



From young to adult trees: How spatial patterns of plants with different life strategies change during age development in an old-growth Korean pine-broadleaved forest



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ARTICLE INFO

Keywords:

Point pattern
Recruits
Old-growth
Life strategy
Korean pine
Temperate forest

ABSTRACT

We used point pattern analysis (pair-correlation function, K_2 function, distance to k th neighbor D_k , and spherical contact distribution function H_s) to describe the process of plant pattern formation for five dominant tree species with different life strategies in a mixed-forest stand with Korean pine (*Pinus koraiensis* Sieb. et. Zucc.) in the southern part of the Sikhote-Alin mountain range (southeastern Russia). We subdivided each species pattern using an ontogenetic classification of individuals: immature, virginal, and generative. We also analyzed stump pattern structure, which marks canopy gap formation locations in recent decades. We also studied the shade tolerance changes of pre-generative plants during their development. As a result, we found similarities between the processes of pattern transformation for the different species. Namely, they transform from pronounced aggregated distributions of plants at several spatial scales (immature plants) to a random pattern (middle-aged and old generative plants). This transformation of pattern structure occurs because the immature plants accumulate under a canopy and require significantly improved light conditions that can only be found in gaps to transition into the virginal and young-generative stage. In turn, the process of gap formation is stochastic, and the stand is characterized by a low-intensity disturbance regime. Thus, the pre-generative plant patterns are filtered by randomly formed gaps, and thus only individual randomly distributed plants reach the middle-aged and old generative ontogenetic states.

1. Introduction

The study of spatial and temporal patterns of plants is crucially important for solving a wide range of ecological problems connected to community dynamics, the coexistence of species and biodiversity maintenance (e.g., Chesson, 2000; Wright, 2002; Brown et al., 2011; May et al., 2015). Community spatial pattern is the result of plant interactions with each other and the environment (e.g., Harms et al., 2001; John et al., 2007; Lai et al., 2009; Zhang et al., 2010a, 2010b). However, it also presents the peculiarities linked to species life-strategies such as seed spreading strategies and the maximal distance of their distribution, shade-tolerance, plant lifetimes, and sizes (Brzeziecki and Kienast, 1994; East-European Forests (Russia), 2004). By studying the spatial pattern of the species in a stand, we can better understand its life-strategy traits (Seidler and Plotkin, 2006; Jara-Guerrero et al.,

2015). Comparisons of the features of different species' patterns provide clues for understanding how life strategy features are expressed and thus which life-strategy traits differ and which are similar. Finally, considering the formation of different species' patterns all together, we can make conclusions regarding the formation of community spatial structures.

The processes leading to some kinds of patterns differ in duration depending on plant lifetime and development peculiarities. The formation of patterns by trees may last up to hundreds or even thousands of years (Smirnova, 2004). These patterns consist of plants that substantially differ in size, age and stages of development (Smirnova and Bobrovskii, 2001). Thus, for a meaningful analysis, we should divide tree patterns into functionally similar components, which is usually done by their heights (Hao et al., 2007), diameters (Liu et al., 2014; Punchi-Manage et al., 2014) or ages (Garcia-Cervigon et al., 2017). The

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<https://doi.org/10.1016/j.foreco.2018.01.023>

Received 18 September 2017; Received in revised form 11 January 2018; Accepted 13 January 2018
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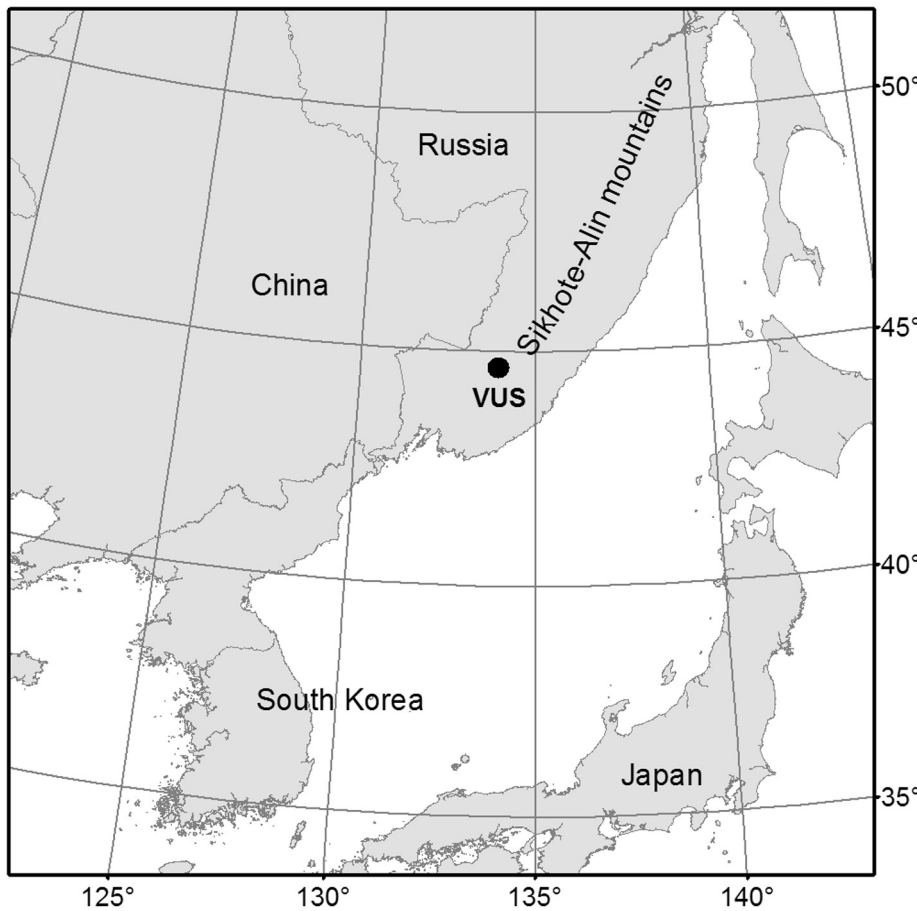


Fig. 1. Location of the study area on the Sikhote-Alin Mountains, South-Eastern Russia. VUS is Verkhneussyriysky Research Station of the FSC of Terrestrial Biodiversity FEB RAS.

Table 1
Characteristics of the dominant tree species.

Species	H _{max} (m)	DBH _{max} (cm)	A _{max} (years)	Shade tolerance	Life strategy
<i>Abies nephrolepis</i>	25	50	214	Shade tolerant	R-C
<i>Betula costata</i>	30	100	340	Light-demanding	R-C
<i>Picea jezoensis</i>	35	110	317	Shade-tolerant	C-S-R
<i>Pinus koraiensis</i>	42	150	527	Shade-tolerant	C
<i>Tilia amurensis</i>	30	100	250	Mid-tolerant	R-C

Note: H_{max} – maximum tree height (Usenko, 1968); DBH_{max} – maximum tree diameter at 1.3 m height (Usenko, 1968); A_{max} – maximum age (Petrenko et al., 2016; Omelko et al., 2016; Ukhvatkina and Omelko, 2016; Ukhvatkina et al., 2017). Life strategy (Grime 1979). Shade tolerance (Usenko 1968). Note that Wang et al. (2010) consider *T. amurensis* as shade-tolerant and *P. koraiensis* as a mid-tolerant species. In our opinion, such differences may be due to differences in the methods of determining shade tolerance.

concept of discrete descriptions of plant ontogenesis is promising for that purpose. In that concept, the populations of each species consist of sets of individuals at different stages of ontogeny development (East-European Forests (Russia), 2004). A similar approach is used to divide the individuals of populations when developing stage-structured matrix models (Caswell, 2001). The special feature of this approach is that although the individuals may differ in size and absolute age, they are at the same stage of ontogenetic development and play a similar role in a stand (Smirnova and Bobrovskii, 2001; Evstigneev and Korotkov, 2016). Using that concept, we can divide the population of any species into functionally homogeneous components – sets of plants at the same

stage of ontogenetic development (East-European Forests (Russia), 2004) which, therefore, are under the influence of similar factors. Each of those components presents a certain stage of the stand dynamics. The pattern of such stages can be regarded as a snapshot of the process structuring the formation. By analyzing the snapshot, we can describe how it proceeds.

The object of our research are the Korean pine-broadleaved forests situated in north-eastern Asia, which are remnants of the Turgai flora that once existed across the entire territory of Eurasia (Krestov, 2003). These forests cover the southern part of the Russian Far-East, the north-eastern part of China, and parts of the Korean peninsula and Japanese islands (Krestov, 2003). The scarce land development in the Russian territory has contributed to the preservation of old-growth stands as well as unique sites that have not experienced human impacts and fires in the past 1500–2000 years (Omelko et al., 2016).

However, information on the structure and dynamics of those forests is fragmentary. The sparse materials presented in the literature on species ecological peculiarities (Usenko, 1968; Ishikawa et al., 1999; Orekhova, 2005; Komarova, 1986; Komarova and Trofimova, 2010; Komarova et al., 2010; Ukhvatkina et al., 2010) cannot fully characterize life strategy traits and the process of forest dynamics. Studies of mixed broadleaved-Korean pine forests conducted in north-eastern China (Zhang et al., 2008; Zhang et al., 2010a, 2010b; Wang et al., 2010; Liu et al., 2014) also cannot present a complete picture because of the considerable variability in climatic conditions and land development history; the described forests differ greatly from those studied in the stand structures and dominant species list.

For the detailed analysis of the patterns structure, it is necessary to use several summary statistics (Illian et al., 2008; Wiegand et al., 2013). These allow discerning whether the aggregation of plants was really due to plant-plant (i.e., interacting through their crowns or root

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