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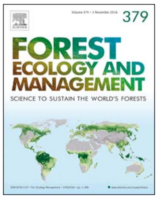

Spatial patterns of tree species in Suserup Skov – a semi-natural forest in Denmark

Shaaban Ghalandarayeshi[a,b,*], Thomas Nord-Larsen[a], Vivian Kvist Johannsen[a], Jørgen Bo Larsen[a]

[a] Department of Geosciences and Natural Resource Management, University of Copenhagen, Denmark
[b] Department of Statistics, Gonbad Kavous University, Gonbad Kavous, Iran

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ABSTRACT

In Europe, concerns regarding the provision of ecosystem services from forests, such as biodiversity, has led to a widespread conversion from even-aged to close-to-nature forest management. These concerns have also led to a demand for quantifying stand structure, dynamics, and species diversity in order to evaluate ecosystem status and devise management action. In this study, species distribution, species association, and size diversity in a semi-natural, unmanaged beech forest in Denmark were analyzed using spatial indices including uniform angle index, mingling index, and differentiation index and spatial functions including pair correlation function, bivariate pair correlation function, mark variogram, and the Wiegand scheme. To analyze the spatial patterns of tree species, two plots, one in a less disturbed part of the forest and the other in a more recently disturbed part, was selected. Based on the spatial functions, all species showed a clustered pattern as a result of forest dynamics. *Fagus sylvatica* L. was segregated from other species and was more likely to form pure groups. In contrast, *Ulmus glabra* L.-*Fraxinus excelsior* L. and *Ulmus glabra* L.-*Acer psedoplatanous* L. showed positive association. All species in the less disturbed part of the forest showed positive spatial correlation of tree diameters, probably as a result of gap-phase dynamics. However, a lack of spatial correlation of tree diameters was observed for beech and elm trees in the more recently disturbed part of the forest. Our results indicated that spatial functions using stem-mapped data provide more reliable results and additional insights into the stand structure than neighborhood based indices. The study findings can be used to align forest management practices with goals of protecting biodiversity in managed forest.

1. Introduction

Close-to-nature forest management is claimed to protect biodiversity as well as the ecological structures and functions of the forest and thus to provide long term sustainability, while satisfying the economic needs of the forest owner (Hofle, 1995; Larsen, 1997; Nord-Larsen et al., 2003). When developing silvicultural practices that mimic natural forest structures and processes, natural forests have served as basic reference. In natural forests, the spatio-temporal structure of trees results from a large number of feedback loops of processes caused by the underlying disturbance regime in time and space. For example, current structure (i.e. tree size and occurrence of gaps) have direct impact on seeding and rejuvenation processes, which in turn affects future forest structure. Since different processes modify forest structure, assessment of current forest structure may be used for interpretation of the underlying processes which are commonly difficult to measure (Pretzsch, 2010). As such interactions have implications for designing forest management practices a large scientific effort has been devoted to the assessment and analysis of forest structure.

Previously, natural forest structure has been characterized by the mere distribution of tree sizes (Leibundgut, 1993; Korpel, 1995; Emborg et al., 1996; Emborg, 1998) and the degree of size heterogeneity has been characterized by the Gini coefficient (Lexerod and Eid, 2006; Nord-Larsen et al., 2006). However, indices such as the Gini and Shannon diversity index (Shannon, 1948) do not include the spatial structure and hence interactions between individual trees. Spatial functions such as Ripleys's $K(r)$ function and pair correlation function, $g(r)$, are among several functions that are used for analyzing unmarked point patterns and only describe distribution of trees without consideration of differences in species or size (Ward et al., 1996; Chokkalingam and White, 2001). In contrast, the bivariate pair correlation function and mark variogram, that are used for analyzing marked point patterns, allow simultaneous consideration of positions of trees and their species or size (Stoyan and Penttinen, 2000; Pommerening, 2002; Wiegand and Moloney, 2004; Wälder and Wälder, 2008; Pommerening and Särkkä, 2013). However, all above-mentioned

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[*] Corresponding author at: Department of Statistics, Gonbad Kavous University, Gonbad Kavous, Iran.
E-mail address: sghalandar@yahoo.com (S. Ghalandarayeshi).

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spatial functions require datasets with known tree positions. In contrast, some neighborhood based indices can be used for quantifying forest spatial structure with little effort as by-product during a normal field sampling: the uniform angle index (von Gadow et al., 1998), mingling index (von Gadow, 1993), and dominance index (von Gadow et al., 2012).

In a study of the dynamics in a temperate, semi-natural beech forest in Denmark (Suserup Skov), Emborg et al. (2000), developed a model of the forest cycle that included five sequential phases: innovation, aggradation, early biostatic, late biostatic and degradation. As each phase occurs asynchronously in patches of varying size, the result was characterized as a fine-grained shifting mosaic of successional stages. The characterization of forest structure and thus the underlying processes in Suserup Skov (Emborg et al. op. cit.) and similar examples (Watt, 1925, 1947; Christensen et al., 2007; Heiri et al., 2009) has served as a reference for the development of close-to-nature forest practices (Angelstam et al., 2004; Larsen et al., 2010; Larsen, 2012). However, the methodological approach in these studies was mainly descriptive and the scientific description and understanding of forest structures was likely subjective. In this study we therefore aimed to quantify the observed spatial patterns using a series of different spatial indices and functions. We believe that knowledge on spatial patterns and the relationship between different species in a natural forest will be useful as a reference to devise strategies for close-to-nature forest management.

The research questions may be formulated as:

(1) How is the horizontal distribution of dominant tree species in Suserup,
(2) Are there any interactions between different tree species (segregation or aggregation) or are they independently distributed, and
(3) Is there any spatial correlation between tree diameters, and if so, at what scale are they spatially correlated?

Finally, we examined the consistency of the results on questions 1–3 obtained by neighborhood based indices and spatial functions at small scales. The simplicity of neighborhood-based indices including uniform angle index, mingling index and differentiation index provide more possibilities for the application in a normal inventory, therefore, they are still being used and the papers based on them are still being published in international peer-reviewed journals (Hui et al., 2011; Li et al., 2012, 2014; Zhao et al., 2014; Meng et al., 2016; Li et al., 2017).

It was hypothesized that a deviation from a random distribution towards more aggregated patterns should be found due to gap regeneration processes. Considering the mixed species forest in Suserup, it was expected that the spatial pattern of species and their mingling characteristics would be different, given their differences in terms of requirements and role in the succession. It was also assumed that the results obtained by spatial indices should be consistent with the results from spatial functions at small scales.

2. Materials and methods

2.1. Study area

Suserup Skov is a 19.2 ha semi-natural, nemoral beech (*Fagus sylvatica* L.) dominated forest located on central Zealand (UTM zone 32: E661870, N6139930). The climate is cool-temperate with a mean annual temperature of 8.8 °C and a mean annual precipitation of 674 mm, which is quite evenly distributed across the year. However, the most of precipitation occurs during late summer and autumn (average climatic data 2001–2010 (Wang, 2013)). The soil parent material is a nutrient-rich, calcareous glacial till with approximately 20% clay and the soil has been classified as a Haplic Luvisol (Vejre and Emborg, 1996; Vesterdal and Christensen, 2007).

The forest cover of Suserup Skov dates back to before 4200 BCE (Heilmann-Clausen et al., 2007). According to management plans dating back to the 1850 s, the forest was managed as a minimal intervention forest park. Suserup Skov was formally conserved for biological and recreational reasons in 1925. Although the conservation plan did not exclude fellings, only limited interventions occurred until 1961, when its protection status was changed to a non-intervention forest. A detailed description of the history of Suserup Skov can be found in Heilmann-Clausen et al. (2007).

Today, Suserup Skov is a mixed deciduous forest with an average basal area of 37.5 m^2 ha^{-1}. Beech is the dominating species and occupies 53% of the basal area. Among other important species are pendunculate oak (*Quercus robur* L., 18%), ash (*Fraxinus excelsior* L., 18%), common alder (*Alnus rubra* L., 7%), and sycamore maple (*Acer pseudoplatanus* L., 2%). However, beech, elm (*Ulmus glabra* L.), and ash were the most abundant species in the studied plots.

2.2. Measurements

When the study of Suserup Skov was initiated in 1992 and remeasured in 2002, the forest was divided into a regular grid of 50 × 50 m, and the grid intersections were marked with metal pipes. When measurements were repeated in the autumn of 2012 and the spring of 2013, the original grid was maintained as a practical partition of the research area. The positions of the trees were captured with a Trimble GPS Pathfinder Pro XRS receiver mounted with a Trimble Hurricane antenna and a Trimble Geo Beacon for real-time differential correction. This equipment is expected to yield sub-one meter precision even under dense canopies. All standing live trees with *dbh* > 5 cm were cross callipered at breast height.

In this study, two study areas were selected in Suserup for stand structure analyses: (a) first plot (100 x 200 m) in the western part of the forest and (b) second plot (100 x 60 m) in the eastern part. The western part is dominated by beech trees and shows little evidence of disturbances during the past 200 years. Contrary, the eastern part is dominated by beech and old oak trees, showing evidence of more recent grazing and seeding of oak around 1820 (Emborg et al., 1996). Further, in the eastern part, sycamore maple has more recently spread naturally into the forest from the east, possibly from trees planted outside the forest. Both selected plots were rather uniform with respect to the soil, topography (Heilmann-Clausen et al., 2007), and species distribution while the forest border within a buffer zone of approximately 50 m was avoided.

2.3. Analyses

As general description of the two plots, summary statistics such as mean *dbh*, standard deviation of *dbh*, basal area per hectare, stand density (number of stems/ha), relative species density (number of stems of a species divided by the total number of stems), and Gini index for basal area were calculated for each plot.

The spatial distribution of trees was assessed using both spatial indices (uniform angle index, mingling index, diameter differentiation index) and spatial functions (univariate and bivariate pair correlation function, mark variogram, and the Weigand scheme). The spatial indices were all calculated for each tree and the spatial structure of the forest was characterized by the distribution of the indices. Analyses were only carried out for the most abundant tree species in each plot including beech, ash, elm, and sycamore maple. Spatial indices and spatial functions were calculated using Crancod 1.4 (Pommerening, 2006) and spatstat 1.41–1 (Baddeley and Turner, 2005), respectively.

2.3.1. Spatial indices

The Winkelmass index (W_i) or the uniform angle index (*UAI*) describes the degree of regularity of the spatial distribution of the four trees nearest to a reference tree *i*. The concept is based on the classification of the angles α_j between the immediate neighbors of the four trees with reference to a sample tree. An immediate neighbor is the tree next to a sample tree in a clockwise (or anticlockwise) direction (von Gadow and Hui, 2002). To calculate the Winkelmass index, always the smaller of the two angles is used.

Assuming complete regularity of the position of the four nearest neighbors around a reference tree *i*, the expected standard angle (α_0) between two neighbors would be $\alpha_0 = 360/4 = 90°$. However, based on a simulation study, von Gadow and Hui (2002) found the optimum standard angle producing a random distribution to be 72°.

W_i is defined as the ratio of all the angles α_j smaller than the standard angle α_0 to the total number of α_j (von Gadow et al., 2012):

$$W_i = 1/4 \sum_{j=1}^{4} V_{ij} \text{ with } V_{ij} = \begin{cases} 1, & \alpha_j < \alpha_0 \\ 0, & otherwise \end{cases} \text{ and } 0 \leqslant \mathrm{W_i} \leqslant 1 \tag{1}$$

$Wi = 0$ indicates that the trees in the vicinity of the reference tree are regularly distributed, whereas $Wi = 1$ points to an irregular or clumped distribution. Zhao et al. (2014) argued that the accuracy of the evaluation of the type of spatial distribution is directly related to the confidence interval, and studies were required to estimate the confidence interval for communities with varying densities. To do this, they presented a method for estimating the standard deviation of W_i based on the tree density.

The mingling index (M_i) describes the species variety in the neighborhood of a given reference tree and is defined as the proportion of the four nearest neighboring trees of another species (von Gadow et al., 2012):

$$M_i = 1/4 \sum_{j=1}^{4} V_{ij}, \tag{2}$$

with

$$V_{ij} = \begin{cases} 0, & \text{neighbor } j \text{ belongs to the same species as the reference tree } i \\ 1, & otherwise \end{cases}$$

and $0 \leq M_i \leq 1$.

$M_i = 0$ indicates that all the neighbors belong to the same species as the reference tree (zero mingling, homogenous group or segregation from other species).

$M_i = 1$ indicates that all four neighbors belong to different species (very high mingling, heterogeneous group or the attraction of the reference species to other species).

The differentiation index (T_i) quantifies the size differentiation between neighboring trees and is calculated based on the ratio between thinner and thicker *dbh* of two neighboring trees (von Gadow et al., 2012).

$$T_i = 1 - 1/4 \sum_{j=1}^{4} [\min(d_i,d_j)/\max(d_i,d_j)], \tag{3}$$

where d_i and d_j are diameters of subject tree *i* and the neighbor *j*, respectively.

Index values are between 0 (no differentiation) and 1 (complete differentiation).

2.3.2. Spatial functions

The above-mentioned indices only provide information on spatial patterns of trees at short distances (up to the distance of the four nearest neighbors from the reference trees). However, the interaction between trees might be different at larger scales. In contrast, spatial functions provide information on the spatial distribution at different scales. In our analyses with the spatial functions, we assumed within-plot homogeneity of site conditions with constant density, which was reasonable based on our method of plot selection. To avoid edge effects, translation correction was used in the analyses (Pommerening and Stoyan, 2006; Grabarnik et al., 2011).

We used the univariate pair correlation function, $g(r)$ for assessing the spatial distribution patterns of all living trees and used the bivariate pair correlation function, $g_{12}(r)$ for assessing the spatial interaction between different species. The univariate pair correlation function is a distance-dependent correlation function for mapped point patterns, proportional to the derivative of the widely used *K*-function with respect to distance (*r*) (Ripley, 1977; Stoyan and Stoyan, 1994; Illian et al., 2008), i.e.

$$g(r) = K'(r)/2\pi r \quad \text{for r} > 0, \tag{4}$$

where $K'(r)$ is the derivative of $K(r)$.

The univariate pair correlation function can be interpreted as expected density of points within a given distance *r* of an arbitrary point, divided by the intensity of the pattern (Stoyan and Stoyan, 1994). The univariate pair correlation function can be used to test if the distribution of trees is random, clustered, or regular, and at which scales these patterns occur. When the trees are randomly distributed over the entire plot, $g(r) = 1$, under aggregation $g(r) > 1$, and under regularity $g(r) < 1$ (Wiegand and Moloney, 2004; Baddeley and Turner, 2005; Illian et al., 2008).

The bivariate pair correlation function, $g_{12}(r)$ is the ratio of the observed mean density of points of pattern 2 at distance *r* of an arbitrary point of pattern 1 to the expected mean density of pattern 2 (Stoyan and Stoyan, 1994; Lan et al., 2012). Under the null hypothesis for bivariate spatial analysis, two types of points (here species) are independently and randomly distributed over the entire plot. For an independent distribution $g_{12}(r) = 1$, under attraction $g_{12}(r) > 1$, and under repulsion $g_{12}(r) < 1$ (Wiegand and Moloney, 2004; Baddeley and Turner, 2005; Illian et al., 2008).

In addition to the bivariate pair correlation function, all associations of the tree species were categorized using the scheme developed by Wiegand et al. (2007a). The commonly used bivariate Ripley K function, $K_{12}(r)$ and nearest neighbor distance distribution function, $D_{12}(r)$ statistics were implemented to construct the two axes of the scheme. The statistic $K_{12}(r)$ measures concentration as a ratio of the average number of type 2 events within a distance *r* of an arbitrary type 1 event to the density of the type 2 events ($\hat{\lambda}_2$) in the whole study region. The statistic $D_{12}(r)$ evaluates the fraction of points of the reference type 1 that have their nearest type 2 neighbor within a distance *r* (Diggle, 2003; Illian et al., 2008). In the case of complete spatial randomness, $D_{12}(r) = 1 - \exp(-\lambda_2 \pi r^2)$. The two axes $P(r)$ and $M(r)$ are defined as follows (Getzin et al., 2014):

$$P(r) = \frac{(D_{12}(r) - E[D_{12}(r)])}{SD[D_{12}(r)]}, \tag{5}$$

$$M(r) = \frac{(K_{12}(r) - E[K_{12}(r)])}{SD[K_{12}(r)]}, \tag{6}$$

where $D_{12}(r)$ and $K_{12}(r)$ are estimated from observed data and the operators $E[.]$ and $SD[.]$ indicate the expectation and standard deviation of summary statistics, respectively, in the neighborhood *r* under null model. The theoretical value of the two summary statistics $K_{12}(r)$ and $D_{12}(r)$ under the null model are subtracted from those observed to set the case of null association $P(r) = M(r) = 0$ (Wiegand et al., 2007a; Martinez et al., 2010; Wang et al., 2010; Wiegand et al., 2012).

The statistics $M(r)$ and $P(r)$ evaluate two fundamental aspects of bivariate point patterns. The $P(r)$ will be negative if the proportion of nearest neighbors within distance *r* is smaller than expected, and it will be positive if the proportion is larger than expected. Similarly, $M(r)$ will be negative if the average number of neighbors within distance *r* is smaller than expected, and it will be positive if the average number is larger than expected. In addition to independence, four other types of spatial associations are possible for each neighborhood *r* (Wiegand et al., 2007a, 2012). These are as follows:

Type 0: "independence" in which neither $K_{12}(r)$ nor $D_{12}(r)$ show significant departures from independence. The species pairs in this type will be located close to the origin of the scheme.

Type I: "Segregation" in which both the average number of neighbors within distance *r* and the probability of finding a heterospecific individual within neighborhood of the radius r are less than expected under independence ($M(r) < 0$ and $P(r) < 0$).

Type II: “partial overlap” in which the mean number of trees of species 2 within neighborhoods of radius r around trees of species 1 is larger than expected but the probability that a tree of species 1 has a neighbor of species 2 is smaller than expected ($M(r) > 0$ and $P(r) < 0$). This type is only possible for heterogeneous patterns.

Type III: “mixing” in which species 2 occurs on average more frequently than expected within the neighborhood of species 1 ($P(r) > 0$ and $M(r) > 0$).

Type IV: this association type corresponds to ($P(r) > 0$ and $M(r) < 0$) and is predicted to occur only rarely when trees of species 1 are highly aggregated and few trees of species 2 overlap the cluster of species 1 (Wiegand et al., 2007a).

We used mark variogram to study the spatial correlation of tree diameters. The mark variogram of a marked point process is analogous, but not equivalent, to the variogram of a random field in geostatistics. The mark variogram, $\gamma_m(r)$ is a measure of the similarity of the marks (here tree *dbh*) depending on the distance between points (Wälder and Stoyan, 1996; Stoyan and Penttinen, 2000; Stoyan and Wälder, 2000; Pommerening and Särkkä, 2013) and it provides two important characteristics: range of correlation and the strength of interaction as defined in Eq. (7):

$$\gamma_m(r) = 1/2E(m(x) - m(x+r))^2/\sigma_m^2, \qquad (7)$$

where, x and $x + r$ denote the locations of two arbitrary points. The numerator in Eq. (7) is the mean of the mark difference given that there is a point of the process located both at x and at $x + r$ (Baddeley, 2010). The denominator removes scale effects of marks and normalizes the mark variogram. When the distribution of trees is independent of the tree diameters, $\gamma(r)$ takes the value of 1. In the presence of segregation, correlation is negative and $\gamma(r) > 1$. In contrast, positive correlation indicates that the pairs of trees tend to have similar marks and results in $\gamma(r) < 1$.

2.3.3. General tests of hypotheses for spatial functions

The first null hypothesis of our study was that there was no deviation from complete spatial randomness (CSR) in the spatial distribution of each tree species. The population independence (or random superposition) hypothesis was used to test for inter-specific associations and species aggregation (Goreaud and Pelissier, 2003; Illian et al., 2008; Hui and Pommerening, 2014). The null hypothesis for spatial correlation of tree diameters was complete spatial independence of the tree diameter distribution. This hypothesis was tested using the random labelling test (Diggle, 2003; Illian et al., 2008; Hui and Pommerening, 2014).

Monte Carlo simulations were used to determine the significance of deviations from each null hypothesis by running 999 simulations for each analysis (Illian et al., 2008; Baddeley et al., 2014). In all analyses, if the observed values were outside the simulation envelope, the null hypothesis was rejected. To avoid edge effects, translation correction was used in the analyses (Grabarnik, et al., 2011; Pommerening and Stoyan, 2006).

3. Results

3.1. Non-spatial structural attributes

The species included in the structural analyses made up 90% of the total stem number in the two plots (Table 1). Species and size distributions differed clearly between the two plots. In the less disturbed plot, beech made up 55% of the stems with a mean diameter of 21.8 cm compared to a mean diameter of 42.3 cm and 10% of the stems in the more recently disturbed plot. Oppositely, sycamore maple made up 40% of the stems in the more recently disturbed plot compared to less than 2% in the less disturbed plot. In both plots, elm acted as a subcanopy species with a mean diameter of about 10 cm. Elm and ash had the lowest Gini index among trees in both plots. Shannon species diversity and evenness indices were 1.07 and 0.51 in the less disturbed plot and 1.31 and 0.63 in the disturbed plot respectively.

Overall, the diameter distribution was typical for an old-growth forest covering a wide range of diameter classes (Fig. 1). The distribution of elm and beech in the less disturbed plot showed a decreasing trend with increasing size. In contrast, ash had a bell-shaped

Table 1
Structural characteristics of the plots.

Forest attributes	Less disturbed plot				Disturbed plot			
	Beech	Elm	Ash	Others	Beech	Elm	Sycamore maple	Others
Density (N/ha)	321.5	163.0	82.5	13.5	73.3	291.6	285.0	70.0
Density proportion of species	0.55	0.28	0.14	0.02	0.10	0.40	0.39	0.09
Mean *dbh* (cm)	21.82	10.27	35.40	51.30	42.34	10.21	17.42	33.09
Max *dbh* (cm)	119.4	28.9	71.3	153.1	120.9	65.2	56.9	182.4
dbh (CV)	1.32	2.16	2.61	0.96	1.85	1.55	1.38	0.75
Gini index	0.47	0.39	0.39	0.69	0.50	0.57	0.63	0.83
Basal area (m^2/ha)	18.86	1.64	9.30	5.68	13.26	3.38	10.34	16.43

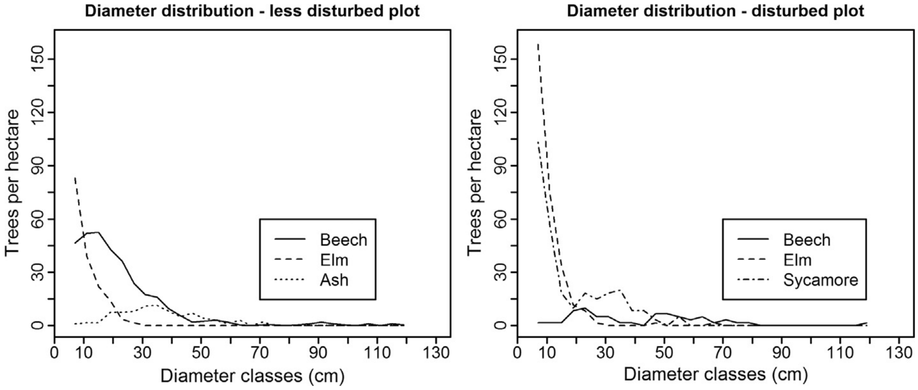


Fig. 1. Diameter distribution of all living trees larger than 5 cm dbh in 4-cm diameter classes.

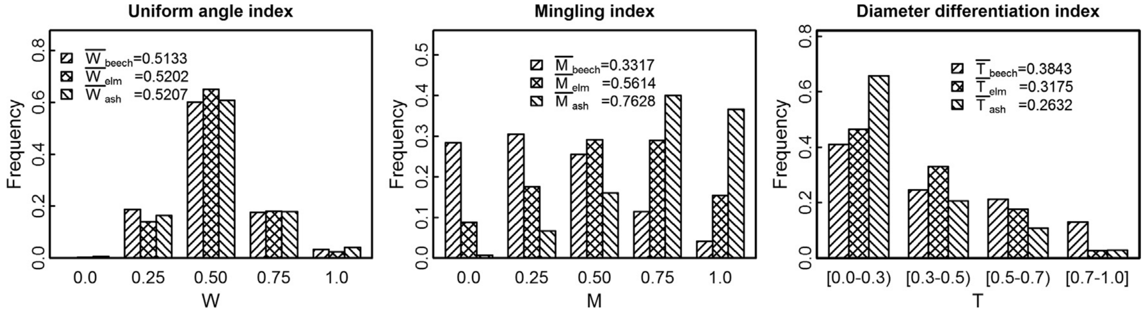


Fig. 2. Frequency distribution of the structural indices for dominant species in the less disturbed plot.

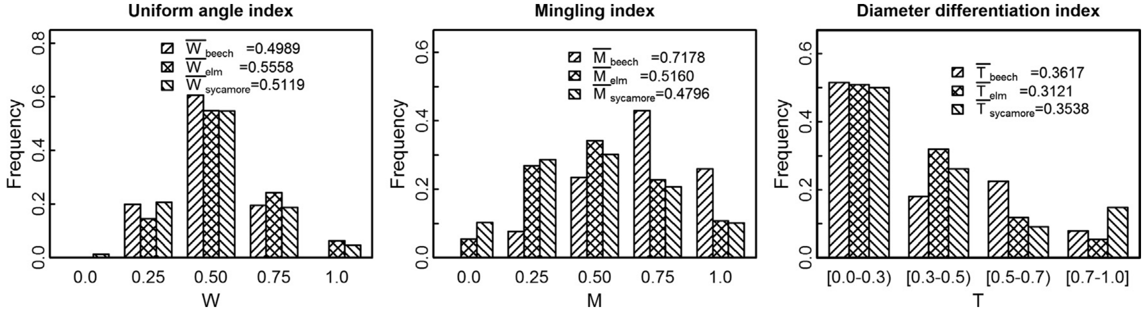


Fig. 3. Frequency distribution of the structural indices for dominant species in the more recently disturbed plot.

Table 2
Uniform angle index results for different species in the plots.

Plot	Species	N	$\overline{W}$	u_w	Confidence interval of $\overline{W}$ (95%)	Distribution pattern of $\overline{W}$ (95%)
Less disturbed	Beech	547	0.5133	1.3773	0.4810–0.5189	Random
	Elm	289	0.5202	1.5315	0.4740–0.5259	Random
	Ash	150	0.5207	1.1391	0.4640–0.5359	Random
More recently disturbed	Beech	30	0.4989	0.0275	0.4183–0.5816	Random
	Elm	147	0.5558	3.0458	0.4637–0.5362	Clustered
	Sycamore maple	150	0.5119	0.6548	0.4640–0.5359	Random

Note: N is the number of trees in the core area, $\overline{W}$ is the mean value of the uniform angle index; u_w is the statistics of the uniform angle index.

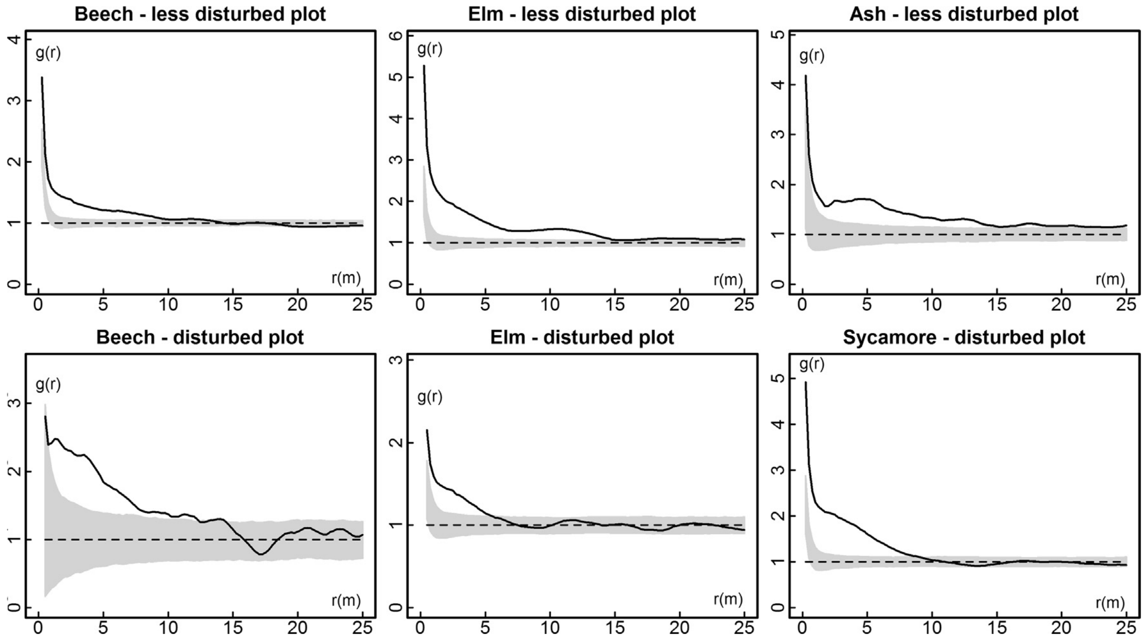
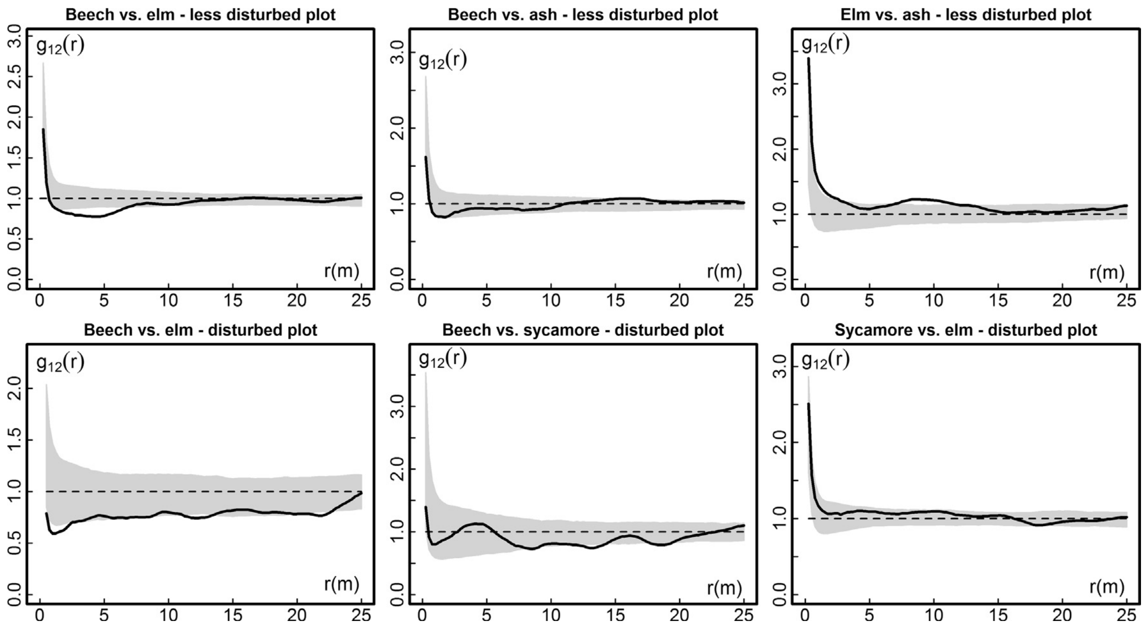


Fig. 4. Univariate pair correlation functions of dominant species. The shaded bands show the 95% confidence envelopes. Dashed lines correspond to expected values for a random distribution. Observed values above the confidence envelope indicate significant clustering, below show significant regularity.



Beech vs. elm - less disturbed plot

Beech vs. ash - less disturbed plot

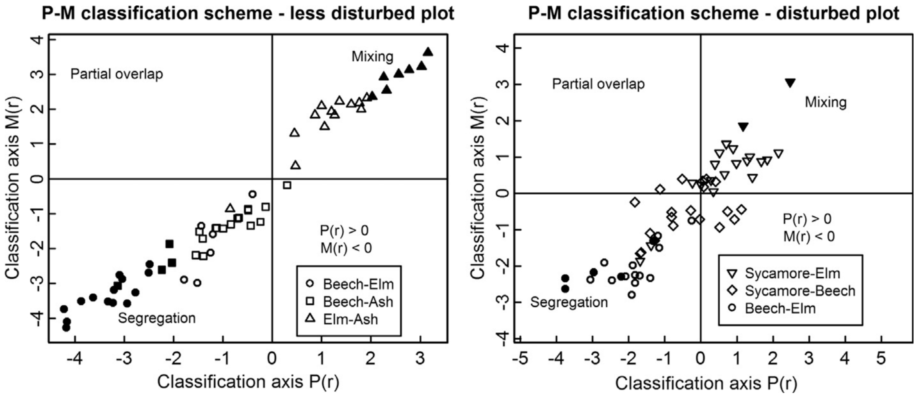
Elm vs. ash - less disturbed plot

Beech vs. elm - disturbed plot

Beech vs. sycamore - disturbed plot

Sycamore vs. elm - disturbed plot

Fig. 5. Bivariate pair correlation functions for analyzing the spatial associations between dominant species. Solid lines are observed values; dashed lines, expected values for independent distribution and shaded bands, the 95% confidence envelope. Observed values above the confidence envelope indicate a significant attraction, below indicate a significant repulsion.



P-M classification scheme - less disturbed plot

P-M classification scheme - disturbed plot

Fig. 6. Species association classification using the Wiegand scheme. Filled symbols represent significant cases.

diameter distribution. In the more recently disturbed plot, both sycamore maple and elm had large numbers of small trees but very few large trees while beech showed an almost bimodal distribution.

3.2. Species distribution pattern

The uniform angle indices (Winkelmass index) of all species in both plots averaged approximately 0.5 (Figs. 2 and 3). Based on the method presented by Zhao et al. (2014), all species except elm in the disturbed plot were randomly distributed (Table 2). In contrast, the univariate spatial distribution of living trees assessed with *g(r)* showed a clustered pattern for most of species at short (5 m) to medium distances (15 m) in both plots (Fig. 4). However, ash trees exhibited a clustered pattern at larger scales (up to 45 m).

3.3. Species mingling and associations

The dominant species in the less disturbed plot showed a variety of mingling constellations (Fig. 2). Compared to the other species, the average mingling index of beech was low (0.33) and most beech trees were distributed in the no mingling to moderate mingling classes. In contrast, ash had a high average mingling index (0.76) and mingling was generally high to very high. Elm occurred in a variety of mingling groups, either in pure groups (about 9%), in groups where half of the trees were elm (about 30%), in groups where three of neighbors belonged to different species (about 30%), and in groups where none of the neighbors were elm (about 15%).

Contrasting the results from the less disturbed plot, beech trees in the more recently disturbed plot (Fig. 3) were mostly mingled with other species and consequently had a high average mingling index (0.72), while elm showed similar values to that in less disturbed plot. Sycamore maple trees were moderately mingled with other species and had an average mingling index of 0.47.

Species association assessed with the bivariate $g_{12}(r)$ in the less disturbed plot showed that elm and ash trees were negatively associated with beech up to 6 and 2 m, respectively (Fig. 5). However, their tendencies towards segregation were visible up to 10 m. In contrast, elm and ash trees showed significant aggregation up to 3 m and at distances between 8 and 12 m. In the more recently disturbed plot, sycamore maple showed an independent distribution versus elm and beech trees.

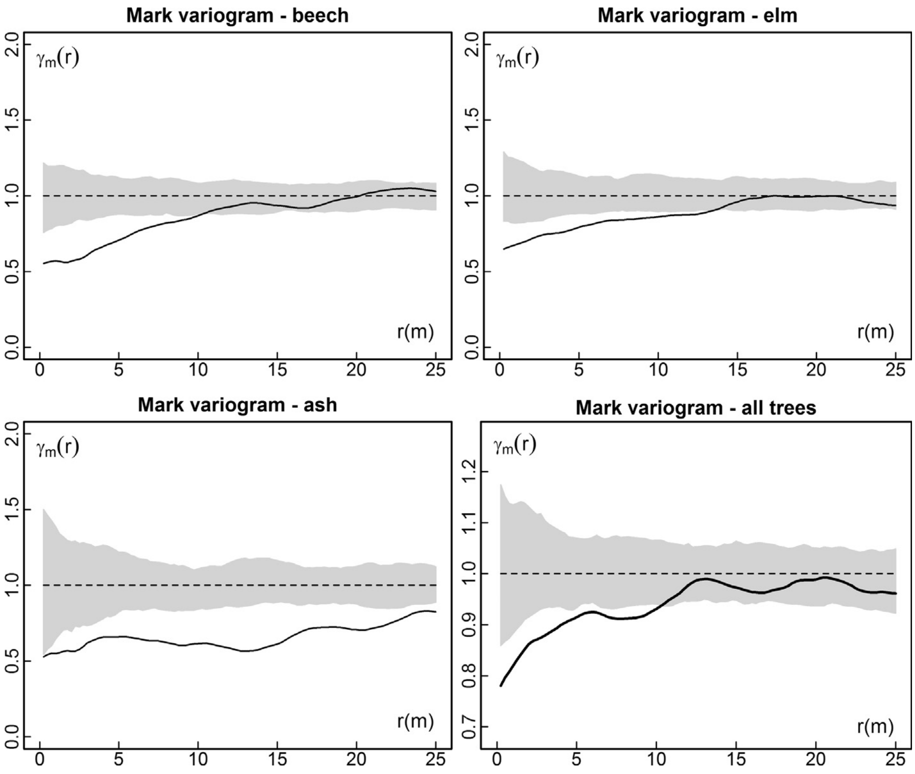


Fig. 7. Mark variograms for dominant species in the less disturbed plot. The shaded bands show the 95% confidence envelopes. Dashed lines correspond to the values for the case with independent mark. The mark variograms were normalized with the mark variance.

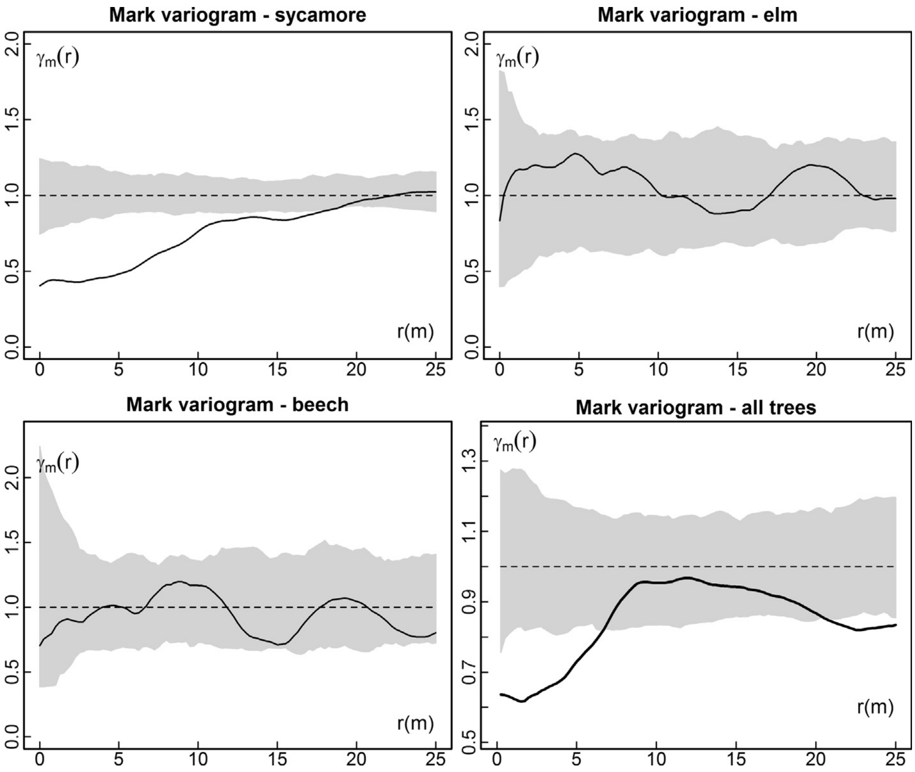


Fig. 8. Mark variograms for dominant species in the more recently disturbed plot. The shaded bands show the 95 percent confidence envelopes. Dashed lines correspond to the values for the case with independent mark. The mark variograms were normalized with the mark variance.

However, the observed summary statistics were above theoretical values for sycamore maple versus elm trees up to 15 m (a tendency towards attraction) while they were below theoretical values at most distances up to 15 m for sycamore maple versus beech trees (a tendency towards segregation). Similar to the less disturbed plot, elm trees showed segregation versus beech trees at short distances and a tendency toward segregation at larger distances. Classification of species association using the Wiegand scheme to a large extent agreed with the results from the bivariate pair correlation (Fig. 6). This analysis also showed that there are no partial overlaps between species, which could be an indication of site heterogeneity.

3.4. Species size diversity

In both plots, the majority of trees had a low diameter differentiation index with respect to their neighbors (class 0.0–0.3) (Figs. 2 and 3).

In the less disturbed plot, the number of trees with low diameter differentiation index was however smaller for beech and elm compared to ash. For all tree species, the smallest share of trees had a high (class 0.5–0.7) or very high (class 0.7–1.0) diameter differentiation index.

In line with our findings from the analysis of the diameter differentiation index, the mark variogram also indicated an aggregation of similar-sized trees (positive correlation) in the less disturbed plot (Fig. 7). However, the aggregation varied between different species. Beech and elm trees had similar size up to 10 and 14 m respectively, while ash had similar size at all distances. In line with these findings, the overall mark variogram showed positive correlation up to 11 m in the less disturbed plot. In the disturbed plot, the overall mark variogram showed correlation up to 8 m. However, the mark variogram of sycamore maple trees (Fig. 8) showed correlation of tree diameter up to 18 m, while elm and beech showed no spatial correlation of tree diameters.

4. Discussion

4.1. Non-spatial structural attributes

Within plots, trees showed a diameter distribution typical of old-growth stands covering a wide range of diameter classes and showing a typical decreasing trend in the less disturbed plot. In the more recently disturbed plot beech had a bimodal diameter distribution. The increase in the frequency of beech trees with *dbh* of 45–75 cm in disturbed plot probably reflects a major natural regeneration event in the decades following 1807, when the forest was fenced and cattle browsing stopped (Emborg et al., 2000). Elm trees as a sub-canopy species represented by many small trees in both plots, whereas sycamore maple regeneration occurs mainly in the disturbed plot. The increase in sycamore regeneration in the eastern part of the forest is likely due to a favorable light regime under the old oaks and ashes and the presence of seed sources to the east of the forest. The bell-shaped diameter distribution of ash trees was probably the result of the pronounced regeneration of ash trees after a major wind throw in 1967 and a reduction in the frequency of appearance of small trees caused by ash dieback in the past decade

4.2. Species distribution pattern

Based on the uniform angle index (winkelmass index), all tree species except elm in the more recently disturbed plot were randomly distributed. In contrast, the univariate spatial distribution of living trees assessed with $g(r)$ showed a clustered pattern for most of the species at short (5 m) to medium distances (15 m) in both plots, while ash trees exhibited a clustered pattern at even larger scales. Clustered distributions at small scales have previously been reported for European beech trees and are presumably caused by heavy seeds and limited seed dispersal (Ward et al., 1996; Rugani et al., 2013; Petritan et al., 2014; Drössler et al., 2016). Clustering at short distances could be attributed to the dependency of regeneration establishment on light availability in gaps, seed dispersal patterns, and tree-tree interactions. Clustering at larger scales usually results from site heterogeneity, the mosaic structure of developmental stages, or large scale disturbance patterns (Szwagrzyk and Czerwczak, 1993; Wiegand et al., 2007b). Site heterogeneity was unlikely the reason for large scale clustering in our study as the plots were selected specifically to present homogenous growing conditions based on soil, topographic, and species distribution maps. A possible explanation is that due to large annual seed production, higher light requirements, and the seed dispersal patterns of ash trees, this species is able to regenerate and survive in large gaps formed by natural disturbances (mainly storms) or by an enlargement in gaps resulting from the mortality of adjacent trees (the domino effect). Therefore, we assume that ash trees are actually clustered up to 16 m where the observed statistics touches the confidence envelope (Fig. 4).

In the less disturbed parts of the forest, the scale of clustering of beech, elm, and ash trees extends up to 11, 15, and 16 m. Therefore, the average gap sizes can be estimated to be small for beech (about 120 m^2) and larger for elm, and ash trees (220–250 m^2). However, the gap sizes estimated at the beginning of the forest cycle is expected to be larger than the gap sizes estimated by this method because the gap area decreases as a result of crown expansion of surrounding canopy trees (Muth and Bazzaz, 2002; Christensen et al., 2007). Based on previous research in the Suserup forest, the average size of gaps for the innovation and degradation phases that are characterized by the occurrence of gaps in the canopy have been estimated to be 430, 368, and 246 m^2 in 1992, 2002, and 2012, respectively (Emborg, 1998; Christensen et al., 2007; Nielsen and Larsen, 2012). There may be several reasons for previously reported large gap sizes. Firstly, only the gaps larger than 100 m^2 were monitored in the field, increasing the average gap size. Secondly, contrary to our analyses the gap sizes were determined based on development stages regardless of species composition. Finally, the gap size estimated in early development stages is relatively unaffected by the crown expansion.

There was some discrepancy between the results of the pair correlation function and the uniform angle index, where the uniform angle index failed to distinguish clustered patterns in most cases. Zhao et al. (2014) compared the results from uniform angle index with Ripley's L function and aggregation index of Clark and Evans and concluded that the uniform angle index can produce results that are equivalent to those obtained by Ripley's L function and is more reliable than aggregation index. However, the advantage of angle measures among neighbors over distance-dependent methods in terms of measurement is questionable (Río et al., 2016). Neumann and Starlinger (2001) compared four different spatial indices and concluded that Clark and Evans index of aggregation, Cox index of clumping and Pielou index of non-randomness perform generally well, and no preference could be given to any of them. However, they recommended using uniform angle index in special cases to distinguish between more regular stands or afforestation. This may suggest that the uniform angle index is less efficient than the pair correlation function in analyzing spatial pattern of trees in natural forests.

4.3. Species mingling and associations

Beech trees showed a low average mingling index (0.33) in the less disturbed plot but a high average mingling index (0.72) in the more recently disturbed plot. The differences in mingling index between the two plots could be caused by differences in the proportion of beech trees, which was lower in the more recently disturbed part of the forest. Graz (2004) found that the mingling index is sensitive to the proportion of a species in a stand and stated that a low proportion of a given species dispersed randomly over a stand will show a high degree of mingling. The results from the bivariate pair correlation function and the Wiegand scheme on spatial association of beech trees in the disturbed plot showed that beech trees were segregated from other species and hence the high mingling values for beech trees in the disturbed plot seem unreliable.

The bivariate pair correlation indicated that beech and elm trees were spatially segregated up to 6 m while ash trees showed segregation from beech trees up to 2 meters. Ash is a gap specialist in the climax forest with pioneering characteristics, producing wind dispersed seeds in most years (Mitchell, 1974; Etherington, 1982; Finegan, 1984; Oldeman and Oldeman, 1990; Dobrowolska et al., 2011). In contrast, beech has periodical seed production with heavy seeds (Watt, 1925). These differences in the seed production of ash and beech trees result in a high probability of establishment of ash trees prior to beech trees in gaps. Further, ash grows faster than beech in the juvenile stage (Petritan et al., 2007). These two characteristics of ash trees result in a long-lasting coexistence of beech and ash trees until beech takes over canopy control because of its longevity and ability to grow through canopies of ash (Emborg, 1998; Emborg et al., 2000). Therefore, depending on the stage of development, we can assume both segregation and independence of these two species. The segregation of beech and ash trees at short distances represented by the bivariate pair correlation function and the Wiegand scheme is a consequence of the light requirements of ash and the deep shadows created by beech crowns. In general, the relative success of ash as compared to beech in gaps may be dependent on the gap sizes as small gaps favor the establishment of beech trees and large gaps favor ash trees.

The negative association of elm and beech trees at larger distances is possibly the result of lower light availability for elm trees because they often occur in the understory. In contrast, ash trees, which are most commonly found in the overstory, have access to light for a longer duration and therefore grow and survive in the vicinity of beech trees. Our findings are in agreement with Oldeman and Oldeman (1990), who found that the preferred habitat for elm trees is the epicentre and periphery of fallen canopy trees. In Suserup Skov, more or less broken elm trees in large gaps formed by canopy trees, often rapidly spread an umbrella of long sprouts that efficiently precluded the establishment of other species. However, in the long run, beech trees seem to suppress elm trees in these gaps (Emborg et al., 2000). The undergrowth behaviour of elm trees is, however, a rather new phenomenon caused by the spread of Dutch elm disease some 30 years ago.

Positive associations was observed between elm and ash trees in the less disturbed plot, and sycamore maple and elm trees in the more recently disturbed plot at short distances. These associations were classified as mixing using the Wiegand scheme (Wiegand et al., 2007b). However, the association between elm and ash is stronger than the association between sycamore maple and elm. Ash is not known to form very dense canopies (Gardner, 1975), as a result, elm trees usually form a subcanopy stratum, utilizing the light penetrating the upper canopy of ash (Emborg, 1998).

Sycamore maple was distributed independently of elm and beech trees at all scales according to the bivariate pair correlation function. However, according to the Wiegand scheme, the species associations were classified as non-significant mixing between sycamore maple and elm and non-significant segregation between sycamore maple and beech. The ability of sycamore maple trees to coexist with other species arises from two main characteristics: firstly, they can easily regenerate naturally in shaded conditions and secondly, they can achieve temporal height dominance because of their rapid height growth (Hein et al., 2009). It will be interesting to study the future role of sycamore maple in Suserup forest because this species is currently only present in the disturbed part of the forest. Future climate warming in the northern parts of Europe may benefit sycamore maple (Weidema and Buchwald, 2010), which could consequently expand throughout the entire forest and take over the role as a gap colonizer in the absence of ash that is currently disappearing due to ash dieback. However, its dominance may alternate with other trees species (Leslie, 2005).

While the species-specific mingling index gave general inspiration on species behaviour in each plot, the bivariate pair correlation function showed more details about species–species relationships. The results of mingling values for the less disturbed plot were in agreement with the results from the bivariate pair correlation function and the Wiegand scheme. However, a discrepancy between the results of this index and the bivariate correlation function was observed in the more recently disturbed plot.

4.4. Species size diversity

According to the differentiation index, all species in both plots showed a decreasing frequency with increasing differentiation classes. This means that in a close neighborhood, the majority of individuals of each species have similar sizes. In line with the differentiation index, the analyses of mark variograms also indicated an aggregation of similar-sized trees (positive correlation) at a small scale in the less disturbed plot.

Positive spatial correlation of tree diameters in natural forest is primarily related to the aggregation of small trees in gaps during the regeneration process. However, their size differentiation increases with size as a result of their competition status, microsite conditions, and genetic makeup. Suzuki et al. (2008) stated that negative autocorrelation is rare in natural forests in which trees are distributed in a spatially random or clustered manner which is the case in our study. Beech trees showed positive correlation at shorter distances (up to 10 m) compared to other species probably due to their limited seed dispersal and their success in smaller gaps in competition with other species. Elm trees showed correlation up to 15 m while ash trees were correlated at all distances. The correlation of ash at larger scales is probably a consequence of ash only developing into the canopy layer when having access to light over the full life-cycle – indicating a large initial gap (corresponding to the defined “stop-and-go” strategy for beech and the “continuous and fast growing” strategy for ash) (Christensen et al., 2007). Another reason may be that neighboring patches often merge together because the diameter differentiation of trees between patches decreases by aging and reaching their maximum *dbh* while there is no regeneration of ash tress according to diameter distribution graph. This is most likely caused by the ash dieback disease, which has affected development for more than 10 years. In line with species-specific mark variograms, the overall mark variogram showed a positive correlation up to 11 m in the less disturbed plot.

Contrary to beech and elm trees in the less disturbed plot, elm and beech trees in the disturbed plot showed no spatial correlation of tree diameter at any scale probably because of disturbances or past management practices (wood pasture). Penttinen et al. (1992) noted the lack of spatial correlation of dbh as a result of several thinning operations in the spruce stand. Sycamore maple trees in disturbed plot showed spatial correlation of tree diameters up to 18 m. However, the overall mark variogram in the disturbed plot showed correlations up to 8 m, meaning that sycamore maple trees are main drivers of positive correlation in this plot. A comparison of the mark variogram and differentiation index for beech and elm trees in the disturbed plot showed no consistency. Until now, the reason for this conflict is not clear and may need investigation using simulation studies in the future. However, it should be noted that the test statistic of the mark variogram is based on the squared difference of the marks, while in differentiation index the test statistic is based on the ratio of the marks.

5. Conclusion

Overall analyses of mark variograms in Suserup Skov, indicated that the semi-natural beech forest is mostly composed of fine-grained patches. Based on our analyses in the less disturbed part of the forest, all tree species showed positive spatial correlation of *dbh*, probably as a result of gap-phase dynamics. The clustering of elm and ash trees occurred at larger scales (~15 m) than beech and sycamore maple trees (~10 m), probably as a result of preference and success of elm and ash regeneration in larger gaps. Beech trees were segregated from other species and were more likely to form pure groups. In contrast, elm-ash and elm-sycamore maple showed a positive association and formed mixed tree species groups.

Our understanding of the spatial distribution of tree species and the underlying dynamics in time and space of such semi-natural forests can be used in practical forestry to mimic recruitment processes, composition and diversity of tree species through silvicultural intervention. Specifically, the distribution of gap sizes created during silvicultural interventions will have implications for species regeneration, survival and diversity and thus for the future provision of forest resources as well as ecosystem services.

Our study provided a comparison of spatial functions based on stem-mapped data with more simple neighborhood-based spatial indices. We demonstrated that these indices may in some cases result in erroneous conclusions, while spatial functions provided more reliable insights into the stand structure and species interactions in Suserup Skov. The neighborhood based indices are commonly used but researchers should be aware of the limitations of these methods, especially when they are drawing silvicultural conclusions based on them.

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