Eesti Maaülikool
Estonian University of Life Sciences

ANALYSIS OF TREE COMPETITION AND STRUCTURAL INDICES WITH A FOCUS ON MODELLING SILVER BIRCH (*Betula pendula* Roth) STANDS

PUUDE KONKURENTSI- JA STRUKTUURIINDEKSITE ANALÜÜS ARUKASE (*Betula pendula* Roth) PUISTUTE MODELLEERIMISE EESMÄRGIL

KOBRA MALEKI

A Thesis
for applying for the degree of Doctor of Philosophy in Forestry

Väitekiri
filosoofiadoktori kraadi taotlemiseks metsanduse erialal

Tartu 2016

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following papers, references to which in the text are given by Roman numerals. The papers are reproduced with the kind permission of the publishers.

I **Maleki, K.,** Kiviste, A., Korjus, H. 2015. Analysis of individual tree competition effect on diameter growth of silver birch in Estonia. *Forest Systems*, 24(2), e023.

II Pommerening, A., **Maleki, K.** 2014. Differences between competition kernels and traditional size-ratio based competition indices used in forest ecology. *Forest Ecology and Management*, 331, 135–143.

III **Maleki, K.,** Kiviste, A. 2016. Individual tree mortality of silver birch (*Betula pendula* Roth) in Estonia. *iForest – Biogeosciences and Forestry*, 9, 643–651.

IV **Maleki, K.,** Kiviste, A. 2016. Effect of sample plot size and shape on estimates of structural indices: A case study in mature silver birch (*Betula pendula* Roth) dominating stand in Järvselja. *Forestry Studies*, 63, 130–150.

The contribution of the authors to the papers was as follows:

	Paper			
	I	II	III	IV
Original idea	HK	AP	All	All
Study design	HK, **KM**	AP	**KM**	All
Data preparation	AK, **KM**	All	All	All
Data analysis	All	All	**KM**	**KM**
Preparation of manuscript	All	All	**KM**	**KM**

AK-Andres Kiviste, AP-Arne Pommerening, HK-Henn Korjus, **KM-Kobra Maleki**, All-all authors of the paper.

ABBREVIATIONS

agg	Aggregation index
AIC	Akaike Information Criterion
AIC_w	Akaike weight
AR(1)	The first order autoregressive structure
AUC	Area Under the Receiver Operating Characteristic Curve
BAL	Total Basal Area of Larger trees
BALMOD	Modified form of BAL
C_{red}	Reduced competition due to thinning
CEA	Competition Elimination Angle
CI	Competition Index
CL	Clustered
cr	Crown ratio
C_r	Crown radius
CSM	Competitor Selection Method
d	Tree diameter at breast height
ddf	Diameter differentiation index
ddm	Diameter dominance index
d_{rel}	Tree relative diameter
ENFRP	Estonian Network of Forest Research Plots
g(r)	Point-pair correlation function
Heg	Spatial CI of Hegyi (1974)
id_5	Five-year diameter growth
id^{pot}	Potential diameter growth
I_{thin}	Thinning intensity
ming	Species mingling index

MSER	Mean Square Error Reduction
NN	Nearest Neighbour
NN1	One Nearest Neighbour
NN4	Four Nearest Neighbours
N-N	Inter-tree relation
RAMI	Radiation Model Intercomparison
RAN	Random
REG	Regular
R^2	Coefficient of determination
RMSE	Root Mean Square Error
r_S	Spearman’s rank correlation coefficient
RS	Relative Spacing
RSC	Reserved Search Cone
sd	Standard deviation
SdrAng	Spatial CI of Rouvinen and Kuuluvainen (1977)
SI	Site Index
sp	Species proportion
ua	Uniform angle index
VIF	Variance Inflation Factor
ZOI	Zone Of Influence
ZOI_r	The radius of the Zone Of Influence

1. INTRODUCTION

The functioning and productivity of forest ecosystems is closely related to their structural properties (Naumburg and DeWald, 1999; Bobiec, 2002; Frolking *et al.*, 2009). The spatial placement of individual trees and tree distribution patterns by their size, condition and species are the main components of forest stand structure (Gadow and Hui, 1999; Laarmann *et al.*, 2009). The dynamic processes of tree recruitment, growth, competition and mortality as well as disturbances are reflected in the structural components of a forest ecosystem. The growth of trees is influenced by the species composition, spatial structure, and dynamics of a forest stand and also by human activities (Rice *et al.*, 2004; Navarro-Cerrillo *et al.*, 2013).

Tree mortality is an important driver of forest stand dynamics as the formation of forest structure follows mortality patterns (Pederson, 1998; van Mantgem and Stephenson, 2007). Trees may die when tree vigour is reduced because of negative stress factors, such as drought or competition among trees. These stress factors can lead to a wide variety of causes of tree mortality, and there have been numerous attempts to categorize them (e.g. Vanclay, 1994; Yang *et al.*, 2003) in order to achieve better understanding of mortality. In a simplified procedure, mortality has generally been classified into regular mortality, because of senescence or tree competition, and irregular mortality, caused by catastrophic and ecological events, such as flood or fire (Monserud, 1976). The regular mortality rates of small and large trees are usually relatively high (mortality probability is U-shaped) because of light competition and senescence, respectively (Lorimer *et al.*, 2001; Fraver *et al.*, 2008). Irregular mortality is triggered by temporally and spatially changing biotic and abiotic factors, therefore it is quite complicated to predict, e.g. diseases or pests, and these attacks may result in relatively small mortality or completely remove the host species throughout the region (Vanclay, 1994). A large number of interacting factors like the stand density; the size and the viability of an individual and the competition with neiughors affect a tree to survive the stress conditions (Hamilton, 1986). However, it can be very difficult to distinguish between these factors and evaluate their importance to tree mortality (Das *et al.,* 2008) in order to adequately maintain forest ecosystems and their benefits, e.g. timber production, carbon sequestration, water cycle, and species habitats (Dietze and Moorcroft, 2011). It is reasonable to look at tree mortality as a primary stimulus of changes in the structure and composition of forest ecosystems as it is closely interrelated with other processes, including tree recruitment, competition and growth.

Competition between neighbouring trees has a major role in tree mortality and it is also important in population dynamics, survival, growth and species replacement (Peet and Christensen, 1987). Competition strongly regulates the mortality of suppressed trees (Keddy, 1989; Szwagrzyk and Szewczyk, 2001) and occurs when several individual trees attempt to utilise the same resources that are limited in supply (Kimmins, 2004). In this context, competition can be seen as either symmetric or asymmetric (Bauer *et al.,* 2004). If competing individuals benefit an equal share of resources then competition is symmetric, otherwise, unequal sharing of resources will be allocated to competing neighbours as a consequence of larger individuals having a competitive advantage over smaller ones because of asymmetric competition (Schwinning and Weiner, 1998; Freckleton and Watkinson, 2001). The competition between individual trees leads to a reduction in the survival, growth and reproduction of some competing individuals (Begon *et al.,* 2006). The identity of a neighbouring tree species is considered as an important factor of their competitive influence (Bella, 1971; Zhao *et al.*, 2006). Competition can occur among con-specific individuals, trees of the same species, and hetero-specific individuals, trees of different species, named respectively as intraspecific and interspecific competition. There are differences between individual trees, some trees die quickly due to competition, some individuals withstand and suffer from competition over long periods of time but they become weak and eventually die because of other reasons (Wyckoff and Clark, 2000; Antos *et al.,* 2008; Lännenpää *et al.,* 2008).

Numerous indices and techniques for quantifying forest stand structure and tree competition have been developed in forestry and ecology. These indices are mathematical functions and algorithms based on stand and tree level data, either spatially explicit or non-spatially explicit (Tomé and Burkhart, 1989). Spatially explicit indices are based on the concept of point process statistics and require dimensions and coordinates of neighbouring trees. Non-spatially explicit indices use stand level variables (or dimensions of the trees) and therefore do not require the locations of trees. Spatial approach is considered to be more effective and precise, particularly in forest stands with a complex structure (Weigelt and Jolliffe, 2003).

Birches, silver birch and downy birch (*Betula pubescens* Ehrh.), are important tree species in Estonia and their stands form 30.3% of the forest area (Raudsaar *et al.*, 2016). In official statistics silver birch and downy birch are not distinguished in Estonia. Silver birch grows naturally in forests of northern temperate and boreal zone in pure and mixed stands and it is an ecologically and commercially essential broadleaved tree species (Hynynen *et al.*, 2010). This thesis focuses on studying the competition and structural indices in silver birch stands for using them in forest assessment and growth modelling. Data analysis is mainly based on the permanent sample plots of the Estonian Network of Forest Research Plots (ENFRP) (Kiviste *et al.*, 2015). Spatially explicit and non-spatially explicit indices are analysed. This study establishes and assesses different approaches of competition quantification incorporated with various competitor selection methods for silver birch in Estonia (I) and for two different forest ecosystems in Europe and one in North America (II). The influence of competition along some other tree and stand variables on the growth (I) and the mortality of silver birch trees (III) are explored and characterised. One actual silver birch stand and five simulated stands are used to quantify structural indices and to analyse how well they can be estimated within the ENFRP (IV).

2. REVIEW OF THE LITERATURE

2.1. The concept of point process statistics in forest modelling

Point processes and marked point processes are powerful tools for modelling and analysing forest ecosystems. A point process is a type of a random set of isolated points falling either in time or geographical space in statistics and a probability theory which studies the probability of random variables, stochastic processes and events (Diggle, 2003). In forest research, the points are tree locations and the marks are tree characteristics such as diameter and height. Considering trees as stationary points in terms of the point process theory, different point processes can be seen in forests depending on their development stages and conditions. A regular pattern (Matérn hard-core process) can be represented in older forests, where trees have been thinned out earlier, due to management activities and/or interspecific/intraspecific competition leading to self-thinning, a clustered pattern (Matérn cluster process) is thought to be found in young forests having trees with heavy seeds or with any heterogeneous conditions arranging trees in clusters, and a random pattern (Poisson process) is common in most forests (Tomppo, 1986; Pommerening, 2002), and it is a situation between the two first patterns (Pommerening, 2006).

Regarding the importance of forest ecosystems and their dynamics, numerous indices and statistical techniques for quantifying and analysing stand structure and its dynamics have been developed and compared (e.g. Gleichmar and Gerold, 1998; Kint *et al.*, 2000, 2003; Pommerening, 2002). The majority of indices have been divided into two main groups: non-spatially explicit (distance independent) and spatially explicit (distance dependent) measures. Non-spatially explicit indices are functions of stand level variables, or of the initial dimensions of trees, and therefore do not require the trees' coordinates. Spatially explicit indices require spatial references and are based on the nearest neighbour (NN) concept of point process statistics where it is expected that the immediate neighbours surrounding a tree, the so-called subject/reference tree, are likely to have interaction effects (Schneider et *al.,* 2006). Therefore, when calculating spatial characteristics, as well as the mathematical formulation, the value of a spatial index depends on the method used to define affecting neighbours for the subject tree (Biging and Dobbertin, 1992) and also the edge effect correction.

In this context, a zone of influence, ZOI, is an imaginary circle the centre of which is constituted of the subject tree (Staebler, 1951) and trees inside this circle are potential interacting neighbours (Fig. 1). Within this zone the subject tree predominantly draws on resources, such as nutrients, water and light (Berger and Hildenbrandt, 2000). In plant ecology it is a common assumption that all plants with overlapping ZOIs interact via competition for resources (Grimm and Railsback, 2005). The radius of this circle should be equal to the expected growing space of open-grown trees in complete absence of interactions between the trees, and is usually a function of tree size (Corral Rivas *et al.*, 2005). Proposed approaches different from the ZOI definition belong either to a ZOI with a fixed radius considering an equal ZOI for all subject trees within a stand or to ZOIs with variable radii, often weighted by dimensions of the subject tree and its neighbours (Ford and Diggle, 1981). Ratios of stand height (Sims *et al.*, 2009) and stand density (Lee and Gadow, 1997) are considered as proxies of the ZOI with a fixed radius. The angle count sampling (Bitterlich, 1952), the reserved search-cone (Pukkala, 1989; Pretzsch, 2009) or the angular height method (Richards *et al.*, 2008) and the crown overlap method (Bella, 1971; Alemdag, 1978) are examples of ZOIs with variable radii.

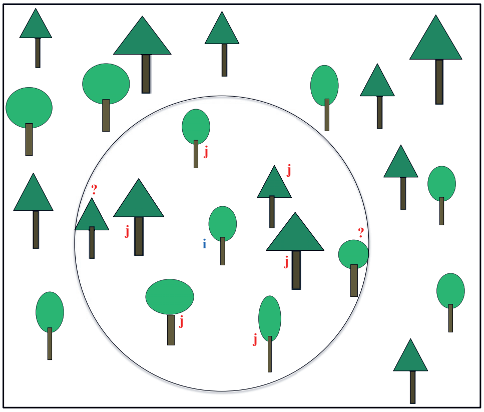

Figure 1. An illustration of the concept of zone of influence in modelling tree competitors: trees are considered as active competitors j for a subject tree i if they occur inside a circle centred by that tree, the radius of the zone of influence and active competitors are selected with different methods based on their size and location relative to the subject tree. Trees marked with a "?" are "shaded" behind the active competitors and therefore do not compete actively with the subject tree and usually are not considered as active competitors.

The edge effect for trees standing near the boundary of monitoring plots is likely to play an important role in spatial indice quantifications and should result in biased statistical estimations. This is due to the lack of information about some of the immediate neighbours of subject trees near the boundary and outside the monitoring plots; the closer the subject tree is to the boundary, the greater the unknown portion of the actual neighbours outside the plots. The edge effect problem was ignored in early studies (e.g. Clark and Evans, 1954; Pielou, 1977). Later, different possibilities for avoiding the edge effects were developed and discussed in the literature (e.g. Gignoux *et al.,* 1999; Pommerening and Stoyan, 2006; Lilleleht *et al.*, 2014). The border method (Ripley, 1981) is one simple possibility to even out this error and is used by many researchers (e.g. Neumann and Starlinger, 2001; Aguirre *et al.*, 2003). Taking a buffer zone near the plot edges includes only interior trees whose entire neighbours are recorded. This method guarantees the removal of all edge effects (Kint *et al.*, 2004); however, special attention should be paid to select the appropriate width of the buffer zone (Diggle, 2003). Yet, the number of subject trees, particularly for small plots and plots with a high circumference to area ratio, is relatively small (Pretzsch, 2009). Other edge correction methods are translation (Diggle, 2003), reflection (Radtke and Burkhart, 1998) and linear expansion (Martin *et al.,* 1977), which extrapolate the stand structure on the monitoring plot beyond the plot boundary and can be speculative. Evidently, translation and reflection create unrealistic and periodic spatial point patterns and neighbourhood situations that do not naturally exist and their application is limited to rectangular plots (Pretzsch, 2002; Diggle, 2003). Finally, structure generation methods produce a hypothetical stand, which is close to a real one, in a given area around the observation plot with similar structural characteristics, applying generalized stem-distance functions that are calibrated for the experimental plot (Pretzsch, 2009). Linear expansion and structure generation methods are applicable in plots of any shape such as circular and amorphous areas (Pretzsch, 2009).

2.2. Approaches to quantifying forest stand structure

Structural indices and characteristics have often been applied for assessing different aspects of forest stands. Diameter distribution and species compositions of trees present some specific structural properties as non-spatial measures, e.g. the Shannon index (Shannon and Weaver, 1949) and the Simpson index (Simpson, 1949), which can be applied for more complex assessments. A significant part of ecological processes in forests is the quantitative characterization of a spatial structure (Pretzsch, 1998; Bauer *et al.,* 2004). Spatial structural indices are categorized as individual tree parameters based on neighbourhood relations; measures of structure at stand level; and continuous functions of inter-tree relations (Pommerening, 2002). The single-tree level indices based on neighbourhood relations of individual trees account either for the first NN (e.g. the diameter differentiation index (Füldner, 1995; Pommerening, 2002) or for more than one NN depending on the objectives of the study (e.g. Füldner, 1995; Aguirre *et al.,* 2003). The indices of diameter dominance (Gadow and Hui, 2002; Aguirre *et al.*, 2003), uniform angle (Hui and Gadow, 2002) and species mingling (Füldner 1995;

Aguirre *et al.*, 2003) consider more than one NN in their quantifications. Therefore, they consider small-scale differences and are easy to calculate where they show the neighbourhood relation with a single value (Kint *et al.*, 2003). Stand-level structural indices, such as the aggregation index (Clark and Evans, 1954) counting for the first NN, also describe the variability of individual tree locations by a single value. Continuous functions, e.g. Ripley's K function (Ripley, 1977); the radial distribution function (Diggle, 2003) or the point-pair correlation function (Cressie, 1993), take all possible inter-tree distances, N-N, within the stand into account to examine the second-order effects, and are more complex (Dale, 2000; Pommerening, 2002).

2.3. Approaches to tree mortality and competition assessment

Tree mortality is a significant process in forest dynamics determining forest structure and its formation (Pederson, 1998; Mantgem and Stephenson, 2007). Different variables as representatives of multiple interacting factors, tree size and viability, stand density and competition (Hamilton, 1986), contributing in tree mortality and determining the survival ability of trees, have been listed and implemented in mortality studies. Variables indicating the size of a tree can be simply measured (e.g. tree diameter and height) or calculated (e.g. tree growth and basal area), and they provide valuable, but insufficient, information about the probability of tree death (Monserud and Sterba, 1999; Yang *et al.,* 2003). The vitality of trees has been proficiently estimated by diameter growth rate (Buchman *et al.,* 1983), or as a substitute, by crown size (Monserud and Sterba, 1999). Stand density can be presented by the number of trees per unit area (N) and total basal area of trees per unit area (G) (Eid and Tuhus, 2001; Burgman *et al.,* 1994), however G can be also considered as a quantification of symmetric competition (Bravo *et al.,* 2001). Many species are not able to withstand the deep shading of high density of their neighbourhoods, thus they are exposed to high density-dependent mortality, also called self-thinning (He and Duncan, 2000, Gómez-Aparicio *et al.,* 2009), specifically in young and clumped stands (Oliver and Larson, 1996). Within a stand the limit of the number of trees with a known average size, so-called limiting density, has been of great interest and several studies (e.g. Zeide, 1987, 2010; Gadow *et al.,* 2014) have been conducted to define it based on environmental conditions and the forest type. In a maturing stand, when the size and required space of surviving trees increase, the density-dependent mortality reduces and tree mortality may be due to other reasons such as pathogen and insect attacks (Franklin and van Pelt, 2004). Consequently, inclusion of the spatial measures of interactive environment surrounding the individual tree is thought to improve the understanding of mortality (Biging and Dobbertin, 1995).

Competition for limited resources is a highlighted ecological process and an important contributor to tree mortality (Szwagrzyk and Szewczyk, 2001). Numerous indices for quantifying the competition level of an individual tree have been introduced and examined, e.g. by Holmes and Reed (1991), Contreras *et al.* (2011). Similarly to structural indices and tree mortality contributors, technically competition can be quantified by non-spatial and spatial measures. Non-spatial competition indices are the functions of trees' initial dimensions, or of the stand level variables, and thus do not require the trees' locations (e.g. Wykoff *et al.*, 1982; Schröder and Gadow, 1999). Spatial indices (e.g. Hegyi, 1974; Alemdag, 1978) usually take several primary response variables along with spatial information (Weigelt and Jolliffe, 2003). Competition kernels have been developed as a different approach in the spatial competition field in the past thirty years (Snyder and Chesson, 2004; Hernández-García *et al.,* 2009). Competition kernels are related to the idea of dispersal kernels used in modelling seed and plant dispersal (Bolker and Pacala, 1999; Nanos *et al.*, 2010) and belong to a group of functions, so-called interaction kernels that explain how the biological processes of an individual (e.g. growth, survival and reproduction) tree depend on its own size and the size of and distance from other individuals (Vogt *et al.,* 2010). According to this approach, every individual of a given community emits a signal termed the competition signal, impulse, local competition effect or attenuation function, which is the largest at the location of an individual and decreases with increasing distance from that individual. These competition signals can be aggregated additively or multiplicatively at any point of the community and result in a competition field imposing a competition pressure on individuals located in that field (García, 2014).

2.4. Research needs

The natural dynamics of growth, mortality, and other changes in stand composition and structure of forest ecosystems are summarized and represented through modelling approaches. Models can be classified based on the details required, provided and utilized. Stand models, using stand parameters, are often simple and robust. Single-tree models employ individual tree characteristics and measures and in spatial studies they also require the spatial position of the tree; more complex single-tree models may be used for forest simulations (e.g. Vanclay, 1988). Size class models are compromises between stand models and single-tree models and provide some information regarding forest stand structure. They turn to stand level models when only one large class is defined and are replaced with single-tree models if each tree is considered as one class. The models may be used either for prediction or for understanding (e.g. process models), since they are applicable tools for joining isolated information of a process and identifying gaps where additional research is required (Vanclay, 1994).

The quantification methods of the dynamics and structure of forests critically influence the final understanding of forest ecosystems. Consequently, the selection and application of different measures/indices of a stand structure and its dynamics, such as tree mortality and competition, are of great importance and in order to draw more appropriate inferences from the outcome of such assessments special care should be paid to proper selection and employment of the mentioned indices. Spatial relationships between trees were found to be a significant component of a forest ecosystem and its dynamics and along with other factors, regulate mortality, competition, growth and regeneration processes of trees (Dieckmann, *et al.,* 2000). On the other hand, the collection and handling of suitable data for such indices, including geographical positions of trees, is expensive and time-consuming (Kint *et al.,* 2004) and if there is no acceptable reason for using them for a specific purpose, non-spatial indices are preferred.

Regarding the importance of spatial pattern heterogeneity of forests at different scales, in their structural complexity (Churchill *et al.,* 2013) and the immediate influence of the size of monitoring plots on the assessment of general stand characteristics, such as stand density and stand basal area (Corona *et al.,* 1998), which are directly or indirectly applicable in tree mortality and reactions studies, proper sampling methods must be used (e.g. Füldner, 1995; Pommerening and Gadow, 2000). Considering the specific objectives of forest studies, various sampling approaches can be appropriately employed to attain the required degree of precision and accuracy through a benefit-cost analysis (Corona and Marchetti, 2007; Travaglini *et al.,* 2013).

3. AIMS OF THE STUDY

Competitive interactions between neighbouring trees are essential in forest ecosystems as they play an important role in the growth and mortality of competing trees and in the formation of structural properties of a forest stand. Consequently devising the forest models with the measures of different aspects of forest dynamics enhances the models' precision and accuracy (Eastaugh *et al.,* 2013). The objective of the thesis is to evaluate different approaches in modelling tree competition and mortality and to incorporate structural assessments into forest growth models. The main aim is to develop a better understanding of non-spatial and spatial assessments of forest stand structure, tree mortality and tree interactions in silver birch stands.

The main hypotheses of the study are:

1. Spatial indices, associated with the tree locations and their surrounding neighbourhoods, provide more precise quantifications of the stand structure and dynamics than non-spatial measures;
2. Competition measures are important contributors to estimate the diameter increment and mortality probability of silver birch trees;
3. Species-specific interaction improves the ability of spatial indices to account for growth and mortality probability of silver birch trees;
4. Enlarging the sample plots and employing plots with a smaller ratio of the perimeter to the surface area increase the accuracy of structural assessments of a forest stand.

The specific aims of the study are:

1. To explore the adequacy of different spatial and non-spatial competition indices to explain single-tree diameter growth and to find the best competitor selection method for silver birch trees in Estonia (I);

2. To characterise the differences between spatial competition indices and competition kernels in two different forest ecosystems (II);
3. To examine the competitive ability of different species by employing Ellenberg's species-specific light indicator values (I) and the effect of species proportion of neighbouring trees of subject trees on mortality probability predictions (III);
4. To filter and to test different variables in an empirical model to predict mortality of silver birch trees (III);
5. To evaluate the structural indices and to assess their sensitivity to the size and shape of monitoring plots in an actual silver birch stand and five simulated stands (IV).

4. MATERIALS AND METHODS

4.1. Study areas and data sets

The data from the ENFRP was used in the studies **I** and **III** (Fig. 2). The ENFRP contains the data for the main forest types in Estonia and are located all over the country.

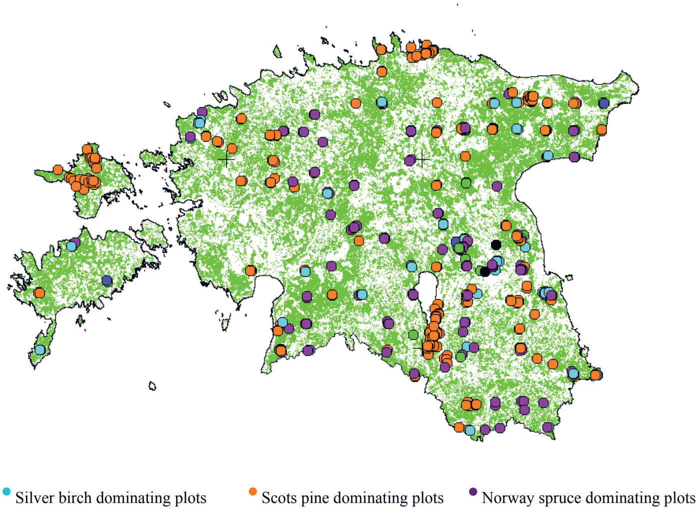

Figure 2. Location of the study area (**I**, **III**) throughout Estonia (Map data: Estonian Land Board, 2016).

Within each plot the azimuth, the distance from the plot centre, the tree species, the diameter at breast height (d), and the health status of each tree were assessed. For every fifth tree, and for dominant and rare tree species, the tree height and the height to the live crown base were also measured. Study **I** included the data from 121 silver birch dominated research plots and their re-measurements with five-year intervals, where more than 65% of the number of trees were birch. The species composition of all trees within the studied plots was 67% silver birch, 24% Norway spruce (*Picea abies* L.) and 9% of several other species, and if there was a thinning operation in the time period between the plot measurements, it was excluded. Study III employed 116 research plots that included silver birch trees. Selected plots had three recorded consecutive measurements and if thinning was practised within a plot before the first or third measurement that plot was excluded from this analysis. The proportion of tree species within the study plots was 33.9% silver birch, 26.8% Norway spruce, 25.6% Scots pine (*Pinus sylvestris* L.) and 13.7% of several other species. The composition of Scots pine, silver birch and Norway spruce as the main tree species is illustrated in Fig. 3.

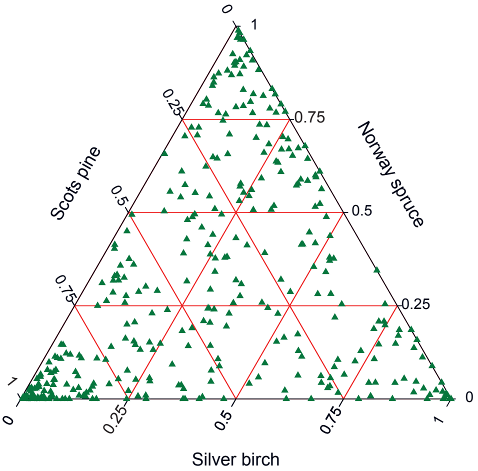

Figure 3. Species composition of study plots by the three major tree species.

To study structural indices and the effect of sample plot size and shape on their assessments (**IV**), a one-hectare sample plot in a birch stand (57% silver birch) established for the Radiation Model Intercomparison (RAMI) study (Kuusk *et al.*, 2013), located in Järvselja Training and Experimental Forest Centre, compartment JS228 and five simulated point pattern stands (two regular patterns REG1 and REG2, moderately clustered CL1, extremely clustered CL2 and random RAN) covering an area equal to the RAMI plot, and with almost the same intensity (N_{ha}=928), similar species composition and diameter distribution (D=20.13 cm), were used as reference stands (Fig. 4). On each stand, 41 different radii ranging from 5 to 45 m and increasing by one meter were considered and for each size, 1,000 random centres were independently generated, in the way that circular plots were thoroughly improvised inside the stand.

Square plots were formed around each random centre defined for the circular plots with the restriction that they cover an area equal to the area of the corresponding circular plot.

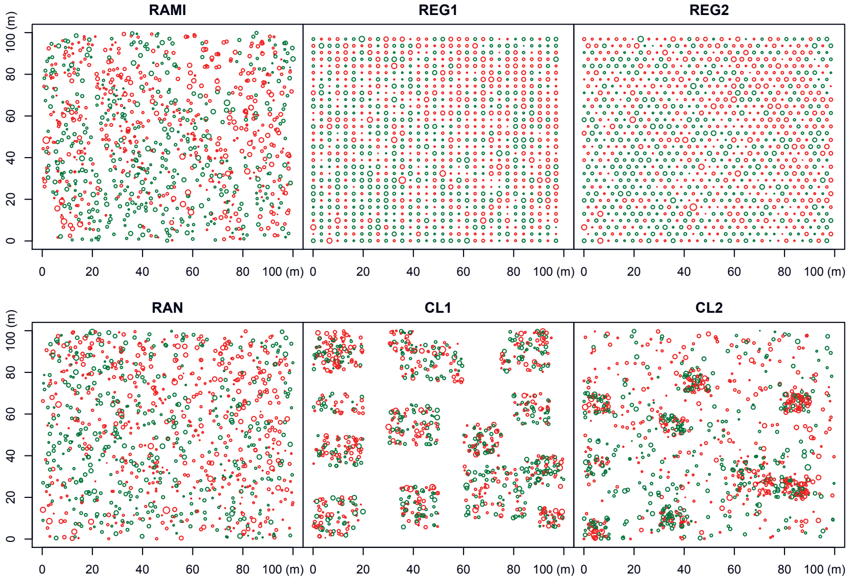

Figure 4. RAMI plot and five simulated point patterns, green circles of different sizes are silver birch trees with their corresponding size and red circles are other species (RAMI – Radiation Model Intercomparison study plot, REG1, REG2 – two regular patterns, CL1 – moderately clustered, CL2 – extremely clustered and RAN – random pattern).

Three mono-species tree populations representing a wide range of growth conditions were used in study **II**: three plots of Swiss spatio-temporal dataset for even-aged European beech (*Fagus sylvatica* L.) at Embrach, six multi-aged interior Douglas fir (*Pseudotsuga menziesii* var *glauca* (Mirb.) Franco) plots in the Alex Fraser Research Forest in British Columbia, Canada, and 16 plots of a replicated thinning experiment in predominantly even-aged Norway spruce stands in Karlstift, Austria.

4.2. Evaluation of tree competition measures as predictors of diameter growth (I, II)

The competition for each subject tree was quantified using a list of non-spatial and spatial competition indices (CIs, Table 1, Eq. 1.1 – 1.18), selected from the literature, taking into consideration the available tree variables and their properties to describe the competition situation of a tree.

Table 1. List of studied competition and structural indices

Eq.	Equation	Description	Sources	Study
1.1	$\sum_{j\neq i}^{n}\left(g_j\right)$	**Non-spatial competition indices;** tree location information is not required for them.	Steneker and Jarvis, 1963	I
1.2	$\sum_{d_i<d_j}^{n}\left(g_j\right)$		Wykoff *et al.*, 1982	I, III
1.3	$\sum_{j\neq i}^{n}\left(d_j/d_i\right)$		Lorimer, 1983	I, II
1.4	d_i/d_g		Hamilton, 1986	I
1.5	$\left(\sum_{j\neq i}^{n} g_j\right)/g_i$		Corona and Ferrara, 1989	I
1.6	$\dfrac{\sum_{j\neq i}^{n}\left(g_{j;dj>d_i}\right)}{G}$		Vanclay, 1991	I
1.7	$\dfrac{\left(\sum_{d_i<d_j}^{n}\left(g_j\right)/G\right)}{RS}$		Schröder and Gadow, 1999	I

1.8	$\sum_{j\neq i}^{n} l_{ij}$	**Influence-zone overlap spatial competition indices;** ZOI_r is a function of tree size and equal to the expected growing space of open-grown trees.	Staebler, 1951	**I**
1.9	$\sum_{j\neq i}^{n}\left(O_{ij}/ZOI\right)$		Gerrard, 1969	**I**
1.10	$\sum_{j\neq i}^{n}\left(\left(O_{ij}\cdot d_j\right)/\left(ZOI\cdot d_i\right)\right)$		Bella, 1971	**I**
1.11	$\left(d_i^2\cdot N_c\right)\Big/\sum_{j\neq i}^{n} d_j^2$	**Size-ratio spatial competition indices;** often weighted by subject-to-competitor distances (distance weighted).	Daniels *et al.,* 1986	**I**
1.12	$\sum_{j\neq i}^{n}\left(d_j/\left(d_i\cdot l_{ij}\right)\right)$		Hegyi, 1974	**I, II, III**
1.13	$2\sum_{j\neq i}^{n}\arctan\left(d_j/2l_j\right)$		Lin, 1974	**I**
1.14	$\sum_{j\neq i}^{n}\arctan\left(d_j/l_{ij}\right)$		Rouvinen and Kuuluvainen, 1997	**I**
1.15	$\sum_{j\neq i}^{n}\left(\left(d_j/d_i\right)\cdot\arctan\left(d_j/l_{ij}\right)\right)$		Rouvinen and Kuuluvainen, 1977	**I**
1.16	$\sum_{j\neq i}^{n}\left\{\frac{\pi\left[\left(l_{ij}\cdot d_i\right)/\left(d_i+d_j\right)\right]^2\left(d_j/l_{ij}\right)}{\sum\left(d_j/l_{ij}\right)}\right\}$		Alemdag, 1978	**I**
1.17	$\sum_{j\neq i}^{n}\left(\left(d_j/d_i\right)/\sqrt{l_{ij}/ZOI_r}\right)$		Lorimer, 1983	**I**
1.18	$\sum_{j\neq i}^{n}\left(d_j/d_i\right)\cdot\exp\left(\left(l_{ij}\right)/\left(d_i+d_j\right)\right)$		Martin and Ek, 1984	**I, II**
1.19	$\sum_{j\neq i}^{n}\frac{d_j^{\alpha_{K,f}}}{1+\left(l_j\left(\xi_i\right)/\beta_{K,f}\right)^2}$	Fractional competition kernel, transformation of Eq. 1.12	Schneider *et al.,* 2006; Pommerening *et al.*, 2011	**II**

1.20	$\sum_{j\neq i}^{n} d_j^{\alpha_{K,e}} \times \exp\left(-\frac{l_j\left(\xi_i\right)}{d_j^{\beta_{K,e}}}\right)$	Exponential competition kernel, transformation of Eq. 1.18	Schneider *et al.,* 2006; Pommerening *et al.*, 2011	**II**
1.21	$agg = \frac{l_{obs}}{E(l)}$ where $E(l) = \frac{1}{2 \cdot \sqrt{n/A}}$	Structural indices counting for NN1	Clark and Evans, 1954	**III, IV**
1.22	$ddf = 1 - \frac{\min(d_i, d_j)}{\max(d_i, d_j)}$		Gadow, 1993; Füldner, 1995; Pommerening, 2002	**IV**
1.23	$ua = \frac{1}{n}\sum_{j=1}^{n=4} w_j$ where $w_j = \begin{cases} 1 \text{ if } \alpha < 360°/5 \\ 0 \text{ if } \alpha \geq 360°/5 \end{cases}$	Structural indices counting for NN4	Gadow and Hui, 2002	**IV**
1.24	$ddm = \frac{1}{n}\sum_{j=1}^{n=4} v_j$ where $v_j = \begin{cases} 1 \text{ if } d_j < d_i \\ 0 \text{ if } d_j \geq d_i \end{cases}$		Gadow and Hui, 2002; Aguirre *et al.*, 2003	**IV**
1.25	$\min g = \frac{1}{n}\sum_{j=1}^{n=4} m_j$ where $m_j = \begin{cases} 1 \text{ if Species}_j \neq \text{Species}_i \\ 0 \text{ if Species}_j = \text{Species}_i \end{cases}$		Gadow, 1993; Füldner 1995; Aguirre *et al.*, 2003	**III, IV**

1.26	$g(r)=\frac{\lambda}{\lambda_0}$ where $\begin{cases} g(r)>1 \rightarrow \text{cluster} \\ g(r)=1 \rightarrow \text{random} \\ g(r)<1 \rightarrow \text{regular} \end{cases}$	Point-pair correlation function (g(r)), counting for N-N	Diggle, 2003; Cressie, 1993	**IV**

Notes: d_i, d_j and d_g are the diameter at breast height of the reference tree, neighbouring tree, and basal area weighted plot diameter (cm), respectively; G, g_i and g_j are the total basal area of the trees within the plot, the basal area of the reference tree and neighbouring tree (m^2ha^{-1}), respectively; l_{ij} and $l_{(ZOI)}$ are the distance between the reference tree and neighbouring tree and the nearest neighbour, and the mean nearest neighbour distance within the influence zone (m), respectively; l_{obs} and E(l) are the mean distance to the first nearest neighbour and the mean nearest neighbour distance in a stand in the case of completely random tree locations, respectively; N_c and n are the number of competitors and the number of trees inside the influence zone/plot, respectively. A and ZOI are the area of the plot (ha) and influence zone, respectively; ZOI_r is the radius of the influence zone (m); RS is the relative spacing index of the plot (see Eq. 3.13); O_{ij}, crown overlap between the neighbour tree j and the subject tree i (m^2); α is the angle pointing away from the reference tree to neighbours; λ is the intensity of points at distance r from an arbitrary point and λ_0 is the expected intensity for a Poisson process; for subject tree i, at location ξ_i; α_K and β_K are the strength of the competition signal and range parameter.

The value of competition depends not only on the mathematical formula of a competition index but also on the method used to define active competitors for the subject tree (Biging and Dobbertin, 1992). Among different proposed competitor selection methods (CSM) four approaches were applied in study **I** to define the radius of influence zone, ZOI_r, and potential competitors within these zones (Table 2). Then, depending on the algorithm of the spatial CIs, they were quantified using all possible CSMs for them. Additionally, to avoid biased estimations due to the interference from the competitive effects of immediate non-measured neighbouring trees outside the plot boundary, a boundary strip inside the plot with a width equal to the ZOI_r was established and, CIs were computed only for interior trees for which the neighbours' information was available.

Table 2. List of competitor selection methods.

Eq.	ZOI	ZOI_r	Equation	Description	Sources	Study
2.1	ZOI_H	Ratio of stand height	$ZOI_r = 0.4 \cdot H$	Fixed radius for all trees in a plot; trees within the ZOI are competitors for the subject tree.	Sims *et al.*, 2009	I, III
2.2	ZOI_k	Ratio of stand density	$ZOI_r = k \cdot \sqrt{\frac{10000}{N}}$ Competitor $\text{if} \rightarrow d_j \geq 0.3 d_i \;\&\; \text{CEA}=30°$		Lee and Gadow, 1997	I
2.3	BAF	Basal area factor	$l_{ij} \leq d_i \cdot \sqrt{\frac{50}{\text{BAF}}}$ $\text{BAF} = 1,2,4$	Variable radii weighted by dimensions of the subject tree and its neighbours; trees falling within l_{ij} are active competitors.	Bitterlich, 1952	I
2.4	RSC	Reserved search-cone/ Angular height method	$l_{ij} < \frac{h_i}{\tan(90-\beta/2)}$ or $\frac{h_i - cbh_i}{\tan(90-\beta/2)}$		Pretzsch, 2009; Richards *et al.*, 2008	I
2.5	ZOI_{Cr}	Crown radius overlap	$l_{ij} = C_{r_i} + C_{r_j}$ $C_r = \frac{a \cdot d}{b + d}$		Michaelis and Menten, 1913; Bolker, 2008	II

Notes: H is stand average height; N is the number of trees per hectare and k is a constant number (set to 2 or 3); l_{ij} is the distance between the subject tree i and its neighbour j; d_i and h_i are the diameter at breast height and height of the subject tree i, respectively; β is the search-cone opening angle (equal to 100°, 80° or 60°); cbh_i is the crown base height of the subject tree i; C_r is crown radius; d is tree diameter at breast height, a is the asymptote of the saturation curve defining the maximum possible ZOI_r and b is the half-maximum.

To proceed with the competition study, the pairwise relationship between five-year diameter growth, id_5 and CIs was characterized using Spearman's rank correlation (r_S) (Pedersen *et al.*, 2013) to pre-select adequate CI candidates to fit in the growth model. The existence of pairwise relationships between id_5 and CIs was tested by the t-test, and then two non-spatial CIs and two spatial CIs were selected for further analyses. In the next step, a linear multiple regression model (Wimberly and Bare, 1996; Jõgiste, 2000) was constructed improvising different combinations of a list of variables (Table 4). The final diameter growth model (Eq. 3.1) was fitted considering the id_5 (cm) as a response variable in relation with stand variables of the site index SI, estimated by Nilson (2005a), and relative spacing (RS, Eq. 3.13) and tree variables of d (cm), integrating the past competitive interactions (Soares and Tomé, 1999), relative diameter (d_{rel}) and crown ratio (cr) depicting the vigour of trees of similar size (Schröder *et al.*, 2002).

The existence of any correlation among residuals was explored fitting the growth function in a mixed effect model with and without an auto-regressive structure, AR(1) (Eq. 3.2). The relative quality of growth functions was evaluated using R^2 (Adjusted-R^2), the root mean square error, RMSE, Akaike information criteria, AIC, and Akaike weights, AIC_w. A model having the smallest value of the AIC and the biggest AIC_w (Wagenmakers and Farrell, 2004) was expected to be the best. Additionally, CIs were added to the final growth function and the contribution of each CI was assessed with the mean square error reduction MSER. Also, the efficiency of CIs in different stand stages (young, <35 years; middle-aged, 35–69 years; and old, ≥70 years) and the contribution of different species in the competition load of a subject tree, weighted by Ellenberg's species-specific light transmission coefficients, from one, plants in deep shade, to nine, plants in full light (Ellenberg *et al.*, 1991), were evaluated. It should be noted that the existence of multicollinearity amongst explanatory variables for each combination was also controlled using the variance inflation factor (VIF) where only the combinations of variables with VIFs<10 were considered (Soares and Tomé, 2001; Corral Rivas *et al.*, 2005).

In another approach (II), tree competition was quantified in two alternative approaches, (1) by using distance-weighted CIs as fractions and as part of exponential functions which account for the ZOI when calculating CIs, (2) based on corresponding competition kernels. The approaches and analyses used in this generic study to compute and qualify competition are summarized as follow:

- Crown radius (C_r) depending on tree size and restricted by environmental resistance (Soares and Tomé, 1999; Burkhart and Tomé, 2012), defines the growing space of trees and was used as a good proxy of the varying ZOI_r (Gspaltl *et al.,* 2012). Crown radius was estimated using a saturation curve (Eq. 3.8, Fig. 5). The C_r was calculated for all neighbouring trees and if their crowns overlapped they were considered as active competitors. The number of competitors for a subject tree was variable depending on the local tree pattern, tree size and tree locations (Table 2, ZOI_{Cr}).
- Competition load for a subject tree was quantified using two spatial CIs (Eq. 1.12 and 1.18) and one non-spatial CI (Eq. 1.3). As alternatives to the traditional concept of CIs, the fractional and exponential local competition effects or signals of any competitor tree j at any location ξ in the forest were calculated and additively aggregated to measure the equivalent competition kernels (Eq. 1.19 and 1.20), respectively, following the shot-noise approach (Pommerening *et al.,* 2011; Pommerening and Särkkä, 2013). These competition signals are continuously defined in space, whereas CI values are only defined at tree locations. Unlike traditional CI, competition kernels do not necessarily require influence zones since their influence zones are automatically included or implicit. Also to reduce edge effects the competition kernels were computed with periodic boundary conditions (Illian *et al.,* 2008).

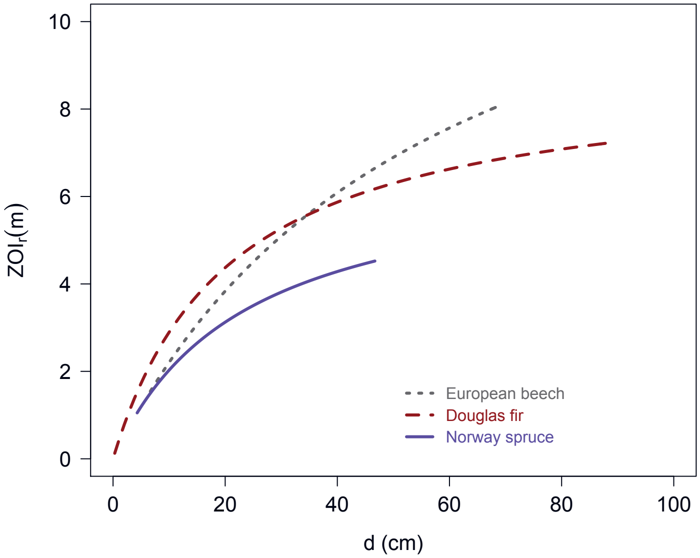

Figure 5. The relationship between stem diameter and the ZOI$_{Cr}$ (Eq. 2.5) for the three species investigated. The three curves reflect the stem diameter ranges of the three time series (**II**).

- Since the impact of competition load depends on the stem diameter of the subject tree i, and its competitors j, and their distances $l_j(\xi_i)$, in order to increase biological plausibility and improve model behaviour a transformation of competition kernels was also measured (Eq. 3.3), which is only defined at the location of trees i, because it requires their size information.
- The quality of competition modelling was assessed by diameter growth as a response variable, applying the potential-modifier approach (Newnham, 1964; Botkin *et al.,* 1972). The potential diameter growth (id^{pot}) was modelled for each tree according to the Chapman-Richards growth function (Eq. 3.4). Finally, both the CIs and the kernels were separately used as growth modifiers, with different modifying terms (Eq. 3.5 and 3.6) and estimated diameter increment were compared by absolute Bias, the RMSE and AIC.

Table 3. List of models used.

Eq.	Equation	Description	Sources	Study
3.1	$id_5 = b_0 + b_1(x_1) + \ldots + b_n(x_n)$	Linear multiple regression growth model	Wimberly and Bare, 1996; Jõgiste, 2000	I
3.2	$id_5 = X\beta + Zu + \varepsilon$	Linear mixed effect growth model	Verbeke and Molenberghs, 2000	I
3.3	$C_{i(trans)} = \frac{CK_i}{d_i^{\alpha_K} + CK_i}$	Transformation of competition kernel to combine the size of the affected tree i with its competition load	Adler, 1996	II
3.4	$id_i^{pot} = D_{max} \cdot k \cdot P \times \exp(-k \cdot d_i) \times (1 - \exp(-k \cdot d_i))^{p-1}$	Chapman–Richards growth function for modelling potential growth	Pienaar and Turnbull, 1973; Zeide, 1993	II
3.5	$id_i^I = id_i^{pot} \times v_I \times \left(\alpha_I - \exp\left(\frac{-\beta_I}{c_i}\right)\right)$	Reduced growth due to competition load calculated by the CI and CK	Ek and Dudek, 1980; Vanclay, 1994; Pretzsch, 2009	II
3.6	$id_i^K = id_i^{pot} \times v_K \times \left(1 - c_{i(trans)}\right)$			
3.7	$C_r = 0.5\left[a \cdot d + \frac{b \cdot d}{h}\right]$	Allometric model to estimate crown radius	Lang *et al.*, 2007	I
3.8	$C_r = \frac{a \cdot d}{b + d}$	Michaelis–Menten saturation curve to estimate crown radius	Michaelis and Menten, 1913; Bolker, 2008	II

3.9	$l = \sqrt{A/N}$	Stand sparsity (m)	Nilson, 2005b, 2006	III
3.10	$l_{lim} = \frac{\left(117 + 14.15 \cdot D^2/H\right)}{134}$	Sparsity of silver birch stands in a self-thinning situation (m)	Vabariigi Valitsuse 2013-eqn. 2).	III
3.11	$\text{logit}(p) = \ln(p/(1-p)) = \alpha + X\beta + Z\gamma + \varepsilon$	Logistic function to model probability of tree mortality	Monserud, 1976, Yao *et al.*, 2001	III
3.12	$\gamma(r) = [2N(r)]^{-1} \Sigma[x_i - x_{i+r}]^2$	Semivariogram to indicate spatial correlation	Cressie, 1993	IV
3.13	$RS = \frac{\sqrt{A/N}}{H_{Dom}}$	Relative spacing of trees	Schröder and Gadow, 1999	I

Notes: d is diameter at breast height; id_5 is five-year diameter growth (cm); D, H and H_{Dom} are stand quadratic mean diameter (cm), stand height (m) and stand dominant height (m), respectively; A and N are the plot area and the number of trees on the plot: b_0-b_n are model coefficients; x_1-x_n are model variables; β is a vector of fixed effects; *u* is a vector of random effects; *ε* is a vector of random errors; *X* and *Z* are design matrices; α_K is the strength of the competition kernel signal; CK is competition kernel; D_{max} represents the maximum diameter for all trees; k scales id rate; P determines the location of the function inflection point; n_I and n_K are additional modifiers allowing equating both sides of the equation; α_I is the strength of the competition signal; β_I is a range parameter: a is an asymptote of the saturation curve; b is the so-called half-maximum; p is the survival probability and (1-p) is the probability of mortality; Xi and Xi+r are values of a variable at locations i and i+r, separated by the vector of directional distance r, and N(r) is the number of pairs of samples considered in the given distance class (lag).

4.3. Characterizing non-spatial and spatial variables associated with individual tree mortality (III)

To investigate the suitability of neighbourhood spatial information to predict tree mortality, a set of variables, representing different factors contributing to tree death or survival (Hamilton, 1986) was assessed; e.g. different measures of a tree and stand (Table 4), measures of competition interactions (Eq. 1.2 and 1.12) and measures of the structural attributes of a stand (Eq. 1.21 and 1.25). Additionally, the were also calculated only for trees within the influence zone around each subject tree. Self-thinning (ST) as an important issue in stand development was also considered in the mortality study and it was defined applying the Eq. 3.9 and 3.10. Trees within study plots cross the ST line if l_{lim}/l is greater than one. Eventually the non-spatial quantification of the thinning intensity within the plots (I_{thin}) and the spatial quantification of the reduced competition within the ZOI due to competing neighbours elimination through thinning practices (C_{red}, using the Eq. 1.12) were done.

Logistic functions are widely used to model the discrete probability of tree mortality that can only take live (value set to 1) or dead (value set to 0) values (e.g. Monserud, 1976, Yao *et al.,* 2001, Bravo-Oviedo *et al.,* 2006), thus generalized linear mixed effects logistic regression was used for binary mortality data to predict mortality probability (Eq. 3.11). Tree mortality was set as a dependent variable, where p is the tree survival probability and 1-p is the tree mortality probability. The variables and indices described and listed in Tables 1 and 3 construct the fixed effects for the logistic mortality model and plot is a random effect.

Table 4: List of variables used for assessment of competition and mortality.

Type	Level	Variables	Description	Study
Non-spatial	Stand	N_{ha}	The number of trees per hectare, ha^{-1}	I, III
		G	Stand basal area, m^2ha^{-1}	I, III
		H	Stand height, m	I
		D	Quadratic mean diameter, cm	I, III
		SI	Site index, m	I, III
		age	Age of overstorey, year	I, III
		I_{thin}	Thinning intensity (Number of thinned trees / total number of trees)	III
Non-spatial	Tree	h	Tree height, m	I
		d	Diameter at breast height, cm	I, III
		d_{rel}	Relative tree diameter in plot	I, III
		id_5	Five-year diameter growth, cm	I, III
		g	Tree basal area, m^2	I, III
		cr	Crown ratio of trees	I
Spatial	Stand	$d_{rel.\ (ZOI)}$	Relative tree diameter in the ZOI	I, III
Spatial	Tree	sp	Species proportion for n nearest neighbours, using Eq. 1.25	III
		ST	Self-thinning situation	III
		C_{red}	Spatial competition measure of thinned trees inside the ZOI	III

For discrete variables, the coefficient of determination is not suitable (Bravo-Oviedo *et al.*, 2006), therefore the goodness of fits of the mortality models was characterized applying a log-likelihood statistic (loglik), AIC, AIC_w and ΔAIC (measuring the difference in AIC values between a given model and the model with the lowest AIC). As Burnham and Anderson (2002) suggested we assumed that models with $\Delta AIC < 2.0$ were almost equal, whereas the models with

ΔAIC>4.0 were considerably different. The predicted probabilities of the logistic fits against the observed mortality were also validated applying the area under the receiver operating characteristic curve (AUC) (Bravo-Oviedo *et al.,* 2006) where values greater than 0.7 indicate good accuracy to correctly distinguish dead trees from living ones (Fawcett, 2006).

The contribution of variables and indices (Tables 1 and 3) to tree mortality was assessed using the analysis of variances (ANOVA) in the pairwise fits, and the 10 most effective variables were selected based on their AIC values. All possible combinations of selected variables were first controlled for existence of multicollinearity using the VIF and were then devised into mortality models with the restriction that no model could simultaneously include variables representing a similar factor. In the end, non-spatial and spatial thinning variables I_{thin} and C_{red} respectively, were separately added to the best models as new predictors, and the changes to the quality measure of the full statistical model were explored.

4.4. Structural assessment of different point patterns through sample plots of varying size and shape (IV)

Structural indices applied for detailed structural analyses are summarized in Table 1 (Eq. 1.21–1.26). The structural analyses were based on repeated samplings of the stands, with randomly placed circular and square plots of different sizes, with areas ranging from 0.007 to 0.636 ha. Similar centre positions (1,000 centres for each size) were considered for plots of different shapes, but the locations of the plot centres differed with size, so that the plots of different sizes were able to cover the maximum possible area of reference stands.

All presented indices except Eq. 1.26 describe the stand spatial structure by single values, and are based on the nearest-neighbour relations; agg and ddf (Eq. 1.21 and 1.22) use the first nearest neighbour, NN1, and ddm, ua and ming (Eq. 1.23–1.25) account for 4 nearest neighbours, NN4. Compared to agg, that is stand level index, single-tree based indices (ddf, ua, ddm and ming) do not result in a single value, but in a value for each tree within the stand; thus, for describing the whole stand, the mean values of single-tree based indices for that stand were calculated. Finally, g(r) (Eq. 1.26) is a continuous function of inter-tree relations, and describes the spatial structure not by a single value but by a function. To eliminate the edge effect error, a border method was applied similarly to studies (**I**, **III**). For a tree located near the stand border, the distance from its n^{th} nearest neighbour and the distance of that tree to the border were controlled, and then the tree was excluded from the calculation if its distance to the border was shorter than its distance from its n^{th} nearest neighbour. However, that tree could only serve as the NN to other subject trees (Pommerening and Stoyan, 2006).

In order to perform statistical analyses for each size class and shape, the mean and the variance of each structural index were calculated. For each stand, the expected values of structural indices, regarding the actual area of that stand covered by sample plots, were computed. Then standard deviation (sd) and the differences of the mean estimates from the expected values were computed to highlight the influence of the plot size and shape on estimate precision and accuracy, respectively.

It should be also noted that due to the spatial variability of forest stands, stand observation through sample plots of various sizes is a tricky issue (Bellehumeur *et al.*, 1997; Chen *et al.*, 2004; Fajardo and Gonzalez, 2009). Subsequently, the semivariogram as an applicable function to indicate spatial correlation between variables characterizing the forest stand at sample locations (Cressie, 1993) was used (Eq. 3.12).

5. RESULTS

5.1. The outcome of competition measurement methods and assessments (I, II)

Three neighbours selecting methods of ZOI_k, when k=3, ZOI_H, and RSC, when β=60°, proved to be more appropriate, respectively. The relationship between diameter at breast height of silver birches and the radius of the interaction zone, where they impose competitive loads on neighbouring trees, calculated with three mentioned approaches is illustrated in Fig. 6. As shown the broader zones are allocated to larger trees, and the ZOI_r (m) increases with d (cm) and this enlargement critically depends on the method of how the zone is defined.

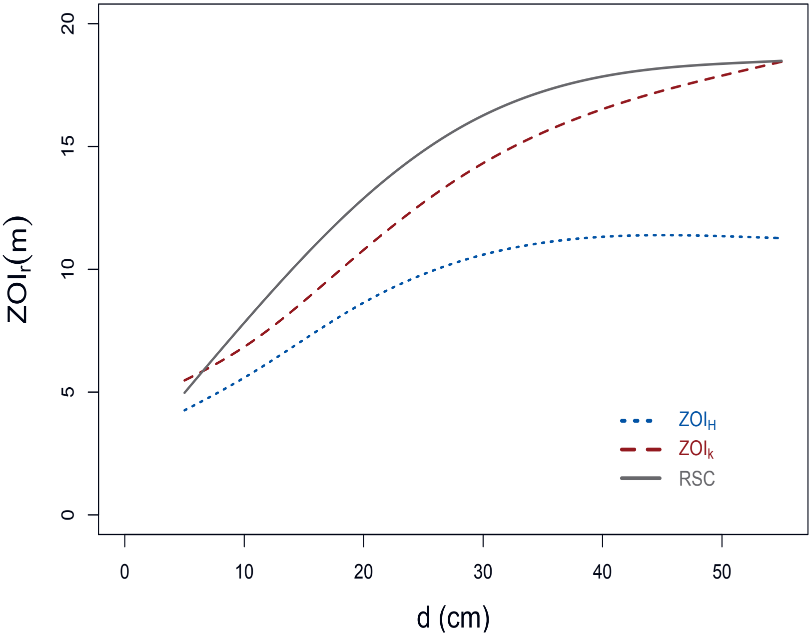

Figure 6. The relationship between diameter at breast height of silver birch trees and the radius of the influence zone determined by three best competition selection approaches in study (I).

Also, the Spearman's rank correlation coefficient (r_S) indicated that the CSMs significantly influence the growth prediction ability of spatial CIs. Spatial CIs of SdrAng (Eq. 1.15) and Heg (Eq. 1.12), when incorporated with selection methods of ZOI_k, ZOI_H, and RSC proved more efficient, respectively. Following the spatial indices, non-spatial CIs of BAL (Eq. 1.2) and BALMOD (Eq. 1.7) also showed to have high correlation with id_5, respectively (Table 5).

Table 5. Spearman's rank correlation between the five-year diameter growth of silver birch trees and CIs combined with different CSMs.

CI	No	ZOI_H	ZOI_k	RSC
SdrAng	-	-0.641	-0.656	-0.616
Heg	-	-0.623	-0.650	-0.597
BAL	-0.598	-	-	-
BALMOD	-0.558	-	-	-

The growth model was fit into linear mixed effect regression with no auto-regressive structure since it performed better than linear multiple regression in terms of the AIC and the ANOVA comparison between the mixed effect models, with and without AR(1), which did not show significant remaining within-group correlation (p-value>0.05). Explanatory variables in Eq. 3.1 were considered as mixed effects and proved significant (p-value<0.05) having no problem with multicollinearity (VIF<8). The statistical measures of mixed effect models illustrated that the contribution of the CIs was significant but not very large in magnitude, and among the CIs added to the model, SdrAng and then Heg presented the most efficiency to improve the growth model, no matter which CSM was used and non-spatial CIs of the BAL and BALMOD showed minor contribution to the growth model, respectively. The analyses of different stand developments and species-specific weighted CIs (Table 6) demonstrated that spatially CIs had stronger prediction ability in younger stands, and proved to be better than non-spatial ones (**I**).

Table 6. Contribution of the un-weighted and species-specific weighted CIs to the five-year diameter growth of silver birch trees in different stand developments.

		Young		Middle-aged		Old	
CSM	CI	r_S	AIC_w	r_S	AIC_w	r_S	AIC_w
	Heg	-0.63	0.008	-0.52	0.011	-0.44	0.034
	Heg^{Ellen}	-0.63	0.023	-0.50	0.004	-0.40	0.007
ZOI_k	SdrAng	-0.69	0.190	-0.61	0.673	-0.54	0.081
	$SdrAng^{Ellen}$	-0.71	0.779	-0.58	0.312	-0.50	0.027
	BAL	-0.62	0.000	-0.56	0.000	-0.60	0.618
	BALMOD	-0.59	0.000	-0.57	0.000	-0.51	0.233
	Heg	-0.61	0.000	-0.48	0.022	-0.38	0.016
	Heg^{Ellen}	-0.62	0.000	-0.46	0.012	-0.31	0.014
ZOI_H	SdrAng	-0.66	0.337	-0.60	0.108	-0.52	0.037
	$SdrAng^{Ellen}$	-0.67	0.663	-0.57	0.076	-0.46	0.004
	BAL	-0.58	0.000	-0.55	0.191	-0.59	0.379
	BALMOD	-0.57	0.000	-0.57	0.592	-0.50	0.549
	Heg	-0.56	0.000	-0.38	0.061	-0.31	0.003
	Heg^{Ellen}	-0.57	0.001	-0.35	0.023	-0.30	0.002
RSC	SdrAng	-0.67	0.033	-0.53	0.835	-0.49	0.110
	$SdrAng^{Ellen}$	-0.69	0.966	-0.48	0.079	-0.46	0.021
	BAL	-0.60	0.000	-0.48	0.001	-0.53	0.222
	BALMOD	-0.59	0.000	-0.49	0.002	0.52	0.642

Notes: Heg and SdrAng are spatial CIs without including the species-specific values. Heg^{Ellen} and $SdrAng^{Ellen}$ are corresponding spatial CIs including Ellenberg's species-specific values for three CSMs. The BAL and BALMOD are non-spatial CIs for the subject trees of the same data set used for analyses in each CSM (**I**).

The competition signal curves are visualised in Fig. 7, where the species, size and the competition kernel type influence the signal scales. When using the exponential competition kernels a larger competition range in European beech and interior Douglas fir are seen and the values of the signal peaks vary considerably between kernels. Norway spruce and interior Douglas fir have the highest and the smallest signal peaks, respectively, and the differences between the species are significant. It is also interesting that the differences in signal strength between a 10-cm-diameter tree and a 20-cm-diameter tree vary as well. They are the largest for Norway spruce followed by European beech. Compared to Norway spruce and European beech, the signal strength of small and large interior Douglas fir trees is much more similar. This pattern is the same for both kernel types. Also, European beech and Norway spruce have the largest and smallest competition signal range, respectively.

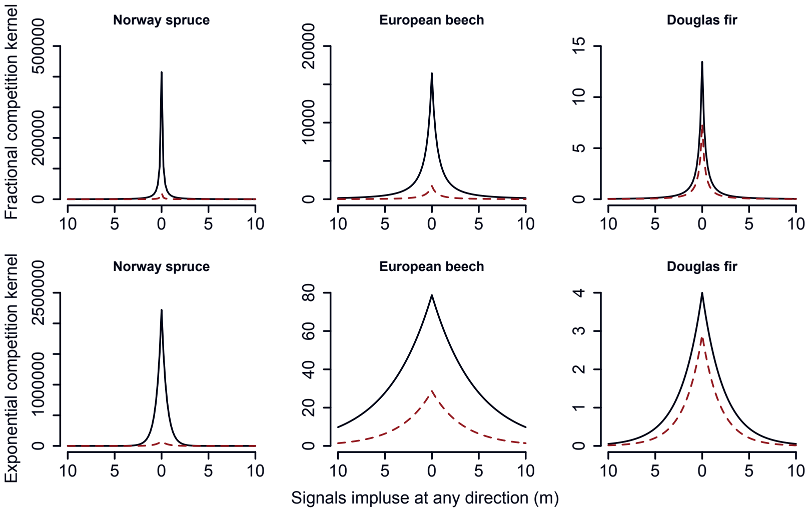

Figure 7. The shape of the exponential and fractional competition kernels estimated from the three spatial time series for hypothetical trees with a diameter of 20 cm (solid line) and 10 cm (dashed line) (II).

The kernel method clearly demonstrated a moderate superiority to CIs for estimating diameter increment (Table 7). In interior Douglas fir, the exponential kernel performs slightly better than the exponential competition index, however, the application of the fractional competition index leads to better results than that of the fractional kernel. These are particularly interesting results, since among three study sites, the Canadian Douglas fir site is the most natural and the most structurally diverse site. Whilst the fractional form of CIs always performs best, the exponential competition kernel always produces better results than the fractional form. Another interesting result is seen in interior Douglas fir and Norway spruce where no distance weight CI performs a slightly better result than the exponential form of distance weighting (**II**).

Table 7. Competition parameters α_I, β_I, α_K and β_K along with the evaluation criteria of Bias, the RMSE and AIC relating to estimated diameter growth (**II**).

Competition measure	**Type**	**Parameters**			**Evaluation criteria**	
		$\alpha_{I,K}$	$\beta_{I,K}$	**Bias**	**RMSE**	**AIC**
		European beech				
CI	Fractional	0.45049	5.20000	-	0.13026	-2165.5
	Exponential	0.24406	44.21367	-	0.13223	-2112.8
	Un-weighted	0.24145	39.52282	- 0.01007	0.13233	-2110.0
Kernel	Fractional	3.24074	1.05879	0.00137	0.12048	-2439.3
	Exponential	1.45772	0.52339	- 0.00163	0.11999	-2453.6
		Douglas fir				
CI	Fractional	0.95916	5.61447	-	0.07200	-7782.2
	Exponential	0.93777	16.65314	-	0.07452	-7561.0
	Un-weighted	0.94979	12.16664	- 0.00065	0.07432	-7578.3
Kernel	Fractional	0.86776	0.55742	-	0.07480	-7537.1
	Exponential	0.46267	0.27992	- 0.00328	0.07311	-7684.2
		Norway spruce				
CI	Fractional	1.67389	6.73727	-	0.17159	-2710.1
	Exponential	0.55300	61.43529	-	0.17230	-2677.9
	Un-weighted	0.53668	55.54871	- 0.00922	0.17228	-2678.5
Kernel	Fractional	4.31822	0.20540	-	0.16955	-2804.9
	Exponential	4.87799	-0.21178	0.00112	0.16874	-2842.8

5.2. Mortality drivers and their associations in logistic mortality functions (III)

The five-year mortality rate of silver birch trees was 9.67%. Out of 6,009 trees 581 died, and this rate decreased from 16.67% in a pure silver birch stand, to 6.09% for single silver birch trees surrounded by other species, mainly by Norway spruce and Scots pine trees. The first 10 mortality contributors based on pairwise analyses are illustrated in Fig. 8. As shown the mortality probability of individual trees was negatively correlated with d, id_5, sp, and agg, but the correlation was positive for competition and stand size (G). In an attempt to take the site quality into consideration, the site index at a reference age of 50, and the site type as a nominal variable, as alternatives to the SI (at a reference age of 100), were also tested and found to be inefficient to improve the mortality model.

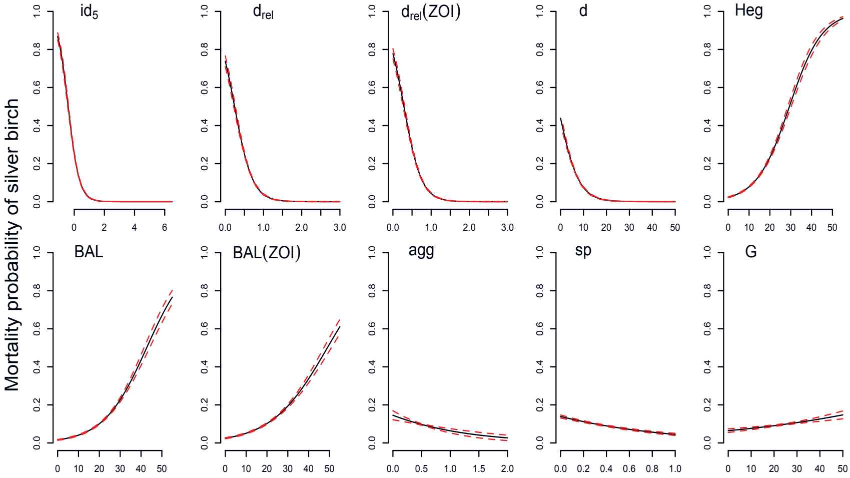

Figure 8. Predicted mortality probability of the most important predictors of the tree mortality (solid lines) with 95% confidence (dashed lines) in pairwise relationship between mortality and predictor variables (III).

The statistical analyses revealed that the logistic models consisting of spatial variables far exceeded those with non-spatial measurements in terms of the AIC and AIC_w. For all combinations, no problem with multicollinearity was detected (VIF<3). Additionally, we tested some transformations of d, d_{rel} and id_5, and found them inferior to their untransformed variables. A comparison of the predicted mortality probability of subject trees with their observed mortality probability for the best logistic model found is presented in Fig. 9.

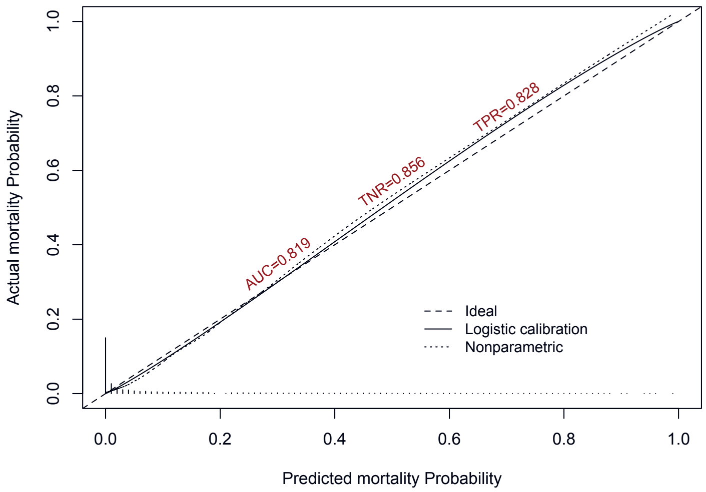

Figure 9. The predicted mortality probabilities of the best logistic model against observed mortality. The dashed line represents the ideal probability estimation and the solid line shows how the model fits observed mortality probabilities. The AUC, TNR and TPR are the area under curve, specificity and sensitivity of the model, respectively.

Despite the good prediction ability of the model, an evidence of trivial overestimation of the mortality prospects of very small silver birch trees ($d_{rel}<0.2$), and also a mild overestimation of survival likelihood of the small proportion of large silver birch trees (d>40 cm, see sensitivity and specificity values in Table 8) were detected. A tendency was also found to overestimate the mortality probability of silver birch trees with a small d_{rel} within the plots with no thinning operations. Finally, the advancement gained by adding C_{red} to the best mortality model indicated that the survival likelihood of silver birch trees increased by thinning (negative model coefficient for C_{red} in Table 8) due to reducing competition; from 89.9% in the plot with no thinning practices to 93.4% in thinned stands, and the spatial thinning measure C_{red} performed better than I_{thin} as the non-spatial measure of thinning intensity. Additionally, the accuracy showed by the AUC was excellent (AUC>0.8) indicating that many of the dead trees (true positives) were correctly classified.

Table 8. The best variable combinations, predicting silver birch mortality, when non-spatial and spatial thinning variables are included (**III**).

Mortality fits	Evaluation criteria		Model Coefficients						
	ΔAIC	AIC$_w$	Intercept	id$_5$	d$_{rel}$	sp	agg	C$_{red}$	I$_{thin}$
With spatial thinning variable	0.00	0.655	2.324	-1.977	-3.263	-1.1053	-1.008	-0.195	-
Without thinning variable	2.49	0.189	2.327	-1.985	-3.232	-1.103	-1.054	-	-
With non-spatial thinning variable	2.86	0.157	2.303	-1.981	-3.262	-1.098	-0.993	-	-1.273

Notes: id$_5$ is the five-year diameter growth of a tree (cm); d$_{rel}$ is the relative dbh of reference trees for each plot; C$_{red}$ is the spatial competition measure of thinned trees inside the ZOI; I$_{thin}$ is the thinning intensity of the plot; agg is the aggregation of trees inside the ZOI and sp is the proportion of species other than silver birch within the ZOI. ΔAIC and AIC$_w$ are the statistical measures of models.

5.3. The efficiency of sample plot size and shape in characterizing structural indices (IV)

Regarding the assessment of the effect of sample plots' properties on quantification of forest structural indices, the exact values of studied structural indices for six one-hectare reference stands were computed (Table 9). The differences between exact and expected values of structural measures were small for circular (<1%) and square (<0.4%) sample plots in all stands, except for the clustered patterns quantified by circular sample plots (varying up to 2.3%); due to the occurrence of the clusters in the corners and the exclusion of a considerably large number of points, specifically for bigger radii, when calculating the expected values.

Table 9. Structural indices of six one-hectare stands (IV).

Index	Stand					
	RAMI	RAN	REG1	REG2	CL1	CL2
agg	1.04	1.01	2.00	2.00	0.67	0.84
ddf	0.32	0.30	0.40	0.37	0.33	0.31
ua	0.60	0.54	0.00	0.50	0.70	0.71
ddm	0.51	0.50	0.50	0.52	0.50	0.50
ming	0.61	0.65	0.66	0.69	0.70	0.65

Variation in structural estimates (sd) declined asymptotically with increasing plot size in the six studied stands. However, the estimates of agg using square plots showed slightly bigger variation in those using the circular plots, specifically in regular stands. Regular stands also showed an expectation in ua estimates; the ua remained constant for all sample plot sizes and shapes, 0 for REG1 and 0.5 for REG2, resulting in sd=0.

Comparing the mean estimates of the expected values, the spatial arrangement of trees defined by the agg showed more accuracy for circular plots in all reference stands. Inaccuracy in RAMI, RAN, REG1 and REG2 declined with increasing size up to 0.1ha. In CL1 there is an evidence of overestimation of clustering when the plot area expands. In CL2, inaccuracy first declines with the plots enlarging up to around 0.1ha and for plots larger than 0.1ha the accuracy starts to decrease again, however when the plot areas exceed 0.5ha, the structural variables of those plots start converging to the structural values of the stand. Also, the estimation accuracy of the ddf for reference stands, RAMI, REG1 and REG2 increased slightly with plot size, regardless of their shapes and reached the maximum for the plot size of 0.40–0.45ha. The differences between the mean estimates and the expected values in estimating the NN4 indices were less than 4% for all stands and accuracy increased by enlarging the plots' size above 0.4ha. Besides, similarly to the sd, the measure of the ua remained constant with the size and/or shape of plots, being always 0 for REG1 and 0.5 for REG2, therefore, the differences of the mean estimates from the expected values were set equal to zero.

The maximum distance within which trees may have direct interactions is illustrated in Fig. 10. As shown the g(r) resulted in thoroughly different pictures for six stands. In RAMI a distance limit of approximately 6 m is evident, where trees tend to be inhibited, and do not tend to be located at shorter distances within the stand. At larger distances of up to 10 m, trees show a more clustering tendency, and after that, their spatial arrangement approaches to randomness. As expected, the g(r) values for RAN are around 1 and the CL1 and CL2 appear to have the values of the g(r) greater than 1, up to inter-tree distances of 10–12 m, and after that critical distance, the pair correlation function behaved similarly to the Poisson process. Finally, the pattern of fluctuations in g(r) values for REG1 and REG2 reflects the current spacing between points within those stands.

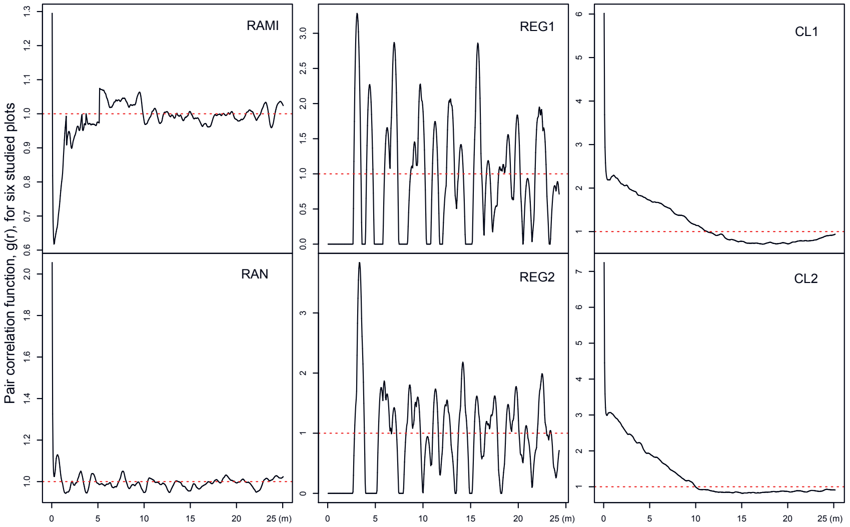

Figure 10. The pair correlation function, g(r), for the RAMI stand and five simulated point patterns, where the dotted lines indicate complete randomness (**IV**).

Finally, the distributions of indices' estimations applying sample plots with radii of 10 and 20 meters, to compute the structural properties of the RAMI, are compared in (**IV**, Fig. 7). As expected the variation in sample plots when calculating structural indices decreased by enlarging the sample plot radius from 10 to 20 m; therefore, the ENFPR sample plots provided more accurate measures of the structural indices for the RAMI stand. In more detailed analyses, the omnidirectional semivariograms of the quantified structural attributes based on 10 m and 20 m sample plots' radii in the RAMI stand are illustrated in Fig. 11. As shown, the spatial variability in all structural estimations varied with the sample plot size, and a more significant spatial trend is evident for sample plots with a radius of 10 m, and also some degree of spatial auto-correlation of the stand structure appeared in plots with a radius of 20 m.

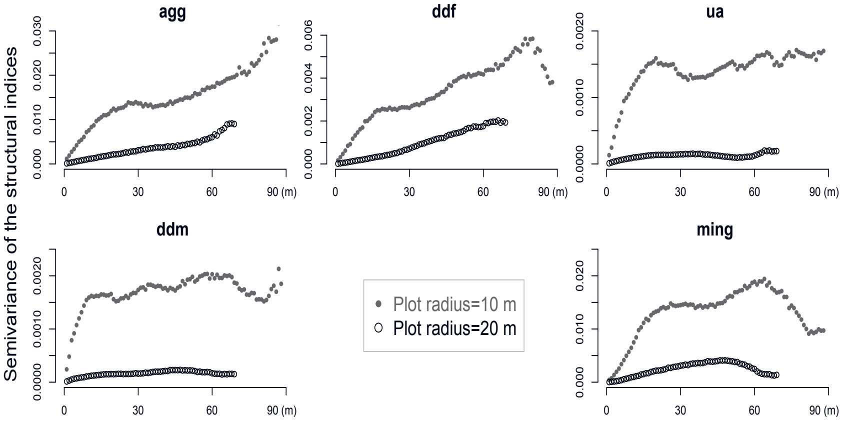

Figure 11. The omnidirectional semivariograms of the numerated structural indices based on 10 m and 20 m sample plots' radii in the RAMI stand (IV).

6. DISCUSSION

6.1. The superiority of spatial measures of competition in estimating diameter growth of individual trees

Tree growth in response to competition, and the evaluation of the efficiency of different competition indices (CIs), has been an important subject of research (Burkhart and Tomé, 2012; Seifert *et al.*, 2014).

Results of comparing non-spatial and spatial CIs showed that spatial CIs, SdrAng and Heg, were more appropriate than non-spatial ones to quantify the competition status of silver birch trees, respectively. However due to the inclusion of d_{rel}, the improvement using CIs was not considerable (I). Relative dimensions are believed to illustrate the hierarchical position of a tree within the stand, and indirectly indicate the competitive status of that tree (Burkhart and Tomé, 2012). Following the hypothesis of Cole and Lorimer (1994) noticeable competitive stress occurs by immediate neighbours surrounding the subject tree crown, SdrAng and Heg assign greater weight to the closer and larger competing neighbours (Wimberly and Bare, 1996). Thus, a considerable amount of variation in growth models can be described by applying SdrAng (Castagneri *et al.,* 2008; Contreras *et al.,* 2011) and Heg (Alemdag, 1978; Pukkala and Kolström, 1987; Holmes and Reed, 1991; Mailly *et al.*, 2003). Eventually, two recent CIs used the d as a size indicator and their efficient contribution in the diameter growth model can be explained by the actual correlation between the subject tree's diameter growth and its d (Holmes and Reed, 1991). However, the competition strength expressed by such correlations may be debatable (Larocque, 2002). Numerous studies, which explored and compared non-spatial and spatial CIs, reached conclusions, which are similar to those in our study. Some found spatial measures to be more precise growth predictors (Boivin *et al.*, 2010; Contreras *et al.*, 2011) and to the contrary, no advantages of spatial CIs over non-spatial CIs were found in other studies (Soares and Tomé, 1999; Stadt *et al.*, 2007; Roberts and Harrington, 2008) and devising non-spatial CIs (e.g. BAL and BALMOD) in some other researches (e.g. Biging and Dobbertin, 1995; Corral Rivas *et al.*, 2005) improved the model performance.

In another study (**II**), kernel functions were employed to measure competition. These methods are not well known despite their theoretical importance (Schneider *et al.,* 2006; Vogt *et al.,* 2010). The first comparison between competition indices and competition kernels was presented by Pukkala (1989) and Miina and Pukkala (2002). However, their competition indices and kernels differed noticeably and they used *multiplicative aggregation* of competition signals instead of *additive* ones, which was common in early applications of the ecological field theory (Wu *et al.,* 1985). Competition kernels were found to be better growth predictors for Scots pine and Norway spruce in Scandinavia (Miina and Pukkala, 2002) and authors attributed this to the multiplicative aggregation of competition signals. However, study (**II**) using additive aggregation revealed that in some forest ecosystems, other factors such as specific neighbourhood effects could result in a better performance of competition kernels. Generally, any superiority of competition kernels cannot only be justified by evaluation criteria relating to a response variable but also by the differences between the two concepts of quantifying competition (**II**, Table 4).

Competition measures with fractional distance weights performed well, which can be due to the term $1/l_{ij}$, the distance weight. This, similarly to the corresponding kernel, includes a robust mechanism to weigh the competition load depending on the competitor's distance to the subject tree. However, the exponential weights appear to be less effective than the fractional ones. Un-weighted CIs are expected to perform notably worse than comparable competition kernels. However, the un-weighted and the weighted CIs did not differ markedly in terms of evaluation criteria and in two cases the un-weighted CI even performed better than the exponentially weighted CIs. Obviously the contribution of the distance weights to the growth estimation should not be overestimated and in some conditions they are not required. It should also be noted that exponential kernels always proved to be better than fractional ones in this study, whilst fractionally weighted CIs were superior to exponentially weighted ones. The potential benefits of competition kernels (Illian *et al.,* 2008) are attained at the expense of complex spatial regression routines that require advanced programming skills, since the competition parameters are included in the spatial algorithm.

6.2. The importance of the selection method of active competitors

The competition status of a tree strongly depends on the selection of the competitive neighbours that affect the growth of that tree and could potentially vary depending on the radius of the influence zone (Pukkala and Kolström, 1987; He and Duncan, 2000; Nanami *et al.*, 2005). Concerning the CSM, the best results were acquired using the ZOI_k (k=3 and CEA=30°) as a multiple of average inter-tree distances within the plot and highly affected by stand density. The angle gauge of 30° has provided a satisfactory selection of active competitors (e.g. Lee and Gadow, 1997; Corral Rivas *et al.*, 2005; Zhang *et al.*, 2009), however some studies achieved better results using a different angle gauge (e.g. Alvarez *et al.*, 2003). Some suggested that the optional ZOI_r strongly depends on the initial dimensions of trees (D'Amato and Puettmann, 2004; Sims *et al.*, 2009), which was also proved valid using the ZOI_H. Similar to several other studies (Biging and Dobbertin, 1995; Pretzsch, 2009; Oheimb *et al.*, 2011), the opening angle of 50°–60° performed properly for the RSC as the third preferable CSM, where bigger angles (80° and 100° in this study) markedly decreased the merit of the RSC method to detect the competitors (Richards *et al.*, 2008). In contrast to the ZOI_k, the two methods of the ZOI_H and RSC assigned a greater weight to tree height than distance, and since in study (I) there was a lack of height measurements for all trees, the selected system of the ZOI_k was preferred to identify competitors of subject trees (I).

In study **II** the C_r was used as a proxy of the variable ZOI_r for computing the exponential and fractional spatial CIs, and trees were considered as active competitors if their crowns overlapped. It is probable that assigning weights to inter-tree distances when computing spatial CIs automatically specifies an implicit ZOI, therefore no additional designing of an explicit ZOI would be required. Some studies have taken this probability into consideration (e.g. Miina and Pukkala, 2002) and some other studies (e.g. Schneider *et al.,* 2006) have employed additional explicit ZOIs and even found superior results. To explore this matter, the same ZOI used for identifying competitors in the case of fractional and exponential CIs was also applied to the corresponding kernels. The results did not present any significant improvements and indicated that competition kernels in fact do not require ZOIs.

6.3. Species mixture effects on diameter growth and mortality of silver birch

Numerous studies (e.g. Kaitaniemi and Lintunen, 2010; Jõgiste, 2000; Hynynen *et al.,* 2011) have concluded that the competition and the growth of silver birch trees, and consequently, their survival potential are noticeably influenced by the attributes of neighbouring species. In study (**I**), regardless of the fact that the identity of neighbouring trees is a substantial factor in the characterization of their competitive effects (Bella, 1971; Zhao *et al.*, 2006; Kaitaniemi and Lintunen, 2010; Bošelá *et al.*, 2013), no remarkable improvement appeared by assigning weights to different species when re-computing the CIs, except for young trees. Therefore, as proposed by Oheimb *et al.*, (2011) the influence of competition on diameter growth was not significantly related to the number of species in the local neighbourhood. One possible explanation is that about two-thirds of the trees were birches with similar weights; consequently, allocating weights to different species did not considerably alter the values of the CIs.

Also, *interspecific* interactions, caused mainly by Norway spruce and Scots pine, appeared to be insignificant, where Norway spruce trees with similar site requirements have different temporal growth patterns and shade-tolerance (Tahvanainen and Forss, 2008; Hynynen *et al.*, 2011) and despite the shade-intolerance of Scots pines, birch trees simply overwhelm Scots pine trees due to their vigorous early growth (Hynynen *et al.,* 2011). In addition, the site requirements of Scots pine and birch are quite different. It must also be noted that Ellenberg's light values refer to the preferences of the early stage of the tree life cycle, when the more light-demanding birch trees rapidly occupy regeneration areas and Norway spruce tends to emerge as more shade-tolerant. Consequently, weighting tree species differently during the early stage (young stands) for competition quantification is a rational approach. Moreover, the adequacy of CIs modestly changed by stand development. Spatial indices performed better in young stands while in older stands, non-spatial indices showed superior results. In the early stage, pioneer birches grow relatively fast and vigorously (Hynynen *et al.*, 2011), and the competitive interactions in dense young stands are well illustrated by spatial CIs, since they account for the inter-tree distances that are critical for competing individuals to allocate resources. As stands reach maturity, mortality induced by different factors, including competition (Sims *et al.*, 2009), reduces the number of trees and consequently stand crowding. Therefore, non-spatial CIs are adequate for competition assessments.

Regarding the mortality assessments of individual silver birch trees (**III**), devising the species mixture of immediate neighbours to the mortality fit improved the mortality estimates as expected. The mortality likelihood of a birch tree decreased from pure stands to mixed stands (tables 1 and 3 in **III**). As discussed earlier, competition-induced mortality among silver birches that have similar demands for light and resources is relatively high and also as the Janzen-Connell type effect explains, this high possibility of mortality may be due to the increased risk of attack by species-specific herbivores or diseases, when a silver birch tree grows in close proximity to many other con-specifics (Janzen, 1970; Connell, 1971).

6.4. Mortality probability and drivers of silver birch

The diameter increment of a tree has frequently been considered as an indicator of tree health and vigour (e.g. Kobe, 1996; Yao *et al.,* 2001; Das and Stephenson, 2015) and from the biological point of view the survival chance of any individual tree can be related to its diameter growth (Waring, 1987). A higher growth rate suggests robust vitality to resist stress factors. However, since diameter growth rates often decline with an increasing diameter, the mortality probability of smaller trees relative to bigger individuals may be underestimated. For this reason, some studies (e.g. Pederson, 1998, Ireland *et al.,* 2014) suggest that the basal area growth rate is a better estimator of tree survival because it is related to tree size (Clark and Clark, 1999, Di Filippo *et al.,* 2012).

The high mortality rate of small birch trees is associated either with the occurrence of self-thinning in young and dense stands (Barnes *et al.,* 1998) or with the suppression by dominant trees in older stands where d_{rel}, showing the hierarchical position of trees, indirectly accounts for competitive interactions among trees (Burkhart and Tomé, 2012). Similar to study **III**, the extensive literature on Estonian forests (e.g. Laarmann *et al.,* 2009; Sims *et al.*, 2009) and on other forests (e.g. Monserud *et al.*, 2004; Temesgen and Mitchell 2005; Bravo-Oviedo *et al.,* 2006; Das *et al.,* 2011) introduced competition as an important mortality driver. The neighbourhood interaction and the stand local density have a positive effect on competition in sparse stands, and subsequently, competition-induced mortality declines (e.g. Gonzalez *et al.,* 2004; Temesgen and Mitchell, 2005). Regarding the deficiency of d_{rel} to account for variation in stand density, equipping the model with spatial measures exhibiting the neighbourhood attributes of subject trees did appear indispensable. Eventually, devising the logistic model with agg and sp successfully assessed the regularity of tree positions (Pommerening, 2002; Aguirre *et al.,* 2003; Brumelis *et al.,* 2005) and species mixture effects on the survival prospects of silver birches.

Finally, thinning operations within the plots reduced the mortality probability of silver birch trees up to 3.5%. The slight significance of C_{red} in improving the mortality model indicated that thinning some interactive neighbours could successfully release the shade-intolerant birch trees to benefit from vigorous growth within a less competitive environment. Depending on the tree species located in sites with different conditions, thinning to different residual densities produces varying effects on tree mortality, (e.g. He and Duncan 2000; Canham *et al.,* 2001; Uriarte *et al.,* 2004). Whilst some authors have admitted that thinning practices may rescue trees from density-dependent mortality (e.g. Powers *et al.,* 2010), some other studies show an increased risk of mortality either because of mechanical damage to the residuals (e.g. Nyland, 1994; Caspersen, 2006), or windfall for the large remaining trees on the margin of cutting areas (e.g. Jönsson *et al.,* 2007; Fortin *et al.,* 2008) and also by shifting the population towards smaller trees with a greater negative influence from various environmental stress factors.

6.5. Effects of varying sample plot size and shape on structural measures

Study **IV** and several other studies (e.g. Johnson and Hixon, 1952; Freese, 1960; Gray, 2003; Frazer *et al.*, 2011; Næsset *et al.*, 2015) indicated improved precision of both circular and square sample plots in estimating stand structure by enlarging the plots. However, it should be noted that the spatial scale of point patterns other than random may cause some fluctuations (Reich and Arvanitis, 1992). Depending on the stand structure and management practices, the sampling errors could increase dramatically (Pommerening and Gadow, 2000; Kint *et al.*, 2004).

The numerical values of agg and any deviation of sample plot estimates from stand values, depend on the area that the sample plots cover, and the intensity of trees (tree crowding) within that area (Eq. 1.21). This fact is also reflected in g(r) values, where, specifically in the studied clustered pattern, small plots often failed to capture the actual point interactions. Spatial clustering is represented applying different methods (e.g. Anselin, 1996; Boots and Getis, 1988) and irrespective of the measurement employed, analyses are always subject to ecological fallacy due to size, or other effects (Wrigley *et al.*, 1996). Thus, to achieve more reliable results, special consideration must be devoted to the scale of the general layout of the underlying process, and the overall distribution of trees within the observed stand. The other approach to assessing the relative locations of trees (ua) behaved as expected: values between 0.5 and 0.6 refer to randomness, more than 0.6 show clustering, and less than 0.5 indicate regularity. However, these distinctions may vary slightly (Albert, 1999).

The values of ming and ddm, higher than 0.5, indicated that, on average, each tree had two neighbours of different species, and the reference tree was greater than at least two of its immediate neighbours. However, the variation in the stem sizes of two immediate neighbours represented by ddf was rather small. As discussed earlier, this finding seems acceptable for light-demanding silver birches willing to dominate speciose areas with relatively less competitive surroundings (Hynynen *et al*., 2010). Furthermore, in shorter inter-tree distances of the RAMI stand (up to 6 m), the g(r) values smaller than 1 revealed that at those distances fewer trees were recorded than what would be expected under random conditions. Self-thinning due to negative interactions between neighbouring trees would result in a random structure or even with some tendency towards regularity (Stoyan and Penttinen, 1998; Pommerening, 2002). Additionally, regarding the accordance of the inter-tree distance of 6 m with the estimated crown diameter of silver birch trees, ranging from 1.5 to 5.8 m, the competition or/and thinning must cause this trend in our study and also in other similar studies quantifying forest structure (e.g. Pommerening, 2002).

Despite the large variation among small sample plots, we were able to detect spatial heterogeneity of the RAMI stand. Lombardi *et al.* (2015) present a similar finding when quantifying the influence of sample size on some structural measures of old-growth forests. Subsequently, increasing the number of small plots as an alternative to enlarging the sample plot size is suggested (Salk *et al.* 2013). This aspect was discussed in a recent review of forest observational studies by Gadow *et al.* (2016).

Several studies on different measures of forest stands using varying plot size and/or shape have also reported considerable gains of precision with small plots, while larger plots proved inefficient (e.g. Conkle, 1963; Loo-Dinkins and Tauer, 1987; Haapanen, 1992; Pommerening and Gadow, 2000; Kint *et al*., 2004; Lombardi *et al*., 2015). However, there are also contrary findings, involving precision gains in larger plot areas due to various reasons and different traits that were investigated (e.g. Johnson and Hixon, 1952; Freese, 1960; Corona *et al*., 1998; Gray, 2003).

When exploring the influence of plot shape, in most cases, circular sample plots usually provide more accurate estimates. This result may be justified by the smaller ratio of the perimeter to the surface area for circular plots compared to square ones of equal size, and this difference increases with plot size. Consequently, the edge effect increases by reducing plot size, and also in square plots, more trees are excluded from the indices' calculations due to edge effect corrections (Pommerening, 2002). Special attention has been paid to minimizing edge effect errors. Although several methods have been developed (e.g. Monserud and Ek, 1974; Martin *et al.*, 1977; Donnelly, 1978) or tested (e.g. Radtke and Burkhart, 1998; Pommerening and Stoyan, 2006), no overall solution has been proposed to be applicable to all structural quantifications and plot shapes for stands with different structural patterns.

Finally, based on variogram analyses it can be concluded that observations at larger spatial resolutions are more similar than those at smaller scales (Arbia *et al.*, 1996; Král *et al.*, 2014), because the proportion of spatial components of variability increases with enlarging the sample plots and possible trends are then more visible (Bellehumeur *et al.*, 1997; Cohen *et al.*, 1990; Král *et al.*, 2014). On the other hand, semivariograms are computed either from discrete point data with a small range (10–100 m) for tree level variables, or from sample plots of various sizes with a larger range (150–300 m) for stand level measurements (Král *et al.*, 2014). As a result, since the structural indices (**IV**) present different attributes of a forest stand, it must be considered that for explaining the spatial variability, the one-hectare study area (RAMI) is quite small and also homogeneous. Consequently, the calculated indices for different sample plots in any location are correlated, showing small variances. However, regarding the algorithms of indices, they might be counted as tree level measures based on the tree's NNs, accounting for small-scale variations (Kint *et al.*, 2003).

For describing a stand by a specific index, the distribution of that index for individual reference trees within the stand is used. The effect of spatial autocorrelation is expected to decrease by combining multiple plots from entirely different stands, and consequently, the variation in estimates probably increases, and becomes larger than the results of the study **IV**. Therefore, for generalizing the outcomes of this study to other forest stands, a separate and careful assessment of the structural measures is necessary in broader scales to illustrate the spatial correlation in observations made at the sample locations.

7. CONCLUSIONS

The influence of tree competition on radial growth was explored in study **I** considering stand development stage, species identity and potential competitor selection methods. In addition to the traditional approaches of non-spatial and spatial competition indices, competition kernels representing a new promising concept were examined in study **II**. The analysis of stochastic and irregular tree mortality showed the important role of competition and stand structure attributes (**III**). Despite the challenges of mortality probability modelling, the final model for silver birch trees did produce satisfactory results for individual tree predictions. The effect of sample plot size and shape on the quantification of structural indices was examined in (**IV**). The choice of plot size and shape depends on the spatial distribution of trees and on the selected structural indices.

Based on the results of this thesis, the main conclusions are the following:

1. When comparing non-spatial and spatial competition in silver birch stands, spatial indices performed better than non-spatial ones, however the differences between the two types of competition indices were relatively small.
2. Despite the moderate superiority of exponential and fractional competition kernels for European beech and Norway spruce and the exponential kernel for Douglas fir, size-ratio competition indices can improve the diameter increment models with sufficient success.
3. Concerning the competitor selection methods, the best results were obtained from two methods: a) using a fixed radius of a zone of influence considering crowding, diameter and position of competitors relative to the subject tree (CZR_k) and the ratio of stand height (CZR_H) and, b) using a variable radius of the zone of influence and applying the competition elimination angle concept (RSC).
4. The flexible kernel approach used in this study was superior in modelling neighbourhood related tree competition

interactions than traditional indices; there was no need to define a zone of influence. An appropriate zone of influence should be separately defined for calculating the traditional spatial competition indices more accurately.

5. Employing Ellenberg's species-specific light values for quantifying tree competition showed only a minor improvement in young stands.
6. Diameter increment, relative diameter of a tree, species proportion of neighbouring trees within the zone of influence, and aggregation were appropriate explanatory variables in modelling the mortality probability of individual silver birch trees. Also the thinning measure improved the predictions of the model.
7. The growth and mortality of silver birch are affected by stand characteristics and competition interactions of neighbouring trees. Silver birch trees showed better growth and higher survival probability in neighbourhoods where trees were less clumped and neighbourhoods contained fewer silver birch trees.
8. The assessment of the effect of the size and shape of plots on the structural indices showed that circular and square sample plots have almost equal estimation accuracy. However, circular plots are preferable due to their smaller ratio of perimeter to surface area. Also, the optimum plot size depends on the stand attributes and structure, with an attempt to keep sample plots small enough to reduce the assessment efforts and costs.

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SUMMARY IN ESTONIAN

PUUDE KONKURENTSI- JA STRUKTUURIINDEKSITE ANALÜÜS ARUKASE (Betula pendula Roth) PUISTUTE MODELLEERIMISE EESMÄRGIL

Sissejuhatus

Puude ruumiline paiknemine ning puude suuruse, seisundi ja koosseisu varieerumise mustrid on puistu struktuuri olulised komponendid, mis mõjutavad otseselt metsaökosüsteemi toimimist, puude kasvu ja puistu tootlikkust. Puudevaheline konkurents ja puude suremine on metsaökosüsteemis tegurid, millel on märkimisväärne roll metsa struktuuri kujunemisel.

Puude kasvu ja elujõudu negatiivselt mõjutava stressi tegureid on mitu, stressi tulemusena võivad puud ka surra. Puude suremine võib olla: 1) tavapärane, puudevahelise konkurentsi ja puude vananemise tõttu ning; 2) erakorraline, erinevate ajalis-ruumiliselt toimivate biootiliste või abiootiliste häiringute tõttu, näiteks kahjurite või haiguste tulemusena. Puu vastupanuvõime stressile sõltub paljudest omavahel seotud näitajatest, nagu puu suurusest, tervislikust seisundist, puudevahelisest konkurentsist ja puistu tihedusest. Selleks et sihipäraselt majandada metsaökosüsteeme ja metsaökosüsteemi teenuseid, nt puidu tootmist, süsiniku sidumist, veerežiimi reguleerimist ja metsaelupaiku, on vajalik süvendada teadmisi puude suremisest, kuna see protsess on tihedalt seotud teiste ökosüsteemis toimuvate protsessidega, sh puistu uuenemisega, puudevahelise konkurentsiga ja puude kasvuga.

Naaberpuude vaheline konkurents on oluline puude suremuse põhjustaja, samuti on puudevaheline konkurents puistu dünaamika ja koosseisu tähtis mõjutaja ning ta vähendab omavahel konkureerivate puude ellujäämist, kasvu ja paljunemist. Puudevaheline konkurents reguleerib tugevasti allajäänud puude suremist eelkõige siis, kui mitu puud püüavad samal ajal kasutada piiratud kättesaadavusega ressursse. Puud reageerivad konkurentsile erinevalt: kui mõned surevad suhteliselt kiiresti, siis mõned muutuvad nõrgaks ja surevad hoopis teistel põhjustel palju aega hiljem.

Puistu struktuuri ja puudevahelise konkurentsi hindamiseks on metsanduses ja ökoloogias välja töötatud mitmu indeksit ja meetodit. Puistu struktuuri- ja konkurentsiindeksid on matemaatilised funktsioonid ja algoritmid, mis põhinevad puistu ja/või puu tasemel andmetel ja võivad arvestada või mitte arvestada puude omavahelist paiknemist. Selles doktoritöös uuritakse erinevaid meetodeid puudevahelise konkurentsi hindamiseks ja aktiivsete konkurentide kindlakstegemiseks arukase puistutes Eestis (I) ning kahes erinevas metsaökosüsteemis Euroopas ja ühes Põhja-Ameerikas (II). Selgitatakse ja iseloomustatakse puudevahelise konkurentsi ning puistu ja puude takseertunnuste mõju arukase kasvule (I) ja suremusele (III). Puistu struktuuriindeksite hindamine tehti ühe reaalse ja viie simulatsioonpuistu andmetel (IV), et tulemusi rakendada Eesti metsa kasvukäigu püsiproovitükkide võrgustikus (ENFRP).

Teoreetiline taust

Erinevate indeksite abil kirjeldatakse ja hinnatakse puistu struktuuri ja selle dünaamikat kahel viisil: mitte-ruumiliselt (naaberpuude kaugusest sõltumata) ja ruumiliselt (naaberpuude kaugusest sõltuvana). Mitte-ruumiline indeks on puistu ja puu enda tunnuste funktsioon ning seetõttu ei ole indeksi arvutamiseks vajalikud puu paiknemise koordinaadid. Seevastu aga ruumilise indeksi arvutamisel on vajalikud nii puu enda kui ka naaberpuude paiknemise koordinaadid. Ruumilise indeksi arvutamine põhineb n-ö lähimate naabrite kontseptsioonil, mis lähtub arusaamisest, et puu lähimad naabrid mõjutavad märgatavalt tema konkurentsiseisundit. Seetõttu on indeksi arvutamisel peale matemaatilise algoritmi väga tähtsad ka meetodid aktiivsete konkurentide väljaselgitamiseks ja proovialade servaefekti korrigeerimiseks prooviala välise serva läheduses paiknevate puude korral.

Puistu struktuuri kirjeldamisel kasutatakse mitmesuguseid indekseid ja tunnuseid. Need võivad olla puistu või puu tasemel, mitte-ruumilised või ruumilised ning arvestada üht või mitut lähimat naaberpuud, et näidata puistu seisundit kas ühe kindla väärtusena, mis arvestab kõikide puude omavahelisi seoseid, või funktsioonina, mis kirjeldab puude seisundit üksikpuude kaupa. Puude suremust kui olulist metsa dünaamika ja puistu struktuuri kujundajat uuritakse paljude omavahel seotud tegurite koosmõjus. Puude suremuse mudelites on need tegurid esitatud puude ellujäämisvõime tunnustena, nt puu suurus ja juurdekasv, või puude suremusele kaasaaitajatena, nt puudevaheline konkurents. Üksikpuude tasemel on kasutusel mitu erinevat tunnust, et kvantitatiivselt hinnata puudevahelist konkurentsi nii mitte-ruumiliste kui ka ruumiliste indeksite abil. Omaette lähenemisviis on konkurentsituumade meetod, mida on arendatud konkurentsi uurimiseks viimase kolmekümne aasta jooksul. Konkurentsituumad kuuluvad nn vastastikuse mõju tuumade funktsioonide rühma, mis kirjeldavad bioloogiliste protsesside (nagu kasv, ellujäämus, paljunemine) sõltumist üksikisendi puhul tema enda suurusest ning kaugusest teistest isenditest ning nende suurusest.

Metsaökosüsteemide koosseisu ja struktuuri, kasvu ja suremuse loomulikku dünaamikat saab kirjeldada kvantitatiivselt matemaatilise modelleerimise vahenditega. Metsade dünaamika ja struktuuri kirjeldamise kvantitatiivsed meetodid mõjutavad olulisel määral inimeste arusaamist metsaökosüsteemide toimimisest. Erinevate indeksite ja tunnuste väljavalimine puistu struktuuri ja dünaamika kirjeldamiseks on seetõttu väga tähtis ning seoste paremaks mõistmiseks tuleb erilise tähelepanuga suhtuda konkreetsete indeksite iseärasustesse ja kasutamisse. Arvestades ruumiliste mustrite mitmekesisuse tähtsust puistute struktuuri keerukuse seisukohast erinevates mõõtkavades ja proovialade suuruse mõju, tuleb andmete kogumisel kasutada sobivaid inventeerimise meetodeid, et saada optimaalsete kulutustega sobiva täpsusastmega andmed.

Materjal ja meetodid

ENFRP andmeid kasutati uurimustes I ja III. ENFRP sisaldab andmeid Eestis esindatumatest metsatüüpidest ja proovialad on paigutatud üle kogu riigi. Eesmärkidest lähtudes kasutati erinevates uuringutes erinevaid proovialade valimeid. Kuna uuringu fookuses oli arukask, siis üldise reeglina pidi valimis olevatel proovialadel esinema arukaske. Uurimuses I oli valiku põhitingimus, et prooviala oleks mõõdetud vähemalt kaks korda ning uurimuses III oli tingimus, et prooviala oleks mõõdetud järjestikuselt vähemalt kolm korda.

Uurimuses II kasutati kolme puhtpuistu andmeid, mis esindasid kasvutingimuste laia spektrit, et uurida konkurentsituumade meetodi efektiivsust üksikpuude diameetri kasvu prognoosimisel. Uurimuses IV kasutati ühe hektari suurust kaardistatud puudega arukase enamusega reaalset puistut (57% puudest olid arukased) ja viit selle puistu andmete põhjal genereeritud virtuaalset puistut (puude paiknemine oli kahel juhul regulaarse paigutusega, ühel juhul mõõduka kobarpaigutusega, ühel juhul äärmusliku kobarpaigutusega ja ühel juhul juhusliku paigutusega), et uurida struktuuriindekseid ning prooviala suuruse ja kuju mõju struktuuriindeksite väärtustele ja varieeruvusele.

Erinevaid mitteruumilisi ja ruumilisi indekseid ning tunnuseid mõõdeti, arvutati ja kasutati vastavates mudelites, et testida konkurentsiindekseid diameetri kasvu kirjeldamiseks lineaarses mitmese regressiooni mudelis ja lineaarses segamudelis ning puude suremuse tunnuseid ja harvendusraie näitajat binaarse suremuse andmestikul üldise lineaarse segaefektidega logistilise regressiooni abil. Puistu struktuuri analüüs ja struktuuriindeksite arvutamine toimus korduvana proovialade moodustamise teel (iga prooviala suuruse ja kuju kohta 1000 prooviala) kõigis uuritavates puistutes juhuslikesse kohtadesse pindalaga 0,007 kuni 0,636 ha. Puudevahelise konkurentsi hindamisel valiti aktiivsed konkurendid mitmel erineval meetodil, et tulemusi omavahel võrrelda. Servaefekti korrigeerimisega püüti vältida proovialalt välja jäävate naaberpuude tõttu tekkivat hinnangute süstemaatilist nihet. Kasutati mitut statistilist meetodit, et hinnata tunnuste erinevate võimalike kombinatsioonide efektiivsust ning autokorrelatsiooni ja multikollineaarsuse esinemist tunnuste vahel. Mudelite lõplikku sobivust ja valitud tunnuseid võrreldi hindamiskriteeriumitega, mis olid rakendatavad neile mudelitele ja tunnustele.

Tulemused

Lõplikuks kasvumudeliks oli lineaarne segamudel, kusjuures mudeli koostamisel arvestati kindlakstehtud autokorrelatsioonidega. Puudevahelise konkurentsi analüüs näitas, et ruumilised konkurentsiindeksid suurendavad kasvumudelite prognoosivõimet rohkem kui mitte-ruumilised indeksid. Prognoosivõime suurenemine osutus olulisemaks noortes puistutes ja siis, kui indeksite arvutamisel anti erinevatele puuliikidele kaalud Ellenbergi valgusnõudlikkuse indikaatorväärtuste järgi. Aktiivsete konkurentide väljaselgitamise meetodite testimisel selgus, et parimaks osutus puistu tunnustest arvutatud puud ümbritseva aktiivse konkurentsi tsoon ning selles tsoonis kindlakstehtud aktiivselt konkureerivad naaberpuud ning nende suurusest ja kaugusest arvutatud konkurentsiindeks (I). Konkurentsituumade meetod näitas veidi paremaid tulemusi puudevahelise konkurentsi hindamisel kui klassikalised konkurentsiindeksid, konkurentsi signaali kõveraid mõjutasid puuliik, puu suurus ja konkurentsituuma tüüp (II).

Arukase viie aasta puude suremuse määr oli 9,67% ja see määr vähenes 16,67%, kui arukase naabriteks olid vaid arukased, kuni 6,09%, kui arukase naabriteks olid vaid teistesse liikidesse kuuluvad puud. Ruumiliste tunnustega logistiline puude suremuse mudel oli parema prognoosivõimega kui ilma ruumiliste tunnusteta mudel. Samuti parandas puude suremuse mudelit harvendusraie esinemise binaarse tunnuse lisamine ja parim mudel näitas, et arukase ellujäämistõenäosus suureneb harvendusraie tulemusena märgatavalt, kuna sellega väheneb olulisel määral puudevaheline konkurents. Saadud mudeli prognoositäpsus on märkimisväärne, kuna enamiku tegelikult surnud puudest osutusid korrektselt klassifitseerituks (III). Puude kasvu ja suremuse mudelite tunnuste kõigi kombinatsioonide puhul ei tuvastatud multikollineaarsuse probleemi.

Hinnates prooviala suuruse ja kuju mõju puistu struktuurindeksite väärtustele, selgus, et struktuurinäitajate varieeruvus vähenes asümptootiliselt prooviala suurenedes ja ringikujulised proovialad osutusid paremaks kui ruudukujulised. Samuti oli prooviala suurusel mõju struktuurinäitajate ruumilisele varieeruvusele, väiksematel proovialadel oli olulisem ruumiline trend ning suurematel proovialadel ilmnes puistu struktuurinäitajate mõningane ruumiline autokorrelatsioon (IV).

Arutelu ja järeldused

Arukase kasv ja suremus on mõjustatud puistu takseernäitajatest ja konkurentsist naaberpuudega. Arukasel oli suurem diameetri kasv ja ellujäämistõenäosus siis, kui tema naaberpuud paiknesid regulaarsemalt ja naaberpuude seas oli vähem arukaski.

Mitte-ruumiliste ja ruumiliste konkurentsiindeksite võrdlus näitas puude kasvu prognoosimisel ruumiliste indeksite paremust, kuid saadud erinevus oli väike. Kuna ruumilised indeksid sõltuvad puude andmetest ja paiknemisest ning sellise informatsiooni kogumine on kallis ja aeganõudev, siis tuleks ruumilisi indekseid eelistada vaid siis, kui kirjeldatakse konkurentsi looduslikes tingimustes noortes, sageli tihedates puistutes, kuna ruumilised indeksid annavad suurema kaalu subjektpuu suhtes lähemal olevatele naaberpuudele.

Võrreldes mitte-ruumiliste ja ruumiliste konkurentsiindeksite klassikalist lähenemist konkurentsituumade meetodiga, selgus, et konkurentsituumade meetodil saadakse puudevahelise konkurentsi hindamisel veidi paremad tulemused. Klassikaliste konkurentsiindeksite eeliseks on aga arvutusalgoritmide lihtsus ning nende jätkuv kasutamine puistute kasvu modelleerimisel aitab prognoositäpsust suurendada. Puu lokaalne ümbrus on kindlasti ala, kus puudevaheline konkurents aktiivselt toimib. Paindlik konkurentsituumade meetod võimaldas kirjeldada paremini neid keerulisi puudevahelisi suhteid, kusjuures klassikalised ruumilised konkurentsiindeksid vajasid eraldi igale puule aktiivse konkurentsi tsooni määramist.

Puude loomulik suremus on stohhastiline ja ebaregulaarne fenomen, mille uurimise eesmärk oli leida suremust kirjeldavad sobivaimad tunnused. Sõltumata puude suremuse modelleerimise keerukusest, annab väljatöötatud arukase suremuse mudel rahuldavaid tulemusi puude individuaalse suremistõenäosuse hindamisel. Hooldusraie tunnuse lisamine mudelisse parandas mudeli prognoosivõimet, hooldusraie järel on puude suremistõenäosus palju väiksem kui hooldusraieta puistus. Hooldusraie vähendab puistu tihedust ja seetõttu on valgusnõudlikul arukasel rohkem kasvuruumi, kuid raie tulemusena võib allesjäävatel puudel esineda kahjustusi, mis kõik mõjutavad nende suremistõenäosust.

Proovialade suuruse ja kuju mõju hindamine struktuuriindeksite väärtusele näitas, et ringikujulised ja ruudukujulised proovialad annavad suhteliselt sarnase headusega hinnangu. Samas on ringikujulised proovialad eelistatumad, kuna nende ümbermõõdu ja pindala suhe on väiksem kui ruudukujulistel proovialadel. Prooviala optimaalne suurus sõltub konkreetse puistu takseernäitajatest ja struktuurist, et piisavalt suurel alal tunnuste varieeruvus ära kirjeldada, kusjuures inventeerimise kulukuse ja ajakulu aspektist tuleks proovialad valida võimalikult väikese suurusega.

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I

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RESEARCH ARTICLE

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Analysis of Individual Tree Competition Effect on Diameter Growth of Silver Birch in Estonia

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Abstract

Aim of study: The present study evaluates a set of competition indices including spatially explicit indices combined with different competitor selection approaches and non-spatially explicit competition indices. The aim was to quantify and describe the neighbouring effects on the tree diameter growth of silver birch trees.

Area of study: Region throughout Estonia.

Material and methods: Data from the Estonian Network of Forest Research Plots was used. After quantifying the selected indices, the best non-spatial indices and spatial indices (combined with neighbour selection methods) were separately devised into a growth model as a predictor variable to assess the ability of the diameter growth model before and after adding competition measures. To test the species-specific effect on the competition level, the superior indices were recalculated using Ellenberg's light indicators and incorporated into the diameter growth model.

Main results: Statistical analyses showed that the diameter growth is a function of neighbourhood interactions and spatial indices were better growth predictors than non-spatial indices. In addition, the best selections of competitive neighbours were acquired based on the influence zone and the competition elimination angle concepts, and using Ellenberg's light values had no significant improvement in quantifying the competition effects.

Research highlights: Although the best ranking spatial competition measures were superior to the best non-spatial indices, the differences were negligible.

Keywords: Competition indices; zone of influence; stem diameter increment; *Betula pendula* Roth.

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Introduction

Competition among individual trees is a fundamental ecological process that plays a major role in population dynamics, survival, growth and species replacement (Peet & Christensen, 1987). By definition, competition is ‘‘an interaction between the individuals, leading to a reduction in the survival, growth and reproduction of the competing individuals” (Begon et *al*., 1996). Several case studies have been conducted in ecology and forestry to develop, improve or modify different competition indices (*CI*s). Such indices quantify the competition level for an individual tree and are classified into two major groups of non-spatially explicit indices (e.g. Biging & Dobbertin (1995) and Schröder & Gadow (1999)) and spatially explicit indices (e.g. Hegyi (1974) and Alemdag (1978)). Non-spatial indices are functions of stand level variables, or of the initial dimensions of the trees, and therefore do not require the trees coordinates. Whenever spatial indices are used to measure the influence of local neighbours on a central tree (the subject tree), the dimensions and the relative location of neighbour trees are required for the computation (Tomé & Burkhart, 1989; Corral Rivas *et al*., 2005).

For several species and forest conditions, the effectiveness of different *CI*s on tree diameter or basal area growth has been examined (Munro, 1974; Martin & Ek, 1984; Pukkala & Kolström, 1987; Holmes & Reed, 1991; Contreras *et al*., 2011). Since several aspects of stand density and neighbour sizes influence the tree growth, non-spatial *CI*s with simple structures are parsimonious to quantify the competitive status of trees in each stand. On the other hand, as ecology is spatial (Berger & Hildenbrandt, 2000), therefore by increasing the interval distance, the negative interaction of neighbours will decrease and spatial *CI*s take the explicit description of tree spacing into account. Additionally the identity of neighbouring species is an important factor in the characterization of their competitive effect (Bella, 1971; Zhao *et al*., 2006). Competition can occur among *conspecific* individuals, plants of same species, and *hetero-specific* individuals, plants of different species, termed *intraspecific* and *interspecific* competition, respectively. The competition behaviour of different species can be differentiated by using Ellenberg *et al*.'s system (1991). It is the most widely used indicator species system, which compares the response of different species to edaphic and climatic parameters, such as light, temperature, moisture and nitrogen at a 9-point scale for each.

To investigate the effect of competition on the diameter growth of trees, we focused our study on silver birch *(Betula pendula* Roth*)*. Silver birch occurs naturally in northern temperate and boreal forests and it is an essential ecological and commercial broadleaved tree species (Hynynen *et al*., 2010). As a pioneer tree species (Fischer *et al*., 2002), birch is light demanding, and if it grows as a dominant tree with low competitive effects of neighbours, in a stand with relatively wide spacing, birch maintains its vitality and vigorous growth (Hynynen *et al*., 2010). In Estonia, birch is the second most abundant tree species in terms of forest cover (31.2%) and the coverage is expanding (Yearbook of Forest, 2013). A few attempts have been made to study birch growth related to the negative interaction of tree competitive status in stands (Jõgiste, 1998; Prévosto *et al*., 1999; Andreassen & Tomter, 2003; Damgaard & Weiner, 2008; Kaitaniemi & Lintunen, 2010).

The main objective of this study was to investigate the adequacy of different spatial and non-spatial *CI*s to explain single-tree silver birch diameter growth in Estonia. Further objectives were to find the best competitor selection method for Estonian birch stands and evaluate the differences in competitive ability of different species by employing Ellenberg's species-specific light indicator values. Specifically, we hypothesized that (i) the *CI*s contribute to explain diameter increments in silver birch; (ii) spatial indices perform better than non-spatial indices; (iii) selecting the potential competitors based on the concept of the influence zone is superior to variable competition zone radii; and (iv) considering the species-specific competition improves the ability of spatial indices to account for growth variability.

Materials and methods

Study data

The study was carried out in Estonia, which lies on the eastern shores of the Baltic Sea across the Finnish gulf (lat. 57.3°-59.5° N, long. 21.5°-28.1° E). Average temperatures range from 16.3°C to 18.1°C in July and from -3.5°C to -7.6°C in February. Average annual precipitation increases from west to east within a range of 600-700 mm. In this study, data from the Estonian network of forest research plots (ENFRP) was used. ENFRP was established during the period 1995–2004 and covers Estonia entirely (Kiviste & Hordo, 2002). The permanent plots were circular with a radius of 10, 15, 20, 25 or 30 m depending on the stand age and density and as a rule, every plot had at least 100 trees in the overstory. For the current study, we benefit the data from 121 silver birch dominated research plots (where more than 65% of the number of trees were birches) consisting of 16,186 trees with 5-year measurement intervals.

Within each plot the azimuth, the distance from plot centre, the diameter at breast height (*d),* and the defects of each tree were assessed. For every fifth tree, and for dominant and rare tree species, the tree height and the height to the live crown base were also measured. Since the height records of all trees were required for some calculations, based on the height-diameter model developed by Kiviste *et al*. (2003), all unmeasured tree heights were estimated.

Species composition of all trees within the studied plots was 67% silver birch, 24% Norway spruce and 9% of several other species (see Table 4). Plots were established in managed and even-aged forests, and if there was a thinning operation in the time period between the plot measurements, they were excluded. Table 1 summarizes main stand variables of study plots and Fig.1 shows the dynamics of average height, basal area, and quadratic mean diameter.

Table 1. Main characterization of the birch dominated permanent plots*

	A	N	d_g	id_5	h	SI_{100}	BA
Minimum	18	223	3.80	0.00	5.60	15.28	3.40
Mean	34	2378	11.88	1.34	14.38	25.76	18.16
Maximum	90	5471	36.00	6.90	32.50	34.10	36.60
Standard deviation	13.80	1465	5.70	0.77	5.61	4.09	5.84

* *A*, stand age (year); *N*, the number of trees per hectare; d_g, the quadratic mean diameter at breast height of trees (cm); i_{d5}, the 5-year tree diameter increment (cm); h, average stand height (m); SI_{100}, site index at reference age 100 years (m); *BA*, stand basal area (m^2ha^{-1}).

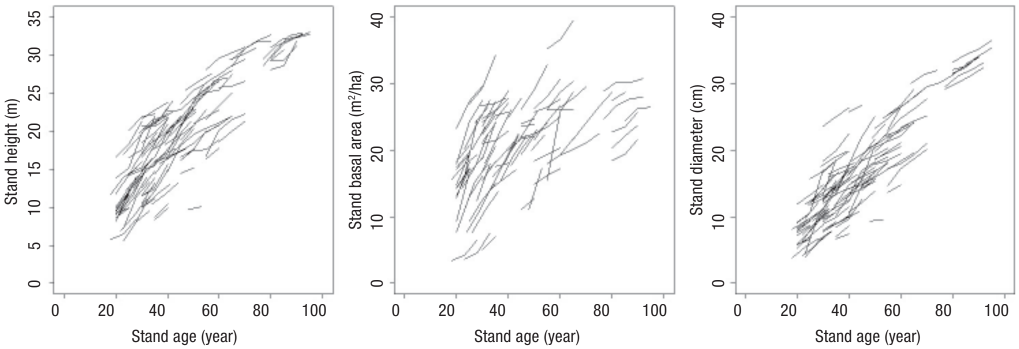

Figure 1. The dynamics of average height (left), basal area (middle), and quadratic mean diameter (right).

Competition indices

The competition for each subject tree was quantified using 18 different *CI*s, consisting of 7 non-spatial and 11 spatial indices (Table 2). The indices described below were selected from the literature, taking into consideration the available tree variables for this study, and their simplicity to describe the competition situation of a tree, as it is difficult to understand the statistical qualities of an index with the combination of several primary variables (Weiglet & Jolliffe, 2003).

The first seven indices in Table 2 are non-spatial indices. In a plot, $BA\text{-}g_j$ *CI* proposed by Steneker & Jarvis (1963), is the sum of the basal area (*g*) of the neighbouring trees *j* for a subject tree *i* (m^2 ha^{-1}); *BAL* presented by Wykoff *et al*. (1982) is the sum of the basal area of trees larger than the subject tree (m^2 ha^{-1}). *Sdr* sums up the *d* of neighbours divided by the subject tree *d* in the plot (ha^{-1}). The index dr_g calculates the ratio of the diameter of the subject tree to the quadratic mean diameter of the plot (Hamilton, 1986) and *BAr* is another form of *Sdr* that considers *g* instead *d*. The index *BALr* is the ratio of *BAL* to the cumulative basal area of the plot (Vanclay, 1991) and finally *BALMOD* (Schröder & Gadow, 1999) modifies *BALr* by dividing it into the relative spacing index as following:

$$RS = \frac{\sqrt{S/N}}{H_{Dom}} \quad (1)$$

where *S* is plot area (m^2), *N* is the number of trees on plot, and H_{Dom} is the stand dominant height (m) (mean height of hundred thickest trees per hectare (Assmann, 1970)).

The next three competition indices *Sl, SOr* and *SOdr* in Table 2 are so-called influence-zone overlap indices, which assume that a horizontal circle surrounding the subject tree can represent the active competition area, and that competition occurs where neighbouring trees overlap their influence zone with the subject tree's influence zone. The radius of these circles is thought to be equal to the expected growing space of open-grown trees, and usually is a function of tree size (Corral Rivas *et al*., 2005).

Finally, the last eight indices in Table 2 are size-ratio spatial *CI*s. The idea of this type of indices was derived from the hypothesis that competition effect has positive relationship with the size of neighbouring trees and negative relationship with their distance from the subject tree (Tomé & Burkhart, 1989). For spatial indices of *Heg* (Hegyi, 1974), *Almdg* (Alemdag, 1978), *Sdrl1* (Lorimer, 1983), *Sdrl2* (Martin & Ek, 1984), and *SBAr* (Daniels *et al*., 1986) the diameter at breast height performs as a tree size indicator. *SAng1* (Lin, 1974) is the sum of horizontal angles. Since the average elevation angle of the brightest region of the sky over the growth season can be approximated by angle of 45° (Stadt & Lieffers, 2000), the 45° gauge was employed for this index. The index *SAng2* sums up the horizontal angles originating from the subject tree centre and spanning the diameter of each competitor (Rouvinen & Kuuluvainen, 1977), and *SdrAng* calculates the sum of the horizontal angles multiplied by the ratios of the diameter of the competitors and the subject trees (Fig. 2).

Methods of competitor identification (*SM*)

As well as the mathematical formulation, the value of a competition index depends on the method used to

Table 2. The list of competition indices tested to use in the tree diameter growth model*

Index	Sources	Equations
Non-spatially explicit indices		
$BA\text{-}g_j$	Steneker & Jarvis (1963)	$\sum_{j\neq i}^{n}\left(g_j\right)\Big/S$
BAL	Wykoff *et al*. (1982)	$\sum_{d_i<d_j}^{n}\left(g_j\right)\Big/S$
Sdr	Lorimer (1983)	$\left(\left(\sum_{j\neq i}^{n}d_j\right)\Big/d_i\right)\Big/S$
dr_g	Hamilton (1986)	d_i/d_g
BAr	Corrona & Ferrara (1989)	$\left(\left(\sum_{j\neq i}^{n}g_j\right)\Big/g_i\right)\Big/S$
BALr	Vanclay (1991)	$\sum_{j\neq i}^{n}\left(g_{j;dj>d_i}\right)\Big/G$
BALMOD	Schröder & Gadow (1999)	$\left[\left(\sum_{d_i<d_j}^{n}\left(g_j\right)\Big/G\right)\right]\Big/RS$
Spatially explicit indices		
Sl	Staebler (1951)	$\sum_{j\neq i}^{n}l_{ij}$
SOr	Gerrard (1969)	$\sum_{j\neq i}^{n}\left(O_{ij}/CZ\right)$
SOdr	Bella (1971)	$\sum_{j\neq i}^{n}\left(\left(O_{ij}\cdot d_j\right)/\left(CZ\cdot d_i\right)\right)$
SBAr	Daniels et al. (1986)	$\left(\left(d_i^2\cdot N_c\right)\Big/\sum_{j\neq i}^{n}d_j^2\right)$
Heg	Hegyi (1974)	$\sum_{j\neq i}^{n}\left(d_j/\left(d_i\cdot l_{ij}\right)\right)$
SAng1	Lin (1974)	$2\sum_{j\neq i}^{n}\arctan\left(d_j/2l_{ij}\right)$
SAng2	Rouvinen & Kuuluvainen (1977)	$\sum_{j\neq i}^{n}\arctan\left(d_j/l_{ij}\right)$
SdrAng	Rouvinen & Kuuluvainen (1977)	$\sum_{j\neq i}^{n}\left(\left(d_j/d_i\right)\cdot\arctan\left(d_j/l_{ij}\right)\right)$
Almdg	Alemdag (1978)	$\sum_{j\neq i}^{n}\left\{\pi\left[\left(l_{ij}\cdot d_i\right)/\left(d_i+d_j\right)\right]^2\left(d_j/l_{ij}\right)\Big/\sum\left(d_j/l_{ij}\right)\right\}$
Sdrl1	Lorimer (1983)	$\sum_{j\neq i}^{n}\left(\left(d_j/d_i\right)\Big/\sqrt{l_{ij}/CZR}\right)$
Sdrl2	Martin & Ek (1984)	$\sum_{j\neq i}^{n}\left(d_j/d_i\right)\cdot\exp\left(\left(16\cdot l_{ij}\right)/\left(d_i+d_j\right)\right)$

*N_c, number of competitor trees; d_i, subject tree *d* (cm); d_j, competitor tree *d* (cm); d_g, basal area weighted plot diameter (cm); l_{ij}, distance between the competitor *j* and the subject tree *i* (m); *G*, basal area of the trees within the plot (m^{2}ha^{-1}); g_i, basal area of subject tree *i* (m^{2}ha^{-1}); g_j, basal area of competitor tree *j* (m^{2}ha^{-1}); *CZR*, the radius of influence zone (m); *RS*, relative spacing index of plot; O_{ij}, crown overlap between the neighbour tree *j* and the subject tree *i* (m^2); *CZ*, the area of influence zone (m^2); *S*, plot area (ha).

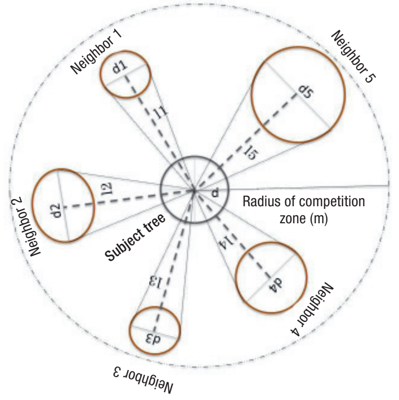

Figure 2. Schematic of the horizontal angles originating from the subject tree centre and spanning the diameter (at breast height) of each competitor tree within the competition zone used to calculate indices *Sang2* & *SdrAng; *dx* is the diameter at breast height (cm), *lx* is the distance between the subject tree and its competitors (m).

define competitors for the subject tree (Bigging & Dobbertin, 1992). Among different proposed methods to choose the potential competitors, we tested four approaches. The first two approaches, approaches 1 and 2, were based on the concept of an influence-zone that assumes an imaginary circle whose centre is constituted by the subject tree (Staebler, 1951) and trees inside this circle are competitors. The last two approaches, approaches 3 and 4, identified competitors based on variable competition zone radii, often weighted by dimensions of the subject tree and its neighbours (Daniels, 1976; Ford & Diggle, 1981):

1. The radius of influence zone was defined as a fraction of the stand's average height for each plot; $CZR_{0.4h}$ was set equal to 0.4 average height of plot (Sims *et al*., 2009).
2. Based on Lee & Gadow (1997) the influence zone radius was calculated using the following equations:

   $$CZR_k = k \cdot \sqrt{\frac{10000}{N}} \qquad (2)$$

   where CZR_k is dynamic radius, N is the number of trees per hectare, and k is a constant number. The function $\sqrt{\frac{10000}{N}}$ calculates average distance between the neighbours. The values of k equal to two (CZR_{k2}) and three (CZR_{k3}) multiply this distance by two and three, respectively to define *CZR*. Within the influence zone, trees were considered to be active competitors if $d_j \geq 0.3 d_i$ (where d_j is d of competitor and d_i is the d of subject tree) and they were beyond the crown projection of other competing trees, considering a competition elimination angle of 30° (*CEA*=30°).
3. The *Bitterlich method* (1952) was used to identify the competitors in variable plot radii samplings. BAF_1, BAF_2 and BAF_4 tested three basal area factors (*BAF*) equal to 1, 2 and 4 $m^2 ha^{-1}$, respectively. A tree was considered a competitor if its distance to the subject tree was:

   $$l_{ij} \leq d_i \cdot \sqrt{\frac{50}{BAF}} \qquad (3)$$

   where l_{ij} is the distance between the subject tree i and the neighbouring tree j and d_i is the diameter of the subject tree. The values of *BAF* equal to 1, 2 and 4 correspond to the opening angles of β=1.15°, 1.62° and 2.30°, respectively. Therefore, when the *BAF* values and boundary angles increase, fewer trees meet the criteria for being considered as competitors (Lorimer, 1983; Tomé & Burkhart, 1989).
4. Finally, the *reserved search-cone method* (Pretzsch, 2009) or angular height method (Richards *et al.,* 2008) applied height angle from the base of the subject tree to identify the competing neighbours. For a search-cone opening angle β, set up at the stem base of the subject tree, competitors are neighbouring trees whose heights are greater than a critical distance, determined as the following:

$$l_{ij} < \frac{h_i}{\tan(90\text{-}\beta/2\ )} \qquad (4)$$

where l_{ij} is the distance between the subject tree and the competitor tree, and h_i is the subject tree height. If the apex of the reversed search-cone is at the crown base height of the subject tree (cbh_j) then a neighbouring tree with height h_j is a competitor when:

$$l_{ij} < \frac{h_i - cbh_i}{\tan(90 - \beta/2)} \qquad (5)$$

We tested the opening angle β equal to 100°, 80°, and 60°, respectively where the apex was set up either at the stem base (SCH_{100}, SCH_{80} and SCH_{60}) or at the crown base height ($SCHCr_{100}$, $SCHCr_{80}$ and $SCHCr_{60}$).

In all the above-mentioned methods, in order to avoid the interference from the competitive effects of non-measured trees beyond the plot borders, we computed *CI*s only for interior trees on each plot where the neighbours' information was available for them. After determining the competitors, we calculated the spatially explicit *CI*s for each subject tree. Four spatially explicit *CI*s (*Sl*, *SOr*, *SOdr,* and *Sdrl1*) were based on the influence zone concept and only the first two approaches of competitor selection ($CZR_{0.4h}$ and CZR_k) were applicable to quantify the mentioned indices. Moreover, the allometric crown radius model, (developed by Lang *et al*., 2007) was used to calculate the crown radius that was required for quantifying indices *SOr* and *SOdr* as well as fitting the Eqs. (7) and (8):

$$R_{cr} = 0.5\left[a_1 d + \frac{a_2 d}{h}\right] \tag{6}$$

where R_{cr} is the crown radius (m), d and h are the diameter at breast height (cm) and the total height of the tree (m) respectively, and a_1 and a_2 are estimation parameters (Table 3).

Table 3. The values of parameters for the used allometric crown model for main tree species

Species	Parameters	
	a_1	a_2
Pinus sylvestris	0.1060	0.6150
Picea abies	0.0830	1.0620
Betula sp.	0.1340	0.9460
Populous termula	0.1370	0.8940
Alnus incana	0.0223	1.1700
Alnus glutinosa	0.1340	1.2300

Statistical and comparative analyses of competition indices

Preliminary analysis was carried out to pre-select adequate *CI* candidates to include in our growth model. As suggested by Pedersen *et al*. (2013) we applied the Spearman rank correlation (Spearman's *rho*) to characterize the relationship between the 5-year tree diameter increment (i_{d5}) and the competition indices. The Spearman correlation is able to consider potential nonlinear trends frequently seen in growth and competition studies, besides it is valid for the data size larger than 10 (Siegel, 1956) which was applicable to our data. The existence of a pairwise relationship between i_{d5} and *CI*s was proved using the *t-test*. Based on the Spearman rank correlation results, the four best *CI*s (two non-spatial and two spatial *CI*s) were selected for further analyses.

Then, we constructed a linear multiple regression model (Wimberly & Bare, 1996; Jõgiste, 2010) between i_{d5} (cm) and some predictor variables that influence diameter growth. In a preliminary assessment, *non-linear extra sum of square method* (Bates & Watts, 1988) was applied to evaluate the effect of plots on growth. For this purpose, we considered the simple model of diameter growth as a function of tree diameter. In order to differentiate the study plots, we introduced dummy variables to the defined simple model. Then, we compared the two mentioned models using *F-test* and a significant effect of plots was detected (F=8.56; P<0.0001). Therefore, predictor variables presenting the initial stand status were also included in the growth models (Eqs. (7) and (8)). Additionally, for each combination of selected variables, the variance inflation factors (VIF) were calculated to certify that our multiple models were not influenced by multicollinearity amongst explanatory variables. We only implemented the combination of variables with VIFs<10 (Soares & Tomé, 2001; Corral Rivas *et al*., 2005). Eventually, the growth model was fitted by improvising some initial stand variables along with the tree variables.

$$\left[\left(\sum_{d_i<d_j}^{n}\left(g_j\right)\Big/G\right)\right]\Big/RS \tag{7}$$

In order to evaluate the efficiency of the chosen *CI*s to improve the prediction ability of growth function, the numerical value of each of those indices, two non-spatial *CI*s and two spatial *CI*s, was independently added to the previous growth function:

$$\begin{gathered} i_{d5} = b_0 + b_1(d) + b_2(cr) + b_3(RS) + \\ b_4(dr) + b_5(SI_{100}) + b_6(CI) \end{gathered} \tag{8}$$

where b_k are coefficients to be estimated, i_{d5} is the 5-year tree diameter increment (cm), d is the subject tree diameter at breast height (cm) that integrates the past competitive interactions (Soares & Tomé, 1999), cr is the ratio between the crown width and the tree height that depicts the vigour of trees of similar size (Schröder *et al*., 2002). The relative diameter dr is the ratio between the subject tree diameter and the quadratic mean diameter of the stand that represents the dominance of the subject tree in relation to other trees in the stand, RS is the stand relative spacing, and SI_{100} is the stand site index. Nilson (2005) model was used to estimate the average height of the stands at reference age 100 years (m) and *CI* is the competition measure for the subject tree. *R* statistical software version 3.1.2 (*R* Development Core Team, 2014) was employed to carry out all the required analyses for this research.

Before proceeding with the subsequent analyses, the existence of any correlation among residuals was explored. For this purpose, the growth model was fit using the *lme* function from the *nlme* package in *R* as following:

$$i_{d5} = X\beta + Zu + \varepsilon \tag{9}$$

For the recent linear mixed effect model, i_{d5} is the dependant variable; *b* is a vector of fixed effects consisting of the same explanatory variables of Eq. (7); *u* is a vector of random effects including tree, plot, and growth interval (measurements); *e* is a vector of random errors; *X* and *Z* are design matrices relating the 5-year diameter growth to fixed and effect random effects, respectively. The previous and recent models were compared in terms of *AIC* (Akaike's Information Criterion) where $\Delta AIC = AIC_{\text{multiple model}} - AIC_{\text{mixed model}}$. In addition, to ensure that there was not any remaining within-group correlation, the recent model was checked with an auto-regressive structure (*AR1*). The mixed effect models, those with and without auto-regressive structures, were compared using *ANOVA* (analysis of variances).

The relative quality of growth functions, with and without *CI*s, were estimated using R^2 (Adjusted-R^2), the root mean square error (*RMSE*, calculated using the *rmse* function for the model residuals in *R*), *AIC* and Akaike weights (AIC_w). The probability that model is the best with the lowest expected information loss is illustrated by the smallest value of *AIC* and the biggest AIC_w (Wagenmakers & Farrell, 2004). Additionally, the performance and the contribution of each *CI* to the growth model were assessed with the mean square error reduction (*MSER*).

$$MSER = 100\left(1 - \frac{MSE_8}{MSE_7}\right) \tag{10}$$

where MSE_7 and MSE_8 are the mean square errors of models 7 and 8, respectively.

Finally, the efficiency of *CI*s in different stand stages and the contribution of different species in the competition load of a subject tree were evaluated. Stand development stages were defined by the age of the silver birch, as the dominant tree species. First, to differentiate the effect of different neighbouring species on competition, tree diameters were weighted differently. For that purpose, tree diameters were multiplied by their corresponding Ellenberg's species-specific light transmission coefficients (Ellenberg *et al.*, 1991) from one (plants in deep shade) to nine (plants in full light); then, the selected spatial *CI*s were recalculated using the new weighted diameters. Table 4 provides the Ellenberg's light values for more frequent tree species in Estonia. Finally, subject trees were divided into three subdivisions of young (<35 years), middle-aged (35-69 years) and old stands (≥70 years). For each age group, the regression analyses for the selected *CI*s and tree diameter growth were repeated separately.

Table 4. The Ellenberg's species-specific light coefficients for more frequent tree species in Estonia

Species	Ellenberg's values
Fraxinus excelsior, *Acer platanoides*, *Ulmus glabra*	4
Alnus glutinosa, *Tilia cordata, Picea abies, Salix fragilis*	5
Populus tremula, *Alnus incana*, *Sorbus aucuparia*	6
Betula pendual, *Pinus sylvestris, Quercus robur*	7
Juniperus communis	8

Results

In Table 5 the Spearman's rank correlation coefficients between the tree diameter growth and non-spatial *CI*s and also the combination of spatially explicit *CI*s and the competitor selection methods are presented. Table 5 shows that the competitor selecting approaches significantly affect the growth prediction ability of spatial indices and the competition selection methods of CZR_{k3}, $CZR_{0.4h}$ and SCH_{60} demonstrated greater values of Spearman's *rho*, respectively. Among different spatial indices in these three neighbours selecting methods, *SdrAng* and *Heg* were well correlated with diameter increment. However, the values of *rho* for *Heg* were slightly lower than *SdrAng*. None of the alternatives of *Bitterlich method* (BAF_1, BAF_2 and BAF_4) showed to be an appropriate selection method of competitors. Furthermore, *BAL* and *BALMOD* as the best non-spatial *CI*s did not perform better than the superior spatial indices *SdrAng* and *Heg*. The results presented in Table 5 are based on the analyses of 2,742 subject trees that were presented in different neighbours' selection methods and 18 different non-spatial and spatial *CI*s are quantified and available for them.

The comparison of the linear mixed effect models and the linear multiple models detected the improve-

Table 5. The Spearman's rank correlation coefficients between the 5-year tree diameter increment and competition indices for a sample of 2,742 subject trees presenting in different neighbours' selection methods

	Plot	$CZR_{0.4h}$	CZR_{k2}	CZR_{k3}	BAF_1	BAF_2	BAF_4	SCH_{100}	SCH_{80}	SCH_{60}	$SCHCr_{100}$	$SCHCr_{80}$	$SCHCr_{60}$
Non–spatial indices													
BA–g_j	–0.160	–	–	–	–	–	–	–	–	–	–	–	–
BAL	**–0.598**	–	–	–	–	–	–	–	–	–	–	–	–
Sdr	–0.320	–	–	–	–	–	–	–	–	–	–	–	–
dr_g	–0.435	–	–	–	–	–	–	–	–	–	–	–	–
BAr	–0.436	–	–	–	–	–	–	–	–	–	–	–	–
BALr	–0.469	–	–	–	–	–	–	–	–	–	–	–	–
BALMOD	**–0.558**	–	–	–	–	–	–	–	–	–	–	–	–
Spatial indices													
Sl	–	–0.285	–0.273	–0.306	–	–	–	–	–	–	–	–	–
SOr	–	–0.225	–0.217	–0.279	–	–	–	–	–	–	–	–	–
SOdr	–	–0.334	–0.292	–0.381	–	–	–	–	–	–	–	–	–
SBAr	–	–0.578	–0.531	–0.590	–0.196	–0.164	–0.098	–0.491	–0.528	–0.551	–0.475	–0.530	–0.532
Heg	–	**–0.623**	–0.504	**–0.650**	–0.241	–0.193	–0.165	–0.456	–0.483	**–0.597**	–0.423	–0.459	–0.481
SAng1	–	–0.359	–0.319	–0.375	–0.214	–0.182	–0.171	–0.303	–0.306	–0.350	–0.282	–0.303	–0.322
SAng2	–	–0.409	–0.363	–0.417	–0.237	–0.231	–0.219	–0.386	–0.378	–0.390	–0.330	–0.348	–0.384
SdrAng	–	**–0.641**	–0.606	**–0.656**	–0.499	–0.430	–0.386	–0.591	–0.598	**–0.616**	–0.579	–0.600	–0.614
Almdg	–	–0.411	–0.368	–0.408	–0.086	–0.065	–0.074	–0.092	–0.228	–0.374	–0.282	–0.289	–0.227
Sdrl1	–	–0.522	–0.501	–0.531	–	–	–	–	–	–	–	–	–
Sdrl2	–	–0.302	–0.225	–0.363	–0.157	–0.131	–0.120	–0.210	0.175	–0.311	–0.135	–0.179	–0.219

ment in linear mixed effect regressions in terms of *AIC*, but the *ANOVA* comparison between the mixed effect models, with and without an auto-regressive structure, did not show significant remaining within-group correlation (P-value>0.05). Subsequently, the growth model was fit into linear mixed effect regression (Eq. (9)) with no auto-regressive structure for further analyses in this study. All explanatory variables used for Eq. (7) were considered as mixed effects and proved significant (P-value<0.05), also *VIF* indicated no problem with multiclollinearity, all values being less than eight. In order to test the contribution of selected *CI*s, they were devised into the recent growth model.

Table 6 illustrates the statistical measures of mixed effect models, including R^2, *RMSE*, *MSER*, *AIC*, AIC_w, and also *DAIC*. The indices comparisons were done for different sample size of subject trees based on each neighbour selection method. Generally, the contributions of *CI*s were significant but not very large in magnitude, and among the *CIs* added to the model, *SdrAng* presented the most significant contribution, no matter which competitor selection method was used. After that, *Heg* was found to be important in efficiency to improve the growth model. Non-spatial *CI*s of *BAL* and *BALMOD* showed less contributions to the growth model than the spatial indices, except for SCH_{60} where *BAL* appeared slightly better than *Heg CI*.

The results of analyses for different age groups (Table 7) demonstrated that competition had stronger prediction ability in younger stands, and spatially *CI*s proved to be better than non-spatial ones. As shown in Tables (6) and (7), the Ellenberg's light values performed a slight improvement for some models in order to describe the species-specific effect. The profiles of the R^2 and *AIC* did not show considerable variation between the two methods of calculating selected spatial *CI*s, with and without Ellenberg's values (Table 6). However, statistical measures for young stands viewed a slight improvement for including species-specific values in competition quantifications (Table 7).

Table 6. Contribution of the competition indices to tree diameter growth model

SM	Model	R^2	RMSE (cm)	MSER (%)	AIC	AIC_w	ΔAIC
CZR_{k3} *(8265 subject trees)*	*No CI*	0.564	0.432	–	6183.70	0.000	249.64
	Heg	0.604	0.422	4.831	5903.26	0.000	328.23
	$Heg^{Ellenberg}$	0.605	0.422	4.796	5894.69	0.002	346.67
	SdrAng	0.607	0.419	6.114	5883.26	0.447	157.43
	$SdrAng^{Ellenberg}$	0.607	0.419	6.107	5882.89	0.551	183.95
	BAL	0.592	0.422	4.627	5992.51	0.000	349.88
	BALMOD	0.589	0.422	4.791	6011.89	0.000	377.56
$CZR_{0.4h}$ *(6426 subject trees)*	*No CI*	0.521	0.471	–	4019.22	0.000	312.57
	Heg	0.569	0.451	8.469	3574.45	0.000	336.94
	$Heg^{Ellenberg}$	0.571	0.449	9.364	3560.08	0.001	363.55
	SdrAng	0.579	0.451	8.700	3485.58	0.779	374.01
	$SdrAng^{Ellenberg}$	0.578	0.451	8.656	3488.11	0.220	343.83
	BAL	0.567	0.460	4.759	3592.26	0.000	381.02
	BALMOD	0.567	0.461	4.576	3596.89	0.000	371.91
SCH_{60} *(3840 subject trees)*	*No CI*	0.485	0.435	–	1325.51	0.000	74.17
	Heg	0.544	0.424	4.758	1184.29	0.003	152.40
	$Heg^{Ellenberg}$	0.544	0.424	4.845	1182.60	0.008	133.32
	SdrAng	0.548	0.419	7.239	1174.16	0.544	128.65
	$SdrAng^{Ellenberg}$	0.548	0.419	7.324	1175.17	0.328	95.03
	BAL	0.546	0.416	8.627	1177.25	0.116	168.91
	BALMOD	0.542	0.419	7.262	1187.65	0.001	177.81

**Heg* and *SdrAng* are spatial indices without including the species-specific values. $Heg^{Ellenberg}$ and $SdrAng^{Ellenberg}$ are corresponding spatial indices including Ellenberg's species-specific values for three different neighbour selecting methods. *BAL* and *BALMOD* are non-spatial indices, for the subject trees of same data set used for analyses in each competitor selecting method.

Discussion

Computing the correlation coefficient of tree growth, and determining the efficiency of *CI*s when added to a tree growth model, have been widely used (Burkhart & Tomé, 2012). In the current study, adding the *CI*s to the growth model slightly improved the model, which can be partially due to the inclusion of relative dimensions of the trees in model. Relative dimensions measure the hierarchical position of the subject tree within the stand, and indirectly indicate the competitive status of the trees (Burkhart & Tomé, 2012).

Results from comparing different *CI*s proposed that spatial *CI*s of *SdrAng* and *Heg* were the best indices suitable to quantify the competition status of birch trees, respectively. Several studies (Castagneri *et al*., 2008; Contreras *et al*., 2011) have reported that *SdrAng* can describe a greater proportion of the investigated variation in growth models. Also, *Heg* demonstrated superior performance to non-spatial *CI*s in many studies (Alemdag, 1978; Pukkala & Kolström, 1987; Holmes & Reed, 1991; Mailly *et al*., 2003). The indices of *SdrAng* and *Heg* assign greater weight to the closer and bigger competitor trees (Wimberly & Bare, 1996) and it was following along the Cole & Lorimer (1994) hypothesis that noticeable competitive stress occurs by immediate competitors surrounding the subject tree crown.

The results we obtained for non-spatial *CI*s showed that *BAL* and *BALMOD* improved the predictive ability of Eq. (9), although in a smaller amount than when using the *CI*s of *SdrAng* or *Heg*. Some studies including *BAL* or *BALMOD* found an improvement (large or modest) in model performance (e.g. Biging & Dobbertin, 1995; Corral Rivas *et al*., 2005). However, similar to our study, several other studies suggested that spatial measures provided more precise growth prediction (Boivin *et al*., 2010; Contreras *et al*., 2011), and to the contrary, many studies did not report

Table 7. Contribution of the competition indices to tree diameter growth in different age groups

Age group	Model	SM								
		CZR_{k3}			$CZR_{0.4h}$			SCH_{60}		
		rho	AIC	AIC_w	rho	AIC	AIC_w	rho	AIC	AIC_w
Young stands	*Heg*	–0.625	3908.56	0.008	–0.611	2594.14	0.000	–0.559	2608.35	0.000
	$Heg^{Ellenberg}$	–0.633	3906.50	0.023	–0.619	2593.95	0.000	–0.573	2604.73	0.001
	SdrAng	–0.694	3902.25	0.190	–0.655	2575.26	0.337	–0.669	2597.93	0.033
	$SdrAng^{Ellenberg}$	–0.714	3899.43	0.779	–0.671	2573.91	0.663	–0.694	2591.17	0.966
	BAL	–0.618	3920.17	0.000	–0.578	2615.14	0.000	–0.602	2612.23	0.000
	BALMOD	–0.586	3918.31	0.000	–0.570	2609.71	0.000	–0.594	2612.72	0.000
Middle-aged stands	*Heg*	–0.522	3603.31	0.011	–0.480	2497.72	0.022	–0.376	2041.02	0.061
	$Heg^{Ellenberg}$	–0.496	3605.24	0.004	–0.458	2498.98	0.012	–0.353	2043.01	0.023
	SdrAng	–0.614	3595.05	0.673	–0.600	2494.53	0.108	–0.534	2035.80	0.835
	$SdrAng^{Ellenberg}$	–0.583	3596.59	0.312	–0.565	2495.22	0.076	–0.481	2040.52	0.079
	BAL	–0.564	3636.79	0.000	–0.549	2493.38	0.191	–0.475	2050.31	0.001
	BALMOD	–0.566	3636.18	0.000	–0.565	2491.12	0.592	–0.486	2047.96	0.002
Old stands	*Heg*	–0.442	587.34	0.034	–0.382	308.67	0.016	–0.311	260.53	0.003
	$Heg^{Ellenberg}$	–0.402	590.46	0.007	–0.311	308.97	0.014	–0.300	261.92	0.002
	SdrAng	–0.544	585.59	0.081	–0.515	306.99	0.037	–0.492	253.44	0.110
	$SdrAng^{Ellenberg}$	–0.498	587.77	0.027	–0.455	311.24	0.004	–0.463	256.76	0.021
	BAL	–0.603	581.52	0.618	–0.589	302.36	0.379	–0.532	252.03	0.222
	BALMOD	–0.507	583.47	0.233	–0.504	301.62	0.549	0.518	249.91	0.642

any superiority of spatial indices to non-spatial ones (Soares & Tomé, 1999; Stadt *et al*., 2007; Roberts & Harrington, 2008). The superiority of size-ratio *CI*s of *SdrAng* and *Heg* that used the *d* as indicator of size was probably because of the actual correlation between the subject tree's diameter increment and its *d* (Holmes & Reed, 1991); however, the strength of competitive stress explained by such correlations might be unclear (Brand & Magnussen, 1988; Larocque, 2002).

While non-spatial *CI*s are simple functions of the stand or a tree's dimensions, the selection of the neighbours that affect the growth of a subject tree is of crucial importance when calculating spatial indices. Concerning the competitor selection methods, the best results were acquired with those based on the influence zone and competition elimination angle concepts. Several studies showed that the competition status of a tree could potentially vary depending on the radius of influence zone (Pukkala & Kolström, 1987; He & Duncan, 2000; Nanami *et al*., 2005). The CZR_k was a multiple of average distance between the trees in the plot and highly affected by stand density. In our study plots, considering *k* equal to three and *CEA* equal to 30° proved to be a good fit to select the adequate number of active competitors. Although some studies (e.g. Alvarez *et al*. 2003) found better results using a different angle gauge, the angle gauge of 30° provided satisfactory results in some other studies (e.g. Lee & Gadow, 1997; Corral Rivas *et al*., 2005; Zhang *et al*., 2009).

The next superior competition selection approach, $CZR_{0.4h}$, was simple in practice and in accordance with studies showing that, the optimal influence zone radius strongly depended on the tree's initial dimensions (D'Amato & Puettmann, 2004; Sims *et al*., 2009). Considering the third suitable competitor selection method, similar to several other studies, the opening angle of 50°-60° performed well (Biging & Dobbertin, 1995; Pretzsch, 2009; Oheimb *et al*., 2011) where bigger angles (80° and 100° in this study) mainly decreased the merit of the search-cone method used to detect the competitors (Richards *et al*., 2008). In contrast to the CZR_{k3}, the two methods of $CZR_{0.4h}$ and SCH_{60} gave more weight to tree height than distance, and since in our study, there was a lack of height measures for all trees, the selecting system of CZR_{k3} was preferable to identify competitors for central trees.

Despite the fact that the identity of neighbouring species is an important factor in the characterization of their competitive effects (Bella, 1971; Zhao *et al*., 2006; Kaitaniemi & Lintunen, 2010; Bošelá *et al*., 2013), no significant improvement appeared in recalculating the selected indices using Ellenberg's light values except for young trees. One possible explanation is that in our study plots about two-thirds of the trees analysed were birch with the same light factors. Consequently, giving weight to different species did not significantly change the values of measured competition. In addition, *interspecific* competition mainly caused by Norway spruce appeared inferior due to differences in temporal growth patterns and shade-tolerance (Tahvanainen & Forss, 2008; Hynynen *et al*., 2011). Furthermore, the influence of competition on diameter growth was not strongly impacted by the number of species in the local neighbourhood as suggested by Oheimb *et al*. (2011). The slight improvement in young stands might be due to the nature of Ellenberg's light values that refer to the preferences of the early stage of the tree life cycle. During the early stage, when light-demanding birch trees rapidly occupy regeneration areas, Norway spruce tends to appear more shade-tolerant; consequently, weighting them differently in competition measures is justified. Moreover the performance of *CI*s changed slightly by stand development. In young stands spatial indices performed better while in older stands, non-spatial indices showed superior results. In the early stage, pioneer birches grow quite fast and vigorously (Hynynen *et al*., 2011), and spatial *CI*s explain competition effects better in dense young stands, since they account for the short distances between the neighbouring trees, that are competing for resources. In older stands, due to mortality induced by different factors, including competition (Sims *et al*., 2009), the number of trees decline and non-spatial *CI*s are adequate for competition studies.

The overall results of this study provided a better understanding of competition in birch stands. Although spatial *CI*s performed better than non-spatial *CI*s, the reported differences between the spatial and non-spatial indices are relatively small. The spatial indices require tree attributes and locations, and the recording of such information is expensive and time consuming. Therefore, we suggest applying the spatial indices only when studying the competition in the natural development of young stands, where the stands are usually dense, because these types of indices give more weight to trees that are closer to the subject tree. In the middle-aged and old managed stands, an efficient measure of competition is possible by employing the non-spatial indices that do not require as many field measurements.

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Differences between competition kernels and traditional size-ratio based competition indices used in forest ecology

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ABSTRACT

Both traditional competition indices and competition kernels are used in many studies to quantify competition between plants for resources. Yet it is not fully clear what the differences between these two concepts really are.

For characterising the two approaches we selected two fundamental types of competition indices based on distance weighted size ratios, an additional competition index without distance weighting and developed similar competition kernels. In contrast to the latter approach, competition indices require individual influence zones that for example can be derived from tree crown-radius measurements. We applied these competition measures to two spatio-temporal forest datasets in Europe and one in North America. Stem diameter increment served as observed response variable.

The results of both methods indicated similar performance, however, the use of competition kernels produced slightly better results with only one exception out of six computer experiments.

Although the performance of both competition measures is not too different, competition kernels are based on more solid mathematical and ecological grounds. Particularly the question of defining the local neighbourhood of a given tree seems to be better handled by competition kernels. Consequently, applications of this method are likely to increase. The trade-off of the use of competition kernels, however, is the need for more sophisticated spatial regression routines that researchers are required to program. Finally, a tabulated summary of differences between competition indices and competition kernels is included.

1. Introduction

Plant-to-plant competition is a fundamental notion in plant ecosystems and occurs when two or more individuals attempt to utilise the same resources that are limited in supply (Kimmins, 2004, p. 422). Competition sets in motion an interaction between individuals leading to a reduction of the performance (e.g. in terms of survival, growth and reproduction) of at least some of the competing individuals (Begon et al., 2006, p. 132).

In this context, *symmetric* competition is regarded as an equal sharing of resources among individuals whilst *asymmetric* competition is an unequal sharing of resources as a consequence of larger individuals having a competitive advantage over smaller ones (Schwinning and Weiner, 1998; Freckleton and Watkinson, 2001; Begon et al., 2006, p. 151f.). Symmetric and asymmetric competitions are collectively referred to as *mode of competition* (Bauer et al., 2004).

On a practical note, Freckleton and Watkinson (1999, p. 286) state that the interpretation of the outcome of competition can critically depend on the way competition is measured. In other words, the selection and use of competition measures by researchers has an important bearing on the way competition is assessed, which in turn may condition the inferences drawn from plant competition experiments (Weigelt and Jolliffe, 2003). Technically competition can be quantified by *spatial* and *non-spatial measures*. Spatial competition measures specifically take the locations of plants into account. As a spatial assessment of plant interactions has theoretical advantages and is often more effective particularly in ecosystems with complex structures (Berger and Hildenbrandt, 2000; Martin and Ek, 1984; Weigelt and Jolliffe, 2003), we focus on spatially explicit measures in this study. Spatial competition measures usually amalgamate several primary response variables along with spatial information (Weigelt and Jolliffe, 2003). *Indices* of spatial competition are based on the *nearest-neighbour* (NN)

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concept of point-process statistics following the idea, that the immediate neighbours surrounding a subject plant are likely to have a competitive effect (Schneider et al., 2006). Using this approach, a competition index is calculated for each plant as a measure of the competition load exerted by neighbouring plants. Competition index values typically are associated with the point locations of the subject plants.

By contrast a different approach producing spatial competition fields has been developed in the past thirty years. As a consequence potential competition pressure is known for every point in a research or monitoring plot. The concept has origins in different fields of natural sciences including *ecological field theory* (Wu et al., 1985; Walker et al., 1989; Li et al., 2000; Pukkala, 1989; Miina and Pukkala, 2002), *shot-noise fields* in physics (Baccelli and Blaszczyszyn, 2001; Baccelli et al., 1997), *individual-based modelling* (Adler, 1996; Bezzi et al., 1999; Berger and Hildenbrandt, 2000; Snyder and Chesson, 2004; Adams et al., 2011; Grabarnik and Särkkä, 2011) and *competition kernels* (Snyder and Chesson, 2004; Hernández-García et al., 2009; Baptestine et al., 2009; Vogt et al., 2010). Competition kernels belong to a group of so-called *interaction kernels* that are functions describing how biological processes such as growth, survival and reproduction of an individual depend on its own size and the size of and distance to other individuals (Snyder and Chesson, 2004; Vogt et al., 2010). Competition kernels are therefore also related to the idea of *dispersal kernels* used in modelling seed and plant dispersal (Bolker and Pacala, 1999; Nanos et al., 2010). For all of these approaches, every plant of a given community emits a signal termed *competition signal*, *impulse*, *local competition effect* or *attenuation function*, which is largest at the location of a plant and decreases with increasing distance from that plant. At any point in the community the plants' competition signals can be aggregated additively or multiplicatively to obtain the total amount of competition pressure at that point. This aggregation or superposition essentially results in a competition field. Competition signals are modelled by competition kernels and in the remainder of the text we will use this term to collectively refer to all approaches that have the aforementioned definition in common. For a good practical overview also refer to García (2014).

The practical use of competition kernels has recently been much facilitated by the fast development of powerful computer technology (Berger and Hildenbrandt, 2000). A historic shortcoming of competition kernels has been the effort necessary for their computation compared to the simpler competition indices. This, however, is no longer a serious constraint and consequently as shown above many applications of this modelling technique have been published in recent years. However, to our knowledge there has so far not been any study directly comparing both competition measures and elaborating the merits of both concepts based on comparable computational principles.

For this generic study, we have selected the most widespread type of competition indices, i.e. that of size ratios. Size ratios are very common expressions of competition. They have frequently been used in modelling and usually involve stem diameters, total heights and crown sizes (of trees for example) (Biging and Dobbertin, 1992; Martin and Ek, 1984; Burkhart and Tomé, 2012, Chapter 9). The ratios typically include the size of a competitor divided by the size of a subject plant. In our study, we used tree stem diameter as the size variable, since it is the most common primary tree variable available whilst crown or height measures are often estimated from stem diameter. However, any other size variable including volume and biomass is possible.

For many competition indices, size ratios are often weighted by subject-to-competitor distances to account for the decreasing effects of competitors with increasing distances. There are two basic strategies of expressing distance weights, as *fractions* and as part of *exponential* functions. The well-known Hegyi competition index (Hegyi, 1974) is an example of a size ratio weighted by the reciprocal of the distance. It is a comparatively simple competition index and has proved to be very effective and robust at the same time (Daniels, 1976; Radtke et al., 2003; Sandoval and Cancino, 2008; Contreras et al., 2011). Exponentially weighted size ratios are a little less common as competition indices and a good example is the competition index by Martin and Ek (1984). By contrast, exponential competition kernels are frequently used (Schneider et al., 2006). Asymmetric competition emerges from both the competition indices and the kernels.

A straightforward comparison between competition indices and kernels is not easy. In this case study, we have compared the indices to similar fractional and exponential competition kernels and we devised the kernels for this study so that they share as many similarities with the indices as possible. In addition we also included a simple size ratio competition index without distance weight to find out whether weighting matters at all.

The objective of this paper is therefore to establish and to characterise the differences between competition indices and competition kernels. Using trees as examples, we apply both concepts to two different forest ecosystems in Europe and one in North America.

2. Methods

2.1. Quantifying competition

In this study, we quantified plant-to-plant competition in two alternative ways, (1) by using the aforementioned two basic types of traditional competition indices and (2) based on corresponding competition kernels.

The first method commonly involves (1a) the definition of a zone of influence (ZOI) and (1b) the actual competition index sensu stricto (Burkhart and Tomé 2012, p. 204). A ZOI is an assumed circular area around a tree in which it predominantly draws on resources like light, water and nutrients (Berger and Hildenbrandt, 2000; Grimm and Railsback, 2005, p. 201). It is a common assumption in plant ecology that all plants whose ZOIs overlap, interact via competition for resources (Grimm and Railsback, 2005, p. 201).

Whilst putting this definition into modelling practice, we found that crown radius is a good proxy of ZOI radius, since this measure is directly where photosynthetic processes take place. This is why crown radius has been used before in many studies to define the growing space of trees (see for example Gspaltl et al., 2012). This modelling approach predominantly takes care of competition for light and Genet et al. (2014) demonstrate how the ZOI approach can be extended to other kinds of competition. To estimate crown radius, r, we exploited the allometric relationship between *dbh* and crown radius. We collected crown radius and stem diameter data from the same sites or regions as the main data of this study and calculated the quadratic mean of four to sixteen measurements (depending on the number of records available) following a recommendation in Hasenauer (1997). Alternatives to this approach include the use of crown data of open-grown trees, i.e. trees that have grown in complete absence of tree competition (Hasenauer, 1997). As no data from open-grown trees were available to us, we used data from predominant trees as a surrogate and identified them by quantile regression (Cade and Noon, 2003). Assuming that ZOIs increase with tree size and are restricted by environmental resistance (Soares and Tomé, 1999; Burkhart and Tomé, 2012, p. 205f.), we selected the Michaelis–Menten saturation curve (Eq. (1), Michaelis and Menten, 1913; Bolker, 2008, p. 77ff.). The model implies that ZOI size is different for every tree depending on stem diameter, *dbh*, at 1.3 m above ground level. Model parameter a can be interpreted as the asymptote of the saturation curve thus defining the maximum possible ZOI size whilst b is the so-called half-maximum.

$$r = \frac{a \cdot dbh}{b + dbh} \tag{1}$$

When testing whether a neighbouring tree j is a competitor of subject tree i, we calculated Eq. (1) twice, i.e. once for the subject tree i yielding r_i and once for the potential competitor j resulting in r_j. Tree j is a competitor of tree i, if $r_i + r_j > dist_{ij}$, i.e. if the ZOIs of both trees overlap. The estimated model parameters that define the ZOIs are provided for the three tree species in Table 1. Fig. 1 illustrates the species-specific relationships between stem diameter (cm) and ZOI radius (m). The curves typically reflect the large demand on space of broadleaved trees compared to conifers, which is also expressed by the values of the asymptote parameter a.

The competition index (denoted by “I” in the upper index) type based on a size ratio with fractional distance weight (denoted by “f” in the upper index) for tree i and its k competitors can be expressed by Eq. (2); Hegyi, 1974). The number of competitors, k, is variable and depends on the local tree pattern with respect to tree size and tree locations.

$$c_i^{\text{I,f}} = \sum_{j=1}^{k} \frac{dbh_j}{dbh_i} \times \frac{1}{dist_{i,j}} = \frac{1}{dbh_i} \sum_{j=1}^{k} \frac{dbh_j}{dist_{i,j}} \tag{2}$$

In this context, inter-tree distances are used for two purposes, firstly for identifying competitors and secondly for deriving weights modelling their contribution to the overall competition load of a given subject tree. An important alternative competition index type is the exponentially weighted size ratio (denoted by “e” in the upper index). As a typical example we have used a generalised version of Martin and Ek’s (1984) competition index (Eq. (3)).

$$\begin{aligned} c_i^{\text{I,e}} &= \sum_{j=1}^{k} \frac{dbh_j}{dbh_i} \times \exp\left(-\frac{dist_{i,j}}{dbh_i + dbh_j}\right) \\ &= \frac{1}{dbh_i} \sum_{j=1}^{k} dbh_j \times \exp\left(-\frac{dist_{i,j}}{dbh_i + dbh_j}\right) \end{aligned} \tag{3}$$

Finally, to check up on the importance of the distance weight we also used an unweighted size ratio as in Eq. (4). In this case, competitors further away from the subject tree have the same influence as those of the same size nearby.

$$c_i^{\text{I},\cdot} = \sum_{j=1}^{k} \frac{dbh_j}{dbh_i} = \frac{1}{dbh_i} \sum_{j=1}^{k} dbh_j \tag{4}$$

As alternatives to the traditional concept of competition indices we applied equivalent competition kernels to the spatio-temporal datasets. There are many different competition kernels and Schneider et al. (2006) provide a good overview. To mimic the idea of fractionally and exponentially weighted size ratio we used a *fractional* or *hyperbolic* and an *exponential* competition kernel that we modified from Adler (1996), Schneider et al. (2006) and Pommerening et al. (2011). This resulted in the local competition effects or signals $p_j^{\text{f}}(\xi)$ and $p_j^{\text{e}}(\xi)$ of a competitor tree j at any location ξ in the forest given in Eqs. (5) and (6), respectively. Figs. 2a and 2b illustrate the shape of $p_j^{\text{f}}(\xi)$ and $p_j^{\text{e}}(\xi)$ for the three species considered in this study. “f” and “e” in the upper index have the same meaning as in the case of the competition indices.

Table 1
Estimated model parameters of the Michaelis–Menten model (Eq. (1); Michaelis and Menten, 1913) defining the zones of influence of the three species investigated.

Species	ZOI definition Eq. (1) with a and b		R^2
Beech	14.73798	56.861277	0.99182
Interior Douglas fir	8.92849	20.84195	0.99077
Norway spruce	6.80408	23.54801	0.99631

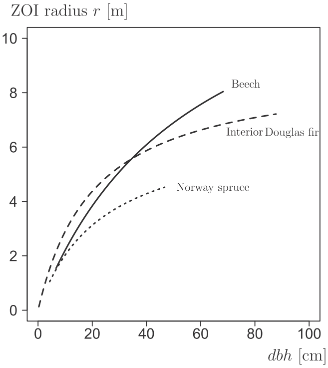

Fig. 1. The relationship between stem diameter and ZOI radius based on Eq. (1) for the three species investigated. The three curves reflect the stem diameter ranges of the three time series.

$$p_j^{\text{f}}(\xi) = \frac{dbh_j^{\alpha_{\text{K,f}}}}{1 + \left(dist_j(\xi)/\beta_{\text{K,f}}\right)^2} \tag{5}$$

$$p_j^{\text{e}}(\xi) = dbh_j^{\alpha_{\text{K,e}}} \times \exp\left(-\frac{dist_j(\xi)}{dbh_j^{\beta_{\text{K,e}}}}\right) \tag{6}$$

These competition effects are defined continuously in space, whereas competition index values (Eqs. (2)–(4)) are only defined at tree locations.

To calculate the competition load of a given tree, i, at its location, ξ_i, following the shot-noise approach (Pommerening et al., 2011; Pommerening and Särkkä, 2013) we additively aggregate the competition effects of all other trees j according to Eqs. (7) and (8). “K” in the upper index denotes “competition kernel”.

$$c_i^{\text{K,f}}(\xi_i) = \sum_{j \neq i} p_j^{\text{f}}(\xi_i) = \sum_{j \neq i} \frac{dbh_j^{\alpha_{\text{K,f}}}}{1 + \left(dist_j(\xi_i)/\beta_{\text{K,f}}\right)^2} \tag{7}$$

$$c_i^{\text{K,e}}(\xi_i) = \sum_{j \neq i} p_j^{\text{e}}(\xi_i) = \sum_{j \neq i} dbh_j^{\alpha_{\text{K,e}}} \times \exp\left(-\frac{dist_j(\xi_i)}{dbh_j^{\beta_{\text{K,e}}}}\right) \tag{8}$$

The aggregation, $c^{\text{K,f}}(\xi)$ and $c^{\text{K,e}}(\xi)$, of competition impulses at any point, ξ, in a research plot is a pre-requisite for producing competition load maps as shown in Pommerening et al. (2011). Eq. (7) has similarities with the second term in Eq. (2) after the equal sign except for $1/dbh_i$. Likewise Eq. (8) is similar to the second term of Eq. (3).

Unlike traditional competition indices, competition kernels do not necessarily require ZOIs. As an approximation the competition signals of other trees are aggregated at the location of the subject tree rather than integrated over a larger area. The competition signal for example of a small tree j with large distance, $dist_j(\xi_i)$ is per definition near zero or zero at the location of tree i. Thus competition kernels are mathematically elegant as their ZOIs are automatically included or implicit.

In our study, we computed the c_i^{K} values with periodic boundary conditions (Illian et al., 2008, p. 184) to reduce edge effects. Note that the value of c_i^{K} is only dependent on the stem diameter

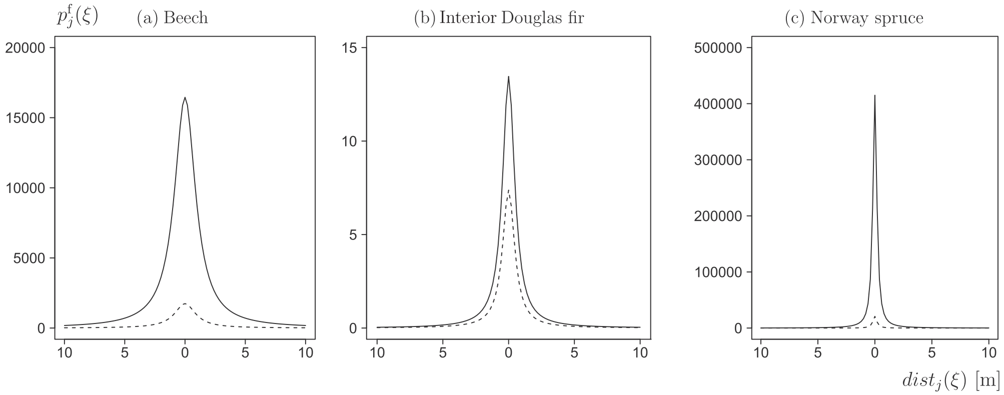

Fig. 2a. The shape of the fractional competition kernel $p_j^f(\xi)$ estimated from the three spatial time series for hypothetical trees j with 20 cm (solid line) and 10 cm (dashed line) dbh_j. The corresponding values of $\alpha_{K,f}$ and $\beta_{K,f}$ are provided in Table 3.

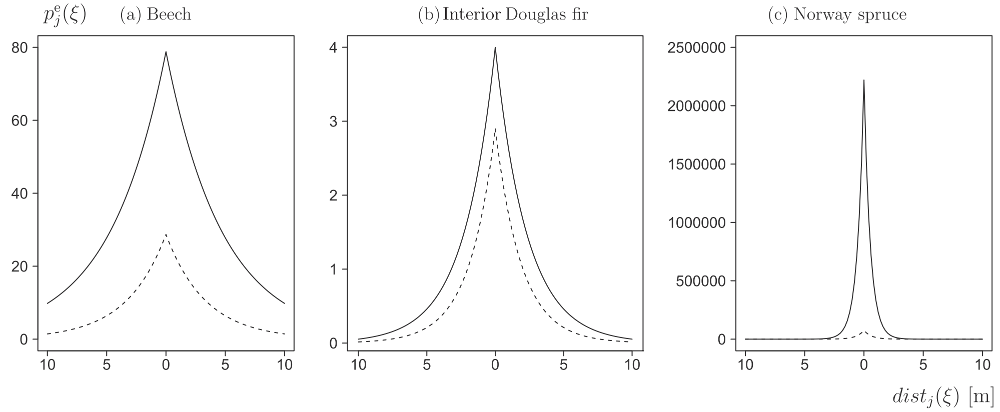

Fig. 2b. The shape of the exponential competition kernel $p_j^e(\xi)$ estimated from the three spatial time series for hypothetical trees j with 20 cm (solid line) and 10 cm (dashed line) dbh_j. The corresponding values of $\alpha_{K,e}$ and $\beta_{K,e}$ are provided in Table 3.

of the trees influencing tree i and the distance $dist_j(\xi_i)$ between tree i and tree j.

However, the impact of competition load also depends on the size of the affected tree i. Therefore, for estimating the effect of the aggregated competition load c_i^K on tree i a transformation of c_i^K is required, which was inspired by Adler (1996). This transformation applies to both kernel types used in this study and combines the size of the affected tree i with its competition load c_i^K and is given by:

$$c_i^{trans} = \frac{c_i^K}{dbh_i^{\alpha_K} + c_i^K} \tag{9}$$

By construction, c_i^{trans} is scaled between 0 and 1. Note that the exponent α_K in Eq. (9) is the strength parameter in Eqs. (5)–(8). In contrast to c_i^K, c_i^{trans} values are only defined at the location of trees i, as they require their size information. From Eqs. (5)–(9) it is clear that the effect of competitors is initially separated from that of the subject tree for retaining the option of a continuous random field, which is an important property of competition kernels and the shot-noise approach. Note that this transformation is not a "compulsory" modelling step. It just increases biological plausibility and improves model behaviour. Earlier approaches to modelling competition kernels have not included any transformation.

The parameters of the competition kernel can be easily interpreted: A large value of α_K increases the *strength* of the competition signal, i.e. the magnitude of the peak. β_K, on the contrary, scales the decrease or attenuation of the competition signal with distance $dist_j(\xi)$: A large value of β_K stretches the range of the competition impulse. β_K is therefore a *range* parameter.

In modelling and applying the competition indices we have made an effort to give these traditional competition measures the best possible "starting conditions" for a meaningful characterisation of their performance. To this end, we also considered the same number of three model parameters for both competition models.

2.2. Stem diameter increment as response variable

In this study, we used stem diameter increment as a response and performance variable to assess the quality of competition modelling, i.e. the stem diameter increments estimated by the models were compared with the observed stem diameter increments. To link competition with diameter growth, we applied the potential-modifier approach (Newnham, 1964; Botkin et al., 1972). Potential diameter growth was estimated from predominant trees using quantile regression as specified in the section "Parameter estimation". The competition load a subject tree is facing reduces the potential diameter increment.

Note that we have omitted indices relating to time throughout this paper to simplify the notation of the formulae used for ease of reading.

The potential diameter increment id_i^{pot} was modelled for each tree i according to the Chapman–Richards growth function (Pienaar and Turnbull, 1973; Zeide, 1993):

$$id_i^{\text{pot}} = Akp \times \exp(-k \cdot dbh_i) \times (1 - \exp(-k \cdot dbh_i))^{p-1} \tag{10}$$

where A, k and p are model parameters. In the corresponding Chapman–Richards growth function, parameter A is the asymptote representing the maximum diameter for all trees of a given forest, parameter k scales the growth rate and p determines the location of the inflection point of the growth function, as explained in Pienaar and Turnbull (1973). Parameters A, k, p and as a consequence id_i^{pot} are the same regardless which of the two competition measures are used. Fig. 3 shows the potential annual diameter increment function according to Eq. (10) in relation to the observed periodic annual increments of the three species investigated.

Finally, both the competition indices and the kernels are separately used as growth modifiers with a view to reduce the potential diameter increment to match the real increment. Depending on whether we work with traditional competition indices or with the corresponding kernels, the modifying term is different. Traditional competition indices need to be wrapped in a modifier function (Pretzsch, 2009, p. 454f.). In preparatory calculations, we identified from several available modifier functions (Ek and Dudek, 1980; Vanclay, 1994; Pretzsch, 2009, p. 454f.) the bracket term of Eq. (11) as the best.

$$id_i^{\text{I}} = id_i^{\text{pot}} \times \nu_{\text{I}} \times \left(\alpha_{\text{I}} - \exp\left(\frac{-\beta_{\text{I}}}{c_i^{\text{I}}}\right)\right) \tag{11}$$

α_{I} and β_{I} are less straightforward to interpret than their kernel counterparts. For the competition kernel Eq. (11) simplifies to Eq. (12).

$$id_i^{\text{K}} = id_i^{\text{pot}} \times \nu_{\text{K}} \times (1 - c_i^{\text{trans}}) \tag{12}$$

In Eqs. (11) and (12) ν_{I} and ν_{K} are further model parameters, which can be interpreted as additional modifiers. These parameters allow us to equate both sides of the equation. Without ν_{I} and ν_{K} both terms in Eqs. (11) and (12) would only be proportional (Pommerening et al., 2011). Table 2 gives the species-specific values of A, k, p (Eq. (10)) and ν_{I} and ν_{K} of (Eqs. (11) and (12)).

2.3. Parameter estimation

For each forest all model parameters were estimated separately. The ZOI radius (Eq. (1)) required for the traditional indices was estimated from stem and crown diameter records by using quantile regression (Cade and Noon, 2003) with $\tau = 0.995$ for beech, $\tau = 0.985$ for interior Douglas fir and $\tau = 0.999$ for Norway spruce calculated with the R Quantreg package.

In contrast to traditional competition indices (Weigelt and Jolliffe, 2003; Biging and Dobbertin, 1992) the estimation of competition parameters α_{K} and β_{K} (Eqs. (5)–(9)) must be processed simultaneously with parameter ν_{K} (Eq. (12)). This is the main computational difference to traditional competition indices and makes the estimation of competition kernel parameters more sophisticated: For the former it suffices to simply compute the competition indices and in a second step to estimate parameters α_{I} and β_{I} of the modifier function in Eq. (11). This is computationally easier to accomplish. By contrast, competition kernels require a complex spatial regression routine that we programmed partly in R (R Development Core Team, 2013) and partly in C++ using the Rcpp package (Eddelbuettel and François, 2011; Eddelbuettel, 2013) to take advantage of a tremendous gain in computation time. For estimating parameters $\alpha_{\text{I,K}}$ and $\beta_{\text{I,K}}$ we used nonlinear regression based on maximum likelihood and the Nelder–Mead simplex algorithm Nelder and Mead (1965).

From periodic diameter growth records the mean annual diameter increments were derived. These were used to estimate the parameters A, k and p (Eq. (10); Table 2) through nonlinear quantile regression applying the R Quantreg package.

2.4. Study data

Three tree populations representing a wide range of growth conditions were selected to test the performance of the two alternative concepts of quantifying competition. To obtain clearer results the investigation was intentionally limited to mono-species woodlands to focus on intra-specific competition at this stage.

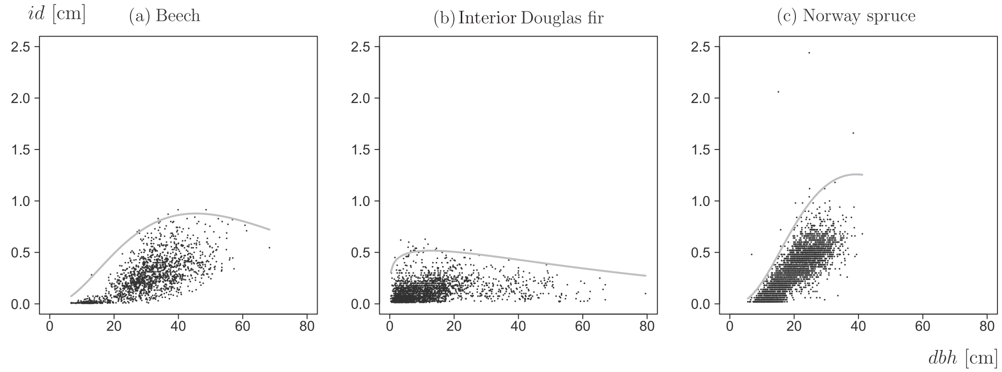

Fig. 3. Annual periodic diameter increment, id, over stem diameter, dbh, of the three time series. The grey curves represent the potential annual diameter increment, id^{pot}, as defined in Eq. (10).

Table 2
Parameters of A, k and p relating to the potential diameter increment model (Eq. (10)) and diameter increment parameters ν_{I} (Eq. (11)) and ν_{K} (Eq. (12)) of the three spatial time series. “No distance” means that no distance weight was applied to the index term, see Eq. (4).

Parameter	Description	Type	Beech	Interior Douglas fir	Norway spruce
A	Parameter in the potential diameter increment model (Eq. (10))	–	75.03706	53.87373	83.35942
k	Parameter in the potential diameter increment model (Eq. (10))	–	0.02700	0.01358	0.03590
p	Parameter in the potential diameter increment model (Eq. (10))	–	3.41053	1.18914	4.09376
R^2	Coefficient of determination of the potential diameter increment model	–	0.93632	0.75735	0.91827
ν_{I}	Parameter in the diameter increment estimation (Eq. (11))	Fractional	1.11986	0.59512	0.29867
		Exponential	2.12753	0.83389	0.87511
		No distance	2.15364	0.93199	0.90215
ν_{K}	Parameter in the diameter increment estimation (Eq. (12))	Fractional	0.65357	0.60133	0.50343
		Exponential	3.33278	1.46721	0.49036

Table 3
Competition parameters α_{I}, β_{I}, α_{K} and β_{K} along with the evaluation criteria *Bias*, *RMSE* and *AIC* relating to estimated diameter increment. “No distance” means that no distance weight was applied to the index term, see Eq. (4).

Species	Competition measure	Type	Parameters		Evaluation criteria		
			$\alpha_{\mathrm{I,\ K}}$	$\beta_{\mathrm{I,\ K}}$	*Bias*	*RMSE*	*AIC*
Beech	Index	Fractional	0.45049	5.20000	−0.00524	0.13026	−2165.5
		Exponential	0.24406	44.21367	−0.00976	0.13223	−2112.8
		No distance	0.24145	39.52282	−0.01007	0.13233	−2110.0
	Kernel	Fractional	3.24074	1.05879	0.00137	0.12048	−2439.3
		Exponential	1.45772	0.52339	−0.00163	0.11999	−2453.6
Interior Douglas fir	Index	Fractional	0.95916	5.61447	−0.00034	0.07200	−7782.2
		Exponential	0.93777	16.65314	−0.00064	0.07452	−7561.0
		No distance	0.94979	12.16664	−0.00065	0.07432	−7578.3
	Kernel	Fractional	0.86776	0.55742	−0.00136	0.07480	−7537.1
		Exponential	0.46267	0.27992	−0.00328	0.07311	−7684.2
Norway spruce	Index	Fractional	1.67389	6.73727	−0.00763	0.17159	−2710.1
		Exponential	0.55300	61.43529	−0.00917	0.17230	−2677.9
		No distance	0.53668	55.54871	−0.00922	0.17228	−2678.5
	Kernel	Fractional	4.31822	0.20540	−0.00089	0.16955	−2804.9
		Exponential	4.87799	−0.21178	0.00112	0.16874	−2842.8

Plots 41-193, 41-194 and 41-700 (0.22, 0.25, 0.25 ha in size) are part of a Swiss spatio-temporal dataset from an even-aged beech (*Fagus sylvatica* L.) forest at Embrach (longitude: 8°10′22.13″, latitude: 47°22′18.32″). The plots were established between 1891 and 1905 and re-measured every 5–10 years until 1991. However, spatial information is available only since 1940. The site has a mean annual precipitation of 1030 mm, a mean annual temperature of 8.3 °C and is located at 590 m a.s.l. (Pommerening et al., 2011).

The multi-aged interior Douglas fir (*Pseudotsuga menziesii* var *glauca* (Mirb.) Franco) plots (6 plots with 0.05–0.10 ha in size) are part of a larger study in the Alex Fraser Research Forest in British Columbia (Canada, longitude: 52°3′, latitude: 121°52′). The site has a mean annual precipitation of 450 mm, a mean annual temperature of 4.2 °C and is located at approximately 1000 m a.s.l. The plots were established in 1988 in an uneven-aged interior Douglas fir forest and re-measured three times until 2004. For at least 20 years there have been no cuttings in this forest and the site has been protected from large-scale fires which frequently happen in this forest type (LeMay et al., 2009).

16 plots with 0.12 ha in size are part of a replicated thinning experiment in predominantly even-aged Norway spruce (*Picea abies* (L.) Karst.) at Karlstift (Austria, longitude: 14°45′59.7″, latitude: 48°34′50.8″). The site has a mean annual precipitation of 950 mm, a mean annual temperature of 4.5 °C is located at 930 m a.s.l. (Pommerening et al., 2011). The plots were established in 1964 and re-measured every five years until 2004.

The interior Douglas fir forest can be considered as natural woodland with a complex forest structure while the beech and the Norway spruce woodlands are influenced by human disturbances and have a relatively uniform structure.

3. Results

Table 3 presents the values of the competition parameters α_{K} and β_{K} which determine the competition signal curves visualised in Figs. 2a and 2b. Particularly Figs. 2a and 2b show that the scales of the signals are influenced by species, size and by the competition kernel type. The use of the exponential competition kernel for example seems to lead to a larger competition range in beech and interior Douglas fir and the values of the signal peaks also vary markedly between kernels. The signal peaks are highest for Norway spruce and smallest for interior Douglas fir and the differences between the species are considerable.

It is also interesting to note that the differences in signal strength between a 10-cm-diameter tree and a 20-cm-diameter tree vary as well. They are largest for Norway spruce followed by beech. In interior Douglas fir, the signal strength of small and large trees is much more similar than with the other two species. This pattern is the same for both kernel types.

The competition signal range is largest for beech whilst it is smallest for Norway spruce.

For beech and Norway spruce absolute *Bias*, *RMSE* and *AIC* relating to estimated diameter increment clearly demonstrate a moderate superiority of the kernel method (see Table 3). However, the differences are small. In interior Douglas fir, however, the evaluation criteria of the indices more or less break even with those of the two kernel methods, i.e. the application of the fractional

Table 4
Comparison of the two concepts of quantifying plant competition.

Competition index	Competition kernel
• Straightforward calculation and parameterisation	• Complex parameterisation, requires special programming skills
• Modifier function necessary	• No modifier function required
• Competition parameters (of modifier function) difficult to interpret	• Competition parameters are easy to interpret and reveal much about plant interaction
• Usually require a ZOI and as a consequence only considers nearest neighbours	• Usually does not require a ZOI and as a consequence considers all plants in a given research plot
• Only produces competition values at the location of a plant (variables of subject plant and competitor not separated)	• Produces competition fields that can be used for other modelling purposes (variables of subject plant and competitor separated)
• Models asymmetric competition	• Models asymmetric competition

Table 5
Model parameters and performance statistics relating to the simultaneous use of the fractional and exponential competition kernels in Eqs. (5) and (6) and of ZOIs as defined in Eq. (1) and in Table 1.

Species	Kernel type	Parameters			Evaluation criteria		
		α_K	β_K	ν_K	*Bias*	*RMSE*	*AIC*
Beech	Fractional	3.25341	1.39347	0.65587	0.00113	0.11989	−2456.3
	Exponential	2.47535	0.27360	0.80384	0.00156	0.12027	−2445.5
Interior Douglas fir	Fractional	0.93316	0.87405	0.73243	−0.00065	0.07289	−7703.3
	Exponential	0.65311	0.36695	1.72530	−0.00472	0.07188	−7793.1
Norway spruce	Fractional	4.06725	0.28802	0.50615	−0.00078	0.16909	−2826.2
	Exponential	4.87506	−0.21157	0.49038	0.00111	0.16874	−2842.9

competition index leads to better results than that of the fractional kernel. However, in interior Douglas fir the exponential kernel performs slightly better than the exponential competition index. These results are particularly interesting, since the Canadian Douglas fir site is the most structurally diverse and also the most natural of all three study sites.

As far as the three competition indices are concerned, the fractional form of distance weighting always performs best. The opposite tendency is shown by the kernels, the exponential competition kernel always produces better results than the fractional form. Interestingly in interior Douglas fir and Norway spruce using no distance weight leads to a slightly better result than the exponential form of distance weighting.

4. Discussion

Despite more than 30 years of research in the areas of the ecological field theory, shot-noise fields, individual-based modelling and competition kernels and despite their theoretical importance Schneider et al. (2006) as well as Vogt et al. (2010) state that we still know comparatively little about kernel functions. Our study is a contribution towards a better understanding of the differences and similarities between traditional competition indices and competition kernels based on simulation experiments.

Pukkala (1989) and Miina and Pukkala (2002) made a first step in this direction, however, their competition indices and kernels differed markedly and they used *multiplicative aggregation* of competition signals instead of *additive*, which was common in early applications of the ecological field theory (Wu et al., 1985). In their study, Miina and Pukkala (2002) concluded that for Scots pine (*Pinus sylvestris* L.) and Norway spruce in Scandinavia competition kernels were better predictors of tree growth than competition indices and they attributed this to the multiplicative aggregation of competition signals. However, our study using additive aggregation reveals that other factors such as a better handling of neighbourhood effects must be responsible for the better performance of competition kernels in some forest ecosystems.

Our results clearly emphasise that any superiority of competition kernels cannot be justified by evaluation criteria relating to a response variable like plant growth alone. It is necessary to interpret the results in the context of the differences between the two concepts of quantifying plant-to-plant competition highlighted in this and in other papers. To this end we have compiled Table 4 as a summary. Going through these six most important differences it seems evident that the main advantages of competition kernels are in their theoretical foundation: Modifier functions and ZOIs that are not easy to define from a mathematical and ecological point of view. The competition parameters α_K and β_K, are clearly interpretable and help to understand the ecological processes in an ecosystem. Revisiting Figs. 2a and 2b, for example, the wide range of the competition impulses in the beech forest can be explained by the high degree of shade tolerance and shade casting of this species. In a similar way on the dry interior Douglas fir site there is long-range competition for water (LeMay et al., 2009).

Competition kernels produce a field of competition load values that are useful for follow-on modelling like the modelling of offspring. Illian et al. (2008, p. 45, 423), for example, show the connection between competition kernels and spatial statistics. The potential benefits of competition kernels come, of course, at the expense of complex spatial regression routines that need to be programmed by the researcher or by a specialist and require advanced programming skills, because the competition parameters are included in the spatial algorithm.

One reason for the good performance of the competition index with fractional distance weights may be that the term $1/dist_{ij}$, the distance weight, – similar to the corresponding kernel – includes a robust mechanism by which the competition load is weighted depending on how close the competitor is located in relation to the subject tree. However, the exponential weights appear to be less effective than the fractional ones. One should expect that competition indices without such a term perform markedly worse than comparable competition kernels. The results in Table 3, however, show that the differences between the evaluation criteria of the unweighted and the weighted indices are not big at all and in two cases the unweighted competition index even produced better results than the exponentially weighted competition index. Obviously the contribution of the distance weights to the increment estimation should not be overestimated and in some situations they are not necessary.

One could also argue that the inclusion of distance weights in both competition measures automatically defines an implicit ZOI so that no additional modelling of an explicit ZOI is required. This certainly also seems to be the understanding of competition kernels in Miina and Pukkala (2002), although other authors like Schneider et al. (2006) use additional explicit ZOIs and even found superior results. To check up on this we applied the same ZOI definition that we successfully used for identifying competitors in the case of traditional competition indices to the corresponding kernels as well (see Table 5). The results reveal only marginal improvements (if any). Minor improvements can be reported for two of the fractional kernels and for two of the exponential kernels. These results indicate that competition kernels in fact do not require ZOIs.

It is interesting to note that exponential kernels always performed better than fractional ones whilst fractionally weighted indices on the other hand were superior to exponentially weighted indices.

5. Conclusions

Competition kernels are an intriguing concept and we can expect more interesting findings connected to them in the future. The theoretical grounds – both in terms of ecology and mathematics – are well established and promising. Our results also imply that traditional size-ratio measures of competition can still be used with sufficient success if there are good reasons for not abandoning them. As expected, the local neighbourhood or zone of influence of a tree definitely is the area in a forest stand where most interactions with other trees take place. However, judging by the results of this study the more flexible kernel approach appears to handle these complex interactions better. Since we used generic competition concepts, the authors believe that the findings of this study are also relevant to a wide range of other plant science experiments that make use of competition kernels (e.g. Purves and Law, 2002; Snyder and Chesson, 2004; Vogt et al., 2010). Generic and freely available R packages such as the recently published *siplab* package (García, 2014) further reduce the computational effort and may contribute to continued systematic research in this area.

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III

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Individual tree mortality of silver birch (*Betula pendula* Roth) in Estonia

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The functioning of complex forest ecosystems is intimately related to their structural properties. Tree mortality is a major driver of forest stand dynamics and therefore plays an important role in the formation of forest structure. Data from the Estonian Network of Forest Research Plots (ENFRP) was used to estimate the mortality probability of silver birch trees (*Betula pendula* Roth) by using logistic models. In this study several spatial and non-spatial variables were tested to determine the most important mortality explanatory factors. Additionally, thinning variables were defined and implemented into the mortality models, to examine whether thinning practices could modify the stand structure and density, then leading to a lower mortality rate. The results of this study showed that tree mortality models that included either a five-year diameter growth rate (id_5) as a measure of tree vitality, or the tree relative diameter (d_{rel}) as a measure of competition, or both these two variables, were substantially better than any models not including these variables. In addition, any measures of spatial aggregation (agg) and species proportion (*sp*) within the zone of influence markedly improved the model predictions, though the mortality probability of trees declined where there was higher aggregation and species mixture. Our results also suggested that if thinning were conducted around the birch trees, depending on the thinning intensity, the number of neighbors is effectively reduced, and consequently the competition load within the influence zone decreases, leading to healthier growth and lower mortality rates of the shade-intolerant birch trees. We thus recommend to adopt thinning regimes in mixed forest stands to foster tree species diversity, and at the same time provide adequate growing space for birch trees within the stands. This will improve the forest structure and increase the adaptive capacity of forests, which is increasingly important under changing climatic conditions.

Keywords: *Betula pendula* Roth, Diameter Growth, Species Proportion, Aggregation, Competition

Introduction

Tree mortality is an important driver of forest stand dynamics as it determines the formation of forest structure (Pederson 1998, Van Mantgem & Stephenson 2007). Structural properties of forests are of great importance since they are related to ecosystem functioning and productivity, in its growth and productivity (Bobiec 2002, Frolking et al. 2009).

Tree mortality occurs when tree vigor declines due to intolerance of the tree to the negative influence of stress factors, such as drought and competition. These stress factors can lead to a wide variety of causes of tree mortality. To achieve a better understanding of mortality, numerous attempts to categorize its causes have been reported (Vanclay 1994, Pederson 1998, Yang et al. 2003). As a simplified approach, mortality has been generally considered either as regular, due to competition or ageing, or as irregular, caused by ecological and catastrophic events, such as storm or fire (Monserud 1976). The probability of regular mortality is believed to be U-shaped, indicating relatively high mortality rates for small and large trees due to light competition and senescence, respectively (Monserud & Sterba 1999, Lorimer et al. 2001, Fraver et al. 2008). The probability of irregular mortality is rather fluctuating, and thus quite difficult to predict, since it may be triggered by various biotic and abiotic factors, which change temporally and spatially, *e.g.*, the attack of pests or diseases may cause a comparatively small mortality in one year, or eliminate the host species from the region (Vanclay 1994).

The ability of a tree to withstand stress factors is affected by a multitude of interacting factors such as tree size, tree viability, competition among trees and stand density (Hamilton 1986). However, diagnosing these factors as contributors to tree mortality and evaluating their relative importance can be very difficult (Das et al. 2008); especially in times of global changes it is important to broaden our understanding of tree mortality as a primary driver of changes in the composition and structure of forest communities. Maintaining a forest is essential to provide important services, such as carbon sequestration, water purification, and timber production, as well as future habitats for a large diverse number of species (Dietze & Moorcroft 2011).

Measurements of tree size can be easily

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collected (tree diameter and tree height) or computed (tree growth and tree basal area) and to some extent they contain valuable, but not sufficient, information about the probability of tree mortality (Monserud & Sterba 1999, Yang et al. 2003). Diameter growth rate (Buchman 1983), or as a substitute, crown size (Avila & Burkhart 1992, Monserud & Sterba 1999) have proven to be suitable measures of tree vitality in mortality studies.

Competition is the next well-documented contributor to tree mortality. Competition for limited resources (such as water, light and nutrients) is a fundamental ecological process, which has strongly modulated the mortality of suppressed trees (Keddy 1989, Szwagrzyk & Szewczyk 2001). Competition among individuals can be either asymmetric or symmetric. Under asymmetric competition, larger trees are not affected by smaller trees and can therefore benefit of a greater share of resources, whereas in symmetric competition all trees have an equal share of resources, and therefore impose some competitive influence on their neighbors, regardless of their sizes (Cannell et al. 1984, Freckleton & Watkinson 2001). Occasionally, some trees may withstand the competition pressure, but will eventually end up in a "death spiral" (Franklin et al. 1987), since trees suffering competition over long periods will weaken and eventually die due to other reasons (Wyckoff & Clark 2000, Antos et al. 2008, Lännenpää et al. 2008).

Theoretically, inclusion of the spatial effects in modeling the competitive environment that surrounds an individual tree is expected to improve the prediction ability of mortality (Biging & Dobbertin 1995). An increment in local density is assumed to increase the density-dependent mortality, or self-thinning, since many species are unable to endure deep shading in their dense neighborhood (He & Duncan 2000, Gómez-Aparicio et al. 2009). In young dense stands where trees are subjected to self-thinning, such assumption was proven to be valid (Oliver & Larson 1996). Several studies have been conducted to define the limit to the number of trees with a given average size growing in a stand (the so called "limiting density"), depending on the forest type and the environmental conditions (Reineke 1933, Zeide 1987, Hynynen 1993, Nilson 2006, Von Gadow et al. 2015). On the other hand, when stands grow to maturity, generally the size of surviving trees and their spacing increase, and stands become less clumped. In such stands the density-dependent mortality decreases, and trees may die because of other factors, such as pathogen and insect attacks (Kenkel 1988, Franklin & Van Pelt 2004).

Regarding the fact that any desired tree species may be absent due to self-thinning in a final regular stand, thinning during the early self-thinning years is an acceptable management tool to control stand quality and supports favorable tree species (Simard et al. 2004). Early thinning improves the tree growth by reducing the competition stress for the remaining trees (Oliver & Larson 1996), while the thinning of suppressed trees at intermediate development stages reduces economical loss from tree deaths (Perry 1985). Thinning to different reduced densities influences the tree mortality rate, and individual trees may react differently to the same treatment. For example, small trees survive better in a less competitive neighborhood (Uriarte et al. 2004), while the mortality rate of large trees increases due to exposing their crowns to strong winds when neighboring trees are removed (Thorpe et al. 2008).

We focused our study on the mortality of silver birch trees (*Betula pendula* Roth), an ecologically essential broadleaf tree species (Hynynen et al. 2010) and the second most important tree species in Estonia in terms of forest cover (31.2% and this coverage is expanding – Yearbook of Forest 2013). As a pioneer tree species (Fischer et al. 2002), silver birch grows naturally in boreal and northern temperate biomes. This species is intolerant to shade and remains vital and vigorous where it occurs as a dominant species in a relatively wide spacing, and under less favorable environmental conditions for other tree species (Hynynen et al. 2010).

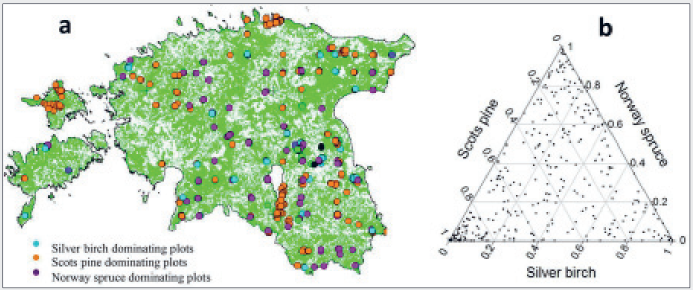


Fig. 1 – (a) The distribution of study plots throughout Estonia, and (b) the proportion of three major tree species within the study plots.

The main objectives of this study were to: (i) filter the variables that are meaningful for the mortality of silver birch trees; (ii) test these variables in an empirical model for their ability to predict mortality of silver birch trees; and (iii) examine whether thinning practices effectively minimize the rate of tree mortality in managed forests.

Materials and methods

Study data

Data from the Estonian Network of Forest Research Plots (ENFRP) was used for this study. This network, consisting of 730 permanent plots, was established during the period 1995-2004, and contains the data for all the main forest types in Estonia (Kiviste et al. 2015). The Republic of Estonia lies on the eastern shores of the Baltic Sea and along the southern shore of the Gulf of Finland (57.3°-59.5° N, 21.5°-28.1° E). The climate varies from maritime to continental. Average temperature ranges from 16.3 to 18.1 °C in July (the warmest month) and from -3.5 to -7.6 °C in February (the coldest month). Mean annual precipitation is within the range 600-700 mm, and decreases from east to west (Tarand et al. 2013).

Clear cutting is the predominant management system in Estonia; consequently overstory trees are mostly even-aged. Most stands have been managed to maintain pure stands, though near-natural situations can occur under good forest growth conditions in any stand after some decades without management. The ENFR permanent plots were circular with a radius ranging from 10 to 30 meters. Depending on the stand age and density, they were delineated so that every plot contained at least 100 trees in the overstory. Within each plot the azimuth, the distance from plot center, the diameter at breast height (d), the tree species identity, and any defects of trees were recorded. For every fifth tree, and also for dominant and rare tree species, the tree height and the height to the live crown base were also measured. The measurements were repeated at intervals of five years.

To carry out this study, we selected 422 research plots with three consecutive measurements where silver birch was present. Other plots of the ENFRP network were excluded because either the plots did not include silver birch or at least three measurements taken at five-year intervals were not available. We used the first five-year interval, *i.e.*, the period between the first and second measurements, for the evaluation of growth and thinning rates, and the second five-year interval, *i.e.*, the period between the second and third measurements, for the mortality study. During the first period, trees were harvested within 93 plots with different thinning intensity ranging from 0.1 to 80% of the total number of trees (0.3-60% of the basal area). Seventy-four plots were discarded from the analysis because thinning was practiced within the plots in the second interval, or before the first interval. Overall, 61 685 recorded tree measurements were considered in 348 selected plots. The species composition of the plots was 25.6% Scots pine (*Pinus sylvestris* L.), 33.9% silver birch, 26.8% Norway spruce (*Picea abies* L.) and 13.7% of several other species (*e.g., Alnus glutinosa* L., *Alnus incana* L. and *Populus tremula* L.). Fig. 1 shows the distribution of the selected study plots throughout Estonia (a) and the proportion of the three major tree species within those plots (b).

Predictors of tree mortality

Based on the concept of the influence-zone (Staebler 1951) we assumed an imaginary circle in which the center is defined by a tree, and its radius is 40% of the average height of trees in the first storey on each plot (Sims et al. 2009, Maleki et al. 2015). In order to avoid biased estimations due to the interference from immediate non-measured neighboring trees outside the plot boundary, we established a boundary strip (buffer zone) inside the monitoring plot with a width equal to the radius of the influence zone. The mortality study was performed only for trees inside the reduced plot (reference trees) for which the neighbors' information was available. The distribution of plots by the number of reference trees, and the plots with an average number of neighbors within the reference trees' influence zones by the radius of the influence zone are presented in Fig. 2a and Fig. 2b, respectively.

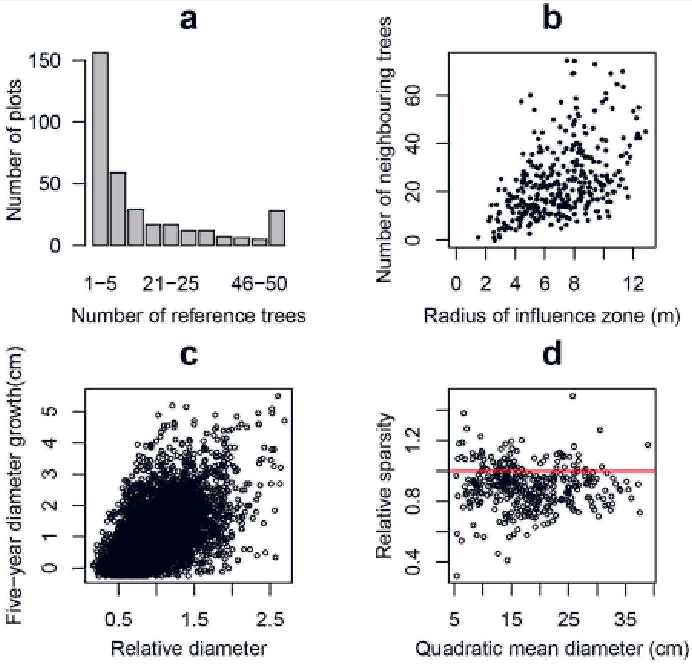


Fig. 2 – (a) Distribution of plots by number of reference trees within the studied plots; (b) relationship between the radius of the influence zone and the average number of neighbors within the reference trees' influence zones; (c) relationship between the five-year diameter growth and relative diameter in reference tree data set; (d) relationship between quadratic mean diameter and relative sparsity, where plot relative sparsity was calculated as limiting sparsity relative to stand sparsity: L_{lim} / L.

A list of selected variables studied for the contribution in tree death is provided in Tab. S1 of the Supplementary Material. As we here aimed to investigate the suitability of neighborhood spatial information to predict tree mortality, the variables were classified into spatial (where the neighboring trees' co-ordinates within the influence zones were required) and non-spatial (where the neighboring trees' co-ordinates were not used).

Non-spatial variables are simple functions of stand or tree level measurements. In Tab. S1 of the Supplementary Material the most common stand variables like density (N_{ha}), basal area (G, m^2/ha), site index (SI_{100}, m) and stand age (*age*, year), were calculated from plot data. Variables N_{ha} and G can be treated as measures of stand density (Eid & Tuhus 2001, Burgman et al. 1994), while G can be considered as a measurement of symmetric competition (Bravo et al. 2001). The site index SI_{100} was used to measure the site productivity, calculated as the average height of a stand at the reference age of 100 years (Nilson 1999).

For non-spatial tree level measurements the following variables were used: tree diameter at breast height (*dbh*, cm), relative tree diameter (d_{rel}) calculated as the ratio of tree and stand diameters, tree five-year diameter growth (id_5, cm), tree basal area (g, m^2), and the sum of the trees' basal areas (per plot) larger than the reference tree (BAL, m^2 ha^{-1} - Wykoff et al. 1982). The tree diameter integrates the past competitive interactions of the reference trees (Soares & Tomé 1999), while d_{rel} shows the dominance of a reference tree related to other trees in the stand. The tree diameter growth rate (id_5) is a measure of tree vitality often used in mortality models (Hamilton 1986, Das et al. 2007). Fig. 2c shows the relationship between the diameter growth and the relative diameter in the reference tree data set. Trees with negative diameter increment were not excluded from the data set in order to avoid bias toward positive growth, because the occurrence of undetectable overestimation of growth is unavoidable. The value of BAL can be used as a measure of asymmetric competition (Monserud & Sterba 1999, Yang et al. 2003). When considering the influence of the neighborhood, the alternative estimates of the relative diameter and the sum of the basal area of larger trees ($d_{rel.cz}$ and BAL_{cz}) were calculated only for trees within the influence zone around each reference tree.

Spatial variables in Tab. S1 of the Supplementary Material consisted of the well-known Hegyi (1974) competition index (CI) as a measure of neighbouring trees' competition, an aggregation index (agg - Clark & Evans 1954) to measure clumping and the different measures of species proportion (sp). Aggregation illustrates the spatial pattern of neighboring trees within the influence zone, where values < 1.0 indicate an aggregated distribution of trees, and values > 1.0 indicate a tendency toward a regular distribution. The species proportion defines the degree of spatial segregation of tree species in the stand. In this study the different values of sp were calculated as follows: (i) the proportion of silver birch trees (sp_{sb}); (ii) the proportion of other species that are not silver birch (sp); (iii) the proportion of Norway spruce trees (sp_{ns}); and (iv) the proportion of Scots pine and other deciduous trees (sp_T), for all neighboring trees within the influence zone.

An important issue in stand development is the self-thinning, when an increased density-dependent mortality rate is expected due to high competition among individuals. Traditionally, the allometric relationship between stand density (N_{ha}) and diameter (D) has been applied for approximating the self-thinning line (Burkhart & Tomé 2012). However, Nilson (2005, 2006) showed the advantage of using stand sparsity (L, m) by a transformation of the stand density (N_{ha} – eqn. 1).

$$L=\frac{100}{\sqrt{(N_{ha})}}$$

On the basis of normal growth and yield tables used in Estonia (*i.e.*, assuming that they describe the highest possible stand density), sparsity of silver birch stands in a self-thinning situation were calculated as follows (Vabariigi Valitsuse 2013 – eqn. 2).

$$L_{\lim}=\left(117+14.15\cdot\frac{D^2}{H}\right)/134$$

where D and H are stand quadratic mean diameter (cm) and mean height (m), respectively. Fig. 2d presents the relationship between mean square diameter and relative density ($L_{\lim}/L$) where dots with relative sparsity greater than 1.0 (69 studied plots including 17% of reference trees) crossed the self-thinning line.

Finally the thinning variables I_{thin} and CI_{red} were quantified, where I_{thin} is the non-spatial measure of the thinning intensity within the plots, and CI_{red} is the spatial measure of the reduced load of competition within the zone of influence, because of the removal of competitors during any thinning practices.

Model fitting and statistical analyses

Mortality is a discrete event that can only take two values (alive or dead), hence logistic functions are widely applied to model probability of tree mortality (Monserud 1976, Yao et al. 2001, Bravo-Oviedo et al. 2006). Since data from many plots were used and the number of reference trees were not equal for studied plots, we devised the mortality probability in a generalized linear mixed effects logistic regression for binary mortality data (eqn. 3). The predictors were combinations of different contributors to mortality (see Tab. S1 in the Supplementary Material) and the plot character was considered as a random effect that estimated the variability in different studied plots. The dependent variable was tree mortality during the second interval (last five-year period). The value of mortality was set equal to 1.0 when a tree was still alive at the time of the third measurement; otherwise the value was set to zero. Given p as the probability of tree survival, 1-p is the probability of tree mortality (eqn. 3):

$$logit(p)=\ln\left(\frac{p}{1-p}\right)=\alpha+\beta X+\gamma Z+\varepsilon$$

Assuming that v is the number of predictors, N is the number of observations, and n is the number of plots, then α is the model intercept, X is a $N\cdot v$ matrix of the v predictor variables, β is a v column vector of the fixed effects model coefficients, Z is the $N\cdot n$ design matrix for the random effect (the random complement to the fixed X), γ is a vector of the random effect (the random complement to the fixed β) and ε is a N column vector of the residuals for that part of p that is not explained by the model $X\beta+Z\gamma$.

Since the coefficient of determination is not appropriate when discrete variables are modeled (Bravo-Oviedo et al. 2006), the goodness-of-fit of the models was assessed using a log-likelihood statistic (loglik), Akaike Information Criteria (AIC), and Akaike weights (AIC$_{\text{w}}$). The probability that the model was the best with the lowest expected information loss was determined by the smallest value of AIC and the biggest AIC$_{\text{w}}$ (Wagenmakers & Farrell 2004). ΔAIC indicates the differences in AIC values between a given model and the model with the lowest AIC value. According to Burnham & Anderson (2002), we assumed that the models with ΔAIC < 2.0 had a "substantial empirical support" and that these models were almost equal, whereas the models with ΔAIC > 4.0 were considerably different. The accuracy of the models in correctly classifying the trees in dead/alive groups was also tested by the area under the receiver operating characteristic (ROC) curve (Bravo-Oviedo et al. 2006). The area under a ROC curve (AUC) quantifies the accuracy of the model, where values > 0.7 indicate good accuracy (Fawcett 2006). Also, a classification of alive and dead trees for each model was performed using the ideal cut-point, where the sensitivity (true mortality rate) and specificity (true survival rate) curves crossed (Hosmer & Lemeshow 2000). The *val.prob* function of the *rms* package in the R statistical software (R Development Core Team 2014) was used to assess the accuracy of the models, and to validate the predicted probabilities of the logistic fits against the observed mortality.

Models were developed and selected as follows. Initially, pairwise models were calculated between mortality and each variable presented in Tab. S1 (Supplementary Material). The importance of each variable in the pairwise fits was evaluated using the analysis of variances (ANOVA) and the 10 most effective variables were selected based on their AIC values. The significance of thinning variables, I_{thin} and CI_{red}, on mortality probability of silver birch trees was also tested. About 400 models were fitted with all possible combinations of these selected variables with the restriction that no model could simultaneously include variables representing a similar factor (*e.g.*, one model could only have either CI or BAL as a measure of competition). Models were then compared using AIC values, and the best models, as well as the models with an AIC$_{\text{w}}$ value greater than zero, were selected.

Finally, the contribution of thinning to the mortality of individual trees was assessed. To this purpose, variables I_{thin} and CI_{red} were separately added to the selected model as new predictors, and the changes to the quality measure of the full statistical model were investigated. For all models, the *glmer* function from the *lme4* package in the R statistical software was applied. Furthermore, for each combination of variables the variance inflation factor (VIF) was determined to ensure that the models were not strongly biased by multicollinearity.

Results

Over the 348 selected research plots the five-year mortality rate of silver birch trees was 9.67%, *i.e.*, out of 6009 silver birch reference trees 581 died. The mortality rate in pure stands was higher than in mixed stands (Tab. 1). There was a stronger survival probability for a silver birch tree when growing in a neighborhood that consisted of species other than birch, as the mortality rate decreased from 16.67% in a pure silver birch stand to 6.09% for single silver birch trees surrounded by other species, mainly Norway spruce and Scots pine.

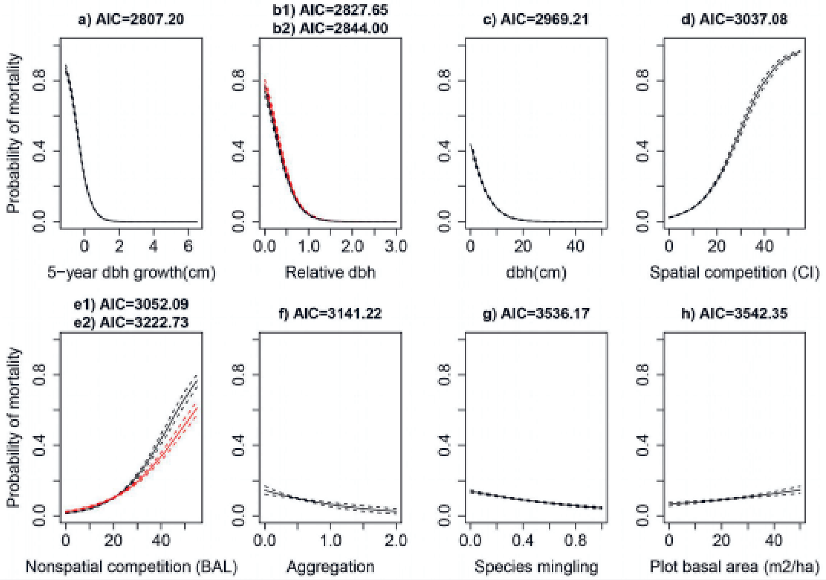
The results from the pairwise analyses indicated that tree growth (id_5), tree size (dbh), as well as competition ($d_{\text{rel.cz}}$, CI and BAL_{cz}), structure (agg and sp), and stand size (G), were the most important predictors of individual tree mortality (Fig. 3). The mortality probability of individual trees was negatively correlated with dbh, id_5, sp, and agg, but the correlation was positive for competition and stand size. The other studied variables (see Tab. S1 in the Supplementary Material) showed non-significant effects in the current mortality study. In an attempt to take the site quality into consideration, the site index at reference age of 50, and the site type as a nominal variable, as alternatives to SI_{100}, were also tested, but they did not provide any improvement to the model performance.

The highest ranked logistic models with different combinations of variables are presented in Tab. 2 in two categories: some models included only non-spatial mortality predictors, and both spatial and non-spatial variables were fitted into other models. The models consisting of spatial variables far exceeded those with non-spatial measurements in terms of AIC and AIC$_{\text{w}}$. The VIF values for all combinations were less than 3.0, indicating a low multicollinearity. Additionally, we tested different transformations of dbh, d_{rel} and id_5, and found them

Tab. 1 - Mortality rate of silver birch trees depending on silver birch proportion.

Proportion of birch in influence zone (%)	Number of reference trees	Number of plots	Mortality to survival rate	Mortality rate (%)
81-100	864	39	0.20	16.67
61-80	1606	88	0.13	11.27
41-60	1526	138	0.08	7.55
21-40	1274	173	0.08	7.53
0- 20	739	246	0.06	6.09

Fig. 3 - Predicted mortality probability of the most important predictors of the tree mortality (solid lines) with 95% confidence (dashed lines) in pairwise relationship between mortality and predictor variables. b1 (black lines) and b2 (red lines) refer to variables d_{rel} and $d_{rel.cz}$, while e1 (black lines) and e2 (red lines) refer to the variables BAL and BAL_{cz}, respectively.



Tab. 2 - Mortality probability analyses of silver birch using different spatial and non-spatial variables. id_5 is the five-year diameter growth of reference trees (cm); dbh is the diameter of reference tree at breast height (cm); d_{rel} and $d_{rel.cz}$ are the relative dbh of reference trees for each plot and zone of influence, respectively; G is the total basal area of trees within the plot (m^2ha^{-1}); BAL and BAL_{cz} are the sum of basal area of trees larger than the reference tree within the plot and the influence zone, respectively (m^2ha^{-1}); CI is the Hegyi's competition measure of neighbouring trees inside the zone of influence; agg is the aggregation measure of trees inside the zone of influence and sp is the proportion of other species than silver birch within the influence zone. AIC, ΔAIC, AUC and loglik are the statistical measures of the models. TPR and TNR are the sensitivity and specificity of the models, respectively.

Variables	AIC	ΔAIC	AUC	TPR	TNR	loglik
Id_5, d_{rel}, sp, agg	2583.64	0.00	0.819	0.828	0.856	-1285.8
Id_5, d_{rel}, sp	2590.37	6.73	0.819	0.833	0.853	-1290.18
Id_5, d_{rel}, agg	2593.54	9.90	0.820	0.812	0.866	-1291.77
Id_5, $d_{rel.cz}$, sp	2593.82	10.18	0.818	0.816	0.861	-1291.91
Id_5, $d_{rel.cz}$, sp, agg	2596.56	12.92	0.818	0.818	0.862	-1294.78
Id_5, d_{rel}, dbh	2600.86	17.22	0.820	0.816	0.862	-1295.43
Id_5, $d_{rel.cz}$, agg	2601.25	17.61	0.817	0.809	0.864	-1295.63
Id_5, d_{rel}	2603.11	19.47	0.820	0.833	0.854	-1297.55
Id_5, d_{rel}, G	2605.08	21.44	0.820	0.831	0.854	-1297.54
Id_5, $d_{rel.cz}$, dbh	2605.17	21.53	0.818	0.831	0.851	-1297.58
Id_5, $d_{rel.cz}$, G	2617.09	33.45	0.818	0.809	0.860	-1303.55
Id_5, dbh, CI	2619.02	35.38	0.818	0.833	0.855	-1304.51
id_5, dbh, BAL	2619.27	35.63	0.818	0.821	0.858	-1304.63
id_5, dbh, agg	2625.64	42.00	0.818	0.833	0.852	-1307.82
id_5, dbh, BAL_{cz}	2629.66	46.02	0.817	0.819	0.859	-1309.83
id_5, dbh, G	2633.34	49.70	0.818	0.824	0.859	-1312.67

inferior to the untransformed variables (data not shown).

Fig. 4 shows a comparison of the predicted mortality probability of reference trees with their observed mortality probability for the best logistic model. The predictive performance of the best model was good; however, a closer analysis of the estimated mortality probability revealed an evidence of negligible overestimation of the mortality prospects of very small silver birch trees (d_{rel}<0.2) with low survival probability, and also a slight underestimation of the mortality probability of the small proportion of large silver birch trees (dbh > 40 cm, see sensitivity and specificity values in

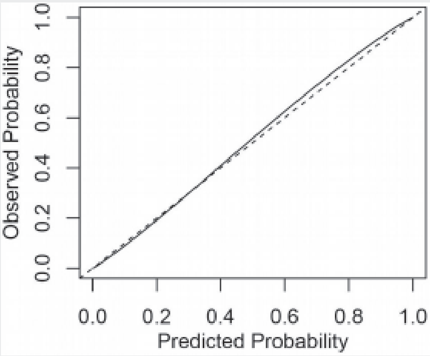


Fig. 4 - The predicted mortality probabilities of the best logistic model against observed mortality. The dashed line represents the ideal probability estimation and the solid line shows how the model fits observed mortality probabilities.

Tab. 3 - The best combinations of variables predicting silver birch mortality when thinning is included as predictor in the model used. (id_5): five-year diameter growth of tree (cm); (d_{rel}): relative *dbh* of reference trees for each plot; (Ci_{red}): Hegyi's competition measure of thinned trees inside the zone of influence; (I_{thin}): thinning intensity of the plot; (*agg*): aggregation of trees inside the zone of influence; (*sp*): proportion of other species than silver birch within the influence zone. ΔAIC and AIC_w are the statistical measures of models. AUC, TPR and FPR are area under curve, true positive rate and false positive rate of dead trees, respectively. $Coeff_i$ are coefficients of the models. TPR and TNR are the sensitivity and specificity of the models, respectively.

Variables	ΔAIC	AIC_w	AUC	TPR	TNR	Intercept	$Coeff_1$	$Coeff_2$	$Coeff_3$	$Coeff_4$	$Coeff_5$
id_5, d_{rel}, sp, agg, CI_{red}	0.00	0.655	0.819	0.833	0.856	2.324	-1.977	-3.263	-1.1053	-1.008	-0.195
id_5, d_{rel}, sp, agg	2.49	0.189	0.819	0.828	0.856	2.327	-1.985	-3.232	-1.103	-1.054	-
id_5, d_{rel}, sp, agg, I_{thin}	2.86	0.157	0.819	0.811	0.863	2.303	-1.981	-3.262	-1.098	-0.993	-1.273

Tab. 3). More detailed examinations also revealed that some models had overestimated the likelihood of smaller tree survival. Moreover, a tendency to underestimate the survival likelihood of silver birch trees with small relative diameters in the unthinned plots was detected.

As shown in Tab. 3, the inclusion of the non-spatial variable I_{thin} in the best model did not seem to improve its performance. However, a significant improvement was observed when the spatial thinning variable Ci_{red} was included. Thus, thinning practices in silver birch stands demonstrated that there was a negative influence on the probability of tree mortality (see $Coeff_5$ in Tab. 3) by reducing the competition. Therefore, an excessive decrease in the number of trees due to high thinning intensity, and consequently a reduction in competition, could also decrease the tree mortality rate (from 10.1% in unthinned plots to 6.6% in thinned plots). Additionally, the accuracy estimated by AUC was excellent (AUC>0.8) for all the models in Tab. 3 (Hosmer & Lemeshow 2000). These high values indicated that many of the dead trees (true positives) were correctly classified.

Discussion

Drivers of silver birch mortality

In this study, the silver birch trees with an increasing diameter growth rate clearly indicated an increment in survival. Recent radial growth has been frequently used as an indicator of tree health and vigor (Kobe 1996, Yao et al. 2001). Accordingly, it is biologically meaningful to assume an improved survival for trees showing higher growth rates, while the opposite is expected for trees showing feeble growth. As a consequence, the probability of any tree to survive can be inferred from its diameter increment (Waring 1987). On the other hand, since radial growth rate varies systematically by tree size after an initial increase, the radial growth rate often decreases as the tree diameter increases, and therefore, diameter growth rate tends to overestimate the mortality probability of bigger trees as compared with smaller trees. It has been proposed that basal area growth rate is a better measure of tree survival than diameter growth rate (Pederson 1998, Ireland et al. 2014). Basal area growth rate represents the tree mass growth more closely, as it increases with tree size (Clark & Clark 1999, Di Filippo et al. 2012). Similar to Das & Stephenson (2015), our results did not indicate any better prediction of tree mortality when basal area growth is included in the model (data not shown). On the other hand, we observed a systematic overestimation of the mortality probability of small birch trees.

While the mortality of small birch trees in young and dense stands increased due to self-thinning (Barnes et al. 1998), in older stands the high mortality of small trees can be attributed to the suppression by dominating trees- where the non-spatial explanatory variable d_{rel} appeared superior to capture this trend. By some means, the hierarchical position of trees within the stand is measured by d_{rel} and indirectly indicates their competitive status (Burkhart & Tomé 2012). We found that competition is a significant mortality driver, in accordance with the extensive literature corroborating such relationships in the Estonian forests (Laarmann et al. 2009, Sims et al. 2009) and in other forests (Monserud et al. 2004, Temesgen & Mitchell 2005, Bravo-Oviedo et al. 2006, Das et al. 2011). Moreover, the reversed J-shaped (L-shaped) size-dependent mortality pattern of our studied trees (Fig. 3) can be explained by the insufficient number of large trees, and the high mortality rates of young trees within the stands where the competition for resources is high (Coomes & Allen 2007, Olano et al. 2009, Dietze & Moorcroft 2011).

The competition-induced mortality is presumed to decline as local tree density decreases, and the overall plot density showed to be related to the strength of competitive effects (Gonzalez et al. 2004, Temesgen & Mitchell 2005). The variable d_{rel} could have served as a simple index of competition, but it did not take the variation of stand density into account. Therefore, equipping the model with spatial measures that represented the neighborhood properties of reference trees did appear unavoidable. Surprisingly, contrary to our assumption, adding the new calculations of BAL (BAL_{cz}) and d_{rel} ($d_{rel.cz}$) only for immediate neighbors inside the influence zone diminished the predictive power of the model. This can be explained by the expected increasing uniformity in tree spacing with tree age or size, due to mortality from competition (Jose et al. 1991, Moeur 1997, Druckenbrod et al. 2005). Therefore, for some small birch trees in old and regular stands, and also for some big birch trees in young and clumped stands, the real values of competition and relative diameter may not be measured by considering the influence zone (here as a ratio of stand height). Finally, the inclusion into the model of the aggregation measure (agg) could take into consideration the horizontal spatial arrangement of tree positions inside the influence zone. The aggregation index has been successfully used to assess the regularity of tree positions (Pommerening 2002, Aguirre et al. 2003, Brumelis et al. 2005). In our study, agg efficiently proved the negative influence of clumping (agg<1) on the survival prospects of birch trees (see Tab. 3, negative coefficients for agg in the mortality models).

Several studies reported that the competition and growth of silver birch trees, and consequently their survival prospects, are strongly related to the identity of neighboring species (Kaitaniemi & Lintunen 2010, Jõgiste 2010, Hynynen et al. 2011). Their findings are consistent with our results, in that including sp to the best non-spatial mortality model definitely improved its fit. The mortality likelihood of a birch tree was negatively related to the species mixture of its immediate neighbors (decreasing from pure stands to mixed stands - Tab. 2, Tab. 3). According to the Janzen-Connell's type effect, this may be caused either by the increased risk of attack by species-specific herbivores or diseases, when a silver birch tree grows in close proximity to many other con-specifics (Janzen 1970, Connell 1971). Also, the inter-specific competition among hetero-specific individuals (mainly Norway spruce and Scots pine) appeared lower than the competition among conspecific individuals (*i.e.*, neighboring silver birch trees). Due to a similar demand for light and resources, the competition among neighboring silver birch individuals increases, and therefore the competition-induced mortality is relatively high. Norway spruce and birch trees have similar site requirements, but when occurring together the formers seem more shade-tolerant than the light-demanding birches, and also show different temporal growth patterns (Tahvanainen & Forss 2008, Hynynen et al. 2011). Moreover, birch trees easily overwhelm and suppress the shade-intolerant Scots pine trees due to their vigorous early growth (Hynynen et al. 2011); however, their co-occurrence is relatively infrequent due to different site requirements.

The effect of thinning on silver birch mortality

Thinning to different residual densities produces varying effects on tree mortality, depending on the tree species with different characteristics and site conditions (He & Duncan 2000, Canham et al. 2001, Uriarte et al. 2004). Some studies have found a higher mortality risk during the first years after thinning, either due to mechanical damage to the remaining trees (Nyland 1994, Caspersen 2006), or by shifting the population towards smaller trees more prone to environmental stresses, or even to windfall for larger residual trees on the margin of cutting areas (Jönsson et al. 2007, Fortin et al. 2008). In contrast, some studies have reported that thinning operations may rescue trees from density-dependent mortality (Powers et al. 2010). In our case, the mortality of silver birch trees was affected negatively by thinning operations within the plots (up to 3.5% decline in mortality rate of birch trees in thinned stands). The slight improvement of performance of the mortality model obtained by including CI_{red} indicated that the competition imposed by neighboring trees, which were cut during the thinning operation, partially limited the survival of birch trees. As explained before, density-dependent mortality or self-thinning (Drew & Flewelling 1977) occurs when the stand sparsity is smaller than the limiting sparsity. Thinning operations have successfully increased the stand sparsity, and released the shade-intolerant birch trees that showed a vigorous growth within a less competitive environment.

Data limitation

The areas included in the Estonian Network of Forest Research Plots (ENFRP) were mostly located in managed forests, *i.e.*, only a few old dense stands were measured in this study. The record of the age of individual trees was not available and the age was only determined for tree cohorts. Since regular mortality of a tree could be dependent on its age (Monserud 1976), including the exact age of trees may have improved the model's strength. However, determining the age of individual trees in practical forest management is too laborious. Another factor of uncertainty is the inclusion of small plots when applying spatial variables. As mentioned above, a buffer zone inside the plot (near the plot boundary) was applied to avoid the biased estimations due to edge effects. Consequently, a relatively large number of trees were excluded from mortality analyses, and this loss was more relevant for small plots. However, for the simulation of the neighborhood, a border method (Ripley 1981) was used as a means to eliminate this effect, as described by Lilleleht et al. (2014). This method is simple to implement in comparison with other methods, and guarantees the removal of all edge effects (Kint et al. 2004).

Additionally, one might expect that building the mortality model to include soil descriptors and climate variables will also improve its performances. In this study, mortality was assessed over periods of five years as the exact year of tree death was unknown. Thus, it was difficult to connect extreme events, such as very cold temperatures or hot summers, which can usually cause high tree mortality. Regarding the costly assessment of annual tree mortality and soil analysis around individual trees for large data sets, a dendrochronological analysis seems to be a more effective method for climate studies (Linares et al. 2009). Further studies are needed to investigate the efficiency of the mentioned variables and other possible mortality predictors in defining the live/death status of individuals.

Conclusions

Natural mortality of individual trees is a stochastic and irregular phenomenon for which we attempted to find the most relevant explanatory variables. Although a number of known and unknown factors affecting tree mortality makes its modeling complicated, the fitted models used in this study did produce results that satisfactorily explained mortality of Estonian silver birch trees. Five-year diameter growth, relative diameter, species proportion, and aggregation were the most appropriate explanatory variables in our mortality models. In order to maintain high survival probabilities, forest management plans and practices should pay a special attention to growth performances of trees, species compositions, tree density and forest stand structure. Furthermore, the reduction of stand density would provide more growing space for light-demanding birch trees, as demonstrated by the reduced mortality predicted by our model when thinning was included as predictor. However, root and stem damage caused by heavy machinery used for thinning operations, and the higher wind exposure of trees after thinning should also be considered. Finally, based on our results, silver birch trees should preferably be managed in mixed stands where they occur along with other tree species, and attempts should be made to minimize the clumping (*agg*>1) within their neighborhoods.

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Supplementary Material

Tab. S1 – List of variables used to study silver birch mortality.

Link: Maleki_1672@suppl001.pdf

IV

Maleki, K., Kiviste, A. 2016. Effect of sample plot size and shape on estimates of structural indices: A case study in mature silver birch (*Betula pendula* Roth) dominating stand in Järvselja. *Forestry Studies*, 63, 130–150.

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Effect of sample plot size and shape on estimates of structural indices: A case study in mature silver birch (*Betula pendula* Roth) dominating stand in Järvselja

Kobra Maleki[*] **and Andres Kiviste**

Maleki, K., Kiviste, A. 2015. Effect of sample plot size and shape on estimates of structural indices: A case study in mature silver birch (*Betula pendula* Roth) dominating stand in Järvselja. – Forestry Studies | Metsanduslikud Uurimused 63, 130–150. ISSN 1406-9954. Journal homepage: http://mi.emu.ee/forestry.studies

Abstract. Structural indices and characteristics have often been employed for assessing different aspects of forest stands. In order to assess the performance of such measures in forest sample plots of different size and shape, the current study is based on a data set for a relatively large (1 ha) silver birch dominated stand, and five simulated planar point patterns (a Poisson process, two clustered and two regular patterns) with similar intensity of points distributed on an area equal to the silver birch stand as reference stands. The analyses was based on repeated samplings of the stands, with randomly placed circular or square shaped plots of different sizes, with area ranging from 0.007 to 0.636 ha. Similar centre positions were considered for plots of different shapes, but the locations of the plot centres differed with size, so that plots of different sizes were able to cover the maximum possible area of reference stands. Some structural indices accounting for one or four nearest neighbours, and also the Point-pair correlation function was then quantified for each random sample plot. We used standard deviation and the differences of the mean estimates from the expected values to assess the sensitivity of the structural measures to the size and shape of sampling plots. The results indicated the significant effect of plot size and shape on structural indices. The correlation between plot size and estimates precision was positive, and small plots, regardless of their shapes, showed big variation among them while circular plots often provided more accurate estimates. Even though, as expected, expanding the plots increased the precision of the neighbourhood-based indices' estimates (spatial measures), and also resulted in inaccurate estimates for some reference stands, depending on the arrangement of trees/points within that stand.

Keywords: *Betula pendula*, spatial indices, point patterns, circular plot, square plot, nearest neighbour.

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Introduction

Forests are complex ecosystems and their structural attributes are of great importance (Franklin *et al.*, 2002; Kint *et al.*, 2004). Spatial alignment of individual trees and distribution patterns of their size and species are known as major components of forest stand structure (Gadow & Hui, 1999; Lingua *et al.*, 2008). The structural properties of forests are believed to be related to their ecosystem functioning (Naumburg & DeWald, 1999; Bobiec, 2002; Sallabanks *et al.*, 2002; Frolking *et al.*, 2009). Evidently, growth of trees is influenced by the species composition, spatial structure, and dynamics of forest stands and also anthropogenic effects (Navarro-Cerrillo *et al.*,

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2013), and in return the dynamic processes of growth and disturbance are reflected in the structural components of forests (Rice *et al*., 2004; Unger *et al*., 2013).

Regarding the importance of the mentioned components in analysing forest ecosystems and their dynamics, numerous indices and statistical techniques for quantifying stand structure have been developed and compared (e.g. Gleichmar & Gerold, 1998; Kint *et al*., 2000, 2003; Pommerening, 2002). The majority of structural indices have been divided into two main groups: non-spatial and spatial measures. Some specific structural properties of forests, such as tree diameter distribution and tree species composition belong to the first group, which do not need any spatial reference and often they are quite simple to assess, and can be used for more complex assessments (Palace *et al*., 2015). The second group is based on positions of trees and it can be subdivided into the following subcategories: individual tree parameters based on neighbourhood relations, spatial measures of forest stand structure at stand level, and continuous functions of inter-tree relations (Pommerening, 2002). Neighbourhood relations of trees, based on their nearest-neighbours, account for small-scale differences and are appropriate, as well as easy to calculate and interpret (Kint *et al*., 2003). Stand level spatial indices often describe aspects of variability of individual tree locations within stands by a single value whilst continuous functions are more complex, using techniques to examine the second-order effects, and take all possible inter-tree distances within the stand into account (Dale, 2000; Pommerening, 2002; Law *et al*., 2009). Forests in different development stages and conditions, when considering the trees as stationary points, represent different point processes. For instance, (1) older forests may present a regular pattern, where trees have been thinned out earlier, either due to inter- and/or intra-specific competition leading to self-thinning, or because of management activities, (2) a clustered pattern may be found in young forests consisting of trees with heavy seeds or with any heterogeneous conditions forming trees in groups, and finally (3) a random pattern, Poisson process, is common in most forests (Tomppo, 1986; Pommerening, 2002), and it is a situation between two recent patterns (Pommerening, 2006).

Since spatial indices require information about tree positions, and obviously the collection of such data is expensive and time-consuming (Kint *et al*., 2004). Considering the facts that forest spatial pattern heterogeneity at different scales is an important component of their structural complexity (Churchill *et al*., 2013) and the plot size has a direct effect on the assessment of general stand characteristics, such as stand density and stand basal area (Corona *et al*., 1998), appropriate sampling methods, either in size or by shape, must be used (e.g. Füldner, 1995; Pommerening & von Gadow, 2000). Various sampling approaches can be properly applied, considering the specific objectives of designing forest monitoring plots, in order to define the degree of precision and accuracy required through a benefit-cost analysis (Corona & Marchetti, 2007; Travaglini *et al*., 2013; Lombardi *et al*., 2015).

To date, several data sources have been established in Estonia for forest growth assessment and yield modelling, the main sources being those of the National Forest Inventory (NFI) and the Estonian Network of Forest Research Plots (ENFRP). The NFI sample plots are circular with systematic design, and cover the entire area of Estonia, and are planned in a five-year cycle. The sampling intensity is the same throughout the country, having a cluster distribution with the aim of increasing the efficiency of the survey, and keeping the accuracy requirements at a national level. Trees are measured in the NFI sample plots with radii of 7 and 10 m, for temporary and permanent plots, respectively (Adermann, 2010). The ENFRP consists of

729 permanent plots, containing the data for all the main forest types in Estonia (Kiviste *et al.*, 2015). The permanent plots are circular with a radius ranging from 7 to 30 m and are measured at intervals of every five years.

For this study, in order to check how well the stand structure variables can be estimated within the Estonian plots, we carried out an experiment for a detailed investigation to view the influence of the sampling plot size on the assessment of some structural indices for a one-hectare silver birch dominated plot and five simulated point patterns. Since circular and square-shaped sample plots are commonly used in forest mensuration (van Laar & Akça, 2007), the square plots of varying size were also implemented, and compared with the circular plots for the forest structural study. Therefore, the main objective of our study is to assess the sensitivity of the structural indices' estimates to the size and/or shape of the sample plots, within the varying structural complexity of a silver birch dominated stand and five other simulated point patterns.

Material and Methods

Study area

The study area consisted of one hectare (100 m × 100 m) stand which was dominated by 54 years old silver birch trees, established for Radiation Model Intercomparison (RAMI) study (Kuusk *et al.*, 2013), located in Järvselja Training and Experimental Forest Centre; compartment JS228 (latitude: 58° 15′ 54.60′′, longitude: 27° 16′ 57.97′′). Within the stand the growth conditions are good and the total number of 968 trees on the typical brown gley-soil was re-measured in 2013, and with the first measurement done in 2007. The RAMI stand consists primarily of deciduous tree species including: 57% silver birch (*Betula pendula* Roth), 29.5% common alder (*Alnus glutinosa* (L.) Gaertn.) and 11% aspen (*Populus tremula* L.). A thinning operation was carried out in the stand during September-October 2004. Based on the social status of the trees, the mentioned deciduous species formed the first layer, and the second tree layer mostly consisted of small leafed linden/lime (*Tilia cordata* Mill.) and Norway spruce (*Picea abies* (L.) H. Karst.) while the understory vegetation was dominated by a mixture of several grass species (Kuusk *et al.*, 2013).

Sampling simulation

The analysis of the effect of sample plot size and shape consisted of several simulated samplings of the stand with randomly placed plots. For our circular sample plots, with 41 different radii ranging from 5 to 45 m and increasing by one meter, were then selected so that the Estonian plot sizes were included within this range. For every plot size, 1,000 random centres were independently generated. Also, depending on radius, a buffer zone of trees near the stand borders was considered when determining the sample plot centres, with its width equal to the sample plot radius. Subsequently, the simulated sample plots could be always, thoroughly improvised inside the RAMI stand. Square plots were formed around each random centre defined for the circular plots with the restriction that they cover an area equal to the area of the corresponding circular plot.

A forest stand can be reduced to a finite set of points to represent the horizontal locations of trees in the stand, and the assumption is that the two-dimensional alignment of tree positions in a stand can be described by a point process (Penttinen *et al.*, 1992). Therefore, in order to test the sensitivity of structural indices to different point patterns, five different planar point patterns were generated with the condition that these virtual plots cover an area equal to the RAMI stand, and with almost the same intensity. In those patterns, each point defined by its position can represent a tree in the virtual plot using

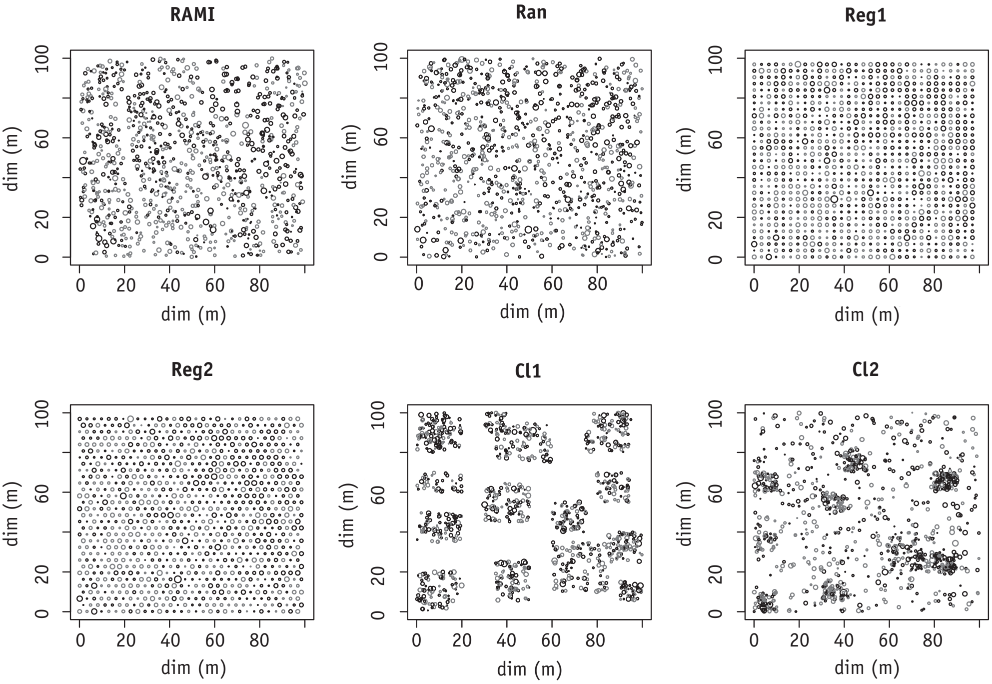

Figure 1. Reference stands patterns including RAMI stand and five simulated point patterns; grey circles of different sizes are silver birch trees with their corresponding size and black circles are other species.

Joonis 1. Uurimisala RAMI puistu ja viie simuleeritud virtuaalse puistu puude paigutuse mustrid; hallid ringid vastavad arukasele, mustad ringid teistele puuliikidele ja ringi raadius on võrdeline puu diameetriga.

two-dimensional Cartesian coordinates (Pommerening & Stoyan, 2006). The simulated patterns are: 1) a Poisson process or random pattern (Ran); 2) an extreme clustered pattern (Cl1); 3) a moderate clustered pattern (Cl2), where both cluster centres follow the Poisson process and the cluster points are randomly distributed in circles of various radii around the centres; or 4) & 5) two types of regular patterns (Reg1 & Reg2). Also in order to keep the similar species composition and diameter distribution, the diameter and species identity of trees within the RAMI stand were assigned to the points in the simulated stand. For this step, the trees in the RAMI stand and the points in the simulated patterns were ranked based on their distances and angles from the stand centre, and the points got the diameter and species identity of trees in the RAMI stand having similar ranks. Therefore, the next step was to explore the effect of the sample plot size and shape on structural indices' estimates, and we were also able to test the effect of different spatial alignment of trees. For the five simulated patterns a sampling method similar to the RAMI stand with the same plot centres was applied. Therefore the RAMI stand and five simulated patterns, as shown in Figure 1, formed our reference stands for this study.

Structural indices

Structural indices applied on simulated sample plot data are presented in Table 1. Five indices describe stand spatial structure by single values, and are based on

Table 1. List of structural indices used for the study.

Tabel 1. Uurimuses kasutatud struktuuriindeksite loetelu.

Variable *Muutuja*	Description *Kirjeldus*	Calculation *Arvutusvalem*	Type *Tüüp*
agg	Aggregation index *Agregatsiooniindeks*	$\frac{L_{obs}}{E(L)}, E(L) = \frac{1}{2 \times \sqrt{n/A}}$	NN1
ddf	Diameter differentiation index *Diameetri diferentseerumisindeks*	$1 - \frac{\min(dbh_i, dbh_j)}{\max(dbh_i, dbh_j)}$	NN1
ua	Uniform angle index *Puude paiknemisindeks*	$\frac{1}{n}\sum_{j=1}^{n=4} w_j \text{ where } w_j = \begin{cases} 1 \text{ if } \alpha < 360°/5 \\ 0 \text{ if } \alpha \geq 360°/5 \end{cases}$	NN4
ddm	Diameter dominance index *Diameetri domineerimisindeks*	$\frac{1}{n}\sum_{j=1}^{n=4} v_j \text{ where } v_j = \begin{cases} 1 \text{ if } dbh_j < dbh_i \\ 0 \text{ if } dbh_j \geq dbh_i \end{cases}$	NN4
ming	Species mingling index *Liikide segunemisindeks*	$\frac{1}{n}\sum_{j=1}^{n=4} m_j \text{ where } m_j = \begin{cases} 1 \text{ if } Species_j \neq Species_i \\ 0 \text{ if } Species_j = Species_i \end{cases}$	NN4
g(r)	Point-pair correlation function *Radiaaljaotuse funktsioon*	$g(r) = \frac{\lambda}{\lambda_0}$	N-N

Notes: L_{obs} and $E(L)$ are the mean distance to the first nearest neighbour and the mean nearest neighbour distance in a stand in the case of completely random tree locations, respectively; n and A are the number of trees and area of the observation window, respectively; dbh_i and dbh_j are the diameter at breast height of the reference tree i and its neighbour j, respectively; α is the angle pointing away from the reference tree to neighbours; λ is the intensity of points at distance r from an arbitrary point and λ_0 is the expected intensity for a Poisson process.

Märkused: L_{obs} ja $E(L)$ on puu keskmine kaugus lähima naabrini ja lähima naabri oodatav keskmine kaugus puude täiesti juhusliku paigutuse korral, kus n and A on vaatlusakna puude arv ja pindala; dbh_i ja dbh_j on vaadeldava puu i ja naaberpuu j rinnasdiameetrid; α on vaatluspuu ja kahe naaberpuu vaheline nurk; λ on puude tihedus juhuslikust punktist kaugusel r ja λ_0 on puude oodatav tihedus puude täiesti juhusliku paigutuse korral.

nearest-neighbour relations as follows: the aggregation index (Clark & Evans, 1954) and diameter differentiation index (Füldner, 1995; Pommerening, 2002) using only the nearest neighbour while diameter dominance (von Gadow & Hui, 2002; Aguirre *et al.*, 2003), uniform angle index (Hui & von Gadow, 2002) and species mingling (Füldner 1995; Aguirre *et al.*, 2003) are single tree based indices accounting for 4 nearest neighbours.

The aggregation index (*agg*) describes the aspects of the variability of tree locations in the stand and is defined as:

$$agg = \frac{L_{obs}}{E(L)}, E(L) = \frac{1}{2 \times \sqrt{n/A}} \quad (1)$$

where L_{obs} is the mean distance to the first nearest neighbour, $E(L)$ is the mean nearest neighbour distance in a stand, in the case of completely random tree locations, A is the area of sample plots, as observation windows, and n is the number of trees. The expected value of the aggregation index in the case of completely random tree locations is equal to 1, where values less than 1 indicate a clustered distribution of trees, and values greater than 1 point to a tendency to being regular.

Diameter differentiation index (*ddf*) as a single-tree based measure of biodiversity of tree dimensions illustrates the spatial distribution of tree sizes as follows:

$$ddf_i = 1 - \frac{\min(dbh_i, dbh_j)}{\max(dbh_i, dbh_j)} \qquad (2)$$

where dbh_i and dbh_j are diameter at breast height for tree i and its nearest neighbour j. Values equal to zero indicate equal size of neighbouring trees.

Diameter dominance index (*ddm*) is another measure of biodiversity of tree dimensions and is calculated as follows:

$$ddm_i = \frac{1}{n}\sum_{j=1}^{n=4} v_j \qquad (3)$$

where $v_j = 1$ if the neighbour for a tree has smaller dbh than that tree, otherwise $v_j = 0$. The *ddm* value ranges between 0 and 1 and values equal to 1 refer to the dominance of the tree to its nearest neighbours by dbh.

Uniform angle index (*ua*) defines the degree of regularity of the spatial distribution of tree positions in a stand, and it is considered as a single-tree based alternative to the *agg* (von Gadow *et al.*, 1998):

$$ua_i = \frac{1}{n}\sum_{j=1}^{n=4} w_j \qquad (4)$$

If $\alpha_0 = 360°/5$ and α is the angle pointing away from a tree to its neighbours; $w_j = 1$ when $\alpha < \alpha_0$, otherwise $w_j = 0$. The *ua* value ranges between 0 and 1, where value equal to 0 refers to regularity and value equal to 1 shows clustering.

Species mingling index (*ming*) defines the degree of spatial segregation of the tree species in a stand, and gives the proportion of four nearest neighbours which do not belong to the same species as the reference trees:

$$ming_i = \frac{1}{n}\sum_{j=1}^{n=4} m_j \qquad (5)$$

where $m_j = 1$ if the neighbour for a tree is of a different species, otherwise $m_j = 0$. The *ming* value ranges between 0 and 1, where values equal to 0 refer to the tendency of species to be segregated and values equal to 1 show that a tree is surrounded by other species. Compared to *agg*, single-tree based indices do not result in a single value, but in a value for each tree within the stand, for describing a whole stand by a specific index, the mean value for that stand is calculated.

Finally, in order to describe the spatial structure of the RAMI stand and the five simulated point patterns on a continuous basis, not only by a single value but also with a function, the radial distribution function (Diggle, 1983) or on the other hand, the point-pair correlation function (Cressie, 1993), depending on the inter-tree distance, was calculated:

$$g(r) = \frac{\lambda}{\lambda_0} \qquad (6)$$

where, λ is the intensity of points at a distance r from an arbitrary point and λ_0 is the expected intensity for a Poisson process. The interpretation is similar to *agg*, where $g(r) = 1$ refers to randomness, where spatial distribution of trees/points are not correlated, $g(r) < 1$ suggests inhibition between points and $g(r) > 1$ shows clustering.

The edge effect correction

An important issue which should be addressed when dealing with spatial indices is the edge effect of trees standing near the edge of a sample plot, and the fact that the detected neighbours may not be their actual or real nearest neighbours. Ignoring this effect could result in inaccurate statistical estimates. To eliminate this error a border method was applied (Ripley, 1981). To apply this method a buffer zone was implemented near the stand boundary. Depending on the indices, for a tree located within or near the stand border, the distance from its nth nearest neighbour (e.g. first or fourth nearest neighbour) and the distance of that tree to the border were checked, and then the tree was excluded from the spatial indices calculation if its distance to the border was shorter. However, that tree could only serve as the nearest neighbour to other trees (Pommerening & Stoyan, 2006). This method guarantees the removal of all edge effects and, in comparison with other methods, it is simple to use (Kint *et al.*, 2004).

Statistical analyses

In order to evaluate the variation of structural indices for each size class and shape, the mean and the variance of each index were calculated. For reference stands, the expected values of any specific index, regarding the actual area of reference stands covered by sample plots, were computed. Since circular plots do not cover the areas near the corners of the reference stands, due to their circular shape and the square shape of reference stands, the uncovered areas (increasing with circular plot size) were considered and excluded when calculating the expected values. The effect was different for square sample plots. Since the attempt was to keep the same plot centres for circular and square sample plots with equal size, the square plots did not cover the areas of reference stands near the borders. In order to avoid the plots outside the stand area, for each sample plot size a buffer zone with a width equal to the circular plot radius was considered, and the dimensions of square plots were slightly smaller than circular plot diameters with equal size.

Standard deviation (*sd*) and the differences of the mean estimates from the expected values were calculated to highlight the effect of the sample plot size and/or shape on estimate precision and accuracy, respectively. The calculation of *sd* is straightforward and the differences of the mean estimates from the expected values indicate the inaccuracy of the mean of the thousand sample plots estimations to measure the true values of structural indices. All calculations and analyses were performed using the R statistical software.

Results

Table 2 presents exact values of structural indices for all six one-hectare plot reference stands. In the case of the circular sample plots, the differences between exact values and expected values of structural indices were small (< 1%) for all reference stands, except for clustered patterns Cl1 and Cl2, varying up to 2.3 percent. In the case of the square sample plots, the differences between exact values and expected values

Table 2. Summary of reference stands and their structural measures used for this study.

Tabel 2. Uuritud struktuuriindeksite oodatavad väärtused RAMI puistus ja viies simuleeritud virtuaalpuistus.

Reference stands / *Puistu*	N	D	agg	ddf	ua	ddm	ming
RAMI	968	20.132	1.04	0.315	0.603	0.514	0.610
Ran	968	20.132	1.01	0.303	0.539	0.501	0.654
Reg1	961	20.079	2.00	0.397	0.000	0.499	0.661
Reg2	961	20.132	2.00	0.373	0.500	0.521	0.689
Cl1	968	20.132	0.67	0.329	0.699	0.495	0.702
Cl2	968	20.132	0.84	0.306	0.706	0.496	0.647

Notes: N is number of trees on the one hectare reference stand; D is the mean square diameter of the reference stand.

Märkused: N on ühe hektari suuruse puistu puude arv, D on puistu ruutkeskmine diameeter.

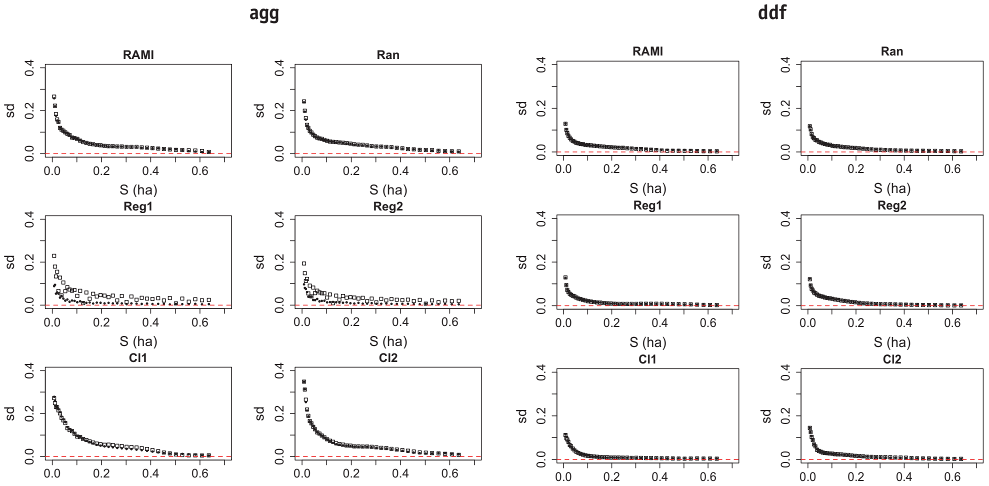

Figure 2. Standard deviations of structural indices counting for the first nearest neighbour, where ● and ☐ signs represent the standard deviations for circular and square plots, respectively.

Joonis 2. Lähima naaberpuu statistikal põhinevate struktuuriindeksite hinnangute standardhälbed sõltuvana proovitüki pindalast ja kujust (märgid ● ja ☐ vastavad ringile ja ruudule).

of structural indices were even smaller (< 0.4%). Figure 1 shows that the greater difference in the case of the circular sample plots with a clustered pattern is caused due to the occurrence of the clusters in the corners, when compared with the area excluded from the quantifications of expected values, and a considerably larger number of points, specifically for bigger radii, were excluded.

Variation of the statistical estimates quantified by the standard deviation *sd* are presented in Figure 2 for the indices based on the first nearest neighbour, and in Figure 3 for the indices based on four nearest neighbours. Variation of structural indices estimates declined asymptotically with increasing sample plot size in six different reference stands. Even though, compared to the circular plots, there is evidence of a slightly bigger variation of the estimate of *agg*, for the square sample plots in almost all reference stands, specifically in regular patterns. Notice that in case of uniform angle index *ua* the regular patterns Reg1 and Reg2 caused different *sd* trend than that from the other simulated patterns. In the case of a regular pattern, *ua* remained constant for all sample plot sizes and shapes, 0 for Reg1 and 0.5 for Reg2, resulting in *sd* = 0.

The differences of the mean estimates from the expected values of structural indices for different sample plot size and shape are illustrated in Figure 4 for the indices based on the first nearest neighbour and Figure 5 for the indices based on four nearest neighbours. The spatial arrangement of trees/points defined by *agg*, shows less inaccuracy for circular plots in all reference stands. In RAMI, random and regular reference stands inaccuracy declines with the sample plot area increasing up to 0.1 ha; however an underestimation of *agg* (or overestimation of clustering) is seen for the reference stand Cl1 when the plot area expands. In Cl2, the differences of the mean estimates from the expected values for *agg* first decrease with the plot increasing in size up to around 0.1 ha and

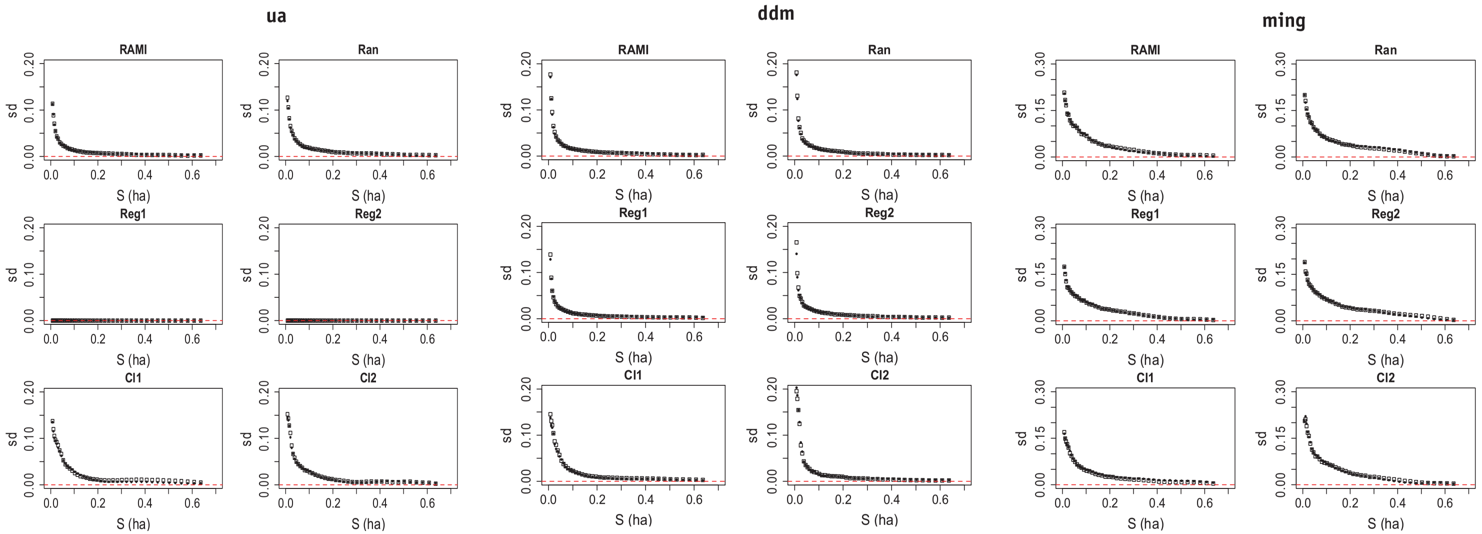

Figure 3. Standard deviations of structural indices counting for four nearest neighbours, where ● and ☐ signs represent the standard deviations for circular and square plots, respectively.

Joonis 3. Lähima nelja naaberpuu statistikal põhinevate struktuuriindeksite hinnangute standardhälbed sõltuvana proovitüki pindalast ja kujust (märgid ● ja ☐ vastavad ringile ja ruudule).

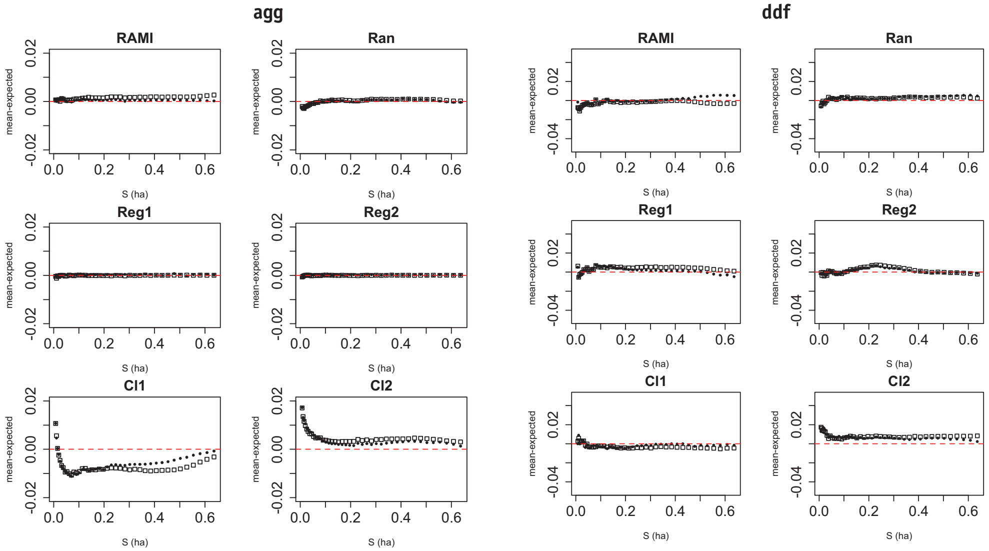

Figure 4. The differences of the mean estimates from the expected values of structural indices counting for the first nearest neighbour, where ● and ☐ signs represent the differences for circular and square plots, respectively.

Joonis 4. Lähima naaberpuu statistikal põhinevate struktuuriindeksite hinnangute keskmine erinevus oodatavast väärtusest sõltuvana proovitüki pindalast ja kujust (märgid ● ja ☐ vastavad ringile ja ruudule).

for sample plots bigger than 0.1 ha the differences start to increase again, however when the plot areas exceed 0.5 ha, the structural variables of those plots start converging to the structural values of the reference stand. Also, the estimate accuracy of *ddf* for reference stands, RAMI, Reg1 and Reg2, increased slightly with sample plot size, regardless of their shapes and the differences of the mean estimates from the expected values reached the minimum for sample plot size of 0.40–0.45 ha. The differences of the mean estimates from the expected values at estimating the indices based on four nearest neighbours were very small for all reference stands (less than 4%). Small sample plots produced mainly satisfactory results and, more or less, circular and square plots exposed the similar trends. Although the bigger sample plots slightly estimated a greater mixture of different species in a neighbourhood with all reference stands expect Cl1, accuracy increased by enlarging the plots' size above 0.4 ha. Besides, similar to *sd*, the measure of *ua* remained constant with the size and/or shape of sample plots, always 0 for Reg1 and 0.5 for Reg2, therefore, the differences of the mean estimates from the expected values were equal to zero.

Figure 6 illustrates the information about the maximum distances within which trees/points may have direct interactions. As shown the pair correlation function resulted in thoroughly different pictures for considered reference stands. The pair correlation function in the RAMI stand shows a distance limit of approximately 6 m, where trees intend to be inhibited, and do not tend to be located in shorter distances within the stand. In further distances up to 10 m, they show a more clustering behaviour, and after that, their spatial arrangement approaches to randomness. As expected the *g(r)* values for random patterns are around 1 and the

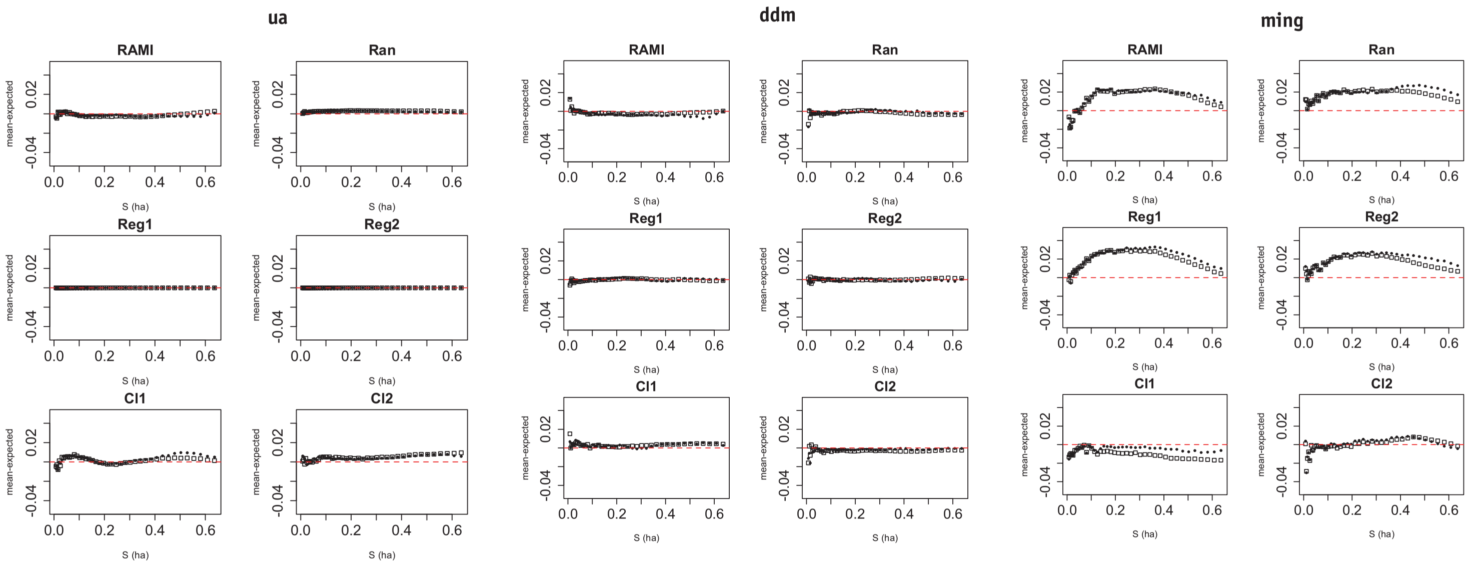

Figure 5. The differences of the mean estimates from the expected values of structural indices counting for four nearest neighbours, where ● and ☐ signs represent the differences for circular and square plots, respectively.

Joonis 5. Lähima nelja naaberpuu statistikal põhinevate struktuuriindeksite hinnangute keskmine erinevus oodatavast väärtusest sõltuvana proovitüki pindalast ja kujust (märgid ● ja ☐ vastavad ringile ja ruudule).

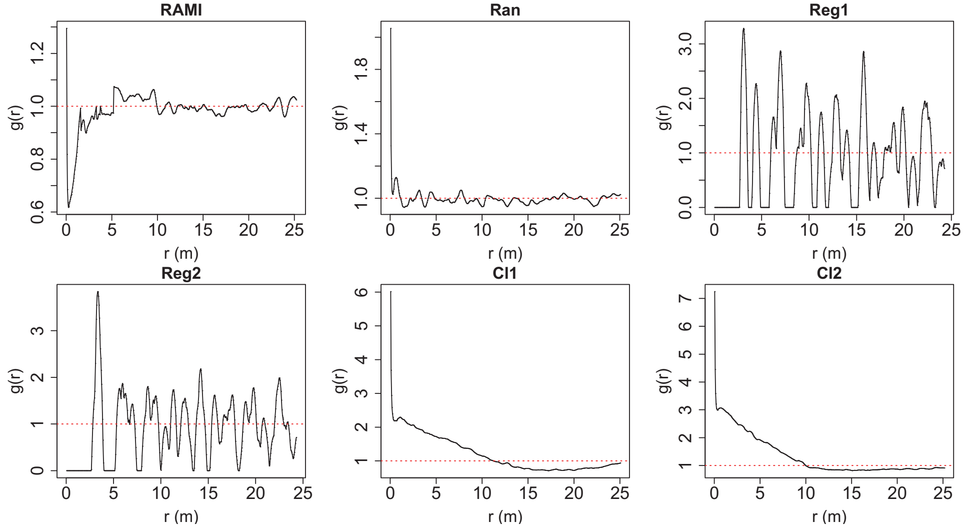

Figure 6. The pair correlation function, *g(r)*, for the RAMI stand and five simulated point patterns, where the dotted lines indicate complete randomness.

Joonis 6. Radiaaljaotuse funktsioon g(r) uurimisala RAMI puistu ja viie simuleeritud virtuaalse puistu jaoks. Punktiirjoon vastab puude täiesti juhuslikule paigutusele.

cluster patterns appear to have the values of correlation function greater than 1, up to inter-tree distances of 10–12 m, and after that critical distance, the pair correlation function behaves similar to the Poisson process for the mentioned patterns. Finally, the pattern of fluctuations in *g(r)* values for regular reference stands reflects the current spacing between points within those patterns.

Discussion

This study evaluated the estimation errors of several spatial structural indices for different sizes and shapes of sampling plots using a silver birch dominated stand located in Järvselja, RAMI, and five different planar point patterns. The analyses revealed that the estimation precision of random sample plots increased with size for circular and square plots. This finding is well documented based on many other studies (e.g. Johnson & Hixon, 1952; Freese, 1960; Gray, 2003; Frazer *et al.*, 2011; Næsset *et al.*, 2015). Also as explained, some fluctuations for precision estimates of structural indices with increasing sample plots size in regular and clustered patterns were indicated. This finding is consistent with some previous studies where they concluded that the spatial scale of point patterns other than random affects the mentioned relationship between size and estimation precision (Reich & Arvanitis, 1992) and depending on the stand structure and management, the sampling errors and inaccuracy could often increase considerably (Pommerening & von Gadow, 2000; Kint *et al.*, 2004).

The relative locations of trees/points within reference stands were described by spatial indices of *agg* and *ua*. The results of the statistical analyses for the two indices were slightly different due to different algorithms of calculating *agg* and *ua*. Where *ua* shows the expected trend of reduction in *sd* and inaccuracy with increasing size in most cases, as explained, some exceptions were evident for *agg* in

RAMI and clustered patterns. However, when the variations declined with plot size, the bigger sample plots (> 0.01 ha) in Cl1 pattern underestimated the *agg*, which means a larger degree of clustering. Also sample plots bigger than 0.12 ha in RAMI and Cl2 slightly overestimated the aggregation, where smaller sample plots (< 0.12 ha) in Cl2 estimated more randomness than the actual existing clustering. As already explained *agg* is the ratio of average observed distances from the first nearest neighbour to the expected distance for a Poisson point process of the same intensity (see eq.1) and depending on the area that the sample plots cover, and the intensity of trees/points, the mentioned expected distance may be smaller, or bigger, than that for the one-hectare plot. Besides, this fact is reflected with the pair correlation values bigger than 1 ($g(r) > 1$) for clustered patterns, showing that inter-tree interactions exist up to the distances of 10–12 m, and after that $g(r)$ curves reach 1, or even slightly less. Therefore, smaller plots fail to capture the actual points interacting. Various methods exist to represent spatial clustering (e.g. Anselin, 1996; Boots & Getis, 1988) and irrespective of the measurement employed, analyses are always subject to ecological fallacy by size, or other effects (Wrigley *et al.*, 1996). Subsequently, in order to achieve appropriate measurements, special consideration must be devoted to the scale of the general layout of the underlying process, and the overall distribution of points within the selected stand. The uniform angle index obtained for different reference stands were in accordance with their aggregation values, and behaved as expected: values between 0.5 and 0.6 refer to randomness, more than 0.6 show clustering, and less than 0.5 indicate regularity. However these distinctions may vary slightly (Albert, 1999, p. 67).

In the RAMI stand, the measures of structural indices *ming* and *ddm*, while only considering the four nearest neighbours, revealed that trees of different species and diameter sizes were assigned as neighbours, and the stand had quite a mixed structure. The values of two recent indices, bigger than 0.5 (see Table 2), indicated that, on average, each tree had two neighbours of different species, and the tree was larger than at least two of its immediate neighbours. However, the variation in the stem sizes of two immediate neighbours illustrated by *ddf* was rather small. This outcome seems acceptable for a silver birch-dominated stand, since as a pioneer tree species (Fischer *et al.*, 2002), silver birch is intolerant to shade, and the most favourable condition for this tree species is growing as a dominant tree with relatively less competitive surroundings (Hynynen *et al.*, 2010). Additionally, self-thinning due to negative interactions between neighbouring trees would result in a structure similar to the Poisson process with trees located randomly within a stand or even more regularly (Stoyan & Penttinen, 1998; Pommerening, 2002). The estimates of the structural indices considering the diameter and species identity for the five other reference stands were similar to the RAMI stand because of the method applied to assign *dbh* and species to points in this study. The aggregation and uniform angle measures for the RAMI stand when compared to those for random and regular patterns showed the same trend. Also, in shorter inter tree distances (up to 6 m), the pair correlation function values smaller than 1 ($g(r) < 1$) revealed that at those distances fewer trees were observed than what would be expected under random conditions. Regarding the compliance of inter-tree distance of 6 m with the estimated crown diameter of silver birch trees ranging from 1.5 to 5.8 m, the competition or/and thinning must cause this inhibition as explained earlier in this study, and also in other similar studies quantifying forest structure (e.g. Pommerening, 2002).

The results obtained for structural estimates in the RAMI stand showed that the small plots with the area about 0.15 ha were able to provide quite accurate estimates, and increasing the plot size did not significantly reduce the differences of the mean estimates from the expected values. Although, the smaller plots can show large variation among them, they captured the spatial heterogeneity of the RAMI stand more efficiently than larger plots, and similar behaviour was also observed in Lombardi *et al*. (2015) when quantifying the effect of sample size on some structural indices in old-growth forests. Subsequently, changes can be detected by increasing the number of smaller plots as an alternative to enlarging the sample plot size (Salk *et al*., 2013). Several practical matters must be considered when adopting research sample plots. The introduction of efficient plots, either by size or by shape, allows the reduction of the total area assigned for sampling, or also lessens the total efforts and cost to measure the plot while maintaining the desirable accuracy. However, the influences of the studied traits are, of course, consequential. Several studies on the impact of plot size and/or shape on various measures of forest stands have also acquired considerable gains with small plots, while the efficiency analyses for larger plots proved impotent (e.g. Conkle, 1963; Loo-Dinkins & Tauer, 1987; Haapanen, 1992; Lombardi *et al*., 2015). Although there are reports of opposite gains due to various reasons and different traits that were investigated (e.g. Corona *et al*., 1998; Gray, 2003).

When applying spatial structural indices an important issue to be considered is the edge effects, where the neighbourhood relationships are not truly shown for trees near the plot boundary due to the uncertainty of the neighbours' selection, as actual neighbours may lie outside the plot. Also depending on the algorithms of indices, when they count only for one nearest neighbour, or four nearest neighbours, this effect varies with shape and the reference stands' patterns. As the results of this study showed, although the inaccuracy of the estimate of circular and square plots are similar, the estimation errors among plots of the same size are more likely less for circular plots. When exploring the effect of shape, in most cases, circular sample plots come up with more accurate estimates. This attitude may be explained by the ratio of the perimeter to the surface area of monitoring plots, which is smaller for circular plots compared with square ones. Consequently, the edge effect becomes more significant with decreasing the plot size, and also for square plots, as more trees will be excluded from the indices' calculations (Pommerening, 2002). Despite several methods developed (e.g. Monserud & Ek, 1974; Martin *et al*., 1977; Donnelly, 1978) or tested (e.g. Radtke & Burkhart, 1998; Pommerening & Stoyan, 2006) in order to eliminate the edge effect, there is no overall solution that can be applied to all structural indices and plot shapes for stands with whatever pattern. However, the outcome of the current study presented slightly different estimates of structural measurements of reference stands for different plot shapes. In general, applying the circular plots provided much better approximations of considered structural indices for the studied RAMI stand and the simulated point patterns.

Potential variation of structural indices on Estonian forest sample plots

The distributions of indices' estimations applying sample plots with radii of 10 m, more common in NFI, and radii of 20 m, more common in ENFRP, to measure structural properties in the RAMI reference stands are compared in Figure 7. As it is shown, and also explained earlier, when the sample plot radius increases from 10 to 20 m, the variation of sample plots when calculating structural indices decreases, and therefore the larger sample plots provide more accurate measures of the structural indices for the RAMI reference stand.

The *agg* and *ua* values of RAMI are very close to randomness (see Table 2),

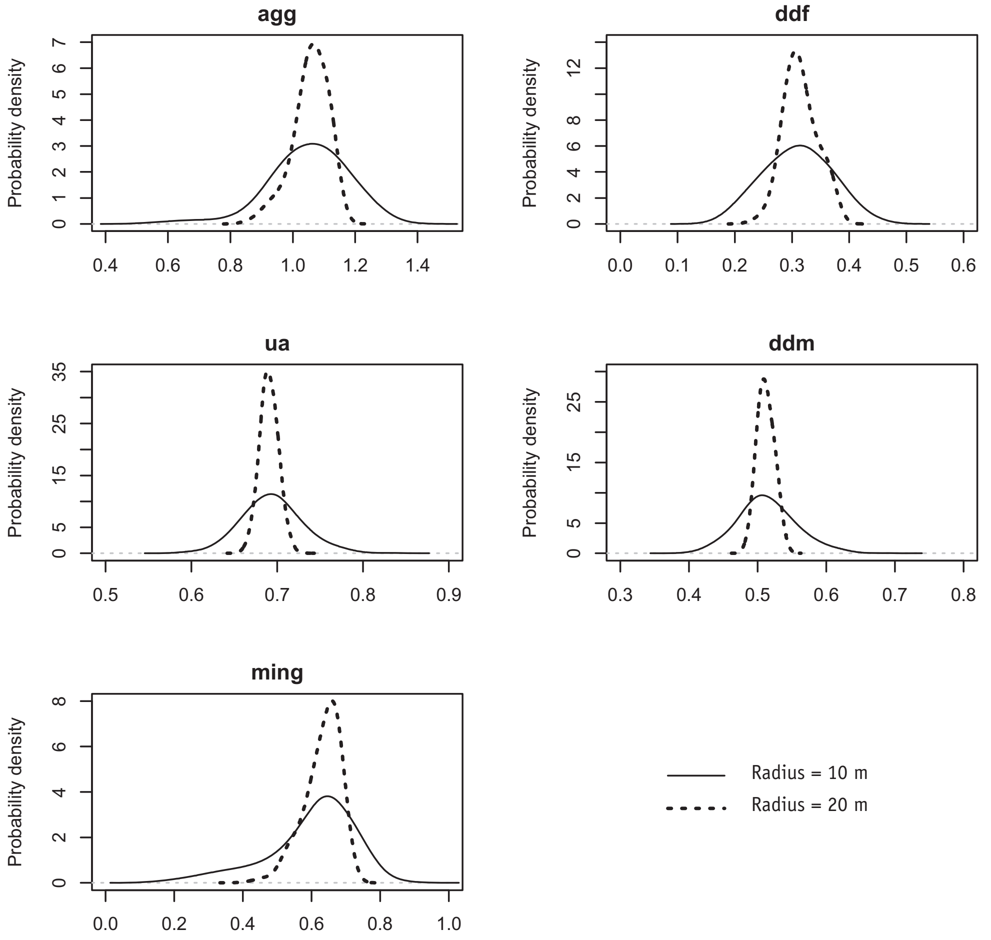

Figure 7. The probability density of structural indices for sample plots radii equal to 10 m (solid lines) and 20 m (dashed lines) in the RAMI reference stand.

Joonis 7. Puistu struktuuriindeksite valimhinnangute tõenäosustiheduse funktsioonid RAMI puistu andmeil proovitüki 10 m (pidevjoon) ja 20 m (katkendjoon) raadiuse korral.

and as it has been already discussed, several studies suggest that the bigger sample plots would result in more precise and accurate estimates (e.g. Johnson & Hixon, 1952; Freese, 1960; Gray, 2003). Some other findings demonstrated that the spatial point patterns, other than random, may show different results (Reich & Arvanitis, 1992), and the sampling errors as well as the differences of the mean estimates from the expected values could increase with increasing the plot size, depending on the stand structure and the management activities (Pommerening & von Gadow, 2000; Kint *et al*., 2004). Consequently, when estimating different variables such as structural indices, special attention should be paid to the optimal size of the sample when considering the spatial distribution of the trees within the forest stands. On the other hand, as discussed earlier, the observation of a forest stand through sample plots with different sizes is a tricky issue because of spatial variablity of forest stands (Bellehumeur *et al.*, 1997; Chen *et al.*, 2004; Fajardo & Gonzalez, 2009). As a spatial statistics tool the semivariogram is an applicable function to indicate the spatial correlation of variables characterizing the forest stand at sample locations (Cressie, 1993):

$$\gamma(r) = [2N(r)]^{-1}\sum[X_i - X_{i+r}]^2 \qquad (7)$$

where X_i and X_{i+r} are values of a variable at locations i and i+r, separated by the vector of directional distance r, and N(*r*) is the number of pairs of samples considered in the given distance class (lag, here 1 m).

Figure 8 shows the omnidirectional semivariograms of the studied structural indices based on 10 m and 20 m sample plots' radii in the RAMI stand. The spatial variability of all stand structure estimations change with the sample plot size, and a more significant spatial trend is seen for the smaller sample plots with radius of 10 m, and also some degree of spatial auto-correlation of the stand structure appears for sample plots with a radius of 20 m. Therefore, it can be concluded that observations at bigger spatial resolutions are more similar than of those at smaller scales (Arbia *et al.*, 1996; Král *et al.*, 2014), because the proportion of spatial components of variability increases with enlarging the sample plots and possible trends are then more visible (Bellehumeur *et al.*, 1997; Cohen *et al.*, 1990; Král *et al.*, 2014). On the other hand, semivariograms are

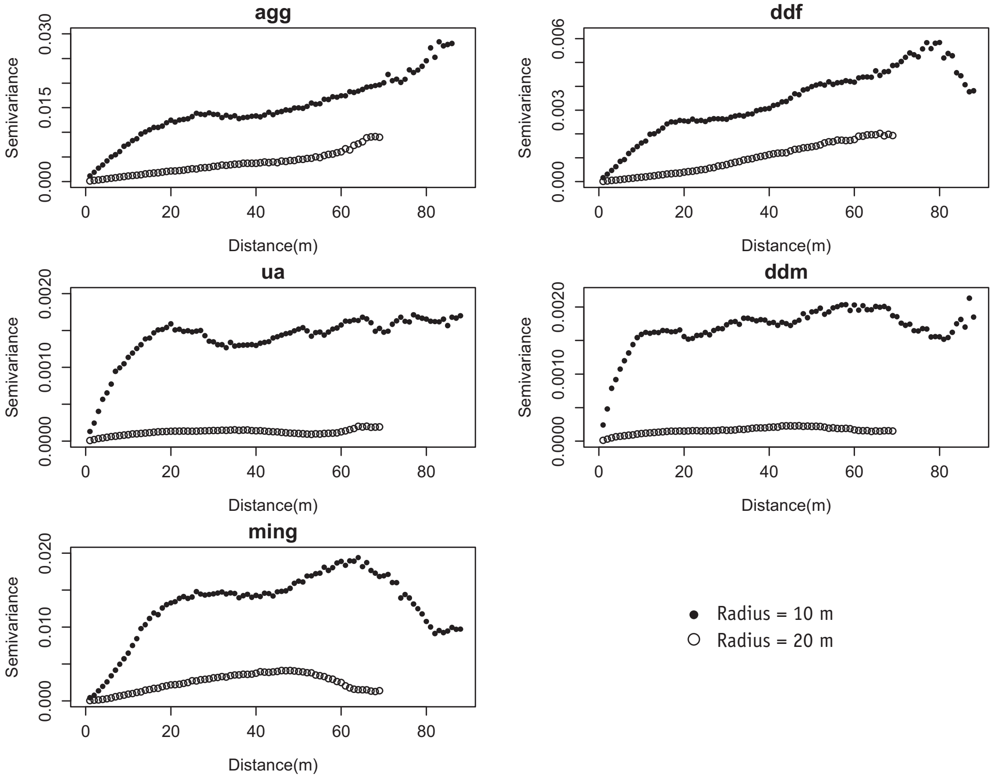

Figure 8. The omnidirectional semivariograms of the studied structural indices based on 10 m and 20 m sample plots' radii in the RAMI reference stand.

Joonis 8. RAMI puistu struktuuriindeksite igasuunalised semivariogrammid proovitüki 10 m ja 20 m raadiuse korral.

calculated either from discrete point data with a small extent (10–100 m) for tree level variables, or from sample plots of various sizes with a larger extent (150–300 m) for stand level measurements (Král *et al*., 2014). Subsequently, since the studied structural indices present different attributes of forest stand, it must be noted that for studying the spatial variability, the study area is quite small (one-hectare) and also homogeneous, and as is shown in Figure 8, the effects of the spatial correlation over short distances are non-negligible. Consequently, the calculated indices for different sample plots with any location are correlated, showing small variances. However, regarding the algorithms of calculated indices, they might be considered as tree level measures based on the tree's nearest-neighbours, accounting for small-scale differences (Kint *et al*., 2003) and, for describing a stand by a specific index, the mean value of that index for individuals within the stand (or sample plot) is calculated.

In summary, the study was carried out on a small and quite homogenous area, and because of that, the variations among the structural estimates of different sample plots, specifically within shorter distances, were small and spatially correlated. The effect of spatial autocorrelation is expected to be diminished by using multiple plots from entirely different stands, and consequently, the variation of estimates would probably increase, and be larger than the results of the current study. However, the trend of this increment strongly depends on the algorithm of structural indices and the spatial alignment of trees within the stands with different development stages, growth conditions and species compositions. Therefore, before generalizing the outcome of this study to other forest stands, a separate and careful evaluation of the structural indices is required in broader scales to depict the spatial correlation in observations measured at the sample locations.

Conclusions

The size and/or shape of the sampling plot is crucial to the extent that quantifying the same structural index for different sizes and/or shapes may yield different, or even inconsistent, results so that the appropriate size and shape of the sampling plot produce a high level of accuracy. The study results clearly demonstrated that the optimal choice of plot size and shape varies according to the spatial distribution of trees inside the stand and the algorithm of desired indices. The sensitivity of structural indices and characteristics to the size and shape of monitoring plots, was also demonstrated, where implementing square plots almost resulted in quite similar structural estimation accuracy compared to the accuracy estimations of circular plots. In addition, circular plots often provided satisfactory estimates of studied structural indices. On the other hand, not only should the sample plots be proper representatives of a real stand, but they also must be small enough, and simple to implement, in order to guarantee a minimum measurement expense. Therefore, referring to the results obtained for this study, circular plots are preferable, with the size depending on the stand attributes for structural considerations.

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Proovitüki suuruse ja kuju mõju metsa struktuuriindeksite hinnangutele arukase (*Betula pendula* Roth) enamusega puistus Järvseljal

Kobra Maleki ja Andres Kiviste

Kokkuvõte

Metsa kirjeldamisel leiavad puistu traditsiooniliste takseertunnuste kõrval üha laiemat kasutamist mitmesugused puistu struktuuri ja puude ruumilise paiknemise mustrit iseloomustavad struktuuriindeksid ja karakteristikud. Eesti metsavarude hindamine ja kasvukäigu uurimine tugineb peamiselt suhteliselt väikestel proovitükkidel tehtavatele mõõtmistele (statistilise metsainventeerimise (SMI) proovitükid on raadiusega 7 või 10 m, puistu kasvukäigu püsiproovitükkide võrgustiku (KKPRT) proovitükid on olenevalt puistu tihedusest raadiusega 15 kuni 25 m), mistõttu tekib küsimus, millisel määral sõltuvad puistu struktuuri iseloomustavad näitajad proovitüki suurusest ja kujust.

Siinne uurimisala on ühe hektari (100 m × 100 m) suurune 54 aasta vanune arukase enamusega puistu (RAMI puistu) Järvselja Õppe- ja Katsemetskonna kvartalil JS228, millel asuvad puud mõõdeti ja kaardistati metsa kiirguslevi mudelite võrdlemise eesmärgil 2007. a. Puistus oli tehtud harvendusraie 2004. a. sügisel, mille käigus tekitati põhja-lõunasuunalised väljaveoteed. 2013. a tehtud kordusmõõtmisel oli uurimisalal 968 eluspuud, millest 57% olid arukased, 29,5% sanglepad ja 11% haavad ning puude rinnasdiameetri ruutkeskmine oli 20,13 cm. Erinevate struktuuriindeksite iseloomustamiseks ja omavaheliseks võrdlemiseks simuleeriti lisaks viis virtuaalset puistut, mis vastavad puude erinevatele paigutusmustritele metsas: (1) puude juhuslik paigutus ehk Poissoni protsess (Ran), (2) puude äärmuslik kobarpaigutus (Cl1) ja (3) puude mõõdukas kobarpaigutus (Cl2),

mis koostati kahetasemelise juhusliku liitprotsessi tulemusena, ning (4 ja 5) kaht tüüpi puude regulaarne paigutus (Reg1 ja Reg2). Simuleeritud puistutes järgiti RAMI puistu liigilist koosseisu ja rinnasdiameetri jaotust.

Puistu struktuuri kirjeldamiseks uuriti järgnevaid karakteristikuid: agregatsiooniindeksit (agg) (Clark & Evans, 1954), diameetri diferentseerumisindeksit (ddf) (Füldner, 1995; Pommerening, 2002), diameetri domineerimisindeksit (ddm) (von Gadow & Hui, 2002; Aguirre *et al.*, 2003), puude paiknemisindeksit (ua) (Hui & von Gadow, 2002) ja liikide segunemisindeksit (ming) (Füldner 1995; Aguirre *et al.*, 2003) ning radiaaljaotuse funktsiooni g(r) (Diggle, 1983). Agregatsiooniindeks (agg) ja diameetri diferentseerumisindeks (ddf) tuginevad lähima naaberpuu statistikale ning diameetri domineerimisindeks (ddm), puude paiknemisindeks (ua) ja liikide segunemisindeks (ming) nelja lähima naabri statistikale. Radiaaljaotuse funktsioon g(r) iseloomustab suvalisest punktist kaugusel r olevat puude tiheduse suhet puude tihedusse juhupaigutuse (Poissoni protsessi) korral ja on tõlgendatav sarnaselt agregatsiooniindeksiga (agg).

Proovitüki suuruse mõju uurimiseks vaadeldi 41 erineva raadiusega ringproovitükki alates raadiusest viis meetrit kuni raadiuseni 45 meetrit ühemeetrise sammuga. Iga proovitüki suuruse jaoks tekitati ühe hektari suuruse uurimisala kohta 1000 juhuslikult paigutatud proovitüki tsentrit nii, et proovitükid jääksid uurimisala sisse. Samu proovitüki tsentreid kasutati ka ruudukujuliste proovitükkide tekitamiseks. Iga proovitüki suuruse ja kuju jaoks arvutati puistu struktuuriindeksite oodatavad väärtused. Proovitüki suuruse ja kuju mõju struktuuriindeksite hinnangute täpsusele analüüsiti 1000 juhuvalimi hinnangute keskmiste ja standardhälvete abil. Tulemustest ilmnes, et puistu struktuuriindeksite hinnangud sõltuvad proovitüki suurusest ja kujust. Üldiselt vähenes struktuuriindeksite hinnangute varieeruvus (standardhälve) proovitüki suurenedes asümptootiliselt kõigi kuue puistu puhul. Erandiks oli puude paiknemisindeks (ua) regulaarse puude paigutusega puistutes (Reg1 ja Reg2), kus proovitükkidel saadud hinnangud olid alati täpsed. Sama pindala korral osutusid struktuuriindeksite hinnangud ringproovitükkidel mõnevõrra vähem varieeruvamaks kui ruudukujulistel proovitükkidel. See tendents ilmnes selgelt agregatsiooniindeksi (agg) hinnangutes regulaarse puude paigutusega puistutes (Reg1 ja Reg2). Struktuuriindeksite hinnangute keskmised erinevused oodatavatest väärtustest olid mõnevõrra vastuolulised, teatud punktimustrite juhtudel jäi isegi proovitüki suurenedes püsima mõningane erinevus struktuuriindeksi keskmise hinnangu ja oodatava väärtuse vahel. Radiaaljaotuse funktsioon g(r) RAMI puistul näitas, et kuni kauguseni 6 m on puud pigem regulaarse kui juhupaigutusega, kaugusel 6 kuni 10 m pigem kobarpaigutusega ja alates 10 m juhupaigutusega. RAMI puistu andmeil ilmnes selgelt, et kõigi töös käsitletud struktuuriindeksite hinnangud on 10 m raadiusega (SMI) proovitükkide puhul tunduvalt varieeruvamad kui 20 m raadiusega (KKPRT) proovitükkidel. Igasuunalise semivariogrammide analüüs viitab siiski asjaolule, et ühe hektari suurusel puistul esineb struktuuriindeksite hinnangute autokorrelatsioon, mistõttu suurel metsamaastikul võib üksteisest kaugel olevate proovitükkide struktuuriindeksite hinnangute varieeruvus olla mõnevõrra suurem, kui on esitatud selles uurimuses.

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Kiviste, A., **Maleki, K.** 2015. The Effect of Thinning on Survival of the Silver Birch Trees in Estonia. Sustaining ecosystem services in forest landscapes, IUFRO Landscape Ecology Conference. August 23–30, 2015, Tartu, Estonia. A poster presentation.

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Presentations at local conferences and meetings

Maleki, K. 2016. Analysis of competition and structural indices for modelling silver birch (Betula pendula Roth) stands. June 22, 2016, Eesti Maaülikool, Tartu, Estonia. An oral presentation.

Maleki, K., Kiviste, A., Korjus, H. 2015. Individual tree mortality of silver birch in Estonia. RMK seminar, February 12, 2014. Tartu, Estonia. A poster presentation.

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PARAMEETRITE JA ELUKÄIGUOMADUSTE ANALÜÜS
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