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Investigating distribution pattern of species in a warm-temperate conifer-broadleaved-mixed forest in China for sustainably utilizing forest and soils

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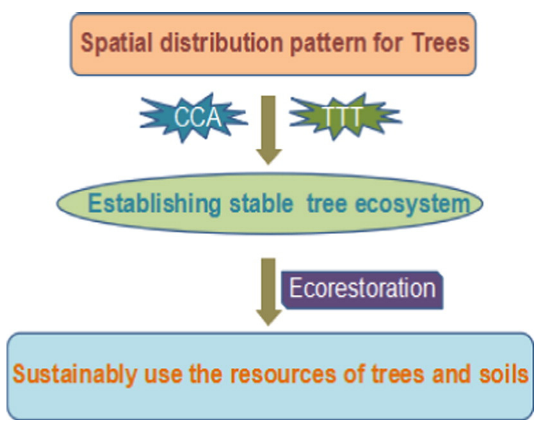
HIGHLIGHTS

- Maintaining mechanisms and ecological processes of species diversity in conifer-broadleaved-mixed forest are far from understanding
- Aggregated distribution is the dominant pattern by CCA and Torus-translation test
- Dispersal limitation and habitat heterogeneity have contributed to regulating the spatial distribution pattern of species in warm-temperate-forest.

GRAPHICAL ABSTRACT



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ABSTRACT

The maintaining mechanisms and potential ecological processes of species diversity in warm temperate- conifer-broadleaved-mixed forest are far from clear understanding. In this paper, the relative neighborhood density Ω was used to analyze the spatial distribution patterns of 34 species with ≥11 individuals in a warm- temperate-conifer-broadleaved-mixed forest, northern China. Then we used canonical correspondence analysis (CCA) and Torus-translation test (TTT) to explain the distribution of observed species. Our results show that aggregated distribution is the dominant pattern in warm-temperate natural forest and four species regular distribution at the spatial scale >30 m. The aggregated percentage and intensity decline with spatial scale, abundance and size classes increasing. Rare species are aggregated more than intermediate and abundant species. These results prove sufficiently the effects existence of scale separation, self-thinning and Janzen-Connell hypothesis. In addition, functional traits (dispersal modes and shade tolerance) also have a significant influence on distribution of species. The results of CCA confirm that slope and convexity are the most important factors affecting the distribution of tree species distribution, elevation and slope of shrub species though the combination of topographic variables only explained 1% of distribution of tree species and 2% of shrub species. Most species don't have habitat preference; however 47.1% (16/34) species including absolutely dominant tree (*Pinus tabulaeformis* and *Quercus*

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wutaishanica) and shrub species (*Rosa xanthina*) and most other species with important value in the front, are strongly positively or negatively associated with at least one habitat. The valley and ridge are most distinct habitat with association of 12 species in the plot. However, high elevation slope with 257 quadrats is the most extensive habitat with only four species. Therefore, there is obvious evidence that habitat heterogeneity play an important role on shaping spatial distribution of species in warm temperate forest. Our research results provide significant evidence that dispersal limitation and habitat heterogeneity have a contribution jointly to regulating the spatial distribution pattern of species in warm-temperate-forest in China.

1. Introduction

Spatial distribution pattern of species in forest is helpful to reveal the formation mechanisms and potential ecological processes of species coexistence (Tuomisto et al., 2003; Wiegand et al., 2007). Aggregated distribution is the dominant pattern in natural forests. The seed for dominant pattern formation is mainly a consequence of many ecological processes, for example habitat heterogeneity, dispersal limitation, competition of intra-species or inter-species, stochastic recruitment, etc. Habitat heterogeneity and dispersal limitation are most profile and preventive among the several different processes (Lin et al., 2011).

Habitat heterogeneity usually affects spatial distribution of species at regional scale in most tropical forests and sub-tropical forests (Harms et al., 2001; Jiangshan et al., 2009; Legendre et al., 2009; Medjibe et al., 2011; Scherrer and Körner, 2011; Shen et al., 2013; Gorman and Turra, 2016), such as topographical factors (Sachot et al., 2003; Yamada et al., 1997) and soil heterogeneity (Tuomisto, 2006). The heterogeneity of topographical variables will influence the species distribution through the preferred habitat of species. Nevertheless, there are some differences in previous results. For example, local habitat association played a limited role in distributions of species, although several species were strongly related to the specific habitats (Harms et al., 2001), but the result of species-habitat associations in a Sri Lankan dipterocarp forest was on the contrary (Gunatilleke et al., 2006). In the Earth system, soils play a key role in controlling biological, erosional, hydrological and geo chemical cycles (Keesstra et al., 2012; Smith et al., 2015; Keesstra et al., 2016). The interaction between soil and plant formed a complex and ever-changing spatial pattern, for example distribution of 36–51% species in three tropical forest was influenced by soil elements (John et al., 2007), and plant spatial distribution was influenced by some soil factors at small scales. In addition, plant can also lead to the soil heterogeneity by changing organic matter circulation and improving microclimate condition at the same time, and the change of soil traits is compatible with the dynamic of plant community and distribution pattern.

Compared with habitat heterogeneity, distribution of species aggregated may have a closed relation to dispersal limitation at local scale (Scherrer and Körner, 2011; Wang et al., 2011). The weaker is more easily gathered and its aggregated intensity is higher than the well-dispersal species (Condit et al., 2000; Wang et al., 2010). Dispersal limitation can affect species diversity strongly (Rosindell and Cornell, 2007), but it still can't provide a good interpretation on pattern of species diversity by oneself. Additionally, Functional traits play an important role on affecting spatial distribution of species in the forests (Condit et al., 2006; Stoll and Newbery, 2005; Wang et al., 2010). However, the potential ecological processes of maintaining species diversity are highly still debated but largely unresolved.

In the past few decades, a large number of substantial researches have been made in studying the underlying mechanisms or processes on spatial distribution, and mainly focus on tropical rain forests (Condit et al., 2000; He et al., 1997; Kubota et al., 2007; Lan et al., 2012; Wiegand et al., 2007) and subtropical forests (Li et al., 2009; Luo et al., 2009), but rarely derived from warm temperate and temperate forests (Piao et al., 2013; Wang et al., 2010). Moreover, there are significant differences among the results. For example, habitat heterogeneity which plays an important role on spatial pattern in tropical (BCI plot at Panama) and subtropical forest (Fushan plot at Taiwan) does not have any effects on spatial pattern of woody plant in temperate Changbaishan plot at Northeast China (Shen et al., 2013). There may be several factors contributing jointly to the variance.

Warm-temperate-forest that owns rich plant resources is one of the main vegetation types in China, and it has distinct regional representative. Because of serious human activity disturbance, there is few remaining natural forest. The Lingkong Mountain (LKS) National Nature Reserve in Shanxi Province is the most typical and representative region of warm temperate deciduous broad-leaved forest in China, and it is known as "the hometown of *Pinus tabulaeformis*", an endemic species in China. The data information from the 4 hm^2 LKS warm temperate forest plot provide a good platform to address what is the dominate pattern of species and the species assemblage maintaining in warm forest. The main objectives of this work are to (1) analyze and explain the spatial pattern of species in the 4 hm^2 warm temperate forest and compare the spatial pattern which have been reported in other forest; (2) to investigate the aggregated intensity of species varies with scale, abundance and different functional groups; (3) to examine whether or not the habitat heterogeneity or dispersal limitation has an influence on distribution pattern of species in plot. It is expected that our analysis provide important insights into understanding species coexistence in warm temperate forests.

2. Materials and methods

2.1. Study site

The area of Lingkong Mountain National Nature Reserve (36°33′–36° 43′N, 111°59′–112°08′E) is located in the middle of Taiyue Mountain, central-south of Shanxi Province, North China. The reserve was established in 1993, promoted to National Nature Reserve in 2013. It is known as "the hometown of *Pinus tabuliformis*" in north China. The region has a warm temperate continental climate with a distinct four seasons. Annual mean temperature in the region is 6.2 °C. Annual mean precipitation is 662 mm, majority of which occurs between July and September.

The 4 hm^2 (200 m × 200 m) plot (36°35′N, 112°05′E) was established in Lingkong Mountain National Nature Reserve in the July and finished the first census in August of 2011, following the standard field protocol of CTFS (Centre for Tropic Forest Sciences, http://www.ctfs.si.edu). The plot is characterized by rugged terrain: altitude varies from 1583.5 m to 1660.2 m, and the mean elevation is 1618.1 m (Fig. 1). The slope ranges from 1° to 45°, and the mean slope in plot is 22.1°.

2.2. Data collection

The plot was divided into 400 10 × 10-m grid,and all free standing trees in these grids were identified, tagged, and mapped. There were 14,765 genotype individuals, belonging to 19 families, 36 genera, and 57 species. According to their growth forms, there are 23 tree species with 5361 individuals DBH (diameter at breast height) ≥1 cm, 33

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