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Relative importance of density dependence and topography on tree mortality in a subtropical mountain forest

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ABSTRACT

Tree mortality is an important process in forest dynamics, and potentially affects species coexistence and community assembly. Detecting spatial pattern of tree mortality and examining the possible driving factors are critical to understand the determinants of tree death. In 2015, we conducted a census of snags (with dbh ⩾ 10 cm) of woody plants in the 25-ha Badagongshan (BDGS) forest dynamics plot. Based on this survey data, we used the univariate, bivariate pair correlation function, g(r), to analyze the spatial distribution pattern of snags and the association between snags and living trees. In addition, we used generalized linear mixed models (GLMM) to examine the relative importance of neighbor and topographical factors on tree mortality. Analyses demonstrated two main results. First, at the community level, snags showed a consistent aggregated distribution at 0–30 m scales, and snags and living trees were significantly negatively correlated at 1–12 m scales. At the species level, 10 of the 18 common species (with ⩾25 snag individuals) displayed significant negative associations between living trees and snags at different scales in the 0–50 m range. Second, both basal area of conspecific neighbors and basal area of heterospecific neighbors showed a significant positive relationship on the occurrence of snags at different levels (community, guild and species). Topographic factors showed limited correlations with the occurrence of snags. Additionally, tree size was significantly negatively correlated with adult and large tree mortality, but non-significantly correlated with old trees. In summary, tree mortality is nonrandom and mainly driven by interspecific competition and intraspecific negative density dependence in this subtropical mountain evergreen and deciduous broad-leaved mixed forest in China. Topographic conditions had little relation on tree mortality, but tree size was an important predictor of tree death at the community level. Our study demonstrates that interactions of species tended to be more important in affecting tree mortality than habitat variables in this forest, which can further improve our understanding of forest dynamics and provide guidance to forest management.

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1. Introduction

Tree mortality is one of the critical processes in forest dynamics (Franklin et al., 1987). It can influence the pathways of succession and the composition of forest communities (Shugart, 1987), create gaps for regeneration (Canham et al., 2001), alter carbon and nutrient cycling, and enhance tree species coexistence (Runkle, 2000; Lutz and Halpern, 2006). A proper understanding of the spatial patterns and drivers of tree mortality may help us to predict forest dynamics precisely (Wang et al., 2012). However, tree mortality is in general not as well understood as tree growth (Luo and Chen, 2011). For instance, does tree mortality occur randomly in forests? And what factors strongly influence tree mortality? There are no consistent and clear answers to these basic questions.

Tree mortality is generally affected by many factors, especially the local neighborhood conditions including biotic and abiotic variables (Wang et al., 2012). In communities, tree mortality was observed to be higher where conspecific neighbors were denser or closer (Zhao et al., 2006; Castagneri et al., 2010). This phenomenon was known as negative conspecific density dependence, which was commonly recognized as a major mechanism of species coexistence and community assembly (Volkov et al., 2005). However, some studies demonstrated that competitive density-dependent mortality ceased to play an important role for large trees because of their widely spaced distribution and permissive understory regeneration (Franklin et al., 2002). Aakala et al.

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(2012) found that mature tree mortality was essentially a random process in old-growth red pine forests. Stronger evidence for density-dependent mortality in old-growth forests was evidenced through analysis of the spatial patterns of tree mortality (He and Duncan, 2000; Getzin et al., 2006; Lutz et al., 2014).

On the other hand, the abiotic local micro-environment also affects tree mortality. Trees located in their preferred habitat were more abundant and larger than when located in other habitats (Hubbell and Foster, 1983; Tilman and Pacala, 1993), and tree mortality was higher when species were located in an adverse habitat (Wang et al., 2012). Studies suggested that topography (i.e. elevation, slope, aspect and convexity) was one of the most important habitat factors, because it affected the distribution of soil nutrients, light and precipitation and thus influenced the spatial patterns of species, tree growth and mortality (Bellingham and Tanner, 2000; John et al., 2007; Zhang et al., 2011).

Tree mortality is not only affected by local neighborhood conditions, but also be correlated to its intrinsic attributes. Tree size is one of the important intrinsic attributes of trees, and many studies have shown that it strongly influences tree death. Ganey and Vojta (2011) found that tree mortality was nonrandom with respect to tree size classes. Recently, metabolic ecology theory suggested that tree mortality decreased with tree size on the assumption that different size classes gained and used the same amount of energy, and large trees had asymmetric advantage in the competition of resource over small trees (Brown et al., 2004; Coomes, 2006). However, other studies found that tree mortality lost the negative association with tree size for very large trees (Coomes and Allen, 2007; Lines et al., 2010; Wang et al., 2012). Therefore, there is no consensus on the association between tree size and tree mortality.

Snags are the most common result of tree mortality in forests, so the analysis of snags can help reveal characteristics of tree mortality in forest systems (Ganey and Vojta, 2011). Detecting the spatial pattern of snags and driving factors of tree death will increase our understanding of factors controlling tree mortality, laws of population dynamics, and mechanisms of species coexistence. In this study, we used the univariate, bivariate pair correlation function, g(r), to analyze the spatial distribution pattern of snags and the association between snags and living trees for trees whose diameter at breast height (DBH) exceeded 10 cm. The effect of neighbor and topographic variables on the occurrence of snags were examined with generalized linear mixed models. We aimed to address the following questions: (1) Is tree mortality spatially nonrandom in this subtropical forest? (2) Is density-dependent tree mortality evident for adult or larger trees? (3) How does tree size relate to tree mortality spatial patterns? (4) Which is more strongly related to tree mortality, neighbor effects or topographic variables?

2. Methods

2.1. Study sites

The study site is located in Badagongshan (BDGS) National Nature Reserve (29°46.041′ N, 110°5.248′ E) in central China, northern Wuling Mountains, at the northern boundary of the mid-subtropical zone. Annual mean rainy days and frost-free days are 170 and 220, respectively. Annual precipitation averages 2105.4 mm, up to 2840.1 mm, comparable to tropical rain forest. Mean monthly temperature ranges from 0.1 °C in January to 22.8 °C in July with an annual mean of 11.5 °C. The topography is characterized by deep valleys, steep slopes and flat hilltops; main soil types are yellow soil and yellow-brown soil (Wang et al., 2014). The common vegetation type in the region is evergreen and deciduous broad-leaved mixed forest, dominated by *Cyclobalanopsis multinervis* and *Fagus lucida*. Other important species include *Cyclobalanopsis gracilis*, *Quercus serrata* var. *brevipetiolata*, *Schima parviflora*, *Carpinus fargesii*, *Sassafras tzumu*, *Litsea elongata* and *Rhododendron stamineum* (Lu et al., 2013; Wang et al., 2014).

2.2. Data collection

A 25-ha (500 m × 500 m) permanent forest plot was established in 2011 in the Badagongshan National Nature Reserve. Elevations in the plot range from 1355 m to 1456 m above mean sea level. All living and dead trees ⩾1 cm dbh (diameter at breast height; 1.3 m above the forest floor) were tagged, measured, identified to species, and mapped following standard field protocol (Condit, 1998). According to the 2010–2011 census, the plot had 186,556 individuals belonging to 53 families, 114 genera, and 238 species (94 evergreen and 144 deciduous) (Guo et al., 2013). Among all the individuals, there were 25,499 individuals with dbh exceed 10 cm. However, most of the dead trees were not identified to species in the 2010–2011 census. In the summer of 2015, we conducted a census of the snags (dbh ⩾ 10 cm) of woody plants in the entire plot. This census includes species name, dbh, height and decay class, as well as geographic coordinates. The total number of the snags in the census was 2569, and these individuals belong to 34 families, 54 genera and 79 species (27 individuals only identified to genus, 13 individuals unknown).

2.3. Neighbor variables

To quantify local neighbor density effects, we calculated basal area of conspecific (ConBa) and heterospecific (HetBa) neighbors ⩾10 cm dbh within a 20-m radius of each focal tree, divided by the distance between the neighbor tree and the center of the focal tree, and summed for all individuals:

$$\text{Ba} = \sum_{i}^{n}(\text{Ba}_i/\text{Distance}_i),$$

where *i* is a living tree or snag. A 20-m radius was selected as it had the lowest Akaike's information criteria (AIC) value based on preliminary analyses comparing models with 5-, 10-, 15- and 20-m radii (Table A1).

2.4. Topographic variables

Elevation, slope, convexity and aspect of every 5 m × 5 m grid were used as topographic variables. Elevation was measured at the corner of each 20 m × 20 m quadrat in the 25 ha plot. Elevation values for these 20 m × 20 m quadrats were interpolated to calculate the elevation of the corners of the 5 m × 5 m grid. Slope, convexity and aspect values were then calculated for each grid. Convexity was the elevation of the grid of interest minus the mean elevation of the eight surrounding plots. For the edge grids, convexity was the elevation of the centre point minus the mean of the four corners (Legendre et al., 2009). Aspect was the direction in which a slope faced. Aspect is a circular variable; sin(Aspect) and cos(Aspect) were computed before data analysis to provide linear predictors. Slope was not included because it was highly correlated with elevation (Pearson correlation coefficient = 0.893, Table A2).

2.5. Data analysis

2.5.1. Tree mortality pattern analysis

We used the univariate and bivariate pair correlation function, g (r), to examine the spatial patterns of snags and the relationship

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