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Tree spatial patterns of *Fagus sylvatica* expansion over 37 years

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ABSTRACT

Fagus sylvatica (European beech) populations in Central Europe are currently expanding their dominance in many forest types. In this study we focused on the spatio-temporal dynamics of beech recruitment as a mechanism for successful expansion. Specifically we investigated: (1) the developmental trend of the tree community composition and spatial pattern in an unmanaged *Picea abies-F. sylvatica* forest over 37 years, (2) the pattern of decrease in clustering along increasing tree size gradient of beech, and (3) the spatial patterns of beech regeneration in relation to gap-makers.

The study was conducted in the Žofín Forest Dynamics Plot, which is part to the Smithsonian Institution's Forest Global Earth Observatory (ForestGEO) as the research plot representing European natural mixed temperate forests.

To quantify these dynamics, we used the stem map of trees with DBH $\geqslant$ 10 cm carried out in 1975, 1997, 2008 and a census of trees with DBH $\geqslant$ 1 cm from 2012 to calculate recruitment, growth, mortality and, from those vital rates, population change. Various types of the pair correlation function were applied to the data to describe the tree density variability over time.

Our analyses revealed a trend of increasing *F. sylvatica* representation at the expense of *P. abies* and *Abies alba* over the 37 years. Increased clustering of *F. sylvatica* trees with DBH $\geqslant$ 10 cm correlated with new recruits at plots where *F. sylvatica* replaced declining *P. abies*. On the other hand, the decrease in *F. sylvatica* clustering at some plots was likely due to strong intra-specific competition. The analysis of the spatial patterns of *F. sylvatica* individuals along DBH gradient 1–9 cm showed a trend of increasing clustering up to 5 m distance. *F. sylvatica* saplings to 4 cm of DBH were positively spatially correlated with other conspecific individuals, although at larger sizes (DBH 7–9 cm), this relationship reversed to a negative correlation. Analysis of relationships between saplings and gap-makers did not reveal a clear pattern.

We concluded that without a coarse-scale disturbance capable of restructuring the community, *F. sylvatica* will become the only dominant tree species in this forest type. *F. sylvatica* gradually replaces *P. abies* through its space occupation strategy because its recruits are already present before a canopy disturbance. Our results indicate that *F. sylvatica* saplings can grow up to 4 cm DBH under a closed canopy, but require a canopy disturbance to advance to a larger size class.

1. Introduction

European beech (*Fagus sylvatica* L., hereafter "beech") is the dominant tree species of forests with natural vegetation and moist to moderately dry soils of the sub-mountainous regions of Central Europe (Ellenberg, 1996). Beech populations in Central Europe–especially in the eastern Alps-Slovenia and Moravia–have increased their representation and are currently expanding their dominance to the north (Magri, 2008). Beech has increased its dominance in various forest types. In natural fir-beech forests of western Carpathians, beech has become the only dominant tree species over the past 100 years (Vrška et al., 2009). Increasing representation of beech in sessile oak – beech natural forests in western Romania has also been documented (Petritan et al., 2012).

In the past century, the development of the Žofín Forest, one of the oldest unmanaged reserves in Europe (from 1838, Welzholz and Johann, 2007), has been intricately connected to the

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interactions between beech and *Picea abies* (hereafter "spruce"). The dynamics between beech and spruce is emblematic of a process occurring in many other European forests (Šebková et al., 2011). In 2012 the Žofín Forest Dynamics Plot became part to the Smithsonian's Forest Global Earth Observatory (ForestGEO, www.forestgeo.si.edu) as the research plot representing European natural mixed temperate forests. The Smithsonian inventory protocol (Condit et al., 1999) combines two features important to understanding the spatial development and dynamics of forests: the large size of the plots (⩾16 ha), and the measurement of individuals of small sizes (stems ⩾ 1 cm of diameter at breast height, hereafter DBH). This protocol offers windows into how the biomass of dominant species emerges from the distribution of species recruitment across environmental gradients and disturbance patterns so that both a range of stems across a large spatial scale can be analysed. A long-studied forest plot in the southern Czech Republic now offers a new opportunity to gain insight into the dynamics of the beech-spruce associations and the possibility of comprehensive beech expansion, with important implications for both managed and unmanaged European forests.

In addition to analyzing population trends (Condit et al., 1999), in this paper we focus on the development of tree spatial patterns within and among populations. Information derived from the spatial patterns of individual stems 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). Further, spatial patterns are critical to the assessment and prediction of future forest conditions that emerge from processes such as competition and dispersal—fundamentally spatially explicit mechanisms of forest dynamics. We thus believe that a detailed investigation of spatial patterns in a forest can illuminate and quantify some of the mechanisms of beech expansion in European temperate forests.

Tree spatial patterns of beech have been investigated in many studies. A clustered pattern of small-sized beech trees was observed by von Oheimb et al. (2005), Rozas (2006), Petritan et al. (2014) or Law et al. (2009), where the intensity and scale of clumping decreased for trees in the upper canopy and for larger size categories (Rozas, 2006; von Oheimb et al., 2005). Similar results were found for spruce. Law et al. (2009) showed higher values of spruce clustering in comparison with beech, and Šebková et al. (2011) documented long-term (~160 year) stability of the pattern of beech in the Boubín forest. In the same forest, however, spruce frequently shifted from a clustered to a more random spatial pattern. These findings are consistent with many studies of coarse spatial distributions that have shown that there is often a shift from aggregated distributions for smaller size classes to uniform distributions for larger size classes (Ghent and Franson, 1986; Stewart, 1986; Moeur, 1993). Causal mechanisms for the aggregated distribution of trees include edaphic patterns, seed dispersal patterns, gap colonization, vegetative reproduction, and other factors (Aldrich et al., 2003; Ward et al., 1996; Wolf, 2005). Changes towards regular spacing, however, may be indicators of competitive interactions between neighboring trees (Lepš, 1990). Such patterns suggests that density-dependent processes operate through higher mortality in high density neighborhoods but allow increased ingrowth in low density neighborhoods (Ward et al., 1996).

Remarkably, even with this diversity of data, the specific strategy and spatial patterns of beech recruitment in European forests remain unclear. von Oheimb et al. (2005) noticed that the small diameter trees were aggregated in some areas, where the density of dominant trees was low or in canopy gaps, but Debeljak and Mlinšek (1998) found that dead dominant trees are readily replaced by subdominant trees from the upper canopy layer and trees from the middle canopy layer. Kucbel et al. (2010) observed different mechanisms of gap-filling dependent on gap size. Although the lateral expansion of adjacent trees determined the closure of small canopy openings, the intermediate and large gaps closed at a rate dependent on the height growth of natural regeneration and understory trees. This observation of European forest associations matches well the theoretical models proposed by tropical biologists to explain forest successional dynamics (Hubbell and Foster, 1986).

Opportunities for spruce to successfully establish itself against the competitively dominant beech was documented from a study in the Slovenian Alps where post-disturbance forest development was dominated by the release of a shade tolerant regeneration, especially beech (Firm et al., 2009). Firm et al. also noticed that fir and spruce populations were established after windthrow disturbance, and their high recruitment rates could be explained by the higher light and temperature conditions found in these windthrow gaps. Simon et al. (2011) also studied the influence of windthrow microsites on tree regeneration in the spruce-fir-beech Rothwald forest. They observed the total failure of spruce at microsites with undisturbed soil. It thus seems that spruce can successfully regenerate only in cases of coarse-scale disturbances, such as larger storm.

The long-life cycle of trees allow different species to employ different life-history strategies to operate at different life stages (Nakashizuka, 2001). Studying the spatial pattern of aggregated categories of sizes fails to reflect how the spatial arrangement of trees operates over long time periods (Stewart, 1986). Moreover, single studies are limited by the threshold parameters of recorded trees, the size of studied plots, etc. Investigations of stand development and dynamics particularly requires data on the spatial pattern of small trees (DBH < 10 cm), as this period of thinning is critical to understanding how endogenous and exogenous mechanism might drive forest development. In this study we measured and analysed spatial sequences of beech trees with DBH ⩾ 1 cm to reveal statistically significant changes in the spatial patterns of species across size classes. The main aims of this paper are to describe the development of the population structure of an unmanaged spruce-beech forest and to test whether the spatio-temporal dynamics of beech recruitment defines a strategy for expansion. We ask the following research questions and related hypothesis:

(i) How did tree species composition in these classic European forest change over four decades?
   – We expect significant changes in species representation due to long-term decline of fir population and due to recent disturbances caused by Kyrill and Emma hurricanes in 2007 and 2008 respectively.

(ii) What is the specific pattern of decrease in clustering along increasing tree size gradient of beech?
   – We hypothesize gradual decrease in intensity and distance of clustering along increasing tree size gradient.

As an alternative hypothesis, the clustering will reveal some break points reflecting species strategy of recruitment.

(iii) What are the spatial patterns of beech regeneration in relation to the presence of gap-makers?
   – We hypothesize high variability in the spatial relationship between saplings and gap-makers in intensity of association and in relation to size of individuals. As an alternative hypothesis, the bigger saplings will be positively associated with gap-makers.

(iv) What spatial relationships between beech and spruce determine the potential dominance of beech?