



Conspecific and phylogenetic density-dependent survival differs across life stages in two temperate old-growth forests in Northeast China

Xucai Pu, Guangze Jin*

Center for Ecological Research, Northeast Forestry University, Harbin 150040, China



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ABSTRACT

Factors that control individual survival dynamics are pivotal determinants of forest diversity. Numerous studies have examined the relative importance of habitat variables and neighborhood effects on individual survival, while few studies have examined this importance in different forest types that largely vary topography. We examined the role of conspecific negative density dependence (CNDD), phylogenetic negative density dependence (PNDD) and habitat variables across life stages in two temperate old-growth forests in Northeast China. Using generalized linear mixed models (GLMMs), we tested whether individual survival is related to neighborhood effects and habitat variables. Our results showed that the relative importance of neighborhood effects and habitat variables to focal individual survival varied among life stages and sites. However, the best-fit models for three life stages (with the exception of seedling stage in the BKPF) at both sites all included habitat variables, indicating that these variables contribute to the patterns of focal individual survival. We found evidence of a CNDD effect, and the strength of this effect decreased as the life stages progressed and varied from a negative effect at the seedling stage to a positive one at the adult stage. This result confirms that the importance of CNDD-based survival at the seedling stage plays a particularly significant role in promoting the coexistence of tree species and maintaining forest diversity. We found evidence of PNDD in our forest, and the impact of hetero-specific phylogenetic relatedness on focal individual survival was significantly negative; the strength of PNDD increased as the life stages progressed. The CNDD and PNDD widely varied among species, indicating the importance of including the relative abundance, life history strategies and functional traits of species when determining the factors that affect species sensitivity to neighborhood effects. The results of our study demonstrated that CNDD, PNDD and habitat variables all influence the individual survival of these temperate old-growth forests, but the relative importance of these factors vary among life stages and species. Our results highlight the importance of combining multiple species, life stages, functional traits and large-scale studies for investigating elements that affect species coexistence in tree communities.

1. Introduction

How species coexist locally is a fundamental question in community ecology, and answering this question has long been a challenge for ecologists. Traditional experiments have focused on resource-niche partitioning. However, all plant species depend mainly on similar resources for growth, and multiple mechanisms can simultaneously foster plant communities; thus, resource-niche partitioning may not be the only mechanism that maintains species coexistence (Schoener, 1974; Chesson, 2000; Comita et al., 2014). Another important mechanism underlying the maintenance of species diversity relates to the Janzen-Connell hypothesis (JCH), which focuses on biotic neighborhood interactions. This hypothesis is that species diversity is promoted by host-specific enemies, such as pathogens and herbivores, and is called

negative density dependence (NDD) (Janzen, 1970; Connell, 1971).

NDD may be expanded to both conspecific negative density dependence (CNDD) of conspecific neighborhoods and phylogenetic negative density dependence (PNDD) of heterospecific neighborhoods. Conspecific neighbors usually exhibit strong intraspecific competition for resources and strong indirect effects of host-specific enemies, so an individual will have increased mortality when they are surrounded by more conspecific neighbors or when they are near conspecific neighbors, and therefore providing more space for other species to grow and survive (Queenborough et al., 2007; Comita and Hubbell, 2009; Comita et al., 2010; Johnson and Clay, 2012; Lin et al., 2012; Zhu et al., 2015). Phylogenetic relatedness of heterospecific neighbors also influences tree performance; therefore, the phylogenetic relatedness of heterospecific neighbors to focal individuals represents another important

* Corresponding author.

E-mail address: taxus@126.com (G. Jin).

biotic neighborhood effect. However, results of this nature are conflicted and remain under debate (Webb et al., 2006; Metz et al., 2010; Uriarte et al., 2010; Lebrija-Trejos et al., 2014; Wu et al., 2016).

The relative importance of CNDD and PNDD may shift throughout the lifetime of a tree (Hubbell, 2001; Newbery and Stoll, 2013; Piao et al., 2013; Zhu et al., 2015; Chen et al., 2017). Numerous studies have found that, compared with that at adult stages, CNDD is evident at early life stages because of high original densities resulting from seed dispersal limitations, combined with higher sensitivity of seedlings to natural enemies (Gilbert et al., 1994; Harms et al., 2000; Nathan and Muller-Landau, 2000; Zhu et al., 2015). Conspecific neighbor densities may be thinned at early stages as the strength of CNDD is strong, in part because of more intense competition for light, water and soil nutrients between conspecific neighbors than between heterospecific neighbors at later life stages. Therefore, examining the degree to which these two interactions function during the assembly of plant communities requires multiple life stages.

Community-level studies have shown that the patterns of CNDD and PNDD are prevalent in plant communities, but the strength of these effects varies widely among species, as the different attributes of species result from differences in life history strategies, such as leaf habit and dispersal mode (Coley and Barone, 1996; Clark et al., 2005; Comita and Hubbell, 2009; Comita et al., 2014; Zhu et al., 2018). Furthermore, recent studies have reported that the effect of CNDD is related to species abundance, demonstrating that the susceptibility to conspecific neighbors and the enemies specialized extent of a species truly affects species abundance in plant communities; however, the variation among species of heterospecific neighbors was unrelated to species abundance or much less than the variation of between conspecific neighbors (Comita et al., 2010; Johnson and Clay, 2012; Wang et al., 2012; Zhu et al., 2015; Lamanna et al., 2016). If more phylogenetically similar species have stronger impacts on focal individuals, and if the variation in phylogenetic neighbor effects among species are widespread, then the strength of PNDD may affect the spatial distribution and relative abundance of species within plant communities (Zhu et al., 2015). Therefore, it is essential to examine phylogenetic relatedness when determining variation in heterospecific neighborhood effects (Zhu et al., 2015; Chen et al., 2016; Wu et al., 2016; Chen et al., 2017; Zhu et al., 2017b).

The relative importance of biotic neighborhoods and habitat variables also plays an important role in understanding the diversity of natural plant communities (Chen et al., 2010; Pu et al., 2017; Wu et al., 2017; Zhu et al., 2017a). Abiotic factors such as topography and soil properties can influence light conditions, pH, nutrient availability and soil moisture, creating conditions that may favor some species over others (Messaoud and Houle, 2006; Russo et al., 2007; Wang et al., 2012; Johnson et al., 2014). Therefore, habitat variables should be considered when examining local species distributions as well as the relative importance of density dependence and niche partitioning in natural communities (Zhang et al., 2011; Metz, 2012; Piao et al., 2013; Johnson et al., 2014). Furthermore, habitat variables may contribute to individual survival more in a habitat that varies widely than in a habitat that varies little. Although numerous studies have examined the relative importance of habitat variables and neighborhood effects on individual survival, few studies have compared this importance in different forest types whose topography widely varies.

Therefore, to improve our understanding of the factors that affect community dynamics, we compared the effects of neighborhood and habitat variables on individual survival for multiple species across three life stages in two temperate old-growth forests that differ mainly in topography: a typical mixed broadleaved-Korean pine (*Pinus koraiensis*) forest (BKPF), whose elevation ranged from 425 to 509 m, and a spruce-fir valley forest (SPVF), whose elevation varied little (346–352 m). We expected that habitat variables might play a more important role than neighborhood effects in individual survival in the BKPF than in the SPVF. We mainly address the following questions: (1) What is the

relative importance of neighborhood effects and habitat variables in our study, and does this importance differ between the two forest types? (2) Does the relative importance of CNDD and PNDD vary across life stages (seedling, sapling and adult)? Finally, (3) how widely does the sensitivity of species to CNDD and PNDD vary?

2. Methods

2.1. Study site

The study site is located in the Heilongjiang Liangshui National Natural Reserve (47°10'50"N, 128°53'20"E), in the Xiaoxing'an Mountains of Northeast China. The elevation of the study site ranges from 280 m above sea level (a.s.l.) to 707 m a.s.l. The soils are classified as dark brown forest soils; the mean annual surface soil temperature is 1.2 °C, and there are 100–120 frost-free days. The mean annual temperature is −0.3 °C; the mean daily maximum temperature is 7.5 °C, and the mean daily minimum temperature of −6.6 °C. The mean annual precipitation is 676 mm, and the mean total evaporation is 805 mm.

A 9-ha (300 m × 300 m) dynamic forest plot in a typical mixed BKPF and a 9.12-ha (380 m × 240 m) dynamic forest plot in a SPVF were established in 2005 and 2006, respectively. The structure and composition of the BKPF is similar to those of the typical mature forests in this region, and the main canopy species of the BKPF include *Pinus koraiensis*, *Tilia amurensis*, *Tilia mandshurica*, *Betula costata*, *Abies nephrolepis*, *Fraxinus mandshurica* and *Acer mono* (Liu et al., 2014); moreover, topographic and edaphic factors strongly influence the species composition and numbers. The structure and composition of the SPVF is similar to those of typical mature forests in the valley of this region, the temperature is low, while the humidity is high. Furthermore, the thermal inversion layer and insular permafrost are evident. The dominant species include *Abies nephrolepis* and *Picea koraiensis*, but *Pinus koraiensis* and some broad-leaved species are also associated. The local drainage is poor, and the natural aging of *Abies nephrolepis* and *Picea koraiensis* occurs relatively quickly; therefore, the trees within the SPVF died largely from various factors. All woody stems with a diameter at breast height (DBH) ≥ 2 cm in the plots were mapped, measured, tagged and identified to the species level in 2005 and 2006 in the BKPF and SPVF, respectively. Censuses were carried out every five years, and after the first census, we included all woody stems whose DBH ≥ 1 cm (hereafter, large trees). The large trees were grouped by maximum attainable height into five growth forms: shrub (S; height ≤ 5 m), small understory tree (US; height 5 to ≤ 10 m), large understory tree (UL; height 10 to ≤ 20 m), small canopy tree (CS; height 20 to ≤ 30 m) and large canopy tree (CL; height > 30 m) species. In turn, each growth form was divided into two DBH size classes to define the life stages for large trees: sapling and adult stages (Piao et al., 2013; Table 1).

Totals of 900 and 912 seedling quadrats (each 2 m × 2 m in size) were established in a regular pattern in the corner of each 10-m × 10-m subplot in the 9-ha BKPF in 2006 and in the 9.12-ha SPVF in 2007, respectively. In each of the seedling quadrats, all woody seedlings that had a DBH < 1 cm and a height (H) ≥ 30 cm were tagged, identified to

Table 1

Life stage classifications based on DBH (cm) for large trees of different growth forms: shrubs (S), small understory tree species (US), large understory tree species (UL), small canopy tree species (CS), and large canopy tree species (CL). Seedlings were DBH < 1.0 cm and H ≥ 10 cm.

Life stage	S	US	UL	CS	CL
Seedling	< 1.0	< 1.0	< 1.0	< 1.0	< 1.0
Sapling	1.0–1.5	1.0–2.0	1.0–2.5	1.0–5.0	1.0–8.0
Adult	> 1.5	> 2.0	> 2.5	> 5.0	> 8.0

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