

Spatial distribution and association patterns in a tropical evergreen broad-leaved forest of north-central Vietnam

Hong Hai Nguyen, Jaime Uria-Diez & Kerstin Wiegand

Keywords

Dispersal limitation; Neutral theory; Paircorrelation function; Point pattern analysis; Self-thinning; Spatial pattern; Species association; Species herd protection; Tropical evergreen forest; Vietnam

Nomenclature

FIPI (1996)

Received 15 February 2015 Accepted 9 October 2015 Co-ordinating Editor: Richard Michalet

Nguyen, H.H. (corresponding author, hnguyen@uni-goettingen.de)^{1,2}, Uria-Diez, J. (juriadiez@gmail.com, Jaime.Uria.Diez@slu.se)^{3,4}, Wiegand, K. (mail@kerstin-wiegand.de)¹

¹Department of Ecosystem Modelling, Faculty of Forest Sciences and Forest Ecology, University of Goettingen, Buesgenweg 4, 37077 Goettingen, Germany; ²Current address: Faculty of Silviculture, Vietnam Forestry University, Hanoi, Vietnam; ³Department of Environmental Biology, University of Navarra, Irunlarrea *s/*n, 31008, Pamplona, Spain;

⁴Current address: Department of Forest Resource Management, Swedish University of Agricultural Sciences (SLU), Faculty of Forest Sciences, Skogsmarksgränd, SE-901 83, Umeå, Sweden

Introduction

Studies on species-rich tropical forests produced numerous hypotheses on species co-existence (Chesson 2000; Wright 2002; Volkov et al. 2005). The Janzen-Connell hypothesis states that species-specific survival probability of recruits increases with increasing distance from parent trees due to predation or host-specific pests close to the parent trees (Janzen 1970; Connell 1971; Bagchi et al. 2014). Thus, other species with similar habitat requirements but different enemy resistances benefit and establish at these locations. As an extension of the

Abstract

Questions: What are the prevailing types of intraspecific spatial distributions and interspecific association patterns at species and life stage levels of trees in a tropical rain forest? Which ecological processes could structure these patterns? Possible processes include dispersal limitation, self-thinning, facilitation and competition between species and life stages.

Location: A tropical broad-leaved forest in north-central Vietnam.

Methods: We used univariate and bivariate pair-correlation functions to investigate the spatial distribution and association patterns of 18 abundant tree species. To disentangle first- and second-order effects, we used a scale separation approach with the heterogeneous Poisson process as null model.

Results: (1) Sixteen of 18 species had aggregated patterns at various scales and regardless of their abundance. (2) Significant and aggregated patterns were found in 64% of all specific life stages. (3) At scales up to 15 m, 12.4% species pairs showed significant associations, among that 71% were spatial attractions, 5% were spatial repulsions and 24% were non-essential interactions. (4) In different life stage associations, attractions (81%) predominated over repulsions (19%) at small scales of up to 15 m.

Conclusions: Our findings provide evidence that dispersal limitation may regulate the spatial patterns of tree species. Moreover, positive spatial associations between tree species and life stages suggest the presence of species herd protection and/or facilitation in this forest stand, while the persistence of intraspecific aggregation through life stages suggests a very late onset or even absence of self-thinning. Habitat heterogeneity plays an important role for species distribution patterns, and the spatial segregation occurs at a scale around 15 m in this forest.

Janzen-Connell hypothesis, the species herd protection hypothesis explains that species co-existence can be promoted by hetero-specific neighbours because of thwarting the transmission of biotic plant pests (Peters 2003). This leads to fewer encounters between a host and its species-specific pests and pathogens, resulting in higher survival rates of established seedlings (Comita & Hubbell 2009). Therefore, attraction patterns between species may be maintained by the species herd protection even in the case of competitive interactions.

Neutral theory assumes that all tree individuals are demographically equivalent in terms of their rates of birth,

reproduction and death, regardless of species identity (Hubbell 2005). Uriarte et al. (2004) supported this theory and illustrated that a majority of tropical tree species on Barro Colorado Island, Panama, exhibits no neighbour identity. However, in a review, Chave (2004) found little empirical support for the assumption of demographic equivalence in its strict sense. In contrast, niche theory assumes that spatial associations and habitat variation may be exhibited because of interspecific differences in morphology, physiology and life-history traits (Harms et al. 2001; Debski et al. 2002; Coomes & Grubb 2003; Peters 2003). Furthermore, due to low frequencies, pair-wise spatial associations are rare as proximal neighbours (Perry et al. 2009), particularly in tropical forests where tree species are mostly at low density (Luo et al. 2012). Evidence for spatial associations is found mostly in species-poor communities and is detectable in only a few species pair interactions (Lieberman & Lieberman 2007; Wiegand et al. 2007; Perry et al. 2009; Wang et al. 2011). Therefore, in species-rich tropical forests, high species diversity begets low densities leading to intra- and interspecific interactions in complex terms.

Studying species associations is more complicated in cases of habitat heterogeneity, which generally occurs at large scales (Wiegand et al. 2007; Getzin et al. 2008). Under habitat heterogeneity first-order effects (species habitat preference relative to e.g. shading, nutrients, soil moisture) may mask second-order effects (direct plantplant interaction, such as facilitation or competition; Wright 2002; Wiegand et al. 2007). Previous studies have shown that direct interactions between neighbouring plants can occur at distances smaller than 30 m and fade away at larger scales (Hubbell et al. 2001; Uriarte et al. 2004). Therefore, we used current techniques of spatial point pattern analysis to separate first- and second-order effects. Last but not least, plant-plant interactions are likely to change with life stage, which has so far received only little attention, especially in the presence of habitat heterogeneity (the first paper on life-stage dependent interactions among trees controlling for habitat heterogeneity was Piao et al. 2013).

Our specific objectives are to study the spatial distributions and interspecific associations of 18 dominant tree species across life stages in the presence of habitat heterogeneity in a tropical evergreen forest stand, north-central Vietnam. We formulate three hypotheses: (1) species are aggregated, being explained by dispersal limitations; (2) species show a reduction in aggregation with life stages from sapling to adult, being explained by self-thinning; and (3) there are positive interspecific associations at small spatial scales, being explained by species herd protection. We separated first- and second-order effects via an approach of scale separation (Wie-

gand et al. 2007). To retain the large-scale structure of the pattern but remove potential non-random local spatial structure, heterogeneous Poisson processes were used as null models (Wiegand et al. 2007; Wang et al. 2010; Lan et al. 2012). We find partial support for hypothesis (1) and, at the species level, for hypothesis (3). However, we reject hypothesis (2), and find that support for hypothesis (3) is mostly due to interspecific attraction between life stages. Consequently, we find little support for competition in this forest stand, while herd protection and/or facilitation seem to be important mechanisms.

Methods

Study plot

A 2-ha study plot (200×100 m) was established in a location with little human disturbances in Aluoi district, Thuathien-Hue province, north-central Vietnam ($16^{\circ}08.35'$ N, $107^{\circ}16.68'$ E) in 2012 (Fig. 1). This region is situated in the tropical monsoon climate. The average annual temperature is about 25 °C. There is an average of 200 rainy days per year; the average annual precipitation is around 3500 mm. About 70–80% of the total precipitation falls from Sept to Dec, while the dry season lasts from Jan to Aug. Soils are mainly light yellow to dark yellow ferralic acrisols. Elevation ranges from 625 m to 660 m a.s.l, with an average slope of 25°.

Study species

The study plot is located in a late successional forest classified as tropical broad-leaved evergreen forest and dominated by shade-intolerant tree species such as *Syzy-gium zeylanicum, Syzygium wightianum* and *Litsea vang.* All trees with diameter at breast height (DBH) \geq 2.5 cm were mapped and their characteristics (species and DBH) recorded. The relative coordinates (*x*, *y*) of each tree were recorded via a grid system of subplots (10 × 10 m) by using a laser distance measurer (Leica Disto D5) and compass. If trees were multi-stemmed, each stem was considered a separate tree with own (*x*, *y*) coordinates if the branching occurred below breast height (1.3 m).

All tree individuals were classified into three life stages: sapling (DBH < 6 cm), pole (6 cm \leq DBH \leq 15 cm), and adult (DBH > 15 cm). All trees belong to 81 species of 37 families. *S. zeylanicum* was the most abundant species (514 individuals) and had some large individuals with DBH up to 100 cm. Eighteen species had an abundance \geq 50 individuals and were taken into our analysis. Among these, 14 species are fast-growing and light-demanding or moderate inclining to light-demanding (Table 1); and six species had



Fig. 1. Location of the 2-ha study plot in a tropical broad-leaved forest stand, north-central Vietnam.

a low abundance of 25–34 individuals ha⁻¹ (*Nephelium melliferum*, *Quercus platicalyx*, *Dillenia scabrella*, *Adina pilulifera*, *Archidendron balansae* and *Ormosia balansae*).

Spatial point pattern analysis and null models

Summary statistics

Ripley's *K*-function and pair correlation function are based on the distribution of distances between pairs of points (e.g. (*x*,*y*) coordinates of trees). Both functions are standard methods for analysing point patterns in ecology (Wiegand & Moloney 2014). Ripley's *K*-function is defined as the expected number of points within distance *r* of an arbitrary point divided by λ , where λ is the intensity of the pattern in the study area (Ripley 1976). The pair-correlation function *g*(*r*) is the derivative of the *K*-function (Stoyan & Stoyan 1994; Illian et al. 2008), *g*(*r*) = *K*'(*r*)/(2 π *r*). Particularly, the *g*-function is non-cumulative and related to the expected density of points at a distance radius *r* from a randomly chosen point.

The univariate pair-correlation function $g_{11}(r)$ describes the spatial distribution of points at a given radius r using a standardized density. $g_{11}(r) = 1$ under complete spatial randomness (CSR), $g_{11}(r) > 1$ indicates aggregation and $g_{11}(r) < 1$ indicates regularity at distance r between the points of a pattern. The bivariate pair-correlation function $g_{12}(r)$ is an extension to describe point patterns between two types of points, for example, two tree species. $g_{12}(r)$ is related to the expected density of points of type 2 at distance *r* from an arbitrary point of type 1: $g_{12}(r) = 1$ indicates independence, $g_{12}(r) < 1$ indicates repulsion and $g_{12}(r) > 1$ indicates attraction between two types of points at distance *r*.

To assess the significance of the summary statistics under given null models, we tested null hypotheses related to ecological questions (see Analyses 1 and 2 below). Significant departure from the null models was evaluated in two steps, as outlined in Wiegand & Moloney (2014). First, we generated simulation envelopes from the fifth lowest and fifth highest values of 199 Monte Carlo simulations. If the test statistic falls outside these simulation envelopes, this indicates departure from the null model, approximately at a 5% level. The advantage of this first approach is the scale-dependent visualization of the results. Second, to evaluate significant departures from the null models, we used a goodness-of-fit test (GoF; Diggle 2003; Loosmore & Ford 2006) for a distance interval of 0-30 m (see below for justification of scale). Significant deviations from the null models were taken into account if the observed P-value of the GoF test was smaller than 0.05. In case of significant departure from the null model (based on GoF test), we used the simulation envelopes to identify the scale(s) and the direction(s) of the departure(s). Null model specific details are given below. All point pattern analyses were performed with the grid-based software Programita (Wiegand & Moloney 2004, updated version Feb 2014 from http://programita.org/; settings: ring width = 2, cell size = 1 m).

Table 1. Species properties of a 2-ha plot of tropical evergreen broad-leaved forest.

No	Species	Family	Abundance	Mean DBH (cm)	Basal Area (m ²)	Properties	Fruits (mm, <i>D</i> - Diameter)
1	Syzygium zeylanicum	Myrtaceae	514	10.05	6.67	Moderate inclining to light demanding	Drupe, D: 7, one seed
2	Syzygium wightianum	Myrtaceae	351	9.54	3.93	Light demanding	Berry, 15 long & 8 wide, one seed
3	Litsea vang	Lauraceae	266	18.35	5.18	Fast growing	Calyx-tube, 23 long &, 12 wide
4	Microcos paniculata	Tiliaceae	189	21.37	7.48	Light demanding	Drupe, D: 10
5	Polyathia nemoralis	Annonaceae	171	5.61	0.51	Light & wet demanding	Follicles, D: 8–10
6	Sterculia lanceolata	Sterculiaceae	157	11.94	2.32	Shade tolerant inclining to neutral	Two-four seeds, ca. D: 10
7	Diospyros eriantha	Ebenaceae	112	5.33	0.28	Shade tolerant inclining to light demanding	Berry, 10–15 long
8	Endospermun sinensis	Euphorbiaceae	90	25.26	5.23	Light demanding & fast growing	Drupe, D: 10–15
9	Aphanamixis polystachya	Meliaceae	81	14.79	2.2	Light moderate	Capsule D: 25, seed D: 10
10	Ardisia lindleyana	Myrsinaceae	79	3.78	0.09	Shrub	
11	Macaranga denticulata	Euphorbiaceae	76	14.23	1.41	Light demanding & fast growing	Globose capsule, D: 5, two seeds
12	Schefflera octophylla	Araliaceae	71	14.43	1.87	Light &wet demanding	Globose berry, D: 3–4, five-seven seeds
13	Nephelium melliferum	Sapindaceae	64	19.53	2.96	Light demanding	
14	Quercus platicalyx	Fagaceae	63	29.96	5.22	Light demanding & fast growing	Obovate, 35 height, D: 17–19
15	Dillenia scabrella	Dilleniaceae	62	14.32	1.64	Light demanding & fast growing	Globose, D: 80–100
16	Adina pilulifera	Rubiaceae	61	8.9	0.49	Found under the shade of forest	Capsule, 7–8 long
17	Archidendron balansae	Mimosoideae	54	12.35	0.83	Moderate inclining to light demanding	Two to six seeds, D and length:45
18	Ormosia balansae	Fabaceae	50	29.71	4.5	Light demanding & fast growing	Pod containing one seed
19–81	Others		643	13.76	13.75	5 5	
	All trees	37	3154	13.4	66.56		

Analysis 1: Intraspecific spatial distributions

We used the heterogeneous Poisson process to analyse intraspecific patterns of (1) each of 18 species and (2) their life stages. After visual inspection of simulation envelopes, species-specific life stages with less than 30 individuals were excluded from analyses to ensure accuracy of spatial pattern modelling. Heterogeneity of our study plot was established based on rejection of the null model of CSR for all adult trees of all species at large scales, as described in Wiegand & Moloney (2004; results not shown). The heterogeneous Poisson process was used to analyse the observed spatial distribution of trees over non-constant intensity. The variable density of tree individuals may be caused by environmental heterogeneity (differences in soil or obstacles e.g. rock outcrops, streams). Here, variation in habitat quality was accounted for with the heterogeneous Poisson process, which accounts for the first-order pattern at large scales. To this end, the constant intensity from the homogeneous distribution was replaced by an intensity

function that varies with location but retains the independence of tree positions from each other (Wiegand & Moloney 2004, 2014).

For a non-parametric kernel estimation of the intensity function based on the Epanechnikov kernel, we used bandwidth R = 30 m and a spatial resolution of 1 m (Wiegand & Moloney 2004; Wiegand et al. 2007). Following Wiegand et al. (2007), we based the choice of the bandwidth on the biological argument of the maximum scale at which second-order effects are expected in tropical forests. The scale of 30 m includes the scales at which tree-tree interactions are typically observed and has been used in previous studies of tropical forests under habitat heterogeneity (e.g. Wiegand et al. 2007; Lan et al. 2012). The heterogeneous Poisson process is an appropriate null model because it retains large-scale effects of environmental heterogeneity, but removes potential non-random local effects at distances smaller than bandwidth R (Wiegand et al. 2007). Therefore, after this scale separation for environmental heterogeneity, we

expected to find second-order patterns caused by plantplant interactions at small scales. In other words, controlling habitat heterogeneity with a heterogeneous Poisson model implies that potential interactions among points may only be evaluated up to the bandwidth [i.e. up to 30 m; Wiegand & Moloney (2014)]. To summarize the results, the numbers of species and life stages with significant spatial patterns (aggregated or regular) were counted at each spatial scale *r*.

Analysis 2: Interspecific spatial associations

We used a null model in which the locations of trees in pattern 1 remained fixed, however, the locations of trees in pattern 2 were randomized using heterogeneous Poisson process according to the intensity function with bandwidth R = 30 m. This null model was applied to address questions related to spatial association of trees. Using the bivariate pair-correlation function $g_{12}(r)$, we performed bivariate analyses concerning: (1) interspecific associations and (2) lifestage associations. Due to the null model applied, the intensity function was built based on the intensity of pattern 2, allowing us to assess whether pattern 2 points were more or less frequent around pattern 1 points than expected under the null model. If the observed $g_{12}(r)$ is above a simulation envelope obtained from Monte Carlo simulations of the null model then the data show positive relation (attraction) at scale r. Inversely, values of $g_{12}(r)$ below the simulation envelope indicate a negative relation (repulsion). In these bivariate analyses, we tested all species and life-stage pairs by the pair-correlation functions $g_{12}(r)$ and $g_{21}(r)$, because we do not know whether biotic interaction is symmetric or not (Wiegand et al. 2007; Lan et al. 2012). Note that species-specific life stages were included in these analyses only if they consisted of at least 30 individuals (cf. Analysis 1).

We did two kinds of summary of the pair-wise combinations of interspecific associations and life-stage associations. First, we counted the number of pairs with significant spatial patterns (positive, negative) at each spatial scale *r*. Second, we classified each species pair and each life stage pair as positive or negative if attraction or repulsion patterns were observed for at least two consecutive scales, respectively, and as non-essential otherwise. To disentangle small-scale effects in the spatial structure of these associations, we report results not only for the full range of scales (0–30 m) but in several cases also restricted to small scales ($r \le 15$ m). The scale of 15 m was chosen *post-hoc* based on the observation that aggregation and association patterns tended to fade away at this scale.

Results

Analysis 1: Intraspecific spatial distributions

Species patterns

Sixteen of 18 studied species showed aggregation at various scales under the heterogeneous Poisson null model. In the nine most significant aggregations (Fig. 2, based on GoF test), six species showed strong aggregations at scales from 0–15 m, while significant effects disappeared at scales larger than 15 m (S. zeylanicum, S. wightianum, M. paniculata, S. lanceolata, A. lindleyana and M. denticulata; see Fig. 2a,b, d–g). The degree of aggregation clearly decreased with larger scales (Fig. 2), corresponding to the observed spatial distributions in the plot (small insets). Particularly, A. lindleyana and M. denticulata (Fig. 2f,g) were highly aggregated but in low abundance (ca. 40 individuals ha⁻¹). Three highly aggregated species were aggregated at more confined spatial scales (L. vang, A. pilulifera and Q. platicalyx; see Fig. 2c,h,i). Among the remaining species, seven species had weakly aggregated intensities (results not shown) at scales up to 1 m and all of these species were low in abundance (E. sinensis, A. polystachya, S. octophylla, N. melliferum, D. scabrella, A. balansae and O. balansae).

Life-stage patterns

A total of 28 specific life stages were analysed. Four saplings (50%), six poles (75%) and eight adults (66%) showed significant deviations from the heterogeneous Poisson null model based on GoF test, covering 64% of all life stages. Aggregation dominated over regularity at scales up to 15 m (Fig. 3). Almost no regular pattern was found at scales 0–15 m for all three life stages, however few cases of regularity were found at larger scales. The most significant aggregations were found in *S. zeylanicum, S. wightianum* and *M. paniculata*. The number of aggregated patterns decreased with increasing spatial scales in all life stages.

In Analysis 1, the heterogeneous Poisson process indicated significant effects at scales smaller than 30 m with aggregated patterns disappearing within the investigated range of scales (i.e. below 30 m). Therefore, our results confirmed the existence of scale separation in this study plot.

Analysis 2: Interspecific spatial associations

Species associations

In total, 306 bivariate pattern analyses were performed for all interspecific combinations of the 18 species. The GoF test detected that only 38 species pairs (12.4%) significantly deviated from the null model. Among these, 32 pairs (84%) of interspecific associations were symmetric and six pairs (16%) were asymmetric. Also among these 38 species



Fig. 2. Examples of nine abundant species analysed by the univariate pair-correlation function g_{11} (Analysis 1). The insets show the species distribution maps. Observed patterns (dark line) lying beyond the simulation envelopes (grey lines) indicate significant departures from the heterogeneous Poisson null model with bandwidth R = 30 m. n gives the number of individuals.



Fig. 3. Number of significant patterns (aggregation/regularity) within life stages (a–c) analysed by the univariate pair-correlation function g_{11} under the heterogeneous Poisson null model with bandwidth R = 30 m (Analysis 1). n gives the number of species.

pairs, 71% and 5% species combinations showed significant attraction or repulsion patterns at two or more consecutive spatial scales, respectively, while 24% showed nonessential associations (e.g. at only one scale, or not on consecutive scales; Appendix S1). Significant associations were highly concentrated below 15 m (Fig. 4).

The three strongest attractors in terms of the number of attraction patterns with other species were *S. zeylanicum*, *S.*



Fig. 4. Number of significant interspecific associations analysed by the bivariate pair-correlation function g_{12} (Analysis 2). Null model was pattern 1 fixed and pattern 2 randomized by heterogeneous Poisson process, bandwidth R = 30 m.

wightianum and *P. nemoralis* (Appendix S1) and they are high-abundance species (Table 1). Repulsion patterns were found between *S. wightianum* and *S. octophylla* vs *M. denticulata*, a shade-intolerant species. Non-essential associations were found in high abundance species like *S. wightianum*, *L. vang*, *P. nemoralis* and *A. polystachya* (Appendix S1).

Life-stage associations

A total of 244 pairs of same life stages and 512 pairs of different life stages were analysed (paired by eight saplings, eight poles and 12 adults). Among the same stages, only 6% of species pairs were significantly different from the null model (GoF test). At any scale, there were very few significant associations (attraction or repulsion) within the same life stages (Fig. 5a–c). Only 12% of sapling, 9% of pole and 1% of adult pairs showed significant attraction or repulsion patterns at any scale up to 30 m. Overall, significant associations were found in only a few species at life stage levels (Fig. 5a–c) while they were much more common at species level (Fig. 4).

For different life stages, 16% of the pairs deviated significantly from the null model (GoF test). Among these, significant associations were found in 13% of adult–pole, 11.9% of adult–sapling and 27.3% of pole–sapling combinations (Fig. 5d–f), with symmetric pairs in 40%, 34% and 34% of these combinations, respectively. Attraction (81%) dominated repulsion (19%) patterns and attraction decreased with increasing spatial scales up to 15 m. Interestingly, repulsion patterns were rare in associations with adults but more frequent in pole–sapling associations (Fig. 5d–f).

Overall, the heterogeneous Poisson null models were used to account for possible environmental heterogeneity at scales beyond 30 m and to reveal species associations (attraction, repulsion) at scales below 30 m. Attraction patterns dominated at small scales up to 15 m, whereas attraction patterns were rare at larger scales. Repulsion patterns were rare at all scales up to 30 m in both species



Fig. 5. Number of significant spatial associations, analysed by the bivariate pair-correlation functions g_{12} for the same life stages (upper row, **a**–**c**) and different life stages (lower row, **d**–**f**; Analysis 2). Null model was pattern 1 fixed and pattern 2 randomized by heterogeneous Poisson process, bandwidth R = 30 m. n gives the number of pairs.

and life-stage levels with the exception of pole–sapling associations being relatively frequent at scales >15 m (Figs 4 and 5).

Discussion

Our results provide significant evidence that dispersal limitation, species herd protection and facilitation may regulate the spatial patterns of tree species in the studied tropical evergreen broad-leaved forest in north-central Vietnam. Habitat heterogeneity plays an important role for species distribution patterns and there is a spatial segregation that occurs at scales around 15 m. There are only a few species associations but among these, attraction patterns between different life stages are common, thus suggesting the presence of species herd protection and/or facilitation processes.

Intraspecific spatial distributions

Aggregated patterns are very common in tree species distributions in tropical forests, especially in species-rich tropical rain forests containing many rare and few common species (He et al. 1997; Condit et al. 2000; Li et al. 2009). This pattern may be caused by dispersal limitation and habitat heterogeneity (Harms et al. 2000; Getzin et al. 2008; Wiegand et al. 2009). To account for this challenge, we use the approach of scale separation, therefore ambiguous effects are separated (Wiegand et al. 2007; Lan et al. 2012).

All 18 studied species, mainly light-demanding or inclining to light-demanding when becoming mature, may have similar habitat requirements. They exhibit aggregated patterns at various scales and their aggregation strength and extent are not correlated to species abundance. Debski et al. (2002) also found that species sharing a habitat preference exhibit similar distributions. In stochastic geometry of biodiversity, interspecific variation in species abundance shows typically many rare but few common species (McGill et al. 2007). Here, we found that two species with low abundance, *A. lindleyana* and *M. denticulata*, showed stronger aggregations than the more common species *S. zeylanicum*, *S. wightianum* or *M. paniculata*.

There was no evidence for self-thinning and consequently little evidence for intraspecific competition in our plot. Under self-thinning one would expect to observe more regular (or at least less aggregated) patterns with increasing tree size or with increasing life stage. However, the level of aggregation was similar across life stages. Please note that the relatively high levels of aggregation at the smallest scale may be an artifact of our sampling design – stems of multi-stemmed trees were considered separate trees if the branching occurred below breast height. Nevertheless, the aggregations in all life stages observed by us indicate effects of species herd protection or facilitation. The pronounced decrease in aggregation with increasing scales suggests a limitation on the dispersal of seeds. Biotic factors such as limited seed dispersal, for example, due to clumped dispersal by animals, may be responsible for the clumped patterns. The studied tree species mainly produce drupe and berry fruits. The morphological characteristics in type and size of these fruits suggest that seeds may be dispersed by animals and/or gravity and thus they are not dispersed far away from their parent trees (Lan et al. 2012). In addition, Condit et al. (2000) and Li et al. (2009) also found that species dispersed by wind.

Interspecific spatial associations

Attraction patterns have rarely been documented in previous studies of tropical tree species, but recently Lan et al. (2012), Luo et al. (2012) and Wiegand et al. (2012) demonstrated that there can be positive spatial associations between species. Among these, the 12.4% of significant species associations observed by us are much lower than the species associations observed in a tropical seasonal rain forest in Xishuangbanna, southwest China (81%; Lan et al. 2012) but similar to a subtropical evergreen broad-leaved forest in Baishanzu, east China (11%; Luo et al. 2012), a neotropical forest in Barro Colorado Island, Panama (BCI; 5%) and a tropical Dipterocarp forest in Sinharaja, Sri Lanka (6%; both Wiegand et al. 2012). In our study, attraction patterns predominate over repulsion patterns at small scales below 15 m. Results at the speciesrich tropical forest of BCI that almost all significant associations were found at scales of <10 m (Wiegand et al. 2012) also support our findings. Strong attractors are found in the most common species: S. zeylanicum, S. wightianum and P. nemoralis. A possible explanation is that attraction patterns are the result of facilitation at small scales. Specifically, the local environment is modified by large trees or canopy gaps and facilitates small intra- and interspecific associations of trees with similar habitat preferences (Kubota et al. 2007; Luo et al. 2012), e.g. with similar light requirements in our case. Suzuki et al. (2012) highlighted that an attraction pattern may result from similarity in habitat preference of spatially associated species. Alternatively, attraction patterns among species could be consistent with the species herd protection hypothesis which states that hetero-specific neighbours can promote co-existence by preventing the transmission of biotic plant pests (Peters 2003; Lan et al. 2012).

Our results (Analysis 2) showed rare cases of significant association in the same life stages but much more frequent cases of positive associations between different life stages. This is compatible with the classical Janzen-Connell hypothesis that states high hetero-specific crowding leads to an increase of survival from species-specific pests and pathogens, therefore preserving high tree species diversity (Wills et al. 1997). Therefore, survival should increase with density of hetero-specific neighbours (Peters 2003). We would have expected to see repulsion patterns between species at both the species and life-stage levels resulting from direct interspecific competition for light or caused by small-scale habitat heterogeneity such as soil patchiness (Wang et al. 2011). However, we mostly observed positive associations between life stages at small scales, with the only exception of a relatively high prevalence of pole-sapling associations at intermediate scales (15-30 m). In summary, given the low number of repulsion patterns, both intra- and interspecific competition appear to be of little importance in this forest plot.

The low abundance of many species may also contribute to the low number of significant spatial associations (Luo et al. 2012). Moreover, this is a typical characteristic of species-rich communities (Hart et al. 1989; Lieberman & Lieberman 2007). Our finding shows that neutral interaction dominates in species with low abundances, supporting the assertion of independent spatial arrangement of species by Wiegand et al. (2012). In addition, spatial segregation and low abundance of species lead to a decreasing probability of interspecific encounters and interactions (Chesson 2000; Wright 2002; Vazquez et al. 2007).

In conclusion, with 16 out of the 18 most abundant species being aggregated, our results show that aggregated patterns dominate the spatial distribution of a broad-leaved forest in Vietnam. The degree of aggregation is independent of the species' abundance and does not decrease with life stage, i.e. there is no evidence for self-thinning. In this forest, associations at species and life-stage levels occur mostly at scales smaller than 15 m. The spatial aggregation within life stages of different species supports the hypothesis of dispersal limitation. Spatial attraction dominated repulsion in interspecific associations, covering 12.4% of species pairs. The attraction patterns at species and lifestage levels suggest the presence of species herd protection and/or facilitative interactions, while competition seems to be of minor importance. In our study forest, dispersal limitation, species herd protection and facilitation may regulate the spatial patterns of tree species. The relative role of competition and facilitation between and within species and life stages deserves further study as this may help to solve the long-standing challenge of explaining species co-existence.

Acknowledgements

This study was supported with funds from the Ministry of Education and Training of Vietnam. Permission to

work and access to the study site was provided by the People's Committee Administration of Aluoi district and Forest inventory and planning sub-institute central Vietnam. Fieldwork was undertaken by Mr. Phuc and two graduate students. We also thank Barbara Strauss and three anonymous reviewers for helpful comments on the manuscript.

References

- Bagchi, R., Gallery, R.E., Gripenberg, S., Gurr, S.J., Narayan, L., Addis, C.E., Freckleton, R.P. & Lewis, O.T. 2014. Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* 506: 85–88.
- Chave, J. 2004. Neutral theory and community ecology. *Ecology Letters* 7: 241–253.
- Chesson, P. 2000. General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology* 58: 211–237.
- Comita, L.S. & Hubbell, S.P. 2009. Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. *Ecology* 90: 328–334.
- Condit, R., Ashton, P.S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S.P., Foster, R.B., Itoh, A., (...) & Yamakura, T. 2000. Spatial patterns in the distribution of tropical tree species. *Science* 288: 1414–1418.
- Connell, J.H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Proceedings of the Advanced Study Institute on dynamics of numbers in populations*, pp. 298–312. Oosterbeck, September 7-18, 1970. Centre for Agricultural Publishing and Documentalion, Wageningen, NL.
- Coomes, D.A. & Grubb, P.J. 2003. Colonization, tolerance, competition and seed-size variation within functional groups. *Trends in Ecology ∉ Evolution* 18: 283–291.
- Debski, I., Burslem, D., Palmiotto, P.A., Lafrankie, J.V., Lee, H.S.
 & Manokaran, N. 2002. Habitat preferences of Aporosa in two Malaysian forests: implications for abundance and coexistence. *Ecology* 83: 2005–2018.
- Diggle, P.J. 2003. *Statistical Analysis of Spatial Point Patterns*. Arnold, London, UK.
- FIPI 1996. Vietnam forest trees. Agricultural Publishing House, Hanoi, VN.
- Getzin, S., Wiegand, T., Wiegand, K. & He, F. 2008. Heterogeneity influences spatial patterns and demographics in forest stands. *Journal of Ecology* 96: 807–820.
- Harms, K.E., Wright, S.J., Calderon, O., Hernandez, A. & Herre, E.A. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404: 493–495.
- 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. *Journal of Ecology* 89: 947–959.

- Hart, T.B., Hart, J.A. & Murphy, P.G. 1989. Monodominant and species-rich forests of the humid tropics - Causes for their cooccurrence. *The American Naturalist* 133: 613–633.
- He, F.L., Legendre, P. & LaFrankie, J.V. 1997. Distribution patterns of tree species in a Malaysian tropical rain forest. *Journal of Vegetation Science* 8: 105–114.
- Hubbell, S.P. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology* 19: 166–172.
- Hubbell, S.P., Ahumada, J.A., Condit, R. & Foster, R.B. 2001. Local neighborhood effects on long-term survival of individual trees in a neotropical forest. *Ecological Research* 16: 859–875.
- Illian, J., Stoyan, D., Stoyan, H. & Penttinen, A. 2008. Statistical analysis and modelling of spatial point patterns. Wiley, Chichester, UK.
- Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. *The American Naturalist* 104: 501–528.
- Kubota, Y., Kubo, H. & Shimatani, K. 2007. Spatial pattern dynamics over 10 years in a conifer/broadleaved forest, northern Japan. *Plant Ecology* 190: 143–157.
- Lan, G., Getzin, S., Wiegand, T., Hu, Y., Xie, G., Zhu, H. & Cao, M. 2012. Spatial distribution and interspecific associations of tree species in a tropical seasonal rain forest of China. *PLoS ONE* 7: 1–9.
- Li, L., Huang, Z., Ye, W., Cao, H., Wei, S., Wang, Z., Lian, J., Sun, I.F., Ma, K. & He, F. 2009. Spatial distributions of tree species in a subtropical forest of China. *Oikos* 118: 495–502.
- Lieberman, M. & Lieberman, D. 2007. Nearest-neighbor tree species combinations in tropical forest: the role of chance, and some consequences of high diversity. *Oikos* 116: 377–386.
- Loosmore, N.B. & Ford, E.D. 2006. Statistical inference using the G or K point pattern spatial statistics. *Ecology* 87: 1925–1931.
- Luo, Z.R., Yu, M.J., Chen, D.L., Wu, Y.G. & Ding, B.Y. 2012. Spatial associations of tree species in a subtropical evergreen broad-leaved forest. *Journal of Plant Ecology* 5: 346–355.
- McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., Dornelas, M., Enquist, B.J., Green, J.L., (...) & White, E.P. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters* 10: 995–1015.
- 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.
- Peters, H.A. 2003. Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecology Letters* 6: 757–765.
- Piao, T., Comita, L.S., Jin, G. & Kim, J.H. 2013. Density dependence across multiple life stages in a temperate old-growth forest of northeast China. *Oecologia* 172: 207–217.
- Ripley, B.D. 1976. The second-order analysis of stationary point processes. *Journal of Applied Probability* 13: 255–266.
- Stoyan, D. & Stoyan, H. 1994. Fractals, random shapes, and point fields: methods of geometrical statistics. John Wiley & Sons, Chichester, UK.

- Suzuki, R.O., Numata, S., Okuda, T., Noor, N.S.M.D., Kassim, A.R. & Kachi, N. 2012. Species associations among dipterocarp species co-occurring in a Malaysian tropical rain forest. *Journal of Tropical Ecology* 28: 281–289.
- Uriarte, M., Condit, R., Canham, C.D. & Hubbell, S.P. 2004. A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter? *Journal of Ecology* 92: 348–360.
- Vazquez, D.P., Melian, C.J., Williams, N.M., Bluethgen, N., Krasnov, B.R. & Poulin, R. 2007. Species abundance and asymmetric interaction strength in ecological networks. *Oikos* 116: 1120–1127.
- Volkov, I., Banavar, J.R., He, F.L., Hubbell, S.P. & Maritan, A. 2005. Density dependence explains tree species abundance and diversity in tropical forests. *Nature* 438: 658–661.
- Wang, X., Wiegand, T., Hao, Z., Li, B., Ye, J. & Lin, F. 2010. Species associations in an old-growth temperate forest in northeastern China. *Journal of Ecology* 98: 674–686.
- Wang, X., Wiegand, T., Wolf, A., Howe, R., Davies, S.J. & Hao, Z. 2011. Spatial patterns of tree species richness in two temperate forests. *Journal of Ecology* 99: 1382–1393.
- 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*. Chapman & Hall/CRC, Boca Raton, FL, US.
- Wiegand, T., Gunatilleke, S. & Gunatilleke, N. 2007. Species associations in a heterogeneous Sri Lankan dipterocarp forest. *The American Naturalist* 170: E77–E95.
- Wiegand, T., Martinez, I. & Huth, A. 2009. Recruitment in tropical tree species: revealing complex spatial patterns. *The American Naturalist* 174: E106–E140.
- Wiegand, T., Huth, A., Getzin, S., Wang, X., Hao, Z., Gunatilleke, C.V.S. & Gunatilleke, I.A.U.N. 2012. Testing the independent species' arrangement assertion made by theories of stochastic geometry of biodiversity. *Proceedings of the Royal Society B-Biological Sciences* 279: 3312–3320.
- Wills, C., Condit, R., Foster, R.B. & Hubbell, S.P. 1997. Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proceedings of the National Academy of Sciences of the United States of America* 94: 1252–1257.
- Wright, S.J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130: 1–14.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Interspecific associations at scales below 15 m: Analysis 2.

Appendix S2. Interspecific associations at scales below 30 m: Analysis 2.