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Density-dependent and distance-dependent effects in a 60-ha tropical mountain rain forest in the Jianfengling mountains, Hainan Island, China: Spatial pattern analysis

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ABSTRACT

To understand the density-dependent and distance-dependent effects on the spatial patterns of trees in tropical mountain rain forest, we used the recent developed O-ring statistic, which is a point pattern analysis method, to explore spatial distribution patterns and spatial associations of trees of different size-classes in a 60-ha tropical mountain rain forest plot in the Jianfengling Nature Reserve, Hainan Island, China. We describe four main findings. (1) As the size-classes of live trees increased, the live trees became more regular. (2) Densities of saplings, small trees, and dead trees tended to decrease with increasing distances, while densities of medium trees, big trees, and old-growth trees initially increased and then decreased at greater distances, showing a skewed inverted *V*-shaped pattern. (3) Densities of saplings, small trees, and medium trees first increased rapidly from 0 m to 5 m to 7 m radius (distance from old-growth trees) and then decreased continuously away from old-growth trees, showing consistent patterns expect from the distance-dependent effect. (4) Mortality was non-random, and dead trees were significantly aggregated with live trees at scales < 2 m, showing clustering of dead (or surviving) trees and clear density dependence where stems with more neighbors had a higher risk of mortality. We concluded that size and spacing effects play important roles in determining spatial distribution patterns of the trees in the Jianfengling tropical mountain rain forest plot.

1. Introduction

Generally, spatial patterns and interactions are expected to be especially important for plants which cannot move (except via births and deaths) and are, therefore, likely to respond directly to their immediate neighborhood (Miriti, 2007; Das et al., 2008; Raventós et al., 2010). Different ecological processes may leave a particular signature on the spatial arrangement of individuals; therefore, studying spatial patterns may help to reveal the importance of underlying mechanisms (McIntire and Fajardo, 2009). At a community scale, spatial patterns of trees are determined by multiple controlling factors, which vary across spatial and temporal scales, related to disturbance (Nagel et al., 2006; Franklin et al., 2007; Yu et al., 2009; Castilla et al., 2012), competition (Stoll and Bergius, 2005; Getzin et al., 2006; Berger et al., 2008; Gray and He, 2009; Das et al., 2011), density-dependent processes (He and Duncan, 2000; Gray and He, 2009; Yu et al., 2009; Chen et al., 2010; Comita et al., 2010; Lin et al., 2012), dispersal limitation (Albani et al., 2005; Hu et al., 2012; Shen et al., 2013), etc. Among those factors, density-dependent and distance-dependent effects have been commonly studied in specific species, and, in most cases, the tree species studied were dominant species (He and Duncan, 2000; Getzin et al., 2006; Gray and He, 2009; Yu et al., 2009; Hu et al., 2012). However, in tropical forests, where there are many tree species with few or no obvious dominant species, density-dependent and distance-dependent effects remain unclear. Current research has emphasized general distance-dependent effects and density-dependent effects of large-size trees on seeds and/or seedlings (Harms et al., 2000; Getzin et al., 2008; Fajardo and McIntire, 2011; Lin et al., 2012). Those results are discussed in light of seeds and seedling ecology, especially with regard to seedling and sapling gap-dependence, which likely has affected the recruitment of juvenile trees, and, therefore, the spatial patterns of the resultant older trees. However, there are few studies on distance-dependent effects and

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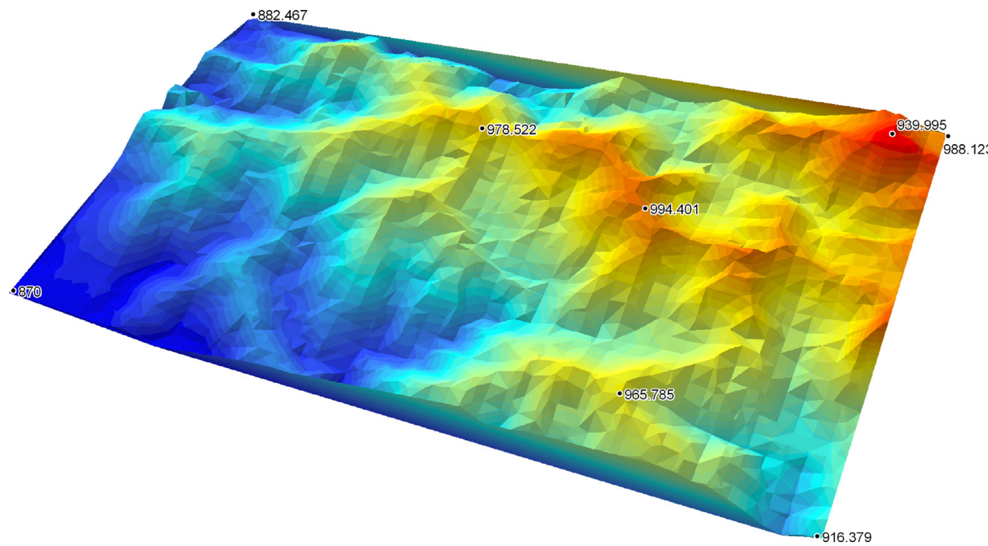

Fig. 1. Topographical image of the 60 ha tropical mountain rain forest plot in the Jianfengling Nature Reserve.

density-dependent effects across multiple life stages (Zhu et al., 2015, 2018).

Tropical forests play an important role in conserving global biodiversity and maintaining the functions of the earth's ecosystems (Deng et al., 2008). The Jianfengling Mountains, located in southwestern Hainan Island, is one of few areas in China where there are well-protected primary tropical forest. The mountain rain forest in the Jianfengling Mountains corresponds to subtropical/warm-temperate zones. Floristically, subtropical/warm-temperate elements dominated, especially Fagaceae and Lauraceae, while tropical elements were subordinate. Plant species richness in the Jianfengling mountain rain forest was lower than in typical Indo-Malayan tropical rain forests but somewhat higher than dry tropical forests with low rainfall. Thus, the Jianfengling mountain rain forest is a transitional forest type from tropical to subtropical/warm-temperate rain forests (Fang et al., 2004).

In this study, we used spatial pattern analysis to reveal spatial distribution patterns and spatial associations of different tree size-classes in a 60-ha plot in the tropical mountain rain forest of Hainan Island, China. Our analyses are guided by the following hypotheses. First, increasing size-classes will be expected to show more regular patterns. With the increasing of size-classes, stems in a natural primary stand should show more regular spatial patterns at small scales, due to thinning caused by competition (Kenkel, 1988; Barot et al., 1999; Getzin et al., 2006; Li et al., 2009; Wang et al., 2010; Guo et al., 2013) (analysis 1). Second, smaller trees are positively associated with large dead trees. In general, mortality is higher for trees at higher densities and for smaller sized trees, regardless of the relative species mix. Large dead trees showed positive associations with juveniles (Franklin et al., 2002; Salas et al., 2006). Saplings were significantly aggregated and positively correlated with dead trees, which suggests that regeneration mostly occurred in canopy gaps (Wolf, 2005). Therefore, we hypothesized that saplings and small trees will show aggregative patterns with large dead trees (analysis 2). Third, for the distance-dependent hypothesis (Hu et al., 2012; Miao et al., 2014), we tested the distance-dependence effect by sizes (~age). Because independence may indeed be a good approximation in the limit of very species-rich communities (Wiegand et al., 2012), we hypothesize that young individuals are expected to show higher densities within close proximity to (i.e., under the canopy of) old-growth trees. However, beyond the canopy of old-growth trees, we would expect to see a typical gradual decline with distance as a result of distance-dependence effect (analysis 3). Fourth, for the random mortality hypothesis (Kenkel, 1988; He and Duncan, 2000; Getzin et al., 2006; Yu et al., 2009), we expect that dead trees are more clumped than expected under random mortality. Additionally, we expect mortality to be spatially correlated in a density-dependent way where stems located in areas of higher stem density have a higher mortality (analysis 4). Our findings may contribute to the conservation and management of the ecosystem and biodiversity of the tropical mountain rain forests over their historical range in China.

2. Materials and methods

2.1. Data collection

We conducted this study in the 60-ha (1000 m × 600 m) Jianfengling montane rain forest plot located in the Jianfengling Nature Reserve, Ledong County, Hainan province, South China, with latitude N 18.73079° and longitude E 108.90491°. This tropical mountain rain forest is located at the northern edge of the Indo-Malayan rain forest, and has relatively distinct species composition and community structure from typical Asian tropical forests. This forest plot was established in 2011, and the first census was completed in 2012. At the time, this plot was established, it was the largest plot and had the highest number of tree stems by one census (in 2012) of all large-scale permanent plots recorded by the Center for Tropical Forest Science (CTFS) of the Smithsonian Tropical Research Institute (http://www.ctfs.si.edu) (Xu et al., 2015a).

The elevation of the Jianfengling plot ranges from 866.3 m to 1016.7 m above sea level and includes valleys and a low mountain peak. Slopes vary from 1.74° to 49.25° at the 20 m × 20 m spatial scale (Fig. 1). The climate is strongly seasonal with distinct alternations between the dry season (November 1–April 30) and the wet season (May 1–October 31), as this area is situated at the north edge of the tropics and has a typical monsoon climate. The National Forest Ecosystem Research Station's meteorological station in the Jianfengling Mountains was just 4 km from the Jianfengling study plot and at a similar elevation (893 m). Based on the records at the meteorological station from 1980 to 2005, the annual precipitation (rain fall) in this montane rain forest varied from 1305 mm to 3686 mm with an annual average of 2449.0 mm. The precipitation fell mainly in the wet season, which accounts for an average of 86.7% of the entire annual precipitation (Zhou et al., 2013). The annual average temperature was 19.8 °C from 1980 to 2005, with the coldest and warmest monthly average temperatures being 10.8 °C and 27.5 °C, respectively. The Jianfengling Mountains is one of the areas with highest biodiversity in China. The total number of plant species in the Jianfengling area is 2849, consisting of 1250 genera from 244 families, including 562 alien species (Li et al., 2012).

All free-standing tree stems ≥1 cm diameter at breast height (DBH)