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Breaking through beech: A three-decade rise of sycamore in old-growth European forest

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A B S T R A C T

European beech (*Fagus sylvatica*) increases its dominance in various forest types in Central Europe. In this context we investigated a very exceptional process, in which beech have been partly outcompeted by sycamore maple (*Acer pseudoplatanus*) in unmanaged forest without severe disturbances. Main research questions were as follows: (i) How did the spatial patterns of beech and sycamore develop, and can these patterns be described by known spatial models?; (ii) What were the spatial relationships between beech and sycamore?; (iii) Does the spatial relationship of advance regeneration to gap-makers differ for the two species?; (iv) Did the presence of a road influence the spread of the sycamore population?

The study was conducted in beech-dominated forest Žákova hora in the central part of the Czech Republic which has been left to spontaneous development for 85 years. We studied long-term forest dynamics using stem position maps of trees with DBH $\geqslant$ 10 cm carried out in 1974, 1995 and 2011. We used standard methods for calculating recruitment, mortality and population change. Various types of the pair correlation function were applied to describe the development of tree spatial patterns.

Our results showed that sycamore regenerated in the close vicinity of other conspecific trees. Sycamore recruits were not spatially associated to individual gap makers. Sycamore individuals had a highly clustered distribution, and the number of individuals grew mostly through the increasing of existing clusters. We successfully fitted the Matérn cluster process for sycamore spatial patterns. The radius of the model cluster ranged between 6 and 16 m. By contrast, beech recruits were negatively correlated to older conspecific trees and showed independence or positive correlation to sycamore veterans. The vicinity of the road significantly promoted sycamore recruitment (opposed to the beech). If the sycamore expansion is connected with the vicinity of the road and thickening of existing sycamore clusters only, as our results indicate, then it can be spatially and temporally limited process.

1. Introduction

European beech (*Fagus sylvatica* L., hereafter beech) forests represent the most important forest communities in near-natural forested landscapes in Central Europe (Peterken, 1996). They cover a wide range of environmental conditions from southern Sweden to the Italian mountains and from northern Spain to Bulgaria (Leuschner et al., 2006). Beech is the most competitive tree species on sites with moderate soil moisture and acidity (Bohn et al., 2004). Recently, beech has become more frequent and has expanded to the north in the eastern Alps and Moravia (Magri, 2008); in Slovenia it has increased its area by more than 1200 ha per year on average over the period 1975–2005 (Poljanec et al., 2010). Beech is very successful also in the north-east of its distribution range, i.e. northern and eastern Poland and the southern regions of the Baltic States (Bolte et al., 2007). In fir-beech forests of western Carpathians, beech has become the dominant tree species over past 100 years (Vrška et al., 2009).

Chmelař (1987) noticed that beech outcompetes other, more light-demanding species in suitable stands, which results in the formation of pure beech stands. The strategy of beech is based on the maintenance of space occupation (Pretzsch and Schutze, 2005). Through superior efficiency in lateral crown expansion and space occupation, beech is able to maintain a multi-layered canopy that holds back competitors from the understorey. It fills gaps in the canopy immediately after self-thinning processes within the stand (Pretzsch and Schutze, 2005). Other tree species are likely to be favoured by the occurrence of large canopy openings, caused by infrequent, severe wind events (Zeibig et al.,

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2005). In the Slovenian Alps, Firm et al. (2009) documented that post-disturbance forest development was dominated by the release of shade tolerant regeneration, especially beech.

We know of no examples when beech would have been outcompeted by other species in unmanaged Central European forests with sufficient water and nutrient availability and without severe disturbances.

In light of the above, the long-term development of the tree species composition at Žákova hora, one of the best preserved remnants of Central European beech dominated forests, is rather surprising. Between 1974 and 1995, a significant increase in the number of sycamore maple (*Acer pseudoplatanus* L., hereafter sycamore) individuals was recorded at the expense of the dominant beech (Vrška et al., 2009). The principal objective of this paper is to understand why tree dominance is shifted in that area and describe the spatial relations that enabled this exceptional success of sycamore over beech.

Sycamore growth was thoroughly reviewed by Hein et al. (2009). This tree is rarely found in pure stands. Its most important characteristics, which can give competitive advantage over other tree species, are that sycamore can easily regenerate naturally and can achieve temporal dominance through its rapid early height growth. In the seedling and sapling stage of development, it has similar light requirements and growth dynamics as beech. However, with increasing light, sycamore constantly gains superiority in length increment over beech (Petritan et al., 2009). On the other hand, at low light, beech shows lower mortality than sycamore (Petritan et al., 2007). Sycamore needs high amounts of soil and air moisture, but it does not tolerate waterlogging (Chmelař, 1987). It is also nutrient-demanding.

Besides the classical methods of analyzing population trends by vital rates (Condit et al., 1999), in this paper we focus on the development of tree spatial patterns within and amongst populations. We use the method of spatial point process analysis. ‘Points’ are tree locations and ‘marks’ are tree characteristics, such as species, diameter, height, and canopy status (Stoyan and Penttinen, 2000). The interpretation of tree spatial pattern analysis is governed by the principle that it is not possible to derive a process from a pattern directly, but patterns can be used to test hypotheses about underlying mechanisms (Dale, 1999; Lepš, 1990) providing important insights into processes that drive population and community dynamics (Illian et al., 2009; McIntire and Fajardo, 2009; Miriti, 2007; Rayburn and Monaco, 2011). Information on the spatial patterns of individual plants within forests may refine our understanding of ecological processes, such as forest establishment, growth, competition, reproduction and mortality (Ward et al., 1996; Woodall and Graham, 2004).

Tree spatial patterns of beech were investigated in many studies (Law et al., 2009; Petritan et al., 2009; Rozas and Prieto, 2000; Šebková et al., 2011; von Oheimb et al., 2005), but sycamore patterns attracted much less attention. Szwagrzyk and Czerwczak (1993) noticed a negative association between beech and sycamore trees and between sycamore and *Ulmus glabra*. Atkinson et al. (2007) revealed evidence of sycamore clustering up to ca. 15 m, but not for larger distances.

Some information on the spatial distribution of sycamore can also be found in studies that did not directly analyse tree spatial patterns. Marinšek and Diaci (2004) noticed that sycamore regeneration occurred in larger openings created by windthrow in a beech dominated old-growth forest. Nagel et al. (2010) documented that recruitment into pole-sized trees only occurred in gaps. Savill et al. (1995) recorded that sycamore tended to regenerate better under the canopy of other species and may establish a cyclical pattern with dominance alternating between two species (Waters and Savill, 1992).

To explain the successful spreading of *A. pseudoplatanus* into a *F. sylvatica* forest, our research questions and hypothesis were:

(i) What was the development dynamics of tree species composition (what were vital rates like) in the period 1974–2011?
(ii) How did the spatial patterns of beech and sycamore develop, and can these patterns be described by known spatial models? We hypothesize that spatial patterns of sycamore and beech will differ, especially in recruit patterns which reflect ways of regeneration.
(iii) What were the spatial relationships between beech and sycamore? Due to direct competition between species on the locality we hypothesize generally negative spatial associations. Due to sycamore expansion we assume changes of intensity of negative associations over time.
(iv) Does the spatial relationship of advance regeneration to gap-makers differ for the two species? We hypothesize that sycamore will show stronger positive relationship to gap-makers than beech.
(v) Did the presence of a forest road influence the spread of the sycamore population? We hypothesize that the presence of a forest road, as a disturbance factor, will have a positive influence on sycamore expansion.

2. Material and methods

2.1. Study area

The detailed surveys presented here were performed in the core area of Žákova hora national nature reserve (N49°39′, E15°59′, total area 38.10 ha) with size 17.46 ha. Žákova hora lies in the Bohemian–Moravian Uplands in the central part of the Czech Republic (Fig. 1). The elevation above sea level ranges from 730 to 808 m, and the terrain is characterized by slopes of various inclinations (up to 20°). The geological basement is Crystalline, built of migmatites and dual-mica gneisses. Sandy and loamy-sand Dystric Cambisols predominate within the locality. Mean annual total precipitation is 740 mm, and mean annual temperatures range from 5 to 6 °C (Tolasz et al., 2007). The growing period lasts for about 120 days. Plant communities can be most often classified into the association *Galio odorati-Fagetum sylvaticae* Sougnez et Thill 1959 (Chytrý, 2013); tree community includes *F. sylvatica*, *Picea abies*, *Abies alba*, *A. pseudoplatanus* and *Acer platanoides*. The site has been left to spontaneous development without deadwood removal since the beginning of the 1930s (Vrška et al., 2002). In 1937–1938 the forest road was built and the reserve was split into two parts (13.9 ha and 3.6 ha) which particularly disturbed the small, south-western part of forest reserve (Vrška et al., 2002). The forest road was originally built from the local acid granite and road surface was reconstructed in 1970.

2.2. Datasets and plots

We used the results of complete tree censuses and stem mappings of trees with diameter at breast height (hereafter DBH) ⩾ 10 cm carried out in 1974 (Průša, 1985), 1995 (Vrška et al., 2002) and 2011. In the period 1974–1995, tree positions were measured using tripod-based theodolites. In 2011, we used Field-Map technology (http://www.fieldmap.cz). A unique identification number was assigned to each stem to enable repeated identification, remeasurement and the recording of recruits and dead trees. For the purposes of this paper, we used a dataset of trees that contains tree position coordinates (x, y), species, DBH and stem status: living or dead.