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Topography related spatial distribution of dominant tree species in a tropical seasonal rain forest in China

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ABSTRACT

The degree to which variation in species distribution is predictable from topographic variation is of considerable current interest. In this paper, canonical correspondence analysis (CCA), linear regression and principal coordinates of neighbour matrices (PCNM) models were used to explain the variation in the distributions of the 13 dominant species in a 20-ha tropical rain-forest plot in China. The results showed that: (1) Tree distribution maps show that some species are mainly found in the gullies of the plot, whereas others occur on the slopes. Which indicates topographic variables are important factors for the distribution pattern of species. (2) Both linear regression and CCA results show that convexity and elevation are the most important variables effecting distribution of trees. For saplings, elevation, convexity and aspect explain 15.3%, 9.0% and 10.1% of the total variation of species abundance. For poles, elevation and convexity explain 19.3% and 11.4% respectively. However, only 5.3% of the total variation is explained for adults. (3) The PCNM results showed that topography alone explained 20%, 24% and 5% of the total variation of species abundance for saplings, poles and adults, respectively. Overall evidence for topographic control of the tropical tree distribution is strong, but the explanatory power of topographic variables was a small part of the total of variation.

1. Introduction

The theory of spatial dispersion of individuals in a species is a central concept in ecological theory. Patchiness, or the degree to which individuals are aggregated or dispersed, is crucial to how a species uses resources, to how it is used as a resource, and to its reproductive biology (Condit et al., 2000). Several studies related to distribution patterns have documented that clumped spatial distributions amongst tropical tree species are extremely common (Condit et al., 2000; Bunyavejchewin et al., 2003; Lan et al., 2009). Dispersal, biotic interactions, and gap dynamics are likely to produce spatial structure most evident at relatively fine scales, whereas topographic variation may produce structure at different scales depending on underlying geomorphology (Jones et al., 2008). Associations between plant distributions and environmental conditions in tropical forests have been studied (Harms et al., 2001; Gunatilleke et al., 2006). In Sinharaja forest, it was found that nearly four-fifths 79% of the species examined were associated with topographically defined habitats (Gunatilleke et al., 2006). In a plot on Barro Colorado Island, 61% of species were significantly positively or negatively associated with at least one habitat type according to the torus-translation tests (110 out of 171) (Harms et al., 2001).

The degree to which variation in plant distribution is predictable from topographic variation is of considerable current interest (Jones et al., 2008). We investigated this question by analysing the data of the 13 dominant tree species in a 20-ha dipterocarp tropical seasonal rain forest in Xishuangbanna Prefecture, China. Canonical correspondence analysis was used to analyse the relationship between species distribution and environmental variables. We modelled the environmental component using mean elevation, convexity and mean slope of each 400-m^2 quadrat and the spatial component with a more flexible model, principal coordinates of neighbour matrices (PCNM). We hypothesised that the spatial patterns of species correlate (negatively or positively) with the topographic variables slope, elevation, convexity and aspect). We are further interested in the relative contributions of topographic and spatial variables to the species distribution and the degree to which variation in a species distribution can be predicted from environmental and spatial variables.

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2. Methods

2.1. Study site

The study site was located in the Xishuangbanna National Nature Reserve in south-western China (101°34′E, 21°36′N). Xishuangbanna situates in the southwestern Yunnan Province of China. It borders Myanmar in the southwest and Laos in the southeast, and has mountainous topography, with mountain ridges running in a north–south direction, decreasing in elevation southward. The uplift of the Himalayas leads to the penetration of warm and moist tropical air mass from the Indian Ocean to Xishuangbanna in the summer, and forms a barrier preventing cold air mass from the north reaching the region in the winter, allowing for the existence of tropical rain forest in its altitudinal and latitudinal northern limits. The region is dominated by a typical monsoon climate with an alternation between a dry season and a rainy season. As recorded by a weather station 14 km from the study site, the mean annual temperature is 21.0 °C, and the mean annual precipitation is 1532 mm, of which approximately 80% occurs between May and October. The dry season is from November to April (Zhang and Cao, 1995). Under these climatic conditions, the tropical seasonal rain forest grows in the lowlands, valleys and hills that have a good water supply (Wu, 1987; Cao and Zhang, 1997; Zhu, 2006; Zhu et al., 2006). The tropical seasonal rain forest has three or four indistinct tree layers: the top layer consists largely of emergent trees (more than 30 m tall the tallest up to 60 m); the second layer, the main canopy layer, contains trees up to 30 m high with almost continuous crowns; the third layer consists of small trees and juveniles 5–18 m tall of species from the upper layers. This forest occurs mainly on laterite and lateritic red soils with pH values of 4.5–5.5. The study site had suffered human disturbance about 40 years ago, some trees, especially trees on the slope had been cut down.

A 20-ha permanent plot was established in the Xishuangbanna National Nature Reserve in 2007. The plot is roughly square in shape and measures 400 m (north–south) by 500 (east–west). The elevation of the plot ranges from 709 to 869 m above sea level; the highest elevation occurs in the north-west corner of the plot. Three perennial creeks wind through the plot and join together in the south-eastern corner of the plot (Fig. 1). The forest was dominated by *Parashorea chinensis*, an emergent tree species of Dipterocarpaceae.

2.2. Species data collection

The plot was established following the field protocol of the Center for Tropical Forest Science (Condit et al., 1996; Condit, 1998; Ayyappan and Parthasarathy, 1999). All trees ($\geqslant$1 cm in diameter at breast height DBH) were mapped and tagged with unique numbers. Tree diameters were measured 1.3 m from the ground. Trees with multiple stems were counted as a single individual, but each stem was measured and assigned a tag number. All stems $\geqslant$1 cm DBH were identified to species. There were in total 95,498 stems belonging to 468 species. We selected the 13 most abundant species, which had more than 1000 individuals in the plot (Table 1). These 13 species comprised 56% of the total stems (95,834) $\geqslant$1.0 cm DBH (Lan et al., 2008). Individuals of each of these species were classified into three life stages: saplings (1 to $\leqslant$5 cm DBH), poles (5 to $\leqslant$D950.1 cm DBH) and adults (>D950.1 cm DBH). Here, D950.1 is the 95th percentile of diameter of all trees $\geqslant 0.1 \times$ Dmax, and Dmax is the diameter of the thickest tree (King et al., 2006). For treelets (with maximum DBH no more than 20 cm), stems between 1 and 3 cm in diameter were classified as saplings. And poles included stem diameters between 3 and D950.1 cm.

2.3. Topographic data

Topographic attributes include mean elevation, convexity, slope and aspect. We divided the 20-ha plot into 500 samples, each with an area of 400 m^2. For each 400-m^2 quadrat, the mean elevation of a cell was defined as the mean of the elevations of its four corners, convexity was the mean elevation of the cell of interest minus the mean elevation of the eight surrounding cells, and slope was the mean angular deviation from the horizontal of each of the four

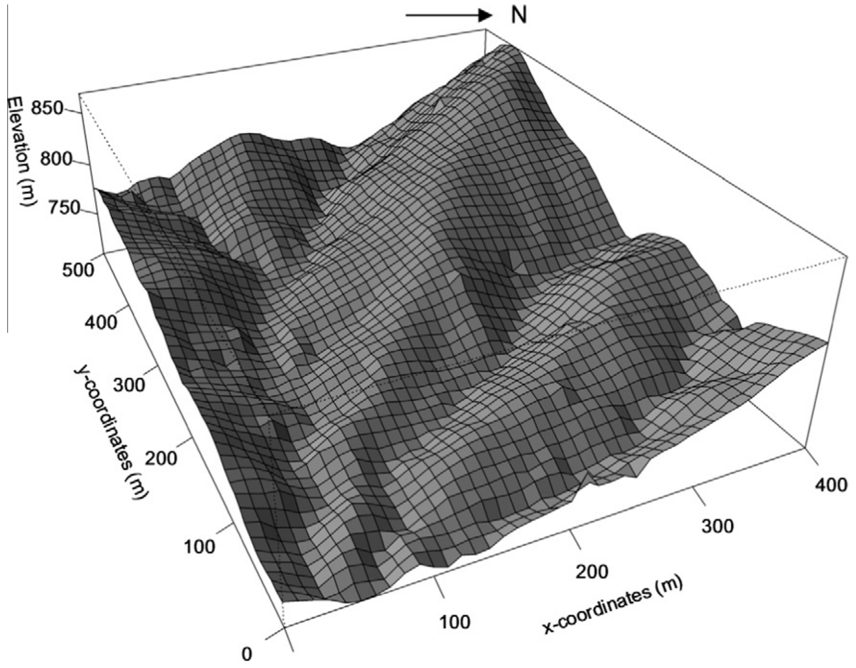

Fig. 1. Topographic map of the 20-ha permanent plot of tropical seasonal rain forest in Xishuangbanna Prefecture of China.

Table 1
The 13 most abundant species (with >1000 individuals) in the 20-ha plot in a tropical seasonal rain forest in Xishuangbanna Prefecture.

Rank	Species	Species code	Family	Maximum DBH of saplings	Maximum DBH	Mean DBH	Minimum DBH of adult	No. of sapling	No. of poles	No. of adults	Total abundance	Percentage
1	*Pittosporopsis kerrii* Craib	PITTKE	Icacinaceae	5	44.3	3.5	15	16,439	4453	26	20,918	21.83
2	*Parashorea chinensis* Wang Hsie	PARACH	Dipterocarpaceae	5	191.1	5.2	50	6492	1308	119	7919	8.29
3	*Garcinia cowa* Roxb.	GARCCO	Guttiferae	5	45.7	5.3	21	2795	1448	90	4333	4.52
4	*Mezzettiopsis creaghii* Ridl.	MEZZCR	Annonaceae	5	49.0	6.9	25	1744	1514	42	3300	3.44
5	*Baccaurea ramiflora* Lour.	BACCRA	Euphorbiaceae	5	31.9	5.8	21	1814	1365	33	3212	3.35
6	*Knema furfuracea* (Hook. f. and Thomson) Warb.	KNEMFU	Myristicaceae	5	47.8	4.1	27	2543	578	39	3160	3.30
7	*Saprosma ternata* Hook. f.	SAPRTE	Rubiaceae	3	13.0	2.0	5	2332	345	21	2698	2.82
8	*Phoebe lanceolata* (Nees) Nees	PHOELA	Lauraceae	3	18.1	4.0	12	895	1496	18	2409	2.51
9	*Cinnamomum bejolghota* (Buch.-Ham.) Sweet	CINNBE	Lauraceae	5	72.6	5.5	30	938	376	23	1337	1.40
10	*Ficus langkokensis* Drake	FICULA	Moraceae	5	37.7	6.3	21	761	537	39	1337	1.40
11	*Dichapetalum gelonioides* (Roxb.) Engl.	DICHGE	Dichapetalaceae	3	20.1	3.8	12	704	473	45	1222	1.28
12	*Nephelium chryseum* Blume	NEPHCH	Sapindaceae	5	79.6	7.2	31	713	343	42	1098	1.15
13	*Leea compactiflora* Kurz	LEEACO	Vitaceae	3	24.2	1.8	4	974	64	13	1051	1.10
	Total										53,994	56.36

triangular planes formed by connecting three of its corners (Harms et al., 2001; Gunatilleke et al., 2006). Aspect in degrees from north was calculated using the formula

$$\text{Aspect} = 180 - \arctan(fy/fx) \times (180/3.14) + 90(fx/|fx|),$$

where *fx* and *fy* are the changes in elevation from east to west and from north to south, respectively.

2.4. Canonical correspondence analysis (CCA)

Field surveys yielded a data matrix of 500 samples (each representing an area of 400 m^2) and the corresponding life-stage counts of 13 tree species. Then we performed the CCA by forward selecting the independent variables and employing a Monte Carlo permutation test to evaluate their significance level. Each variable was tested at the 5% confidence level with 1000 random permutations. Scatter diagrams and simple linear regressions were used to explore the correlation between environmental variables and species abundance.

2.5. Variation partitioning

We ran variance partitioning (Borcard et al., 1992) to quantify the proportion of the variation in the species distribution explained by variation in the topographic and spatial explanatory variables. We generated a sets of continuous spatial variables (x and y, x^2, y^2, xy, x^3, y^3, x^2y and xy^2) from the x and y coordinates in the *R* program. Topographic variables include mean elevation, convexity, slope and aspect as stated above. Then we adjusted the correlation coefficients (R^2 values) to account for the numbers of sampling sites and explanatory variables, as unadjusted R^{2-}values are biased (Jones et al., 2008). We report the adjusted values (Ra^2) throughout. We recorded the proportion of variation explained (Ra^2) in CCA analyses by either the significant spatial (PCNM) or the significant topographic variables, or both simultaneously. Using these Ra^2 values, we calculated the purely topographic, purely spatial, and spatially structured environmental fractions of the total explained variation in species distribution (Borcard et al., 1992). We tested the significance of the purely spatial and purely environmental fractions by means of 999 permutations under the reduced model (Jones et al., 2008).

3. Results

3.1. Tree distribution maps

Most of the dominant species appeared to be distributed nonrandomly in the habitat. For instance, most individuals of *Pittosporopsis kerrii* grew on the slopes of the plot, whereas *P. chinensis* and *Mezzettiopsis creaghii* occurred in the gullies. *Knema furfuracea* and *Phoebe lanceolata* preferred a higher-elevation habitat, but *Saprosma ternata* occurred at lower elevations. Most trees of *Dichapetalum gelonioides* were distributed on mid-elevation slopes. Distribution maps of the three abundant species across three life stages were plotted (Fig. 2a–c). These maps clearly show that trees are not uniform across the plot: some species are found in the gullies whereas others are found on the slope.

3.2. Linear regression of abundance topographic variables

To assess the influence of topographic variables on species distribution, linear regression analysis of abundance with elevation, convexity, slope and aspect was performed. The correlation coefficients (Table 2) of tree abundance with topographic variables indicate that elevation and convexity are the two most important factors effecting the species distribution, and slope is not essential. For example, the correlation coefficients of six species *P. kerrii*, *Garcinia cowa*, *M. creaghii*, *S. ternata*, *Nephelium chryseum* and *K.*

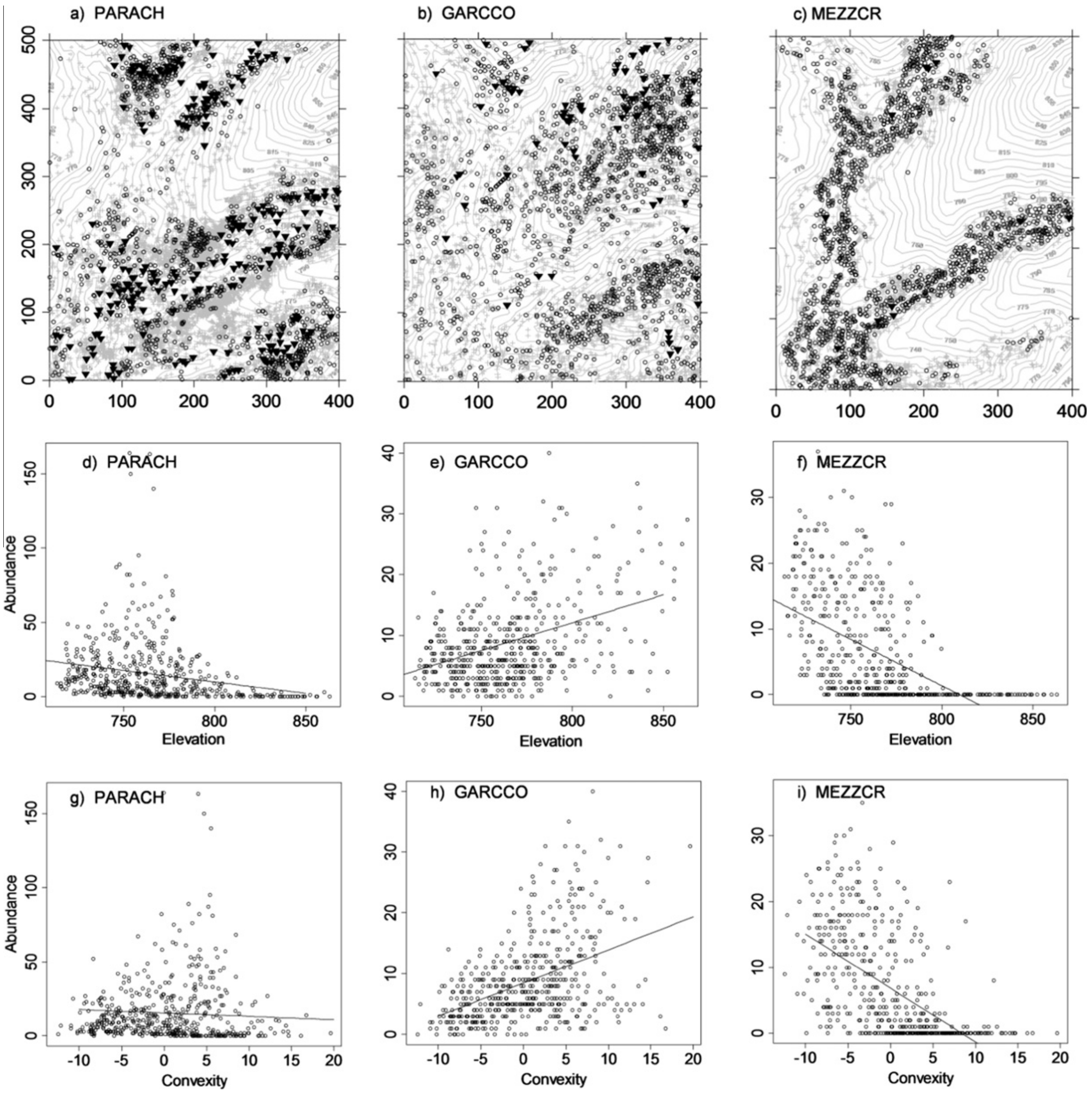

Fig. 2. Distribution maps of the three species (*Parashorea chinensis*, *Garcinia cowa* and *Mezzettiopsis creaghii*) and linear regression of tree abundance with elevation and convexity in the tropical seasonal rain forest in Xishuangbanna Prefecture of China. (Grey cross: saplings; black circle: poles; back triangle: adults) Species codes are given in Table 1.

Table 2
The correlation coefficients of tree abundance with topographic variables (including elevation, convexity, slope and slope aspect). Species codes are given in Table 1. Number in bold indicates the correlation coefficients are greater than 0.0800.

Rank	Species code	Elevation	Convexity	Slope	Aspect
1	PITTKE	**0.0897**	**0.3325**	0.0212	**0.1101**
2	PARACH	0.0492	0.0018	0.0012	0.0244
3	GARCCO	**0.1614**	**0.2013**	0.0126	0.0027
4	MEZZCR	**0.2718**	**0.3324**	0.0009	0.0011
5	BACCRA	0.0011	0.0481	0.0042	0.0225
6	KNEMFU	**0.2037**	0.0019	0.1001	**0.0872**
7	SAPRTE	**0.1095**	0.0128	0.0278	0.0001
8	PHOELA	0.0676	**0.2014**	0.0157	0.0263
9	CINNBE	0.0200	0.0201	0.0018	0.0006
10	FICULA	0.0009	**0.1004**	0.0084	**0.1205**
11	DICHGE	0.0014	0.0336	0.0408	0.0156
12	NEPHCH	**0.1047**	0.0008	0.0553	0.0262
13	LEEACO	0.0013	0.0405	0.0072	**0.0903**

furfuracea) are greater than 0.08 indicates elevation is very important variable for these species. The scatter diagrams (Fig. 2d–i) show the correlation of three species abundance with elevation and convexity.

3.3. Canonical correspondence analysis

Four topographic variables (elevation, slope, convexity and aspect) and life-stage abundance data from 13 species in the 500 quadrats were used for the redundancy analysis. This combination of variables explained 25.3% of the total variance in species abundances. The first axis of ordination is strongly positive correlated with elevation, and explained 15.6% of the total variance $P = 0.001$; Monte Carlo permutation test with 1000 permutations). However the second axis of ordination is positively correlated with convexity but negatively correlated with slope and explained an additional 4.2% (Fig. 3).

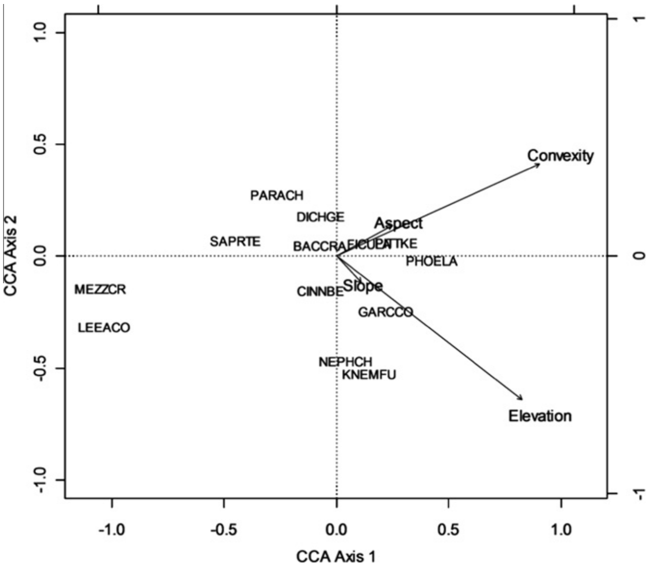

Fig. 3. Canonical correspondence analysis diagram showing the relationship of species with the topographic variables (elevation, slope, convexity and aspect). Species codes are given in Table 1.

3.4. Variation partitioning

Variation partitioning is shown in Fig. 4. For all life stages of the 13 species, topography alone explained 26% of the total variation, and space explained 5%. Topography and space together explained 1% and 68% of the variation could not be explained. For saplings and poles of the 13 species, pure topography explained 20% and 24%, respectively. However, topography alone explained only 5% for adults.

Results of variation partitioning of the 13 species for different combinations of spatial data and topographic data are shown in Fig. 5. For saplings and poles, topographic variables explained more variation than for adults, especially in *P. kerrii*, *G. cowa*, *M. creaghii*, *K. furfuracea*, *S. ternata*, *P. lanceolata*, *D. gelonioides* and *N. chryseum*. Thus, we can conclude that the saplings and poles of these species have distribution patterns related to topography, which could be confirmed by the distribution maps of these species. In contrast, topographic variables played a less important role in the distributions of adults.

4. Discussion

The topography of our site was very diverse, with an elevation ranging from 709 to 869 m above sea level and three perennial creeks that joined together in the south-eastern corner of the plot. This heterogeneity explains why most of the studied species, especially *M. creaghii* and *P. kerrii*, showed a distribution pattern related to topography. The 13 dominant species in our plot also had a clumped distribution (Lan et al., 2009). This pattern supports the ubiquity of clumped spatial distributions amongst tropical tree species (He et al., 1997; Condit et al., 2000; Bunyavejchewin et al., 2003). In our plot, the diverse topography may have contributed to the clumped distribution of the 13 species. This result was confirmed by the CCA, linear regression and variation partitioning analysis. For example, *M. creaghii*, *P. chinensis*, *S. ternata* and *L. compactiflora* were mainly distributed in gullies with a relatively low elevation; in the CCA ordination diagram, these four species had a negative score in the *x*-coordinates, which was positively

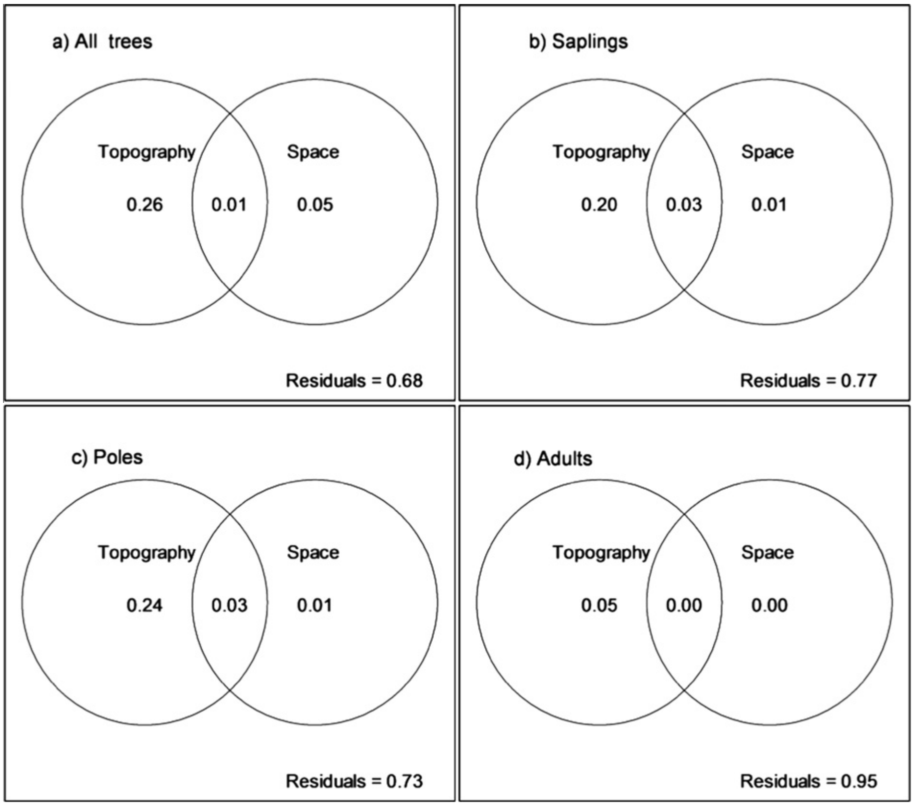

Fig. 4. Partitioning of the variation of the dominant species using topographic and spatial data. The numbers in the circles within the box indicate the fraction of explained variation attributable to environmental and spatial data. All of the testable model fractions (i.e. the unique contributions) were significant, with $P = 0.001$ after 999 permutations. Species codes are the same as in Table 1.

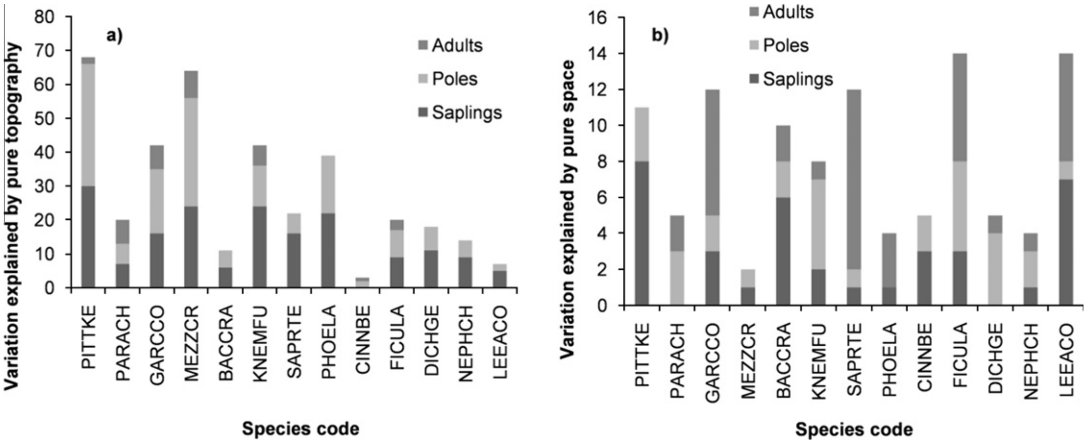

Fig. 5. Variation explained using topographic (elevation, slope, convexity and aspect) and spatial data (PCNM variables) of the 13 dominant species. All of the testable model fractions (i.e. purely spatial or purely environmental fractions) were significant, with $P = 0.001$ after 999 permutations. Species codes are given in Table 1.

correlated with elevation. In contrast, *G. cowa*, *K. furfuracea*, *P. lanceolata* and *N. chryseum* had greater *x*-coordinates and mainly occurred on slopes with high elevation.

It is interesting that topography alone explained 20% of the total variation for saplings and 24% for poles but only 5% for adults. This pattern arises because seedlings or saplings were apparently dispersing and establishing widely, but suffering higher mortality outside the optimal habitat type; thus, topography could explain more variation for poles than for saplings. The lower variation explained for adults may arise from high survival of rare recruits in suboptimal habitats and high density-dependent mortality of abundant seedlings in optimal habitats. Most young trees (saplings) in our plot have a significantly clumped distribution, but adults have a random distribution (Lan et al., 2009). These differences indicate that density-dependent mortality of the offspring is ubiquitous in our plot.

Notably, topography (or environment) explained more variation than did space in our plot. The purely spatial fraction of explained variation has sometimes been interpreted as predominantly a dispersal effect (Gilbert and Lechowicz, 2004; Cottenie, 2005; Karst et al., 2005). Pure space explained only 5% of the total variation, which may indicate that dispersal is not strong in our plot. Seed dispersal by animals predominates in tropical forest plant species (Willson et al., 1989) and involves a tremendous diversity of animal species and behaviours. Animals may consume fruit and drop, spit or defecate the seeds, carry seeds in their coats or scatter hoarded seeds for later consumption. Most types of fruits, such as drupe, berry, capsula and syncarp are dispersed by animals. The dominant canopy species, *P. chinensis*, has samaras nearly 60–70% of its seeds of fall within a circle of 1–8 m near the conspecific adults. Most studies where space explained more variation than environment used no data on soil chemical for trees (Borcard et al., 1992; Svenning et al., 2004; Chust et al., 2006). In those studies where environment explained more variation than space, soil chemical data were included (Duivenvoorden, 1995; Gilbert and Lechowicz, 2004; Cottenie, 2005; Duque et al., 2005; Karst et al., 2005). Soil chemical data were not used in our study, which decreased the fraction of variation explained by the environment.

The abundances of many species changed with topography which indicates topography predicts the composition of tree species in a rain-forest plot in the Xishuangbanna Prefecture, China. Valencia et al. (2004) found the same pattern in eastern Ecuador. However, a relatively large proportion (68%) of species variation in our dataset was unexplained by either environmental or spatial data. Undoubtedly, this result is partly due to random dispersal and mortality, but it may also include deterministic variation caused by unmeasured environmental variables (Jones et al., 2008).

We found strong evidence of topographic controlling of the distribution pattern of tree species. Amongst the four topographic variables, the convexity and elevation were the two most important factors contributing the distribution patterns of tree species in the plot. It is not difficult to hypothesise that both convexity and elevation might be negatively associated with soil moisture. Thus, soil moisture may be the most important environmental variable affecting species distribution. Soil moisture affects both chemical and physical properties of soils. Menendez et al. (1995) demonstrated a strong dependence of soil solution composition on soil water content. Increases in soil moisture content led to change in the ion distribution, free hydrated metal concentrations, and complexation (Fotovat et al., 1997). Soil moisture variation may thereby influence the field distribution of native plants amongst habitats.

It's worth noting that the tropical seasonal rainforest in southern Yunnan conspicuously decreased from a cover of 10.9% of the total area of the region in 1976 down to 3.6% in 2003, mainly due to rubber planting. Tropical seasonal rain forests have been reduced to patches of protected zones in Xishuangbanna, one of the top rubber-producing regions in China, as voracious economic growth has caused increasing encroachment on China's last remnants of uncultivated land (Zhu, 2008). Local people must be compensated for losses in order to avoid encroachment. As we all known a successful management of conservation areas heavily depends on the behaviour of the local people. In words, local government should pay enough attention on conserving and managing the tropical seasonal rain forests.

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References

Ayyappan, N., Parthasarathy, N., 1999. Biodiversity inventory of tree in a large–scale permanent plot of tropical evergreen forest at Varagalaiar, Anamalais, Western Ghats. India Biodivers. Conserv. 8, 1533–1554.

Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045–1055.

Bunyavejchewin, S., Lafrankie, J.V., Baker, P.J., Kanzaki, M., Ashton, P.S., Yamakura, T., 2003. Spatial distribution patterns of the dominant canopy dipterocarp species in a seasonal dry evergreen forest in western Thailand. Forest. Ecol. Manage. 175, 87–101.

Cao, M., Zhang, J.H., 1997. Tree species diversity of tropical forest vegetation in Xishuangbanna, SW China. Biodivers. Conserv. 6, 995–1006.

Chust, G., Chave, J., Condit, R., Aguilar, S., Lao, S., Pérez, R., 2006. Determinants and spatial modeling of tree diversity in a tropical forest landscape in Panama. J .Veg. Sci. 17, 83–92.

Condit, R., 1998. Tropical Forest Census Plots. Springer–Verlag, NewYork, 17p.

Condit, R., Hubbell, S.P., Foster, R.B., 1996. Changes in tree species abundance in a Neotropical forest: impact of climate change. J. Trop. Ecol. 12, 231–256.

Condit, R., Ashton, P.S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S.P., Foster, R.B., Itoh, A., Lafrankie, J.V., Lee, S.L., Losos, E., Manokaran, N., Sukumar, R., Yamakura, T., 2000. Spatial patterns in the distribution of tropical tree species. Science, 1114–1118.

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

Duivenvoorden, J.F., 1995. Tree species composition and rain forest environment relationships in the middle Caquetá area Colombia NW Amazonia. Vegetatio 120, 91–113.

Duque, A.J., Duivenvoorden, J.F., Cavelier, J., Sanchez, M., Polanía, C., León, A., 2005. Ferns and Melastomataceae as indicators of vascular plant composition in rain forests of Colombian Amazonia. Plant Ecol. 178, 1–13.

Fotovat, A., Naidu, R., Sumner, M.E., 1997. Water:soil ratio influences aqueous phase chemistry of indigenous Cu and Zn in soils. Aust. J. Soil Res. 35, 687–709.

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

Gunatilleke, C.V.S., Gunatilleke, I.A.U.N., Esufali, S., Harms, K.E., Ashton, P.M.S., Burslem, D.F.R.P., Ashton, P.S., 2006. Species-habitat associations in a Sri Lankan dipterocap forest. J. Trop. Ecol. 22, 371–378.

Harms, K.E., Condit, R., Hubbell, S.P., Foster, R.B., 2001. Habitat association of tree and shrubs in a 50- ha neotropical forest plot. J. Ecol. 89, 947–959.

Jones, M.M., Tuomisto, H., Borcard, D., Legendre, P., Clark, D.B., Olivas, P.C., 2008. Explaining variation in tropical plant community composition: influence of environmental and spatial data quality. Oecologia 155, 593–604.

Karst, J., Gilbert, B., Lechowicz, M.J., 2005. Fern community assembly: the roles of chance and the environment at local and intermediate scales. Ecology, 86:2473–2486.

King, D.A., Davies, S.J., Noor, N.S., 2006. Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest. For. Eco. Manage. 206, 152–158.

Lan, G.Y., Hu, Y.H., Cao, M., Zhu, H., Wang, H., Zhou, S.H., Deng, X.B., Cui, J.Y., Huang, J.G., Liu, L.Y., Xu, H.L., Song, J.P., He, Y.C., 2008. Establishment of Xishuangbanna tropical forest dynamics plot: species compositions and spatial distribution patterns in Chinese. J. Plant. Ecol. 32, 287–298.

Lan, G.Y., Zhu, H., Cao, M., Hu, Y.H., Wang, H., Deng, X.B., Zhou, S.S., Cui, J.Y., Huang, J.G., He, Y.C., Liu, L.Y., Xu, H.L., Song, J.P., 2009. Spatial dispersion patterns of trees in a tropical rainforest in Xishuangbanna, southwest China. Ecol. Res. 24, 1117–1124.

Menendez, I., Moreno, G., Gallardo, J.F., Saavedra, J., 1995. Soil solution composition in forest soils of Sierra-de-gata Mountains, Central western Spain: relationship with soil–water content. Arid Soil Res. Rehabil. 9, 495–502.

Svenning, J.C., Kinner, D.A., Stallard, R.F., Engelbrecht, B.M.J., Wright, S.J., 2004. Ecological determinism in plant community structure across a tropical forest landscape. Ecology 85, 2526–2538.

Valencia, R., Foster, R.B., Villa, G., Condit, R., Svenning, J.C., Hernández, C., Romoleroux, K., Losos, E., Magård, E., Balslev, H., 2004. Tree species distributions and local habitat variation in the Amazon: a large forest plot in eastern Ecuador. J. Ecol. 92, 214–229.

Willson, M.F., Irvine, A.K., Walsh, N.G., 1989. Vertebrate dispersal syndromes in some Australian and New-Zealand plant-communities, with geographic comparisons. Biotropica 21, 133–147.

Wu, Z.Y., 1987. Vegetation of Yunnan. Science Press, Beijing, 33p.

Zhang, J., Cao, M., 1995. Tropical forest vegetation of Xishuangbanna, SW China and its secondary changes, with special reference to some problems in local nature conservation. Biodvs. Consrv. 73, 229–238.

Zhu, H., 2006. Forest vegetation of Xishuangbanna, south China. Froest. Stud. China 8, 1–27.

Zhu, H., 2008. Advances in biogeography of the tropical rainforest in southern Yunnan, southwestern China. Trop. Conserv. Sci. 1, 34–42.

Zhu, H., Cao, M., Hu, H.B., 2006. Geological history, flora, and vegetation of Xishuangbanna, Southern Yunnan, China. Biotropica 38, 310–317.