

# Point patterns of tree distribution determined by habitat heterogeneity and dispersal limitation

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**Abstract** Understanding processes underlying spatial distribution of tree species is fundamental to studying species coexistence and diversity. This study modeled point patterns of tree distribution, expressed by Cartesian coordinates of individual trees within a mapped forest stand, for the purpose of identifying processes that may generate spatial patterns of tree communities. We used four primary point pattern processes (homogeneous Poisson process, inhomogeneous Poisson process, homogeneous Thomas process, and inhomogeneous Thomas process) to model tree distribution in two stem-mapped forests in Taiwan, Republic of China. These four models simulate spatial processes of habitat association and seed dispersal, allowing us to evaluate the potential contribution of habitat heterogeneity and dispersal limitation to the formation of spatial patterns of tree species. The results showed that the inhomogeneous Thomas process was the best fit model and described most of the species studied, suggesting that spatial patterns of tree species might be formed by the joint effects of habitat associations and dispersal limitation. The

homogeneous Thomas process that models the effect of dispersal limitation was the second best model. We also found that the best fit models could be predicted by species attributes, including species abundance and dispersal mode. The significant traits, however, differed between the two study plots and demonstrated site-specific patterns. This study indicated that the interactive operation of niche-based (habitat heterogeneity) and neutral-based (dispersal limitation) may be important in generating spatial patterns of tree species in forest communities.

**Keywords** Dispersal limitation · Forest dynamics plots · Habitat associations · Point pattern analysis · Species coexistence

## Introduction

Overwhelming evidence has shown that the majority of tree species in forests worldwide, particularly in tropical forests, are spatially aggregated (Condit et al. 2000; Getzin et al. 2008; Li et al. 2009; Seidler and Plotkin 2006). But how is the aggregation formed?

While it has been widely shown that density-dependent competition would lead to regular distribution of trees (He et al. 1997; Kenkel 1988), spatial aggregation often results from two major processes: habitat association and dispersal limitation (Condit et al. 2000; Harms et al. 2001; Hubbell et al. 1999; Plotkin et al. 2002). Species-habitat association is a niche-based process that can give rise to spatial aggregations of tree species along environmental gradients (Comita et al. 2007; Gunatilleke et al. 2006; Harms et al. 2001; Wiegand et al. 2007a). Such an association, however, is not the only ecological process that generates spatial aggregation. Dispersal limitation, arguably a neutral

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process, predicts that spatial aggregation can arise from the fact that propagules are not able to reach every suitable site in a landscape, regardless of underlying habitat conditions or species specificities (Dalling et al. 2002; Harms et al. 2000; Hubbell et al. 1999; Plotkin et al. 2002; Seidler and Plotkin 2006). A challenging question, however, is how one may disentangle the contributions of these two mechanisms to spatial aggregation of tree species.

This question is fundamental to biodiversity study because understanding the generating mechanisms of aggregations for tree species can provide key spatial signatures for decoding mechanisms of species coexistence (Condit et al. 2000; Law et al. 2009). There has been much debate about the importance of niche-assembly and dispersal-assembly paradigms to species coexistence (Harms et al. 2001; Wiegand et al. 2007a). Empirical tests for these two competing hypotheses have so far led to inconsistent results. For example, the species were not significantly associated with topographically defined habitat types in Harms et al. (2001), but many were associated with topographic features in a Sri Lankan forest (Gunatilleke et al. 2006) or with underlying soil chemical properties in three neotropical forests (John et al. 2007). The separation of these two mechanisms may potentially contribute to reconciling the niche versus neutral debate, thus increasing our ability to understand the mechanisms of species coexistence.

Another important question about spatial distribution of species is to what extent habitat association or dispersal limitation would reflect the biological attributes of species. That is, how relative abundance of species and their life history traits such as dispersal mode and shade tolerance would mediate the intensity of species association with habitat and the degree of dispersal limitation. It has been shown that spatial patterns differ between common and rare species (Condit et al. 2000). Generally, rare species showed a higher degree of clumping than common species (Condit et al. 2000). This implies that the relative abundance of species in a community may, to an extent, reflect consequences of biotic and abiotic interactions on the spatial distribution of species, perhaps through density-dependent processes such as the Janzen–Connell spacing process (Janzen 1970; Connell 1971). Similarly, dispersal mode and shade tolerance of tree species can affect regeneration and establishment and may have long-lasting effects on subsequent adult distributions (Oliver and Larson 1996; Seidler and Plotkin 2006). It is therefore important to investigate the connection between life history traits and the intensity of spatial aggregation.

Recent advances in spatial statistics have provided useful point process models to quantify underlying mechanisms that generate spatial patterns of tree species (Baddeley and Turner 2005; Diggle 2003; Illian et al. 2008).

Because the generating processes for these models are theoretically known, by comparing the goodness-of-fit of these models to empirical data, the relative contribution of habitat associations and dispersal limitation can be modeled and separated. In this study, four major point processes were used to model tree distribution of two large stem-mapped forest stands in Taiwan (Diggle 2003; Illian et al. 2008). The four models are the Poisson homogeneous process (for modeling spatial complete randomness), the inhomogeneous Poisson process (for modeling habitat heterogeneity or spatial gradient), the Thomas process (for modeling dispersal limitation), and the inhomogeneous Thomas process (for modeling the interaction of dispersal and habitat heterogeneity). By comparing the relative performance of the four models, the importance of habitat association and dispersal limitation can be quantified and distinguished (Diggle 2003; Wiegand et al. 2007b).

This study aimed to investigate the potential contributions of habitat heterogeneity and dispersal limitation to the formation of spatial distribution of species in tree communities through modeling tree point patterns in two stem-mapped plots. The potential contribution was evaluated by selecting the best-fit model among four different spatial models that simulated spatial patterns generated by random processes, habitat association, dispersal limitation and the combination of habitat association and dispersal limitation. We addressed three specific questions. First, what is the relative importance of habitat heterogeneity and dispersal limitation in forming tree distribution and do habitat and dispersal limitation interact to affect spatial patterns? Second, do species attributes such as species abundance, dispersal mode, and shade tolerance influence spatial distribution of trees? We predicted that rare, wind-dispersed and pioneer species could be better predicted by the two types of Thomas processes than Poisson processes due to their aggregated nature. And third, does the best fit point process model vary with spatial scales?

## Materials and methods

### Study sites

This study was carried out in two forest dynamics plots, the Lianhuachih (Fig. 1a) and Kenting Forest Dynamics Plots (Fig. 1b), in Taiwan, the Republic of China. The Lianhuachih Forest Dynamics Plot (hereafter, the LHC plot) is located inside the Lianhuachih Experimental Forest in central Taiwan (23°54'N, 120°52'E) which is managed by the Taiwan Forestry Research Institute. Topographically, the LHC plot covers an elevational range of 667–841 a.s.l. and is characterized by steep slopes. According to the meteorological records at the research station from 1961 to 1998, the

mean annual precipitation is 2,211 mm. The rainy season starts from March to September and the driest month is November. The Lianhuachih plot is 25 ha in size (500 × 500 m; Fig. 1a) and was established in 2007. According to the 2007–2008 census, there are 144 species and 153,484 stems within the plot which is dominated by Lauraceae and Fagaceae species. Important canopy species include *Pasania nantoensis* (Hayata) Schottky, *Engelhardtia roxburghiana* Wall., *Schefflera arboricola* (Hayata) Kanehira, *Schima superba* Gard. & Champ., and *Cyclobalanopsis pachyloma* (O. Seem.) Schottky (Chang et al. 2010).

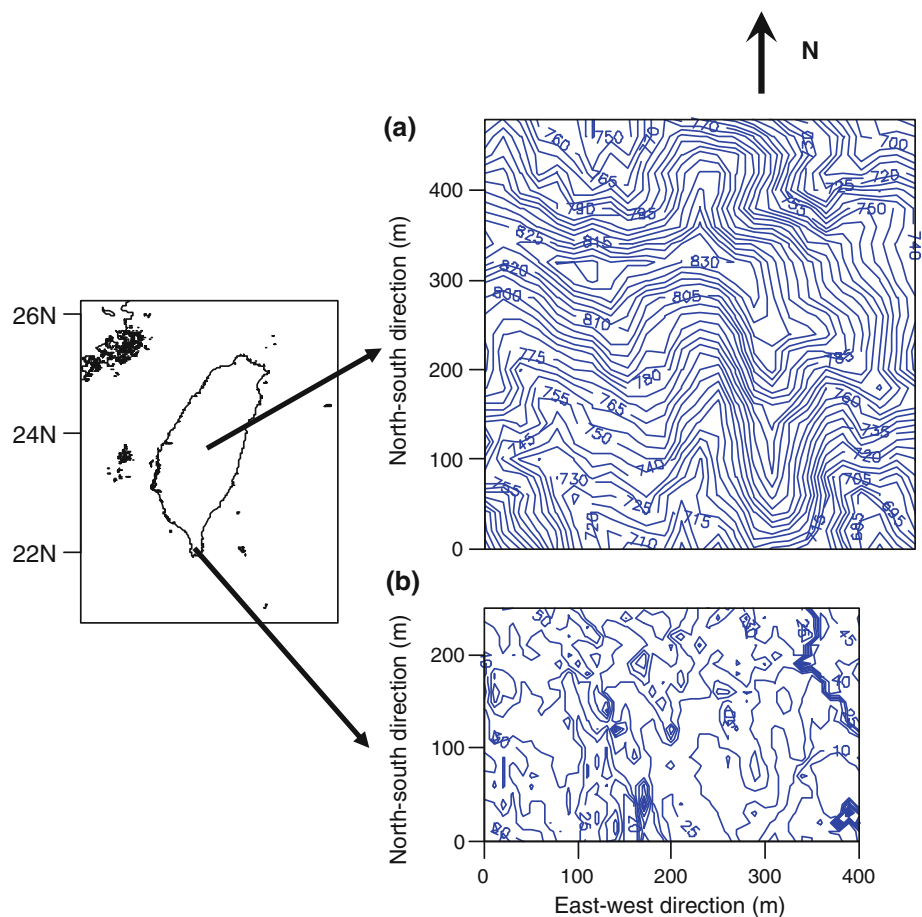
The Kenting plot is established within the Kenting Elevated Coral Reef Natural Reserve (21°58'N, 120°48'E) which is located near the southern tip of Taiwan (Fig. 1b). This reserve is underlain by Miocene rocks and featured by elevated coral reefs (Liao et al. 2006; Wang et al. 2004). The underlying formation is Hengchun limestone that is an organic reef and composed of remains of various organisms, such as corals, foraminifers, mollusks and calcareous algae (Liao et al. 2006). The annual mean temperature and precipitation is 25°C and 1,964 mm during 1997–2002 according to the database of the nearby Hengchun Weather Station. The local climate is characterized by prevailing monsoons between October and March. A 10-ha forest

dynamics plot (400 × 250 m) was established in 1996 (Wang et al. 2004). The plot is dominated by Ebenaceae, Euphorbiaceae and Moraceae species. One hundred and ten species were found within the plot (Wang et al. 2004). The most dominant species, *Diospyros maritima* Blume, accounted for over 50% of the trees in the plot (Wang et al. 2004). Other common species include *Ficus benjamina* L., *Melanolepis multiglandulosa* (Reinw.) Reich. f. & Zoll., *Bischofia javanica* Bl., *Palaquium formosanum* Hayata, *Aglaia formosana* Hayata, and *Pouteria obovata* (R. Brown) Baehni.

#### Field methods

Following Condit (1998), all woody stems with diameter at breast height (DBH) ≥ 1 cm were measured, tagged, mapped, and identified to species (Condit 1998). The census in the LHC plot was carried out in 2008 (Chang et al. 2010) and the census of the Kenting plot was carried out in 1997–2002 (Wang et al. 2004). The 25-ha LHC plot was systematically divided into 625 20 × 20 m quadrats, but the 10-ha Kenting plot was divided into 1,000 10 × 10 m quadrats due to the existence of elevated coral reefs. For each quadrat, three topographical variables (mean elevation, convexity, and

**Fig. 1** Topographic maps of the 25-ha Lianhuachih (a) and 10-ha Kenting plots (b). The contour lines represent 5-m intervals



slope) were derived following Harms et al. (2001) and Valencia et al. (2004). Mean elevation of a quadrat was obtained by averaging elevation measures from the four corners of the quadrat. Convexity was defined as elevation differences between the focal quadrat and mean elevation of the eight neighboring quadrats except for those quadrats on plot edges (Harms et al. 2001; Valencia et al. 2004). Slope was measured by the mean angular deviation from the horizontal plane of each of the four triangular planes by connecting three out of the four corners.

#### Statistical models

Following the presentation of Shen et al (2009), four point processes were used to model spatial distributions of the trees in the two plots. These models simulate tree distributions generated by random processes, habitat association, dispersal limitation and the combination of habitat association and dispersal limitation. The best-fit model among the four was selected for every species of the two plots (Diggle 2003; Illian et al. 2008).

#### Homogeneous Poisson process

This is the simplest point process that represents no underlying biological process, resulting in complete randomness in species distribution. The  $K$  function of the homogenous Poisson process is defined as:

$$K(r) = \frac{1}{A} \sum_{i=1}^n \sum_{j \neq i} \frac{w_{ij}}{\lambda^2} I(d_{ij} < r)$$

In this function,  $A$  denotes the area of the plot,  $\lambda$  is tree density,  $w_{ij}$  is an edge-correction term,  $d_{ij}$  represents the distance between two points, and  $I$  is an index function where  $I = 1$ , if  $d_{ij} \leq r$ , and  $I = 0$  otherwise (Ripley 1976). Tree density,  $\lambda$ , is the parameter to be estimated in this model.

#### Inhomogeneous Poisson process

This process can be used to model heterogeneous habitat association of tree species. In this model, relationships between tree density and habitat heterogeneity are included via a spatially heterogeneous intensity function,  $\lambda(s)$  (Diggle 2003; Illian et al. 2008). The  $K$  function of the inhomogeneous Poisson process is defined as:

$$K(r) = \frac{1}{A} \sum_{i=1}^n \sum_{j \neq i} \frac{w_{ij} I(d_{ij} \leq r)}{\lambda(s_i) \lambda(s_j)}$$

where  $A$ ,  $\lambda$ ,  $w_{ij}$ ,  $d_{ij}$ ,  $I$  are the same as in the homogeneous Poisson process and  $\lambda(s_i)$ ,  $\lambda(s_j)$  are the values of the intensity function at point  $s_i$  and  $s_j$ , respectively. Specifically, the

intensity function,  $\lambda(s)$ , is modeled as a log polynomial regression:

$$\lambda(s) = \exp(\beta^T X(s))$$

where  $X(s)$  is a vector of environmental variables and  $\beta^T$  is a vector of regression parameters. Four different types of log polynomial regressions were used in this study: log linear regressions with 2 or 3 environmental variables and log quadratic regressions with 2 or 3 variables. The environmental variables used in this study were mean elevation, convexity, and slope of the quadrat. Only mean elevation and convexity were selected for the 2-variable regressions. These two variables are selected based on a preliminary study in which slope was not significant in many cases.

#### Homogeneous Thomas process

This is a variety of Poisson cluster process and can be used to model a series of clustered patterns (Diggle 2003; Illian et al. 2008). This model describes processes of dispersal, in which offspring are limited to aggregate around their parent trees. Therefore, it models the effect of dispersal limitation (Diggle 2003; Illian et al. 2008).

The homogeneous Thomas process is modeled by two steps (Diggle 2003; Illian et al. 2008). First, locations of parent trees are generated by a homogeneous Poisson process with a density,  $\kappa$ . Second, a group of offspring are produced around each parent. Their locations are assumed to be independent of one another and isotropically distributed around each parent tree with a Gaussian dispersal kernel,  $N(0, \sigma^2)$ . The number of offspring is determined by a Poisson distribution with mean being  $\mu$  (Baddeley and Turner 2005; Møller and Waagepetersen 2004).

The  $K$  function of the homogenous Thomas process is given by:

$$K(r) = \pi r^2 + \frac{1 - e^{(-r^2/4\sigma^2)}}{\kappa}$$

where  $r$  is distance,  $\kappa$  represents the intensity of parent trees in a Poisson distribution and  $\sigma$  is standard deviation of distance from offspring to the parent. Mean number of offspring per parent in a Poisson distribution,  $\mu$ , can be inferred from estimated intensity  $\lambda$  and  $\kappa$ .

#### Inhomogeneous Thomas process

The inhomogeneous Thomas process is the most complicated model of the four, in which habitat association and dispersal limitation are included simultaneously. This model is used to evaluate the joint effects of habitat association and dispersal limitation (Diggle 2003; Illian et al. 2008). This model is the same as a homogenous Thomas

process, except for the number of offspring per parent,  $\mu$ , which is no longer a constant but must be estimated by a spatially heterogeneous intensity function. The same to the inhomogeneous Poisson process above, intensity functions were modeled by log polynomial regressions.

### Modeling procedure

Field data from the two plots were used to fit the four models. The modeling procedure consisted of two steps: model fitting and goodness-of-fit evaluation. Parameters were estimated via the maximum pseudolikelihood for the homogeneous and inhomogeneous Poisson processes (Huang and Ogata 1999) and the minimum contrast method for the homogeneous and inhomogeneous Thomas processes (Waagepetersen 2007). Goodness-of-fit of the models were evaluated by Akaike's information criterion (AIC) and Monte Carlo simulations. AIC was used to select the best-fit model for each species in the forests. AIC was calculated by the following formula:

$$\text{AIC} = n \ln(R) + 2\kappa$$

where  $n$  is the number of observations,  $R$  is the sum of residual squares and  $\kappa$  is the number of parameters (Møller and Waagepetersen 2004; Shen et al. 2009). Number of parameters ranged from 1 to 12 of various models (Electronic supplementary material, ESM, S1, S2). This AIC was used because parameters were not estimated by the standard maximum likelihood methods in this study. Goodness-of-fit was further evaluated by Monte Carlo simulations which were used to generate 95% confidence intervals of the  $K(r)$  of different models. The modeling process was carried out by R Package Spatsat (Baddeley and Turner 2005).

### Predictability of the best fit model by species attributes

Three species attributes, abundance, dispersal mode and shade tolerance, were used to examine the association between the species attributes and the best-fit models. Multinomial logistic regressions were applied to evaluate the predictability. The dependent variable in the multinomial logistic regression is the type of the best-fit model of a given species. Species abundance, dispersal mode and shade tolerance were considered as independent variables. Species abundance was the number of individuals within the plot. Species were classified into two dispersal modes: wind-dispersed and animal-dispersed. Wind-dispersed species referred to species with winged seeds. Species with fleshy and succulent fruits were classified as animal-dispersed species. The classification of dispersal mode is based upon seed morphology and field observations (Huang et al. 1994). Species which had been recorded as

food species of mammals and birds were recognized as animal-dispersed species (Lin 2000; Su 1991; Sung 2005). No species was solely dispersed by gravity in the two forests. Shade tolerance of a species was classified by a binary index and based on field descriptions and observations (Huang et al. 1994). Multinomial logistic regressions were performed by Proc Logistic in the SAS software (SAS 2000).

### The best model at different spatial scales

To assess the robustness of the models to changing spatial scales, we divided the distance range of the spatial models into six distance classes: <2, 2–5, 5–10, 10–20, 20–40, and 40–60 m. The AIC values of the four models at each distance class were estimated according to the above formula of AIC. Instead of summing residual squares of the entire distance ranges, residual squares were summed within the designated distance ranges for scale-specific AICs. The best models at each of the distance ranges were selected.

## Results

### Best spatial models

Ninety-three and fifty-seven species were analyzed for the LHC and Kenting plots, respectively. Each of the species included in the study had at least 25 stems within the plot.

Our results indicated that the inhomogeneous Thomas process that simulates the joint effects of dispersal limitation and habitat preference performed the best among the four models in both forests. The AIC values of the inhomogeneous Thomas process were the lowest among the four models for 49% and 61% of the species studied in the LHC and Kenting plots, respectively (Table 1; ESM S1, S2). The homogeneous Thomas process mainly representing dispersal limitation was ranked as the 2nd best model (Table 1; ESM S1, S2). It was selected as the best model for 33% of the species in the LHC plot (Table 1; ESM S1) and 30% for the Kenting plot (Table 1; ESM S2). The inhomogeneous and homogenous Poisson processes that reflect random and habitat association were the best models for a small portion of species in these two forests (Table 1; ESM S1, S2). Within the various alternative log polynomial regressions for the inhomogeneous Poisson and Thomas processes, log quadratic regressions with two variables performed the best among the four models.

The results of goodness-of-fit obtained from the Monte Carlo simulations were parallel to the results of AIC. Using *Ardisia sieboldii* in the LHC plot (Fig. 2a) and *Aglaia formosana* in the Kenting plot (Fig. 2b) as examples, at most distances the observed Ripley  $L$  functions were



within the 95% confidence intervals of the inhomogeneous Thomas process, indicating a reasonable goodness-of-fit of the models (Fig. 3d, h). The homogeneous Thomas has the second best goodness-of-fit (Fig. 3c, f). The observed  $L$  functions were greater than the upper limits of the 95% confidence intervals of both the homogenous and inhomogeneous Poisson processes at all distances (Fig. 3a, b, e, f). These results suggested a lack of goodness-of-fit of these two models.

#### Model predictability by species attributes

Predictability of the best models by species attributes was site-specific because model predictability was associated with different traits in LHC and Kenting. Results of multinomial logistic regression indicated that the best-fit model could be predicted by species abundance in LHC (Table 2, Figs. 4a and 5a), but by dispersal mode in Kenting (Table 2; Figs. 4b and 5b). Shade tolerance was independent of the models that best described the species (Table 2).

#### The best model at different spatial scales

The best-fit models differed with spatial scales. The two Poisson processes fit relatively better at smaller spatial scales (Table 3). The relative importance of the inhomogeneous Thomas process increased with distance and was highest at the intermediate spatial scales in both forests (Table 3). Fisher exact tests with 10,000 iterations indicated that the best fit models differed significantly among spatial scales (LHC  $P < 0.001$ , Kenting  $P < 0.001$ ).

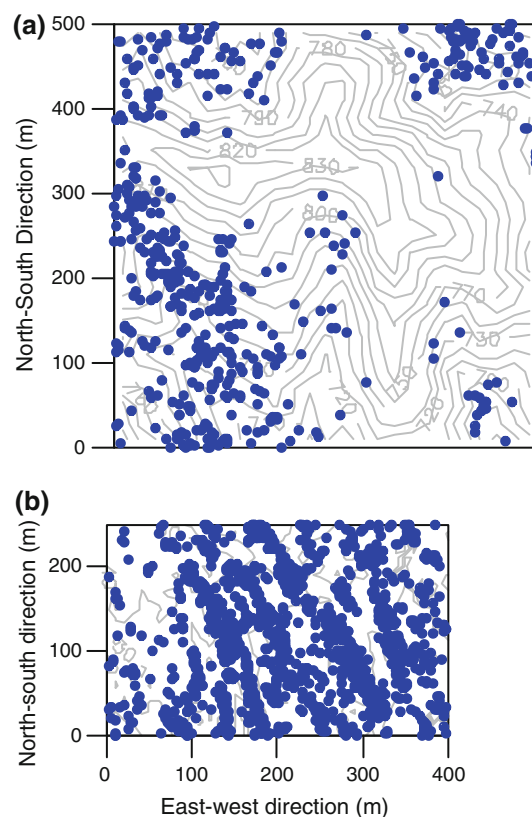
## Discussion

Applying advanced point process models, we were able to evaluate the potential effects of habitat and dispersal limitation on spatial patterning of tree species in the two forests. That the inhomogeneous Thomas process is the best

**Table 1** Proportion of the best models for tree species in the LHC and Kenting plots in Taiwan as judged by the AIC (ESM S1, S2)

Model	LHC	Kenting
Homogeneous Poisson process	3% (3)	4% (2)
Inhomogeneous Poisson process	13% (13)	5% (3)
Homogeneous Thomas process	33% (31)	30% (17)
Inhomogeneous Thomas process	49% (46)	61% (35)

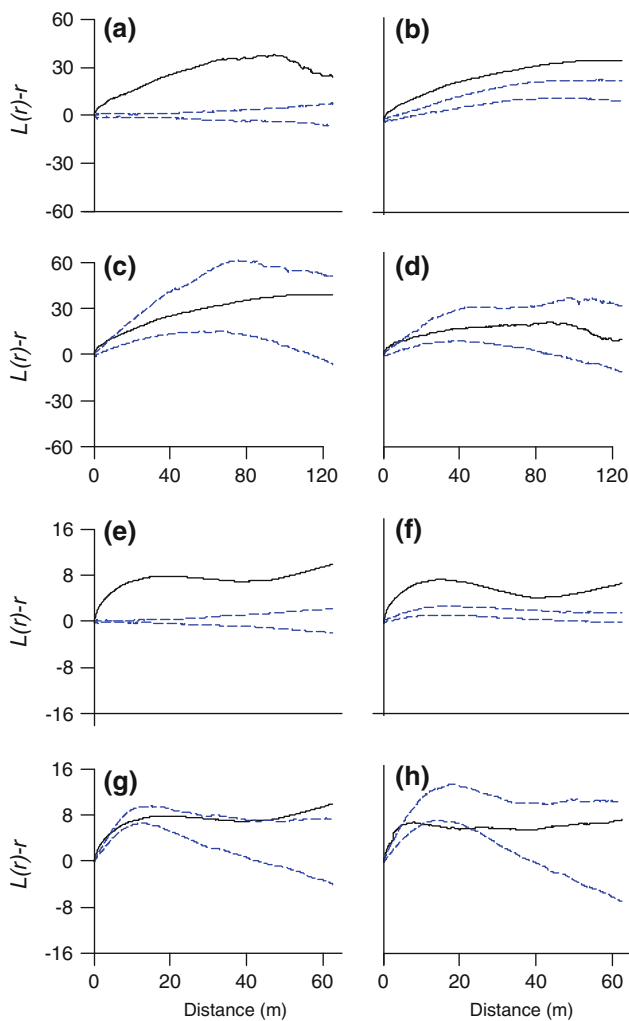
Ninety-three and fifty-seven species which have abundance  $\geq 25$  in the LHC and Kenting plots, respectively, were included in the analysis. Numbers in parentheses are the number of species that are best described by the corresponding models



**Fig. 2** Stem maps of *Ardisia sieboldii* in the LHC plot (a) and *Aglaia formosana* (b) in the Kenting plot. Each dot represents an individual tree

model describing most of the species in the two plots (Table 1) suggests that habitat and dispersal jointly act to determine the formation of spatial aggregation of the species in the plots. The homogenous Thomas process was found to be the 2nd best model. This process together with the inhomogeneous Thomas process implies that dispersal limitation likely plays a major role in spatial patterning of the species in the two plots. The type of dominant ecological processes expressed through the best-fit model is predictable by species attributes, but the significant traits differ between the LHC and Kenting forests.

The result that there was a strong joint effect of habitat and dispersal limitation on species distribution, to some extent, reconcile the inconsistent findings in the literature about the relative effects of habitat heterogeneity and dispersal limitation on species patterns (Dalling et al. 2002; Harms et al. 2001; Wiegand et al. 2007a, b). In these studies, habitat association and dispersal limitation are treated as mutually exclusive hypotheses and tested separately (Dalling et al. 2002; Harms et al. 2001; Wiegand et al. 2007a, b). The inability to model habitat heterogeneity and dispersal limitation in a single process as in the previous studies can lead to incomplete conclusions. For example, weak dispersal limitation is suggested in a Sri



**Fig. 3** Univariate Ripley’s  $L(r)$  of *Ardisia sieboldii* in the LHC plot (a–d) and *Aglaia formosana* in the Kenting plot (e–h) under four alternative spatial models. The observed  $L(r) - r$  values are expressed as solid lines and the dashed lines represent the upper and lower limits of the 95% confidence intervals of  $L(r) - r$  generated by Monte Carlo simulations, where  $r$  represents the distance examined. The four spatial models include homogeneous Poisson process (a, e), inhomogeneous Poisson process (b, f), homogeneous Thomas process (c, g) and inhomogeneous Thomas process (d, h)

Lankan forest, because strong habitat associations are detected (Gunatilleke et al. 2006). In contrast, our study found that both habitat heterogeneity and dispersal limitation worked together to affect species distribution. Therefore, it is important to take account of the two processes simultaneously while studying spatial distribution.

The joint effects of habitat association and dispersal limitation could be common in many forests. A recent study in a subtropical forest in mainland China has highlighted the importance of the joint effects of habitat association and dispersal limitation on the species-area curve (Shen et al. 2009). Similarly, evidence of dispersal limitation and habitat association has been detected in a

**Table 2** Results of multinomial logistic regressions evaluating model predictability by species abundance, dispersal mode and shade tolerance in the Kenting and LHC plots

Factor	<i>df</i>	$\chi^2$	<i>P</i>
<b>LHC</b>			
Abundance	1	4.601	0.032*
Dispersal mode	1	0.640	0.424
Shade tolerance	1	0.510	0.475
<b>Kenting</b>			
Abundance	1	0.142	0.706
Dispersal mode	1	4.413	0.036*
Shade tolerance	1	0.129	0.719

Species were categorized as animal- and wind-dispersed species as well as shade-tolerant and intolerant species (see “Materials and methods” for details)

\* $P < 0.05$

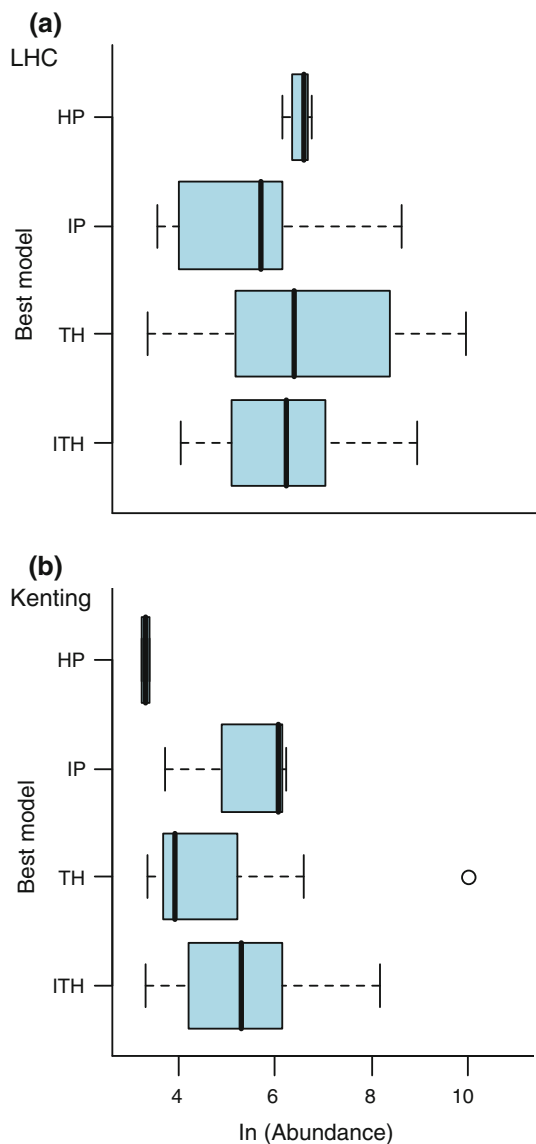
Panamanian forest (Comita et al. 2007). Such results indicate the interactive operation of niche-based (habitat heterogeneity) and neutral-based (dispersal limitation) processes in generating spatial patterns of tree species in forest communities.

How do the joint effects of habitat association and dispersal limitation arise? The interactions between habitat and dispersal limitation may occur during multiple life stages. Dispersal limitation may generate the initial spatial aggregations of seeds. After seed germination, habitat preference of seedlings and saplings may lead to uneven mortality among habitat types and result in a strong association. As a result, spatial patterns of saplings may carry spatial signature of both dispersal limitation and habitat association. Previous research has indicated the importance of habitat heterogeneity in seedling establishment and sapling survival in many forests (Augsburger 1984; Clark et al. 1999) and in the Kenting plot (Shao 2007).

In addition, the strength of the joint effects may vary with spatial scales since the best-fit model differs over spatial scales. Such results are similar to a study of *Shorea congestiflora* in a Sri Lankan forest (Wiegand et al. 2007b). The spatial patterns can be partitioned into several distinct patterns at different spatial scales.

It is worth noting that the homogeneous Thomas process can account for spatial patterns of one-third of species in the two forests studied here. This result heightens the importance of dispersal limitation in explaining spatial distributions and suggests that neutral process may perhaps be a key mechanism underlying the species assemblages of the two forests.

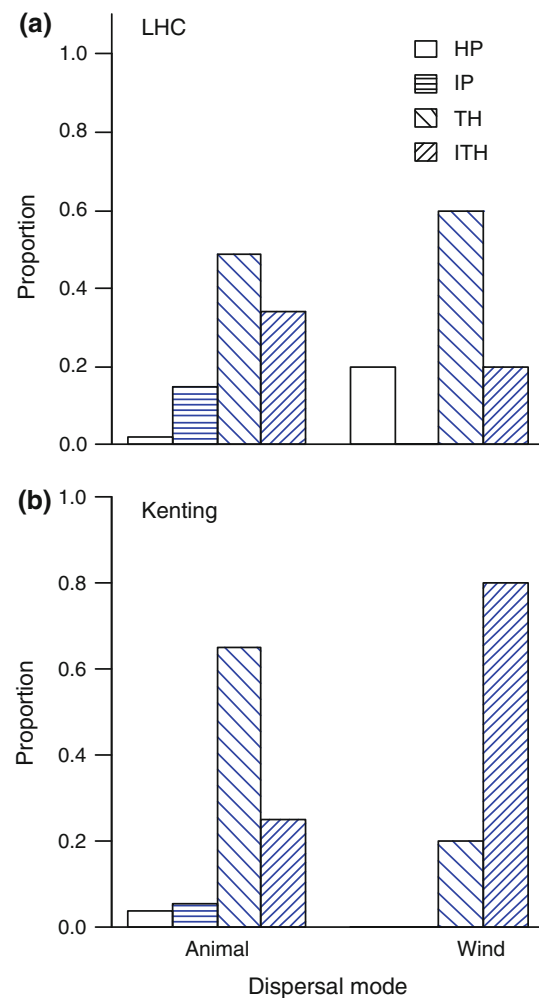
However, we would like to caution the interpretation of our results given the widely recognized limitations of inferring processes from patterns (e.g., a pattern may be generated by multiple processes). We realized that exclusive conclusions could not be drawn from direct evidence



**Fig. 4** Boxplots of species abundance classified by the best-fit model of each species in the LHC (a) and Kenting plots (b). *HP* Homogenous Poisson process, *IP* inhomogeneous Poisson process, *TH* Thomas process, *ITH* inhomogeneous Thomas process. Species abundance was expressed as number of individuals within the plot

of manipulated experimentation which is unfortunately impossible to conduct for the analysis we did. We would also like to mention that the lack of goodness-of-fit of certain models may not suggest insignificance of the processes but rather the violation of model assumptions. For example, the lack of goodness-of-fit of the homogeneous Thomas model may be a consequence of asymmetrical seed distribution which does not satisfy the assumptions of symmetrical distribution of the homogeneous Thomas model.

Some species attributes, abundance and dispersal mode, can be used to predict spatial patterns of tree species. Our



**Fig. 5** Proportion of the best models within each of the two dispersal models in the LHC (a) and Kenting plots (b). *HP* Homogenous Poisson process, *IP* inhomogeneous Poisson process, *TH* Thomas process, *ITH* inhomogeneous Thomas process

results are consistent with previous research (Condit et al. 2000; Li et al. 2009; Seidler and Plotkin 2006) where spatial patterns differ among abundance classes and dispersal modes. Differences in species abundance may arise from differences in fecundity and mortality associated with density dependence, habitat selection and interspecific interactions (Beckage and Clark 2005; Clark et al. 1999; Harms et al. 2000). The underlying mechanisms that contribute to different species abundance may also reflect in the formation of spatial patterns.

Predictability of species attributes, however, differs between the two study forests. This site-specific pattern may be attributed to unique topography and history of the study sites. For example, elevated coral reefs in the Kenting plot may serve as dispersal barriers that block seed dispersal by wind and form seed patches in the study site (Lin et al., in review). As a result, wind-dispersed species



**Table 3** Relative importance of the best fit models in the LHC and Kenting plots at varying spatial scales

Best model	<2 m	2–5 m	5–10 m	10–20 m	20–40 m	40–60 m
<b>LHC plot</b>						
Homogeneous Poisson	3% (2)	1% (1)	0% (0)	0% (0)	0% (0)	2% (2)
Inhomogeneous Poisson	24% (22)	14% (13)	8% (7)	1% (1)	3% (3)	9% (8)
Homogeneous Thomas	28% (21)	23% (21)	16% (15)	16% (15)	32% (30)	37% (34)
Inhomogeneous Thomas	45% (58)	62% (58)	76% (71)	83% (77)	65% (60)	53% (49)
<b>Kenting plot</b>						
Homogeneous Poisson	9% (5)	0% (0)	2% (1)	0% (0)	2% (1)	2% (1)
Inhomogeneous Poisson	44% (25)	25% (14)	7% (4)	5% (3)	4% (2)	22% (13)
Homogeneous Thomas	14% (8)	16% (9)	18% (10)	39% (33)	49% (28)	20% (12)
Inhomogeneous Thomas	33% (19)	60% (34)	74% (42)	56% (32)	46% (26)	56% (33)

The best-fit model was selected by scale-specific AIC (see “Materials and methods” for details). The portion was out of 93 species in the LHC plot and 57 in the Kenting plot. Numbers in parentheses are number of species

in the plot can only be described by aggregation processes, e.g., the homogeneous and inhomogeneous Thomas processes.

In conclusion, we found spatial patterns of tree species may have been dominantly generated by the joint effects of habitat association and dispersal limitation. Such results may lead to reconciling debate on the importance of niche- and neutral-based processes in tree communities. Spatial distribution of species is not independent of life history traits, but can be influenced by species abundance and dispersal mode. However, the significant trait attributes are site-specific, reflecting the unique topographic and history of a study site.

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