

**Spatial pattern and its development from mid- to  
late-successional tree communities in unmanaged  
boreal forests in northern Finland**

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Tiivistelmä — Referat — Abstract <p>This study examined the development of tree communities from mid- to late-successional stages in unmanaged <i>Hylocomium-Myrtillus</i> (HMT) forests in northern Finland using a chronosequence approach. More specifically, this thesis addressed the following study questions: (1) What is the spatial pattern of the overall tree community and does this overall pattern changes as the forest's successional stage changes from mid- to late-successional? (2) What are the spatial patterns of small and large trees and how they differ from mid- to late-successional stages? (3) Is the occurrence of <i>P. abies</i> related to <i>Betula spp.</i> in mid- to late-successional stages and does this potential relation changes as the forest's successional stage changes from mid- to late-successional? (4) Does the tree population displays a mosaic of small patches of <i>P. abies</i> and <i>Betula spp.</i> trees over succession from mid- to late-successional stages?</p> <p>The study was carried out in the Värriö Strict Nature Reserve in north-eastern Finland in 2011. Living and dead trees were recorded within 3 transects (300 m long, 40 m wide) in 3 different stands representing differing mid- to late-successional stages from 180 years to at least 350 years. The stands were classified according to their species composition in <i>Betula spp.</i> dominated, mixed <i>P. abies-Betula spp.</i> and <i>P. abies</i> dominated. Finally, spatial patterns were analysed using Ripley's <i>K</i>-function.</p> <p>The spatial tree patterns were predominantly clustered and this pattern did not vary much over succession. Small trees were generally more clustered than larger trees and regular distributions did not occur. Saplings of both species were predominantly attracted to mature trees of the same species. This, and the repulsion between living mature <i>P. abies</i> and mature <i>Betula spp.</i> suggests clumps composed of only one species and thereby a mosaic of small patches of <i>P. abies</i> and <i>Betula spp.</i> in mid- to late-successional forest stages. At the same time, a successive dependency of <i>P. abies</i> on <i>Betula spp.</i> can be rejected. The lack of regular distributions implies a minor importance of competition in governing the spatial patterning of HMT-forests. In conclusion, suitable regeneration microsites and vegetative regeneration strategies can be assumed to outrun competitive effects on spatial structure in the presence of a thick raw humus layer in HMT-forests. Despite evidence of facilitative effects due the observed intensive clumping, the facilitative effects of <i>Betula spp.</i> on <i>P. abies</i> reported by Doležal et al. (2006) could not be shown in this study. This study thus suggests that facilitation is merely restricted to inter-species tree-to-tree interactions.</p> <p>HMT-forests have barely been studied to date. Concrete scientific benefits by this study are found in its contribution to investigate the actual point process that generates the observed patterns by fitting appropriate point-process models to the observed pattern and evaluate their power. Ultimately, the results derived from this study could thereby contribute to formulate plausible hypotheses concerning the causes for spatial patterning in HMT-forests which could be tested in experimental studies.</p>			
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# 1 Introduction

Spatial patterns within plant communities can be defined as non-random differences in vegetation that appear regularly (Dale & MacIsaac 1989). They can influence significantly ecological features such as interaction of species or variation within plant communities over time. Understanding spatial features in plant communities is thus even considered to be the final frontier in understanding ecological theory (Kareiva 1994). Spatial structure analysis can reveal the existence of the communities' underlying biological processes such as competition or reproduction. The analysis of spatial patterns has consequently been in the focus of numerous studies concerning plant ecology (e.g. Kershaw 1963, Greig-Smith 1979, Frelich & Graumlich 1994). However, most studies have focused on plant communities in grasslands, tropical rain forests or temperate forests while much less attention has been given to the boreal forest biome which covers about 17 % of the earth's land area (Rodin et al. 1975). Additionally, the majority of boreal forest pattern studies deal with the patterns at a certain point in time rather than their dynamics through time (e.g. Leemans 1991, Bartemucci et al. 2002) and there is a large variation in both the scale of the observations and the methods that are applied for analysis.

Since forests constantly react to the changes in their environment, it is generally accepted that the current pattern is the result of processes that have occurred in the past (Watt 1947). Large-scale patterns provide information concerning environmental or biotic heterogeneity whereas small-scale patterns suggest driving factors for the dynamics of forests that have long return intervals of severe disturbances such as gap dynamics i.e. growth, die-off, regeneration and recruitment in small canopy gaps (Kuuluvainen 1994, Kneeshaw & Gauthier, 2003).

A better understanding of the dynamics in forests' spatial patterns might thus contribute to identify the factors that affect the development of forest stands (Malkinson et al. 2003, Harper et al. 2006) which is important for ecological research and for testing ecological theories. Moreover, knowledge concerning these driving factors is needed for research areas that aim to mimic the natural range of variability of forested ecosystems such as modern forest management (Angelstam 1998), nature conservation (Davis et al. 2000) or climate change mitigation (Böttcher 2007). Additionally, knowledge of spatial structure can help to adjust statistical tests and to improve sampling design (Legendre et al. 2002).

Patterns in tree communities are generally grouped into clumped, regular and random patterns. To describe the interactions between different sub-populations, the terms attractive, repulsive and independent interactions are used instead (Perry et al. 2002, Diggle 2003, Doležal et al. 2006). Greig-Smith (1979) states that dominant vegetation components are almost never randomly distributed. Similarly, other studies have described deviations from random distributions in various successional forest stages (Armesto et al. 1986, North et al. 2004, Doležal et al. 2006).

As a stand grows older after regeneration, the trees expand into growing space of their neighbors what causes a competitive stage between individuals. Kershaw (1963) concludes that a high competition among the trees should lead to a regular pattern in the plant community. This theory is supported by findings from Kenkel (1988), who was able to show a significant regular distribution of the surviving trees for Jack pine in a stage of high intra-specific competition. Forests that are subject to high

competition between trees can thus be expected to display a regular pattern.

Mature forests that have escaped large scale disturbances (e.g. fire or wind damage) for long periods of time are expected to be dominated by gap-phase processes (McCarthy 2001). These resulting small scale changes in stand structure again have been shown to result in clumped tree distributions (Bormann & Likens 1979).

Boreal forests of the *Hylocomium-Myrtillus* (HMT) type dominate large areas of northern Fennoscandia (Cajander 1926, Sirén 1955). HMT-forests generally tend to form sparse mixed stands dominated by *P. abies* (L.) Karst. and *Betula spp.* on mesotrophic sites (Doležal et al. 2006) and they typically possess a thick moss layer (Lakari 1920). Another characteristic of these forest types in unmanaged northern Fennoscandian landscapes is the potentially rare occurrence of forest fires on *P. abies* dominated sites (Wallenius et al. 2005). Furthermore, these forests are subject to long and cold winters as well as to short and cool summers.

Extreme climatic conditions have been found to affect the overall spatial pattern. In this case, non-random distributions of individuals generally dominate the overall spatial pattern due to facilitation effects such as seedbed creation, nutrient supply or shelter functions which outweigh competitive effects (Bertness & Callaway 1994).

In the absence of large-scale disturbances such as fire, sexual regeneration in northern Fennoscandian forests is generally limited by seedbed availability (Heikinheimo 1922, Hofgaard 1993), and thus dependent on small-scale disturbances of the thick raw humus layer and punctual nutrient supplies in HMT-forests (Aaltonen 1919, Akhminova 1983 cited in Drobyshev 1999, Kuuluvainen & Ylläsjärvi 2011). Since these disturbances create only an areally limited access to sufficient resources (e.g. nutrients and water), the need for these resources results in a clumped pattern (Armesto et al. 1986, Malkinson et al. 2003). Other factors that may affect a clumped pattern in early-successional stages could be spatially variable seed dispersal or, especially on high-altitude sites, vegetative regeneration strategies (Heikinheimo 1922, Armesto et al. 1986). Despite the fact that HMT-stands are naturally sparsely stocked, they also undergo a stage of an increased competition after regeneration. Sirén (1955) found this stage to occur up to stand ages of 200 years. After this competitive stage is undergone, small-scale disturbances and its resulting gap dynamics start to dominate and contribute to the long-term stability of HMT-forests (Fraver et al. 2008, Aakala & Keto-Tokoi 2011). HMT-forests can thus be expected to display initially clumped distributions in early-successional stages that change to a more regular distribution in competitive mid-successional stages and eventually form again a clumped pattern in late-successional and old-growth stages.

The initially high post-fire proportion of *Betula spp.* trees in HMT-forests decreases over time after the last stand replacing fire following an inverse logistic function with maximum mortality rates at stand ages of 50 years (Sirén 1955). Whereas the proportion of *Betula spp.* decreases, the stand is invaded by *P. abies* up to stand ages of 220-250 years where *P. abies* reaches a maximum stand volume (id.). The following years are characterized by an intense natural mortality of *P. abies*. As the number of suitable regeneration sites for *Betula spp.* increases at stand ages of  $\geq 250$  years due to the mortality of *P. abies*, the stand is reinvaded by a low number of *Betula spp.* trees, thereby forming a secondary

stand and the whole cycle continues (id.). This eventually results in a mosaic of small patches that undergo gradual reciprocal replacement in late-successional HMT-forests (Doležal et al. 2006).

However, a review of the literature concerning spatial pattern development over succession reveals that the present knowledge concerning the importance of different patterns at different successional stages is still limited. Experimental manipulations are practically infeasible in tree community studies and consequently, most of the theories about spatial pattern development in tree communities have been poorly tested so far. Moreover, a considerable number of study results concerning spatial pattern in tree communities even contradict each other. When considering the whole plant community structure for example, Szwagrzyk (1990) and Szwagrzyk & Czerwczak (1993) were not able to find significant deviations of the small-scale pattern from random distributions in natural mid- and late-successional temperate forests in east-central Europe. Kershaw's (1963) results and conclusion regarding the distribution of dominant vegetation elements in a stage of high competition is questioned by findings from Greig-Smith et. al (1963) who state that a tendency towards regular distribution is generally very rare in plant communities. Consequently, Kershaw suggests more research on regular patterns. The study results are also partly contradictory for late successional stages. As opposed to the previously described results, Antos & Parish (2002) were not able to find any patch structure in late-successional subalpine forests in British Columbia, Canada.

## 1.1 Study objectives

The objective of this thesis was to statistically analyze the development of small-scale spatial pattern of trees in an unmanaged HMT-forests in northern Fennoscandia and finally visualize its development using a chronosequence approach. Based on the analyses, the potential mechanisms that caused the observed patterns are discussed. Addressing this objective raised the following specific study questions:

1. What is the spatial pattern of the overall tree community and does this overall pattern change as the forest's successional stage changes from mid- to late-successional?
2. What are the spatial patterns of small and large trees and how do they differ from mid- to late-successional stages?
3. Does the occurrence of *P. abies* relate to *Betula spp.* in mid- to late-successional stages and does this potential relation change as the forest's successional stage changes from mid- to late-successional?
4. Does the tree population display a mosaic of small patches of *P. abies* and *Betula spp.* trees over succession from mid- to late-successional stages?

## 2 Material and Methods

### 2.1 Study site

The study was carried out in the Värriö Strict Nature Reserve in north-eastern Finland (IUCN category Ia), 67°44'16"N 29°38'58"E. The reserve was established in 1982 and it covers an area of approximately 125 km<sup>2</sup>. It is situated in the northern boreal zone where *Pinus sylvestris* L. and *P. abies* are the dominant tree species. The annual average temperature of the last 20 years has been -0.5 °C and the snow melts completely by the end of May (Puttonen 2011). Gneiss complexes dominate the bedrock in the reserve (Korsman et al. 1997). Access to the reserve is prohibited with the exceptions of local residents who are allowed to pick berries and mushrooms in their own municipality, staff of the research station situated within the nature reserve and for research purposes. Some parts of the park area are also used for reindeer herding (Korsulainen & Väisänen 2003).



Fig. 1. Geographic location of the study site in northern Finland (Maps of Net 2011)

### 2.2 Data collection and analysis

#### 2.2.1 Stand selection

The dynamics of the forest's spatial pattern over time were investigated using the chronosequence approach. A chronosequence substitutes space-for-time, aiming to infer a time sequence of development from a series of plots differing in age since some initial condition. A critical assumption of the chronosequence approach is that each site solely differs in its age and not in its (a)biotic components



(Johnson & Miyanishi 2008).

Within the reserve, Metsähallitus (Finnish state forest service) stand compartmental data derived from aerial photographs was used to preliminary select stands that could serve as a chronosequence. This was performed by defining different successional stages of the forest, based on its proportion of *Betula spp.* trees (cf. Sirén 1955). The stands were selected to be as environmentally homogenous as possible and at the same time to represent different successional developmental stages.

In summer 2011, the preliminary selected stands were visited in the field and finally three stands were chosen which met the selection criteria environmental homogeneity, unmanaged forest with no visible signs of past harvests and representation of different successional stages. Stand A was dominated by early successional *Betula spp.*, stand B was a mixed *P. abies-Betula spp.* stand and stand C was dominated by *P. abies*.

### 2.2.2 Verification of the stands' successional states

To allow for the assignment of the stands to their successional stage, based on the time since the last severe disturbance, increment cores were collected from 16 trees in stand A, 33 trees in stand B and 21 trees in stand C. To capture much of the variability in stand age, the increment cores were not only collected from trees within the sample plot located for tree mapping but also from the close surroundings of the sample plot. The sample trees were chosen according to their dimension and competitive status. About 2/3rd of the samples included the dominant tree status by coring deliberately the oldest looking trees of the stand. The selection criteria for old looking trees were the tree's appearance of bark, health, dimension and species. Co-dominant and dominated trees in the close proximity of dominant trees were also included to account for the shade tolerance of *P. abies*.

The increment cores were taken as low as possible, if possible at the root collar. Since *P. abies* dominated boreal forest stands are prone to severe forest fires which leave only few surviving trees, the oldest verified tree age within a stand was assumed to represent the minimum time since the last stand replacing fire (Wallenius et al. 2005). Some of the increment cores could not be gained at the stem base due to e.g. stones surrounding the stem base or stem rot. These cores were taken as low as possible above the root collar. Taking increment cores above the root collar without applying individual age corrections results in serious underestimations of tree ages because year rings that have laid down between the root collar and the actual coring point are not counted (Gutsell & Johnson 2002). In that sense, the calculated age estimations must be understood as minimum ages of the trees.

After the increment cores were taken, they were mounted and sanded to a fine polish using standard methods (Phillips 1985). Afterwards, the ring widths were measured on a sliding-stage stereomicroscope with crosshairs which was connected to a recording device to the nearest 0.01 mm. These measurement results were statistically verified and, if necessary, corrected using the COFECHA-program (Holmes 1983). The age of the off-center and rotten increment cores was estimated using the tracing technique described by Clark & Hallgren (2004), based on the innermost 15 rings for each off-center core. Finally, 5 years were added to the resulting year in order to account for the time span a tree

needs to grow from germination to reach the sampling height at stem base. The year rings for *Betula spp.* were sometimes difficult to count but since the assignment of forest stands to successional stages does not require an accurate year count, the data for *Betula spp.* can still be used for determining the stands' minimum age.

Sirén (1955) found a strong relationship between the depth of the humus layer and the forest stand age. The older the stand, thicker is the humus layer. As a consequence, the humus thickness was additionally used as an indicator of the stands' successional stages. The average humus depth per forest stand was calculated using the humus depth data gained as described in 2.2.4.

### 2.2.3 Tree mapping and measurements

One randomly located large and narrow plot of 1.2 ha (40 x 300 m) was established in each forest stand. These long and narrow plots are effective in reducing the variance per unit-area and the large plot size further contributes to capture most of the structural variance within a stand (Bormann 1954). The plots were located in the field by randomly setting a starting point, choosing an azimuth at random and following this azimuth for 300 m in the field using the precision compass KB-14 (Suunto<sup>TM</sup>). If the end point of the sample plot resulting from this approach was outside the forest stand, a new starting point and azimuth were chosen at random. If the end point was still within the forest stand, both the starting point and the azimuth were used to finally locate the sample plot.

Now, beginning from the starting point, a 50 m long measuring tape was rolled out towards the selected azimuth, representing the bisect line of the sample plot. Finally the position of tally trees on the right and left of the bisect line was defined by walking along the bisect line and determining the point on the measuring tape from where the tally tree can be focused on in an right angle to the chosen azimuth with the precision compass. The distance of the tree to this point on the bisect line was measured up to a distance of 20 m, using the Vertex III clinometer and its transponder T3 (Haglöf<sup>TM</sup>). After walking along the first 50 m of the measuring tape, the tape was fixed at the 50 m position and the whole measurement was repeated until the end point was reached (see fig. 2).

All standing living trees of height  $\geq 1.3$  m and diameter at breast height (d.b.h.)  $\geq 1$  cm within the plot were measured. Dead trees and stumps were included if their d.b.h. was  $\geq 10$  cm. For each tally tree, the tree characteristics (1) species, (2) d.b.h. (measured 1.3 m above the ground to the closest cm; the d.b.h. of stumps was measured using the log), (3) height (measured to the closest cm decimal), (4) lower crown limit (measured to the closest cm decimal), (5) coordinates (measured to the closest cm) and (6) crown radii (estimated to the closest 0.5 m) were collected. Furthermore, the trees were classified according to (7) structural classes (intact standing, snapped  $\geq 1.3$  m or stumps) and (8) health status (living or dead).

Stems that sprouted from one stump were assigned the same x- and y-coordinates as the mother tree's coordinates for the spatial analysis and sprouts with a d.b.h.  $< 5$  cm were not treated as separate trees. Tree height and lower crown limit were measured using the T3 transponder and the clinometer. The d.b.h. was measured using a caliper.

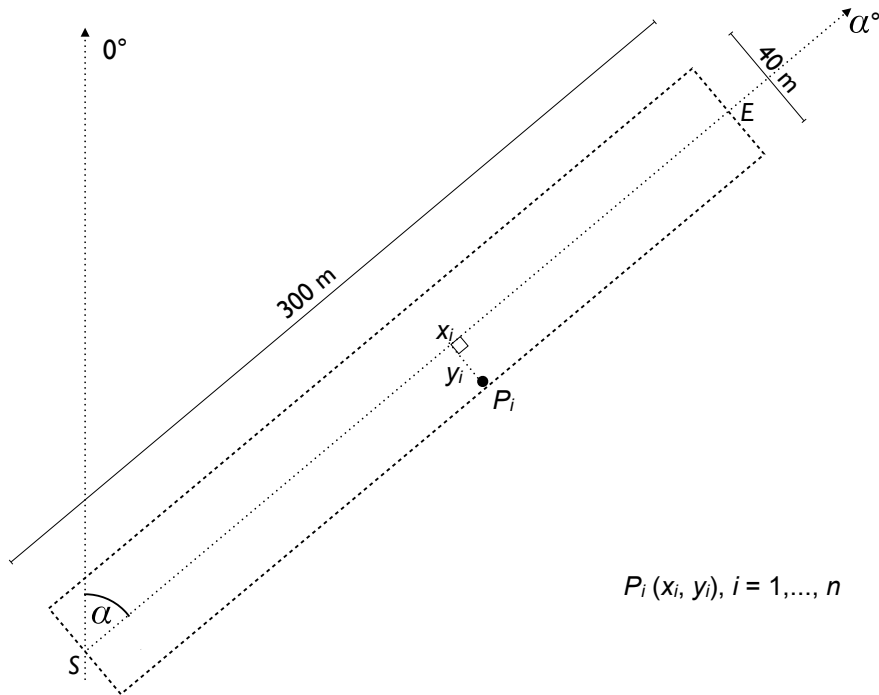


Fig. 2. Plot design for tree mapping.  $S$  = starting point (relative coordinates:  $x_S = 0$  m,  $y_S = 20$  m),  $\alpha$  = azimuth,  $E$  = end point (relative coordinates:  $x_E = 300$  m,  $y_E = 20$  m),  $P_i$  = position of the  $i$ th tally tree,  $x_i$  = point on the measuring tape where  $P_i$  is in a right angle with  $\alpha$  =  $x$ -coordinate of the  $i$ th tally tree,  $y_i$  = distance of tally tree  $i$  to the bisect line =  $y$ -coordinate of the  $i$ th tally tree

#### 2.2.4 Stand structural characteristics

General stand characteristics (e.g. mean height, stem numbers or histograms of diameter distributions for living and dead stems) were calculated using spreadsheet applications (Mac OS X) and the statistical package R (version 2.12.0) (R development core team 2005). *P. sylvestris* was not included in the non-spatial analysis because its proportion in the total stem number recorded was very low (< 2 %) in all three stands. The results of the non-spatial structure allow for a more detailed comparison of the three stands, for a comparison of the species-specific population size structure and for making results of other studies more comparable with this study.

#### 2.2.5 Spatial pattern analysis

Spatial patterns were analyzed using univariate and multivariate statistical analyses (Dixon 2002). To get an impression of local spatial variations in intensity, a kernel estimate of intensity was plotted (Baddeley 2010). Univariate analyses simply analyze the locations of any given event (e.g. tree location) and describe the distribution of these events. Multivariate analyses take into account biological information, called marks, about each event such as e.g. tree species, height or health status and describe the interaction between these marks respective to one another (id.). Bivariate analyses thus requires a classification of mark-variables into two discrete event types  $i$ -events or  $j$ -events.

The mapped locations for *P. abies* and *Betula spp.* were analyzed using the SPATSTAT package in R (Baddeley & Turner 2005). Also in the spatial analysis, *P. sylvestris* was not included because its

proportion in the total stem number was  $< 2\%$  in all studied stands. The spatial point pattern data were analyzed for large mature trees (d.b.h.  $> 15$  cm), small mature trees ( $10$  cm  $<$  d.b.h.  $\leq 15$  cm), large saplings ( $5$  cm  $<$  d.b.h.  $\leq 10$  cm) and small saplings (d.b.h.  $\leq 5$  cm) on a small scale, meaning inter-tree distances  $t \leq 10$  m. Stationarity (meaning that the probability statements about the process do not vary under translation of study area) and isotropy (meaning that the probability statements about the process do not vary under rotation e.g. no directional effects) of the observed point processes were assumed.

The first step in the spatial pattern analysis was a test for complete spatial randomness (CSR) using the Kolmogorov-Smirnov test. If CSR cannot be rejected for a spatial point pattern, there is no reason in conducting further analysis of the data (Diggle 2003). The hypothesis of CSR for a stationary spatial point pattern  $\mathbf{X}$  states that (1) the number of events in any planar region  $A$  with area  $|A|$  follows a uniform Poisson distribution with mean  $\lambda |A|$ ; (2) given  $n$  events  $\mathbf{x}_i$  in a region  $A$ , the  $\mathbf{x}_i$  are an independent random sample from the uniform Poisson distribution on  $A$ . The constant  $\lambda$  is the intensity (mean number of events per unit area). Thus,  $\lambda$  will not vary over the plane in case of CSR (id.).

After performing the Kolmogorov-Smirnov test and rejecting CSR, the square root transformation of the univariate  $K(t)$ -function by Ripley,  $L(t)$ , was used to answer the study questions 1, 2 and 4 and to summarize the point pattern. The analysis of spatial point patterns of trees is a classical application of the  $K(t)$ -function and its square root transformation simplifies the visual assessment and stabilizes the variance of the estimator (Ripley 1981, Dixon 2002, Diggle 2003). The  $K(t)$ -function tests all plant to plant distances instead of only the nearest-neighbor distances. Its form in the univariate case is

$$K(t) = \lambda^{-1} E \quad (1)$$

where  $\lambda$  is the density (number per unit area) of events and  $E$  the number of extra events within distance  $t$  of a randomly chosen event (Ripley 1976). The  $K$ -function describes characteristics of point processes at many distance scales, hence it is also suitable to analyze combinations of characteristic patterns in a plot of the  $K$ -function (Dixon 2002). The  $E$  in the numerator can be expected for many point processes such as CSR (id.). In the case of CSR, the  $K$ -function is

$$K(t) = \pi t^2 \quad (2)$$

The type and density of the pattern distribution is calculated by counting the number of neighbors within a circle of radius  $r$  of each individual in the study plot and comparing the mean number with the expected number  $\lambda K(t)$  (Doležal et al. 2006). To account for edge effects, isotropic edge correction was applied since this is currently the best edge correction for a rectangular window (Ripley 1988).  $K(t)$  was calculated for distances  $t \leq 10$  m.

The  $L(t)$ -function in the univariate case is

$$L(t) = \sqrt{\frac{K(t)}{\pi}} \quad (3)$$

On a graph of the form  $L(t) - t$  positive, negative and zero values of the  $L(t)$ -function indicate clumped, regular and random patterns at distances of  $t$ , respectively.

Interspecific relationships were investigated using the bivariate  $K_{ij}(t)$ -function:

$$K_{ij}(t) = \lambda_j^{-1} E \quad (4)$$

and its square root transformation  $L_{ij}(t)$ :

$$L_{ij}(t) = \sqrt{\frac{K_{ij}(t)}{\pi}} \quad (5)$$

where  $\lambda$  is the density of events and  $E$  is the number of type  $j$  events within distance  $t$  of a randomly chosen type  $i$  event (Dixon 2002). Under the CSR scenario, the corresponding  $K_{ij}$ -function takes the form

$$K_{ij}(t) = \pi t^2 \quad (6)$$

This method reveals attractive, repulsive or independent relationships between two events (e.g. species)  $i$  and  $j$ . It is noteworthy that without applied edge corrections,  $K_{ij}(t) = K_{ji}(t)$ . In case edge corrections are applied,  $K_{ij}(t)$  and  $K_{ji}(t)$  are positively correlated but not equal.

One must bear in mind the bias of the  $K$ -function towards clumping respectively attraction at small scales when interpreting the results. Additionally, randomness will not always correct for the biased effects of clumping respectively attraction at small scales as the distance increases what might result in an exaggerated pattern impression (Wiegand & Moloney 2004).

In all cases, the tested hypotheses were

$$H_0 : P = P_0, \quad H_1 : P \neq P_0 \quad (7)$$

where  $P$  is the observed distribution of the point process and  $P_0$  is the distribution resulting from a uniform Poisson point process. The functions generated from the point pattern data were hence compared with corresponding theoretical functions under CSR generated by 999 Monte Carlo simulations (Diggle 2003). Global significance envelopes were created for a significance level  $\alpha = 0.05$ .

Significance envelopes represent the critical values for the hypothesis test and are nowadays a commonly applied method in spatial point pattern statistics. A significance envelope is created in most studies by calculating the maximum and minimum  $K$ -value of an uniform Poisson point process at every distance  $t$  from a number of Monte Carlos simulations. The observed process is assumed to be different from the uniform Poisson point process if the results exceed the envelope at any distance  $t$  (Loosmore & Ford 2006).

However, Loosmore & Ford (2006) state that this approach is invalid for testing observed point patterns

against a specified spatial model as well as determining the distances at which the observed pattern differs from the spatial model due to an underestimation of the type I error (the test rejects the true  $H_0$ ). The reason for this underestimation of the type I error can be found in the performance of many tests simultaneously, one at each different distance which again yields in the fact that the lower and upper values of the significance envelopes do not equal a  $(1 - \alpha)\%$  confidence interval. Determining the range of distances over which the observed pattern differs from the theoretical model, based on where the results exceed the envelope, is also invalid since the K-statistic is a cumulative function. Thus, results for an observed pattern could lie outside the envelope at a distance where the instantaneous value was not different than the model (Loosmore & Ford 2006).

To account for this issue, the significance envelopes were not calculated in a pointwise but simultaneous manner in R. For a proper analysis with pointwise envelopes, the test is constructed by choosing a fixed distance  $t$  before the analysis and  $H_0$  is rejected, if the result exceeds the envelope at this specified distance  $t$ . In the simultaneous case, the probability that the result exceeds the confidence envelope at any distance  $t$  is exactly  $\alpha$ . The bands are determined by calculating the theoretical  $K(t)$  value and its deviation  $D$  from the model for the number of simulations. Finally, the maximum theoretical deviation  $D_{max}$  serves as the critical value which is, in the case of a Poisson process, defined as (Baddeley & Turner 2005)

$$E = \lambda r^2 \pm D_{max} \quad (8)$$

The univariate and bivariate analysis tested the pattern and interactions of a large set of species, status and size strata combinations (cf. section 3.3).

### 2.2.6 Supplementary data

The chronosequence approach assumes the same (a)biotic components in all study sites under investigation. The more homogeneous the stands are considering their biotic and abiotic factors, the more reliable are the results provided by the analysis. Homogeneity in climatic factors can be assumed due to the close location of the stands to each other. To further assess inter-stand variation in biotic and abiotic factors, supplementary data about soil properties and forest floor vegetation species abundances were collected.

To estimate soil characteristics, 5 randomly distributed sampling plots were implemented in each stand according to Zerva et al. (2005). In each plot, 9 samples were taken from points at randomly selected distances from the centre of the plot in  $40^\circ$  bearing steps in clockwise order and within a radius of 10 m from the centre. The samples were taken by a soil auger with a cross-section of about 5 cm diameter and were visually distinguished in a humus and an earth layer. For each plot, the gradient was determined using a clinometer. Gradients  $< 10^\circ$  were classified as flat. For the humus layer, the depth of the raw humus layer was determined to the closest cm. For the earth layer, soil texture, stone content (%), soil structure and soil type were determined in the field according to Ad-hoc-AG Boden (2005) which provides the fundament for administrative soil descriptions in Germany. According to this manual, the soil features were determined in the field by checking visually and tactually investigated soil properties

against provided descriptions. Besides instructions for soil mapping, the manual contains a definition of essential features for soil classification and respective descriptions.

To characterize the vegetation composition of the studied stands by species cover, four square sites (plots) of 20 x 20 m<sup>2</sup> were sampled for vegetation data according to Wanze et al. (2009). This characterization allows a detailed comparison of the studied stands to other studies. The collected vegetation components were assigned to size strata as trees, shrubs and bottom and field stratum. The tree stratum was sampled within four 10 x 10 m<sup>2</sup> subplots in each plot. The shrub stratum was sampled from four 5 x 5 m<sup>2</sup> quadrats nested at the corners within each 10 x 10 m<sup>2</sup> subplot. The understory stratum was investigated with four 1 x 1 m<sup>2</sup> quadrats nested at the corners within each 10 x 10 m<sup>2</sup> subplot. Thus, a total of 16 subplots and 64 shrub and understory vegetation quadrats were established in each stand. For every subplot and quadrat, a complete floristic inventory was performed for the three strata: (1) bottom and field stratum (moss and herbaceous species < 0.5 m in height), (2) shrub stratum (0.5 - 5 m) and (3) tree stratum (> 5 m). The cover of each species was visually estimated as percent canopy/floor cover within each subplot/quadrat on a 5 % scale (0 %, 5 %, 10 %, 15 %, ..., 100 %).

The soil data were tested for homogeneity using a pairwise Chi-Square test for homogeneity. The test is evaluating the equality of populations and can be used for all scale types. The tested hypothesis was

$$H_0 : \begin{aligned} \pi_{Stand A} &= \pi_{Stand B} \wedge \\ \pi_{Stand A} &= \pi_{Stand C} \wedge \\ \pi_{Stand B} &= \pi_{Stand C} \end{aligned} \quad (9)$$

where  $\pi$  denotes the population of stand A, B and C respectively. The alternative hypothesis  $H_1$  is thus that at least one of the populations differs from the rest. The value of the test statistic is

$$\chi^2 = \sum_{i=1}^n \frac{(O_i - E_i)^2}{E_i} \quad (10)$$

where  $\chi$  is Pearson's cumulative test statistic which asymptotically approaches a  $\chi^2$  distribution,  $O_i$  is the observed frequency,  $E_i$  is the expected (or theoretical) frequency asserted by the null hypothesis and  $n$  is the number of cells in the table. The test statistic is compared to the critical value derived from a chi-square table. In case

$$\chi^2 \leq \chi_{1-\alpha}^2 \quad (11)$$

$H_0$  will be accepted.

The pairwise Chi-Square test for homogeneity included the categories soil textures (1) sand, (2) sandy loam and (3) loamy sand, the soil structures (4) single grain and (5) crumbs and the soil types (6) Podzol and (7) Cambisol.

### 2.3 Stand visualization

The structure of the examined stands was visualized using the Stand Visualization Software (SVS) (McGaughey 1999). The SVS is a freeware provided by the USDA Forest Service, Pacific Northwest Research Station. The system generates graphic images based on a list of individual stand components. It provides a realistic representation of plant and log components in forest stands and furthermore communicates the overall structural diversity of the forest stand. The realistic representations are achieved by allowing the user both to define specific plant forms and colors based on species, plant type and social status and provides tabular and graphical summaries of stand information.

The SVS requires two types of data: a list of stand components and plant form definitions. The first describes the species, size and location of each component in a stand while the latter describes the appearance of each species and, optionally, the appearance of individuals exhibiting different growth forms within a species. The parameters (1) species code, (2) d.b.h., (3) height, (4) expansion factor, (5) optionally plant class, (6) crown class, (7) plant status, (8) felling angle, (9) end diameter, (10) crown radius, (11) crown ratio as well as (12) x- and y-coordinates describe each stand component (id.).

The user can define the appearance of each species represented in a component list using a plant form definition. The plant form describes the overall growth form such as geometry and number or color of branches or leaves. The parameters tree class and crown class can be used to distinguish individuals between a species (id.).



### 3 Results

#### 3.1 Successional stages of the stands

The studied stands represented 3 distinguishable successional stages. However, the cored trees in all sampled transects represented a wide range of tree ages with no visible regeneration waves. Since the classification of trees into successional stages does not require an annual resolution and because age determination of *Betula spp.* trees was difficult due to erratic growth rings, the results of the tree ages are presented at a decadal resolution. The oldest tree in stand A germinated in 1820 while the average year of germination was 1880. The mean of the dated increment cores of stand B lies in 1830 and its oldest tree, *P. sylvestris*, germinated in 1680. The oldest tree in the total increment samples was derived from a *P. abies* in stand C. It germinated in 1660 whereas the average of stand C germinated in 1760 (Fig. 3).

The humus depth results are consistent with these findings. The mean humus layer depth increased from 3.8 cm stand A to 5.1 cm in stand B and reached finally a value of 8 cm in stand C. Thus, stands A, B and C will also be referred to in the following as mid-successional ( $\sim 190$  years old), late-successional ( $\sim 270$  years old) and old-growth ( $\geq 350$  years old) stands respectively.

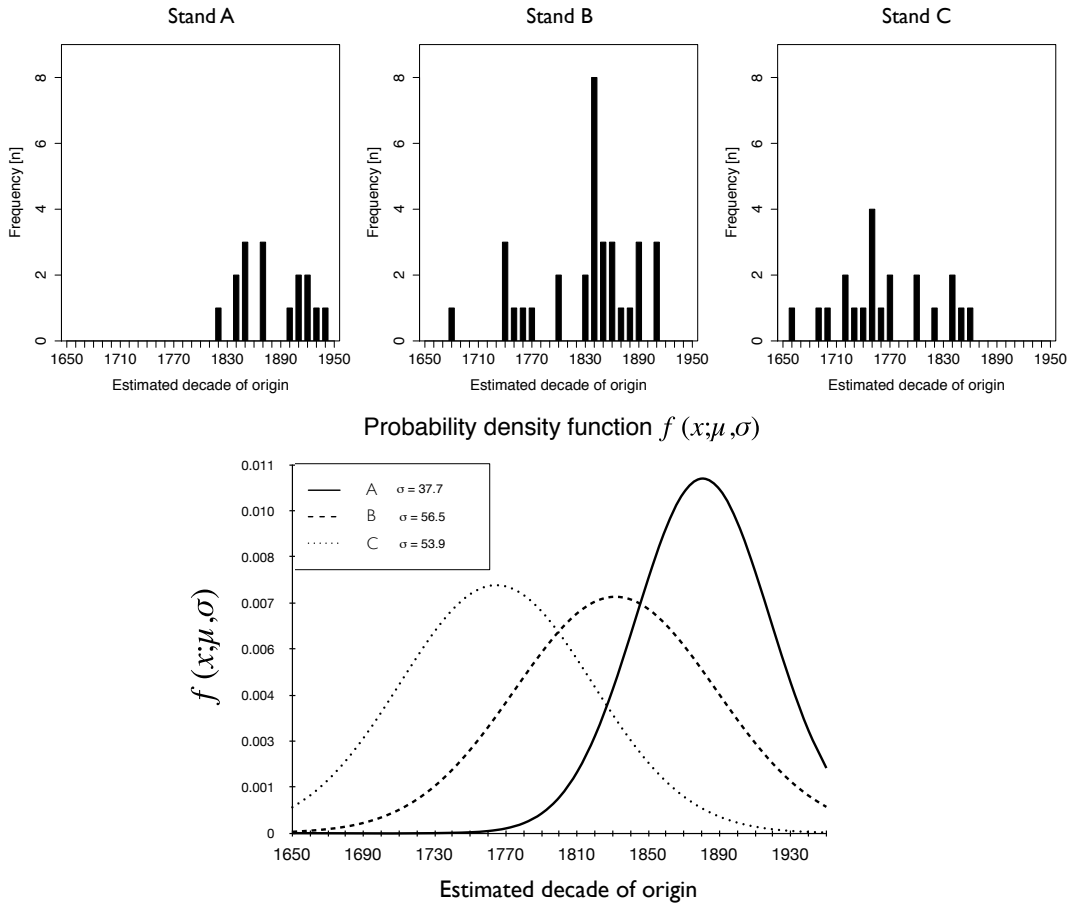


Fig. 3. Age distributions and probability density functions of fitted normal distributions to the stand age. Stand A = mid-successional, stand B = late-successional, stand C = old-growth

### 3.2 Stand structural analysis

There was a clear shift in the species dominance with successional status (Table 1). *Betula spp.* was the dominant species in both the total number of living trees and in the basal area (66.4 % of the total basal area) in the mid-successional stand whereas *P. abies* dominated the late-successional and old-growth stand in both these characteristics. The total living tree stem number was higher in the mid-successional stand (n = 614) than in the old-growth stand (n = 500). Even though the late-successional stand had the highest total number of living stems (n = 872 trees), it still represented a transition stage between the stem number ratios of the mid-successional and the old-growth stand with respect to species stem number ratio. The main changes observed in the *P. abies* population with increasing stand age were an increase in mean tree size, d.b.h. and basal area in both dead and living trees whereas mean tree size and d.b.h. increased less strongly in the *Betula spp.* population and the basal area in both dead and living trees was continuously decreasing (Table 1).

Table 1. Stand structural characteristics of the sample plots representing different successional stages (values per ha). Stand A = mid-successional, stand B = late-successional, stand C = old-growth

Species	<i>P. abies</i>			<i>Betula spp.</i>		
	A	B	C	A	B	C
living trees [n]	182	485	402	432	387	98
living trees [%]	30	56	80	70	44	20
dead trees [n]	3	35	88	194	60	47
dead trees [%]	2	37	65	98	63	35
mean height intact living trees [m]	9	9.2	10.8	9.4	9.5	9.7
max. height [m]	24.2	24.4	24.8	20	21	20
CV height [%]	66.4	62.6	51.3	41.8	41.8	33.7
mean DBH living [cm]	12.6	13.4	17	13	13.5	16.3
max. DBH [cm]	53	60	54	46	40	42
mean crown limit [m]	0.9	1.5	2	4.3	5	3.6
basal area living trees [m <sup>2</sup> ]	3.8	10.5	11	7.4	6.8	2.1
basal area living trees [%]	33.6	60.6	84	66.4	39.4	16
basal area dead trees [m <sup>2</sup> ]	0.1	2	2.8	2.5	1.3	0.9
basal area dead trees [%]	3.2	60	75	96.8	40	25

The tallest and largest trees in the stands were consistently *P. abies*. The total number and number ratio of dead trees steadily increased in the *P. abies* populations with progressing successional status whereas these values steadily decreased in the *Betula spp.* populations. The total number and number ratio of dead stems of the *P. abies* population outran that of the *Betula spp.* population only in the old-growth stand (Table 1).

*P. abies* had a positively skewed diameter distribution of the living trees in all stands, the highest skewness value of 1.28 was reached in the late-successional stand. The diameter distribution of the dead spruce population was slightly symmetric in all stands (no value for the young stand since there

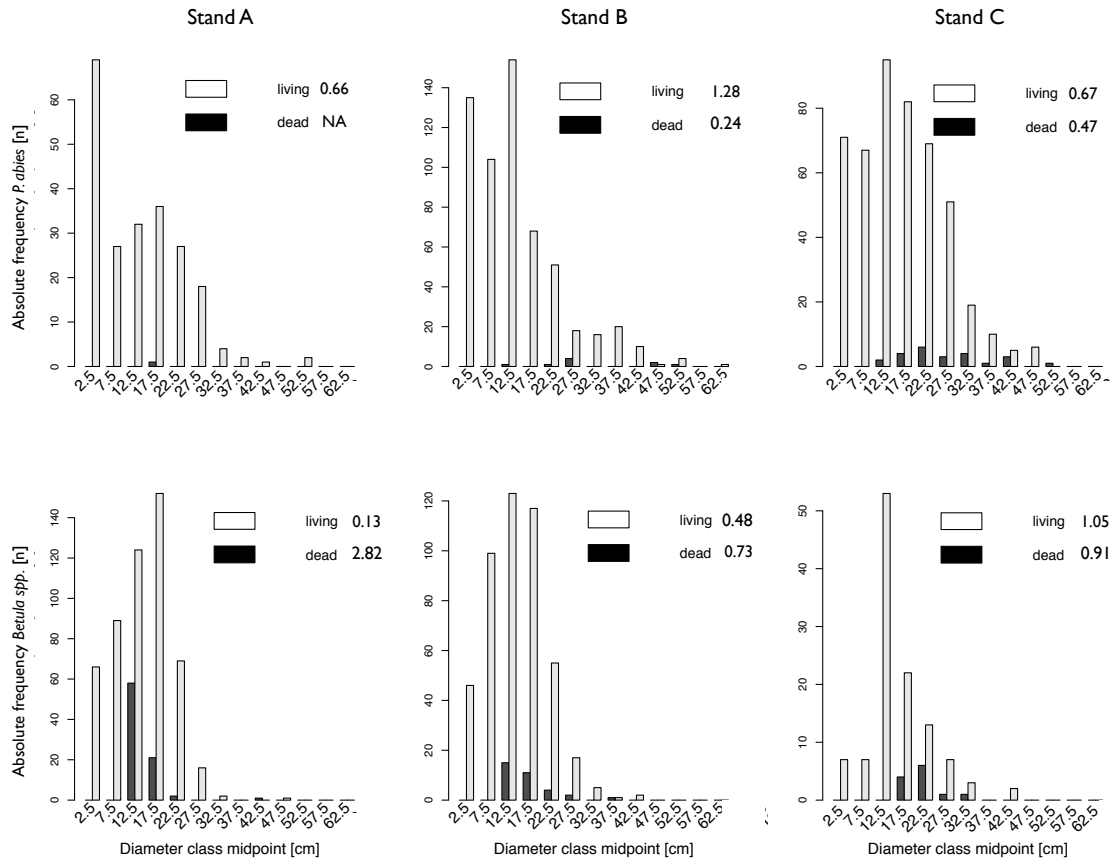


Fig. 4. Diameter histograms. Numbers behind the legend show the skewness value of the standing trees. NA = no value calculated ( $n = 3$ ). Stand A = mid-successional, stand B = late-successional, stand C = old-growth

were only 3 dead trees recorded). The diameter distribution for the standing *Betula spp.* population followed a positive skewness pattern as well. However, the skewness value, indicating an almost symmetric distribution in the mid-successional stand, was steadily increasing with stand age and finally reached a value of 1.05 in the old-growth stand. The diameter distribution of the dead *Betula spp.* population was also constantly positively skewed. The dead *Betula spp.* population in the mid-successional stand showed the highest observed skewness factor (2.82) of all investigated populations.

All stands displayed a local or global maximum in the frequency counts in the diameter classes (10 - 15] or (15 - 20]. Only in the mid-successional stand and for *P. abies*, the highest frequency count coincided with the smallest diameter class but also here, the diameter class (15 - 20] showed a local maximum. Rotated sigmoid forms of the diameter distributions were indicated by the distribution of

*P. abies* whereas an unimodal distribution was indicated for *Betula spp.* (Fig. 4).

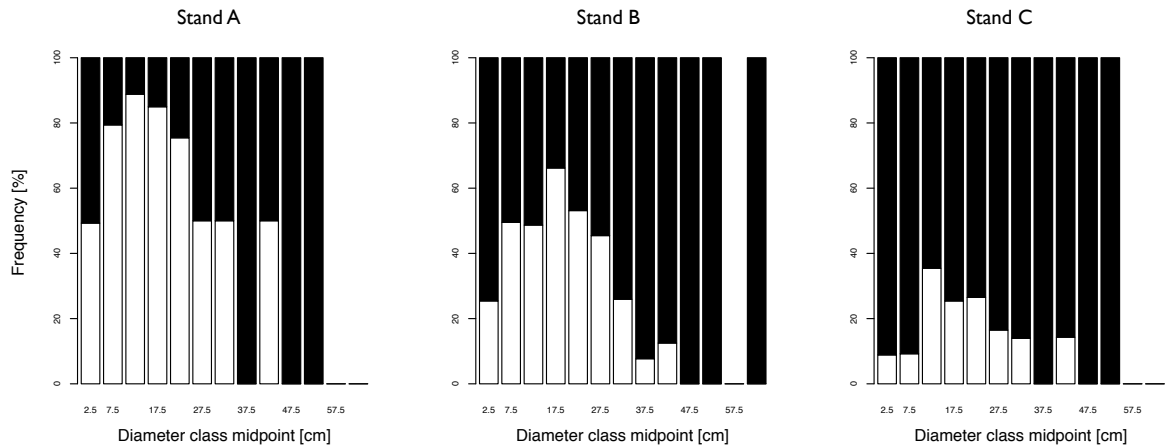


Fig. 5. Diameter frequency distribution of living and dead trees. Filled bars represent *P. abies*, empty ones *Betula spp.* trees. Stand A = mid-successional, stand B = late-successional, stand C = old-growth

Large diameter classes in the tree populations were mainly represented by *P. abies* (Fig. 5). Also the diameter class < 5 cm was mainly represented by *P. abies* trees in all stands. The ratio of *Betula spp.* trees reached its maximum in the diameter classes [10–20] and decreased again afterwards.

### 3.3 Spatial pattern analysis

Overall, in all investigated stands representing different successional stages, trees were nonrandomly distributed. Clumped distributions and attractive interactions dominated the studied successional stages for a variety of tree sizes and species combinations. A regular distribution of trees was never observed, repulsive interactions in just a few cases.

Table 2. Summary results of the pattern analysis for *P. abies* and *Betula spp.* Stand A = mid-successional, stand B = late-successional, stand C = old-growth

Performed analysis	Stand A	Stand B	Stand C
<b>Univariate analysis</b>			
Living trees	cl (0-10)	cl (0-10)	cl (0-10)
Dead trees	cl (0-2)	Random	Random
<i>P. abies</i> living	cl (0-10)	cl (0-10)	cl (0-10)
<i>P. abies</i> living large mature trees	Random	Random	Random
<i>P. abies</i> living small mature trees	Random	cl (8-10)	cl (6-7, 8-9)
<i>P. abies</i> living large saplings	Random	cl (1.5-10)	cl (2-2.5, 6-10)
<i>P. abies</i> living small saplings	cl (0-10)	cl (0-10)	cl (1-10)
<i>P. abies</i> dead	Random	Random	Random
<i>Betula spp.</i> living	cl (0-3, 8-10)	cl (0-10)	cl (1-3)
<i>Betula spp.</i> living large mature trees	cl (1-2)	cl (9-10)	Random
<i>Betula spp.</i> living small mature trees	cl (0.5-1.5)	cl (7-8)	Random
<i>Betula spp.</i> living saplings	cl (0-1)	cl (0-2, 7-10)	Random
<i>Betula spp.</i> dead	cl (0-2)	Random	Random
<b>Bivariate analysis</b>			
living - dead	att (0-2.5)	att (0-1), rep (5-10)	att (0-1)
<i>P. abies</i> living - dead	Independent	Independent	Independent
<i>Betula spp.</i> living - dead	att (0-2.5)	att (0-2)	att (0-3)
saplings - mature trees	att (0-2, 9-10)	att (0-10)	att (0-10)
living mature <i>Betula spp.</i> - living mature <i>P. abies</i>	Independent	rep (3-8)	rep (2.5-3)
living mature <i>Betula spp.</i> - small saplings <i>P. abies</i>	Independent	rep (6-8)	Independent
dead <i>Betula spp.</i> - living small saplings <i>P. abies</i>	Independent	Independent	Independent
living saplings <i>Betula spp.</i> - living mature <i>Betula spp.</i>	att (0-3.5, 7.5)	att (0-10)	Independent
living saplings <i>P. abies</i> - living mature <i>P. abies</i>	Independent	att (1-10)	att (0-10)
living small saplings <i>P. abies</i> - dead downed trees	Independent	Independent	Independent
living small saplings <i>Betula spp.</i> - dead downed trees	Independent	Independent	Independent
living <i>P. abies</i> - dead <i>Betula spp.</i>	Independent	rep (3, 9.5-10)	Independent
dead <i>P. abies</i> - living <i>Betula spp.</i>	Independent	rep (3.5-10)	Independent
living <i>P. abies</i> - living <i>Betula spp.</i>	att (7-10)	Independent	Independent
living mature <i>P. abies</i> - living <i>Betula spp.</i>	rep (1.5)	Independent	rep (2.5-3)
living small saplings <i>P. abies</i> - living large saplings and mature trees <i>Betula spp.</i>	att (8-10)	rep (2.5-5.5)	Independent

cl = clumped, reg = regular, att = attractive, rep = repulsive. Numbers in parantheses are distances [m] at which the observed pattern is significant from the expected distribution under CSR

The resulting  $p$ -values for the Kolmogorov-Smirnov test were 0.0265 (stand A),  $< 0.0001$  (stand B) and 0.0242 (stand C) for all mapped tree locations. The  $H_0$  hypothesis was thus rejected in all stands given a critical  $\alpha$  value of 0.05. Trees were consequently not randomly distributed what made a further analysis of the data reasonable.

The intensity (average density) of the point pattern reached values of 0.0608 (stand A), 0.0842 (stand B) and 0.0572 (stand C) trees  $\text{m}^{-2}$ . Living trees with a d.b.h.  $\geq 10$  cm formed various sized and dense patches. In all stands, patches with low to zero density occurred. Visual assessment of the distribution of dead trees conveyed the impression that dead trees regularly occurred in high to medium dense patches whereas low density patches contained less often dead trees (Fig. 7).

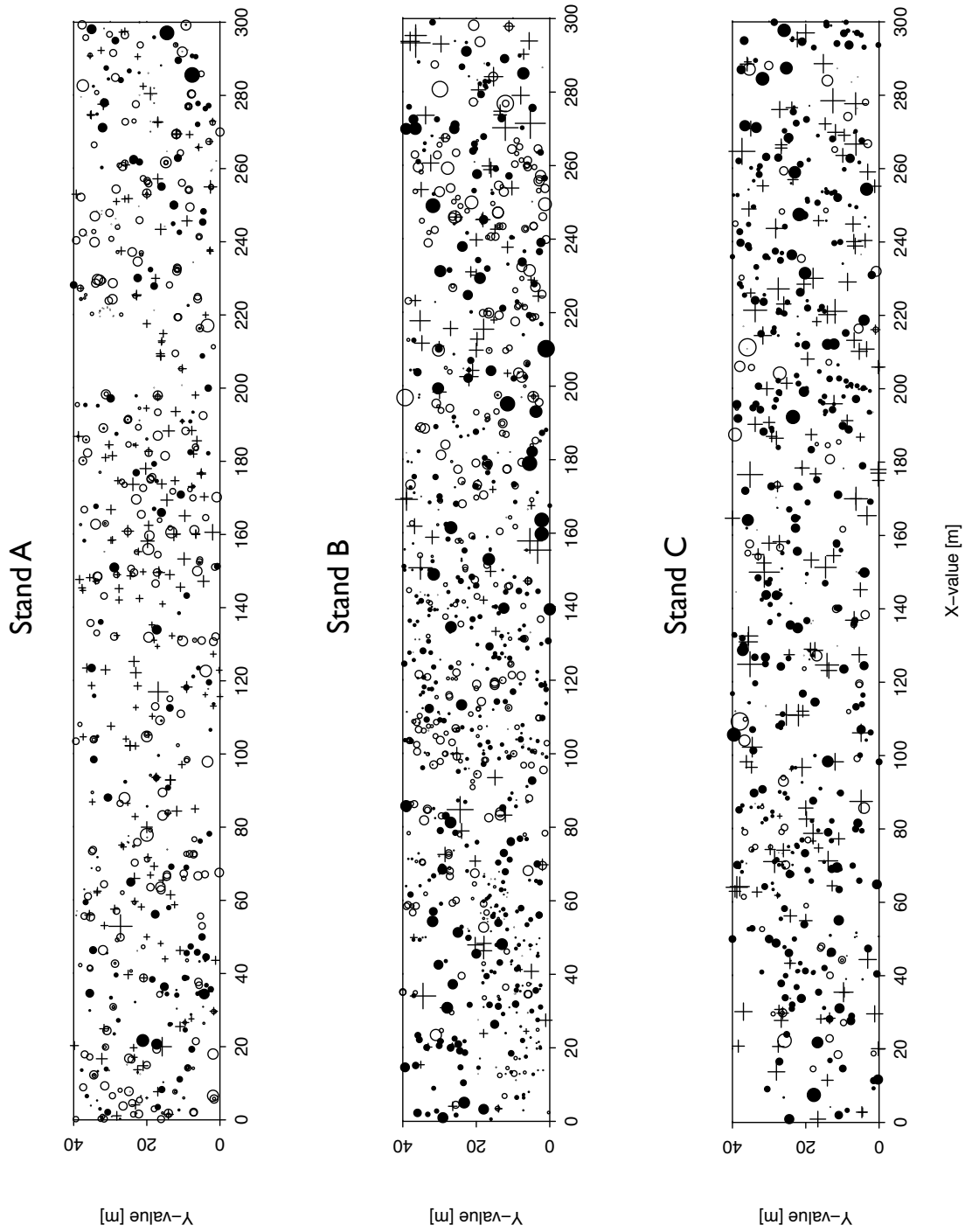


Fig. 6. Spatial point pattern of trees in the studied stands. Open dots represent *Betula spp.*, filled dots *P. abies* trees, + = dead trees/stumps. Stand A = mid-successional, stand B = late-successional, stand C = old-growth. Symbol sizes are drawn proportional to d.b.h. (biggest symbol represents 53, 60 and 54 cm in stand A, B and C respectively) but are disproportionate to the coordinate axes

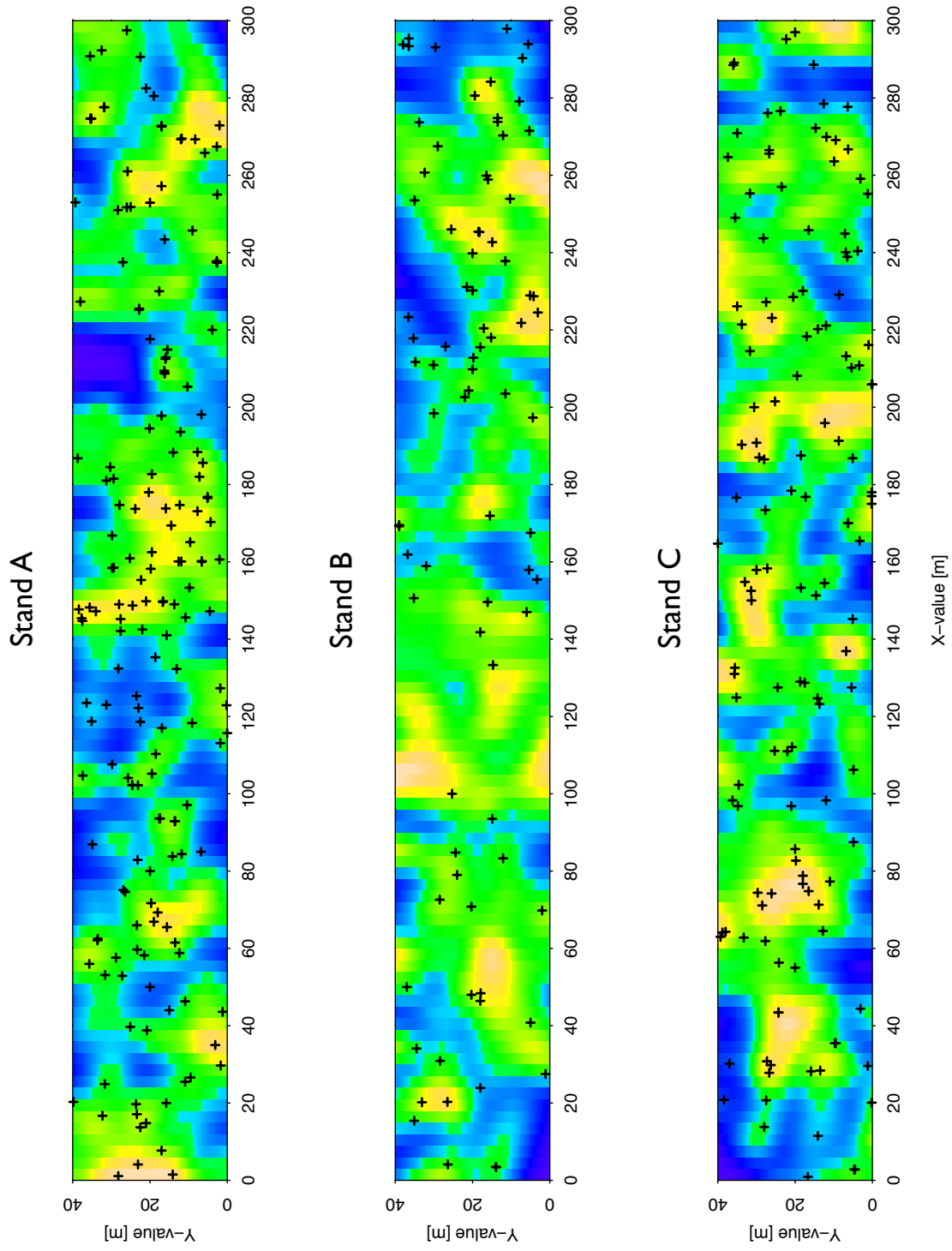


Fig. 7. Kernel estimate of intensity of living trees d.b.h.  $\geq 10$  cm with locations of dead trees (+). Standard deviation  $\sigma$  of the Gaussian smoothing kernel = 4. Brighter colors represent denser patches. Stand A = mid-successional, stand B = late-successional, stand C = old-growth

## Univariate analysis

Trees of both species combined were significantly clumped at all distances in all stands. In both the mid-successional and old-growth stand, the pattern tended towards random distribution at larger distances. However, in the late-successional stand, living trees were even more clumped at the larger scale compared to the pattern at small inter-tree distances (Fig. 8). Dead trees of both species combined were clumped at small distances in the mid-successional stand and randomly distributed in later successional stages (Fig. 9). Small saplings of both species combined were significantly clumped at all scales in the mid-successional stand but randomly distributed in later successional stages (Table 2).

Living *P. abies* trees were significantly clumped in all stands (Fig. 8). The clumping intensity reached its maximum at distances between 3 and 4 meters and decreased slightly afterwards in the mid-successional stand whereas clumping intensity increased steadily in the late-successional stand and remained more or less constant in the old-growth stand. Clumping intensity was also the highest in the mid-successional stand compared to the intensity of clumping in the late-successional and old-growth stands. Dead *P. abies* trees were always randomly distributed.

Large living mature *P. abies* trees were randomly distributed in all stands but small mature *P. abies* trees tended towards a clumped distribution in the late-successional and old-growth stand at large distances ( $> 6$  m). Large saplings of *P. abies* showed a significantly clumped distribution at distances  $> 1.5$  m in the late-successional stand and slightly significant clumped distributions at distances between 2 m and 2.5 m as well as  $> 6$  m in the old-growth stand (Fig. 8). There were too few large saplings in the mid-successional stand to carry out a representative analysis. Small *P. abies* saplings were intensely clumped in the mid-successional stand, with a maximum at 4 m distance and a slight decrease at larger distances. Clumping reached its maximum value in the late-successional stand at 5 m distance and remained more or less constant at larger scales whereas the pattern tended towards a random distribution at distances  $> 5$  m in the old-growth stand (Fig. 8).

*Betula spp.* trees were clumped in the mid-successional stand at distances between 0 m and 3 m, with a maximum value at 1 m. For larger distances, the pattern remained random with a tendency towards clumping. This tendency towards clumping changed into significant clumping at distances  $> 8$  m. The stems were throughout clumped in a constant intensity in the late-successional stand. In the old-growth stand, the pattern reached its maximum clumping intensity at 2 m distance and remained random at distances  $> 4$  m (Fig. 9).

Dead *Betula spp.* trees showed a clumped distribution on just small scales up to a distance of 2 m with a random distribution on larger scales in the mid-successional stand. There were too few dead *Betula spp.* trees to carry out a meaningful analysis in the late-successional and old-growth stand.

The pattern of combined small and large *Betula spp.* saplings was significantly clumped in the mid- and late-successional stand (Fig. 9). In the late-successional stand, the clumped distribution became insignificant at 2 m distance and reached again a significant value at distances  $\geq 6.5$  m. In the old-growth stand, this pattern was consistently distributed randomly.



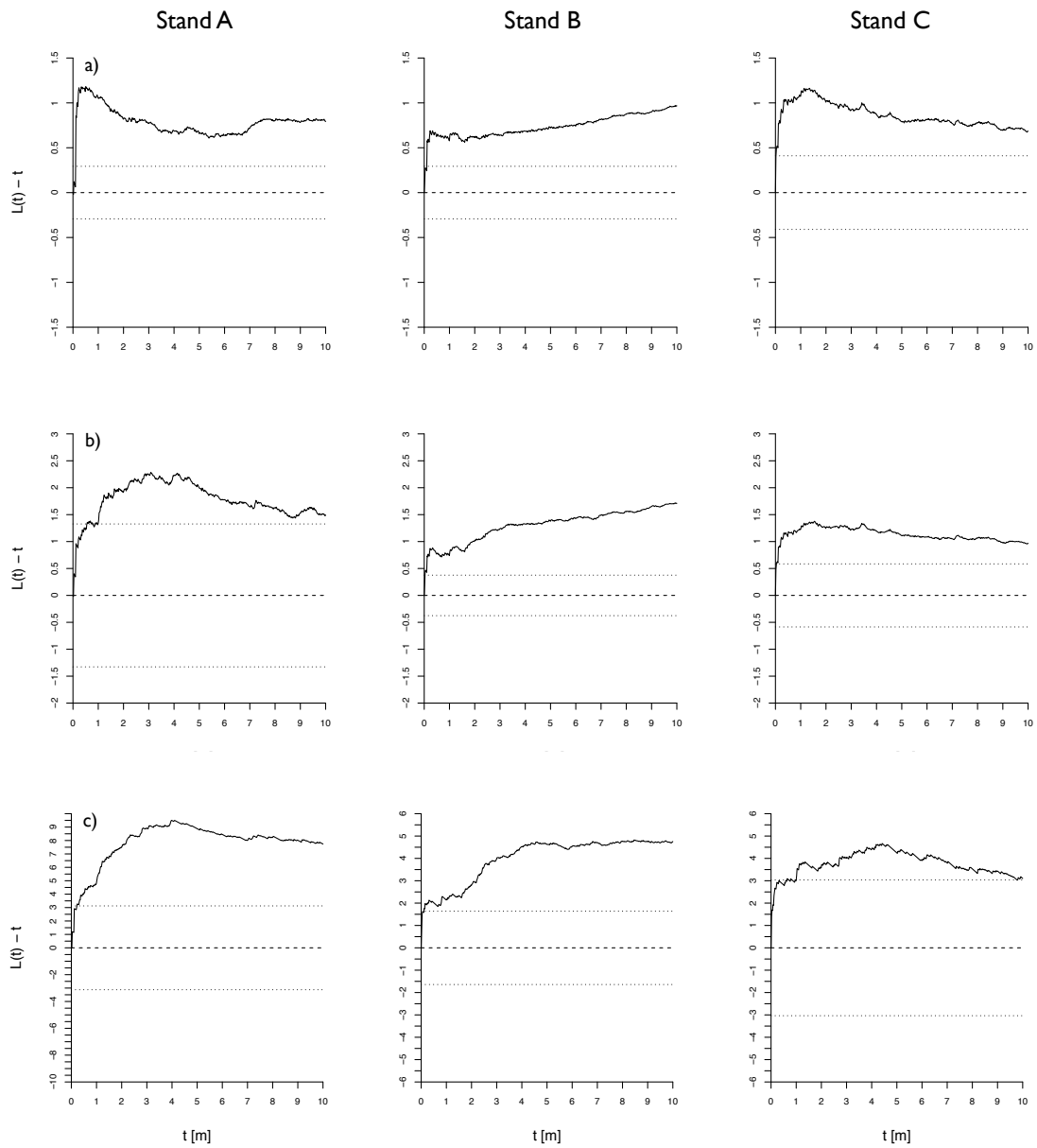


Fig. 8.  $L(t) - t$  plots of univariate analyses. Dashed horizontal line provides a reference for  $L(t)$  under CSR. The dotted lines represent the simultaneous critical bands (0.025 and 0.975 quantiles of  $L(t) - t$ ) estimated from 999 Monte-Carlo simulations). Stand A = mid-successional, stand B = late-successional, stand C = old-growth. a) = living trees, b) = living *P. abies*, c) = living small *P. abies* saplings

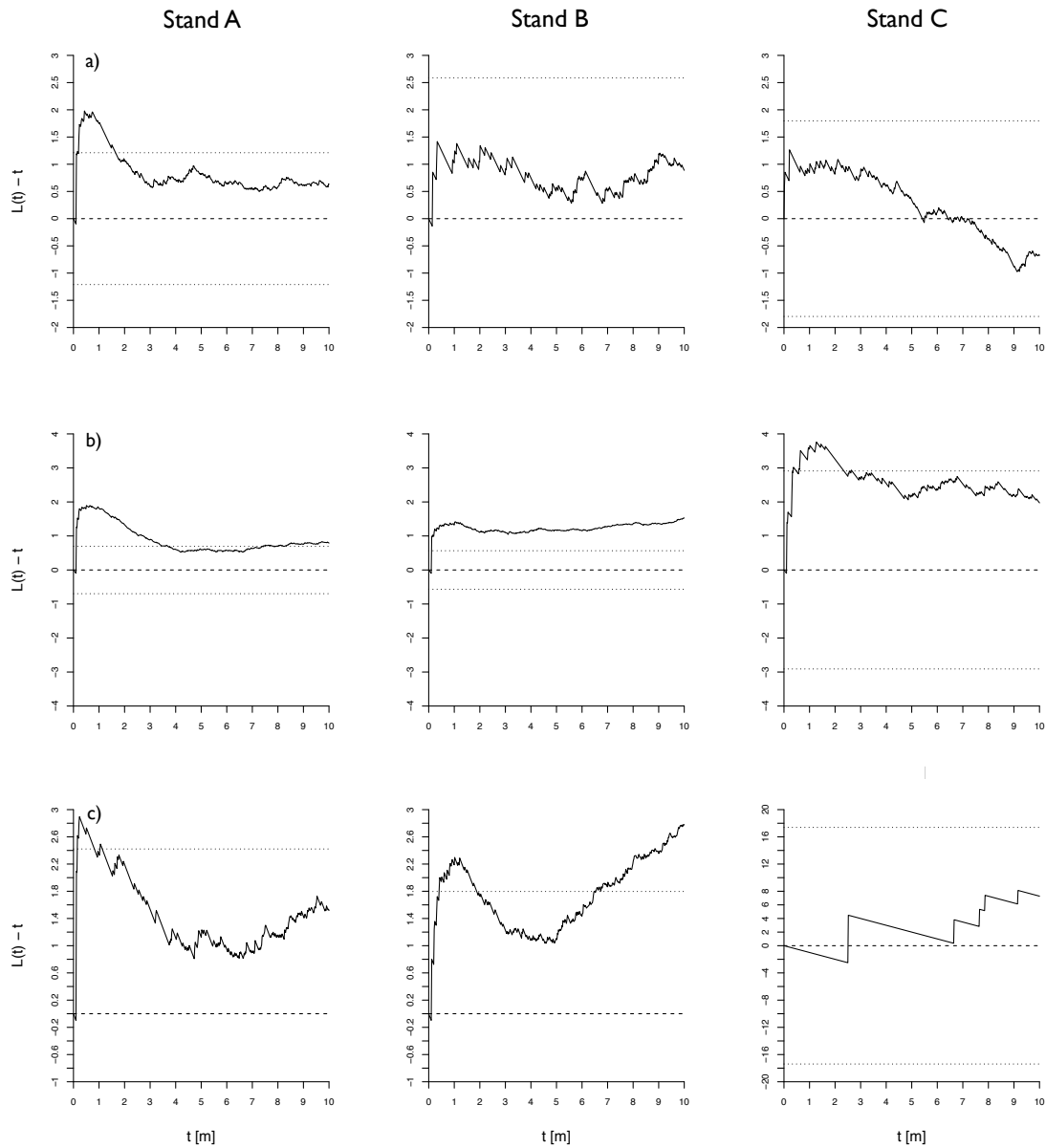


Fig. 9.  $L(t) - t$  plots of univariate analyses. Solid line represents the  $L(t)$ -function. Dashed horizontal line provides a reference for  $L(t)$  under CSR. The dotted lines represent the simultaneous critical bands (0.025 and 0.975 quantiles of  $L(t) - t$ ) estimated from 999 Monte-Carlo simulations). Stand A = mid-successional, stand B = late-successional, stand C = old-growth. a) = dead trees, b) = living *Betula spp.*, c) = living *Betula spp.* saplings

## Bivariate analysis

Dead and living trees were significantly attracted to each other at small distances in all stand ages. This significant attraction changed to independent interactions at distances  $> 1\text{m}$  in the old-growth stand. In the late-successional stand, significant attraction vanished at about the same distance and finally living and dead trees repulsed each other significantly at distances  $> 5\text{m}$ . Basically the same pattern was found in the mid-successional stand, but here, the trees were significantly attracted to each other up to 2 m and, even though not significant, trees tended towards repulsion at distances  $>$

4 m (Fig. 10).

Dead and living *P. abies* trees did not show significant spatial interaction. Dead and living *Betula spp.* trees showed only a significant attraction on small distances  $< 2$ ,  $< 2.5$  and  $< 3$  in the mid-, late-successional and old-growth stand respectively. At larger inter-tree distances dead and living stems interacted independently with each other.

Mature *Betula spp.* trees interacted independently with small *P. abies* saplings at all scales in the mid-successional and old-growth stand. In the late-successional stand, there was a tendency towards repulsion at small distances which changed towards significant repulsion at distances  $> 6$  m. Analysis of the interaction between large saplings as well as small and large mature *Betula spp.* trees and small *P. abies* saplings changed this result. Now, the pattern leaned towards clumping at distances  $> 7$  m which becomes significant at distances  $> 8.5$  m in the mid-successional stand. The pattern retained its tendency towards repulsion at all scales with significant values at inter-tree distances between 2.5 m and 5.5 m in the late-successional stand. In the old-growth stand finally, the pattern displayed a strong but not significant trend towards repulsion at distances  $> 2.5$  m (Fig. 10).

Living *P. abies* trees interacted independently with respect to dead *Betula spp.* trees in the mid-successional and old-growth stand but tended to repulsion. Repulsion only reached significant values in the late-successional stand at 3 m and again at large inter-tree distances  $> 9.5$  m (Fig. 10).

Small *P. abies* saplings occurred independently of dead or living *Betula spp.* trees. Also mature living *Betula spp.* trees and dead *P. abies* trees did not interact significantly.

Analysis of all social strata of *P. abies* and *Betula spp.* showed highly variable interactions. In the mid-successional stand, the species repulsed each other, although not significantly, at distances between 1 m and 2.5 m and were finally significantly positively associated at distances  $> 7$  m. Whereas both species interacted independently in the late-successional stand, the species showed again a tendency towards repulsion in the old-growth stand (Fig. 11).

*Betula spp.* saplings and mature *Betula spp.* trees attracted each other significantly in the mid- and late-successional stand but showed no significant interaction in the old-growth stand. Saplings and mature trees of both species combined attracted each other at distances  $< 2$  m and reached again a significant value of attraction at 9 m distance in the mid-successional stand. The late-successional and old-growth stand showed almost constant significant attraction for saplings and mature trees over all investigated distances (Table 2).

Dead trees of *Betula spp.* and *P. abies* did not significantly interact in any successional stage. Mature *P. abies* and mature *Betula spp.* trees repulsed each other at small scales in the late-successional (between 3 and 8 m) and old-growth stand (between 2.5 and 3 m) whereas no significant interaction was found in the mid-successional stand for these size strata (Fig. 12). Small saplings of either *Betula spp.* or *P. abies* and downed dead trees did not significantly interact in any successional stage.

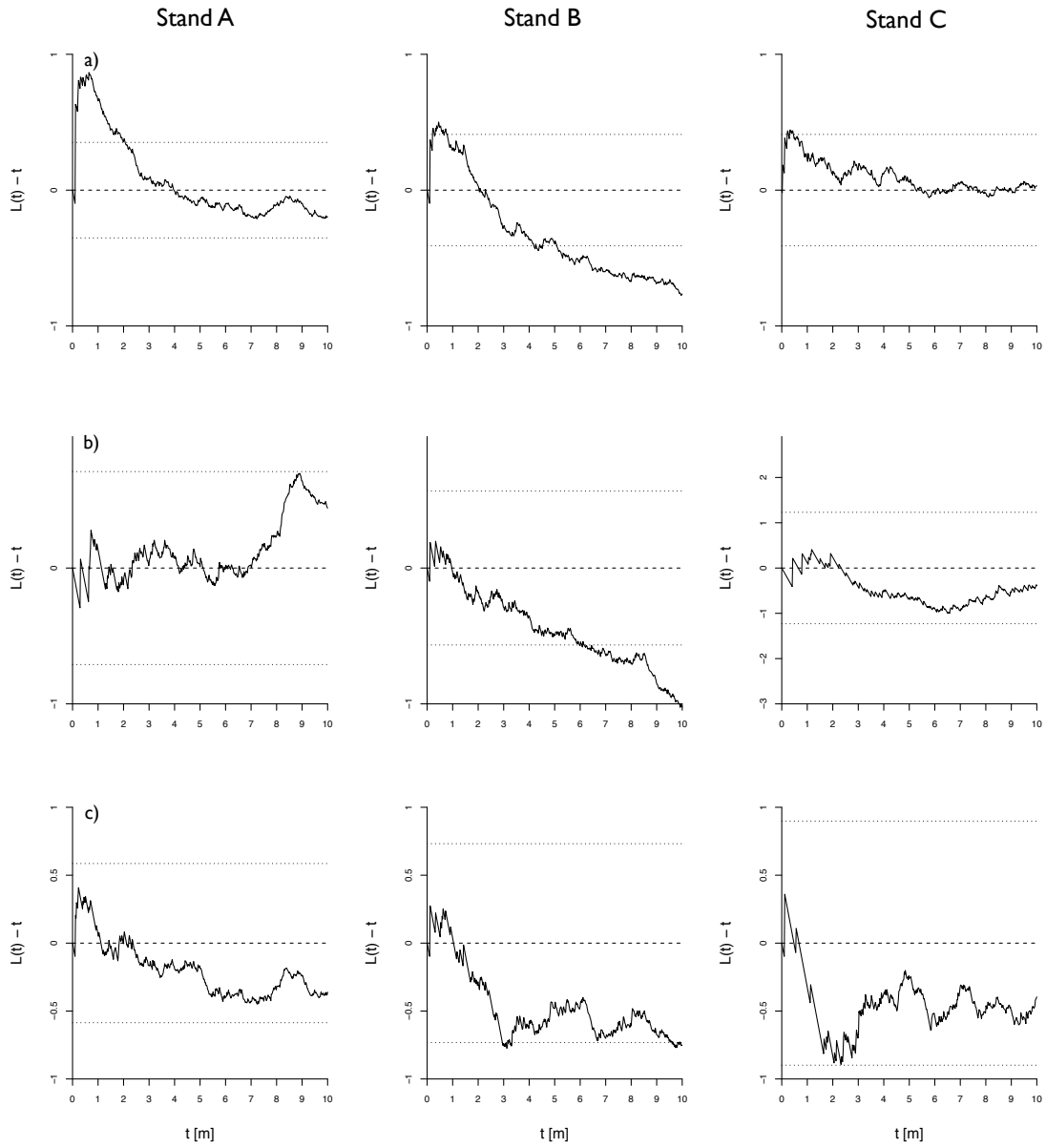


Fig. 10.  $L_{12}(t) - t$  plots of bivariate analyses. Solid line represents the  $L_{12}(t)$ -function. Dashed horizontal line provides a reference for  $L_{12}(t)$  according to  $H_0$ . The dotted lines represent the simultaneous critical bands (0.025 and 0.975 quantiles of  $L_{12}(t) - t$ ) estimated from 999 Monte-Carlo simulations). Stand A = mid-successional, stand B = late-successional, stand C = old-growth. a) = living - dead, b) = living mature *Betula spp.* - living small *P. abies* saplings, c) = dead *Betula spp.* - living *P. abies*

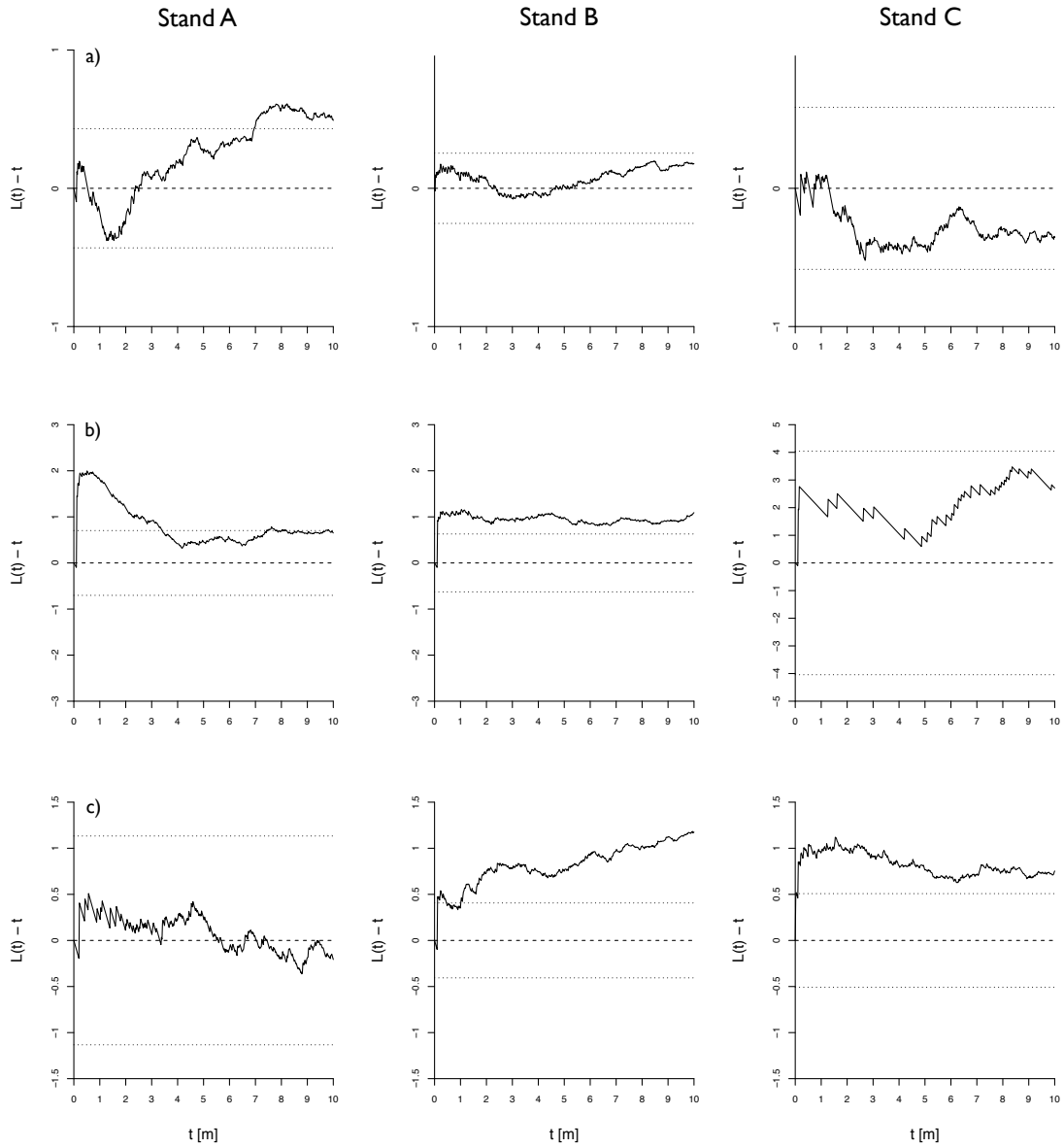


Fig. 11.  $L_{12}(t) - t$  plots of bivariate analyses. Solid line represents the  $L_{12}(t)$ -function. Dashed horizontal line provides a reference for  $L_{12}(t)$  according to  $H_0$ . The dotted lines represent the simultaneous critical bands (0.025 and 0.975 quantiles of  $L_{12}(t) - t$ ) estimated from 999 Monte-Carlo simulations). Stand A = mid-successional, stand B = late-successional, stand C = old-growth. a) = living *Betula spp.* - living *P. abies*, b) = living *Betula spp.* saplings - living *Betula spp.* mature trees, c) = living *P. abies* saplings - living *P. abies* mature trees

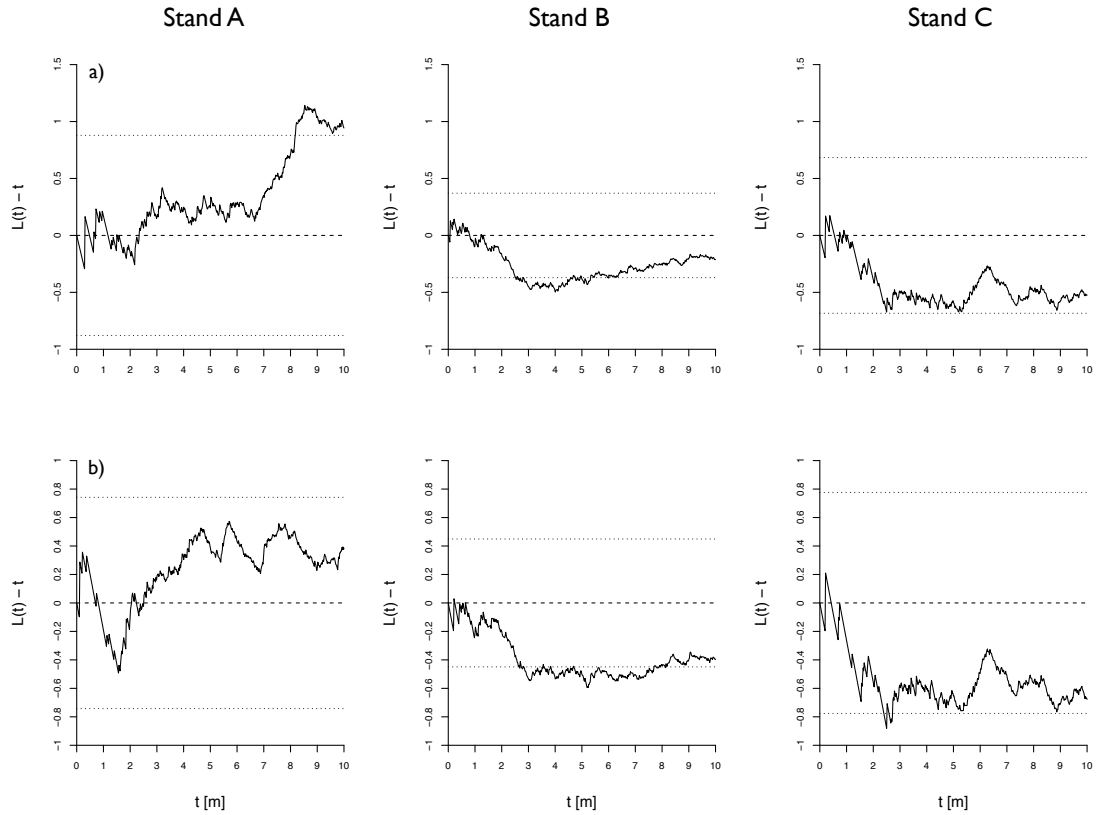


Fig. 12.  $L_{12}(t) - t$  plots of bivariate analyses. Solid line represents the  $L_{12}(t)$ -function. Dashed horizontal line provides a reference for  $L_{12}(t)$  according to  $H_0$ . The dotted lines represent the simultaneous critical bands (0.025 and 0.975 quantiles of  $L_{12}(t) - t$ ) estimated from 999 Monte-Carlo simulations). Stand A = mid-successional, stand B = late-successional, stand C = old-growth. a) = living large *Betula spp.* saplings and mature trees - living small *P. abies* saplings b) = living mature *Betula spp.* trees - living mature *P. abies* trees

### 3.4 Supplementary data

Table 3 displays the stands' soil properties. In each stand, all sample points had slopes  $< 10^\circ$ . The soil type profile of the three stands was very similar, with podzolic soil types strongly dominating. The average soil depth was 10.5 cm in the mid-successional stand, 56.9 cm in the late-successional stand and 16.4 cm in the old-growth stand. Stone contents in the rooting zone were 6.4 % in the mid-successional stand and 2.8 % in the old-growth stand whereas there was no stone content detectable in the late-successional stand. Charcoal residuals between the humus and soil layer were found in few soil samples of the old stand.

The pairwise Chi-Square test for homogeneity resulted in  $\chi^2$  values of 189.23 (comparison stand A - stand B), 45.84 (comparison stand A - stand C) and 167.82 (comparison stand B - stand C). The critical value  $\chi_{0.95}^2$  was 12.6 (degrees of freedom = 6). Thus,  $\chi^2 > \chi_{0.95}^2$  in all pairwise tests and  $H_0$  was consequently rejected. The three stands were thus not homogeneous considering the studied soil characteristics.

All stands were classified as belonging to the northern *Hylocomium-Myrtillus* forest type (HMT) ac-

Table 3. Dominant topography, texture, structure and soil types in the stands (% of the samples). Stand A = mid-successional, stand B = late-successional, stand C = old-growth

Stand	Topography	Texture			Structure		Soil type	
		Sand	Sandy loam	Loamy sand	Single grain	Crumbs	Podzol	Cambisol
A	flat	46.7	8.89	28.89	84.4	15.6	88.9	11.1
B	flat	0.00	51.11	48.89	11.1	88.9	86.9	13.3
C	flat	22.2	44.44	22.22	88.9	11.1	100.00	0.00

According to the Finnish site classification system based on ground- and bottom-layer species composition (Lakari 1920, Cajander 1926). Typical for this forest type are podzolic soils, a continuously growing and thick moss layer and an understory vegetation which is mainly dominated by *Pleurozium schreberi*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and *Juniperus communis*. Trees growing in the northern HMT-forest type do not form dense stands; they are covered by lichen, branches occur down to the stump and the crown is in lower parts relatively wide whereas it is narrow and sometimes dry or broken in upper parts (Lakari 1920).

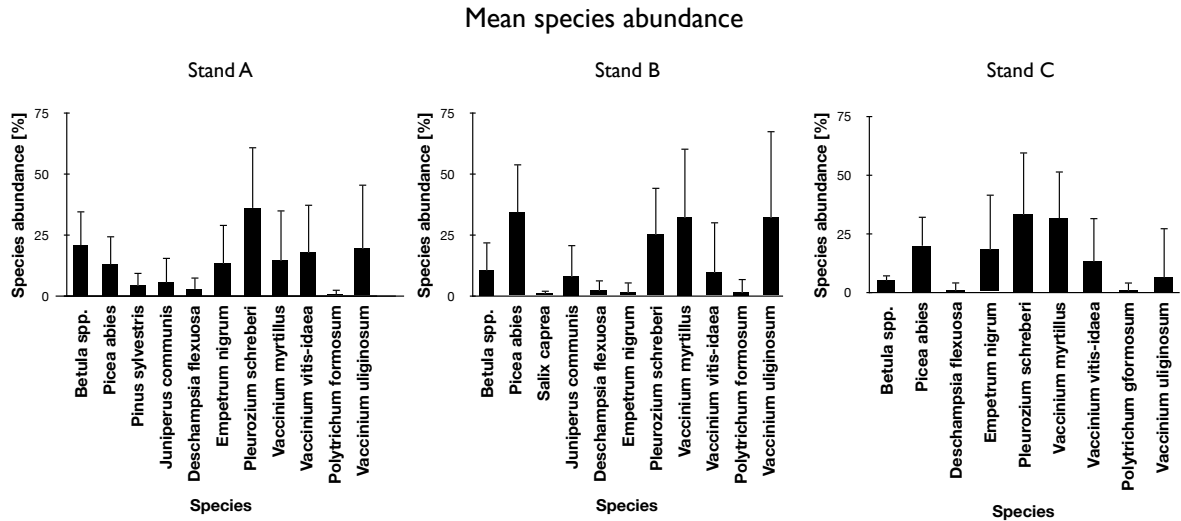


Fig. 13. Mean abundances of the most common species in the studied stands, error bars show the standard deviation. Stand A = mid-successional, stand B = late-successional, stand C = old-growth

Vascular plant species diversity on the plant community level was constant in the mid- and late-successional stand where 11 species were recorded and reached slightly lower values in the old-growth stand with 9 totally recorded species.

### 3.5 Stand visualization

The studied HMT-stands had a sparse tree cover. They were very open forests with partly large unforested patches (Figs 14 - 16).

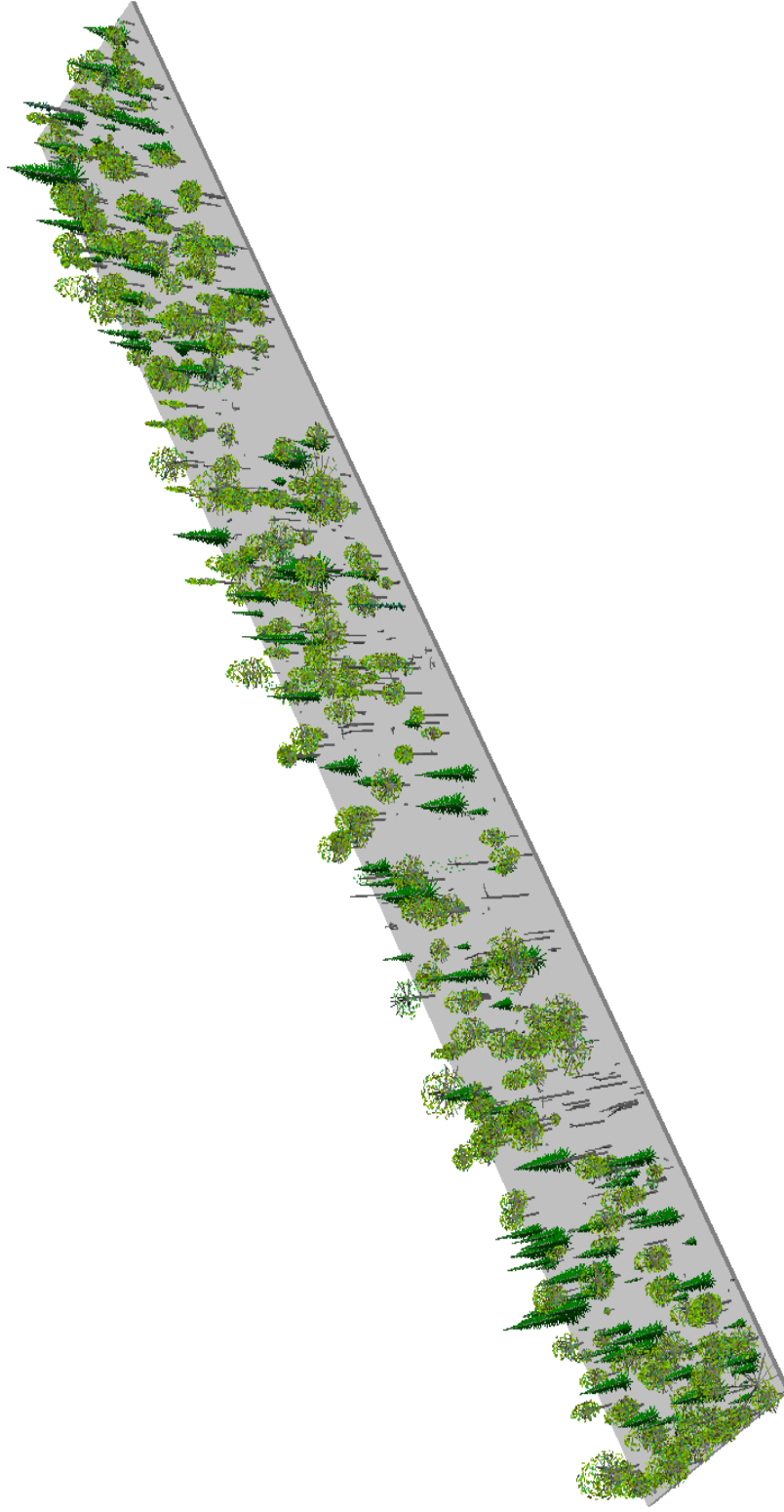


Fig. 14. Image of stand A (mid-successional stage) depicted by the SVS



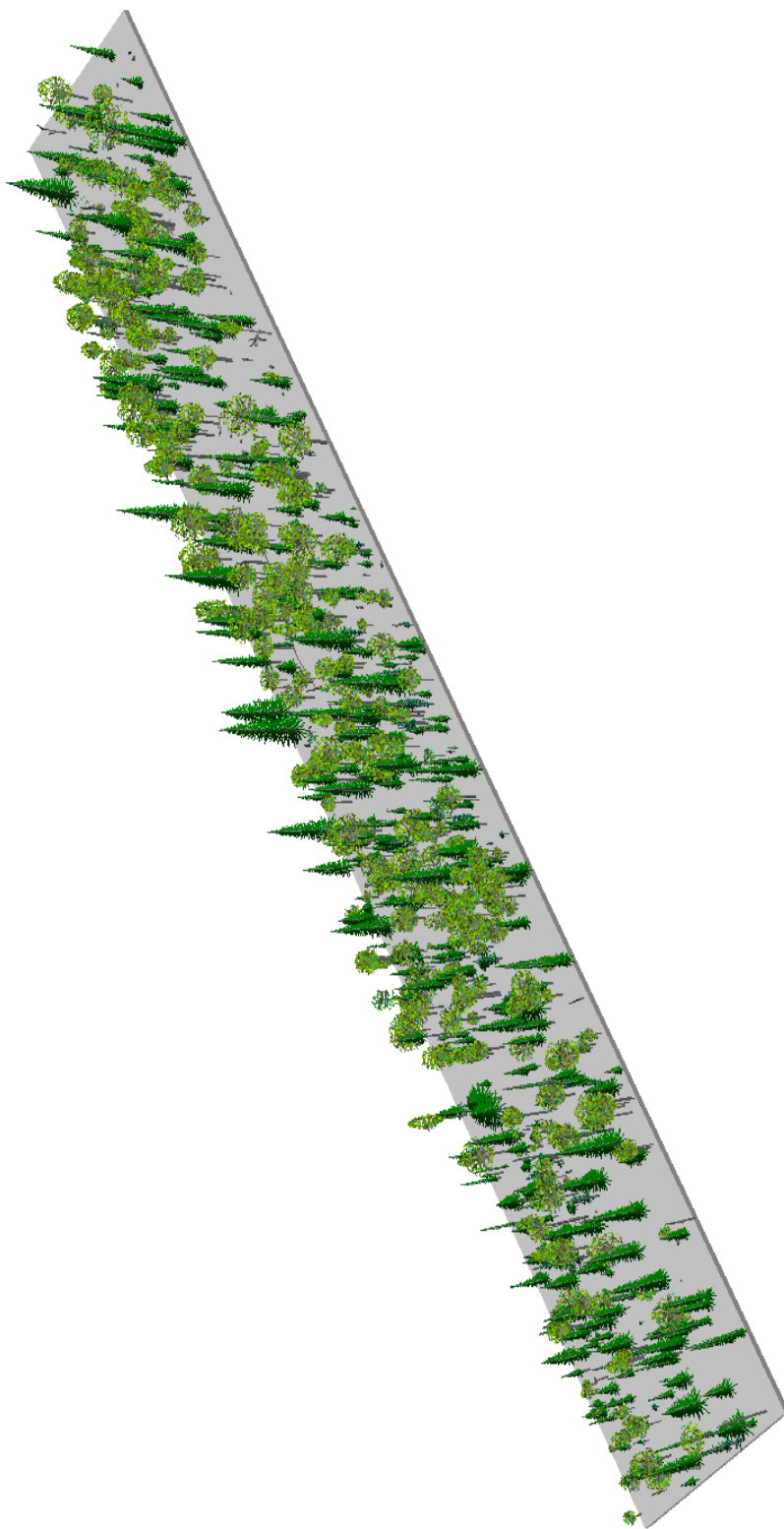


Fig. 15. Image of stand B (late-successional stage) depicted by the SVS

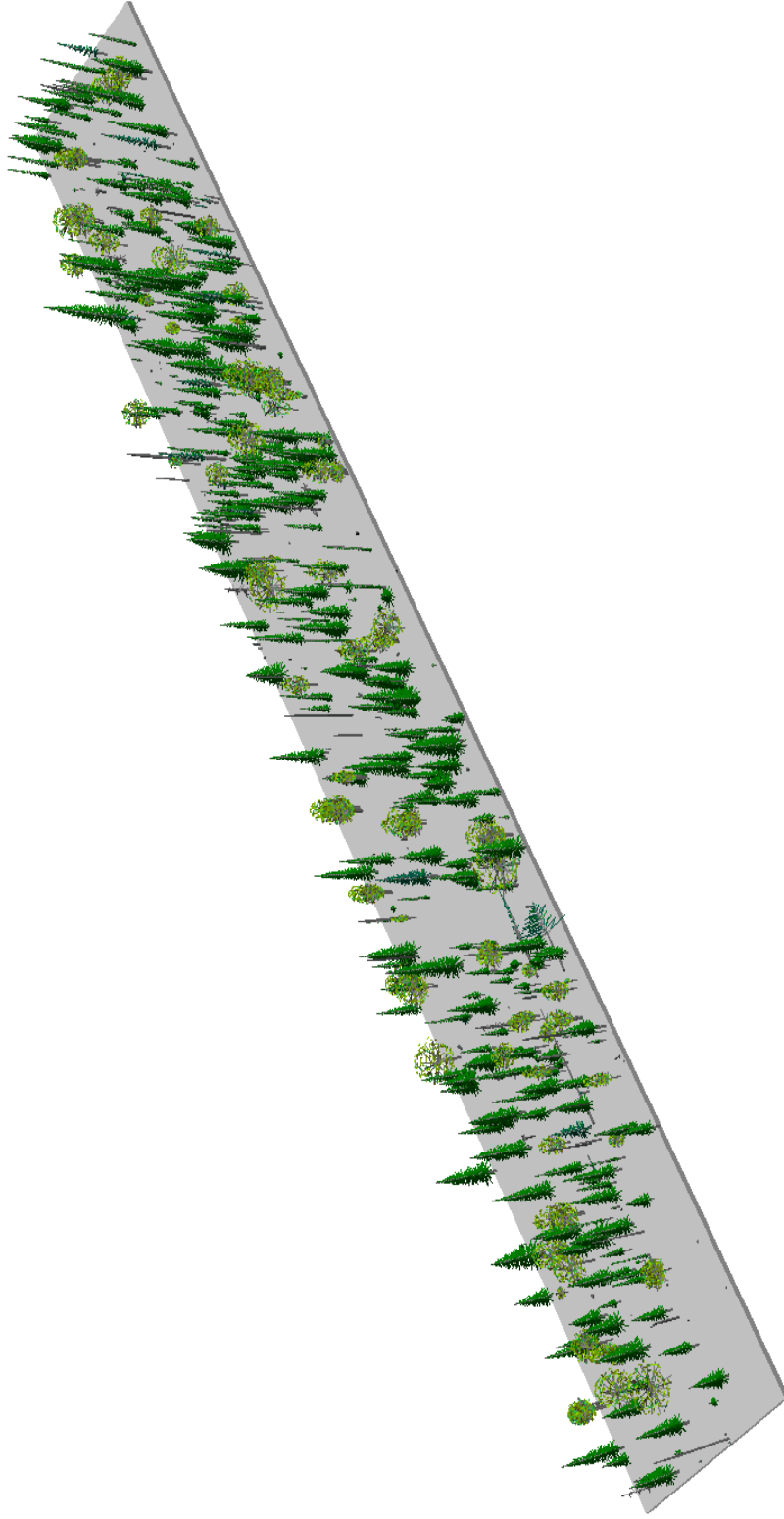


Fig. 16. Image of stand C (old-growth stage) depicted by the SVS

## 4 Discussion

### 4.1 Stand composition and structure

Examination of stand structural characteristics (Table 1) together with the visual observation of the images generated by the Stand Visualization Software (Figs. 14-16) reveal that the studied HMT-forests are rather open and scantily stocked forest stands. The early successional *Betula spp.* dominated the composition of the mid-successional stand where it represented 70 % of the total stem number. Its dominance declined in the subsequent older sample plots to 19% (stem number) whereas the share of *P. abies* increased from 30 % to 81 % from the studied mid-successional to old-growth plots. Thus, according to the successional model of Sirén (1955), *Betula spp.* is gradually replaced by *P. abies* in succession which finally forms a conifer-dominated forest with a small number of remaining *Betula spp.* individuals.

Studies carried out in similar latitudes in HMT forests with varying age since stand replacing fire have reported a similar development. Aakala et al. (2009) reported stand structural characteristics in very old stands, such as a species ratio of *P. abies* of about 70 % or a dead stem number of 103 stems  $\text{ha}^{-1}$  similar to the old-growth stand in this study. Lilja et al. (2006) name a species ratio of *P. abies* of about 90 % and a deciduous tree ratio of 5 % in northern boreal late-successional forest stands. However, in Heikinheimo's (1922) classical study, average stem numbers for *P. abies* in HMT-forests totaled 216 trees  $\text{ha}^{-1}$  which is much less than the numbers observed in this study. This stem number deviation might reflect the natural variability of this forest type what could be due to a productivity gradient along latitude (Sirén 1955) or it could be the result of a different lower diameter limit for tally tree classification.

The successional pathway of secondary HMT boreal forests in northern Finland was first studied by Sirén (1955). While the results for mean diameter, height values or number of dead and living stems in this study are much smaller than the values provided by Sirén, the general structural and compositional changes described by him are also evident in this study. Also Sirén found the dominance of *Betula spp.* to decline at stand ages between 120-300 years and to be replaced over succession by *P. abies* which finally forms a conifer dominated forest. (id.) and this finding was also confirmed by other studies (e.g. Doležal et al. 2006, Lilja et al. 2006). Interspecific differences in the frequencies of dead trees may partly reflect the differences in decomposition rate of the species.

Even though *Betula spp.* is traditionally considered an “early successional” species, it can obviously persist in old-growth boreal coniferous stands as already described by Sirén (1955). One possible explanation for this could be an abundant seed production of *Betula spp.* combined with available suitable seed regeneration microsites created by tree falls (Perala & Alm 1990, Kuuluvainen et al. 1998) and/or the ability of mainly *Betula pubescens* to reproduce vegetatively through sprouting.

Apart from the *P. abies* population in the young stand, all living tree populations displayed their maximum frequency count in the diameter strata of (10–15] respectively (15–20]. The often described “reverse-J” tree diameter distribution of old-growth boreal forests (Linder et al. 1997, Linder 1998, McCarthy & Weetman 2006), which is characterized by a steeply and steadily declining tree number

with d.b.h. (Leak 2001), could not be observed in any stand's tree population. Instead, the tree diameter distribution of *P. abies* followed a rotated sigmoid distribution and that of *Betula spp.* an unimodal distribution in all successional stages. The term rotated sigmoid describes a curve of a number of trees over d.b.h. that has an obvious plateau, near plateau or bump in the mid-d.b.h. range (id.).

Similar diameter distributions for *P. abies* in old-growth boreal forests in Finland and Sweden were also found by Doležal et al. (2006), Lilja et al. (2006) and in a few cases by Linder et al. (1997). Ylläsjärvi & Kuuluvainen (2009) also showed a unimodal distribution of *Betula spp.* for plots dominated by *Betula spp.*, however, they found a “reverse-J” distribution for *P. abies* in HMT-forests.

A “reverse-J” tree diameter distribution is traditionally considered to be a characteristic of natural old-growth forests (McCarthy & Weetman 2006) since it indicates continuous regeneration and recruitment in case of constant regeneration and mortality rates (Kuuluvainen et al. 1998, Linder 1998). Constant regeneration and mortality rates are, however, rare over long time periods due to climatic variability in boreal forests (Hofgaard 1993) and thus, deviations from this distribution have been found regularly (Goff & West 1975, Linder 1998, Leak 2001, Takashi et al. 2001, Lilja et al. 2006). Hunter (1999) names occasional moderate disturbances to be responsible for the often observed deviations from the theoretical “reverse-J”-distribution whereas Goff & West (1975) bring forward the view that medium-diameter classes represent a stage in which the trees have just escaped the stage of competition and are not yet vulnerable to size-related mortality. Results by Linder (1998) also showed that the 15–20 cm diameter class in virgin boreal forests in central Sweden had minimum mortality rates. The rotated sigmoid distribution would thus result from a combination of U-shaped mortality by relatively higher mortality rates in understorey and senescent overstorey (Fraver et al. 2008) and high growth rates in mid-diameter classes that drop sharply at some point, given sufficient seedbed availability. High mortality rates in the understorey might be attributable to low growth rates in northern latitudes (Grenfell et al. 2011). The peaks in diameter distributions might also indicate short favorable regeneration periods, however, this assumption is not supported by the age distribution data of the stands (fig. 3). A lack of young trees might further indicate a poor regeneration situation (Heikinheimo 1922). This is likely due to the thick raw humus layer in HMT-forests which causes a lack of suitable seedbeds for sexual regeneration. A rotated-sigmoid distribution is consequently more likely to reflect equilibrium structures of populations in relatively homogeneous old-growth boreal forests than the “reverse-J” distribution (see also Goff & West 1975).

## 4.2 Spatial pattern analysis

The majority of tree populations in the studied stands displayed a clumped spatial pattern. Trees tended to build densely and sparsely stocked patches. This pattern is emphasized in the whole tree community as well as in the *P. abies* population. A clumped pattern was observed in small *P. abies* saplings (d.b.h.  $\leq 5$  cm) in all successional stages but this clumping was less emphasized in bigger trees, finally resulting in purely random patterns for large mature *P. abies* trees. Also *Betula spp.* possessed a clumped distribution (Table 2).

Other studies done in boreal forests have also found predominantly clumped distributions of trees

(Doležal et al. 2006, Aakala et al. 2007). Bertness & Callaway (1994) state that positive interactions in plant communities dominate in harsh environments. Consequently, Grenfell et al. (2011) showed significant clumping of regeneration for *P. abies* in northern-boreal forests from different regions, whereas *Betula spp.* regeneration was found to be randomly distributed. Small-scale clumping of living *Betula spp.* saplings in Russian boreal forests was also found by Takahashi et al. (2001). In unmanaged boreal forests in southern Finland, a random distribution of large trees was found by Kuuluvainen et al. (1996), which is also in accordance with the results for large mature trees of both species as presented in this study. Armesto et al. (1986) suggested that clumped patterns are typical for forests that are rarely subjected to severe large-scale disturbances.

It is expected that the pattern of a tree community displays a stronger clumping intensity (higher  $L(t)$  values) at large scales ( $> 10$  m) due to large scale environmental heterogeneity (e.g. variation or gradients in soils and geomorphology), compared to small scale effects of competition that should result in a more regular or random pattern (Lepš & Kindlmann 1987, Getzin et al. 2008). Since in this study the clumped pattern was most emphasized at the small studied inter-tree distances and decreasing more or less steadily at larger studied distances (it remained more or less constant in the late-successional stand), this indicates that environmental heterogeneity played a minor role in the formation of the spatial pattern in the mid-successional (ca. 180 years) and old-growth ( $\geq 350$  years) stand. Thus, the main reason for clumping is probably not due to large scale environmental heterogeneity such as changes in site types or climatic variation but to factors operating on a small scale.

One of these factors is possibly the availability of regeneration microsites. Microsites with a disturbed raw humus layer such as logs, stumps and uprooted spots as well as the crown periphery around large trees have been found to be important regeneration microsites in boreal forests (Aaltonen 1919, Sirén 1955, Hofgaard 1993, Grenfell et al. 2011). Relatively higher regeneration rates per area unit on these disturbed microsites may result in clumped patterns in regeneration (Manabe et al. 2000). Indeed, clumped patterns in *Betula spp.* and *P. abies* regeneration in northern boreal forests have been found regularly (e.g. Aaltonen 1919, Sirén 1955, Grenfell et al. 2011). Takahashi et al. (2001) attributed the small scale clumping of *Betula spp.* saplings in Kamtschatkan boreal forests to a vegetative regeneration strategy. Both *Betula pubescens* and *Betula pendula* regenerate vegetatively by root suckers (Kährs 2008). Heikinheimo (1922) found vegetative regeneration of *Betula spp.* and *P. abies* to play an important role in high-altitude HMT-forest regeneration in the presence of a thick raw humus layer. However, no vegetative regeneration of *P. abies* was observed in this study. The humus layer in the studied stands accumulated up to 8 cm and similar values for the humus thickness were found by Heikinheimo (1922) and Sirén (1955) for comparable successional stages. The importance of vegetative regeneration is attributed to the restricted access to suitable seedbeds on microsites created by small-scale disturbances within the thick raw humus layer and the poor seed production in these cold climates. Its importance increases the thicker the raw humus layer has accumulated (Heikinheimo 1922). These results are supported by Johnstone & Chapin (2006) who found decreasing seedling survival rates as the organic layer thickness increases. As the maximum clumping intensity occurs at distances where high tree-to-tree interactions occur, species specific regeneration strategies or regeneration microsite effects are likely to contribute to the observed small-scale clumping.

A significant regular distribution is an indicator of inter-tree competition (Kershaw 1963, Doležal et

al. 2006) but significant regular distributions were not observed in this study for any successional stage or any tree population. However, a regular pattern due to competition will only be the result of sufficient mortality. It is thus obvious that density-dependent mortality is not necessarily occurring on sites with low stem densities (Getzin et al. 2006). Another possible explanation for the observed lack of regular distributions and its implied intra-specific competition is provided by Lepš & Kindlmann (1987). They showed that self-thinning of an initially aggregated population due to strong competition does not necessarily result in a regular distribution but forms a nearly random spatial pattern in the surviving trees. A comparison of the pattern of saplings and mature trees reveals a less intense degree of clumping or even random distributions in the mature trees. Bearing the results of Lepš & Kindlmann (1987) in mind it appears that intra-specific competition leads to the dissolution of the initially clumped regeneration patterns in respective size strata. However, when accounting for the whole tree community and not only certain size strata, the results of this study suggest that significant regular tree distributions in HMT-forests do rarely occur. Intra-specific competition can thus not be considered to be the driving force in governing spatial distribution and population dynamics of the tree populations in HMT-forests.

Attractive spatial pattern interactions between *Betula spp.* and *P. abies* were rare. Overall, the two species had no spatial association, negative or positive; the only exception was the 180 years old stand where both species attracted each other at inter-tree-distances  $> 7$  m (Fig. 11). As Sirén (1955) found the stage of high competition to occur up to stand ages of 200 years, the observed attractive pattern could reflect the replacement of *Betula spp.* by *P. abies* in this successional stage.

On the one hand, attractive interactions between *P. abies* saplings and *Betula spp.* hardly occurred (Tab 2). On the other hand, living *Betula spp.* saplings and mature *Betula spp.* trees predominantly showed attraction as well as living *P. abies* saplings and mature *P. abies* trees in most studied successional stages. Also Aaltonen (1919) documented clustering of seedlings around large mature living trees in dry heath forests but did not provide an explanation for this pattern. Positive interactions between two species in the form of positive density-dependent recruit survivorship have been detected in harsh physical environments where plant neighbors ameliorate the habitat in such a way that it affects the recruitment events positively (Bertness & Callaway 1994). Whereas the study site represents without a doubt a harsh physical environment, the rare attractions between the two species provide only limited support of this hypothesis. Nevertheless, clumped patterns are usually considered to represent facilitation processes, i.e. the presence of individuals enables the establishment and growth of further individuals by e.g. seedbed creation, nutrient facilitation or shelter functions (Armesto et al. 1986, Kuuluvainen 1998). Facilitative effects of mature trees on saplings are strongly suggested in this study by the observed attractive interaction between saplings and mature trees of both species in most stands. The dominance of clumped spatial patterns in this study thus implies an important role of facilitation processes in the studied HMT-forests on spatial patterning besides the role of regeneration strategies or microsite effects. However, this facilitation seems to be restricted to inter-species tree-to-tree interactions.

Small living *P. abies* saplings were not associated with dead trees of any species and small living *P. abies* saplings and living mature *Betula spp.* trees even showed a tendency towards repulsion with significant values in the late-successional stand at distances  $> 6$  m. Similar findings for the

interaction between *P. abies* saplings and *Betula spp.* canopy trees were published by Takahashi et al. (2001) for Kamtschatkan boreal forests. If seedlings have regenerated near dead mature trees of the other species, a successional relationship between the two species can be assumed (id.). The lack to detect a successional relationship combined with the observed inter-specific attraction between seedlings and mature trees in most successional stages suggests that a clumped seedling establishment in the proximity of crowns of the own species is the preferred regenerative process for both species in these stands. Regeneration around mature trees can benefit from higher rates of litterfall and thus nutrient availability in the close surrounding of mature trees (Kuuluvainen & Ylläsjärvi 2011). Similar inter-specific attractive patterns between seedlings and mature trees could be expected if vegetative regeneration is the dominant regenerative process. Bivariate analysis of saplings and mature trees of *Betula spp.* match the clonal regeneration strategy of *Betula spp.* well in the mid-successional stand since the clumping is restricted to a small scale. This further suggests the importance of the humus layer for regeneration as described earlier. Many analyses in this study thus provided no support of a successional dependency of *P. abies* on *Betula spp.* (Duncan 1991). This casts doubt on the often mentioned effect of resource facilitation by *Betula spp.* on *P. abies* in HMT-forests on spatial patterning (Perala & Alm 1990, Doležal et al. 2006).

Mature *P. abies* and *Betula spp.* trees showed a tendency towards repulsive interactions with significant values in > 200 year old stands. The combination of dominant clumped distributions in mature trees of *P. abies* and *Betula spp.* together with the repulsive interactions between mature *P. abies* and *Betula spp.* suggests mono-species clumps that consist of either *P. abies* or *Betula spp.* trees. Also Doležal et al. (2006) found such a mosaic of small patches of *P. abies* and *Betula spp.* in HMT-forests. Stoll & Prati (2001) found that this intra-species aggregation decreases the superiority of those species that would otherwise dominate competitively inferior species whereas the latter benefit from being surrounded by conspecifics in an experimental plant community. Thus, intra-specific clumping could be an adaption by *Betula spp.* to the superiority of *P. abies* in below ground competition simply by reducing inter-specific competition (Duncan 1991, Kuuluvainen 1994). Mid- to late-successional HMT-forests thus do display a mosaic of small patches of *P. abies* and *Betula spp.* trees which is possibly an adaption to intra-specific competition (Gray & He 2009).

Even though some patterns displayed a random distribution of trees or a random interaction between them, this does not necessarily mean that there is no interaction at all between the individual trees nor does it mean that the processes that affect the distribution of trees are purely random processes (Szwagrzyk 1990). On the other hand, it can be said for sure that the processes responsible for non-random distributions of trees are not strong enough to display patterns significantly distinctive from randomness. In case the analyzed population includes only few individuals (e.g. dead tree population), it is also likely to find a random pattern.

### 4.3 Methodological considerations

The value of information concerning past processes in plant communities derived from spatial pattern analyses has been discussed controversial in the past. Even though there is strong evidence of how to interpret the results derived from the point pattern analyses, there are nevertheless drawbacks of these interpretations. Conclusions derived from the analysis of an observed pattern is less reliable than

information derived from manipulative experiments. However, manipulative experiments in forests over long time periods are practically unfeasible (Lepš 1990). The observed spatial pattern of forests is the result of mortality, growth and regeneration processes (Little 2002). Variations in living tree patterns will thus result in different patterns of dead trees even though the disturbance process might be the same. This becomes even more emphasized as the properties of the initial stand replacing disturbances of the studied stands are unknown. Since each disturbance type creates a specific pattern, a variation in the initial spatial point pattern between the studied stands can not be taken into account. In short, it is simply unlikely that all the studied stands have experienced the same (a)biotic disturbance history (Boucher et al. 2006). This casts doubt on the conclusions derived by the chronosequence approach. The supplemental soil data collected to assess environmental heterogeneity of the stands also indicate inhomogeneous stands with respect to the assessed abiotic factors. This further weakens the validity of the results obtained by the chronosequence approach.

The resulting stand ages can not be considered to represent accurate estimates of the true stand age. They rather reflect the minimum time since the last stand replacing disturbance which is usually fire in this region (Wallenius et al. 2005, Kuuluvainen & Aakala 2011). It is however likely that the old-growth stand is much older than the stated 350 years as results of increment core analysis by Aakala et al. (2009) or Lilja et al. (2006) show similar core analysis results but charcoal analysis revealed a potentially much older stand age. When looking at the age distributions of the late-successional stand, it is reasonable to assume that the oldest tree in this stand, *P. sylvestris*, has already germinated before the last disturbance that replaced most of the surrounding vegetation. This is simply attributable to the capacity of *P. sylvestris* to survive forest fires. *P. sylvestris* possesses a thick insulating bark, is able to recover its cambial cells effectively after fire damage and is also resistant to fungal or insect attacks. Additionally, the branch system of *P. sylvestris* makes it less susceptible to surface fires than e.g. that of *Betula spp.* or *P. abies* (Zackrisson 1977). Moreover, results by Wallenius et al. (2004) state that forest fires in eastern Fennoscandia usually leave small unburned patches due to differences in vegetation or site types which could also be the case for the surrounding of this *P. sylvestris*. Whereas age determination of increment cores from *P. abies* and *P. sylvestris* were easy to perform, it was much more difficult to determine the age for increment cores gained from *Betula spp.* The determined ages can thus represent merely minimum ages. However, since the sampled coniferous species are more long-living compared to *Betula spp.*, the results derived from their analysis are more important than the ones from *Betula spp.*

The use of Ripley's  $K(t)$ -function as a suitable tool for plant ecological analyses has been challenged earlier.  $K(t)$  does not define the point process uniquely. Two different processes can thus have the same  $K(t)$ -function (Baddeley & Silverman 1984), respectively the same spatial pattern. The same is valid vice versa, meaning that one distinct past process is very unlikely to produce its own unique footprint in the form of a spatial pattern (Law et al. 2009). Furthermore, the effect of clustering at short distances is only gradually diluted out by randomness at larger distances, and can lead to a superficial impression of clustering over longer distances than operate in reality when Ripley's  $K(t)$ -function is used (Wiegand & Moloney 2004). This study tested deviations of the actual observed point process from a Poisson process. However, Loosmore & Ford (2006) state that a Poisson process is not a very useful null model since purely random spatial processes are rare in nature (Greigh-Smith 1979, Diggle



2003).

Last but not least, the location of the study area in a reindeer herding area with unnaturally high reindeer population densities must be considered. Reindeer herding is likely to cause significant structural and compositional changes to the forest stand through grazing, trampling and fertilization (Greig-Smith 1979, Josefsson 2009). Hence, the results especially for the small diameter strata of birch, which are efficiently grazed by reindeers, might not represent necessarily patterns that could be observed under more pristine conditions.

Yet, despite the mentioned drawbacks, this study also provides strong evidence of reliable results of the spatial pattern analyses. The forest floor species abundance data in this study are consistent with descriptions of Finnish HMT-forests by Cajander (1926), Sirén (1955) and Lakari (1920). The studied stands can consequently be assumed to represent an adequate and accurate sample of HMT-forests. Also the implemented plot sampling contributes to a high accuracy of the the spatial pattern analyses results. The plot size of 1.2 ha is much larger than that of most similar studies, e.g. 0.3 - 0.4 ha in Doležal et al. (2006), 0.36 - 1 ha in Getzin et al. (2006) or 1 ha in Gray & He (2009). Since large plot sizes contribute to capture much of the within stand variance, the results of this study for the spatial analysis can be considered to be more reliable than those of most similar studies.

## 5 Conclusions

The aim of this study was to statistically analyze the small scale spatial pattern development of trees in an unmanaged boreal HMT-forests in northern Fennoscandia and eventually visualize its development based on the chronosequence approach. Furthermore, this study aimed to discuss potential mechanisms causing the observed patterns.

The spatial tree patterns were predominantly clustered and this pattern did not vary much over succession. Small trees were generally more clustered than larger trees and saplings of both species were predominantly attracted to mature trees of the same species. This attraction between saplings and mature trees and the repulsion between living mature *P. abies* and mature *Betula spp.* suggests clumps composed of merely one species in mid- to late-successional forest stages which display a mosaic of small patches of *P. abies* and *Betula spp.* At the same time, a successive dependency of *P. abies* on *Betula spp.* can be rejected.

In addition, the prevalent attraction between saplings and mature trees implies vegetative regeneration to be an important regeneration strategy. The thick raw humus layer in HMT-forests potentially contributes to vegetative regeneration and the clumped pattern in the small tree population by restricting suitable microsites for sexual regeneration. As regular distributions did not occur, the availability of suitable regeneration microsites and vegetative regeneration strategies can be assumed to outrun competitive effects on spatial structure in the presence of a thick raw humus layer in HMT-forests. In conclusion, competition has a minor importance in governing the spatial patterning of this forest type.

Despite evidence of facilitative effects due to the observed intensive clumping, the facilitative effects

of *Betula spp.* on *P. abies* as reported by Doležal et al. (2006) could not be shown in this study. It can thus be concluded that facilitation is merely restricted to inter-species tree-to-tree interactions.

A thorough literature review showed that this study - in addition to the study conducted by Doležal et al. (2006) - the only studies on the spatial point pattern in HMT-forests so far. Further research could investigate the actual point process that generates the observed patterns by fitting appropriate point-process models to the observed pattern and evaluate their power. Ultimately, the results derived from this study could thereby contribute to formulate plausible hypotheses concerning the causes for spatial patterning in HMT-forests - which could be tested in experimental studies.

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## References

- Aakala, T., & Keto-Tokoi, P. (2011). The old Norway spruce forests of northern boreal Fennoscandia are alive and well: A review of Sirén (1955). *Scandinavian Journal of Forest Research*, *26*, 25–33.
- Aakala, T., Kuuluvainen, T., De Grandpre, L., & Gauthier, S. (2007). Trees dying standing in the northeastern boreal old-growth forests of Quebec: spatial patterns, rates and temporal variation. *Canadian Journal of Forest Research*, *37*, 50–61.
- Aakala, T., Kuuluvainen, T., Wallenius, T., & Kauhanen, H. (2009). Contrasting patterns of tree mortality in late-successional *Picea abies* stands in two areas in northern Fennoscandia. *Journal of Vegetation Science*, *20*, 1016–1026.
- Aaltonen, V. T. (1919). *Über die natürliche Verjüngung der Heidewälder im finnischen Lappland I.* Valtioneuvoston Kirjapaino.
- Ad-hoc-AG Boden (2005). *Bodenkundliche Kartieranleitung*. Bundesanstalt für Geowissenschaften und Rohstoffe (German Federal Bureau of Geosciences and Resources), Hannover, 5. ed. In German.
- Akhminova, M. (1983). On methods of suppression and substitution of spruce seedlings by mosses. *Nauka Leningrad*, (pp. 289–291). In Russian.
- Anderson, D. (1967). Studies on structure in plant communities: III. data on pattern in colonizing species. *Journal of Ecology*, *55*(2), 397–404.
- Angelstam, P. K. (1998). Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *Journal of Vegetation Science*, *9*, 593–602.
- Antos, J. A., & Parish, R. (2002). Structure and dynamics of a nearly steady-state subalpine forest in South-Central British Columbia, Canada. *Oecologia*, *130*, 126–135.
- Armesto, J. J., Mitchell, J. D., & Villagran, C. (1986). A comparison of spatial patterns of trees in some tropical and temperate forests. *Biotropica*, *18*(1), 1–11.
- Baddeley, A., & Silverman, B. (1984). A cautionary example on the use of second-order methods for analyzing point patterns. *Biometrics*, *40*, 1089–1093.
- Baddeley, A., & Turner, R. (2005). Spatstat: an R package for analyzing spatial point patterns. *Journal of Statistical Software*, *12*(6), 1–42. URL: [www.jstatsoft.org](http://www.jstatsoft.org), ISSN: 1548- 7660.
- Bartemucci, P., Coates, K. D., Harper, K. A., & Wright, E. F. (2002). Gap disturbances in northern old-growth forests of British Columbia, Canada. *Journal of Vegetation Science*, *13*(5), 685–696.
- Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Tree*, *9*(5), 191–193.
- Bormann, F. H. (1954). The statistical efficiency of sample plot size and shape in forest ecology. *Ecology*, *34*(3), 474–487.
- Bormann, F. H., & Likens, G. E. (1979). Catastrophic disturbance and the steady state in northern hardwood forests. *American Scientist*, *67*, 660–669.

- Böttcher, H. (2007). *Forest Management for Climate Change Mitigation - Modeling of Forestry Options, their Impact on the Regional Carbon Balance and Implications for a Future Climate Protocol*. Ph.D. thesis, University of Freiburg im Breisgau.
- Boucher, D., Gauthier, S., & De Grandpré, L. (2006). Structural changes in coniferous stands along a chronosequence and productivity gradient in the northeastern boreal forest of Québec. *Ecoscience*, *13*(2), 172–180.
- Cajander, A. K. (1926). The theory of forest types. *Acta Forest. Fennica*, *29*(3), 1–108.
- Clark, S. L., & Hallgren, S. W. (2004). Age estimation of quercus marilandica and quercus stellata: applications for interpreting stand dynamics. *Canadian Journal of Forest Research*, *34*, 1353–1358.
- Dale, M. R. T., & MacIsaac, D. A. (1989). New methods for the analysis of spatial pattern in vegetation. *Journal of Ecology*, *77*(1), 78–91.
- Davis, L. S., Johnson, K. N., Bettinger, P., & Howard, T. (2000). *Forest management*. New York: McGraw-Hill Series in Forest Resources, 4th ed.
- Diggle, P. (2003). *Statistical Analysis of Spatial Point Pattern*. Arnold, London, UK.
- Dixon, P. (2002). Ripley's k-function. *Encyclopedia of Environmetrics*, *3*, 1796–1803.
- Doležal, J., Šrutek, M., Hara, T., Sumida, A., & Penttilä, T. (2006). Neighborhood interactions influencing tree population dynamics in nonpyrogenous boreal forest in northern Finland. *Plant Ecology*, *185*, 135–150.
- Drobyshev, I. V. (1999). Regeneration of Norway spruce in canopy gaps in Sphagnum-Myrtillus old-growth forests. *Forest Ecology and Management*, *115*, 71–83.
- Duncan, R. (1991). Competition and the coexistence of species in a mixed podocarp stand. *The Journal of Ecology*, *79*, 1073–1084.
- Fraver, S., Jonsson, B. G., Jönsson, M., & Esseen, P. (2008). Demographics and disturbance history of a boreal old-growth Picea abies forest. *Journal of Vegetation Science*, *19*, 789–798.
- Freilich, L. E., & Graumlich, L. J. (1994). Age-class distribution and spatial patterns in an old-growth hemlock-hardwood forest. *Canadian Journal of Forest Research*, *24*, 1939–1947.
- Getzin, S., Dean, C., He, F., Trofymow, J. A., Wiegand, K., & Wiegand, T. (2006). Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. *Ecography*, *29*, 671–682.
- Getzin, S., Wiegand, T., Wiegand, K., & He, F. (2008). Heterogeneity influences spatial patterns and demographics in forest stands. *Journal of Ecology*, *96*, 807–820.
- Goff, F. G., & West, D. . . D. (1975). Canopy-understory interaction effects on forest population structure. *Forest Science*, *21*, 98–108.
- Gray, L., & He, F. (2009). Spatial point-pattern analysis for detecting density-dependent competition in a boreal chronosequence of Alberta. *Forest Ecology and Management*, *259*, 98–106.

- Greig-Smith, P. (1979). Pattern in vegetation. *Journal of Ecology*, 67(3), 755–779.
- Greig-Smith, P., Kershaw, K. A., & Anderson, D. J. (1963). The analysis of pattern in vegetation: A comment on a paper by D. W. Goodall. *Journal of Ecology*, 51(1), 223–229.
- Grenfell, R., Aakala, T., & Kuuluvainen, T. (2011). Microsite occupancy and the spatial structure of understorey regeneration in three late-successional Norway spruce forests in northern Europe. *Silva Fennica*, 45(5), 1093–1110.
- Gutsell, S. L., & Johnson, E. A. (2002). Accurately ageing trees and examining their height growth rates: implications for interpreting forest dynamics. *Journal of Ecology*, 90, 153–166.
- Harper, K. A., Bergeron, Y., Drapeau, P., Gauthier, S., & De Grandpre, L. (2006). Changes in spatial pattern of trees and snags during structural development in *Picea mariana* boreal forests. *Journal of Vegetation Science*, 17, 625–636.
- Heikinheimo, O. (1922). *Pohjois-Suomen kuusimetsien hoito. Referat: Über die Bewirtschaftung der Fichtenwälder Nordfinnlands*. MKJ 5. Helsinki.
- Hofgaard, A. (1993). 50 years of change in a Swedish boreal old-growth *Picea abies* forest. *Journal of Vegetation Science*, 4(6), 773–782.
- Holmes, R. L. (1983). Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, 44, 69–75.
- Hunter, M. L. (1999). *Maintaining Biodiversity in Forest Ecosystems*. Cambridge University Press.
- Johnson, E., & Miyanishi, K. (2008). Testing the assumptions of chronosequences in succession. *Ecology letters*, 11, 419–431.
- Johnstone, J. F., & Chapin III, F. S. (2006). Effects of soil burn severity on post-fire tree recruitment in boreal forest. *Ecosystems*, 9, 14–31.
- Josefsson, T. (2009). *Pristine forest landscapes as ecological references. Human land use and ecosystem change in boreal Fennoscandia..* Ph.D. thesis, Swedish University of Agricultural Sciences.
- Kareiva, P. (1994). The final frontier for ecological theory. *Ecology*, 75(1), 1.
- Kenkel, N. C. (1988). Pattern of self-thinning in Jack pine: Testing the random mortality hypothesis. *Ecology*, 69(4), 1017–1024.
- Kershaw, K. A. (1963). Pattern in vegetation and its causality. *Ecology*, 44(2), 377–388.
- Kneeshaw, D., & Gauthier, S. (2003). Old growth in the boreal forest: A dynamic perspective at the stand and landscape level. *Environmental Reviews*, 11, S99–S114.
- Korsman, K., Koistinen, T., Kohonen, J., Wennerström, M., Ekdahl, E., Honkamo, M., Idman, H., & Pekkala, Y. (1997). Suomen kallioperäkarta - berggrundskarta över Finland - Bedrock map of Finland 1 : 1 000 000.
- Korsulainen, E., & Väisänen, R. (2003). Metsähallituksen päätös - värriön luonnonpuiston järjestyssäännöstä. In Finnish, not published.



- Kuuluvainen, T. (1994). Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. *Ann. Zool. Fenn.*, *31*, 35–51.
- Kuuluvainen, T., & Aakala, T. (2011). Natural forest dynamics in boreal Fennoscandia: A review and classification. *Silva Fennica*, *45*(5), 823–841.
- Kuuluvainen, T., Syrjänen, K., & Kalliola, R. (1998). Structure of a pristine *Picea abies* forest in northeastern Europe. *Journal of Vegetation Science*, *9*(4), 563–574.
- Kuuluvainen, T., & Ylläsjärvi, I. (2011). On the natural regeneration of dry heath forests in Finnish Lapland: a review of V. T. Aaltonen (1919). *Scandinavian Journal of Forest Research*, *26*, 34–44.
- Lakari, O. J. (1920). Pohjois-suomen metsätyypeistä - Untersuchungen über die Waldtypen in Nordfinnland. *Acta Forest. Fennica*, *14*(4), 1–85. Finnish and German.
- Law, R., Illian, J., Burslem, D. F. R. P., Gratzner, G., Gunatilleke, C. V. S., & Gunatilleke, I. A. U. N. (2009). Ecological information from spatial patterns of plants: insights from point process theory. *Journal of Ecology*, *97*, 616–628.
- Leak, W. (2001). Origin of sigmoid diameter distributions. Cited 12.04.2012.  
URL <http://nrs.fs.fed.us/pubs/5958>
- Leemans, R. (1991). Canopy gaps and establishment patterns of Spruce (*Picea abies* (L.) Karst.) in two old-growth coniferous forests in central Sweden. *Vegetatio*, *93*(2), 157–165.
- Legendre, P., Dale, M., M., F., Gurevitch, J., Hohn, M., & Myers, D. (2002). The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography*, *25*, 601–615.
- Lepš, J., & Kindlmann, P. (1987). Models of the development of spatial pattern of an even aged plant population over time. *Ecol. Modelling*, *39*, 45–57.
- Lilja, S., Wallenius, T., & Kuuluvainen, T. (2006). Structure and development of old *Picea abies* forests in northern boreal Fennoscandia. *Ecoscience*, *13*(2), 181–192.
- Linder, P. (1998). Structural changes in two virgin boreal forest stands in central Sweden over 72 years. *Scandinavian Journal of Forest Research*, *13*(1), 451–461.
- Linder, P., Elfving, B., & Zackrisson, O. (1997). Stand structure and successional trends in virgin boreal forest reserves in Sweden. *Forest Ecology and Management*, *98*, 17–33.
- Loosmore, N. B., & Ford, E. D. (2006). Statistical inference using the G or K point pattern spatial statistics. *Ecology*, *87*(8), 1925–1931.
- Manabe, T., Nishimura, N., Miura, M., & Yamamoto, S. (2000). Population structure and spatial patterns for trees in a temperate old-growth evergreen broad-leaved forest in Japan. *Plant Ecology*, *151*, 181–197.
- Maps of Net (2011). Finland locator map. Cited 26.09.2011.  
URL <http://mapsof.net/map/finland-locator-map.ToLmms3MueY>
- McCarthy, J. (2001). Gap dynamics of forest trees: A review with particular attention to boreal forests. *Environ. Rev.*, *9*, 1–59.

- McCarthy, J., & Weetman, G. (2006). Age and size structure of gap-dynamic, old-growth boreal forest stands in Newfoundland. *Silva Fennica*, *40*(2), 209–230.
- McGaughey, R. J. (1999). Stand visualization system. Cited 01.02.2012.  
URL <http://faculty.washington.edu/mcgoy>
- North, M., Chen, J., Oakley, B., Song, B., Rudnicki, M., Gray, A., & Innes, J. (2004). Forest stand structure and pattern of old-growth western hemlock/Douglas-fir and mixed-conifer forests. *Forest Science*, *50*(3), 299–311.
- Perala, D. A., & Alm, A. A. (1990). Reproductive ecology of birch: a review. *Forest Ecology and Management*, *32*, 1–38.
- Perry, J. N., Liebhold, A. M., Rosenberg, M. S., Dungan, J., Miriti, M., Jakomulska, A., & Citron-Pousty, S. (2002). Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. *Ecography*, *25*, 578–600.
- Phillips, R. L. (1985). *Collecting, preparing, cross-dating and measuring tree increment cores*. Geological Survey, Water-Resources Investigations Report 85-4148. Reston, VA.
- Puttonen, P. (2012). Weather data of the värrö subarctic research station. Cited 26.03.2011.  
URL [http://www.helsinki.fi/metsatieteet/varrio/tutkimus/weather\\_1971.html](http://www.helsinki.fi/metsatieteet/varrio/tutkimus/weather_1971.html)
- R Development Core Team (2005). *R: A language and environment for statistical computing, reference index version 2.13.2.*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, Available at: <http://www.R-project.org>.
- Ripley, B. (1976). The second-order analysis of stationary point processes. *Journal of Applied Probability*, *13*, 255–266.
- Ripley, B. (1981). *Spatial Statistics*. Wiley, New York.
- Ripley, B. D. (1988). *Statistical inference for spatial processes*. Cambridge University Press.
- Rodin, L. E., Bazilevich, N. I., & Rozov, N. N. (1975). Productivity of the world's main ecosystems. In *Productivity of World Ecosystems*, (pp. 13–26).
- Sirén, G. (1955). The development of spruce forest on raw humus sites in northern Finland and its ecology. *Acta Forest. Fennica*, *62*, 1–363.
- Stoll, P., & Prati, D. (2001). Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology*, *82*(2), 319–327.
- Szwagrzyk, J. (1990). Natural regeneration of forest related to the spatial structure of trees: A study of two forest communities in Western Carpathians, Southern Poland. *Vegetatio*, *89*, 11–22.
- Szwagrzyk, J., & Czerwczak, M. (1993). Spatial patterns of trees in natural forests of East-Central Europe. *Journal of Vegetation Science*, *4*(4), 469–476.
- Takahashi, K., Homma, K., Vetrova, V. P., Florenzev, S., & Hara, T. (2001). Stand structure and regeneration in a Kamchatka mixed boreal forest. *Journal of Vegetation Science*, *12*, 627–634.

- Wallenius, T. H., Kuuluvainen, T., & Vanha-Majamaa, I. (2004). Fire history in relation to site type and vegetation in Vienansalo wilderness area in eastern Fennoscandia, Russia. *Canadian Journal of Forest Research*, *34*, 1400–1409.
- Wallenius, T. H., Pitkänen, A., Kuuluvainen, T., Pennanen, J., & Karttunen, H. (2005). Fire history and forest age distribution of an unmanaged *Picea abies* dominated landscape. *Canadian Journal of Forest Research*, *35*, 1540–1552.
- Wanze, Z., Song, C., Xiaohu, C., Fei, H., & Jinxi, W. (2009). Changes in plant species diversity along a chronosequence of vegetation restoration in the humid evergreen-broadleaved forest in the Rainy Zone of West China. *Ecol. Res*, *24*, 315–325.
- Watt, A. (1947). Pattern and process in the plant community. *The Journal of Ecology*, *35*(1), 1–22.
- Wiegand, T., & Moloney, K. A. (2004). Rings, circles and null-models for point pattern analysis in ecology. *Oikos*, *104*, 209–229.
- Ylläsjärvi, I., & Kuuluvainen, T. (2009). How homogeneous is the boreal forest? Characteristics and variability of old-growth forests on a *Holocomium-Myrtillus* site type in the Pallas-Yllästunturi National Park, northern Finland. *Ann. Bot. Fennici*, *46*, 263–279.
- Zackrisson, O. (1977). Influence of forest fires on the North Swedish boreal forest. *Oikos*, *29*(1), 22–32.
- Zerva, A., Ball, T., Smith, K., & M., M. (2005). Soil carbon dynamics in a Sitka spruce (*Picea sitchensis* (Bong.) Carr.) chronosequence on a peaty gley. *Forest Ecology and Management*, *205*, 227–240.