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Intra- and interspecific interactions of Scots pine and European beech in mixed secondary forests

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A B S T R A C T

By the mid successional stages, secondary forests of Scots pine in Europe are dominated by mixed stands of pioneer Scots pine and late-successional European beech. The objective of this study was to explore the interactions of pine and beech with their conspecific and heterospecific neighbours in these forests. To accomplish the objective, pine and beech trees were stem-mapped in forty 500 m^2 plots randomly located within 18 mixed stands in Milomlyn Forest District, northern Poland. The interactions within and between the species were analysed through two structurally different univariate and bivariate second-order summary statistics, i.e. pair correlation function $g(r)$ and mark correlation function $k_{mm}(r)$. Field measurements showed that the overstorey was dominated by even-aged pine, whereas uneven-aged beech was the only species in the understorey. Pine trees presented an aggregation, while beech trees exhibited a dispersed structure in all stands. In addition, pine trees showed strong attraction to beech trees at small spatial scales (0–2 m). Negative correlation was found between tree height and diameter at breast height of beech, while there was no correlation between height and diameter of pine trees. We conclude that pine trees exhibit negative intraspecific interactions at small spatial scales that are mostly driven by their competitive interactions. Beech trees show strong positive intraspecific interactions and form clumps within pine canopy cover. The strong positive interspecific interactions of pine and beech are the outcome of their different shade tolerance. Our results help to explain successful coexistence of pine and beech in the study site and highlight detailed tree-tree interactions of the species in mixed stands.

1. Introduction

Characterisation of the spatial distribution of tree species within forest stands is one of the key aspects of forest ecology theory that receives increasing attention in recent years. The arrangement of trees gives forest ecologists significant information about inter- and intraspecific interactions of tree species, with important consequences for both forest dynamics and management (Greig-Smith, 1983; Dale, 2000; Getzin et al., 2006; Miao et al., 2014). Furthermore, it carries information about the ecological processes which operated in the past and the processes which will take place in the future since a number of these ecological processes such as competition, facilitation, mortality, and dispersal tend to follow specific types of spatial patterns in a forest stand (Cale et al., 1989; Stoyan and Penttinen, 2000; Law et al., 2009). These ecological relationships and processes are also key drivers that markedly affect forest structure and functioning that should be considered when developing efficient guidelines for their conservation and management (Batista and Maguire, 1998; Pommerening, 2002).

It is well known that tree species are not randomly distributed in forest ecosystems due to the influence of processes such as environmental heterogeneity, dispersion of seeds, and uneven age distribution; which cause trees to be often spatially dispersed or aggregated at one or multiple spatial scales (He et al., 1997; Rayburn et al., 2011). The spatial distribution of trees may be influenced by biotic (e.g., competitive and facilitative relationships of species) and abiotic (e.g., soil moisture, nutrient availability, light) factors during stand development (Wiegand et al., 2003; McIntire and Fajardo, 2009). For instance, competition between and within species can lead to mortality and decrease in growth of

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trees located close to each other and cause a significant repulsion among individuals (Hou et al., 2004; Martinez et al., 2010; Wang et al., 2015). In contrast, species that coexist due to their facilitative interactions with other species, usually present aggregated spatial patterns. In general, spatial arrangement of trees influenced by biotic processes (e.g., competition and facilitation) may reflect the interspecific interactions between two or more species or intraspecific interactions between different cohorts of the same species (Baumeister and Callaway, 2006; Moustakas et al., 2008). On the other hand, spatial distribution of trees can also be influenced by abiotic factors. Previous studies showed that soil properties or availability of resources in some parts of a site may be responsible for non-random spatial distribution of plants (Sher et al., 2010). In general, the same species growing under different environmental conditions may present completely different spatial patterns due to spatial availability of resources (Kearns et al., 2003; Law et al., 2009). Previous studies have revealed the scale-dependency of spatial distribution of plants and different biotic and abiotic factors (Sher et al., 2010; Benot et al., 2013). Therefore, assessment of spatial patterns of tree species as one of the scale-dependent structural components of a stand may quantify its hierarchies of vertical and horizontal structures. Moreover, scale-dependent analysis of spatial patterns in forest stands is able to reconstruct the underlying ecological processes such as intra- and interspecific competition that reduces growth and induces mortality or facilitation that enhances establishment and growth which are important to forest management (Pommerening, 2002; Wiegand and Moloney, 2014).

Most stands of pioneer species (e.g., sliver birch, Scots pine) were naturally developed on abandoned lands that were previously used for pastoral and agricultural activities during the second half of twentieth century in Europe. The main objective of sustainable forest management (SFM) in these secondary forests within Europe is to create stands that are richer in species diversity due to richer economical, socio-economical, and ecological forest goods and services of mixed stands (Dieler and Pretzsch, 2013; Metz et al., 2013; Pretzsch et al., 2015). Therefore, it was planned to transform monospecific Scots pine (*Pinus sylvestris* L.) (hereafter termed just pine) stands as one of the most frequent colonies on the abandoned lands into mixed pine-beech stands by introducing European beech (*Fagus sylvatica* L.) (hereafter termed just beech) as a deciduous broadleaved species. In addition, it was observed that beech progressively infiltrates natural pine stands and naturally regenerates by seeds, probably disseminated by birds and small rodents (Prevosto et al., 2000; Curt and Prévosto, 2003; Kint et al., 2006; Buczko et al., 2007). The natural transformation of pure pine stands to mixed pine-beech stands have significant impacts on the underlying ecological interactions of pine and beech that have so far been poorly investigated in the literature (Prevosto and Curt, 2004; Pretzsch et al., 2015).

The objective of this study was to reveal spatial associations of pine and beech trees in a secondary forest in northern Poland to quantitatively identify their ecological relationships and explain possible causes of their successful coexistence in these forest ecosystems in Europe as illustrated in previous investigations (Curt and Prévosto, 2003; Pretzsch et al., 2015). Pine is a shade intolerant species that has high light compensation point and significantly compete for light with other species (Curt and Prévosto, 2003; Dieler and Pretzsch, 2013). While beech has a lower light compensation point compared to pine and benefit from light intercepted throughout canopies of trees in overstorey (Rio et al., 2014; Pretzsch et al., 2015). Therefore, we tested the hypotheses that (i) strong intraspecific competition (for light or other biotic and abiotic factors) will lead to a strong repulsion between pine individuals in the study region, i.e. negative intraspecific interactions, (ii) beech trees will have a spatial attraction to their conspecific neighbours, probably due to their shade tolerance or favorable environmental conditions under pine canopy and consequently, aggregated spatial patterns of beech may be observed within the first few meters of pine, i.e. positive intraspecific interactions, (iii) pine, a shade intolerant species, will allow beech as a shade tolerant species to survive and grow within its canopy cover suggesting positive interspecific interactions between the species. Competitive and facilitative interactions of species significantly influence their growth rate and the correlation between tree sizes (e.g., tree height) at different spatial locations may reveal negative or positive relations between trees (Getzin et al., 2008; Law et al., 2009). Therefore, we used univariate and bivariate mark correlation functions $k_{mm}(r)$ and $k_{m1m2}(r)$, respectively, to evaluate the hypothesis (iv) that we would expect to observe the effects of intra- and interspecific interactions of pine and beech on spatial distribution of sizes (i.e., DBH and tree height) of the individuals and there will be a significant spatial correlation between the sizes of investigated species. Analysis of spatial patterns of the species will aid in interpreting the underlying ecological processes of mixed stands mainly composed by these two species. Moreover, this analysis will be useful to design forest management practices intended to be applied in conversion of pure pine or beech stands to mixed stands. Our findings may provide useful information to better understand the spatial dynamics and ecological mechanisms of pine and beech mixed stands and the development of effective forest management plans.

2. Materials and methods

2.1. Study area

Milomlyn Forest District is one of thirty-three forest districts included in the Regional Directorate of State Forests in Olsztyn. It is situated in Warmia-Mazury, districts Ostroda and Ilawa. The total area of the district is 479.39 km^2 and 19116 ha. The average age of forest stands is 70 years and the average stock volume is 302 m^3/ha. The dominant species are pine (*Pinus sylvestris* L.) covering almost 70% of the Milomlyn Forest District forest area, beech (*Fagus sylvatica* L.) (11%), alder (*Alnus* spp.) (6%), birch (*Betula pendula* L.) (5%) and oak (*Quercus* spp.) (4%). We selected 18 stands covered only by mixture of pine and beech in Milomlyn Forest District based on forest digital maps (Fig. 1). The environmental characteristics such as soils, topographic characteristics, and age within the stands showed apparent heterogeneity among stands.

Forty random points were selected in the stands as the center of circular plots 500 m^2 in area (Fig. 1). The plots were located in stands with different environmental conditions, therefore it was expected to observe significant heterogeneity between the environmental characteristics of the plots. In each plot, all of the trees with a DBH greater than 7 cm were recognized to the species level, and their locations were recorded using azimuth (to the nearest degree) and distance (to the nearest cm) from the plot center. Furthermore, for each tree in the study plots, we measured tree height (using Vertex Haglof instrument with 0.1 m precision) and DBH (using a steel Codimx calliper with 1 mm precision). In addition, we implemented paired sample *t*-test to assess the significance of differences between the mean values of tree height and DBH of the species.

2.2. Spatial pattern analysis

A powerful and reliable tool to characterise the spatial distribution of trees is to analyse their fine-scale spatial patterns by point pattern analysis and related summary statistics, which shows the