

Species-area relationships explained by the joint effects of dispersal limitation and habitat heterogeneity

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Abstract. Species-area relationships (SARs) characterize the spatial distribution of species diversity in community ecology, but the biological mechanisms underlying the SARs have not been fully explored. Here, we examined the roles of dispersal limitation and habitat heterogeneity in shaping SARs in two large-scale forest plots. One is a 24-ha subtropical forest in Gutianshan National Nature Reserve, China. The other is a 50-ha tropical rain forest in Barro Colorado Island, Panama. Spatial point pattern models were applied to investigate the contributions of dispersal and habitat heterogeneity and their interactions to the formation of the SARs in the two sites. The results showed that, although dispersal and habitat heterogeneity each could significantly contribute to the SARs, each alone was insufficient to explain the SARs. Their joint effects sufficiently explained the real SARs, suggesting that heterogeneous habitat and dispersal limitation are two predominant mechanisms for maintaining the spatial distributions of the species in these two forests. These results add to our understanding of the ecological processes underlying the spatial variation of SARs in natural forest communities.

Key words: *Barro Colorado Island, Panama; dispersal limitation; Gutianshan National Nature Reserve, China; heterogeneous habitat; point pattern modeling; Poisson processes; species-area relationship (SAR); subtropical forest; Thomas processes; tropical forest.*

INTRODUCTION

A species-area relationship (SAR) describes how the number of species changes with the size of the sampling area (Gleason 1922, Connor and McCoy 1979). This relationship has been studied for more than one hundred years, and its importance has long been appreciated in biogeography, community ecology, and conservation biology (de Candolle 1855, Sugihara 1980, Higgs 1981, He and Legendre 1996, 2002, Desmet and Cowling 2004, Thomas et al. 2004). However, current understanding of SARs mainly comes from empirical data fitting by various statistical and ad hoc models (e.g., exponential and power curves; Tjørve 2003), and the processes that produce the SARs are still not fully understood (McGuinness 1984, Storch et al. 2007).

Conventionally, three principle hypotheses have been proposed to account for SARs. The random placement hypothesis proposes that nothing other than a random

placement of species and individuals in an area is responsible for the shape of SARs, thus leaving no room for habitat differences and other ecological processes for explaining species richness (Arrhenius 1921, Coleman 1981). On the contrary, the habitat diversity hypothesis attributes the increase of species to the addition of new habitats when the size of sampling area increases (Williams 1964). Meanwhile, the equilibrium theory assumes that the number of species in an island is a result of dynamic equilibrium between the effect of immigration and extinction (Preston 1960, 1962, MacArthur and Wilson 1963, 1967).

The recently developed neutral theory of macroecology introduces speciation and dispersal limitation into the mechanisms for interpreting species diversity and SARs (Hubbell 2001). It has been shown that dispersal limitation is a key process generating species-area curves (Hubbell 1999). Different dispersal kernels (e.g., narrow vs. fat tails) can generate SARs varying from log-log linear to triphasic shape (Hubbell 2001, Chave et al. 2002). Rosindell and Cornell (2007) showed a triphasic SARs with a log-log linear central phase in an infinite landscape.

It has been well recognized that each of the above hypotheses can be applied to explain the observed

Manuscript received 3 September 2008; revised 19 January 2009; accepted 17 February 2009. Corresponding Editor: N. J. Gotelli.

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TABLE 1. A comparison of the two forest plots (Gutianshan, China, and Barro Colorado Island, Panama [BCI]).

Characteristic	Gutian plot	Barro Colorado Island
Plot location	29°10'19"–29°17'41" N, 118°03'50"–118°11'12" E	9°9'4.5"–9°9'20.7" N, 79°51'18.6"–79°51'19.1" W
Community type	subtropical forest, old-growth evergreen, broad-leaved	tropical forest, old-growth, rain, semi-deciduous plants
Plot setting-up year	2005	1980
Plot size (ha)	24	50
Mean annual temperature	15.3°C	27°C
Mean annual precipitation (mm)	1964	2600
Species richness (number of species with dbh \geq 1 cm)	159	301
Number of individuals	140 676	229 049

species-area curve in some kinds of communities (Connor and McCoy 1979). These hypotheses emphasize roles of different ecological and evolutionary processes (Gotelli and Graves 1996), but the method for quantitatively assessing the contributions of individual processes remains to be explored. This has been a major challenge to the study of the SARs and a source of controversies.

In this study, we address this challenge using the recently developed spatial statistics methods (Waagepetersen 2007, Waagepetersen and Guan 2009). The spatial statistical models can be used to analyze spatial distribution of individuals through either single process or multiple processes (Stoyan 2000, Cottetie 2005), thus allowing for assessing the additive effects of different generating mechanisms. Because the new methods do not require the unrealistic assumptions of stationary and isotropic spatial distribution (Baddeley and Turner 2005), more accurate estimates of the joint effects of dispersal and habitat heterogeneity can be obtained (John et al. 2007).

Our interest here is to investigate the individual effects of random placement, dispersal limitation, habitat heterogeneity, and their joint effects on the formation of the SARs. We start by testing the effect of the random placement model and then examine more complex spatial models by including the processes of dispersal limitation and habitat heterogeneity. Specifically, four models were assessed: (1) the homogeneous Poisson process for examining the effect of a pure random process; (2) the heterogeneous Poisson process for examining the effect of habitat heterogeneity; (3) the Poisson cluster process for examining dispersal limitation. Hereafter, this process is called homogenous Thomas model based on previous studies (Plotkin et al. 2000, Seidler and Plotkin 2006, John et al. 2007); and (4) the heterogeneous Thomas model for examining the joint effects of dispersal and habitat heterogeneity. These different spatial models were applied to generate SARs at different spatial scales and the results obtained from each of the above four models were compared across scales. Inferences on the effect of each of these models on SARs were then drawn from comparing the goodness of fit of the models.

MATERIALS AND METHODS

Subtropical and tropical forest community data sets

Two different types of tree communities were chosen to examine the mechanisms generating the SARs. The first data is a 24-ha stem-mapped subtropical forest plot, located in Gutianshan National Nature Reserve, western Zhejiang Province, China (Table 1, hereafter called Gutian plot). Detailed descriptions of the climate, geology, flora, and fauna in the Gutian plot can be found in Zhu et al. (2008) and Legendre et al. (2009). The Gutian plot was stem mapped in 2005. There are in total 140 676 stems (dbh \geq 1 cm) belonging to 159 species. The second data is the widely known 50-ha Forest Dynamics Plot of Barro Colorado Island (BCI), Panama (Table 1). Detailed descriptions of the climate, geology, flora, and fauna of BCI can be found in Croat (1978), Leigh et al. (1982), and Gentry (1990). The BCI data we used is the sixth census data collected in 2005. The climate and community composition of the two plots are summarized in Table 1. Because the accuracy of spatial pattern modeling relies on reasonable minimum population size (Baddeley and Turner 2005), rare species with fewer than 50 individuals were not included in all analyses.

In order to quantify the effect of habitat heterogeneity on the SARs of Gutian and BCI plots, we included four topographical variables, the tree density per quadrat, and 12 soil nutrient elements and pH value in the soil in our analysis. Specifically, the topographic variables are mean elevation, mean convexity, mean aspect, and mean slope in each 4 \times 4 m quadrat (Harms et al. 2001, Valencia et al. 2004). Similarly, based on the original BCI soil data, we generated the maps of 4 \times 4 m² scale for the concentrations of nutrient elements including Zn, Al, B, Ca, Fe, K, Cu, Mg, Mn, N, P, and N (mineralization) and pH value in the soil using geo-statistical methods. The total tree density in each 4 \times 4 m² quadrat was used as a comprehensive bioenvironmental index for analysis.

Testing the effects of random placement, dispersal limitation, and habitat heterogeneity on SARs

Four distinct processes with a progressive increase in complexity were used to explain the SARs in the two

plots. The first is a homogeneous Poisson process where the spatial location of a given point (tree) is independent of any other trees. This process only has one parameter, α , the average tree density per unit area for each species (Table 2, Appendix).

The second model is a heterogeneous Poisson process where the density of each tree species in each quadrat is associated with the environmental factors in the quadrat. Compared with the homogeneous Poisson process, heterogeneous Poisson process has additional parameters, β_j ($j = 1, 2, \dots$), for describing the correlations between the tree density and habitat conditions (Table 2, Appendix). This process can be used to examine the effects of the interaction between tree density and habitat factors (e.g., topography and soil nutrient properties) on the SARs.

The third model is a homogeneous Thomas process where the aggregative distribution of offspring due to dispersal limitation is considered, distinct from the previous two processes. Homogeneous Thomas process is a cluster process, which is formed by the distribution of parent trees generated by a Poisson process (κ), together with the distribution of a random number of offspring around each parent tree. Here, the number of offspring for a parent is also assumed to be a Poisson distribution (μ), and the locations of the offspring of each parent are assumed to be independent and isotropically normally distributed around the parent tree, with mean being zero and standard deviation δ (Table 2, Appendix).

The fourth model is a heterogeneous Thomas process where the relation between the density of each tree species and the environmental factors in each quadrat is considered in addition to the three parameters in the homogeneous Thomas process (Table 2, Appendix). Thus, the joint effects of dispersal limitation and habitat heterogeneity are included.

In our analysis, parameters in each of the above four processes were estimated using Waagepetersen and Guan's two-step approach (Waagepetersen and Guan 2009; Appendix). The maximum likelihood method, Eq. A.4 in the Appendix, was used to estimate the environmental (habitat heterogeneous) parameters. The minimum contrast method, Eq. A.5 in the Appendix, was used to estimate the dispersal related parameters. In the heterogeneous models with soil nutrient variables, we calculated principal components (PCs) from 13 soil variables and used only the first three components (condensed variables, explained 80.2% of total variance in soil nutrient variables) together with four other topographic parameters and the tree density per quadrat for analysis. This approach was also used by John et al. (2007) and can help to minimize the possibility of overfitting the models. To compare different models, Akaike's information criterion (AIC) was calculated to assess the gain in explanatory power due to the addition of more parameters. Since the parameters were estimated through two-step approach, our AIC calculations

TABLE 2. Four different processes and their parameters used for testing species-area relationships (SARs) pattern at different spatial scales in Gutian and BCI plots.

Processes	Parameters
Homogeneous Poisson	α
Heterogeneous Poisson	α, β_j ($j = 1, 2, \dots$)
Homogeneous Thomas	κ, μ, δ
Heterogeneous Thomas	$\kappa, \mu, \delta, \alpha, \beta_j$ ($j = 1, 2, \dots$)

Note: Parameters are: α , the tree density per unit area; κ , the density of parent trees per unit area; μ , the expected number of offspring trees per parent tree; δ , the standard deviation for the location distribution of the offspring for a given parent, which is assumed to be independently and isotropically normally distributed for the spatial distances between a parent and its offspring; and β_j , the log linear regression coefficients of the tree density on the j th environmental factor in the focal quadrat.

were based on the sum of residuals and the number of parameters used in different processes (Webster and Mcbratney 1989; Appendix).

For each of the four processes, we used the parameterized processes to simulate spatial distribution of each species, and then overlaid each species distribution generated by the simulations to recover a community that was estimated from the actual community. A species-area curve was then constructed by randomly throwing quadrats onto one simulated community, similar to the method used in previous studies (Dungan et al. 2002, Manly 2006). Finally, the predicted SARs of each model were calculated by averaging the SARs on 100 simulated communities and a 95% confidence interval (CI) was constructed for each predicted SARs. The observed (true) SARs from the original data of Gutian and BCI plots were compared against the predicted SARs. The model is considered adequate if the observed SARs fall within the 95% CI of each predicted SARs, otherwise, the model is rejected. For illustration, we presented the observed and four simulated spatial distribution maps of *Cupania seemannii* (Triana & Planch.) in the BCI plot. The nearest neighbor distance function $G(r)$ was also calculated for those different distributions to evaluate the goodness of fit of each model (Ripley 1988, Møller and Waagepetersen 2004). All calculations were conducted using the program R package "spatstat" and the main codes for analyses were included in the Supplement.

RESULTS

Homogeneous Poisson process

Our results showed that the SARs produced by the homogeneous Poisson process significantly overestimated species diversity at most scales in both Gutian and BCI plots (Fig. 1, cyan lines). In each plot, the observed SAR was distributed outside the range of 95% CI generated by the homogeneous Poisson process. Fig. 1B, D, F clearly show the discrepancies between the predicted and observed SARs at different scales. The AICs of homogeneous Poisson process models were the highest in the two plots. These significant differences

indicated that the random placement model is not adequate for explaining the SARs for Gutian and BCI plots. This is because species in both plots are not randomly distributed. For example, results in Fig. 2A, E show that the homogeneous Poisson process fails to describe spatial distribution of *C. seemannii* in the BCI plot. This result strongly suggests that nonrandom processes should be invoked to explain the SARs for the two forests.

Note that the seemingly “good” estimates of the SARs near the two ends of the SARs curve, i.e., near 0 and 24 ha in the Gutian plot (or near 0 and 50 ha in the BCI plot), were an artifact. If the results were magnified at very small scales, the SARs driven by the homogeneous Poisson process significantly overestimated species richness at most small scales (Fig. 1). The artifact arises from the fact that the total richness is fixed at the large spatial scale regardless what models are used. Thus, with the sampling area approaching the total plot, the predicted species richness is forced to converge to the total species richness. This was also true in the following analyses with different processes.

Heterogeneous Poisson process

Compared with the results of the homogeneous Poisson process, a better predicted SAR was obtained using the heterogeneous Poisson process (green lines in Fig. 1). The AICs of the heterogeneous Poisson process model were smaller than those of the homogeneous Poisson process model in the two plots (Table 3). However, the SAR predicted using the heterogeneous Poisson process still significantly overestimated species richness at most scales, especially when some important heterogeneity habitats (e.g., topography and soil nutrients) were not included (green lines in the middle of Fig. 1). The green lines in middle of Fig. 1, generated by the heterogeneous Poisson process, included four topographic parameters (elevation, slope, aspect, and convex) and the total tree density indices. These green lines were significantly different from those generated by the homogeneous Poisson process at most large spatial scales. The difference in species richness at each spatial scale and the difference in the AICs between the homogeneous and heterogeneous processes indicated that topography and the total tree density were important for explaining the SARs.

Soil nutrients and pH value are important factors which can change the SAR pattern. The inclusion of five aboveground habitat factors (four topography variables plus the number of trees in each quadrat) and three main PCA components from 13 soil parameters with the BCI plot data, substantially improved the prediction of the SARs (green lines at the bottom of Fig. 1). Fig. 2B shows the spatial distribution of *C. seemannii* in the BCI plot predicted from the heterogeneous Poisson process. The inclusion of the effects of local soil nutrient properties produced the clustered distribution that was closer to the real situation (Fig. 2E). However, there is

still noticeable overestimation in species richness at most spatial scales even when information of 17 habitat variables was considered in the BCI plot. This overestimation is largely due to the underestimation of aggregation of species. Fig. 3 exactly shows that heterogeneous Poisson model underpredicts the aggregation of the spatial distribution of *C. seemannii* in the BCI plot. These results indicated that random placement and habitat heterogeneity together were still insufficient to explain the SARs.

Homogeneous Thomas process

Our results showed that the homogeneous Thomas process fitted the SARs better than the homogeneous Poisson process, with smaller AICs (Table 3). This suggests that dispersal limitation could be an important factor in affecting the SARs. The homogeneous Thomas process predicted aggregated distribution of species. For example, Fig. 2C shows the distribution of *C. seemannii* in the BCI plot predicted from the homogeneous Thomas process.

In contrast to the overestimation with the homogeneous Poisson process, the homogeneous Thomas model underestimates species richness at intermediate spatial scales (blue lines in Fig. 1). The homogeneous Thomas process in general overpredicts the degree of aggregation that causes the underestimation of the SARs (Fig. 3). The underestimations at the scale of 0.015–6.000 ha in the Gutian plot or at 0.04–6.00 ha in the BCI plot indicated that the sole dispersal process was not sufficient to explain species distribution pattern. This suggested that other aggregation processes, such as the heterogeneous habitats, could affect the SARs as well. The presence of other aggregation processes could bring above biased estimation of the clustering intensity of each species.

Heterogeneous Thomas process

The last model was the heterogeneous Thomas process which significantly improved the explanation of the SARs in both plots. No significant differences were observed between the predicted and observed SARs at most sampling scales, except a very slight underestimation at the scale of 0.04–2.2 ha for the BCI plot (red lines in Fig. 1C–F), and at the scale of 0.02–0.18 ha for the Gutian plot (red lines in Fig. 1A, B). The heterogeneous Thomas process models had the lowest AIC (Table 3). Apparently, the heterogeneous Thomas process is the best-fitted process among the four processes studied here.

Fig. 2D shows the spatial distribution of *C. seemannii* predicted using the heterogeneous Thomas process in the BCI plot. Differences in spatial patterns of *C. seemannii* (Fig. 2) and nearest neighbor distance curves (Fig. 3) again show heterogeneous Thomas process is the best process of the four studied here. The same qualitative results were also observed in most of other species (not shown here). These results explicitly

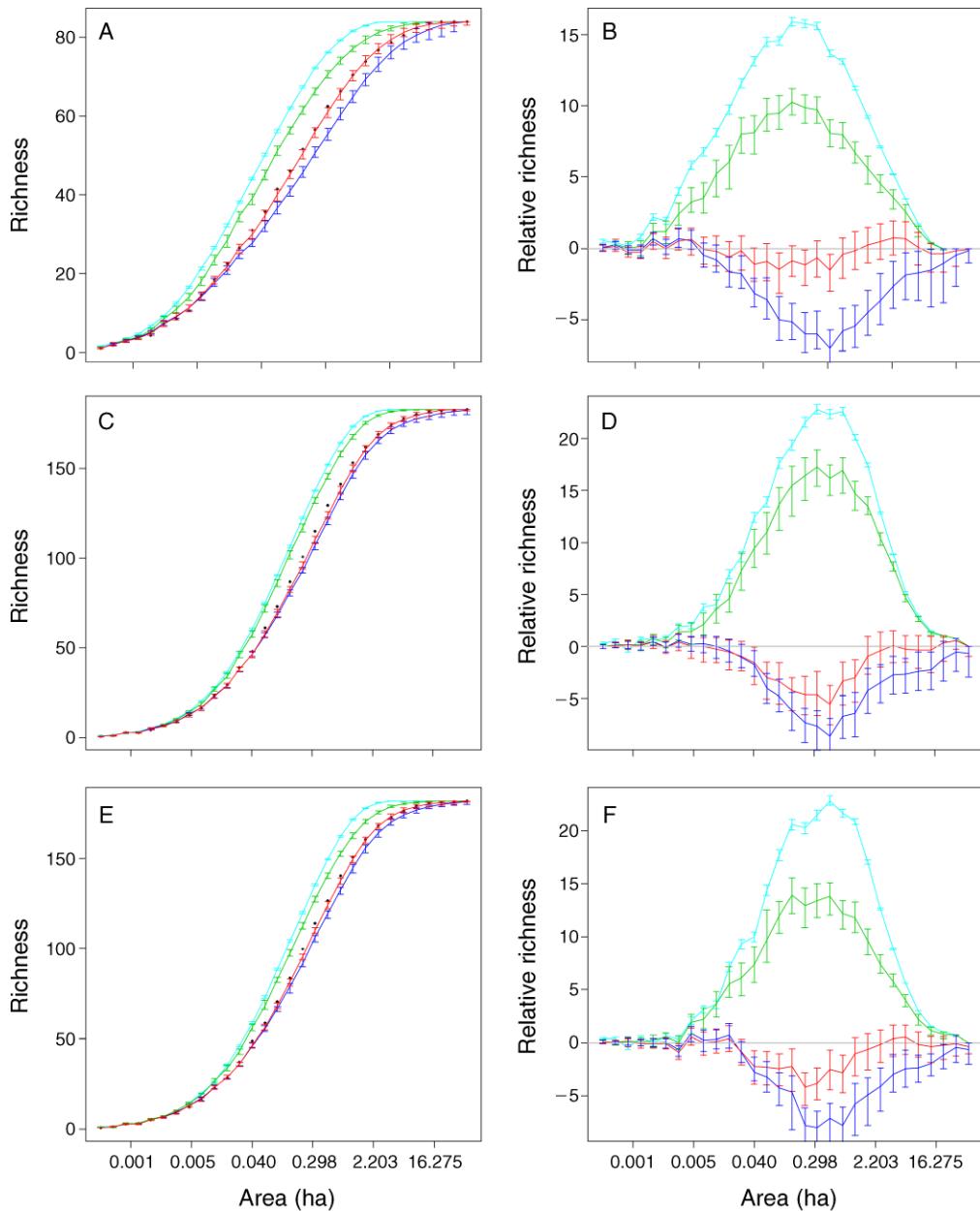


FIG. 1. The observed (black dots) and predicted species-area curves for the two data sets (A, C, E) and their differences (B, D, F). (A, B) Gutian plot (China) without soil data, (C, D) Barro Colorado Island (BCI; Panama) plot without soil data, (E, F) BCI plot with soil data. In each figure, the cyan line is the species-area curve predicted from the homogeneous Poisson process, the green line is the prediction of the heterogeneous Poisson process, the blue line is the prediction of the homogeneous Thomas process, and the red line is that of the heterogeneous Thomas process. The differences between results with soil data and results without soil data by the same analysis method reflect the potential impact of soil nutrients and soil pH values on species-area relationships. The vertical bars indicate the 95% confidential intervals.

demonstrated that the joint effects of habitat heterogeneity and dispersal limitation determine the SARs in both Gutian and BCI plots.

DISCUSSION

Using different types of spatial point pattern models, we demonstrated that the joint effects of dispersal

limitation and heterogeneous habitats could explain the pattern of SARs in both Gutian and BCI forest plots. Compared with the significant effects of dispersal limitation or habitat heterogeneity, their joint effects increase the predictive power of the SARs in forest communities (Table 3). These results are consistent with the previous studies observed from seed trapping

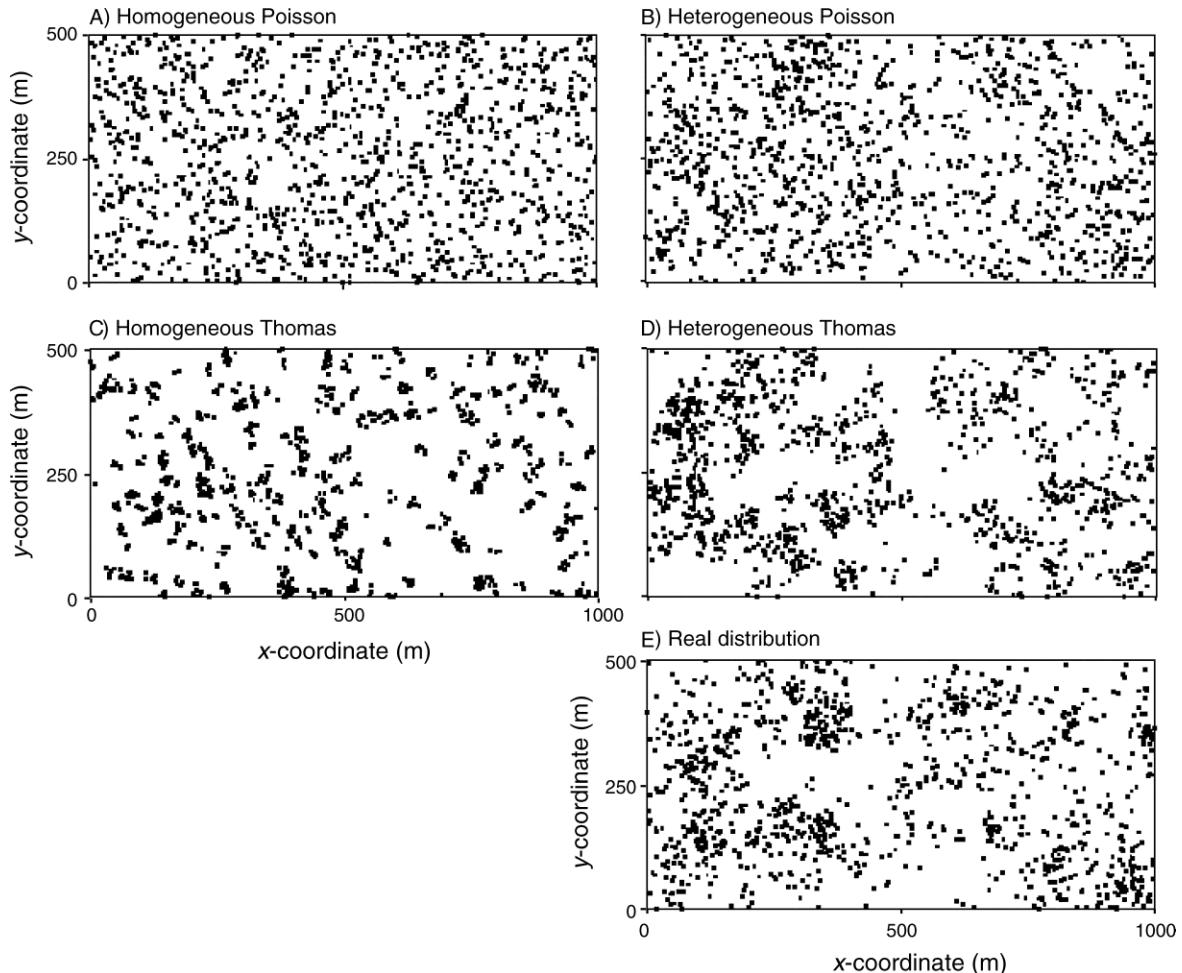


FIG. 2. The natural distribution of *Cupania seemannii* (Triana & Planch.) in the BCI plot and its distribution predicted from four different processes. (A) Distribution predicted by the homogeneous Poisson process, with parameter $\hat{\alpha} = 0.0026$. (B) Distribution predicted by the heterogeneous Poisson process, with parameters $\hat{\alpha} = 17.2541$, $\hat{\beta}_1 = -4.1274$ for elevation, $\hat{\beta}_2 = -0.1113$ for slope, $\hat{\beta}_3 = 0.0261$ for aspect, $\hat{\beta}_4 = 0.4145$ for convex, $\hat{\beta}_5 = 1.6390$ for tree density, $\hat{\beta}_6 = 0.2057$ for the first component of soil nutrients, $\hat{\beta}_7 = 0.2057$ for the second component of soil nutrients and pH value, and $\hat{\beta}_8 = -1.6736$ for the third component of soil nutrients and pH value. (C) Distribution predicted by the homogeneous Thomas process, with parameters $\kappa = 0.0005$, $\mu = 4.8786$, and $\delta = 5.8189$. (D) Distribution predicted by heterogeneous Thomas process, with parameters $\kappa = 0.0003$, $\mu = 40.7715$, $\delta = 17.0692$, and the same $\hat{\beta}_j$ ($j = 1, \dots, 8$) as those in panel (C). (E) Natural distribution of *Cupania seemannii*.

experiments and environmental association tests (Levine and Murrel 2003, John et al. 2007). Although the importance of dispersal limitation and habitat heterogeneity in explaining species diversity have been separately stressed in forest or other communities (Boecklen 1986, Hart and Horwitz 1991, Plotkin et al. 2000, Condit et al. 2002, Clark et al. 2004, Wiegand et al. 2007), our results highlight the significance of their joint effects in determining the SARs. This result has not been emphasized in lowland rain forest in Panama (BCI) although effects of dispersal limitation have been reported (Condit et al. 2002, Seidler and Plotkin 2006).

Although the random placement hypothesis explains the SARs quite well in some communities, it often overestimates species richness in other cases (Ryti 1984,

TABLE 3. A comparison of Akaike's information criterion (AIC) among the four spatial process models.

Plot	Poisson		Thomas	
	Homo-geneous	Hetero-geneous	Homo-geneous	Hetero-geneous
Guian	235.5	217.6	178.8	91.7
BCI	251.4	246.2†, 239.5‡	187.2	164.5†, 150.1‡

Note: AICs were calculated according to the sum of residuals and the number of parameters used in different processes (see Appendix). The differences between results with soil data and results without soil data by the same analysis method reflect the potential impact of soil nutrients and soil pH values on species-area relationships.

† Without soil data.

‡ With soil data.

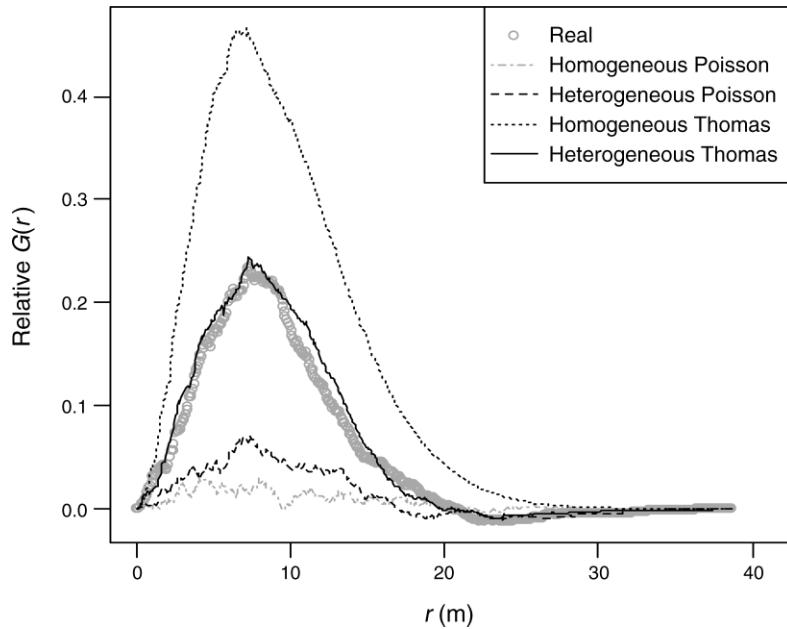


FIG. 3. The relative nearest-neighbor distance (r) function $G(r)$ (the observed G function minus that for a completely random point process) for *Cupania seemannii* in the BCI plot and the theoretical $G(r)$'s for the fitted homogeneous Poisson, heterogeneous Poisson, homogeneous Thomas, and heterogeneous Thomas processes.

Gotelli and Graves 1996, Poltkin et al. 2000, He et al. 2002), similar to the results of our homogeneous Poisson process models. Rytí (1984) suggested that overestimation of richness by this process might be caused by habitat heterogeneity and dispersal limitation. Habitat heterogeneity and dispersal limitation could cause the assumption of random spatial distribution of individuals and species invalid. Habitat diversity hypothesis assumes that species diversity is controlled by the availability of different habitat types (Williams 1964). However, our results from the heterogeneous Poisson models and other habitat-associated tests suggest that habitat heterogeneity is an important but not sufficient process in affecting spatial species diversity. Dispersal limitation is likely to be another important factor that changes the SARs (Levine and Murrel 2003). Theoretical and empirical studies both showed that species diversity depended on the strength of dispersal limitation (Hubbell et al. 1999, Chave et al. 2000, Levine and Murrel 2003, Rosindell and Cornell 2007). Our results from the Thomas process model confirmed it and further indicated that dispersal limitation was not the sole main force in changing the SARs. In summary, the dispersal limitation hypothesis and habitat diversity hypothesis only emphasize different individual process but not the joint processes. Heterogeneous Thomas process used in this study fills the gap in this area.

The results of our study suggest that the mechanisms for maintaining species diversity in forest community could be distinct from those of other types of communities, such as forest bird (Boecklen 1986) and herbivore communities (Rigby and Lawton 1981) where

habitat heterogeneity is considered as the dominant process. An important feature of forest community is that seed dispersal first sets the template for tree distribution. This template is subject to the effects of local environments through a variety of forms of environmental filtering. Although the real dynamics of forest communities may be more complicated, dispersal and environmental filtering are perhaps the two most fundamental steps to determine spatial distribution of species and our study supports this hypothesis. Further inquiries on the effects of different types of processes, such as density-dependent selection and interspecific competition, could be interesting in predicting SARs, and more sophisticated analyses are needed. Our study shows the effectiveness of the spatial point process for describing species distribution. This is consistent to the finding of He and Legendre (2002) who have shown that spatial distribution of species is one of the two primary factors that directly determine the shape of SARs, and the other factor is abundance. The contribution of any other factors to SARs is through their indirect effects on the spatial distribution and the abundance of species.

The advantage of the point pattern modeling method used in this study is that it can incorporate both dispersal and heterogeneous habitats into the point pattern models (Stoyan 2000, Cottetie 2005, John et al. 2007). This method relaxes two unrealistic assumptions (stationarity and isotropy) that are required in traditional statistical analysis (Baddeley and Turner 2005), and hence can more accurately estimate the effects of dispersal and habitat heterogeneity. However, we also noticed some limitations in the present modeling

framework. For instance, the spatial statistics cannot evaluate the processes in a manner analogous to the methods of variance partitioning (Dungan et al. 2002, Baddeley et al. 2005), owing to the fact that there is no natural generalization of the conditional intensity of a temporal process given the “past” or “history” up to time t (Ripley 1988, Møller and Waagepetersen 2004). This begs for the development of more advanced spatial models for modeling species distributions.

ACKNOWLEDGMENTS

Foremost, we are grateful to Fangliang He for supporting the establishment of the Gutian plot. This work was inspired from the many discussions G. Shen had with him. We thank Joshua Plotkin and James Rosindell for very useful comments on the manuscript. We also thank Jianhua Chen, Teng Fang, Shengwen Chen, Binyang Ding, Chaozong Zheng, and many field workers who provided support on field investigation. This work was supported by Key Innovation Project of CAS (KZCX2-YW-430) and NSFC (30200034) and was conducted while G. Shen visited Fangliang He’s lab in 2008. The BCI forest dynamics research project was made possible by National Science Foundation, 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 two decades. The plot project is part of the Center for Tropical Forest Science, a global network of large-scale demographic tree plots.

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APPENDIX

Main algorithms for the four spatial point models and the steps for estimating parameters used in addressing the joint effects of habitat heterogeneity and dispersal limitation on the species-area relationships (SARs), and calculations of AIC (*Ecological Archives* E090-217-A1).

SUPPLEMENT

R program code for estimating parameters of spatial point models and generating the expected SARs for each model (*Ecological Archives* E090-217-S1).