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



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#### 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 ( $20 \times 20$  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

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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 (Villeger 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 Enguist, 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 tradeoff 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  $\geq$ 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  $20 \times 20$  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:

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

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  $(S \ge S_{\text{mean}}, E < E_{\text{mean}})$ ; High slope  $(S \ge S_{\text{mean}}, E \ge E_{\text{mean}}, \text{ concavity > 0})$ ; High-gully  $(S \ge S_{\text{mean}}, E \ge E_{\text{mean}}, \text{ concavity < 0})$ ; Ridge top  $(S \le S_{\text{mean}}, E \ge E_{\text{mean}})$ ; 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, Download English Version:

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