Flora 231 (2017) 21–28

Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.com/locate/flora

Original research

Effects of topography and spatial processes on structuring tree species composition in a diverse heterogeneous tropical karst seasonal rainforest

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ARTICLE INFO

Article history:
Received 8 December 2016
Received in revised form 2 April 2017
Accepted 5 April 2017
Edited by Karsten Wesche
Available online 7 April 2017

Keywords:
Spatial distribution
Redundancy analysis (RDA)
Variation partitioning
Topographic control
Habitat heterogeneity

ABSTRACT

Aggregated patterns of tree species originate either from the physical forcing of habitat heterogeneity or from community processes. In both cases, spatial structuring plays a functional role in ecosystems. This study examines the spatial patterns of tree species, and discusses the degree to which variation in species distribution patterns depends on topographic variation. We first analyzed the spatial distribution patterns of tree species by using the univariate pair correlation function. We used redundancy analysis to identify the main structures explained by the measured topographic variables. Then, we used variation partitioning in combination with Moran's eigenvector maps and seven topographic variables to determine the relative importance of the effects of pure topographical, pure spatial, and spatially structured environmental processes on spatial patterns of tree species composition in a large-scale stem-mapping plot located in a diverse heterogeneous tropical karst seasonal rain forest of south China. Although aggregated distribution was the dominant pattern for tree species as we expected in this tropical karst forest, the degree of aggregation was lower than in other tropical or subtropical forests. Most species showed random patterns after controlling for habitat heterogeneity in a parametric heterogeneous Poisson process null model. The seven topographical variables explained about 16.7%, 31.0% and 47.2% of the total variance in species abundances by redundancy analysis for cell sizes of 10 m × 10 m, 20 m × 20 m and 50 m × 50 m, respectively. The pure spatial component was most important at the three spatial scales, which accounted for about one-third of total variance in species composition, while the spatially independent habitat contributed a negligible effect. This indicated that the overall evidence for topographic controls of the tropical tree species spatial pattern was strong, but the explanatory power of the topographic variables was negligible compared to the total variation of pure spatial processes, especially the broad-scale space. The results suggest that topographical and neutral progresses jointly contribute to the maintenance of species composition, and their relative importance varies with spatial scale in the Nonggang tropical karst seasonal rain forest.

1. Introduction

The spatial distribution of tree species in forest stands is a central tenet in ecological theory, as it often determines patterns of understory species diversity, biotic and abiotic interactions (Perry et al., 2008; Wiegand et al., 2009). Tree species are often patchily distributed in natural forests (He et al., 1997; Condit et al., 2000; Zillio and He, 2010). Such aggregated distribution of tree species has implications for species coexistence, because it can directly affect species interaction and resource use (Ives and May, 1985). Many processes, such as habitat heterogeneity, species dispersal limitation and biotic interactions, have been proposed to explain spatial distribution of species (Harms et al., 2001; Seidler and Plotkin, 2006; John et al., 2007; Pinto and MacDougall, 2010).

Habitat heterogeneity caused by environmental variation in space is considered an important determining factor in spatially

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http://dx.doi.org/10.1016/j.flora.2017.04.002
0367-2530/

aggregated patterns of species (Whittaker, 1956; Bray and Curtis, 1957). The environmental variables are always differentially segregated along environmental gradients, and their effects are generally reflected in species distribution due to species-habitat association (Harms et al., 2001). Most species may show significant habitat association in natural forests. For instance, Lai et al. (2009) found that in a subtropical forest in China 86.7% of the tree species examined were associated with topographically defined habitats. The degree to which variation in tree species distribution is predictable from topographical variation is of considerable current interest (Jones et al., 2008; Lan et al., 2011).

In addition, spatial patterns may also be generated by stochastic processes and spatial structuring processes of community dynamics, and in particular by dispersal limitation which can produce aggregated patterns through the neutral theory (Hubbell, 2001). This theory ignores the possible effects of local environmental conditions on the differences in species composition among sampling sites (McGill et al., 2006). Spatial structure in species composition is mainly driven by dispersal limitation and independent of habitat under neutral theory (Etienne and Alonso, 2007). Niche and neutral theories emphasize different processes but jointly contribute to the maintenance of species composition and should leave different structures in species assemblages (Legendre et al., 2009; Punchi-Manage et al., 2014). However, relatively little is known about the relative importance of topographic variables, stochasticity, and spatial processes in structuring local species compositions, especially in tropical forests.

Limestone karsts are sedimentary rock outcrops that primarily consist of calcium carbonate. Over millions of years, the softer sediments covering these karsts were removed by mechanical and chemical weathering. This process usually produced “tower” and “cockpit” karst formations in the tropics (Clements et al., 2006). South China is one of the largest karst regions in the world and is considered fragile because of the unique geology and high habitat heterogeneity. A previous study showed that most of the common species in a tropical karst forest in south China were positively associated with at least one topographically defined habitat (Guo et al., 2017). We hypothesize that the spatial patterns of tree species has an obviously correlation with the topographic variables in this diverse heterogeneous system. We are interested in the spatial distribution of tree species and the degree to which variation in a species distribution can be predicted from the topographic and spatial variables. Partitioning the variation in species assemblages among sampling units between topographic and spatial variables according to this framework provides a useful ground for separating niche and neutral mechanisms in community structure studies.

Our study is based on detailed information about topography and species composition within a 15 ha northern tropical karst seasonal rain forest in south China, which is topographically very heterogeneous. This region is one of the fourteen key areas of protecting the biodiversity in the world (Chen, 1993). Using these data, the main objectives are to show the spatial patterns of conspecific tree species and how topographical variables and spatially structured environment influence the spatial distribution of species. Ultimately, this will increase our understanding of the mechanisms that drive species assembly in tropical karst seasonal rain forests with pronounced topographical variation.

2. Materials and methods

2.1. Study site

Our study site was in the Nonggang northern tropical karst seasonal rain forest dynamics plot located in the Nonggang National Natural Reserve (22°13′56″ –22°33′09“N, 106°42′28”–107°04′54″E), Guangxi Zhuang Autonomous Region, in south China. The forest has not been subjected to human disturbance over ca. hundred years. This forest reserve preserves the most typical and aboriginal karst seasonal rain forest of China. Topographically, the area is characterized by typical karst Fengcong-Depression (‘tower’ and “cockpit”), a combination of clustered peaks with a common base and funnel landscape with the altitude ranging from 150 to 600 m (Su et al., 1988). Mean annual temperature of the reserve is 22 °C with mean daily maximum temperature of 37–39 °C and minimum temperature of 13 °C. Annual precipitation ranges from 1150 to l550 mm but can reach up to 2043 mm, calculated from data from 1970 to 2000 (Fig. 1). Most of the precipitation occurs between May and September.

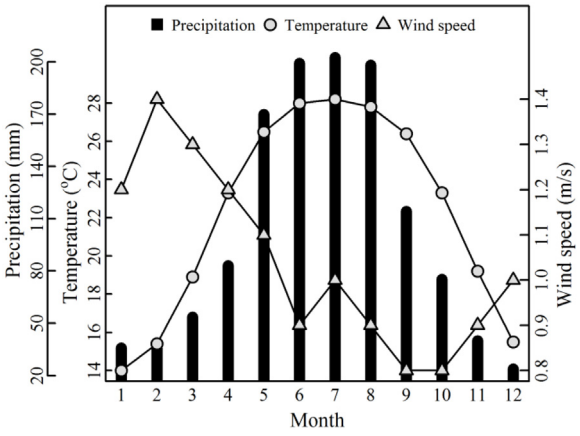

Fig. 1. Monthly variations of precipitation, air temperature and wind speed between 1971 and 2000 in the Nonggang National Nature Reserve.

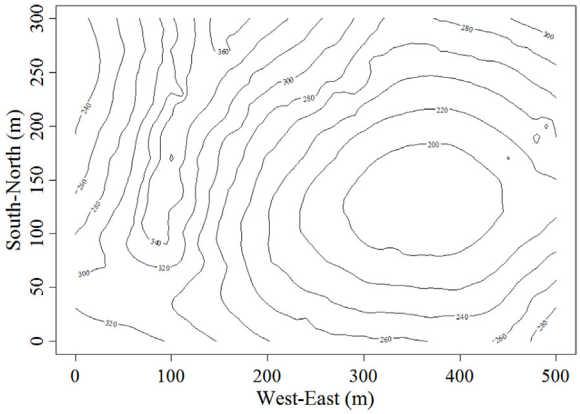

Fig. 2. Contour map with 20-m intervals of the 15-ha (500 m × 300 m) Nonggang plot.

2.2. Site history and data collection

2.2.1. Permanent plot

A 15 ha (500 m × 300 m) plot was established between May 2010 and October 2011 as a node of the CForBio (Chinese Forest Biodiversity Monitoring Network) with the aim to monitor long-term dynamics in a northern tropical karst seasonal rain forest (hereafter Nonggang plot). To date, this is the largest long-term monitoring forest plot in the karst region of south China (Guo et al., 2017). The plot encompasses a complicated and steep terrain (3.7–78.9°) with elevation ranging from 180 to 370 m above sea level (Fig. 2). All woody stems ≥ 1 cm in diameter at breast height (DBH) in the plot were mapped, measured, identified to species level and tagged. This work was conducted based on the Forestry Standards “Observation