Point process models, the dimensions of biodiversity and the importance of small-scale biotic interactions

Xiangcheng Mi[1], Lei Bao[2], Jianhua Chen[3] and Keping Ma[1],*

[1] *State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, 20 Nanxincun, Xiangshan, Beijing 100093, China*
[2] *College of Life Science, Beijing Normal University, 19 Xinjiekouwai Street, Haidian District, Beijing 100875, China*
[3] *College of Chemistry and Life Sciences, Zhejiang Normal University, 688 Yingbin Road, Jinhua, Zhejiang 321004, China*
*Correspondence address. State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, 20 Nanxincun, Xiangshan, Beijing 100093, China. Tel: +86-10-62836223; Fax: +86-10-82599518; E-mail: kpma@ibcas.ac.cn

Abstract

Aims

Recent mechanistic explanations for community assembly focus on the debates surrounding niche-based deterministic and dispersal-based stochastic models. This body of work has emphasized the importance of both habitat filtering and dispersal limitation, and many of these works have utilized the assumption of species spatial independence to simplify the complexity of the spatial modeling in natural communities when given dispersal limitation and/or habitat filtering. One potential drawback of this simplification is that it does not consider species interactions and how they may influence the spatial distribution of species, phylogenetic and functional diversity. Here, we assess the validity of the assumption of species spatial independence using data from a subtropical forest plot in southeastern China.

Methods

We use the four most commonly employed spatial statistical models—the homogeneous Poisson process representing pure random effect, the heterogeneous Poisson process for the effect of habitat heterogeneity, the homogenous Thomas process for sole dispersal limitation and the heterogeneous Thomas process for joint effect of habitat heterogeneity and dispersal limitation—to investigate the contribution of different mechanisms in shaping the species, phylogenetic and functional structures of communities.

Important Findings

Our evidence from species, phylogenetic and functional diversity demonstrates that the habitat filtering and/or dispersal-based models perform well and the assumption of species spatial independence is relatively valid at larger scales (50×50 m). Conversely, at local scales (10×10 and 20×20 m), the models often fail to predict the species, phylogenetic and functional diversity, suggesting that the assumption of species spatial independence is invalid and that biotic interactions are increasingly important at these spatial scales.

Keywords: point process model, niche, neutral theory, dispersal limitation, habitat filtering, assumption of species spatial independence, community phylogenetic structure, community functional structure

INTRODUCTION

In order to simplify the complexity of natural systems, species spatial independence is a default assumption in many theoretical models (Harte *et al.* 2005; Volkov *et al.* 2007) and empirical studies (Shen *et al.* 2009; Wang *et al.* 2011) of community assembly. Over the past decade, two opposing families of hypotheses have been at the center of the debate regarding what processes underlie community patterns: the niche theory that invokes the important role of niche-based habitat filtering and the neutral theory that emphasizes the central role of seed dispersal and demographic stochasticity in shaping patterns of community structure and diversity. This debate has led to a general consensus that the observed patterns of community structure and diversity are simultaneously shaped by niche-based environmental processes and dispersal-based

spatial processes. Thus, it appears that the observed patterns of community structure and diversity can be largely explained by only habitat filtering and dispersal limitation without having to consider other important ecological processes such as direct and indirect species interactions. For example, recent research, that assumes spatial independence of species by default, utilizes spatial point process models to show that the species–area relationship (Shen *et al.* 2009), the species abundance distribution (Cheng *et al.* 2012) and species beta diversity (Wang *et al.* 2011) can be explained quite well by models that incorporate only dispersal limitation and habitat filtering (invoked by carrying capacity of populations alone in these studies).

However, the assumption of species spatial independence is inconsistent with other evidence that shows intraspecific and interspecific interactions are important determinants of community structure and diversity (Brooker *et al.* 2008; Maestre *et al.* 2009; Terborgh 2012). For example, Wiegand *et al.* (2007) found that species that have negative and positive facilitative interactions with other species dominated the tropical forests in Barro Colorado Island, Panama and Sinharaja, Sri Lanka at local scales (<20 m) and were therefore not well modeled using spatial point processes models that assume spatial independence. Further, many studies that investigate spatial scale and co-occurrence have demonstrated an increase in the phylogenetic and functional dissimilarity of species at local scales (Kraft and Ackerly 2010; Stubbs and Wilson 2004; Swenson and Enquist 2009; Swenson *et al.* 2007). These findings challenge the assumption of species spatial independence in above-mentioned studies and suggest that strong biotic interactions should produce some detectable spatial structure of community diversity that would be significantly different from those shaped by species spatial independence. Here, we assess the validity of the species spatial independence assumption across scales with respect to species, phylogenetic and functional diversity and argue that community assembly is more than habitat filtering and dispersal limitation particularly at local scales.

We performed an assessment of the assumption of species spatial independence and tested the prediction of species, phylogenetic and functional dimensions of biodiversity across spatial scales from the same spatial point processes by Cheng *et al.* (2012), Lin *et al.* (2011), Shen *et al.* (2009), Wang *et al.* (2011) and Wiegand *et al.* (2007). Spatial point processes are stochastic models that describe the spatial pattern formed by the locations of objects in two or more dimensional space. We utilized these spatial point processes to simulate the effect of habitat heterogeneity assumed by habitat filtering-based approaches, dispersal limitation as assumed by neutral approaches, and their combination. Specifically, the approaches used in these previous studies include four spatial statistical processes: (i) homogeneous Poisson processes simulating pure random effects, (ii) heterogeneous Poisson processes for the effect of habitat heterogeneity, (iii) homogeneous Thomas processes, also called Poisson cluster models, implementing the effect of dispersal limitation without habitat heterogeneity (Plotkin *et al.* 2000; Potts *et al.* 2004; Seidler and Plotkin 2006) and finally

(iv) heterogeneous Thomas processes for the joint effect of habitat heterogeneity and dispersal limitation (Waagepetersen 2007; Waagepetersen and Guan 2009). Using these four models, Cheng *et al.* (2012), Lin *et al.* (2011), Shen *et al.* (2009) and Wang *et al.* (2011) successfully explained species aggregation, species–area relationships, beta diversity and species abundance distributions in tree communities. However, these four models focus on only three ecological processes of community assembly, i.e. completely random spatial distributions (random effects), the effect of habitat heterogeneity and dispersal limitation: they do not consider species interactions occurring at any spatial scale. Here, we show that the above four spatial statistical models representing random effects, habitat heterogeneity, dispersal limitation and their joint effect are not sufficient to explain species richness and phylogenetic and functional structure of communities at local scales, but they perform relatively well when predicting these biodiversity patterns at larger spatial scales. We demonstrate this by comparing the simulated species richness and phylogenetic and functional structure from the four spatial statistical models with empirical data from a tree inventory plot in a subtropical forest in southeastern China.

MATERIALS AND METHODS

Our analyses used data from the Gutianshan 24-ha forest dynamics plot. The plot is rectangular (600×400 m) in which all trees with DBH (i.e. diameter at breast height, which is 1.3 m above ground) ≥1 cm in the plot were tagged, identified, measured and spatially mapped. The evergreen broad-leaved subtropical forest in the plot is the representative vegetation of subtropical China dominated by *Castanopsis eyrei* (Fagaceae), *Schima superba* (Theaceae) and *Pinus massoniana* (Pinaceae). A total of 140 700 individuals belonging to 48 families and 159 species were recorded in the plot during the 2005 census. Detailed descriptions of climate, topography and the flora can be found in Cheng *et al.* (2012), Legendre *et al.* (2009) and Shen *et al.* (2009).

Data and spatial statistical models

A total of 102 tree species with DBH ≥1 cm and abundance ≥24 individuals were used in this study to meet the requirements of minimal population sizes for accurate spatial modeling (Cheng *et al.* 2012; Shen *et al.* 2009). The habitat heterogeneity in the Gutianshan plot was represented by topographic and edaphic variables (Cheng *et al.* 2012). Specifically, we first obtained the elevation of the four corners for every 5×5-m subplot from an ordinary kriging analysis using the elevation data measured in a topographic survey of the plot. The topographic variables of each 5×5-m quadrat, including mean altitude, convexity, slope and aspect, were then calculated using elevation of every 5×5-m quadrat (Legendre *et al.* 2009). Soil moisture, bulk density, nitrogen mineralization rate (Nmin), pH, together with 16 soil nutrients including total carbon, total nitrogen, total phosphorus, available Fe, Mn, Zn, Cu, K,

P, Ca, Mg, Na, B, Si, N (including NH_4^+ and NO_3^-) and Al were all quantified following the lab protocol outlined in John *et al.* (2007) and these data were interpolated to a spatial grain of 5 × 5 m using ordinary kriging following John *et al.* (2007). We then performed a principal component (PC) analysis on the topographic and soil variables and chose the first four PCs of 25 topographic and edaphic variables explaining 99.94% of the variation of 25 variables to reduce redundant information among covarying habitat variables and to minimize the possibility of overfitting (John *et al.* 2007; Shen *et al.* 2009). The details of soil sampling and measurement of soil nutrients can be found in Cheng *et al.* (2012) and Zhang *et al.* (2011).

A molecular community phylogeny was reconstructed for the tree community in the Gutianshan plot. Specifically, three commonly used plant DNA barcode loci (*rbcL*, *matK* and *trnH-psbA*) were sequenced and assembled into a three-locus supermatrix. The supermatrix was generated by globally aligning the *matK* and *rbcL* and aligning the *trnH-psbA* sequences within families using MUSCLE (Edgar 2004). Maximum likelihood and maximum parsimony algorithms were subsequently used to reconstruct community phylogenies for the plot using RAxML (Stamatakis *et al.* 2008). A bootstrap analysis with 1000 replicates was conducted to assess the percentage support for each node. Finally, an ultrametric tree was obtained using the nonparametric rate smoothing approach in the r8s software package (Sanderson 2003). Detailed methods regarding the extraction, sequencing, alignment and phylogenetic inference can be found in Kress *et al.* (2009).

We measured leaf area (LA), specific leaf area (SLA), wood density (WD), seed mass (SM) and documented maximum height (MH) for the species in the Gutianshan plot. The trait collection protocols for the Gutianshan plot followed Cornelissen *et al.* (2003) with the exception of WD, which followed the protocols of Wright *et al.* (2010). The MH values for species in the Gutianshan plot were estimated using values reported in the Flora of China (Wu *et al.* 1994–2009). Previous work has suggested that these traits have significant phylogenetic signal in the Gutianshan forest plot (Swenson *et al.* 2012). For each trait, a dendrogram was constructed using UPGMA (Unweighted Pair Group Method with Arithmetic Mean) clustering based on a Euclidean distance matrix representing interspecific trait similarity with species-level mean trait values of each species.

To compare our results with the results from Cheng *et al.* (2012), Lin *et al.* (2011), Shen *et al.* (2009) and Wang *et al.* (2011), we modeled the same four spatial statistical processes, i.e. the homogeneous Poisson process representing pure random effect, the heterogeneous Poisson process for the effect of habitat heterogeneity, the homogenous Thomas process for sole dispersal limitation and the heterogeneous Thomas process for the joint effect of habitat heterogeneity and dispersal limitation, to investigate the contribution of different mechanisms in shaping the species, phylogenetic and functional structure of communities. The model details and model parameterization can be found in Cheng *et al.* (2012), Lin *et al.* (2011), Shen *et al.* (2009) and Wang *et al.* (2011).

We first parameterized the four spatial statistical models using the spatial distributional data of each species in the Gutianshan plot. Subsequently, we used the four parameterized models of each species to simulate the spatial distribution of each species in the entire plot. Then we used an assumption of species spatial independence to overlay simulated tree distributions of all species to acquire the simulated community composition. In this study, we obtained 100 simulated communities for each model. Finally, we grouped the trees of observed community and simulated communities into territory units corresponding to three grain sizes of 10 × 10, 20 × 20 and 50 × 50 m and counted the individuals of the 102 tree species in each subplot.

To test our hypothesis regarding the effect of habitat heterogeneity and dispersal limitation on species richness and phylogenetic and functional structure, we first calculated the mean pairwise distance (MPD) and mean nearest neighbor distance (MNND) using the molecular phylogeny or a functional trait dendrogram (Webb *et al.* 2008). Then we calculated a standardized effect size (SES) of MPD and MNND using the mean and standard deviation of the null distribution as follows (Swenson *et al.* 2006; Webb *et al.* 2002):

$$\text{SES} \cdot \text{MPD} = -1 \times \left(\text{MPD} - \text{rndMPD}\right)/\text{sdrndMPD}$$
$$\text{SES} \cdot \text{MNND} = -1 \times \left(\text{MNND} - \text{rndMNND}\right)/\text{sdrndMNND}$$

Where rndMPD and rndMNND are, respectively, the mean of MPD and MNND from 999 randomly generated local community phylogeny for each quadrat by randomly shuffling the names of taxa across the tips of the phylogeny or trait dendrogram, and sdrndMPD and sdrndMNND are the corresponding standard deviations of the randomly generated local communities. Next, we compared the species richness and the community phylogenetic or functional structure between the observed communities and the average value of 100 simulated communities for each quadrat using major axis regression and adjusted mean sum of squared residual (Legendre and Legendre 1998). If the regression line is below the 1:1 identity line, the model underestimates the species richness and the degree of phylogenetic or functional clustering of communities, whereas if the regression line is above the 1:1 identity line, the model overestimates the species richness and the degree of phylogenetic or functional clustering of communities. An adjusted mean sum of squared residual (MR_a) was calculated as follows (Cheng *et al.* 2012; Efron and Tibshirani 1993; Hilborn and Mangel 1997):

$$MR_a = R/(n - 2k)$$

where *n* is the number of subplots, *k* is the number of parameters in a model and *R* is the sum of squared residuals of each subplot (see detail in the Supplementary Material Appendix 1).
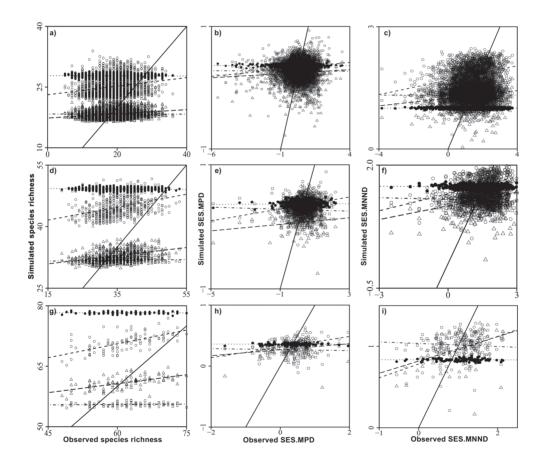
The PCs of environmental variables were extracted using the R package 'vegan' (Oksanen *et al.* 2012), simulations of spatial distribution were carried out using the R package

'spatstat' (Baddeley and Turner 2005), the SES·MPD and SES·MNND were calculated using the software 'phylocom' (Webb *et al.* 2008) and major axis regression was implemented using the R package 'lmodel2' (Legendre 2009).

RESULTS

The correlation results and the adjusted mean sum of squared residual (MR_a) between species richness of the observed and simulated communities showed that species richness estimated by all four spatial statistical models was only weakly correlated with that of observed communities at scales of 10×10 and 20×20 m (Fig. 1a and d; Table 1). In contrast, species richness estimated by the heterogeneous Poisson process, representing the effect of habitat heterogeneity, and the heterogeneous Thomas process, representing the joint effect of habitat heterogeneity and dispersal limitation, was strongly

correlated with that of observed communities at scale of 50×50 m (Fig. 1g; Table 1). We do note that there were some minor differences between results from correlation coefficient and MR_a, where the heterogeneous Thomas processes more accurately estimated species richness compared to other three processes (Fig. 1a and d; Table 1).

Our phylogenetic analysis confirmed our pattern analysis of species richness where the simulated community structure measured by SES·MPD and SES·MNND had higher MR_a and was less correlated with the observed than the estimated species richness at the scales of 10×10 and 20×20 m. The heterogeneous Poisson and heterogeneous Thomas processes also estimated community phylogenetic structure better at scales 50×50 m (Fig. 1; Table 1). The heterogeneous Poisson and heterogeneous Thomas processes estimated community phylogenetic structure relatively better than the homogeneous Poisson and homogeneous Thomas processes

Figure 1: comparison of species richness between observed and simulated communities. (**a**) 2400 10×10-m subplots, (**d**) 600 20×20-m subplots, (**g**) 96 50×50 m, SES·MPD between observed and simulated communities of (**b**) 2400 10×10-m subplots, (**e**) 600 20×20-m subplots, (**h**) 96 50×50-m subplots and comparison of SES·MNND between observed and simulated SES·MNND of (**c**) 2400 10×10-m subplots, (**f**) 600 20×20-m subplots, (**i**) 96 50×50-m subplots in Gutianshan forest dynamic plot. Filled circles represent the comparison of SES·MPD or SES·MNND between observed communities and simulated communities by homogeneous Poisson process, while open circles stand for the heterogeneous Poisson process, open triangles represent homogeneous Thomas process and open squares represent the heterogeneous Thomas process. The solid line stands for the identity relationship with equal values of SES·MPD or SES·MNND for observed and simulated communities, the dotted line for major axis regression line between SES·MPD of observed and simulated communities by homogeneous Poisson process, the dashed line for the heterogeneous Poisson process, the dot-dashed line for the homogeneous Thomas process and the long-dashed line for the heterogeneous Thomas process.

Table 1: correlation and adjusted mean sum of squared residual (in the bracket) of species richness, SES·MPD and SES·MNND of community phylogeny and SES·MPD and SES·MNND of WD between observed and simulated communities by four spatial point pattern models at different scales

Correlation types	Scale (m^2)	Homogeneous Poisson (purely random)	Heterogeneous Poisson (niche)	Homogenous Thomas (dispersal)	Heterogeneous Thomas (niche + dispersal)
$r_{richness}$	10×10	−0.036*** (100.269)	0.192*** (61.102)	−0.011** (23.725)	0.221*** (22.501)
	20×20	−0.073** (228.308)	0.329*** (122.627)	0.126** (46.167)	0.383*** (36.069)
	50×50	−0.014*** (320.831)	0.615*** (126.106)	0.096** (83.009)	0.575** (38.024)
$r_{SES·MPD}$ of phylogeny	10×10	−0.018 (0.640)	0.119*** (0.632)	−0.005 (0.658)	0.071*** (0.646)
	20×20	0.022 (0.430)	0.211*** (0.416)	−0.036 (0.461)	0.115*** (0.445)
	50×50	0.017 (0.280)	0.441*** (0.272)	−0.040 (0.319)	0.338*** (0.324)
$r_{SES·MNND}$ of phylogeny	10×10	−0.027 (0.966)	0.245*** (0.942)	−0.003 (0.833)	0.172*** (0.803)
	20×20	−0.043 (0.548)	0.315*** (0.503)	−0.063 (0.595)	0.270*** (0.533)
	50×50	−0.024 (0.349)	0.415*** (0.285)	−0.098 (0.342)	0.372*** (0.314)
$r_{SES·MPD}$ of WD	10×10	0.005 (0.440)	0.103*** (0.387)	0.016 (0.350)	0.090*** (0.350)
	20×20	0.028 (0.288)	0.181* (0.245)	0.028 (0.219)	0.182*** (0.216)
	50×50	0.161 (0.138)	0.326*** (0.122)	−0.091 (0.128)	0.329*** (0.122)
$r_{SES·MNND}$ of WD	10×10	0.033 (0.676)	0.025 (0.638)	0.002 (0.542)	0.090*** (0.523)
	20×20	0.014 (0.259)	0.130*** (0.243)	−0.022 (0.236)	0.170*** (0.213)
	50×50	−0.091 (0.071)	0.592*** (0.056)	−0.064 (0.075)	0.637*** (0.050)

$r_{richness}$: correlation coefficient between species richness of observed and simulated communities; $r_{SES·MPD}$ of phylogeny: correlation coefficient between SES·MPD of observed and simulated communities; $r_{SES·MNND}$ of phylogeny: correlation coefficient between SES·MNND of phylogeny for observed and simulated communities; $r_{SES·MPD}$ of WD: correlation coefficient between SES·MPD of WD for observed and simulated communities; $r_{SES·MNND}$: correlation coefficient between SES·MNND of WD for observed and simulated communities. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

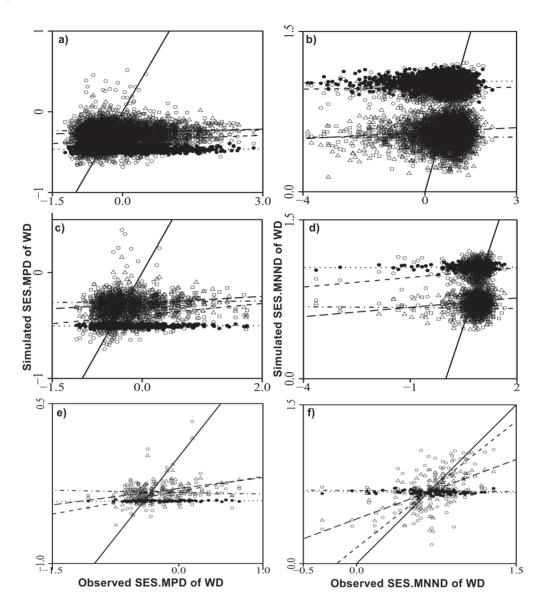from results of correlation coefficient and MR_a (Fig. 1; Table 1).

Our functional analyses showed similar results to the species richness and phylogenetic analyses with the exception of SLA (Fig. 2; Table 1; Supplementary Material Appendix 2 and 3). For WD, LA, SM and MH, the four spatial statistical models underestimated the degree of functional overdispersion and clustering at smaller scales (10×10 and 20×20 m) (Fig. 2; Supplementary Material Appendix 2), and the functional SES·MNND and SES·MPD of simulated communities has larger MR_a, and were only weakly correlated with the functional SES·MNND and SES·MPD of the observed communities (Table 1; Supplementary Material Appendix 2). Similar to the community phylogenetic structure, the heterogeneous Poisson and the heterogeneous Thomas processes performed better at larger scales based on results of correlation coefficient and MR_a (Fig. 2; Table 1; Supplementary Material Appendix 2 and 3). The one exception was SLA, where the heterogeneous Poisson and heterogeneous Thomas processes estimated the community structure quite well even at small scales.

DISCUSSION

The assumption of species spatial independence is frequently used to reduce the complexity of natural communities in ecological studies. Point process models have recently been used to explore the mechanisms of community assembly particularly in tree communities. The assumption of the species

spatial independence is often used to simplify the spatial modeling or in other words, it is explicitly hypothesized in the assumption that interspecific interactions do not dictate the spatial distributions of trees. Here, we tested the validity of the assumption of species spatial independence across scales with respect to species, phylogenetic and functional diversity, using the four spatial statistical models used in recent studies (Cheng *et al.* 2012; Lin *et al.* 2011; Shen *et al.* 2009; Wang *et al.* 2011), representing effect of random process, habitat heterogeneity, dispersal limitation and their joint effect.

At larger scales (50×50 m), our results show that point process models do adequately predict the diversity patterns in our example dataset and that the spatial independence assumption used in previous studies (Cheng *et al.* 2012; Lin *et al.* 2011; Shen *et al.* 2009; Wang *et al.* 2011) may be adequate at these scales and that species interactions were, perhaps unsurprisingly, relatively unimportant at these scales. Specifically, the evidence from pattern analysis of species, phylogenetic and functional diversity supports that the community diversity patterns simulated by the habitat heterogeneity and the joint effect of habitat heterogeneity and dispersal limitation were strongly correlated with the observed community diversity patterns (Fig. 1; Table 1; Supplementary Material Appendix 2 and 3). Further, the heterogeneous Poisson and heterogeneous Thomas processes explained patterns of community biodiversity better at larger scales, suggesting a lack of species interactions and stronger habitat filtering and dispersal limitation at larger scales (50×50 m) (Brunbjerg *et al.* 2012; Cheng

Figure 2: comparison of SES·MPD of WD between observed and simulated communities of (**a**) 2400 10×10-m subplots, (**c**) 600 20×20-m subplots, (**e**) 96 50×50-m subplots and comparison of SES·MNND of WD between observed and simulated communities of (**b**) 2400 10×10-m subplots, (**d**) 600 20×20-m subplots, (**f**) 96 50×50-m subplots in Gutianshan forest dynamic plot. Filled circles represent the comparison of SES·MPD or SES·MNND between observed communities and simulated communities by homogeneous Poisson process, while open circles stands for the heterogeneous Poisson process, open triangles represent homogeneous Thomas process and open squares represent the heterogeneous Thomas process. The solid line stands for the identity relationship with equal values of SES·MPD or SES·MNND for observed and simulated communities, the dotted line for major axis regression line between SES·MPD of observed and simulated communities by homogeneous Poisson process, the dashed line for the heterogeneous Poisson process, the dot-dashed line for the homogeneous Thomas process and the long-dashed line for the heterogeneous Thomas process.

et al. 2012; Shen *et al.* 2009; Swenson and Umaña 2014; Wang *et al.* 2011).

At local scales (10×10 and 20×20 m), however, community species richness and phylogenetic and functional diversity could not be predicted by any of the point process models (Fig. 1; Table 1). Although greater sample size at local scales may affect the relationship between observed and simulated patterns of community species richness and phylogenetic and functional diversity, the great discrepancy between the results at larger scales (50×50 m) and those at local scales

mainly indicates a failure of these models to incorporate important biological information. In particular, these results suggest strong local biotic interactions such as negative density dependence and positive facilitation among species that are not modeled dominate at these local scales (Brooker *et al.* 2008; Raventós *et al.* 2010; Terborgh 2012; Wiegand *et al.* 2007). One exception to this general finding was SLA, where the heterogeneous Poisson and the heterogeneous Thomas processes explained the diversity of this trait quite well even at local scales (10×10 and 20×20 m). This suggests that SLA

is related to habitat characteristics more strongly than other functional traits on these scales (MH, WD, LA and SM), which may not be surprising given that SLA represents species-specific strategies of construction investment, growth rate and resource acquisition (Reich *et al.* 1997; Wright *et al.* 2004).

In summary, here we have discussed the increasing usage of point process models to investigate the biological processes underlying the spatial distribution of biodiversity and the default utilization of the assumption of species spatial independence in these models. These models have generally been used to investigate one dimension of biodiversity, species diversity, but they can be easily extended to other dimensions of biodiversity such as functional and phylogenetic diversity as we have shown here. The previous success of these models in predicting patterns assures that they will continue to be utilized. Despite the success of these models in previous work, we argue that the utilization of the assumption in these models that species are independently distributed in space may be not hold particularly at local scales. We approached this problem by examining the ability of the four commonly used point process models to predict the three dimensions of biodiversity across spatial scales. We found that these models often perform well at larger scales for each dimension of biodiversity, thereby demonstrating their power when operating at large scales. However, we also found that at local scales, the models often fail to predict the dimensions of biodiversity observed. We infer that this failure is due to a lack of information regarding species interactions in the models. This is not to suggest that point process models are without merit on these or other scales. Rather we suggest two important points. First, observed deviations from modeled levels of biodiversity across spatial scales can be useful in identifying when, where and why habitat filtering and dispersal limitation are not enough to explain the spatial distribution of biodiversity. Second, if researchers are interested in modeling tree biodiversity across spatial scales, additional biological processes such as competition and facilitation may have to be incorporated into point process models using Gibbs point process models in the future although the practical fitting of complex point process models incorporating interspecific interactions of tens to hundreds of species in a community remains difficult (Haas *et al.* 2011; Illian and Hendrichsen 2010). We suggest that phylogenetic and functional information could be useful in simplifying the complexity modeling of interspecific interactions in point process models.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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