Dominant species and dispersal limitation regulate tree species distributions in a 20-ha plot in Xishuangbanna, southwest China

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Habitat heterogeneity and dispersal limitation are widely considered to be the two major mechanisms in determining tree species distributions. However, few studies have quantified the relative importance of these two mechanisms at different life stages of trees. Moreover, rigorous quantification of the effects of dominant tree species in determining species distributions has seldom been explored. In the present study, we tested the hypothesis that the distribution of tree species is regulated by different mechanisms at different life history stages. In particular, we hypothesised that dispersal limitation regulates the distribution of trees at early life stages and that environmental factors control the distribution of trees as they grow, because of niche differentiation resulting from environmental filtering. To test this, trees in 400-m² quadrats in a 20-ha plot in Xishuangbanna, southwest China were grouped into four classes on the basis of the diameter at breast height (DBH) that roughly represent different stages in the life history of trees. A neighbourhood index was computed to represent a neutral spatial autocorrelation effect. We used both biotic (dominant species) and abiotic (topography and soil) predictor variables to model the distribution of each target species while controlling for spatial autocorrelation within each of the DBH classes. To determine which factors played the largest role in regulating target species distribution, the simulated annealing method was used in model selection based on Akaike information criterion (AIC) values. The results showed that the relative importance of neutral and niche processes in regulating species distribution varied across life stages. The neutral neighbourhood index played the most important role in determining the distributions of small trees (1 cm $\leq$ DBH $\leq$ 10 cm), and dominant species, as biotic environmental predictor variables, were the next most important regulators for trees of this size. Environmental predictor variables played the most important role in determining the distributions of large trees (10 cm $\leq$ DBH). This finding builds on previous research into the relative importance of neutral and niche processes in determining species distributions regardless of life stages or DBH classes.

Over the past century, numerous theories, including the Janzen–Connell hypothesis (Janzen 1970, Connell 1978), niche assembly theories (Hutchinson 1957, Wright 2002) and unified neutral theory (Hubbell 2001), have been proposed to explain species coexistence. Niche theory, and more specifically niche-assembly theory, has been proposed as a major mechanism for the coexistence of tree species (Silvertown et al. 1999). The core concept of niche theory stems from Darwin's theory of evolution by natural selection, in which species are predicted to be closely associated with particular environmental conditions (Losos and Ricklefs 2009). Niche theory itself can be traced back to half a century ago, when Hutchinson (1957) proposed that each species has its own niche. Niche-assembly theory has motivated numerous studies to model and test the effects of habitat on the spatial and temporal distributions of species. These studies have contributed greatly to our understanding of species coexistence in various ecosystems, including tropical (trees: John et al. 2007, palms: Tuomisto et al. 2003), subtropical (evergreen forest plants: Legendre et al. 2009, Wang et al. 2009), temperate (understory ferns: Gilbert and Lechowicz 2004) and savanna ecosystems (tree-grass mixtures: Sankaran et al. 2004).

Habitat variations are also important factors in the regulation of species distributions, and species can vary in their responses to environmental factors (Gilbert and Lechowicz 2004, Legendre et al. 2009, Tuomisto et al. 2003). For example, some species may be positively correlated with particular explanatory variables whereas others respond negatively. To understand the habitat associations of individual species, precise field-oriented studies are typically required (Clark et al. 1998). For example, Levine and HilleRisLambers (2009) conducted an experiment on serpentine annual plants to test the stabilising effects of niche differences. However, this type of experiment may not be suitable for study species that have long life spans, such as trees.

Although various methods have been developed for studying species–habitat relationships, few of them incorporated the effect of spatial autocorrelations in species distribution analysis before Legendre and Fortin (1989). Legendre (1993) suggested that spatial autocorrelation should be treated properly in the analysis of spatial processes. The spatial autocorrelation in tree species distribution is primarily caused by environmental factors and community processes (Legendre 1993). Of the community processes, dispersal limitation has been proposed as the most important mechanism for the maintenance of species diversity (Hubbell et al. 1999, Hubbell 2001). Recently, many empirical and theoretical studies have provided strong support for these hypotheses (Shen et al. 2009, Chen et al. 2010).

Abiotic factors such as soil properties, topographic factors and gap openness are widely considered to be important factors in the regulation of species distributions (Hubbell et al. 1999, Harms et al. 2001, John et al. 2007). At mesoscales ($\approx$ 1–100 km^2), abiotic factors have been verified to be important in regulating species distributions (Clark et al. 1998, 1999), but at the local scale (0–1 km^2), more studies are still required. In addition, biotic factors such as neighbourhood effects are also important in determining species distributions (Hubbell 2001, Uriarte et al. 2004, Canham and Uriarte 2006). Traditionally, ecologists have tended to use all of the surrounding neighbour trees to analyse the performance of a target species (Uriarte et al. 2004). The dominant species have rarely been considered separately as predictor variables in quantifying the distributions of target tree species.

Another issue that is often ignored in species–habitat studies is that conspecific trees may not respond to the same explanatory variables consistently across life stages. So far, few studies have taken individual tree size into consideration in the analysis of species spatial distribution (Comita et al. 2007, Lai et al. 2009). Many studies have assumed that all trees respond similarly to the environment regardless of life stage. Using the entire population of a species regardless of the size classes of trees may obscure our understanding of species–habitat relationships.

Previous studies have shown that the contribution of demographic niches to species distribution is limited (Condit et al. 2006), and trees are more clumped than would be predicted by a random distribution (Condit et al. 2000). We hypothesise that neutral processes play a greater role than niche processes in determining trees distributions, especially at early life stages but that the relative importance of neutral processes is reduced and species–habitat association is enhanced throughout tree growth because of the effects of environmental filtering (Norden et al. 2009). Because the dominant species are the most abundant and widely distributed and have the largest total basal area in the community, they might play an important role in determining the distributions of trees. In this study, we integrated dominant species, edaphic factors and topographic factors into a regression model to fit the spatial distribution of tree species while controlling for a spatial autocorrelation effect along multiple life stages in a seasonal rain forest in southwest China.

Methods

Study area

The study was conducted in a 20-ha tropical seasonal rain forest plot in Xishuangbanna, southwest China (21°37′08″N, 101°35′07″E). This region is located on the northern edge of the Asian tropical rain forests and is identified as a part of the Indo–Burma biodiversity hotspot in the list of the 25 top priorities in global biodiversity conservation (Myers et al. 2000). The elevation of the plot ranges from 708.2 m to 869.1 m (Fig. 1). Three perennial streams traverse the plot and merge together at the southeastern corner. The area is dominated by warm, wet air masses from the Indian Ocean in the summer and by continental air masses from subtropical regions in the winter, resulting in the alternation between rainy (May to October) and dry (November to April) seasons. The soil is derived from both igneous and sedimentary rocks (Cao et al. 2006).

Data collection

The 20-ha plot was divided into 500 quadrats of 400 m^2 each. All trees with diameter at breast height (DBH) $\geq$ 1 cm were tagged, identified and mapped. All branches with DBH $\geq$ 1 cm were also tagged and measured for multi-stemmed trees (trees with more than one stem).

We further divided each 400-m^2 quadrat into 16 sub-quadrats of 25 m^2 each. If 70% or more of the total area of a sub-quadrat consisted of open canopy and the average tree height was under 10 m, the sub-quadrat was classified as a 'gap'. A gap openness value between 0 and 16 was assigned to each 400-m^2 quadrat based on the number of sub-quadrats within that quadrat that were classified as gaps.

Soil was sampled using a regular grid of 30 × 30 m throughout the 20-ha plot. Each of the 252 nodes in this grid was used as a 'base point'. Together with each base
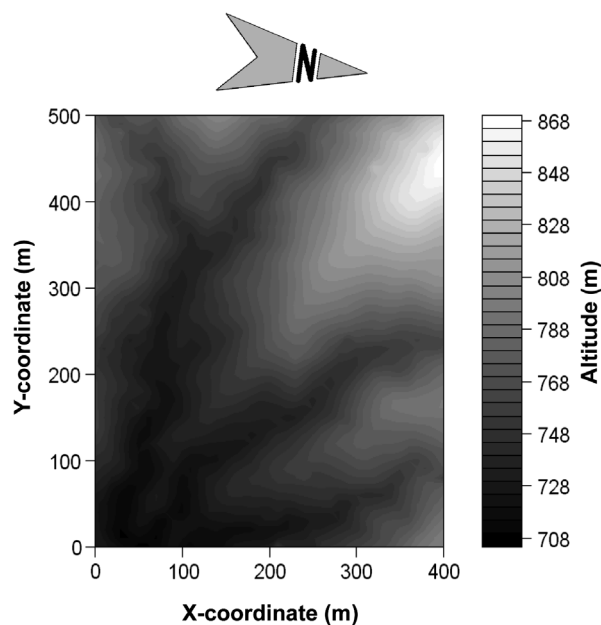

Figure 1. Topographic map of the 20-ha study plot.

point, two additional sampling points were located at random combinations of 2 and 5 m, 2 and 15 m or 5 and 15 m along a random compass bearing away from the associated base point. At each sample point, 500 g of topsoil was collected from a depth between 0 and 10 cm. A total of 756 soil samples were taken. Fresh soil samples were placed into pre-labelled plastic bags and shipped to the Biogeochemistry Laboratory at the Xishuangbanna Tropical Botanical Garden. In the laboratory, the pH values of the soil samples were measured as immediately as possible using a potentiometer in fresh soil after water extraction (soil/water = 1/2.5 weight/volume). The soil samples were then air-dried, smashed, sieved using 1-mm and 0.15-mm mesh and stored in plastic bags for later additional analysis (Liu et al. 1996).

Soil bulk density was measured using the corer method, soil organic matter was measured in soil oxidised with H_2SO_4–$K_2Cr_2O_7$, and carbon content was estimated by volume. The micro-Kjeldahl method was used to evaluate total nitrogen (N) using a mixture of H_2SO_4 and K_2SO_4–$CuSO_4$–Se catalyst, and an automatic steam distilling unit was used to determine the soil N content in the solution. Micro-diffusion was used to determine the available N in the soil.

The soil was digested in HNO_3–$HClO_4$ solution, and the total phosphorus (P) and potassium (K) were determined using an inductively coupled plasma atomic emission spectrometer. Extractable P was released from the soil in a solution containing 0.03 mol l^{-1} NH_4F and 0.025 mol l^{-1} HCl and estimated colorimetrically. Exchangeable K was extracted in a neutral 1-mol l^{-1} CH_3COONH_4 solution, and the total K in the extract was determined using an inductively coupled plasma atomic emission spectrometer. Table 1 presents the basic statistics for the soil measurements described here.

Gamma regression analysis

Tree species distributions are commonly described according to the numbers of individuals of a target species in quadrats of a certain area (Harms et al. 2001). Other measures, however, may provide additional insight into the mechanisms regulating tree species distributions (Morlon et al. 2009). The lattice basal area, which reflects tree size and biomass accumulation of the target species within each quadrat, was used as the response variable in this study. Correspondingly, a gamma regression model was used for regression analysis of the data (Dobson 1990). The gamma regression model is a special case of the generalised linear model in which the

error term follows a gamma distribution. We chose to use this approach to model the total basal area because this variable is not normally distributed and thus not suitable for multiple regression analysis. The flexibility of the gamma regression is more appropriate for modelling the total basal area. To relate the response variable to the various explanatory variables in the gamma regression, we used a commonly used inverse link function.

The basal area of each target species in each 400-m^2 quadrat was summed to obtain a vector. To avoid a zero-inflated effect and thus meet the positive data requirement of the gamma regression, we further removed all zero data and used the final vector as the response variable. Gamma regression models were calculated only for those tree species that were present in at least 30 quadrats and had at least one individual with DBH ≥ 1 cm in each quadrat. Rare species generated unstable models.

The purpose of grouping trees into different DBH classes was to categorise trees on the basis of life stage. For a tree with multiple stems, we computed the basal area of each stem. We then summed all the basal areas to obtain a total basal area for the tree. We then assigned a DBH to the multi-stemmed tree using the equation:

$$\text{multi-stemmed DBH} = 2 \times \sqrt{\frac{\text{total basal area of all stems}}{\pi}} \quad (1)$$

Following this transformation, we treated multi-stemmed trees as single-stemmed trees of the same total basal area. We then grouped all trees into five DBH classes following He et al. (1997):

class 1 = 1 to < 5 cm DBH,
class 2 = 5 to < 10 cm DBH,
class 3 = 10 to < 25 cm DBH, and
class 4 = DBH ≥ 25 cm;

We further defined class 0 = DBH ≥ 1 cm, which encompasses the previous four classes.

After grouping, there were 191, 147, 61, 57 and 22 tree species in classes 0 to 4, respectively (Supplementary material Appendix 1, Table A1).

To explain the spatial distributions of the tree species, we used three groups of explanatory variables. Each variable was centred and divided by its standard deviation, and a value of 4 was then added to each variable in order to transform all the explanatory variables into positive numbers. The first group of variables included soil properties. Using the original soil data, an ordinary kriging was performed to generate a sub-quadrat grid map of 10 × 10 m for each soil variable (Cressie 1993). The values of the soil variables for each 400-m^2 quadrat were calculated as the mean of the values at each of the nine nodes of the 10 × 10 m sub-quadrats within that quadrat, as soil data were originally sampled at a scale of 30 × 30 m. This was performed using the geoR package in the R statistical language (R Development Core Team 2009).

The topographic variables and the presence or absence of gaps comprised the second group of explanatory variables. The topographic variables included the mean elevation, mean convexity, mean aspect and mean slope in each quadrat (Legendre et al. 2009).

Table 1. Basic statistics calculated for 756 soil measurements from the study plot.

Soil explanatory variables	SD	Mean
Organic matter (g kg^{-1})	5.30	18.4
Total N (g kg^{-1})	0.40	1.83
Ammonium N (mg kg^{-1})	41.2	180
Total P (g kg^{-1})	0.10	0.34
Extractable P (mg kg^{-1})	6.27	4.89
Total K (g kg^{-1})	3.46	11.2
Exchangeable K (mg kg^{-1})	89.8	181
pH	0.64	4.91
Soil bulk density (g cm^{-3})	0.12	1.13

The third group of explanatory variables consisted of the total basal areas of the five most dominant tree species in each quadrat (*Castanopsis echidnocarpa*, *Garcinia cowa*, *Mezzettiopsis creaghii*, *Parashorea chinensis* and *Pittosporopsis kerrii*). These five tree species were identified as the most dominant according to their relative importance values, calculated using the method described by Cao et al. (1996).

The neighbourhood index was calculated by averaging the total basal area of conspecifics of the target species in each of the adjacent neighbour cells. The definition of neighbourhood index used here is similar to that of Wang et al. (2009), but we used the total basal area per quadrat of a target species instead of stem counts. This neighbourhood index represents the spatial autocorrelation effect.

The gamma regression model was expressed as:

$$Y = X\beta_1 + \beta_2 NI + \varepsilon \qquad (2)$$

where Y is a response variable, in this case the quadrat-based total basal area vector of a target tree species within a given DBH class, X is the explanatory variable matrix consisting of the five dominant neighbours and the edaphic and topographic variables, β_1 and β_2 represent the slopes associated with the explanatory variables in the original explanatory variable matrix X, NI is the isotropic second-order spatial autoregressive factor and ε is a random error term. For each quadrat, neighbours were defined as those quadrats with which the target quadrat shared a common edge or border.

Parameters of the gamma regression models were estimated using maximum likelihood with an inverse link function. Because not all of the explanatory variables were important in structuring the distribution of each species of tree, we constructed more parsimonious models using simulated annealing on the set of explanatory variables (Kirkpatrick et al. 1983). This optimisation approach determines the best model by applying mutations to the model (i.e. adding, removing or changing a variable). A 'better' model is selected if it has a lower Akaike information criterion (AIC, Akaike 1974) value than the one selected previously. If the model does not yield a lower AIC value than the previous one, a probability function is used to evaluate whether the model should be kept. In the analyses, we used the probability function used by Kirkpatrick et al. (1983), which is based on an acceptance parameter that defines how often a 'bad' model will be accepted. For all of the model selection procedures, we used a parameter of mutation acceptance equal to 200, a start time equal to 10 and an annealing temperature equal to 0.5 (Supplementary material Appendix 2, R language code A2). This approach was used because it does not require normal distribution of the variables.

To assess the relative importance of each of the explanatory variables in determining species distributions, a principal component analysis (PCA) was conducted on a transformed matrix of the p-values generated by the gamma regression models. Following model fitting and model selection, each selected explanatory variable was assigned a coefficient and a corresponding p-value. Because the magnitudes of the coefficients can vary greatly across species, they are not suitable for assessing the relative importance of the explanatory variables. The p-values associated with these coefficients reflect the relationship between the response variable and each explanatory variable, and these p-values do not differ in magnitude across species and thus are suitable for PCA. The p-values were transformed by log(1/p) to generate the p-value matrix for the PCA. A value of 0 was assigned to any explanatory variable that was removed by the model selection procedure. Five transformed p-value matrices were then constructed, one for each of the five DBH classes. Using the scores of each of the explanatory variables on the first two principal component axes, we drew biplots to indicate the relative importance of each explanatory variable based on the length of each associated vector.

To demonstrate the relative importance of each of the three groups of explanatory variables in explaining the distribution of tree species, we plotted Venn diagrams based on the number of tree species that responded to each of the seven combinations of the three groups of explanatory variables in the most parsimonious models for each of the five DBH classes. When the explanatory variables in a most parsimonious model matched one of the combinations, we added 1 to that combination. The procedure was repeated for the most parsimonious models for all species, and the numbers of responses to each of the seven combinations of variable groups were shown in the Venn diagram.

Results

The neighbourhood index yielded the longest vectors in the PCA analyses for DBH classes 0 and 2 (Fig. 2a, 2c) and the third longest vector in the analysis for DBH class 1 (Fig. 2b). This indicates that the neighbourhood index is the most important factor in determining the distribution of small trees in the study plot. The lengths of the vectors representing the abiotic environmental factors gradually increased as the DBH of the trees increased (Fig. 2d, 2e). This was consistent with our prediction that the relative contributions of neutral and niche processes change across life stages. Of the abiotic environmental predictors, elevation yielded the longest vectors in the PCA analyses for DBH classes 1, 2 and 3 and thus had the strongest effect on the distribution of trees in these classes. The edaphic variables only showed a significant impact on the distribution of large trees: the total and extractable N, P and K levels in the soil were negatively correlated with the distribution of the trees in DBH class 4 (Fig. 2e).

The five most dominant tree species together covered 27.85% of the total basal area in the plot. *Mezzettiopsis creaghii*, with the fourth highest importance value (Supplementary material Appendix 3, Table A3), had significant effects on the distributions of smaller trees: the vectors representing *Mezzettiopsis creaghii* were among the three longest in the PCA analyses for DBH classes 0, 1 and 2 (Fig. 2a–c). *Mezzettiopsis creaghii* did not have as prominent an effect on the distributions of trees in DBH classes 3 and 4 (Fig. 2d–e).

The median variance explained in the gamma regression models became higher as tree size increased: for classes 1
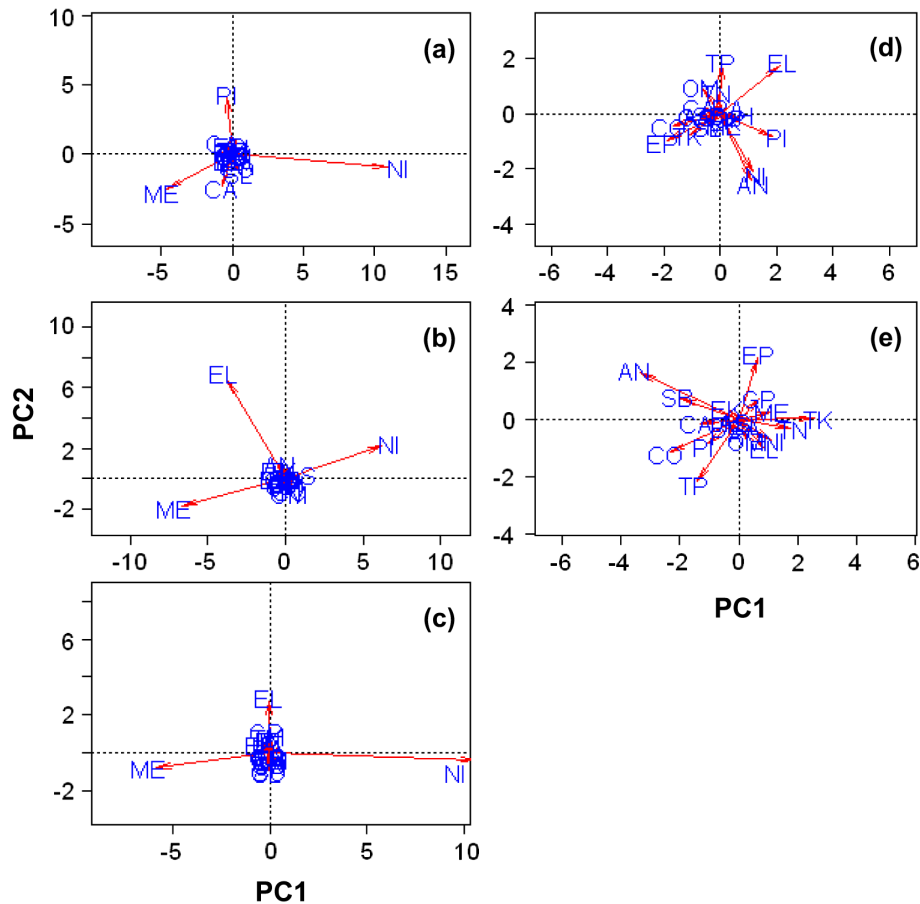
Figure 2. The variance explained by the most parsimonious gamma models of all species in each of 5 classes: (a) class 0 (DBH ≥ 1 cm), (b) class 1 (1 cm ≤ DBH < 5 cm), (c) class 2 (5 cm ≤ DBH < 10 cm), (d) class 3 (10 cm ≤ DBH < 25 cm) and (e) class 4 (DBH ≥ 25 cm).

to 4, the explained variances were 0.21, 0.22, 0.29 and 0.49, respectively (Fig. 3). The median explained variance for class 0 was 0.36. The median variance explained in the gamma regression model for class 4 was significantly higher than for classes 1 and 2 (Kruskal–Wallis rank-sum test, Supplementary material Appendix 4, Table A4). Except for class 0, the amount of variation explained in the gamma regression models became smaller with increasing total basal area of a tree species (Fig. 4).

The numbers of tree species responding to each of the seven combinations of the three groups of explanatory variables varied greatly across DBH classes (Fig. 5). The combination of all of the variables explained the most responses in each of the five DBH classes, but this pattern was less pronounced in the larger DBH classes, suggesting that most of the factors that affect the distribution of trees exert this effect when trees are at younger life stages. The results of the Kruskal–Wallis rank sum test on the seven parts of each of the five Venn diagrams showed that the numbers in the central portions were significantly greater than the numbers in each of the other six portions. There was no difference among these six other numbers. This result indicates that the joint effects of the three groups of factors predominate in regulating most of the tree species distributions throughout all life stages.
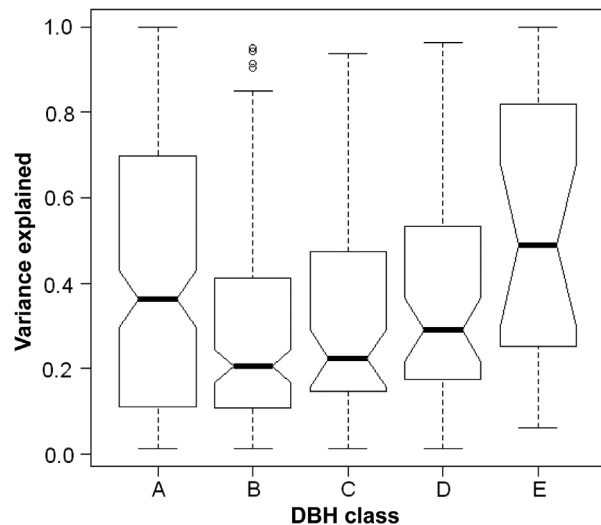

Figure 3. Boxplot with 95% confidence intervals indicating the distributions of the variance explained in each species by the most parsimonious gamma regression models for each of the 5 DBH classes. A to E on the x-axis denote class 0 (DBH ≥ 1 cm), class 1 (1 cm ≤ DBH < 5 cm), class 2 (5 cm ≤ DBH < 10 cm), class 3 (10 cm ≤ DBH < 25 cm) and class 4 (DBH ≥ 25 cm), respectively.

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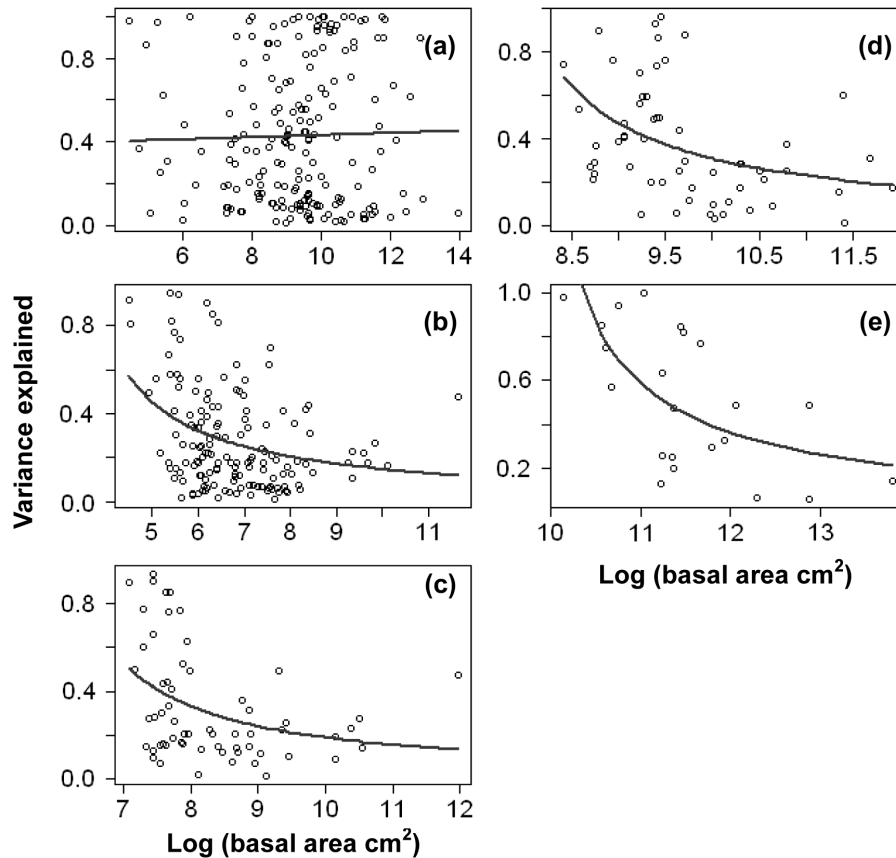
Figure 4. Principal component analysis ordinations of the explanatory variables for each of the five tree size classes: (a) class 0 (DBH ≥ 1 cm), (b) class 1 (1 cm ≤ DBH < 5 cm), (c) class 2 (5 cm ≤ DBH < 10 cm), (d) class 3 (10 cm ≤ DBH < 25 cm) and (e) class 4 (DBH ≥ 25 cm). Matrices of the transformed p-values from the gamma regression models were used to compute the ordinations. Scores on the first two ordination axes were plotted for the following explanatory variables: AN (available nitrogen), AS (aspect), CA (*Castanopsis echidnocarpa*), CO (convexity), EK (exchangeable potassium), EL (elevation), EP (extractable phosphorus), GA (*Garcinia cowa*), GP (gap), ME (*Mezzettiopsis creaghii*), NI (neighbourhood index), OM (organic matter), PA (*Parashorea chinensis*), pH (soil pH), PI (*Pittosporopsis kerrii*), TK (total potassium), TN (total nitrogen), TP (total phosphorus), SB (soil bulk density) and SL (slope).

Discussion

Mechanisms regulating species distributions across life stages

Our study revealed that dispersal limitation, represented as a neighbourhood index, has the largest effect on the distribution of trees across life stages whereas environmental factors mainly affect the distribution of large trees. For example, *Mezzettiopsis creaghii*, the fourth most dominant tree species, was significantly correlated with its own neighbourhood index in all five size classes. However, the relative roles of neutral and niche processes in determining species distributions are still controversial. Gilbert and Lechowicz (2004) reported that niche-structuring predominantly determines species distributions in a temperate forest understory. Tuomisto et al. (2003) showed that although both environmental factors and dispersal limitation jointly contribute to floristic differences in western Amazonian forests, environmental factors are more important than dispersal limitation. Legendre et al. (2009) suggested that environmental factors and neutral processes performed equally in partitioning the beta diversity of tree species in a 24-ha subtropical forest plot in Gutian, China.

In a tropical forest in Panama, recruitment limitation has been reported as the predominant factor controlling tree species diversity (Hubbell et al. 1999). He et al. (1997) suggested that the relative contribution of any factor to explaining species coexistence could change over time and space. The results of our study suggest that both neutral and niche process are important in determining tree species distribution but that these processes play different roles at different life stages of the trees. Neutral processes are more important in regulating the distribution of smaller trees, and niche processes become dominant in shaping the distribution of larger trees.

Most tropical rain forest tree species tend to display aggregated distributions (Condit et al. 2000). In a similar study by Wang et al. (2009), few negative associations between tree species distributions and neighbourhood index were found in a subtropical forest. In the plot studied here, dispersal limitation, indicated by the neighbourhood index, showed similar numbers of positive and negative effects (Supplementary material Appendix 5, Table A5). According to the Janzen and Connell hypothesis (Connell 1978, Janzen 1970), density-dependent effects cause conspecific individuals to escape from maternal trees, and this provides a theoretical explanation for the negative effect of neighbourhood index.
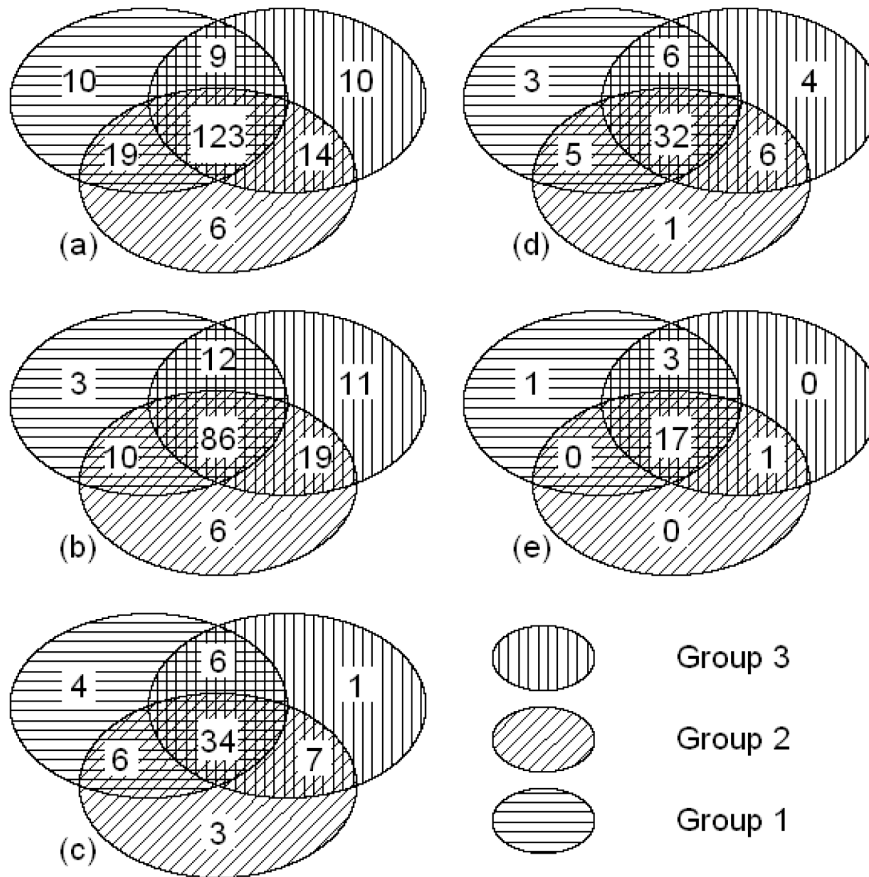
Figure 5. Venn diagrams displaying the number of species responding to each of the seven combinations of the three groups of explanatory variables, according to the most parsimonious gamma regression models, for each tree size class: (a) class 0 (DBH $\geq$ 1 cm), (b) class 1 (1 cm $\leq$ DBH $<$ 5 cm), (c) class 2 (5 cm $\leq$ DBH $<$ 10 cm), (d) class 3 (10 cm $\leq$ DBH $<$ 25 cm), (e) class 4 (DBH $\geq$ 25 cm). Explanatory variables are represented as follows: Group 1 represents soil parameters, Group 2 represents topography and gap and Group 3 represents dominant neighbours and neighbourhood index.

Stoll and Newbery (2005) also found strongly negative neighbourhood effects on larger trees of the genus *Shorea* in Sabah, Malaysia.

It is widely accepted that topographic and edaphic factors affect species distributions in both subtropical and tropical forests (John et al. 2007). In the present study, environmental predictors differed greatly in explaining the distributions of large trees, and edaphic factors contributed very little to explaining species distributions for DBH classes 0 to 2. However, the edaphic factors did explain a large proportion of the variation in the distributions of larger trees. Topography is generally correlated with many environmental factors, such as water regime (Daws et al. 2002) and the physical and chemical properties of the soil (Bourgeron 1983). In our study, elevation showed a strong effect on the distribution of trees in most DBH classes.

Our results suggest that failing to classify trees into multiple life stages may lead to a biased interpretation of the mechanisms contributing to tree distributions. We found different results for trees at different stages of life history. At early stages, when trees are small, their distribution is largely determined by dispersal limitation. This result is consistent with the finding that the distribution of seedlings is mainly affected by seed dispersal and the presence of heterospecific neighbours (Comita and Hubbell 2009). Thus, we assume

that the habitat preferences of many tree species are consistent across the sapling and juvenile stages. However, as the habitat associations of most tree species becoming stronger as trees reach the mature stage (Lai et al. 2009), the habitat preferences of tree species change at mature stage. Our results do indicate that environmental predictors affecting species distributions shifting across life stages (Fig. 4). Thus, environmental predictors do have filtering effects on species distributions, as Norden et al. (2009) suggested. Consequently, analysing species distributions based on the assumption that all individuals of a target species respond similarly across life stages may obscure the true process by which species distribution patterns are generated.

The effects of dominant species on species distributions

Our gamma regression model of tree species distributions indicated that the dominant tree species were important in regulating species distributions. This result is consistent with the finding that forest composition is highly deterministic (Yu et al. 1998) and that the dominant species play important roles in shaping community composition. Comita and Hubbell (2009) found that dominant tree species play an important role in shaping the distributions of

non-dominant tree species across life stages and that cross-species neighbourhood effects have a prominent influence on seedling survival. Our results extended the effects of inter-species interactions to established trees (DBH ≥ 1 cm). One possible explanation for the effect of dominant tree species on the distributions of other tree species is that dominant species have the ability to restructure multiple aspects of their surrounding environment, including light availability, soil textures and temperature (Eviner 2004). A recent study further hypothesised that plants alter competition by modifying the bioavailability of nutrients in the rhizosphere (Raynaud et al. 2007). Moreover, although dominant species often compete with other species, they may also facilitate the establishment of other non-dominant species (Supplementary material Appendix 6, Table A6). The species herd hypothesis (Wills 1996) provides one possible explanation for the cooperation between dominant and non-dominant tree species. This hypothesis states that an increasing density of heterospecific tree species can slow the rate or reduce the chance that natural predators, pathogens or viruses will encounter their host species. We conclude that it is important to pay more attention to the influence of dominant neighbours on species distributions.

Conclusions

The results of our study support the concept that neutral and niche processes jointly affect species distributions (Cottenie 2005, Leibold and McPeek 2006). We further develop this concept by showing that the relative importance of each of the two processes varies across life stages. This implies that if species are not analysed at multiple life stages, a biased conclusion may be reached regarding the mechanisms maintaining species coexistence. The negative impact of the neighbour index on species distributions that we observed in some cases provides empirical support to the Janzen and Connell hypothesis. Our results also present a quantitative perspective on how dominant species can regulate species distributions.

References

Akaike, H. 1974. A new look at the statistical identification model. – IEEE T. Automat. Contr. 19: 716–723.

Bourgeron, P. S. 1983. Spatial aspects of vegetation structure. – Elsevier.

Canham, C. D. and Uriarte, M. 2006. Analysis of neighborhood dynamics of forest ecosystems using likelihood methods and modeling. – Ecol. Appl. 16: 62–73.

Cao, M. et al. 1996. Tree species composition of a seasonal rain forest in Xishuangbanna, southwest China. – Trop. Ecol. 37: 183–192.

Cao, M. et al. 2006. Tropical forests of Xishuangbanna, China. – Biotropica 38: 306–309.

Chen, L. et al. 2010. Community-level consequences of density dependence and habitat association in a subtropical broad–leaved forest. – Ecol. Lett. 13: 695–704.

Clark, D. B. et al. 1998. Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. – J. Ecol. 86: 101–112.

Clark, J. S. et al. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. – Ecology 80: 1475–1494.

Comita, L. S. and Hubbell, S. P. 2009. Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. – Ecology 90: 328–334.

Comita, L. S. et al. 2007. Developmental changes in habitat associations of tropical trees. – J. Ecol. 95: 482–492.

Condit, R. et al. 2000. Spatial patterns in the distribution of tropical tree species. – Science 288: 1414–1418.

Condit, R. et al. 2006. The importance of demographic niches to tree diversity. – Science 313: 98–101.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a non-equilibrium state. – Science 199: 1302–1310.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. – Ecol. Lett. 8: 1175–1182.

Cressie, N. A. C. 1993. Statistics for spatial data, revised edition. – Wiley.

Daws, M. I. et al. 2002. Topographic position affects the water regime in a semideciduous tropical forest in Panama. – Plant Soil 238: 79–90.

Dobson, A. J. 1990. An introduction to generalized linear models. – Chapman and Hall.

Eviner, V. 2004. Plant traits that influence ecosystem processes vary independently among species. – Ecology 85: 2215–2229.

Gilbert, B. and Lechowicz, M. J. 2004. Neutrality, niches, and dispersal in a temperate forest understory. – Proc. Natl Acad. Sci. USA 101: 7651–7656.

Harms, K. E. et al. 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. – J. Ecol. 89: 947–959.

He, F. L. et al. 1997. Distribution patterns of tree species in a Malaysian tropical rain forest. – J. Veg. Sci. 8: 105–114.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. – Princeton Univ. Press.

Hubbell, S. et al. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. – Science 283: 554–557.

Hutchinson, G. E. 1957. Concluding remarks. – Cold Spring Harbor Symp. Quant. Biol. 22: 415–427.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. – Am. Nat. 104: 501–528.

John, R. et al. 2007. Soil nutrients influence spatial distributions of tropical tree species. – Proc. Natl Acad. Sci. USA 104: 864–869.

Kirkpatrick, S. et al. 1983. Optimization by simulated annealing. – Science 220: 671–680.

Lai, J. S. et al. 2009. Species–habitat associations change in a subtropical forest of China. – J. Veg. Sci. 20: 415–423.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? – Ecology 74: 1659–1673.

Legendre, P. and Fortin, M. 1989. Spatial pattern and ecological analysis. – Plant Ecol. 80: 107–138.

Legendre, P. et al. 2009. Partitioning beta diversity in a subtropical broad-leaved forest of China. – Ecology 90: 663–674.

Leibold, M. A. and McPeek, M. A. 2006. Coexistence of the niche and neutral perspectives in community ecology. – Ecology 87: 1399–1410.

Levine, J. M. and HilleRisLambers, J. 2009. The importance of niches for the maintenance of species diversity. – Nature 461: 254–258.

Liu, G. S. et al. 1996. Soil physical and chemical analysis and description of soil profiles. – Standards Press of China, in Chinese.

Losos, J. B. and Ricklefs, R. E. 2009. Adaptation and diversification on islands. – Nature 457: 830–836.

Morlon, H. et al. 2009. Taking species abundance distributions beyond individuals. – Ecol. Lett. 12: 488–501.

Myers, N. et al. 2000. Biodiversity hotspots for conservation priorities. – Nature 403: 853–858.

Norden, N. et al. 2009. Interspecific variation in seedling responses to seed limitation and habitat conditions for 14 Neotropical woody species. – J. Ecol. 97: 186–197.

Raynaud, X. et al. 2007. Plants may alter competition by modifying nutrient bioavailability in rhizosphere: a modeling approach. – Am. Nat. 171: 44–58.

Sankaran, M. et al. 2004. Tree-grass coexistence in savannas revisited - insights from an examination of assumptions and mechanisms invoked in existing models. – Ecol. Lett. 7: 480–490.

Shen, G. C. et al. 2009. Species–area relationships explained by the joint effects of dispersal limitation and habitat heterogeneity. – Ecology 90: 3033–3041.

Silvertown, J. et al. 1999. Hydrologically defined niches reveal a basis for species richness in plant communities. – Nature 400: 61–63.

Stoll, P. and Newbery, D. 2005. Evidence of species-specific neighborhood effects in the Dipterocarpaceae of a Bornean rain forest. – Ecology 86: 3048–3062.

Tuomisto, H. et al. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. – Science 299: 241–244.

Uriarte, M. et al. 2004. A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. – Ecol. Monogr. 74: 591–614.

Wang, Z. et al. 2009. Species-topography association in a species-rich subtropical forest of China. – Basic Appl. Ecol. 10: 648–655.

Wills, C. 1996. Safety in diversity. – New Sci. 149: 38–42.

Wright, S. J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. – Oecologia 130: 1–14.

Yu, D. W. et al. 1998. Can high tree species richness be explained by Hubbell's null model? – Ecol. Lett. 1: 193–199.