



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 ≥ 10 cm carried out in 1975, 1997, 2008 and a census of trees with DBH ≥ 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 ≥ 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.

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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

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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, Welzhof and Johann, 2007), has been intricately connected to the

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 Žofin 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?

- We hypothesize negative spatial associations between spruce and beech due to limited successful establishment of spruce in areas without coarse-scale disturbances.

As an alternative hypothesis we assume that random spatial associations will prevail due to competitive interactions between species, which gradually reshape the original distribution of beech and spruce.

2. Methods

2.1. Research plot

The Zofin Forest Dynamics Plot (ZFDP) is situated in the Novohradské Hory Mts. It lies in South Bohemia near the border with Austria (48°40'N 14°42'E) (Fig. 1). ZFDP with size 25 ha is located within a 75 ha research area that has been intensively studied since the 1975 (Fig. 1). The terrain is characterized by gentle NW slopes that predominate (Fig. 1). Bedrock is almost homogenous across this plot, and consists of finely to medium-grained porphyritic and biotite granite. The dominant soils (classified according to Michéli et al., 2006) at xeric sites are Entic Podzols and Haplic and Dystric Cambisols. At mesic sites there are Histic and Haplic Gleysols, Endogleyic Stagnosols, or Fibric, Hemic, and Sapric Histosols (Šamonil et al., 2011). Mean annual temperature at the site is 6.2 °C, and mean annual precipitation is 866 mm.

F. sylvatica L. dominates in tree species composition stem number, followed by *P. abies* L. Karsten and *Abies alba* Mill. Other tree species have a minor representation – *Acer platanoides* L., *Acer pseudoplatanus* L., *Betula pendula* Roth, *Populus tremula* L., *Salix caprea* L., *Sambucus racemosa* L., *Sorbus aucuparia* L., *Ulmus glabra* Huds. (Král et al., 2010).

Žofín is the oldest reserve in the Czech Republic. The long-term history of human impact started in the last three decades of the 18th century when this part of Novohradské Mountains was step by step colonized and the glassworks were established in the surrounding of Zofin forest reserve. Zofin represented the last complex

of virgin forest in the region. As early as 1838 the Count Buquoy – the owner of the forest – banned tree cutting in two stands, which today form the core zone of the nature reserve. The first detailed records on tree species composition are from 1847, and at that time the most common tree species were *A. alba* Mill. (hereafter fir), followed by *P. abies* L. and *F. sylvatica* L. During the next 100 years, older firs died out and spruce and beech became the most common species (Průša, 1985).

2.2. Data-sets

All living trees of DBH ≥ 1 cm within the ZFDP (25 ha) were measured and mapped according to Smithsonian protocol in 2012 (Condit et al., 1999). We additionally had stem mappings of trees with DBH ≥ 10 cm within ZFDP borders carried out in 1975 (Průša, 1985), 1997 and 2008 too. An identification number was assigned to each stem to enable repeated identification, re-measurement and the recording of recruits and dead trees. For the purposes of this paper, we used a dataset of trees that contained tree position coordinates (x, y), species, DBH, and the stem status, living or dead.

To perform our spatial analysis, we chose seven 1-ha square plots (100 × 100 m) within the ZFDP (Fig. 1). The plots were selected according to the following criteria: (i) Plots did not include intensively wet sites; (ii) plots did not overlap with each other; (iii) plots were situated at least 50 m from the protected area border to eliminate border effect; and (iv) rock areas without trees were excluded. On these plots, tree spatial patterns were analysed for the categories: *Saplings 0102* (DBH 1–2 cm), *Saplings 0304* (DBH 3–4 cm), *Saplings 0506* (DBH 5–6 cm), *Saplings 789* (DBH 7–9 cm), *All trees* (DBH ≥ 10 cm), *Small-sized trees* (DBH 10–24 cm), *Mid-sized trees* (DBH 25–54 cm), *Large-sized trees* (DBH ≥ 55 cm), *Recruits* (new trees that reached the minimum DBH of 10 cm since the previous census), *Surviving trees* (live trees with DBH ≥ 10 cm which survived since the previous census) and *Gap-makers* (Large-sized trees with DBH ≥ 55 cm which dead in the period 1997–2012). To perform spatial analysis the minimum number was 10 individuals within each category and plot.

2.3. Tree demography

We used standard methods for calculating recruitment, mortality and the resulting population change (Condit et al., 1999), as follows: let the census interval be t , and the population sizes at time 0 and time t be n_0 and n_t . The survivors at time t are of S_t and number of recruits is $n_t - S_t$. Then recruitment was defined as $r = (\ln n_t - \ln S_t)/t$; mortality as $m = (\ln n_0 - \ln S_t)/t$ and population growth as $\delta = (\ln n_t - \ln n_0)/t$.

2.4. Tree spatial pattern analysis

2.4.1. Pair correlation function - description

To describe tree and sapling density variability we used a pair correlation function (e.g. Stoyan and Stoyan, 1994). According to Law et al. (2009), this function is suitable for describing spatial relationships of neighboring plants with different species identity or size class, as is the case in our study. Stoyan and Penttinen (2000) define the pair correlation function as follows: consider two infinitesimally small discs of areas dx and dy at distance r . Let $p(r)$ denote the probability that each disc contains a point of the process. Then $p(r) = \lambda^2 g(r) dx dy$, where λ is density of trees. In a different way, the pair correlation function $g(r)$ is the probability of observing a pair of points separated by a distance r , divided by the corresponding probability for a Poisson process (Baddeley, 2008). It is related to the K function (Ripley, 1977) by:

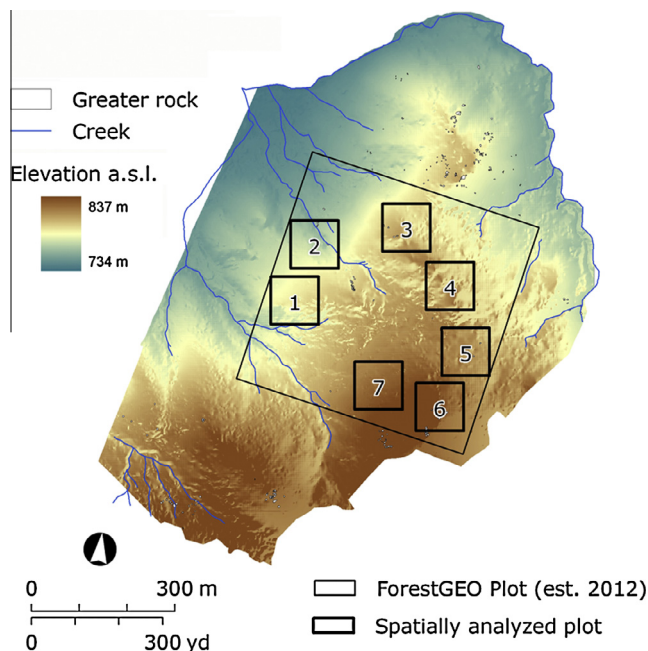


Fig. 1. Natural conditions of the study site with locations of plots for spatial analysis.

$$g(r) = \frac{d}{dr} K(r) / (2\pi r) \quad \text{for } r \geq 0 \quad (1)$$

The definition of K function is $K(r) = \lambda^{-1}E$, where λ is density of trees and E is the number of trees within distance r of an arbitrary tree. The essential difference between the pair correlation function and the K function is its non-cumulative character; the pair correlation function uses annuli as distance classes, not circles. Under the assumption of a homogenous Poisson process, $g(r) = 1$. Values of $g(r)$ larger than one indicate clustering, while values smaller than one indicate regularity.

2.4.2. Univariate analysis

To test spatial patterns of saplings (DBH 1–9 cm), the pair correlation function $g(r)$ was estimated for each of the seven plots at steps of 0.25 m up to 20 m. 95% non-parametric bias-corrected and accelerated (BC_a) confidence intervals based on 1000 bootstrap replications (Efron and Tibshirani, 1993) were constructed for the mean values of $g(r)$. The BC_a limits were given by percentiles of the bootstrap distribution. The percentiles used depend on acceleration and bias correction (Efron and Tibshirani, 1993; Miller, 1964).

To analyse spatial patterns of trees (DBH ≥ 10 cm) we tested a null model of complete spatial randomness (hereafter CSR). This model was used on the assumption that the first-order intensity λ is constant within particular plots. To verify this assumption we used a test of homogeneity of point density, and we did not find a trend in point density within particular plots (Illian et al., 2008). We used 99 Monte Carlo simulations of CSR to obtain pointwise critical envelopes for $g(r)$ (Besag and Diggle, 1977). In the context of point processes we can consider the significance level of this pointwise Monte Carlo test was 0.02 (Illian et al., 2008).

2.4.3. Multivariate analysis

To describe tree spatial patterns of mortality and spatial dependency of particular DBH categories on neighbors, we used the ‘i-to-any’ summary $g_i(r)$, which is the corresponding analogue of the pair correlation function (Baddeley, 2008). A randomization test was used to test the null hypothesis of random labelling: given the locations X , the marks are conditionally independent and identically distributed. In randomization tests, the simulated patterns X are generated from the dataset by holding the point locations fixed and permuting the marks randomly. Under random labelling, $g_i(r) = g(r)$; we thus used $g_i(r) - g(r)$ to make a test statistic for random labelling. We generated 99 simulations of our null model to obtain pointwise critical envelopes for this model.

To investigate the spatial relationship of *Recruits* to *Surviving trees* and *Gap-makers*, *Saplings* to *Gap-makers* and relationships between heterospecific individuals (beech to spruce trees and saplings) we used an ‘i-to-j’ pair correlation function, which is the extended $g(r)$ function to multitype point patterns. We tested the null hypothesis of independence of components. In a randomisation test of the independence-of-components hypothesis, the simulated patterns X are generated from the dataset by splitting the data into sub-patterns of points of one type, and randomly shifting these sub-patterns, independently of each other (Baddeley, 2008). We generated 99 simulations of this null model to obtain pointwise critical envelopes. All edge effects were corrected using Ripley’s isotropic correction (Ripley, 1988).

All spatial analyses were conducted using the package ‘spatstat’ (Baddeley and Turner, 2005) in the statistics software R (R Core Team, 2015). Package ‘bootstrap’ (Efron and Tibshirani, 1993) was used for constructing BC_a confidence intervals. Summary of all spatial analysis and research questions is provided in Table 1.

Table 1
Summary of research questions and related spatial analysis.

Research question	Point pattern analysis ~ null models	Related figures
What is the specific pattern of clustering along increasing tree size gradient of beech?	Pair correlation function ~ null model of Complete Spatial Randomness, ‘i-to-any’ pair correlation function ~ random labelling null model	Figs. 3–5
What are the spatial patterns of beech regeneration in relation to the presence of gap-makers?	‘i-to-j’ pair correlation function ~ null model of independence of components hypothesis	Fig. 6
What are the spatial relationships like between beech and spruce?	‘i-to-j’ pair correlation function ~ null model of independence of components hypothesis	Figs. 7 and 8

3. Results

3.1. Species composition of trees with DBH ≥ 10 cm within all ZFDP over 37 years

For the entire ZFDP plot (25 ha), our results show a clear trend of increasing representation of beech stems from 65% in 1975 to 95% in 2012 (Fig. 2). The representation of spruce sharply decreased (from 28% to 4%) and fir effectively disappeared over 37 years. Other tree species – *A. pseudoplatanus*, *A. platanoides*, *B. pendula*, *S. caprea*, *S. aucuparia*, *U. glabra* – persisted as rare species, with under 0.5% representation in 2012. Beech recorded the highest recruitment and population growth of all species (Table 2). The highest mortality rates were recorded for spruce.

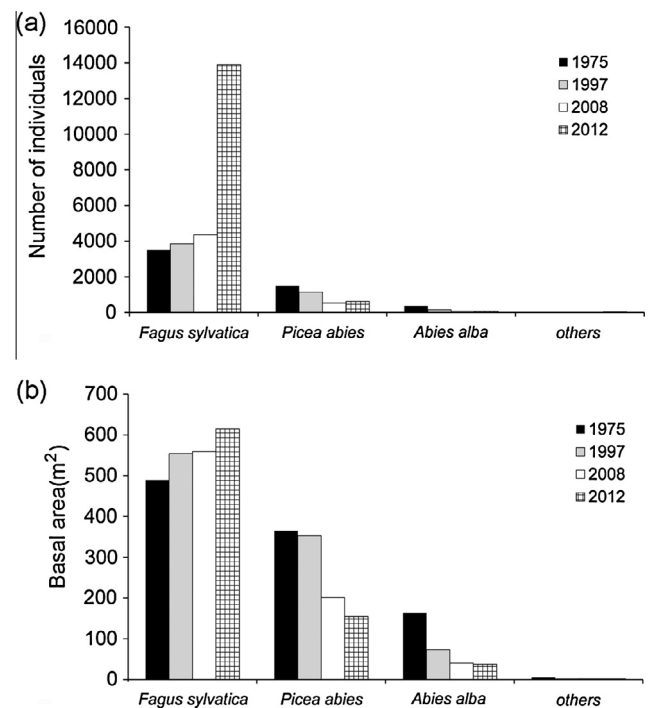


Fig. 2. Development of number of trees (DBH ≥ 10 cm) (a) and basal areas (m²) (b) for the main tree species on Zofin Forest Dynamic Plot over the period 1975–2012. Others: *Acer pseudoplatanus*, *Acer platanoides*, *Betula pendula*, *Populus tremula*, *Salix caprea*, *Sambucus racemosa*, *Sorbus aucuparia*, *Ulmus glabra*.

Table 2

Recruitment rates, mortality rates and population growth rates of main species at the Žofín Forest Dynamics Plot over the study period.

Species	Time period	Recruitment rate (%)	Mortality rate (%)	Population growth rate (%)
<i>Fagus sylvatica</i>	1975–1997	1.68	1.19	0.49
	1997–2008	2.49	1.39	1.10
	2008–2012	29.37	0.32	29.04
<i>Picea abies</i>	1975–1997	0.45	1.77	–1.32
	1997–2008	0.69	7.66	–6.97
	2008–2012	11.02	7.19	3.83
<i>Abies alba</i>	1975–1997	0.00	4.39	–4.39
	1997–2008	0.00	5.95	–5.95
	2008–2012	0.67	1.63	–0.97

3.2. Tree spatial analyses on 1-ha plots

3.2.1. Tree spatial patterns of trees with DBH ≥ 10 cm over 37 years

The spatial pattern of beech showed a characteristic alternation of clustered and random tree distribution (Fig. 3). Clustering was the most common in the category *Small-sized trees* and the least common in the category *Large-sized trees*. Regular distribution occurred sporadically at short intervals, most often in the category *Large-sized trees* (3–5 m).

The development of the spatial pattern of beech in individual plots partly reflected the development of the number of individuals in the tree-size categories. Plots 1, 2 and 7 showed the highest increase in the number of individuals in the study period and at the same time demonstrated the most clustering in the category *Small-sized trees* (1.5–20 m) in 2012 (Fig. 3). Simultaneously the sharp decrease in number of spruce trees and its basal areas was recorded in these plots over study period (Table 3). By contrast, plot 6 in 1975 had the highest number of beech individuals overall as well as in the category *Small-sized trees*. During the study period the number of individuals decreased and clustered distribution in 1997 and 2012 was almost completely absent while basal area of beech did not change over time (Table 3). A similar dynamic was observed in plots 3 and 5, where the number of trees slightly

increased but clustering decreased in the categories *All trees* and *Small-sized trees*. Plot 4 showed no change in the proportion of individual tree-size categories in the study period, and the proportion of clustering was continuously low (Fig. 3).

Beech mortality appeared to be randomly distributed across the plot (Fig. A1). Clustering did occur, however, in plots with more frequent dead trees (plot 3, 6). In plots with fewer dead trees, these dead trees typically showed a random spatial distribution. In plots 4 and 7 we also observed signs of regular distribution in dead trees. Random mortality prevailed for spruce in both study periods too (Fig. A1).

The number of spruce stems decreased in all plots where spruce occurred and clustered distributions were typical for trees across size categories (Fig. A2). Regular distribution was observed only exceptionally.

3.2.2. Spatial patterns of saplings (DBH 1–9 cm)

The analysis of the spatial patterns of beech individuals with DBH < 10 cm showed a trend of increasing average values of the pair correlation function, i.e. increasing clustering, along DBH gradient at least to 5 m distance (Fig. 4). On the other hand, there is an apparent trend of shortening distances at which trees are significantly clustered. While in category *S0102* individuals are significantly clustered over the entire study interval, in category *S0304* they are clustered to 18.5 m (low BCa limit for $g_{\text{mean}}(r) = 1.01$, Fig. 4) and in category *S789* to 14.5 m (low BCa limit for $g_{\text{mean}}(r) = 1.02$, Fig. 4).

Spruce saplings showed clustering up to 20 m (Fig. A3).

We analysed spatial relations between size categories as well (Fig. 5). We found a transition in the influence of neighbors across beech sampling sizes in all plots. The null hypothesis of random labelling is true if the probability of an occurrence is independent of the neighborhood. The occurrence of small beech saplings (*S0102* and *S0304*) was positively correlated with the presence of all other beech individuals, in the category *S0102* up to 12 m in average from all plots, in the category *S0304* up to 8 m in average from all plots. Intermediate sized saplings, however, showed independence (class *S0506*). At larger sizes, beech saplings and larger beech

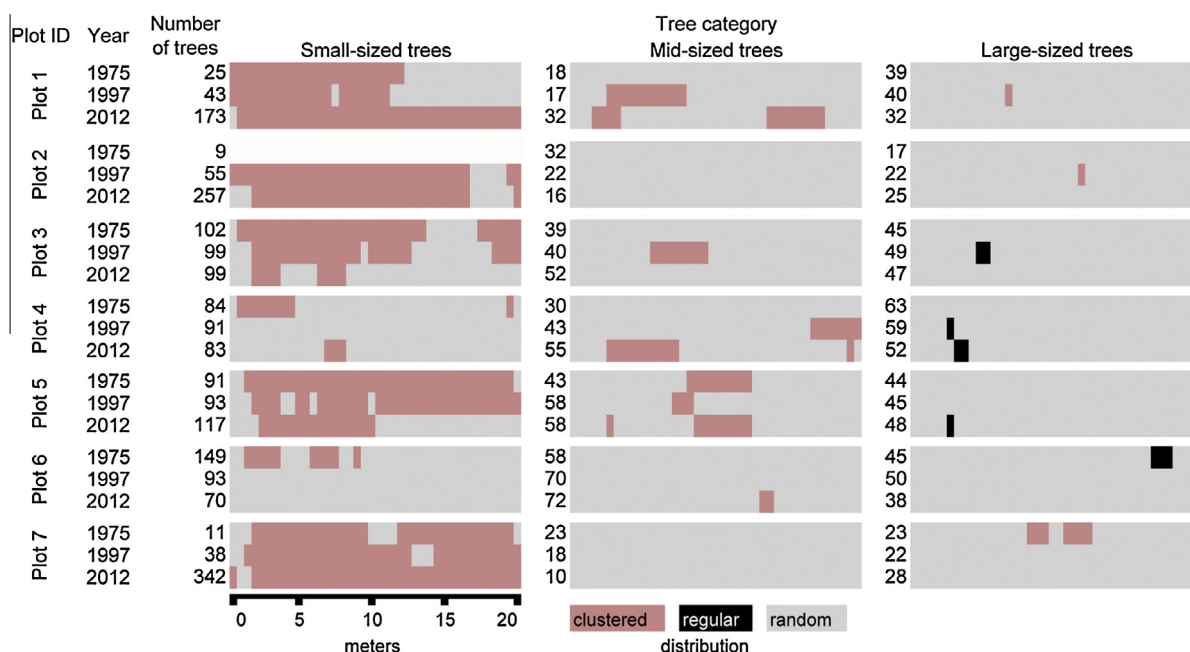
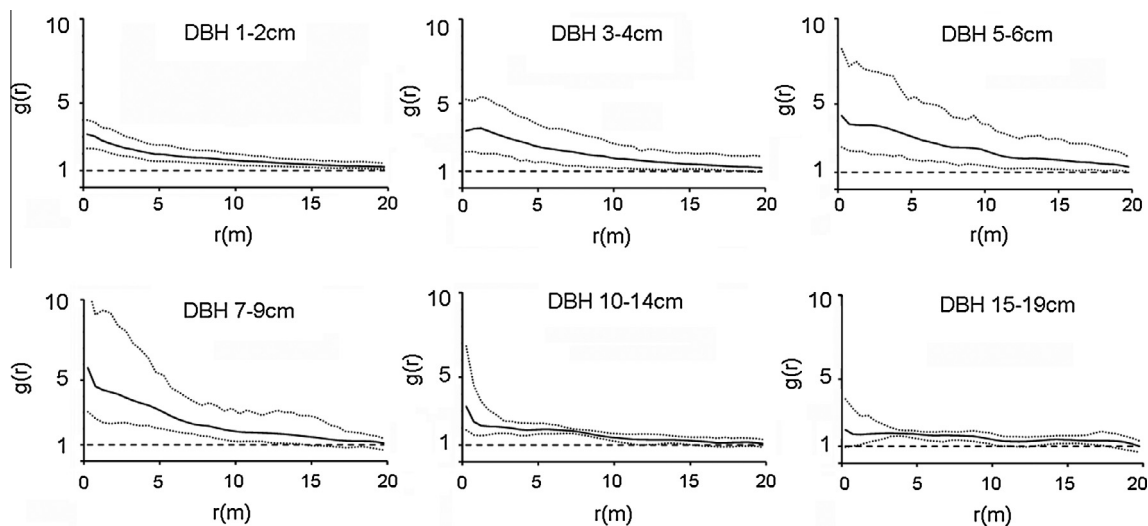


Fig. 3. Tree spatial patterns of *Fagus sylvatica* trees (DBH ≥ 10 cm) on 1-ha plots analysed by pair correlation functions over the period 1975–2012. For single values of r (1–20 m, step 0.5 m) significant spatial distributions were determined through 99 Monte Carlo simulations of the null model of complete spatial randomness. All trees – trees with DBH ≥ 10 cm, Small-sized trees – DBH 10–25 cm, Mid-sized trees – DBH 25–55, Large-sized trees – DBH ≥ 55 cm.

Table 3

Numbers of trees and basal areas on seven 1-ha plots which were used for spatial analysis.

Plot ID	Year	<i>Fagus sylvatica</i>		<i>Picea abies</i>		Others		Total	
		Number of trees	Basal area (m ²)	Number of trees	Basal area (m ²)	Number of trees	Basal area (m ²)	Number of trees	Basal area (m ²)
Plot 1	1975	82	20.54	77	24.45	11	4.94	170	49.93
	1997	100	20.51	62	27.13	4	1.51	166	49.15
	2012	237	25.94	33	15.81	5	1.69	275	43.44
Plot 2	1975	58	10.94	127	35.75	29	14.96	214	61.65
	1997	99	13.62	93	32.21	11	6.24	203	52.07
	2012	298	20.33	48	22.34	5	2.26	351	44.93
Plot 3	1975	186	25.75	5	1.92	12	5.46	203	33.13
	1997	188	29.57	4	2.04	3	1.23	195	32.84
	2012	198	32.10	1	0.92	1	1.19	200	34.21
Plot 4	1975	177	35.70	9	5.87	8	3.72	194	45.29
	1997	193	34.25	5	2.90	2	0.54	200	37.69
	2012	190	37.48	3	2.64	1	0.12	194	40.24
Plot 5	1975	178	26.91	13	4.31	10	3.54	201	34.76
	1997	196	31.20	12	5.33	3	0.79	211	37.32
	2012	223	34.45	8	2.97	2	0.28	233	37.7
Plot 6	1975	252	28.34	8	3.06	29	12.46	289	43.86
	1997	213	32.52	6	2.73	10	4.29	229	39.54
	2012	180	28.93	0	0.00	3	1.92	183	30.85
Plot 7	1975	57	13.05	172	45.84	7	13.05	236	71.94
	1997	78	12.14	115	41.24	2	0.71	195	54.09
	2012	380	24.14	7	1.24	0	0.00	387	25.38

Others: *Acer pseudoplatanus*, *Acer platanoides*, *Betula pendula*, *Populus tremula*, *Salix caprea*, *Sambucus racemosa*, *Sorbus aucuparia*, *Ulmus glabra*.**Fig. 4.** Tree spatial patterns of *Fagus sylvatica* saplings and trees in the DBH range 1–19 cm represented by pair correlation function $g(r)$ in 2012. We calculated mean value of $g(r)$ from seven 1 ha plots (solid line) and its 95% nonparametric bias-corrected and accelerated confidence intervals (dotted line). If the values of BC_a confidence interval are larger than theoretical value of Complete Spatial Randomness (CSR, dashed line) then the trees show clustering. If the values of BC_a confidence interval are smaller than theoretical value of CSR then the trees show a regular distribution. The variable “r” refers to distance.

stems show a negative correlation (class S789) (Fig. 5). Beyond saplings, *Small-sized trees* (DBH 10–24 cm) showed the highest and the longest negative spatial relationship with other individuals. By contrast, in the category *Large-sized trees* (DBH ≥ 55 cm), the interval with negative association to other individuals of the same population was shortened. We did not perform these analyses for spruce due to the low numbers of individuals.

3.2.3. Spatial associations to gap-makers and surviving trees

Generally we did not find any typical shape in the spatial relation between beech saplings from 2012 and gap-makers of all species from 1997 to 2012 (Fig. 6). The similar pattern of relationship between saplings and gap-makers appeared on plots 1, 2, 7, where the sharp decrease of spruce population in number of trees

and basal area (Table 3) occurred over study period. On these plots the marks of negative relationships for lower sapling categories were replaced by marks of positive correlation from categories S0506 and S789.

As far as the relationship between beech recruits and conspecific surviving trees is concerned, we could not reject independence of components hypothesis in most cases, but there were tendencies towards a negative correlation between recruits and surviving trees to the distance 2.5 m (Fig. A4).

3.2.4. Spatial relationships between beech and spruce

In each plot where the spatial relationship between beech and spruce could be evaluated over the study period 1975–2012 (Plots 1, 2), we observed a similar dynamic (Fig. 7). In 1975 beech and

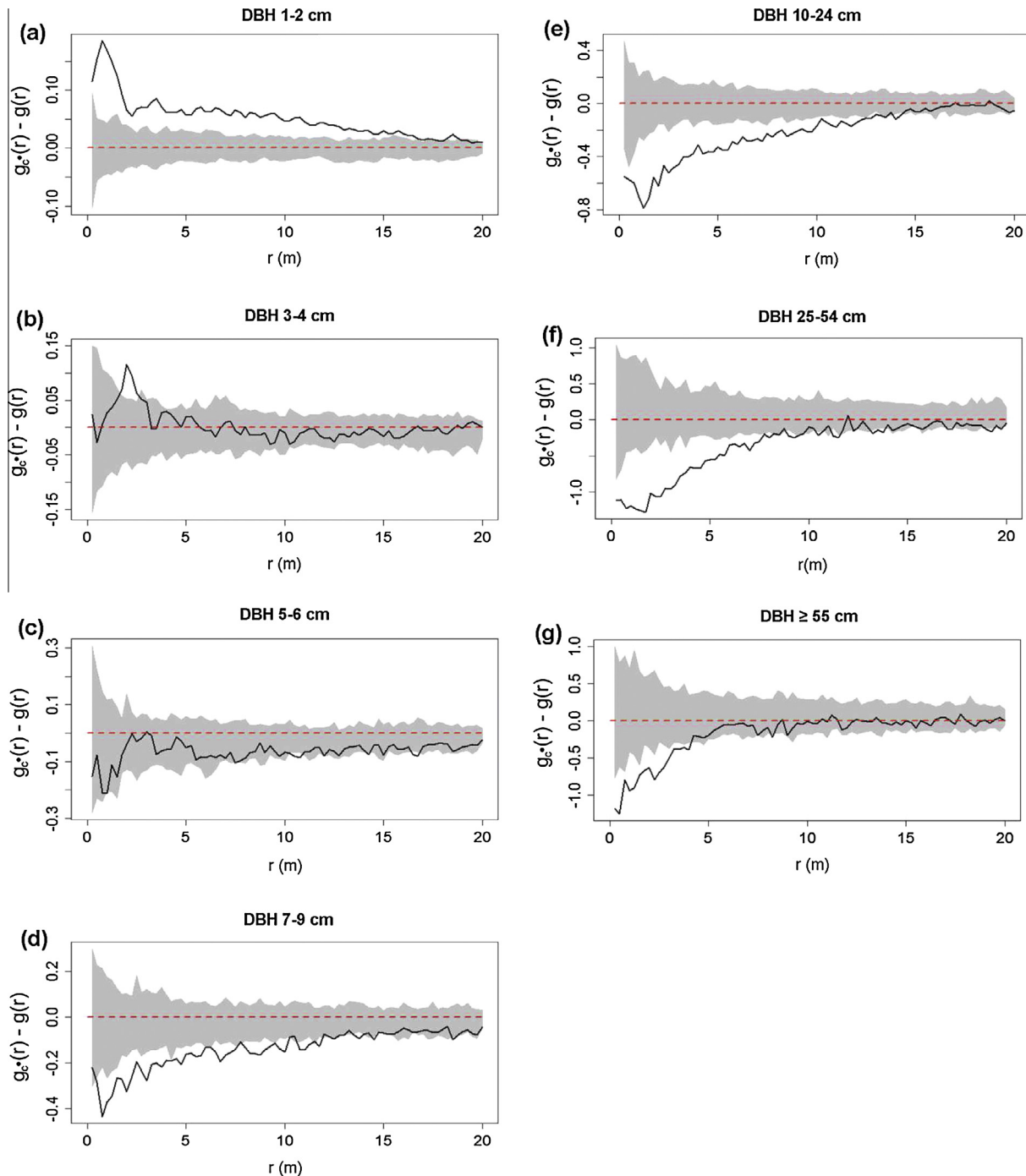


Fig. 5. Test statistic for random labelling of *Fagus sylvatica* tree (sapling) categories from the Plot 1 shows spatial relations between size categories. We generated 99 simulations of our null model to obtain pointwise critical envelopes for this model (grey lines). If the value of our observed statistic (solid line) is larger than the value of pointwise critical envelopes then the tree (sapling) category show positive spatial correlation to other conspecific individuals. If the value of our observed statistic is smaller than value of pointwise critical envelopes then tree (sapling) category show negative spatial correlation to other conspecific individuals. In the grey zone, we cannot reject the null hypothesis of random labelling. The variable “r” refers to distance.

spruce trees were negatively spatially associated. In 1997 zero spatial relationships dominated with short intervals of negative correlation, for example at 3 m on Plot 1 and 16 m on Plot 2 (Fig. 7c, d). The tendency towards the disappearance of negative relationships was fully realized in 2012, when once again zero spatial relationships were typical and even positive relationships occurred at ca. 17 m (Fig. 7).

The spatial pattern between saplings and trees of other species differed for beech and spruce (Fig. 8). Beech saplings

showed no significant spatial relationships with spruce trees, while spruce saplings were negatively correlated with beech trees to 5 m.

We could not reject the null assumption of independent of components for spatial relationship between beech and spruce saplings (Fig. A5). However, the development of the function as well as the short deviation intervals from the null model indicated a weak trend towards negative spatial correlation with increasing size of individuals.

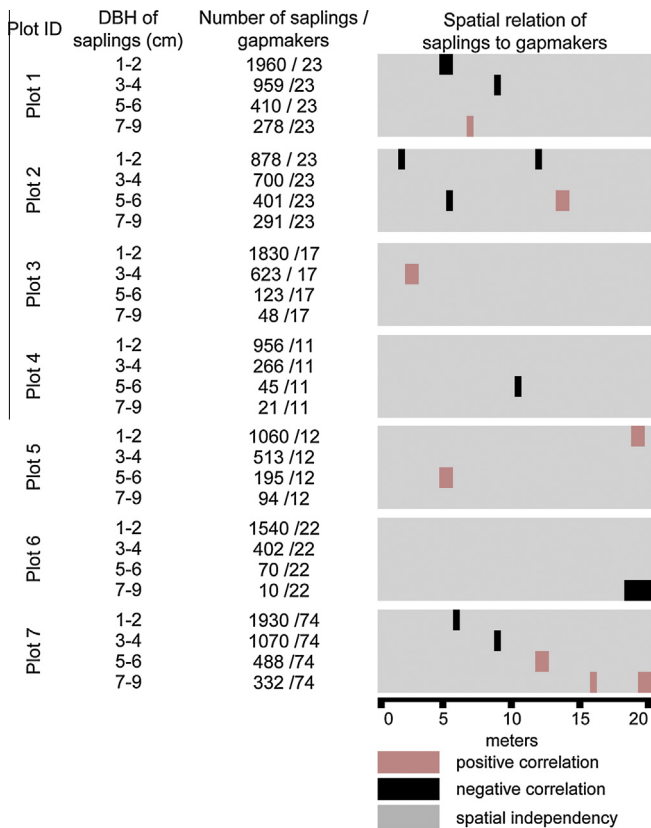


Fig. 6. Spatial relationships between *Fagus sylvatica* saplings of 2012 and *Gap-makers* of all species from the period 1997–2012. *Gap-makers* - trees with DBH ≥ 55 cm which dead in the period 1997–2012. We tested null model of the independence of components hypothesis. For single values of r (1–20 m, step 0.5 m) significant spatial distributions were determined through 99 simulations obtained by random shifts of sub-patterns (saplings, gap-makers), independently of each other.

4. Discussion

Over the past 37 years, the beech population in this iconic unmanaged European forest has been characterized by an increase in the number of individual stems, with high recruitment and population growth. In 2012 beech dominated tree species composition. Over the same period, the number of spruce and fir stems, traditionally important European forest species, sharply decreased. Significant decreases of spruce population followed three major disturbances: hurricanes Kyrill (2007) and Emma (2008) as well as a subsequent bark-beetle outbreak. It seems that beech will become the only dominant tree species in forests like the upland Zofin habitats, and that spruce will persist only on strongly water affected sites (i.e. 15% of ZFDP area). It is only in saturated habitats where the spruce escapes from the competitive pressure of beech.

The tree spatial patterns of beech trees (DBH ≥ 10 cm) were rather variable in the study period of 37 years. Unsurprisingly, the new recruits tended to show clustered spatial patterns, indicating the accelerated growth of advance regeneration in gaps (Aldrich et al., 2003; Ward et al., 1996; Wolf, 2005). However we observed few dead beech trees in these plots in the study period, which suggests that beech were not responsible for the large gaps of which they took advantage. However plots with the highest increase in recruits were in 1975 characterized by the highest numbers of spruce stems. The numbers of spruce sharply decreased to 2008 and beech filled former areas of spruce growth.

By contrast, we observed a strong pattern of self-thinning in Plot 6, where small-sized beech trees entirely dominated in

1975. The number of dead beech trees was the highest in this plot and clustering disappeared in 1997. This process was also connected with the highest proportion of clustering mortality. This appears to show that although small-sized trees were randomly distributed in the plot, intensive competition for space can be discerned from these clear patterns.

As opposed to beech, the distribution of spruce was generally more clustered even in the category *large-sized trees*. Higher clustering can be connected to the spatial restrictions of spruce (Firm et al., 2009; Simon et al., 2011) as well as to the lower intensity of competition as compared to the beech populations (Pretzsch and Schütze, 2005; Zeide, 1985).

Our analysis of the spatial relations between beech recruits and other conspecific trees (surviving trees) either showed zero association or suggested negative association to 2.5 m. This is in accordance with the conclusions of Martínez et al. (2013), who studied younger regeneration stages. They noticed a positive association from 5 m between beech seedlings and conspecific adult trees as well as a relative lack of beech seedlings near old conspecifics with respect to its overabundance at medium to large scales. They explained this by Janzen–Connell dynamics (Janzen, 1970), which proposes that survival of seedlings declines with increasing density or proximity to con-specific neighbors, primarily due to the mortality caused by natural enemies and strong intraspecific competition.

As expected, the spatial distribution of beech saplings (DBH 1–9 cm) was clustered in all categories. However, in larger size classes, we observed an increase in the average values of the pair correlation function. Increasing clustering with the increasing size of individuals contradicts the classical theory that clustering in such cases gets reduced under the influence of competition (Lepš, 1990). We argue that this phenomenon can be connected to the spreading strategy of beech. Saplings in the smallest categories fill in larger spaces, which are more loosely defined than the growing conditions of individuals in larger DBH size-class categories. This can lead to a relative increase in clustering in places more favourable for advanced growth. Furthermore, the shortening of the interval in which clustering is significant can indicate higher spatial restrictions. Szwagrzyk and Szewczyk (2001) noticed that emergence of beech seedlings was almost independent of relative light intensity, and so random spatial patterns of distribution prevailed. However, the long-term survival of seedlings was strongly related to higher levels of relative illumination. This was confirmed by Chmelař (1957), who connected the successful growth of beech recruits to places with increased light availability. On the other hand, our analysis of spatial relationships between saplings and gap-makers did not reveal a clear pattern. Spatial associations appeared to be weakly positively correlated. Similar relationships between gap-makers and the growth of larger beech recruits have been observed in a fir-beech forest (Janík et al., 2014). Although fir recruits were strongly connected to gap-makers, beech recruits were not.

In mountain spruce-beech forests, the dominant coarse-scale disturbance agent is wind, followed by insects and pathogens. Splechna et al. (2005) found that most disturbance events thin rather than clear stands. Small gaps predominate in most old-growth forests (Kneeshaw and Bergeron, 1998). It was documented that beech closes small gaps via the growth of lateral branches (Lemoine et al., 2002). The strategy of beech is evidently based on the maintenance of space occupation. 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 the self-thinning stage (Pretzsch, 2005). Collet et al. (2008) found that thirteen years after gap creation all gaps were fully closed and regeneration was almost exclusively dominated by

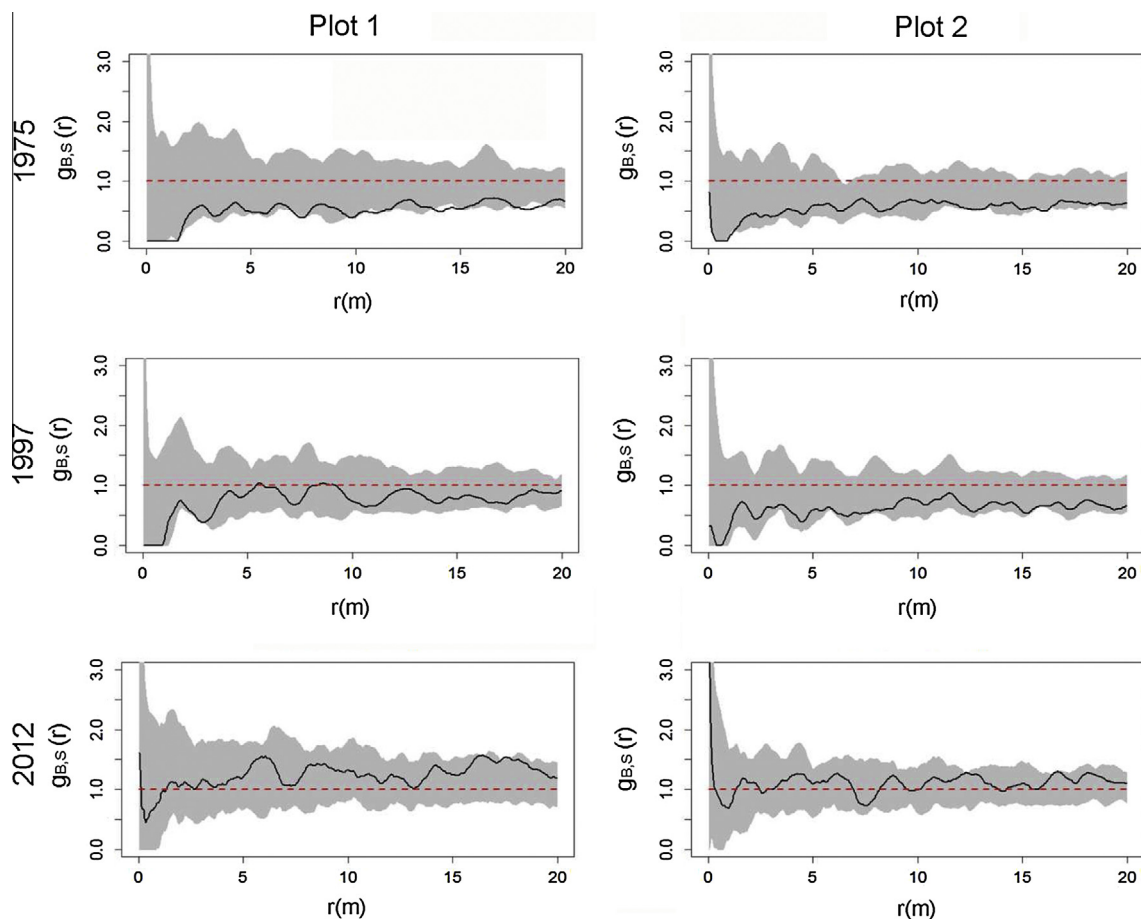


Fig. 7. Spatial relationships between (a) *Fagus sylvatica* and *Picea abies* trees (DBH ≥ 10 cm) at Plot 1 (a, c, and e) and Plot 2 (b, d, and f) in 1975 (a and b), 1997 (c and d) and 2012 (e and f). We constructed pointwise envelopes resulting from 99 simulations of the null model of independence of components hypothesis (grey line). If the value of observed cross-pair correlation function (solid line) is larger than the value of the pointwise envelopes then the *Fagus sylvatica* trees and *Picea abies* trees are positively associated. If the value of observed function is smaller than value of the pointwise envelopes then species are negatively associated. In the grey zone, we cannot reject the null hypothesis of independency of components. The variable “r” refers to distance.

beech and *A. pseudoplatanus* seedlings in former coppice with-standards forest with high broadleaved tree species diversity. However, 85% of the dominant seedlings were already established when the storm occurred. This is in accordance with our previous findings (Janik et al., 2014) documenting that advanced beech regeneration can successfully grow under a closed canopy.

The question is how long can beech saplings persist in low-light conditions? We used the random labelling null hypothesis for the analysis of spatial relationships between individual size categories of beech saplings and trees to other individuals to answer this question. The random labelling null hypothesis is appropriate when the size categories are considered to result from different growing conditions affecting a posteriori a single even-aged cohort (Goreaud and Pélissier, 2003). In our study, we were looking for size categories that begin to spatially differ from the other categories. Results in all plots were consistent. Saplings to 4 cm were positively spatially correlated with other individuals and did not create spatially isolated groups. In category S0506 random spatial distribution prevailed. Category S789 was already decidedly negatively spatially correlated to other individuals. We believe that this negative association with other individuals could be caused by a quick growth reaction to spatially limited higher light availability. This idea is supported by the results of clustering in individual categories as well. The highest average values of the pair correlation functions and their confidence intervals were reached for categories S0506 and S789. Clustering in thinner and thicker trees

was lower. Moreover in category S0506, we observed the most signs of positive spatial relationships to gap-makers. It appears that advanced beech recruits can grow to 4 cm DBH under a closed canopy, but to grow larger, they generally require a significant canopy disturbance.

The spatial relationship between beech and spruce markedly changed over 37 years. As a result of hurricane Kyrill and the subsequent bark-beetle outbreak, the number of living spruces markedly decreased in all plots. At the same time, in 2012 we observed a massive wave of beech recruits in all plots where spruce had occurred in larger quantities. In 1975 the spatial relationship between beech and spruce was typically negative. This disappeared during the 30-year study period, and in 2012 zero spatial relationship prevailed with signs of positive correlation at larger distances. From this it follows that the wave of recruits did not occur only on those places earlier occupied by spruce but happened over the entire area. However, it did not avoid earlier spruce-dominated places. Considering that the bark-beetle attack followed hurricane Emma in 2008, the wave of new beech recruits did not appear as a result of this disturbance. It is more likely that higher light availability facilitated the growth of beeches already present, which then exceeded the 10 cm boundary en masse. As a vertical fast growing tree, spruce is efficient in space exploitation under constant conditions, but far more susceptible to disturbances and less well equipped to overcome them when compared with beech (Pretzsch and Schütze, 2005).

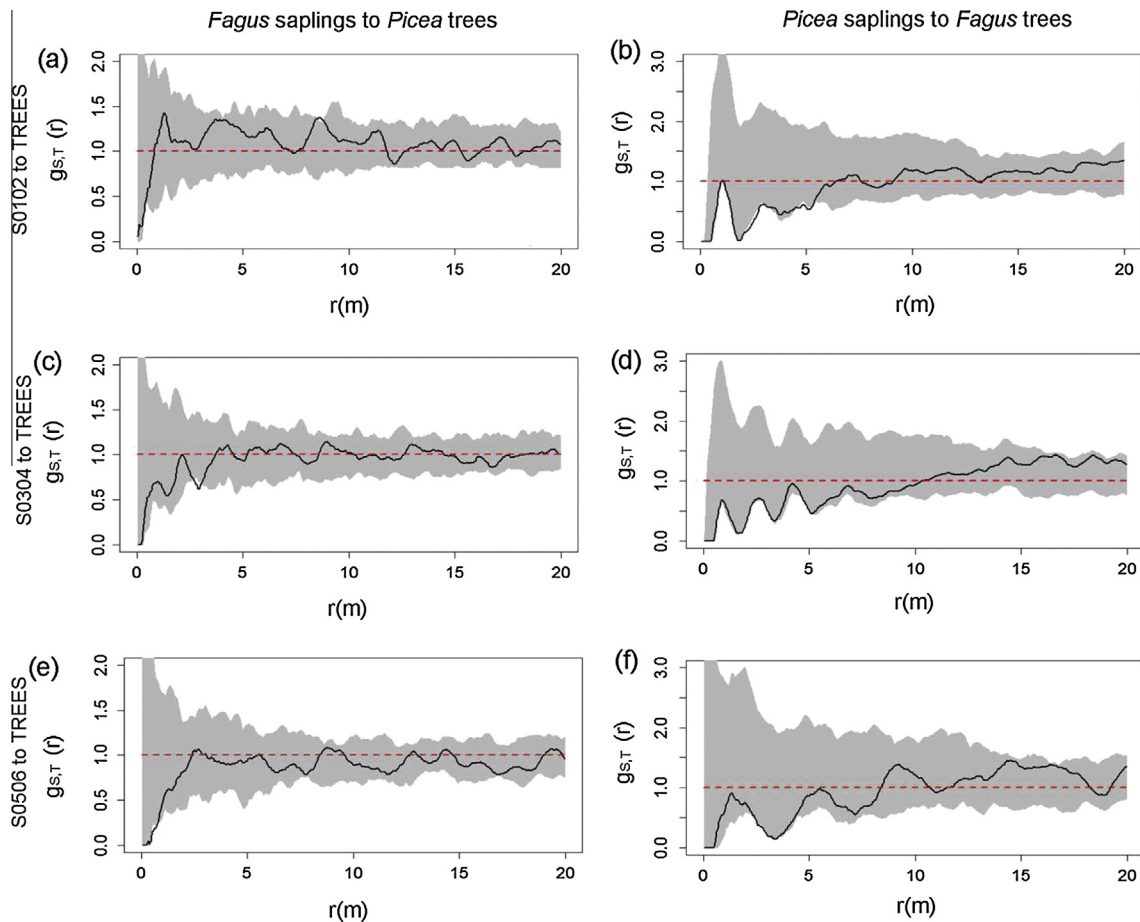


Fig. 8. Spatial relationships between *Fagus sylvatica* saplings and *Picea abies* trees (a, c, and e) and *Picea abies* saplings to *Fagus sylvatica* trees (b, d, and f) at Plot 2 in 2012. Trees – trees with DBH ≥ 10 cm, S0102 – DBH 1–2 cm, S0304 – DBH 3–4 cm, S0506 – DBH 5–6 cm. We constructed pointwise envelopes resulting from 99 simulations of the null model of independence of components hypothesis (grey lines). If the value of observed cross-pair correlation function (solid line) is larger than the value of the pointwise envelopes then the saplings and heterospecific trees are positively associated. If the value of observed function is smaller than value of the pointwise envelopes the saplings and heterospecific trees are negatively associated. In the grey zone, we cannot reject the null hypothesis of independency of components. The variable “r” refers to distance.

The results of the spatial relationship analysis between saplings and adult trees of other species are also of interest. While spruce saplings are negatively correlated to beech trees, beech saplings have no detectable spatial relationship with spruces. It follows from our results that although beech regeneration does not primarily focus on spruce stands, beech gradually replace spruce through a space-occupation strategy because its recruits are already present before beech or spruce canopy disturbance.

Two questions arise from the fact that beech continued to dominate despite storms Kyrill and Emma: (1) what other disturbances might allow other species to colonize beech-dominated stands? and (2) why did this forest contain such a strong presence of spruce and fir over the last 200–400 years if beech is currently so dominant? In our research in Žofin, we found a high amount of charcoal in the soil (*unpublished data*). These footprints of fire originated from early Holocene, and fire events were clearly an important component of forest dynamics until circa 6000 years before present. At that time, fire presence (based on the charcoal record) diminished to reappear again in the Middle Ages. Changes in fire frequencies are probably connected with the development of tree species composition (particularly increasing representation of *F. sylvatica*) or with colonization of the mountains by humans, but timing and interaction between fires and woody species compositions remain an important research challenge. According to Giesecke et al. (2007) the presence of frequent fire disturbances could limit the range of beech as fire sensitive tree. On the other

hand the role of fire in beech spreading is intriguing and existing research often differs in conclusions (Bradshaw and Lindblath, 2005; Tinner and Lotter, 2006).

5. Conclusions for management

According to our results, the main change in the spatial distribution of beech emerges in the 4–6 cm dbh size class. In this phase, the beech is changing from being positively correlated with conspecific stem density to being negatively correlated. Beech is light-demanding, and therefore responds with fast growth when light availability increases (due to a lower density of neighboring trees). This pattern may be of service in improving near-natural silviculture practices. The traditional silviculture system used in European beech dominated forests is the shelterwood system. It has two variants: (i) a large-scale regular shelterwood system (Schirmschlag) and (ii) an uneven “dark” shelterwood system (Femelschlag) (Röhrig et al., 2006). In the first case the last two phases of this large-scale shelterwood system (release felling and final felling) are done if the new generation of trees is shorter than 4 m. If we follow the natural processes (presented in Žofin) the natural spatial selection (i.e., self thinning) and the light release comes when tree height is greater than 6 m (\sim DBH 4–6 cm). This means that beech responds to light later in development than the shelterwood system predicts. We therefore propose a silviculture

experiment in which a more prolonged “shade” growing phase is implemented. It is necessary to test not only the growth reaction, but also the morphological stem quality of beeches as well. In the second case, small gaps enlargement would create the high-light conditions that release young beech – which recommends enlarging gaps when tree height is 6–7 m. This would also be appropriately tested in a silviculture experiment.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.05.017>.

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