



Topography related habitat associations of tree species traits, composition and diversity in a Chinese tropical forest



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ARTICLE INFO

Article history:

Received 8 May 2014

Received in revised form 25 June 2014

Accepted 27 June 2014

Keywords:

Community assembly
Environmental filtering
Functional diversity
Functional traits
Limiting similarity
Topography

ABSTRACT

Several studies have demonstrated that topography, as a proxy for resource availability, plays an important role in shaping tree species distribution patterns in tropical forests. Here we take a functional approach by assessing changes in plant functional traits along topographical gradients in a 20-ha forest dynamics plot in Xishuangbanna, southern Yunnan, China. We hypothesized that observed changes in trait composition and diversity along the topographic gradient should reflect tree life-history strategies linked to resource (water and nutrients) availability. We measured and compiled data of the maximum height, leaf area, seed mass and wood density of 334 tree species in 500 subplots (20 × 20 m). We found that species composition and diversity changed significantly along the topographical gradient. This change was accompanied by increasing community average seed mass and wood density, and decreasing leaf area and tree maximum height with higher elevations and steeper slopes. Higher slopes and ridges were being dominated by tree communities that, possibly due to environmental filtering, converged on a combination of traits characteristic of slow growth and low turn-over. Lower slopes and valleys, on the other hand, were dominated by tree communities that showed high trait evenness and divergence, and tree species characterized by traits indicative of fast growth and turn-over, i.e. competition for resources may be responsible for complementary trait combinations and resource use in this habitat type. Our study shows that functional traits can provide a mechanistic understanding of the processes shaping tropical tree community assembly along topographical gradients and supplements information obtained using species composition and diversity data. Some practical outcomes of our study include: (1) plant species compositional trends in tropical forests can be predicted with GIS technology, focusing on topographical gradients; (2) forest communities on ridges may become more dominant and expand in the future due to increasing drought severity; (3) a considerable number of tropical tree species may currently be under threat of local extinction due to topographically biased deforestation trends and (4) trait based survey approaches improve our understanding of the mechanisms behind species compositional trends.

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1. Introduction

Determining the relative contribution of the factors influencing the structure and diversity of ecological communities along environmental gradients has been a persistent theme in ecology (Anderson et al., 2011), and is crucial for informed forest management practices such as selection of protected areas. Most previous studies have focused on taxonomic information such as species composition and richness, which ignores phylogenetic and

functional information (Swenson et al., 2011), and thus the link between functional traits and the environment. At the community scale, plant traits are strongly correlated with soil resources and water availability (Cornwell and Ackerly, 2010; Katabuchi et al., 2012). Hence, they have been widely used in explaining the community assembly process based on niche theory (Kraft et al., 2008). Nowadays, functional diversity indices, including functional richness, functional evenness and functional divergence, are widely used to shed light on community assembly processes among different forest types (Villegger et al., 2008; Pakeman, 2011; Laliberté et al., 2013; Purschke et al., 2013), and to evaluate forest management impacts (Maeshiro et al., 2013).

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Topography has been identified as an easily measured proxy for environmental resource availability and spatial pattern in plant species composition (Costa et al., 2005; Bohlman et al., 2008). Topography is strongly linked to microhabitat gradients of soil water and nutrient availability at local scales (Balvanera et al., 2011), with sites near valleys being moister and more nutrient rich than sites near ridge tops (Gibbons and Newbery, 2003; Segura et al., 2003). Also, steeper sites have higher water and nutrient output and thus generally have less soil water and nutrients available than flatter areas (Comita and Engelbrecht, 2009; Balvanera et al., 2011). Given these clear links between topography and soil/water resource availability, it is not surprising that many studies have found evidence of habitat associations of plant species along topographical axes (Gunatilleke et al., 2006; Wang et al., 2009; PUNCHI-Manage et al., 2013).

To identify and understand the underlying processes behind the observed changes in species composition along topographical gradients a functional approach is advantageous as this provides a direct link between species traits and observed habitat characteristics. This is especially useful in mega-diverse tropical forests where ecological data for the majority of species is lacking and most tree species are rare (Tuomisto et al., 2003; Meier et al., 2010). Here we focus on four traits (maximum height, seed mass, leaf area and wood density) that provide information concerning plant life-history strategy, especially the 'slow' versus 'fast' growth and productivity trade-off (*sensu* Reich, 2014). They represent multiple axes of functional differentiation and several studies have previously found strong linkages between these traits and the abiotic environment (Cornwell and Ackerly, 2010; Swenson and Weiser, 2010). Wood density was used to represent the wood economics spectrum (Chave et al., 2009) where a species falls along a continuum between high volumetric growth rates, low construction costs, and high mortality rates vs. low volumetric growth rates, high construction costs, and low mortality rates (Swenson and Enquist, 2007; Chave et al., 2009). Maximum height was used to indicate the adult light niche and colonizing strategy (Moles et al., 2009; Thomson et al., 2011). Seed mass was used to represent a trade-off between producing many small seeds per energy unit vs. producing a few large seeds per energy unit and is linked to colonizing ability and plant establishment strategy (Moles and Westoby, 2006). Leaf area was used to indicate photosynthesis and respiration rates, which are linked to plant productivity (Wright et al., 2004; Malhado et al., 2009).

In this paper, we analyze the composition and diversity of plant functional traits in a 20-ha tropical rainforest dynamics plot in southwestern China to test the following hypotheses: (1) functional trait shifts along topographical gradients reflect a change in life-history from 'fast' to 'slow' (*sensu* Reich, 2014) linked to the declining resource availability at steeper slopes and higher topographic positions; (2) as 'fast' species need more resources per time unit, competition may be particularly high in 'fast' species dominated habitats and those communities may therefore show high trait diversity indicating complementary resource use; at the same time (3) we expect species communities growing under low resource conditions, i.e., dominated by 'slow' species to show lower trait diversity as the species community there is under strong environmental selection towards the best adapted trait combinations to cope with the relatively harsh conditions.

2. Materials and methods

2.1. Study site

Our study took place in the 20-ha permanent seasonal rainforest dynamics plot (Fig. 1) managed by the Xishuangbanna Tropical

Botanical Garden, Chinese Academy of Sciences, at Xishuangbanna, southwest China (101°34'26–47"E, 21°36'42–58"N). This plot is part of the Chinese Forest Biodiversity Monitoring Network, which has sponsored four large permanent dynamic plots that cover a range of typical vegetation types spanning temperate, subtropical and tropical forests. It is 400 m in width and 500 m in length, and elevation ranges between 710 and 866 m above sea level. The plot location is characterized by a monsoon climate with an alternation between a dry, cool winter season and a rainy, hot summer season, with a mean annual temperature of 21.0 °C and mean annual precipitation of about 1532 mm according to a weather station near the study site. The canopy is dominated by Dipterocarpaceae, Icacinaceae and Lauraceae. In 2007, all trees and shrubs ≥ 1 cm DBH (diameter at breast height, 1.3 m above ground) in the plot were tagged, measured, mapped and identified to species according to the field protocol of the Center for Tropical Forest Science (Lan et al., 2011). For our study, stems with unknown species names or whose exact locations were unknown, were excluded (1.02%). In total the dataset contained 334 species and 94,856 stems, of which 51 species were represented by just a single individual.

2.2. Topographical variables

The plot was subdivided into subplots ($n = 500$) of 20×20 m for each of which slope, convexity and elevation was measured following the methods described in Harms et al. (2001). Elevation for each subplot was calculated as the mean of the elevation at its four corners. Slope was based on the mean angular deviation from the horizontal of each of the four triangular planes formed by connecting three corners. Convexity was calculated as the difference between the mean elevation of the focal subplot and the mean elevation of the eight surrounding subplots. Low lying sites have a negative value (depressions) while high sites have a positive value (hilltops). Aspect refers to the North/South exposure of slope faces and was calculated as follows:

$$\text{Aspect} = |\text{aspect} \cdot \text{degree} - 180| \div 57.3$$

Using this formula, aspect values vary between zero (full South exposure) and 3.14 (full North exposure).

On the basis of the topographical variables, we identified six types of habitat. The six habitat types were: Valley (slope (S) $< S_{\text{mean}}$, elevation (E) $< E_{\text{mean}}$); Lowslope ($S \geq S_{\text{mean}}$, $E < E_{\text{mean}}$); High slope ($S \geq S_{\text{mean}}$, $E \geq E_{\text{mean}}$, concavity > 0); High-gully ($S \geq S_{\text{mean}}$, $E \geq E_{\text{mean}}$, concavity < 0); Ridge top ($S \leq S_{\text{mean}}$, $E \geq E_{\text{mean}}$); Gap (Canopy cover less than 50%) (Fig. 1). Since gap habitat was related to light availability rather than topography, gap plots were excluded in further analyses.

2.3. Traits collection

The functional trait data for this study were collected from literature sources and large publically available trait databases (i.e. TRY website: <http://www.try-db.org/>), but most data were measured from specimens present in the herbaria of the Xishuangbanna Tropical Botanical Garden (XTBG), the Kunming Institute of Botany (KIB) and the Institute of Botany (IB), China. We aimed to measure at least 10, but preferably 20 specimens for each species. Species in the permanent plot are mostly tropical and, within China, occur almost exclusively in Yunnan province meaning that the variation between the species in the herbaria and the ones in the plots is small. We measured leaf areas for 5778 individuals belonging to 318 species. Morpho-species data were measured from vouchers collected in the 20-ha plot. For species without specimens in the herbarium, we searched the leaf trait data from the Flora of China website (<http://www.tropicos.org/Project/FC>) and local flora (Zhu,

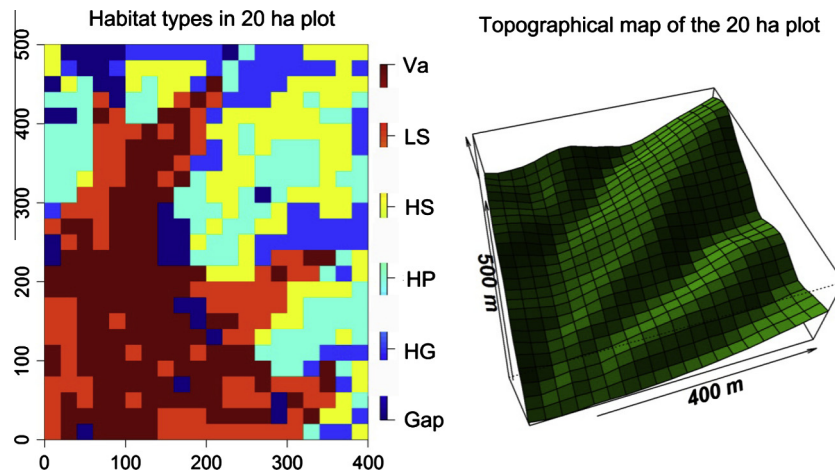


Fig. 1. Habitat types (left) and topographic map (right) of the Bubeng 20-ha permanent plot in Xishuangbanna, Southern Yunnan, China. Habitats include Gap, high gully (HG), high plateau (HP), high slope (HS), low slope (LS), valley (Va).

2008). For tree maximum height, we collected maximum height data from herbarium labels. For species with more than 10 mature individuals we ranked the observed tree heights from highest to lowest, fitted a logarithmic curve and used the intercept as the predicted maximum height. For trees with less than 10 height observations we used the maximum height reported in the Flora of China (<http://www.tropicos.org/Project/FC>). Seed mass data was derived primarily from the XTBG Seed Bank, and partly from the literature (Chen and Huang, 2000), the Kew Seed Information Database (<http://data.kew.org/sid/>) and from the KIB Seed Bank. Wood density data (oven-dry) was taken from the global wood density database (<http://datadryad.org/repo/handle/10255/dryad.235>) and literature focusing specifically on Chinese tree species (Zhang et al., 2011). For species without wood density data we used the genus average wood density values because previous studies have found insignificant variation in congeneric trait values for such traits as seed mass (Moles et al., 2005) and wood density (Slik, 2006; Swenson and Enquist, 2007). We generated the community weighted functional trait values for each 20 m by 20 m subplot of the 20-ha forest dynamics plot. Leaf area, maximum height and seed mass data were log-transformed before analysis to normalize their distributions.

2.4. Species and functional diversity indices

We used Nonmetric Multidimensional Scaling (NMDS) for the floristic composition analysis. For species richness we used the number of species for each 20 by 20 m subplot. Additionally, we used the Simpson index, which calculates the probability of finding different species when two random stems are sampled from the population, and the Shannon-Wiener diversity indices for each subplot. The Vegan package in R program 2.12 (R Core Development Team, 2008) was used for these calculations. For functional diversity we used distance-based indices (Mouchet et al., 2010): (1) functional richness (F_{ric} - volume of the functional space occupied by the community), (2) functional evenness (F_{eve} - regularity of the distribution of abundance in this volume) and (3) functional divergence (F_{div} - divergence in the distribution of abundance in this volume). The functional diversity indices were calculated per 20 × 20 m subplot using the “FD” package (Laliberté and Shipley, 2010) within the R program.

2.5. Data analysis

For each functional trait, functional diversity index and species diversity index (response variables) we calculated all possible

multiple-regression models linking them to the topographical variables (predictor variables). Before running the multiple regressions we first checked whether all individual regressions were linear and residuals normally distributed. We also checked for multi-collinearity of the variables by calculating their variable inflation factors (VIFs) in the full models, which showed that all VIFs were below 1.3, indicating no serious multi-collinearity between the variables. The most parsimonious model for each of the response variables were subsequently selected using the Akaike Information Criterion (AICc). All selected models were checked for spatial autocorrelation of residuals. If spatial autocorrelation was detected we applied Simultaneous Autoregression (SAR) as applied in the software Spatial Analysis in Macroecology (Rangel et al., 2010) to eliminate or reduce its impact. By doing this, we could disentangle the effect of space and topography on the response variables. We used ANOVA to compare functional diversity indices among different habitat types.

3. Results

Species composition in the form of NMDS axis 1 was highly correlated with topographical gradients ($R^2 = 0.662, p < 0.001$, Table 1, Fig. 2), showing that floristic composition changed with elevation, convexity and slope (Fig. S1). The optimum models linking species diversity with topography explained limited data variance and were mostly negatively affected by convexity, i.e. diversity increased towards concave terrain (valleys). Species richness, however, showed a positive correlation with convexity (higher richness

Table 1
Best ordinary least squares models (based on lowest AICc) for the response variables and their explained variance based on predictor variables only and predictor variables plus space. Direction of correlation indicated by positive (+) and negative (-) signs.

Response variables	Best AICc model	R ² Pred.	R ² Pred. + Space
NMDS1	+elev+convex-slope	0.662	0.653
Species Richness	+aspect+convex+slope-elev	0.08	0.082
Simpson	-convex	0.153	0.161
Shannon	-convex	0.137	0.144
Max. height	+elev-convex-slope-aspect	0.134	0.157
Leaf area	+slope-convex+aspect	0.208	0.201
Wood density	+convex+elev	0.167	0.189
Seed mass	+convex+elev+slope	0.129	0.167
Trait richness	+aspect+convex+slope-elev	0.079	0.081
Trait evenness	+elev-convex	0.055	0.056
Trait divergence	+convex+slope+elev	0.105	0.102

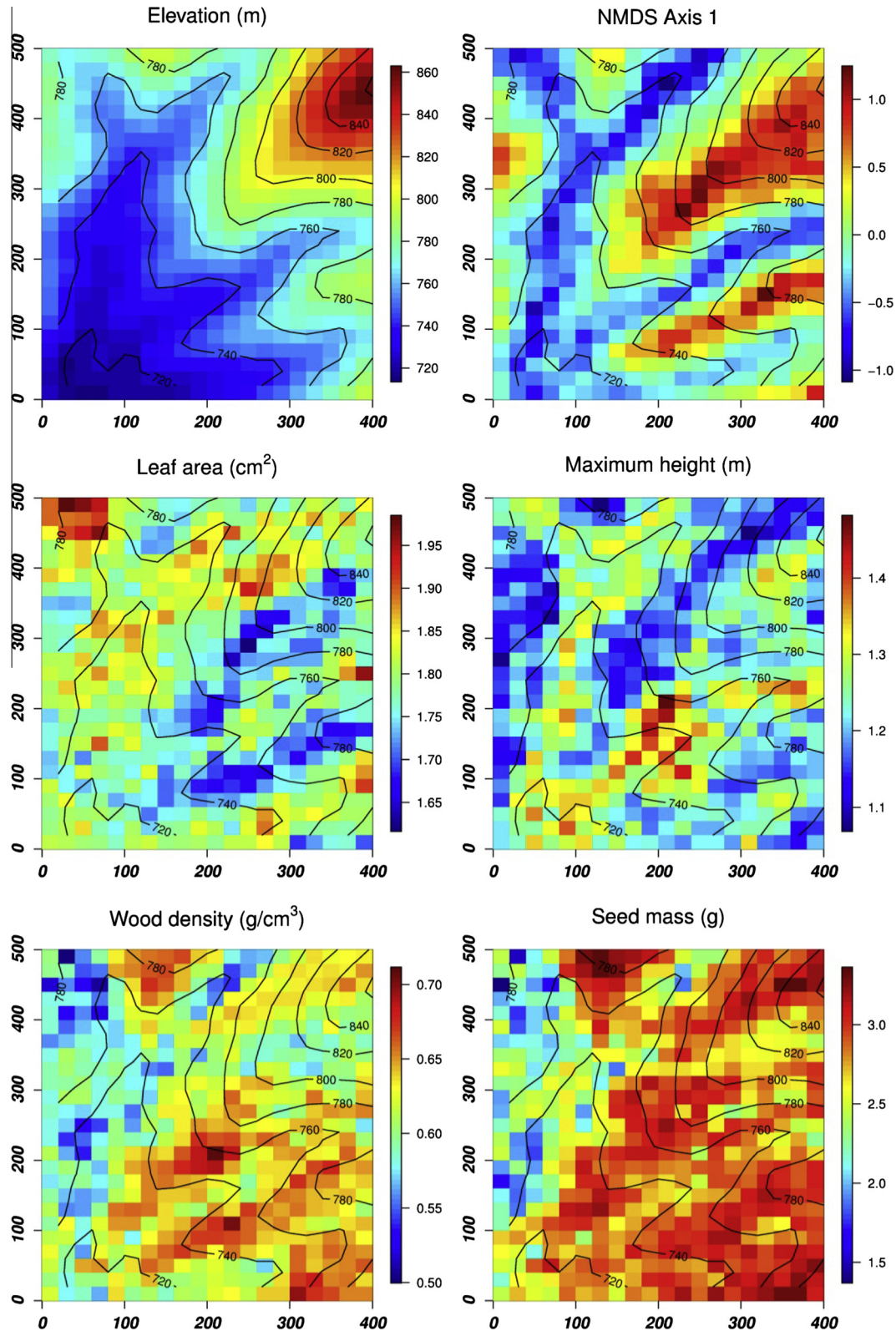


Fig. 2. Maps of elevation, NMDS-axis1 scores and the mean abundance weighted trait values in the 20-ha plot. Each grid represents a community weighted trait value of a 20 m by 20 m subplot. All traits except wood density were \log_{10} -transformed before analysis. Elevational contours are indicated by black lines.

on upper slopes and ridges), and additional associations with aspect (higher richness towards northern exposures), slope (higher richness on steeper slopes) and elevation (lower richness at higher elevations) (Table 1).

Functional traits were correlated with topographical factors although explained variance was low (Fig. 2, Table 1). Subplots in low depressions (concave) were dominated by species that had high tree maximum height ($r = -0.256$, $p < 0.001$) and large leaf

area ($r = -0.413$, $p < 0.001$), but low wood density ($r = 0.31$, $p < 0.001$) and seed mass ($r = 0.387$, $p < 0.001$).

Functional diversity indices were significantly but weakly correlated with topographical variables (Tables 1 and 2), notably elevation and convexity. Functional richness was especially high on north-facing and steep slopes, while functional evenness and divergence were highest in valleys and lower slopes (Tables 1 and 2).

4. Discussion

4.1. Functional traits and topography

Functional trait structure and diversity were significantly correlated with topography, indicating that tree species composition was, at least partly, shaped by habitat filtering at the community scale. This supports the hypothesis that environmental filtering is a fundamental process in community assembly in tropical forests.

In our study plot, the soil water and nutrient content decreased from the valley to the ridge top, especially during the dry season (Yan and Cao, 2008). This is consistent with the observed increase in community seed mass and wood density towards higher slopes and ridges, and the decrease in leaf area and maximum tree height along the same gradient. High seed mass, high wood density, small stature and small leaf area are generally indicative of slow tree growth, shade and drought tolerance, and investment in long-term survival through mechanical and chemical defense against damage (Davies, 2001; Slik et al., 2008; Reich, 2014). These are characteristics of plants growing under low resource availability (soil water, soil nutrients, light) (Russo et al., 2008; Reich, 2014). The large leaf area and maximum potential tree height in combination with low wood density and small seed mass of trees growing on lower slopes and valleys, indicates high turn-over and investment in fast growth at the expense of defensive measures (Coley et al., 1985; van Gelder et al., 2006; Reich, 2014). These are characteristics of plants growing under high resource availability (Poorter, 2009). Topography has been shown to represent such a resource gradient, with higher and steeper sites having lower soil nutrient content and water availability (Segura et al., 2003; Balvanera et al., 2011). Our results therefore indicate that species distributions along topographical gradients are partly shaped by habitat filtering through a selection of functional traits that are linked to tree resource-use and growth strategies (Lebrija-Trejos et al., 2010).

Among the topographical variables, elevation and convexity were the main drivers of traits distribution patterns, although combined they only explain ca. 10–20 percent of the total observed data variance. This value is similar to that found for the influence of elevation on tree traits at Sinharaja tropical rainforest in Sri Lanka (Baldeck et al., 2013). In Sri Lanka, however, the topographical variables explained only 25% of the variance in species composition (Punchi-Manage et al., 2013) versus more than 60% in our, more species rich, Chinese tropical forest. Despite this difference it is

clear that topographical variables are significantly shaping the species and traits distributions in both plots, with the remaining variance possibly related to other clustering processes such as soil and light resources, and dispersal limitation (Chase, 2010; Baldeck et al., 2013). The use of herbarium instead of field measured traits may also have affected the strength of the detected relationships negatively.

4.2. Species versus functional diversity

Species diversity can be positively, negatively and unimodally linked to environmental conditions (Pausas and Austin, 2001), but it does not provide any functional explanation for the detected pattern. In extreme cases, the entire plant community might shift along an environmental gradient, while species diversity would remain unaffected. Plant traits provide a more functional link between the environment and the species community (Diaz et al., 1998), and we therefore expected that functional trait diversity would show a stronger relationship with the environment, in this case topography, than species diversity. However, our results show that both types of diversity show similar levels of association with the environment (Table 1). For example, functional richness and species richness were highly correlated ($R^2 = 0.439$, $p < 0.001$) and affected by the same topographical variables. Previous studies show that the relationship between species and functional trait diversity can differ considerably (Diaz and Cabido, 2001; Naem and Wright, 2003; Mayfield et al., 2005). These differences in the relationship between species and functional diversity were ascribed to differences in functional redundancy (Petchev et al., 2007), i.e. different species may play equivalent roles within ecosystems. High functional redundancy occurs when species overlap in their traits (Flynn et al., 2009). In our case species and functional diversity showed similar correlation values with the environmental gradient, which suggests that functional redundancy is low, i.e. each species added some functional diversity to the community. However, it has to be kept in mind that the majority of data variance in our study remained unexplained, and it is not as yet clear if this represents functional redundancy or linkage of traits to variables not included in our study.

4.3. Functional diversity, community assembly mechanisms and habitat types

Functional diversity indices can be significantly different among forest habitat types (Maeshiro et al., 2013). Our study revealed that sites in valleys and on lower slopes, which are characterized by higher resource availability (Gibbons and Newbery, 2003; Segura et al., 2003), have higher functional evenness and divergence than sites higher along topographical gradients. Functional evenness is an indicator of how functional space is occupied, with a higher value when species abundances are more even or regularly spaced in trait space (Villeger et al., 2008). The high functional evenness in low slope and valley locations, shows that functional trait abundances are more evenly distributed in habitats with high resource availability. Apparently, the co-existing species in these habitat types tend to be dissimilar in their trait values, indicating complementary resource use (Mouchet et al., 2010; Pakeman, 2011; Laliberté and Shipley, 2010).

In contrast, habitats on high slopes and ridges had uneven and more convergent functional diversity. Functional divergence reflects how close the abundant species lie to the center of the functional trait volume (Villeger et al., 2008). The high elevation and ridge environments therefore tended to be dominated by species with similar traits, indicative of a prominent role of environmental filtering in these habitat types. Our results correspond to those of Mason et al. (2012) who found that at high soil fertility

Table 2

Mean \pm SD of trait richness, trait evenness, and trait divergence in the different habitat types found in the 20-ha plot. Significant differences within columns (one way ANOVA with post hoc Tukey test) are character coded.

Habitat	Trait richness	Trait evenness	Trait divergence
Valley	34.85 \pm 10.22ab	0.706 \pm 0.037b	0.822 \pm 0.039b
Low slope	37.29 \pm 8.80b	0.704 \pm 0.034b	0.826 \pm 0.037b
High slope	38.58 \pm 9.57b	0.695 \pm 0.036a	0.794 \pm 0.047a
High gully	37.73 \pm 9.86ab	0.702 \pm 0.036ab	0.796 \pm 0.046a
High plateau	32.99 \pm 10.73a	0.685 \pm 0.042a	0.791 \pm 0.046a
F	4.902	5.398	13.03
p	<0.001	<0.001	<0.001

dominant species differ in resource-use strategy while dominant species became convergent, with a resource-retentive strategy, when soil fertility declined.

5. Conclusions

Our study shows that topography is a good predictor of plant species turnover, with the plant trait composition and diversity providing a functional understanding of the processes that shape this topographic species gradient. Our results have several practical implications:

1. *Plant species compositional trends in tropical forests can be predicted with remote sensing and GIS technology*, focusing on topographical gradients, although the importance of these gradients probably vary with dry season length and topographic variability within the forest area of interest.
2. *Forest communities on ridges may become more dominant and expand in the future* because droughts are expected to become more severe and the tree species on ridges are more tolerant to such changes than the valley forests.
3. *A considerable number of tropical tree species may currently be under threat of local extinction* just because current deforestation trends are generally focused on low elevation, shallow slope, southern aspect, and nutrient rich parts of landscapes (Sandell and Svenning, 2013). This is a consequence of tree species distributions being not randomly but topographically distributed across the landscape. Even largely forested areas can have disproportionate local species extinctions if the forests do not cover the complete topographical range.
4. *Trait based survey approaches improve our understanding of the mechanisms behind the observed species compositional trends* within forest landscapes. This is especially useful in tropical forests, where the ecology of most of the species is still poorly studied.

Acknowledgments

The authors would like to thank the Xishuangbanna Station of Tropical Rain Forest Ecosystem Studies, and especially Deng Xiaobao, for sharing the tree species inventory and topographical data from the Bubeng 20-ha forest dynamics plot with us. Special thanks go to Wang Hong, Lin Qi and Ya Jidong for providing us the chance to collect data from herbaria and seed banks. We are particularly indebted to Chen Sichong and Kyle Tomlinson for their insightful comments on the manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.06.045>.

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