

QUANTITATIVE ASSESSMENT OF STAND STRUCTURAL TRAITS AND HEALTH CONDITION IN HEMIBOREAL FOREST ECOSYSTEMS

PUISTU SEISUNDI JA STRUKTUURITUNNUSTE KVANTITATIIVNE HINDAMINE HEMIBOREAALSETES METSAÖKOSÜSTEEMIDES

ENELI PÓLDVEER

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

Väitekiri filosoofiadoktori kraadi taotlemiseks metsanduse erialal

Eesti Maaülikooli doktoritööd

Doctoral Theses of the Estonian University of Life Sciences



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LIST OF ORIGINAL PUBLICATIONS

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

- I Allikmäe, E., Laarmann, D., Korjus, H. 2017. Vitality assessment of visually healthy trees in Estonia. Forests, 8 (7): 223.
- II Põldveer, E., Korjus, H., Kiviste, A., Kangur, A., Paluots, T., Laarmann, D. 2020. Assessment of spatial stand structure of hemiboreal conifer dominated forests according to different levels of naturalness. Ecological Indicators, 110: 105944.
- III Põldveer, E., Potapov, A., Korjus, H., Kiviste, A., Stanturf, J.A., Arumäe, T., Kangur, A., Laarmann, D. 2021. The structural complexity index SCI is useful for quantifying structural diversity of Estonian hemiboreal forests. Forest Ecology and Management, 490: 119093.

The contributions from the authors to the papers in alphabetical order are as follows:

	I	II	III
Original idea	DL, HK	DL, EP , HK	DL, EP , HK
Study design	All	AK, DL, EP , HK	AK, DL, EP , HK
Data collection	EP	AK, DL, EP , TP	AK, DL, EP
Data analysis	All	AK, EP	AK, AP, EP
Preparation of manuscript	All	All	All

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ABBREVIATIONS

CWD Coarse woody debris

DBH Diameter at breast height, measured at 1.3 m above the root

collar

D_i Deadwood distribution index

DM_i Deadwood mingling index

EU European Union

ENFRP Estonian Network of Forest Research Plots

GAM Generalized additive model

GLM General linear model

 M_i Species mingling index

NM_i Decay mingling index

SCI Structural complexity index

T_i Diameter differentiation index

W_i Uniform angle index

1. INTRODUCTION

Several classical approaches and paradigms require reconsideration in forestry nowadays. Practical forest management is shifting towards promoting heterogeneous stand structures (Ehbrecht et al., 2017) as they are considered to provide a higher level of ecosystem goods and services (Juchheim et al., 2019). The shift towards more heterogeneous forest stands and diverse management is largely induced by ecological issues that have been an active part of the societal and political agenda for several decades in Estonia and worldwide. The change is creating new demands for forest utilization – the focus from timber production is turning to better integration of ecological and social functions with prioritized economical services (Huuskonen et al., 2021). New ideas, technologies and environmental issues require innovations in forest management and planning strategies.

Around 25% of Estonian forests are currently under different conservation regimes (Sims et al., 2020). Setting aside conservation areas and habitats of threatened species are actively implemented policy tools in Estonia that provide protecting of ecologically valuable forest ecosystems and preserving key biotopes in managed forests. Forest conservation is an important step for maintaining biodiversity, however, it does not necessarily provide wanted ecological value if it is done in the wrong place and/or at an inappropriate time. For an example, almost half of the Fennoscandian herb rich Norway spruce (*Picea abies* (L.) H. Karst.) forests, habitat type 9050 in the European Union (EU) habitat directive, have mostly lost their initial conservation value after becoming part of the Natura 2000 network in Estonia (Korjus et al., 2016).

The effort that is on forest conservation similarly should be applied to promoting stand structural diversity in commercial forests in order to foster biodiversity. Much work has been done on raising overall knowledge and developing practical advice on safeguarding forest diversity through specific management decisions (Levin, 2005; Vanha-Majamaa et al., 2007; Seidel et al., 2019). Promoting stand structural heterogeneity is one of the key actions in biodiversity maintenance: the variety of stand structural elements that form structural patterns will promote resources and species using those resources (McElhinny et al., 2005; Mikoláš et al., 2017; Thorn et al., 2017). The three-dimensional

distribution of trees is the most important variable in forests directly affected by silvicultural activities changing forest stand structure, e.g., promoting structural heterogeneity (Seidel et al., 2019; Juchheim, 2020).

Various mathematical methods and indicators are developed to describe. analyse and model forest stand structure. Those include conventional stand characteristics used for forest management planning. Such measures provide valuable information about a forest stand but not about structural traits and patterns within it as stands with similar characteristics may have different tree positioning patterns (Pretzsch, 1995). Proper understanding of forest structural diversity requires more accurate and profound evaluations of spatial forest structure than traditionally used characteristics provide (Maes et al., 2011). Several structural indices describing spatially explicit relationships among neighbouring trees – tree positioning patterns, mingling of tree species and differentiation in trees dimensions (Aguirre et al., 2003; Gadow et al., 2012), tree mortality patterns (Laarmann et al., 2009) and stand-level variability in tree dimensions, (Zenner, 2000; Peck et al., 2014) can be used as guiding measures of stand structural diversity. Structural indices take into account that forests have a spatial nature, and therefore more adequately help to quantify forest stand structure (Zenner and Hibbs, 2000).

The resilience of forest stands, or in other words - the capacity of forests to maintain essential characteristics of their structure, taxonomic composition, ecosystem functions and processes in the face of disturbances – is dependent on biodiversity (Thompson et al., 2009). The loss in biodiversity is negatively affecting forest health and the resistance towards several abiotic and biotic stressors (Alfaro and Singh, 1997; Kuuluvainen, 2016) and the trend is predicted to increase on the backdrop of climate change (Gauthier et al., 2015). Tree's resistance towards different negative causes are crucial for maintaining forest structural and functional integrity but the range within each factor is tolerable, is unique for each organism and depends on the wide variety of indicators (Mandre et al., 2011). The agent strongly influencing Estonian coniferous forests is root rot caused by fungal pathogens Heterobasidion and Armillaria sp. (Hanso and Hanso, 1999; Drenkhan et al., 2018). Root rot is visually difficult or even impossible to detect despite that some visual signs may indicate problems with decreased tree vitality, like extraordinary leaf or needle loss or noticeable fruiting bodies of fungi (Vollbrecht and Agestam, 1995; Laflamme, 2010). The visual assessment of tree vitality during forest inventories gives a biased result of actual condition of trees: decay causes physical deterioration of wood properties (Rinn, 2016) and is affecting management outcomes leading to possible overestimation of round wood assortment. This, in turn, strongly affects forest structure and dynamics, and may lead to wrong estimations in predictions of tree mortality and growth and yield (I).

The current thesis synthesizes several methods that could be used during forest management planning to focus more on ecosystem values. The thesis is based on three papers. Paper I researches if visually healthy coniferous trees in intensively managed stands are affected by decay at the root collar and identifies the proportion of trees with well-developed decay. Paper II examines the differences in structural patterns in conifer dominated managed and unmanaged forests using neighbourhood relationship-based tree-level structural indices. Paper III quantifies stand structural heterogeneity along forest management history and site fertility gradients using tree position and a diameter-based stand-level structural complexity index.

2. REVIEW OF THE LITERATURE

2.1. Structural characterization of forest stands

2.1.1. Forest management shapes the structure of stands

Estonia is rich in forest resources: about 50% of the land is covered with forests (Valgepea et al., 2020) that are in general considered as seminatural (Runnel and Lõhmus, 2017). Semi-natural forests are managed with medium intensity, with tree species diversity maintained mainly through natural regeneration and deadwood supply supported through retention (Lõhmus and Kraut, 2010; Runnel and Lõhmus, 2017). However, in some studies (for an example: Laarmann et al., 2009), such forests can be regarded as forests where no silvicultural treatments have recently been applied. Estonian forests are managed mainly according to the clear-cutting methodology - operations include thinnings, clearcutting and planting. Scots pine (Pinus sylvestris L.), Norway spruce and silver birch (Betula pendula Roth) trees are favoured in the course of reforestation (Raudsaar et al., 2020) because of being easy to establish and manage. Rotation period starts from 30 years in aspen-dominated (Populus tremula L.) stands growing on fertile soils to 120-130 years in pine-dominated and hardwood stands growing on poor soils (Forest management regulation, 2007). To a minor extent, short rotation species such as *Populus* × *wettsteinii* (Hämet-Ahti) plantations have been established in former agricultural lands (Tullus et al., 2007), however, planting short rotation species is not a widespread practice in Estonia.

Human activities, e.g. resource extraction, is continuously changing forest structure and while the economical aspect is often seen as positive and leads to the increase of standing tree volume, the impact on ecological processes (Juchheim, 2020) and the amount of naturally dynamic forests tends to be rather negative (Angelstam and Kuuluvainen, 2004). It is believed that the strongest driver of biodiversity loss is caused by habitat destruction (Dirzo and Raven, 2003). Forest management for timber production is an important reason of forest ecosystems biodiversity loss all over the boreal vegetation zone, caused by the decline in forest structural complexity among others (Gauthier et al., 2015).

In boreal (including hemiboreal) forests, six main forest development stages are formed based on the idea presented by Franklin et al. (2002) and customized by Angelstam and Kuuluvainen (2004): 1) the initiation stage where structural elements left from the pre-disturbance strongly affects the survival, spatial patterns and general progress of regeneration, 2) the young forest stage where tree competition gradually increases canopy cover, light supply decreases and humidity increases, deadwood from pre-disturbance starts decaying and living trees continue growing and form large dimensional trees, 3) the middle-aged stage where severe tree mortality due to tree competition appears if regeneration is dense, and gradual substitution of light-demanding species with shade-tolerant species in understorey vegetation may take place, 4) the mature stage where regenerated trees reach the final height, but the amount of coarse woody debris (CWD) is at its lowest as the deadwood from the pre-disturbance time has decayed and new CWD has not yet formed, competition caused tree mortality decreases and increases due to other agents, the vigour of deciduous tree species decreases and they form important substrates for specialised species, additionally, stand structure may slowly start changing into multi-storey. Managed forests contain mostly these four first development stages after stand-replacing disturbance. Lastly, 5) ageing stage and 6) old-growth stage where structural characteristics vary greatly and create great structural heterogeneity in the tree layer, deadwood structures from different ages and sizes, CWD is abundant and different decay stages are formed, tree diameters get large enough to create habitats for specialized species and gap formation becomes more and more severe creating a diverse horizontal understorey vegetation mosaic. Old forests tend to be complex in the spatial distribution of structures when compared to managed forests (Franklin et al., 2002), however, stands over 120-years-old are rare in Estonia accounting for just 3.1% of the total forest area (Valgepea et al., 2020).

Diverse structural elements and patterns, e.g., multiple tree species and sizes, different (including clumped) spatial distribution, deadwood abundance and spatial distribution that appear in ageing and old-growth forest development stages are associated with high biodiversity (Buongiorno et al., 1994; Lilja and Kuuluvainen, 2005). Furthermore, for example in Finland (Tikkanen et al., 2006), about a half of protected red-listed forest species prefer old-growth forests for living; the majority of those species are associated with different characteristics of a forest stand structure. Excessive homogenization of forest structure during

management also causes the fragmentation of natural forests (Gauthier, 2009). Therefore, important structural elements providing habitats or harbouring large proportions of species (such as CWD and large living trees) are considered as important biological legacies that should be retained as often as possible in the course of forest management activities (Vanha-Majamaa and Jalonen, 2001; Jõgiste et al., 2017). The most serious attempts to preserve forests in Estonia are made primarily in nature conservation areas (Viilma et al., 2001). However, Lõhmus and Kraut (2010) showed that many functional characteristics of an old-growth forests, such as diversity in tree species, volume and different decay-stages of CWD, are present in commercial Estonian forests that are in mature or old-growth condition, however, the appearance of those elements depends largely on the site type.

2.1.2. Tree species composition and diversity

Tree species composition and diversity are usually the most often considered aspects of biodiversity assessment characterizing forest stand structure (Graz, 2004) linked to the temporal stability of ecosystems functioning (Morin et al., 2014). Tree species diversity increasingly promotes forest structural complexity, and the structural complexity of coniferous stands expands with the increasing proportion of broadleaved trees (Juchheim et al., 2019). Furthermore, the majority of redlisted boreal forest species are tied to specific tree species (Tikkanen et al., 2006). Though species diverse forests are often regarded as being more challenging to manage than monocultures (Felton et al., 2010) they are expected to provide more different ecosystem goods and services than pure stands (Juchheim et al., 2019).

Estonian forests are mostly mixed species composition, approximately 18% of the forest are pure stands (National Forest Register, 2019). Many studies of diversity carried out in Europe do not account direct negative effect of forest management on overall species diversity (Duguid and Ashton, 2013; Schulze et al., 2016; Dieler et al., 2017; Ehbrecht et al., 2017). However, Liira et al. (2007) showed that silviculture in Estonia has had a negative effect on tree species richness and on the basal area of deciduous trees.

As an aspect of species diversity, spatial mingling of plants is an important indicator as well, which describes how different tree species

are mixed within a space (Aguirre et al., 2003). Species diversity is more than species composition extending to the way species are mixed spatially in a stand, which can be expressed as species mingling. The species mingling concept takes into account the individuals' perceptions of local diversity (Pommerening et al., 2019) – whether different tree species locate in close proximity to each other or are spatially segregated (Gadow and Hui, 2002).

2.1.3. Deadwood and coarse woody debris

Standing dead trees and logs fallen on the forest ground are of great importance in terms of biodiversity conservation and other ecosystem goods and services (Tomescu et al., 2011). More than half of red-listed boreal forest species depend on deadwood (Tikkanen et al., 2006). Most important substrates for wood inhabiting species are old spruce logs and large aspen logs with branches (Ruokolainen et al., 2018). Many wood-dependent lichens in managed forest live on CWD (Svensson et al., 2016). Saproxylic fungi prefer CWD with dimensions larger than 10 cm; less than 3% of the species are specialised on deadwood smaller than 10 cm (Tikkanen et al., 2006). Quality also is an important structural component of unmanaged forests in Estonia, e.g., the decay stage of CWD (Köster et al., 2005). Decay stages of CWD play an important role in diversity of epixylic plant communities in boreal forests (Kumar et al., 2018).

A serious problem of lacking deadwood as well as vanishing large trees in boreal forests was shown by Swedish researchers more than twenty years ago (Berg et al., 1994). In Estonia, the intensity of management plays a key role in the decrease of the amount of deadwood, snags and logs, and the components and decay classes of CWD (Liira et al., 2007). However, the site type is important too; dry boreal forests tend to be poor in CWD while the quantity of CWD in eutrophic forests can be similar to old-growth forests (Lõhmus and Kraut, 2010). Liira and Sepp (2009) indicated that the amount of deadwood in Estonia is decreasing along a management intensity gradient in productive forests. The amount of CWD varies greatly depending, for instance, on dominant tree species and site conditions, stand age, standing stock volume, protection regime and/or past management decisions and on the location within Estonia, being up to 60 m³ ha-¹ in managed and up to 200 m³ ha-¹ in unmanaged/ protected forests (based on the information received from: Köster et

al., 2005; Lõhmus et al., 2005; Lõhmus and Kraut, 2010; II). In addition to the quantity and quality, the positioning patterns of deadwood is another important factor to be considered: clumping of dead trees indicates future gap formation (Laarmann et al., 2009), an important process inherent for natural boreal forests (Esseen et al., 1997).

2.1.4. Tree positioning patterns and the importance of large trees

Trees within a forest may follow regular, random or irregular patterns (Gadow and Hui, 2002). It often tends to be that most of the trees within a forest are randomly positioned (Motz et al., 2010; Pastorella and Paletto, 2013). More regular tree spacing at the stand-level indicates rather homogenous and less complex structures in comparison to random spacing (Neumann and Starlinger, 2001; Ehbrecht et al., 2017). Irregular patterns in turn indicate the clustering of trees that is characteristic of natural forests with more heterogeneous structures (II). Inter-stand variability of tree positioning also may vary greatly – for instance, large mature trees tend to be randomly distributed and surrounded by clusters of small trees in the forest (Pommerening and Särkkä, 2013).

Pommerening and Uria-Diez (2017) state that large trees tending towards high patterns of species mingling create higher structural and species variability within a forest stand. There is a lack of large trees in Estonian mature stands, especially late-successional deciduous species (Lõhmus and Kraut, 2010). Those large deciduous trees, especially aspen trees, have key importance as they harbour noticeable amount of specialist species (Jüriado et al., 2003; Kivinen et al., 2020). As tree size and species diversity within forest stands are related (Pommerening and Särkkä, 2013), the diameter distribution of trees is an important variable characterising stand structural heterogeneity. For example, diameter distribution of Scots pine in managed stands has a bimodal shape, whereas a descending shape in near-natural and selectively logged stands (Lilja and Kuuluvainen, 2005).

2.2. Quantifying structural traits of forest stands

Spatial forest structure determines short-term ecological processes and, conversely, ecological processes (such as disturbances) are potential drivers modifying spatial forest structure in the long-term (Illian et al., 2008). Forest stands can be defined by the main components of spatial

stand structure: the spatial arrangement of individual trees by their size, condition and species (Gadow and Hui, 2002; Laarmann et al., 2009). General stand measures traditionally used for describing stand structure such as tree species composition, diameter or basal area provide useful descriptions of a forest stand but do not provide description about structural variability within it. Stands with similar stand measures may have very different tree positioning patterns (Pretzsch, 1995). To describe comprehensively forest structure and incorporate its spatial nature, it is necessary to use measures that take into account the spatial dimensions of forest structure (Zenner and Hibbs, 2000).

Numerous structural indices have been developed in order to quantify forest stand structure. Structural indices can either be independent to tree distances or require the exact location of trees within the stand. Well-known are distance independent stand-level characteristics such as Shannon (1948) or Simpson (1949) ecological diversity indices, Pielou (1977) species segregation index and Clark and Evans (1954) spatial aggregation index. A number of structural indices quantifying spatially explicit relationships among neighbouring trees have been developed within the last decades, e.g., based on the nearest neighbourhood approach (Maleki et al., 2015) and general stand-level ones (Zenner, 2000; Peck et al., 2014). Such indices are often used as biodiversity indicators (Pommerening, 2002) as the diversity of spatial forest structure is considered a surrogate measure or a characteristic variable of ecological diversity (Gadow and Hui, 2002).

Monitoring structural patterns inside forest ecosystems based on nearest neighbourhood relationships provides information about how trees with different characteristics locate within a stand (Kint et al., 2001; Gadow and Hui, 2002; Aguirre et al., 2003; Pommerening, 2006; Gadow et al., 2016) – a stand may consist of various tree species that are well mixed (Fig. 1A) or *vice versa*. There may be absence of dead trees or a low number of dead trees positioned far from each other or *vice versa* – a high amount of partially clumped deadwood (Fig. 1B). Trees may have been planted in regular rows (Fig. 1C), be clustered into groups or located completely randomly. All the trees in a stand may have similar dimensions (Fig. 1D) or dominant trees (the trees on the basis of which the diameter of the stand is determined) may have similar dimensions but the overall dimensional variability within a stand is higher. In addition, other differences in spatial forest structure may occur that are

not apparent to the human eye. As large-scale high-resolution remote sensing data has become increasingly available for Estonia (Estonian Land Board, 2018), any kind of structural indices may increasingly gain importance for quantifying forest stand structure.

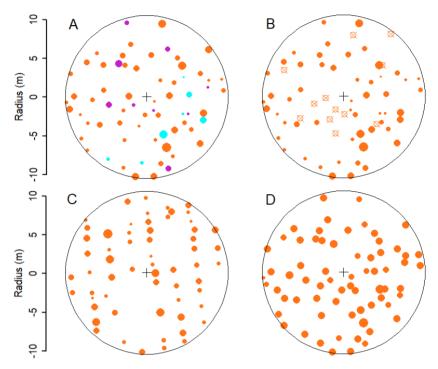


Figure 1. Spatial schemes of different aspects of structural diversity in forest ecosystems: relatively high mingling of species (A), relatively high mingling of deadwood and deadwood clumping (B), regular tree positioning (C) and low diameter differentiation (D). Different colours refer to different tree species, crossed circles to dead trees.

Forest structural elements and legacies carry on important information inherent to natural forest systems (Jõgiste et al., 2017). It does not necessarily mean that the structure of natural forests should completely be taken as a reference in forest management decision making in order to manage our forests well and sustainably, because forest ecosystems and their naturalness are under constant change (O'Hara, 2016). The need is to determine and acknowledge the most important structural components and spatial patterns that are driving forces behind important natural processes to keep the forests as diverse as desired and to provide habitats for different ecologically important species.

2.3. Is forest health condition reflected in the stand structure?

In order to promote desired forest structure, structural components and tree species composition are manipulated during silvicultural practices (Angelstam and Kuuluvainen, 2004). Intensive human influence, e.g., forest structure homogenization, is causing the decrease in forest stability and its main components: resistance and resilience; monocultures, for an example, can lead to an increase in forest disease problems (Larsen, 1995). Tree species diversity in forest plays an important role in fungal diversity as the composition of fungi is tree species-specific (Ruokolainen et al., 2018). Mixed forests tend to be more resistant towards small-scale natural disturbances (Jactel et al., 2017). The study of Haas et al. (2011) about the forest pathogen *Phytophthora ramorum* showed that the risk of disease spreading is lower on sites with higher species diversity.

The loss in forest diversity is negatively affecting forest resistance to different abiotic and biotic factors, and therefore, forest health (Alfaro and Singh, 1997; Kuuluvainen, 2016). The diversity in forests leads to higher resistance of trees to soil-borne fungal diseases (Jactel et al., 2017). Two main soil-borne fungal species in Estonia are *Heterobasidion* and *Armillaria* sp. (Hanso and Hanso, 1999; Drenkhan et al., 2018) causing increased tree mortality, deterioration of the physical properties of the wood, and serious loss in wood industry. The psychical prevention of root rot during forest management is difficult, especially in the case of Norway spruce trees as even stump removal has shown no significant effect on their spreading in Estonia (Aosaar et al., 2020). The interactions between trees and different pathogen species in turn create heterogeneous stand structures (Edman et al., 2007).

2.4. Research needs

Public demands towards forests and forestry are growing in many countries (EU, 2015). Timber production remains an important part of bio-economy and green economy due to several environmental advantages in comparison to use of other resources (Ingrao et al., 2016). Questions arise how to consider various demands towards sustainable forest management, and how to find appropriate management strategies for providing desired levels of ecosystem services (Marques et al., 2013). Forest ecosystem services usually cannot be assessed directly. Therefore, special indicators are necessary to quantify and understand the condition,

trends and rate of change in ecosystem services over time and space (Mendoza and Prabhu, 2003; van Oudenhoven et al., 2012). In forest planning, indicators are often used for measuring the performance of sustainable forest management (Vacik and Wolfslehner, 2004), modelling development of forest stands under various management regimes or environmental factors, searching for management alternatives, and assessing the effectiveness of multifunctional forest management (Knoke et al., 2020). Indicators are diverse forest attributes, usually derived from forest inventories (Andrew et al., 2014; Knoke et al., 2021). Modern forest management requires detailed data about forests than provided during conventional forest inventory in Estonia. Additional information is needed in order to take into account the vitality of trees for proper mortality, growth and yield predictions, and to promote forest structural diversity in order to improve silvicultural targets for ecologically sustainable forestry. Different indices can be used for quantifying forest stand structure and examining the effects of forest management and/or restoration measures. However, there is still very little knowledge on their ecological meaning (Keren et al., 2020) and practical application. Small-scale structural complexity in forest ecosystems and the relationships between structural indices at different spatial scales are probably different in managed and unmanaged forests.

3. AIMS OF THE STUDY

This thesis aims on evaluating methods for assessing stand health, spatial structure and heterogeneity in hemiboreal forest ecosystems. Classical forest inventories produce the data that is often insufficient for forest ecosystem assessments and for advanced forest management practices. Novel approaches can be beneficial for monitoring the structure and dynamics of forest stands, and for developing tools in forest management planning to focus more on ecosystem values and ecological processes.

The aims of the doctoral thesis are:

- 1. To quantify the proportion of visually healthy trees with internal decay indicating decreased vitality in intensively managed conifer forest stands (I);
- 2. To study how often internally decayed trees are clumped in intensively managed conifer forest stands (I);
- 3. To quantify the structural traits, heterogeneity and spatial patterns of stands with different management history (II, III);
- 4. To verify the hypothesis that spatial indices of stand structure are effective quantitative tools for identifying stands with different management histories (II, III).
- 5. To test the hypothesis that thinnings have different short-term and long-term effects on stand structural heterogeneity (III).

4. MATERIALS AND METHODS

4.1. Study area

The papers I, II and III of the current thesis are based on the Estonian Network of Forest Research Plots (ENFRP; Fig. 2). ENFRP was founded in 1995 and the network has been supplemented every year since. Approximately 150 to 200 sample plots are measured or re-measured annually at five-year intervals to collect long-term empirical data about Estonian forests. At present, there are 1,071 plots in the network. Collected data allows study of, among other factors, spatiotemporal patterns, naturalness, silvicultural treatments and growth and yield of Estonian forests (Kiviste et al., 2015).



Figure 2. Geographical location of studied sample plots. Some of the sample plots overlap in different studies.

The study of tree vitality assessment (I) was carried out on 20 sample plots in Southern Estonia (Table 1, Fig. 2). Plots were located in high productivity, intensively managed forest stands in good sanitary condition dominated by Scots pine and Norway spruce on *Oxalis* and *Rhodococcum* forest site types (Lõhmus, 2004).

The study of the assessment of spatial stand structure (II) was based on the data collected from 212 sample plots from all over Estonia (Table 1, Fig. 2). The ecological quality of the stands where sample plots were located was evaluated using a forest naturalness scoring table (Korjus et al., 2012). The scoreboard-type table gives an individual naturalness score to a forest stand (Laarmann, 2014) and was used to assign sample plots into managed (123 plots), recovering (58 plots) and natural e.g., old-growth (31 plots) forest categories. All plots were under observation once, at the time when the naturalness assessment was carried out (between 2006 and 2016). Sites were located on oligo-mesotrophic and mesotrophic mineral soils on *Oxalis*, *Oxalis-Rhodococcum* and *Oxalis-Myrtillus* forest site types (Lõhmus, 2004), dominated by Scots pine and Norway spruce trees.

The study of forest structure quantification using a structural complexity index (III) was based on the measurement data of 852 sample plots collected between 2015 and 2019. Pre-harvest data was included to assess the before and after effects of silvicultural treatments on stand structural heterogeneity. All possible previous measurements were additionally included to follow the dynamics of the structural complexity index over time. Sample plots were located throughout Estonia (Fig. 2): 165 plots belong to conservation forests located in nature protection areas or in woodland key habitats, 622 to managed forests (additionally divided into actively managed stands - 306 plots, and passively managed stands -316 plots) located in commercial forests, and 65 to rehabilitation forests located in former oil-shale open-mined areas. Stands are dominated by Scots pine, Norway spruce and other tree species (Table 1) and include the majority of Estonian forest site types. Site types were divided into fertile and poor sites regarding the site productivity according to Lõhmus (2004).

Table 1. General stand characteristics according to forest categories under study: M/MF-managed, R-recovering, N-natural, QF-rehabilitation and CF-conservation forests. No – number of sample plots under study, A – stand age, SP_d – dominant tree species, D – stand quadratic mean diameter, H – stand mean height, G – basal area, $V_{\rm L}$ – volume of living trees, $V_{\rm DW}$ – volume of standing deadwood, $V_{\rm CWD}$ – volume of CWD. Means are accompanied by \pm standard deviations.

Paper							
	I	II			III		
Forest category							
	M	M	R	N	QF	MF	CF
No	20	123	58	31	65	622	165
SP _d	Norway spruce, Scots pine	Norway spruce, Scots pine			downy biro B. pubescen. (Populus tren glutinosa ((Alnus incana	ruce, Scots pi ch (Betula pena s Ehrh.), com nula L.), black L.) Gaertn.), a (L.) Moench Fraxinus excels	mon aspen alder (Alnus grey alder n), European
A, years	29–95	26–153	44–177	90–178	15–45	20–177	62–250
D, cm	25.6±1.3	26.3±0.8	34.0±1.0	37.8 ± 1.0	12.7±3.9	23.2±6.9	34.9±9.4
H, m	26.1±1.1	25.1±0.6	29.3 ± 0.5	30.2 ± 0.4	12.6±4.4	23.4±5.7	28.6 ± 6.0
G, m ² ha ⁻¹	33.1±1.4	33.1±0.8	39.3±1.0	38.1±1.5	18±7	28±7	30±8
V _L , m ³ ha ⁻¹	415.9±29.2	378.4±12.9	486.9±16.4	477.5±23.5	145±69	236±118	435±140
V_{DW} $m^3 ha^{-1}$	_	_	_	-	2±3	13±18	25±20
V _{CWD} , m³ ha-1	_	22.9±3	37.4±4.2	63.2±9.0	_	_	-

4.2. Data collection

Tree-level data is collected from the sample plots of ENFRP; information includes tree location (polar coordinates), species, diameter at breast height (DBH) in two perpendicular directions, tree mortality agents, damages (mechanical, wind, moose, signs of insect attacks, etc.), and tree height and height to crown base of every fifth tree. All trees – dead, snags, bushes, understorey trees, and stumps of recently cut trees are recorded. In addition, the naturalness of the stand is assessed (Laarmann et al., 2009) and the amount of CWD wider than 10 cm with decay stages are inventoried from time to time (Paluots et al., 2018). The minimum tree diameter threshold is generally set to 4 cm (Kiviste and Hordo, 2002). Tree-level data is accompanied by stand-level information such as the

year of inventory, plot number, plot coordinates and radius, stand age, site type, dominant tree species and others. All sample plots are circular with radius up to 30 metres depending on stand density and other stand characteristics (Kiviste et al., 2015). Three plots are often made within the same stand to describe intra-stand variability.

For evaluating the spatial structure of forest with different levels of naturalness (II) and for quantifying forest stand structural heterogeneity (III), the tree-level data collected from the sample plots were used. For the study of tree vitality assessment (I) 10 to 16 (approximately every 10th tree located on chosen sample plots) randomly selected visually healthy trees (reference tree) were drilled at the root collar for decay detection. Drilling was done with a non-destructive micro-drill RESISTOGRAPH® 4450-P/S. As the resistograph device is measuring its power consumption (Rinn, 2016), it detects tree density changes caused by decay. Altogether, 272 trees (130 Scots pine and 142 Norway spruce) were drilled through the stem or up to 450 mm in depth.

4.3. Data analysis

4.3.1. Evaluation of structural patterns of forests using nearest neighbour structural indices (II)

To model the structure and assess structural patterns of forests with different levels of naturalness, marked point process statistics were used. Point process statistics are mathematical models of point patterns (Illian et al., 2008) where point patterns (stand) consist of individual points (trees) that can be provided with information about marks (e.g., tree species, vitality status, diameter). Every tree located on a sample plot was taken under consideration as a reference tree, as a point in two-dimensional space. To quantify forest stand structure and to analyse spatial tree patterns, structural indices based on the nearest neighbourhood approach (Maleki et al., 2015) were used.

Nearest neighbour indices describe the relationships between a certain point in a point pattern (reference tree) and its nearest neighbourhood where a certain number of closest neighbouring trees are observed. All the indices were calculated at single-tree-level, calculations were done using the equations presented in Table 2. To analyse spatial patterns in forest stands, tree polar coordinates (azimuth and distance) were first

Table 2. Equations for calculating structural indices of a reference tree. The four nearest neighbours of a reference tree are used in this study (k = 4).

Species mingling index (Gadow, 1993)

$$M_i = \frac{1}{k} \sum_{j=1}^k v_j,$$

 $M_i \in [0,1]$

where:

 M_i – species mingling index for reference tree i;

tree i – reference tree;

tree j – neighbouring tree of the reference tree i;

$$v_j = \begin{cases} 1, when species j \neq species i \\ 0, otherwise \end{cases}$$

Deadwood mingling index (Laarmann et al., 2009)

$$DM_i = \frac{1}{k} \sum_{j=1}^k v_j,$$

 $DM_i \in [0,1]$

where:

 DM_i – deadwood mingling index for reference tree i;

tree i – dead reference tree;

tree j – neighbouring tree of the reference tree i;

$$v_j = \begin{cases} 1, when \ neighbour \ j \ is \ a \ dead \ tree \\ 0, otherwise \end{cases}$$

Deadwood distribution index (II)

$$D_i = \frac{1}{k} \sum_{j=1}^k v_j,$$

 $D_i \in [0,1]$

where:

 D_i – deadwood distribution index for reference tree i;

tree i – alive reference tree;

tree i – neighbouring tree of the reference tree i;

$$v_j = \left\{ egin{array}{ll} 1, when \ neighbour \ j \ is \ a \ dead \ tree \ 0, otherwise \end{array}
ight.$$

Uniform angle index (Gadow and Hui, 2002)

$$W_i = \frac{1}{k} \sum_{j=1}^k v_j,$$

$$W_i \in [0,1]$$

where:

 W_i – uniform angle index for reference tree i;

tree i – alive reference tree;

tree j – neighbouring tree of the reference tree i;

 a_j – angle between neighbouring trees, $\leq 180^{\circ}$;

 $\alpha_{\rm o}$ – standard angle (360° / k + 1), 72° when k = 4 (Hui and Gadow, 2002);

$$v_j = \begin{cases} 1, when \ a_j < \alpha_o \\ 0, otherwise \end{cases}$$

Diameter differentiation index (Gadow, 1999)

$$T_i = 1 - \frac{1}{k} \sum_{j=1}^{k} \frac{\min(d_i, d_j)}{\max(d_i, d_j)}$$

 $T_i \in [0,1]$

where:

 T_i – diameter differentiation index for reference tree i;

tree i – alive reference tree;

tree j – neighbouring tree of the reference tree i;

d - DBH

To make T_i frequency distributions compatible with other indices, T_i values for distributions are grouped as follows (based on Gadow and Hui, 2002):

 $T_i=0$ if $T_i\leq 0.05$ – smaller tree has 95% or more of the neighbouring tree's size, dimensions of neighbours and subject tree i are very even $T_i=0.25$ if $0.05 < T_i < 0.15$ – smaller tree has 85% to 95% of the neighbouring tree's size, dimensions of neighbours and tree i are even $T_i=0.50$ if $0.15\leq T_i<0.30$ – smaller tree has 70% to 85% of the neighbouring tree's size, dimensions of neighbours and tree i are moderately uneven

 $T_i=0.75$ if $0.30 \leq T_i < 0.60$ – smaller tree has 40% to 70% of the neighbouring tree's size, dimensions of neighbours and tree i are uneven $T_i=1$ if $T_i \geq 0.60$ – smaller tree has less than 40% of the neighbouring tree's size, dimensions of neighbours and tree i are very uneven

transformed into Cartesian coordinates (x, y). Then, mark information, that can be both qualitative (e.g., tree species, vitality status) or quantitative (e.g., tree dimensions) were taken into consideration: attributes associated with the arrangement of tree positions, tree species and dimensions and deadwood were under observation.

With four neighbouring trees, structural indices have five values -0, 0.25, 0.5, 0.75 and 1 (Table 2). For example, index value 0 (Fig. 3) indicates homogeneous tree species and dimensions, deadwood absence and regular tree positioning patterns within a group of neighbours, and index value 1 refers to heterogeneous tree species and dimensions, frequent occurrence of deadwood and/or deadwood clumping, and irregular or clumped tree positioning within a group of neighbours. The index value was calculated for each tree (shrub species were excluded from data analysis) present in a sample plot based on the information about tree species, vitality status, dimensions and positioning characterizing the spatial diversity in the immediate vicinity of each reference trees close neighbourhood.

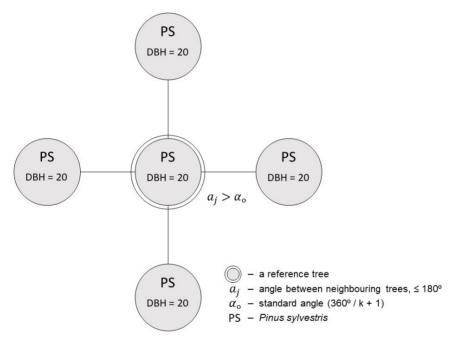


Figure 3. Method of calculating species mingling, uniform angle and diameter differentiation indices involving four neighbouring trees with calculated index value of 0; deadwood mingling and deadwood distribution indices calculations are analogous to species mingling but instead of tree species, tree vitality status (whether tree is dead or alive) is taken under observation. The reference tree is a dead tree in case with deadwood mingling index and alive in case with other indices.

As a second step, as a population characteristic, the mean arithmetic indices were calculated for every sample plot applying the NN1 edge effect correction method (Pommerening and Stoyan, 2006). Edge

correction is needed in cases with small circular plots such as plots in ENFRP (Lilleleht et al., 2014), however, edge effects are minimized with larger observation windows. The edge correction is done in order to avoid or reduce systematic errors in estimates occurring due to the fact that reference trees may have some closest neighbouring trees located outside of the plot that are not recorded. The closer the reference tree is to the plot boundary, the greater is the probability that at least one neighbouring tree is located outside the plot.

Kruskal and Wallis (1952) nonparametric test with Dunn's (1961) multiple comparison test as a post hoc were used to assess the differences between mean index values of managed, recovering and natural forests. Confidence intervals at 95% confidence level for the mean index values were calculated with the bootstrap method (Efron, 1979). Wilcoxon (1945) one sample test (also known as Mann-Whitney test) was used to investigate whether the index values of large trees (DBH \geq 40 cm) were higher than small trees (DBH \leq 40 cm).

4.3.2. Quantification of stand structural heterogeneity using structural complexity index (III)

Structural complexity index (SCI; Zenner, 1998), a stand-level index describing stand structural heterogeneity was calculated for each sample plot using ENFRP tree-level data. All standing trees and shrubs (alive and dead) present on sample plots were used for the index calculation. Tree polar coordinates were first transformed into Cartesian coordinates (x, y) and DBH was used for tree size information (z). The index calculation was performed using the equation presented in Table 3: SCI is calculated as a ratio between the area of faceted surface SCI* (three-dimensional triangles generated by tree x and y coordinates and z coordinate according to tree DBH) and its projection A_T . Possible edge effects were corrected as described in Zenner (2000) by omitting triangles where nearest neighbours may locate outside the plot boundary. First steps of index calculation are illustrated in Fig. 2 in III. The greater is the area of faceted surface depending on tree size variation compared to its projection, the higher is SCI value for sample plot indicating more heterogeneous stand structure.

Table 3. Equations for calculating structural complexity index (Zenner, 2000).

$$SCI = SCI^*/A_T$$

where:

 A_T is the sum of areas of all non-overlapping two-dimensional triangles calculated by tree x and y coordinates using Delaunay triangulation routine.

SCI*

$$SCI^* = \sum_{i=1}^N \frac{1}{2} |a \times b|,$$

where:

N is the number of triangles in the plot, $|a \times b|$ is the absolute value of the vector product of vector AB: coordinates $a = (x_b - x_a, y_b - y_a, z_b - z_a)$ and the vector AC: coordinates $b = (x_c - x_a, y_c - y_a, z_c - z_a)$.

Kruskal-Wallis (1952) nonparametric test with Dunn's (1961) multiple comparison test as a post hoc were used in order to assess the differences in mean SCIs between multiple groups. To study the effect of forest management considering the multiple influence of stand variables, the generalized additive model (GAM) as extension of generalized linear models (Robinson et al., 2011; Mehtätalo and Lappi, 2020) was used (Eq. 1 in III). GAM was also used for modelling and visualizing the relationship between SCI and stand characteristics conventionally used for forest management planning (Table 1 in III). The GAM coefficients were obtained using penalized iteratively reweighted least squares method and the spline approach was used as to smooth functions of the predictor variables (Wood, 2006). Additionally, a linear model with 95% confidence limits was used to model and visualize the SCI trend from 1996 to 2016 (Mehtätalo and Lappi, 2020).

4.3.3. Assessment of tree vitality using non-destructive microdrill resistograph (I)

Resistograph drilling profiles were manually analysed using the Rinntech e.K. DecomTM Scientific program to determine trees with well-developed decay at the root collar (Fig. 4). To detect the areas of

decay on resistograph drilling profiles as accurately as possible, a specific algorithm was written in the Microsoft® Visual FoxPro® environment. The algorithm compares the mean value of the drilling measurement 5 mm before and after a point in the drilling profile and then searches for the absolute maximal difference between the mean values at 2 cm width areas. Then the algorithm establishes the areas where the mean values differ from each other to the greatest extent. This method identifies decayed areas more precisely than visual evaluation of drilling profiles.

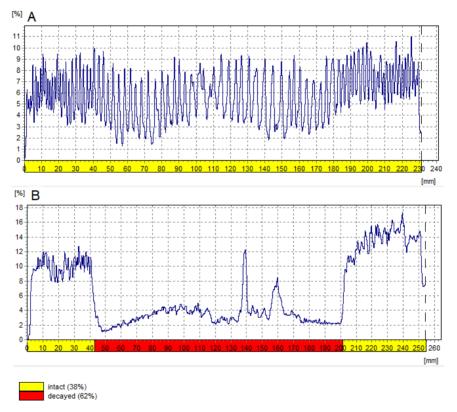


Figure 4. Resistograph drilling profiles of intact (A) and decayed (B) Norway spruce trees. Intact and decayed areas are marked manually. The x-axis is drilling depth (mm) and the y-axis is drilling resistance (%).

The pathogen species causing the decay was not identified. Instead, the clumping of decayed neighbouring trees was assessed using the index NM_i (Eq. 1 in **I**; method is originally based on deadwood mingling (Laarmann et al., 2009) and species mingling indices (Gadow, 1993)). The index of a reference tree with decay is calculated to assess the proportion of the k nearest neighbours j of a reference tree i in order to identify clumping of

decayed trees. The closer the mean index is to 1, the more neighbouring trees are decayed and the stronger is the clumping of decayed trees.

The probability of decay occurrence on trees depending on the main tree species of a stand was tested using a general linear model (GLM; Bates, 2010). The occurrence of decay in a tree was considered as the function characteristic with binary values (1 – tree has internal decay, 0 – tree does not have internal decay). The relative diameters of trees at the root collars were calculated to determine if internally decayed trees have, on average, greater dimensions than drilled trees. A tree was larger than the average drilled tree if its relative diameter value exceeded 1.0.

Data analysis of all the papers (**I**, **II**, **III**) was carried out in the R environment (R Core Team, 2017). The threshold for a statistically significant *p*-value was set to 0.05.

5. RESULTS

5.1. Structural elements and patterns of forests with different levels of naturalness

The results of the assessment of stand structural elements and spatial patterns in Scots pine and Norway spruce dominated forests with different levels of naturalness (II) showed that managed forests in Estonia differ from natural and recovering forests (hereafter also referred to as unmanaged forests) in several aspects. The average stand age, height and diameter, basal area and volume of living trees were noticeably lower, and tree species composition more homogeneous in managed forests (Table 1 in II). Mingling of tree species and dead trees, the distribution of deadwood, differences in tree dimensions and regularity in tree positioning patterns were also lower in managed forests but depend on the dominant tree species (Table 4).

Table 4. Means of structural indices accompanied with confidence intervals at 95% confidence level (II) according to dominant tree species and forest naturalness level. M – managed, R – recovering and N – natural forests; M_i – species mingling, DM_i – deadwood mingling, D_i – deadwood distribution, T_i – diameter differentiation, W_i – uniform angle index. Letters denote significant differences at p < 0.05 between forests in accordance with the Kruskal-Wallis test.

		N	orway spru	ce	Scots pine			
Level		M	R	N	M	R	N	
	$\overline{M_{\iota}}$	0.17 ^a	0.28 ^b	0.35 ^b	0.43a	0.44a	0.44ª	
Index		(0.13, 0.21)	(0.22, 0.34)	(0.29, 0.41)	(0.39, 0.46)	(0.41, 0.47)	(0.37, 0.50)	
	\overline{DM}	0.15^{a}	0.10^{a}	0.12^{a}	0.13^{a}	0.12^{a}	0.18^{b}	
		(0.11, 0.19)	(0.06, 0.15)	(0.06, 0.18)	(0.09, 0.16)	(0.10, 0.15)	(0.14, 0.22)	
	_	0.10^{a}	0.10^{a}	0.08^{a}	0.08^{a}	0.11^{b}	0.15^{c}	
		(0.07, 0.12)	(0.07, 0.13)	(0.06, 0.11)	(0.07, 0.09)	(0.09, 0.13)	(0.12, 0.17)	
	\overline{T}_{l}	0.31 ^a	0.40^{b}	0.45^{b}	0.36^{a}	0.41 ^b	0.44^{b}	
	l	(0.30, 0.33)			(0.34, 0.38)	(0.39, 0.44)	(0.43, 0.46)	
	1/17	0.47^{a}		0.49^{b}		0.49^{a}	0.49^{a}	
	$\overline{W_{\iota}}$	(0.46, 0.48)	(0.47, 0.50)	(0.48, 0.51)	(0.47, 0.49)	(0.48, 0.50)	(0.48, 0.50)	

The mean species mingling (Table 4) was relatively high in all forest groups. Managed Norway spruce dominated stands were significantly more homogeneous in mingling of species when compared to unmanaged ones. The frequency that at least one neighbouring tree

is a different tree species was around 60% in unmanaged and 35% in managed forests (Fig. 5). The stand-level mean index in Scots pine dominated stands did not show any statistically significant differences among different naturalness levels (p = 0.89).

The mean deadwood mingling index (Table 4) in Norway spruce dominated stands showed higher clumping of dead trees in managed forests than in unmanaged forests. However, the differences were not statistically significant (p = 0.36). The frequency distributions indicated that *no statistical difference* may have been caused by the high variability of mean index values between stands as the amount of clumped deadwood (index values 0.75 and 1.00) in managed forests was relatively high (Fig. 5). The mean index value (Table 4) and the frequency distribution (Fig. 5) of Scots pine dominated stands indicated that in natural forests, dead trees were significantly more often clumped than in recovering or managed forests.

The mean deadwood distribution index (Table 4) in Norway spruce dominated stands showed no significant differences (p = 0.67) among different naturalness levels. In Scots pine dominated stands the mean index value indicated that the more natural is the forest conditions, the more often dead trees are interlaced with living trees. The frequency distribution in Scots pine stands (Fig. 5) showed that more than 75% of the living reference trees had all neighbours alive; in unmanaged conditions the amount was around 10% smaller.

Frequency distributions of DBH (Fig. 2 in II) show that trees with small diameters predominate in unmanaged stands. The distribution of the diameter differentiation index in Norway spruce dominated stands (Fig. 5) showed that neighbouring trees in managed forests had mostly moderately uneven, even or very even dimensions. Neighbouring trees in unmanaged forests had inversely more often uneven and very uneven dimensions. The mean index value (Table 4) showed that trees had significantly more often uneven dimensions in recovering and especially in natural forests when compared to managed forests. In Scots pine dominated stands (Fig. 5) the index showed a relatively strong tendency of neighbouring trees to have uneven and very uneven dimensions under unmanaged conditions. The mean indices (Table 4) showed statistically significant differences between naturalness levels; trees had remarkably

more uneven dimensions in recovering and especially in natural forests when compared to managed forests.

The uniform angle index showed that most of the trees were randomly positioned regardless of forest naturalness level or dominant tree species (Table 4, Fig. 5). The positioning of trees in Norway spruce dominated stands in managed forests was significantly more regular than in unmanaged forests (Table 4), neighbouring trees were more often positioned irregularly or very irregularly (Fig. 5). The stand-level mean index in Scots pine dominated stands (Table 4) did not show any statistically significant differences among different naturalness levels (p = 0.09).

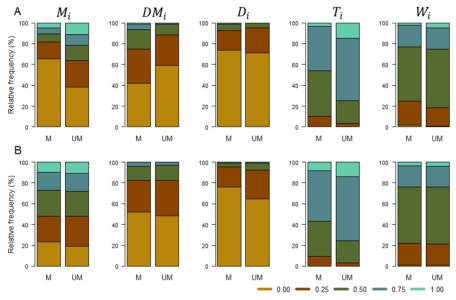


Figure 5. Frequency distributions of structural indices in Norway spruce (A) and Scots pine (B) dominated stands according whether stands are M – managed or UM – unmanaged (II). M_i – species mingling, DM_i – deadwood mingling, D_i – deadwood distribution, T_i – diameter differentiation, W_i – uniform angle index.

The analysis of the importance of large trees on stand structural heterogeneity showed that large trees are especially important in terms of maintaining the diversity of forests (see a visualized example in Fig. 6). Large trees in Norway spruce stands had statistically significantly higher values of species mingling (0.43, p < 0.01) and diameter differentiation indices (0.58, p < 0.01) than smaller trees (0.22, 0.34, respectively). Large trees in Scots pine stands had statistically significantly higher species

mingling (large trees = 0.69, small trees = 0.41, p < 0.01), deadwood distribution (large trees = 0.10, small trees = 0.09, p < 0.05) and diameter differentiation (large trees = 0.55, small trees = 0.38, p < 0.01) indices.

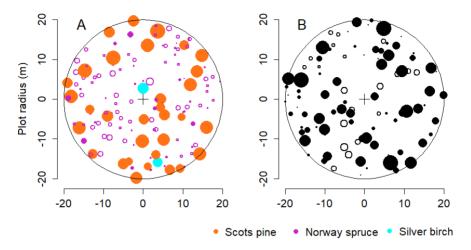


Figure 6. Examples of spatial schemes of trees with high (≥ 0.50) and low structural index values (based on the idea from Pommerening and Uria-Diez (2017) paper) – larger trees are often surrounded with other tree species and therefore experiencing high mingling of species (A), and larger trees are often surrounded by small trees experiencing high diameter differentiation (B). Trees with high index values are presented as filled dots, low index values as empty dots.

5.2. Structural heterogeneity of forest stands with different management history

The results of quantifying stand structure by applying a stand-level structural complexity index SCI (III) showed that the index ranged from 1.36 to 10.78 in Estonian hemiboreal conditions (Table 5).

Table 5. The range of SCI in Estonian forests according to the site fertility (III). CF – conservation forests, MF – managed forests, RF – rehabilitation forests.

		Forest type	
	CF	MF	RF
Fertile sites	3.16 - 10.22	1.86 - 10.78	_
Poor sites	1.99 - 5.90	1.72 - 6.77	1.36 - 4.15

SCI was highest in conservation forests on fertile sites (7.42 \pm 1.20), followed by managed forests on fertile sites (4.74 \pm 1.44), managed forests on poor sites (4.00 \pm 1.02), conservation forests on poor sites (3.85 \pm 0.87) and lowest in rehabilitation forests (2.64 \pm 0.69). The mean SCI was statistically significantly different between forest groups and site types (p < 0.01) according to the Kruskal-Wallis test. The only exception was managed and protected forests growing on poor sites (p = 0.32) according to the post hoc.

The complexity index was statistically significantly correlated (GAM: p < 0.01) with commonly used stand characteristics showing positive relationship with the volume of living trees, stand diameter, stand height, the volume of standing deadwood, stand age and basal area (Fig. 3 in III). Additional modelling of the effects of forest management and site fertility on SCI when considering the multiple influence of stand variables using GAM showed that both, forest management and site fertility have an additional impact on forest structural heterogeneity that commonly used variables do not explain. Management, site fertility and stand characteristics explained 82% of SCI. Silvicultural operations affected SCI negatively (-0.14, p = 0.03) and site fertility affected SCI positively (0.26, p < 0.01).

SCI increased with the increasing number of tree and shrub species present on sample plots (Fig. 7A): group means differed significantly from each other (p < 0.01) according to the Kruskal-Wallis test. The post hoc analysis showed that the difference in SCI was weaker as the number of species increased. Silvicultural operations, on the other hand, had an immediate negative impact on stand structural heterogeneity (Fig. 7B). The SCI decreased significantly (p < 0.01) after thinning on fertile and poor sites. However, the linear trend of SCI values immediately after the thinning from 1996 to 2016 (Fig. 6 in III) indicated that forest management in Estonia may have shifted towards favouring increased structural heterogeneity over the years.

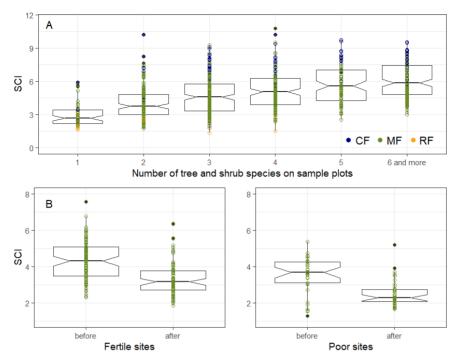


Figure 7. SCI boxplots by number of tree and shrub species occurring on a sample plot (A) based on all 852 sample plots belonging to CF – conservation forests, MF – managed forests, RF – rehabilitation forests; and SCI boxplots before and after thinning (B) based on 125 sample plots belonging to actively managed stands thinned before the last measurement (**III**). The bottom and top of the box denote the interquartile range, black horizontal line medians, black dots outliers, and coloured points observations.

5.3. Visually healthy trees in managed forests

The proportion of visually healthy trees growing in stands with good sanitary condition was determined and the probability of internal decay occurrence at the root collar depending on the main tree species of a stand was tested in paper I. Well-developed decay was identified from resistograph drilling profiles in $8.0 \pm 2.9\%$ of visually healthy Norway spruce trees growing on 50–66-year-old stands and $1.6 \pm 1.4\%$ Scots pine trees growing on 94–95-year-old stands. The radial proportion of decay was higher in Norway spruce trees ($61.1 \pm 16.1\%$) and lower in Scots pine trees ($35.5 \pm 26.1\%$). According to the GLM, trees in Norway spruce dominated stands were significantly more often decayed than in Scots pine stands (p = 0.04).

The clumping of decayed trees assessment showed that 60% of drilled trees with well-developed decay had at least one decayed neighbouring tree. This result indicates a spreading of root diseases in sampled stands. Norway spruce trees experienced clumping of decayed trees more often ($NM_i = 0.42$) than Scots pine trees ($NM_i = 0.13$). The internal decay more often affected trees with larger dimensions – the relative diameter of decayed trees was 1.08 ± 0.32 in Norway spruce and 1.16 ± 0.27 in Scots pine trees. Norway spruce trees were mostly damaged by central decay and Scots pine by peripheral decay.

6. DISCUSSION

Forest stand structural traits and structural heterogeneity, e.g., the spatial arrangement of trees including their size, condition and species are considered as important biodiversity and resilience indicators (Laarmann et al., 2009; Gadow et al., 2012). Accurate estimates of those indicators are needed for different purposes, e.g., for comprehensive forest management planning, for ecologically better forest management practices and for restoring forest structures in simplified forest ecosystems (Laarmann et al., 2013; Pastorella and Paletto, 2013; Peck et al., 2014). In order to comprehensively describe forest structure, it is necessary to use measures that take into account multidimensional characteristics of forest structure (Zenner and Hibbs, 2000). Structural indices are used for quantifying forest stand structural traits and for assessing stand structural heterogeneity. Those include spatially explicit tree-level indices based on the nearest neighbourhood approach (II) as well as stand-level indices (III). The importance of such indices will probably increase in Estonia as large-scale data from high-resolution remote sensing, providing potential tree-level data, such as terrestrial and airborne lasers is increasingly available (Lang et al., 2012; Arumäe and Lang, 2018; Arumäe et al., 2020).

One of the key variables of structural diversity in forests providing spatial heterogeneity is considered to be the variability of tree dimensions (Pommerening and Särkkä, 2013). Different diversity aspects in forests are relevant but the dimensional distribution of trees is the most important attribute directly altered through silvicultural activities (Seidel et al., 2019). The results of the study about quantifying stand structure using SCI calculated on the basis of tree positions and diameters showed that structural heterogeneity was highest in conservation forests on fertile sites in Estonia (III). The diameter differentiation index showed that neighbouring trees have more often uneven dimensions under more natural forest conditions as well (II). The more the structural elements of old forests creating complex patterns are retained during management, the better it is for forest biodiversity: plant species, animals and fungi (Gustafsson et al., 2020). Large old trees showed especially high importance in preserving stand structural diversity for Estonian conditions (II). Another option for preserving dimensional differences of trees in managed forests, suggested by Gauthier et al. (2015), is retaining natural regeneration or keeping seed trees in gaps and patches. It helps maintain stand-level diversity and still follows the main idea of forest management, e.g., maximizing economic gain through homogenizing forest structure (Buongiorno et al., 1994). Maintaining or improving a certain diversity aspect during forest management helps obtaining other aspects. For example, the mingling of tree species and the differentiation of tree dimensions (Pommerening and Uria-Diez, 2017) and the spatial arrangement of trees and tree dimensions (Pommerening and Särkkä, 2013) are related to tree local neighbourhoods. This means that local species richness promotes size hierarchy and *vice versa*, and that mature trees that tend to be randomly distributed within a stand are surrounded by clusters of small trees.

Ecologically sustainable forest management is particularly important in conifer-dominated forests that are under strong pressure to supply wood (Angelstam and Kuuluvainen, 2004). However, the time for homogeneous monocultures seems to be coming to an end due to many shortcomings (Juchheim et al., 2019; Huuskonen et al., 2021). Mixed forests ensure the heterogeneity of stand structure and species diversity (III) and are more easily adapted to uncertain future changes, diluting the impact of disturbance agents such as specialist pathogens (Bauhus et al., 2017). Conifer-oriented forest management does not produce noticeably better economic benefits when compared to mixed forests but has high cost in resilience and diversity (Dieler et al., 2017; Pukkala, 2018). Benneter et al. (2018) found that tree species diversity does not compromise stem quality in most of the European forest types and often has positive effects on forest productivity. Taylor et al. (2020) agrees in part with Benneter et al. (2018), stating that species diversity indeed affects forest productivity but the effect changes during different successional stages. The results of study III clearly showed that species diversity promoted stand structural diversity in Estonia, SCI significantly increased along with the increasing number of tree and shrub species in a stand (Fig. 7 in III). Furthermore, the mingling of different tree species was significantly higher in unmanaged Norway spruce stands when compared to managed stands, however, no statistical differences appeared in Scots pine dominated stands (II).

An important structural feature characterizing forest ecosystem quality in Estonian conditions is deadwood quantity (Kohv and Liira, 2005). A noticeably higher amount of deadwood was present in unmanaged

forests than in managed ones regardless of the dominant tree species in Estonia (II). Tree mortality patterns in Norway spruce dominated forests showed clumping of dead trees mostly in managed forests (II). Norway spruce stands are known to be especially vulnerable to forest diseases and pests (Pukkala, 2018). In Estonia, clumping of dead trees in managed forests often indicated a recent disturbance caused by biotic agents (Laarmann et al., 2009). Dead trees in Scots pine stands were spatially more clumped in natural forests rather than in recovering or managed forests (II); the finding indicated that the start of gap formation is a natural process inherent in hemiboreal old-growth forests (Esseen et al., 1997).

Managed forests are more homogeneous in occurring structural patterns and elements when compared to unmanaged forests in Estonia (II). Stand structural heterogeneity largely depends on forest management intensity and site fertility (III). Many studies state that forest management does not affect forest structure and species composition negatively in Europe (Duguid and Ashton, 2013; Schulze et al., 2016; Dieler et al., 2017; Ehbrecht et al., 2017) but not necessarily (Liira et al., 2007; Horvat et al., 2017). In Estonia, silvicultural operations had a negative immediate impact on stand structural heterogeneity (III). Although the immediate impacts of silvicultural treatments were negative, the trend of SCI values after thinning indicated that forest management in Estonia may have shifted over the past 20 years toward favouring increased structural diversity (Fig. 6 in III). The direction of silvicultural impact on forest stand structural heterogeneity depends on the characteristics of management (Laarmann, 2014). The decisions are largely in the hands of forest managers. Too intensive forest management and homogenization of forest stand structure decreases forest resistance and resilience, leading to a possible increase in forest disease problems (Larsen, 1995).

The internal health condition of trees has not been largely studied and described during forest inventories in Estonia, even though the presence and serious problems with root rot in coniferous stands were noted decades ago (Hanso and Hanso, 1999). The study of tree vitality assessment (I) showed that the proportion of visually healthy trees having well-developed decay is considerable and that larger trees often have more problems with internal decay: the increase in tree diameter contributed to higher probability of a tree being decayed. Almost 10% of the trees in Norway spruce dominated stands that were visually in

good sanitary condition contained well-developed decay. The possible reasons why, are partially explained by the results of studies II and III: the structure of managed forests is usually significantly simplified during forest management in Estonia, especially in Norway spruce dominated stands. Structurally complex species-rich stands tend to be ecologically more stable than homogeneous stands regarding stressors (Thurm et al., 2016). Forest management, e.g., thinning and homogenization of forest stand structure, create perfect conditions for the spreading of root diseases: tree stumps, damaged stems or roots are the primary growing substrates for fungal spores where the spreading expands through root contacts within the stand (Bendel, 2006). Although the exact pathogen species causing tree decay was not determined in paper I, the clumping of decayed trees gave reason to believe that the decay was caused by root diseases in most of the sampled stands. Visual tree vitality assessment only in conifer dominated stands during forest inventories will lead to underestimating the proportion of trees with well-developed decay, which in turn can lead to miscalculating tree mortality and ultimately inaccurate growth and yield predictions (Fig. 2 in I).

The results of the current thesis are mainly focused on the examples of conifer dominated stands growing on productive mineral soils, thus the results are only applicable to particular areas. The mechanisms creating complex patterns of forest ecosystems require further analysis. One of the methods – correlations among the points relative to the distances to the closest neighbours, used in the current thesis, involved perhaps one of the most used approaches of point process statistics. However, there are multiple other ways in marked point process statistics for describing and understanding interactions of trees with different characteristics, which can be continuous variates, vectors of variates, even stochastic processes (Illian et al., 2008).

7. CONCLUSIONS

The knowledge gained from studies I, II, III that provided quantitative information about stand health, spatial structure and heterogeneity is intended to support improved forest management practices focusing more on ecosystem values and ecological processes. Natural forest stands show more heterogeneous stand structures and spatial patterns, identified using structural indices, in comparison to managed stands (II, III). The species and dead tree segregation, deadwood distribution, dimensional differences and irregularity in positioning patterns of trees were generally higher in natural forests and the structure of conservation forests on fertile sites was more heterogeneous than on any other forest type. Therefore, structural indices are effective tools for identifying stands with different management histories. The hypothesis that thinnings have different short-term and long-term effects on stand structural heterogeneity was verified in study III. The short-term effects of thinnings were to simplify stand structural heterogeneity but silvicultural treatments did not show a similar effect over the long-term.

The following conclusions were drawn based on the results of this thesis:

- Structural indices provide quantitative information about spatial forest structure, e.g., how trees of different species, dimensions or vitality status are mixed in space and how heterogeneous is the structure of a forest stand. In-field evaluation of neighbourhood relationship-based structural indices are rather easy to implement and the practical use of these indices in forest inventories can contribute to a more comprehensive ecological planning of forest management. The range of SCI in forests with high ecological quality could be used as a reference or baseline for assessing the suitability of management techniques to enhance the structural heterogeneity of the stand. However, it is not suitable for everyday use due to labour-intensity but could be routinely implemented in the future when remotely-sensed structural data becomes routinely available.
- The variety of structural elements and patterns (multiple tree species and sizes, e.g., large old trees or regrowth, deadwood abundance, different spatial distribution of dead and alive trees)

in forest stands with different ecological quality or management history show significant differences. Heterogeneous stand structures are generally significantly more abundant in natural or conservation forests compared to other forest types.

- Large trees play an important role in sustaining forest stand structural diversity they are more often surrounded with dead trees, trees with different dimensions and species than smaller trees. The key to create and maintain complexity during management is preserving large old trees whenever they exist. Another option for preserving higher stand-level diversity by preserving dimensional differences of trees is retaining regrowth.
- The spatial patterns and dimensions of deadwood and CWD are important indicators of forest ecological quality. Dead trees with different dimensions, species and decay stages create possible habitats for specialist species and should be partially retained. Clumping of dead trees also creates gaps.
- Structural heterogeneity of stands increases with increasing number of tree and shrub species suggesting that species diversity promotes stand structural diversity. Mixed forests add to heterogeneity and complexity of stand structure.
- Managed Norway spruce stands are strongly homogenized during forest management, and are therefore especially vulnerable to biotic agents. Despite the lack of visual symptoms of internal damage, visually healthy conifers in intensively managed stands tend to decay relatively often at the root collar. Species-diverse mixed forests would potentially adapt more easily to disturbances.
- Modelling of forest dynamics depends on growth and mortality predictions of single trees. Errors in tree vitality assessment may lead to biased predictions in forest stand dynamics showing higher growth rates and probability of survival of trees with internal decay.
- Considering stand structural elements and patterns as well as forest growth and yield in forest management planning will lead to the enhanced naturalness and biodiversity of managed forests.

Maintaining or restoring important structural features inherent in stands with higher ecological quality or lower management intensity are essential to maintain habitats of desired species, and to support the overall biodiversity of Estonian forests.

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SUMMARY IN ESTONIAN

PUISTU SEISUNDI JA STRUKTUURITUNNUSTE KVANTITATIIVNE HINDAMINE HEMIBOREAALSETES METSAÖKOSÜSTEEMIDES

Sissejuhatus

Lisaks puidu tootmisele on metsanduses väga oluliselt esile tõusnud metsade majanduslike, ökoloogiliste ning sotsiaalsete funktsioonide omavaheline integreerimine ning ökosüsteemiteenustega arvestamine (Huuskonen et al., 2021). Ligi veerandile Eesti metsadest on kehtestatud erineva tugevusega kaitserežiime (Sims et al., 2020). Kuigi kaitsealadel on oluline roll bioloogilise mitmekesisuse hoidjana (Viilma et al., 2001), ei piisa nendest üksi elurikkuse säilitamiseks, vaid bioloogilise mitmekesisuse hoidmise ja taastamisega tuleb tegeleda ka väljaspool kaitsealasid, praegustes majandusmetsades.

Metsade majandamise peamine eesmärk on siiani olnud optimaalsete kuludega puidu tootmine (Buongiorno et al., 1994) ja seetõttu on metsakasvatuslike tööde mõju metsade struktuuri lihtsustav. Erinevate majandamisvõtetega mõjutatakse puude ruumilist, liigilist, vanuselist jm jaotust puistus (Seidel et al., 2019; Juchheim, 2020). Bioloogilise mitmekesisuse säilitamisel mängivad olulist rolli puistus esinevad struktuurielemendid (nt vanad ja surnud puud, lamapuud erinevas kõdunemisastmes, erinevad puuliigid erineva vanusega jt), mis pakuvad elupaiku erinevatele metsaliikidele (McElhinny et al., 2005; Mikoláš et al., 2017; Thorn et al., 2017). Nii ongi puistute struktuuri mitmekesisena hoidmine ja looduslähedane majandamine üks oluline elurikkuse säilitamise meede metsanduses.

Metsaökosüsteemi võime säilitada häiringute korral oma struktuuri olulisimaid komponente, koosseisu, looduslikke funktsioone ja protsesse sõltub bioloogilisest mitmekesisusest (Thompson et al., 2009). Elurikkuse vähenemine mõjutab negatiivselt metsade tervislikku seisundit ja vastupanuvõimet mitmele abiootilisele ja biootilisele stressitegurile (Alfaro ja Singh, 1997; Kuuluvainen, 2016). Näiteks on Eesti okaspuumetsades suur probleem juure- ja tüvemädanikku põhjustavad seenhaigused (Hanso ja Hanso, 1999; Drenkhan et al., 2018). Hoolimata

visuaalsetest märkidest, mis viitavad puu elujõu vähenemisele, on mädanikku puus sageli keeruline kui mitte võimatu tuvastada (Vollbrecht ja Agestam, 1995; Laflamme, 2010). Kuna mädanik põhjustab puidu füüsikaliste omaduste halvenemist (Rinn, 2016), võib puude tervisliku seisundi silmamõõduline hindamine metsainventeerimise käigus anda kallutatud tulemusi puistu tegeliku tervisliku seisundi kohta. See võib aga omakorda viia valehinnangute saamiseni puude suremuse, puistute ajalis-ruumiliste mustrite, puude kasvu ning puistu saagikuse kohta.

Doktoritöös analüüsitakse erinevaid meetodeid, mida saab rakendada metsakorralduses, et arvestada varasemast enam mitmesuguste ökosüsteemi väärtustega. Doktoritöö põhieesmärgid on 1) hinnata kahjustuse ilminguteta puistutes visuaalselt tervetes puudes juurekaelal mädaniku esinemist (I), 2) uurida puistu mädanikuga kahjustunud puude grupilisust (I), 3) analüüsida erineva majandamisrežiimiga puistutes puistu struktuuri kirjeldavaid indekseid, puistusisest heterogeensust ja puistus esinevaid puude ruumilise paiknemise mustreid (II, III), 4) kinnitada hüpoteesi, et ruumilised struktuuriindeksid on efektiivsed arvulised näitajad, mille abil erineva majandamisrežiimiga puistuid võrrelda või tuvastada (II, III), 5) testida hüpoteesi, et harvendusraiete lühiajaline mõju erineb nende pikaajalisest mõjust puistu struktuuri varieeruvusele (III).

Materjal ja metoodika

Doktoritöö (artiklid I, II, III) põhineb Eesti metsa kasvukäigu püsiproovitükkide võrgustiku andmetel. Esimesed proovitükid rajati 1995. aastal (Kiviste et al., 2015) ning praeguseks on üle Eesti kokku 1071 proovitükki, mis asuvad erineva vanuse, kasvukohatüübi ja majandamisrežiimiga puistutes. Ringikujulistel, raadiusega kuni 30 m püsiproovitükkidel on puude asukohad kaardistatud ning iga viie aasta järel toimub kordusinventuur, kus mõõdetakse puude rinnasdiameeter, märgitakse üles puudel esinevad kahjustused ning mõõdetakse mudelpuude kõrgus koos võra alguse kõrgusega. Lisaks elusatele puudele inventeeritakse ka surnud puud, määratakse puu suremise põhjused, inventeeritakse lamapuud (Paluots et al., 2018) ning hinnatakse puistu looduslikkust (Laarmann et al., 2009).

Visuaalselt tervetes puistutes üksikpuu elujõulisuse hindamine (I) toimus 20 proovitükil (tabel 1). Proovitükid asusid majandatud okaspuupuistutes, vanusevahemikuga 29–95 aastat. Neist 10 proovitükki

rajati jänesekapsakuusikutesse ja 10 pohlamännikutesse. Igal proovitükil puuriti resistograafiga vähemalt 10 visuaalselt tervet puud, et hinnata mädaniku esinemist puu juurekaelal. Mädaniku tuvastamiseks mõõdetakse resistograafi puurile mõjuvat takistust, mis on korrelatsioonis puu tihedusega (Rinn, 2016). Mädaniku tekitajat ei määratud. Kokku puuriti 238 puud: 113 harilikku kuuske (*Picea abies* (L.) H. Karst.) ja 125 harilikku mändi (*Pinus sylvestris* L.). Kui uuritava puu juurekaelal tuvastati mädanik, siis hinnati ka tema naaberpuudel (kokku 29 kuusel ja 5 männil) mädaniku esinemist. Mädanikuga puude grupilisuse hindamiseks arvutati indeks NM_i (Valem 1 artiklis I). Mida suurem on indeksi väärtus (0...1), seda enam esineb mädanikuga naaberpuid.

Erineva looduslikkuse tasemega puistute struktuuri uuring (II) tehti 212 proovitüki andmete põhjal (tabel 1). Puistu looduslikkuse hindamine põhines kolmel komponendil: puistu loodusväärtused, kultuurilisbioloogilised väärtused ja negatiivsed inimmõjud (Korjus, 2002; Laarmann, 2014). Saadud punktiskoori alusel jaotati puistud kolme klassi: majandusmetsad (123 proovitükki), taastuvad metsad (58 proovitükki) ja loodusmetsad (31 proovitükki). Puistu struktuuri arvuliseks kirjeldamiseks kasutati lähimatel naaberpuudel põhinevaid indekseid: liigilise segunemise indeks (M_i , Gadow, 1993), surnud puude ruumilise paiknemise indeks (DMi, Laarmann et al., 2009), elusate ja surnud puude segunemise indeks (D_i , II), diameetrite diferentseerumise indeks (T_i, Gadow, 1999) ning puude ruumilise paiknemise indeks $(W_i, \text{Gadow} \text{ ja Hui, } 2002)$. Igat puud proovitükil referentspuuna, millele arvutati indeksi väärtused, kasutades tabelis 2 toodud valemeid. Erineva looduslikkusega puistute struktuuri uurimiseks ning omavaheliseks võrdlemiseks kasutati nii indeksi puistu keskmist väärtust kui ka indeksi varieeruvust puistus.

Puistu struktuuri mitmekesisuse uuring (III) põhineb 852 proovitükil (tabel 1), mis jaotati vastavalt majandusrežiimile kolme gruppi: kaitsealused metsad (165 proovitükki), majandusmetsad (622 proovitükki), mis omakorda jagunesid passiivselt majandatavateks (316 proovitükki, kus viimase 20 a jooksul pole toimunud raietegevust) ja aktiivselt majandatavateks (306 proovitükki), ning väga tugevate inimmõjudega metsad (65 proovitükki), mis asuvad endises Aidu avatud põlevkivikarjääri taasmetsastatud aladel. Igale proovitükile arvutati puistu struktuuri mitmekesisuse indeks SCI (Zenner, 1998), kasutades tabelis 3 toodud valemeid. Indeks põhineb puu asukohal ja puu suurusel puistus, võimaldades uurida, milline on indeksi ja puistu takseertunnuste

vaheline seos, hinnata metsamajandamise otsest mõju puistu struktuuri mitmekesisusele ja vaadelda, kuidas struktuuri mitmekesisus muutub sõltuvalt metsamajandamise režiimist ja kasvukohast.

Kõiki andmeid analüüsiti R-keskkonnas (R Core Team, 2017). Vaadeldavate tunnuste statistilise olulisuse hindamisel võeti olulisuse nivooks 0,05.

Tulemused

Erineva looduslikkuse tasemega puistute struktuuri uuringus (II) selgus, et majandusmetsad erinevad oluliselt looduslikest ja taastuvatest metsadest (tabel 4). Majandamata kuusikutes on erinevad puuliigid segunenud kui omavahel sagedamini majandatud puistutes $(\overline{M_I})$ (loodusmetsad) = 0,35, $\overline{M_I}$ (taastuvad metsad) = 0,28, $\overline{M_I}$ (majandusmetsad) = 0,17), männikute puhul statistilist erinevust looduslikkuse tasemega puistute vahel ei esinenud. Majandatud kuusikutes paiknevad puud regulaarsemalt (\overline{W}_{i} (majandusmetsad) = 0,47) kui majandamata puistutes (\overline{W}_{i} (taastuvad metsad ja loodusmetsad) = 0,49), männikutes statistiline trend puudub. Lisaks on naaberpuud seda sagedamini erinevate mõõtmetega, mida looduslikum on puistu (kuusikute puhul \overline{T}_{I} (majandusmetsad) = 0,31, \overline{T}_{I} (taastuvad metsad) = 0,40, \overline{T}_{l} (loodusmetsad) = 0,45 ja männikute puhul \overline{T}_{l} (majandusmetsad) = 0,36, \overline{T}_{t} (taastuvad metsad) = 0,41, \overline{T}_{t} (loodusmetsad) = 0,44), ning struktuuri mitmekesisuse säilitamise seisukohalt mängivad olulist rolli vanad jämedad puud.

Majandatud kuusikutes paiknevad surnud puud majandamata puistutega võrreldes sagedamini grupiti $(\overline{DM_l}$ (majandusmetsad) = 0,15, $\overline{DM_l}$ (taastuvad metsad) = 0,10, $\overline{DM_l}$ (loodusmetsad) = 0,12), kuigi lagupuidu (püstised surnud puud, tüükad, lamapuud) maht on kolm korda väiksem kui taastuvates ja üle viie korra väiksem kui looduslikes metsades (artikkel II, tabel 1). Indeksi väärtus eri rühmade vahel ei olnud statistiliselt usaldusväärselt küll erinev, kuid indeksite sagedustabel (joonis 5) näitas, et seda võis põhjustada keskmiste indeksite väärtuste suur varieeruvus. Männikutes oli trend aga vastupidine – loodusmetsas paiknevad surnud puud statistiliselt oluliselt sagedamini grupiti $(\overline{DM_i} = 0,18)$ kui majandatud $(\overline{DM_i} = 0,13)$ või taastuvates $(\overline{DM_i} = 0,12)$ metsades. Männikutes on ka elusad ja surnud puud seda sagedamini omavahel segunenud, mida looduslikum on puistu $(\overline{D_l}$ (loodusmetsad) = 0,15, $\overline{D_l}$ (taastuvad metsad) = 0,11, $\overline{D_l}$ (majandusmetsad) = 0,08), kuid

kuusikutes erineva looduslikkuse taseme vahel statistilist erinevust ei ilmnenud.

Puistu struktuuri mitmekesisuse hindamisel kasutati puude asukohal ja diameetritel põhinevat indeksit SCI (III). Selgus, et SCI on kõrgeim ehk puistute struktuur heterogeenseim viljakates kaitsealustes metsades (SCI = 7.42 ± 1.20), millele järgnevad viljakad majandusmetsad (SCI = 4.74 ± 1.44), väheviljakad majandusmetsad (SCI = 4.00 ± 1.02) ning väheviljakad kaitsealused metsad (SCI = 3.85 ± 0.87), kaks viimast gruppi omavahel statistiliselt ei erine. SCI on statistiliselt oluliselt väiksem endistes karjäärimetsades (SCI = 2.64 ± 0.69). SCI on seda suurem, mida enam puu- ja põõsaliike puistus esineb (joonis 7), toetades seisukohta, et liigiline mitmekesisus toetab struktuuri mitmekesisust. Üldiselt on metsamajanduse mõju SCI väärtustele negatiivne ja puistu boniteedi mõju SCI väärtustele positiivne. Harvendusraietel tuli välja kohene negatiivne mõju puistu struktuuri mitmekesisusele (joonis 7), kuid pikemas perspektiivis on metsamajandus Eestis pigem nihkunud struktuuri heterogeensuse säilitamise poole (artikkel III, joonis 6).

Puistu sanitaarse seisundi hindamise uuring (I) näitas, et sageli on visuaalselt hea tervisliku seisukorraga puistutes puude tegelik seisund halvem, kui paistab. Puu juurekaela kõrguselt tuvastati resistograafi puurimisprofiilide põhjal mädanikku 8% visuaalselt tervetest kuuskedest ja 2% mändidest. Kuusikutes esineb sagedamini mädanikuga puid kui männikutes. Mädaniku osakaal on suurem kuuskedel ja väiksem mändidel ning mädanikku esineb sagedamini just jämedamates puudes. Kuusikutes paiknevad mädanikuga puud sagedamini grupiti ($NM_i = 0,42$) kui männikutes ($NM_i = 0,13$) ning 60% juhtudest esineb mädanikuga puude naaberpuudest vähemalt ühel samuti mädanikku – see võib viidata juuremädanikku tekitavate seenhaiguste levikule uuritud puistutes, eriti kuusikutes.

Kok.k.uvõte

Metsanduses on välja töötatud mitmesuguseid matemaatilisi meetodeid, mis võimaldavad puistute struktuurile arvulisi hinnanguid anda. Puistu struktuur sõltub suuresti metsamajandamise intensiivsusest ja loodusliku dünaamika käigus tekkivatest struktuurikomponentidest, millel on oluline osa elurikkuse säilitamisel. Keerulisema struktuuriga liigirikkad puistud on erinevate stressitegurite suhtes stabiilsemad, seetõttu on oluline

suunata majandusmetsa struktuuri kujunemist looduslähedasemaks, kui seda on ühetaolised puhtpuistud.

Doktoritöös käsitletud uuringute põhjal tehti järgmised järeldused:

- Erineva looduslikkuse tasemega puistute struktuur erineb üksteisest oluliselt nii elusate kui surnud puude paiknemise mustrite, puude liigilise segunemise, elusate puude dimensioonide varieeruvuse, lagupuidu dimensioonide ja koguse ning puistu struktuuri keerukuse aspektist. Majandamata (sh kaitsealuste, looduslike) metsade struktuur on oluliselt heterogeensem kui majandatud metsades.
- Puistu struktuuri kirjeldavad indeksid annavad olulist teavet puude ruumilise paiknemise mustrite erinevate aspektide kohta. Indeksite praktiline hindamine metsainventeerimise käigus aitab potentsiaalselt kaasa terviklikumale metsade majandamise planeerimisele, aidates parandada puistute looduslikkust ja elurikkustmajandatavatesmetsades. Kõrgeökoloogilisekvaliteediga kaitsealuste metsade puhul saab indeksi väärtusvahemikke kasutada lähtealusena majandamismeetodite sobivuse hindamisel puistu struktuuri heterogeensuse säilitamiseks või suurendamiseks.
- Jämedatel (üle 40 cm diameetriga) puudel on oluline roll säilitamaks metsade struktuuri mitmekesisust ning need tuleks metsamajandamise käigus võimalusel säilitada. Võrreldes peenemate puudega ümbritsevad jämedaid puid sagedamini surnud, eri liiki ning erinevate mõõtmetega puud. Kui jämedaid puid puistus ei esine, võimaldab raiete käigus järelkasvu säilitamine puude dimensioonide varieeruvust soodustada.
- Surnud puud ning nende ruumilise paiknemise mustrid on olulised metsade tervislikku seisundit ja ökoloogilist kvaliteeti iseloomustavad näitajad. Erinevate omadustega (sh mõõtmete, liigi ja laguastmega) surnud puud loovad puistus erinevatele metsaliikidele sobivaid elupaiganišše.
- Puistu struktuuri mitmekesisuse erinevad aspektid on omavahel seotud ning metsamajandamise käigus teatud struktuurielementide ja -mustrite (näiteks puude liigilise segunemise) säilitamine või

parandamine edendab teisi mitmekesisuse aspekte (näiteks puude diameetrite diferentseerumist).

- Metsamajandamise käigus ühtlustatakse sageli puistute struktuuri, nt. kuuse enamusega puistute struktuuri ühtlustamisel muutuvad kuusikud biootiliste kahjustajate suhtes eriti vastuvõtlikuks. Vaatamata visuaalsete sümptomite puudumisele esineb majandatud okaspuupuistutes visuaalselt tervetel puudel juurekaelal mädanikku. Metsade ajalis-ruumiliste mustrite modelleerimine sõltub üksikpuude kasvu ja suremuse prognoosidest. Puude tervisliku seisundi silmamõõduline hindamine võib anda ebaõigeid tulemusi puude tegeliku tervisliku seisundi kohta, mis põhjustab puude suremuse ja puude kasvu prognoosides nihkega hinnanguid.
- Eesti metsade jätkusuutlikuks majandamiseks tuleks metsakorralduse käigus tavapärastele takseertunnustele lisaks hinnata erinevaid puistute struktuuri mitmekesisustiseloomustavaid näitajaid. Oluliste struktuurielementide ja -mustrite (sh erinevat liiki, erineva tervisliku seisundi ja dimensiooniga puud, ebaregulaarse asetusega puud, grupiti paiknevad surnud puud, vanad ja jämedad puud) säilitamine on vajalik, et hoida metsade elurikkust ja vastupanuvõimet häiringute suhtes.

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Communication

Vitality Assessment of Visually Healthy Trees in Estonia

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Abstract: Root rots are considered the most important forest diseases in Estonia, causing serious concern in forest management. The majority of trees infected by forest pathogens lack easily-detectable visual symptoms, making it difficult to detect decay in a tree. We assessed the general health condition of visually healthy trees in intensively managed Norway spruce (*Picea abies* L. Karst.) and Scots pine (*Pinus sylvestris* L.) stands with resistography in order to identify trees infected by root rot. We found that 8.0% of Norway spruces and 1.6% of Scots pines had well-developed internal decay on the root collar regardless of having no external symptoms of root rot. Visually healthy trees growing on permanent forest land experienced more decay than trees growing on former agricultural land. The radial proportion of decay of damaged trees was 61% in Norway spruces and 35% in Scots pines. The results suggest that resistography can be used as a reliable method for tree vitality assessment.

Keywords: Norway spruce; Scots pine; forest health; root rot; resistography; mortality

1. Introduction

Modelling of forest stand dynamics depends on growth and mortality predictions of single trees. Tree vitality is often assessed visually in the course of forest inventories as an important indicator of forest condition [1]. Visual signs, including extraordinary leaf or needle loss of a tree and noticeable fruit bodies of fungi, may indicate problems with tree vitality, but often the symptoms of stem or root rot are difficult or impossible to detect visually [2,3]. Tree vitality is usually under-examined in forest inventories, as the use of more precise methods is labour-intensive and may be destructive to the examined trees. Suitable instruments for decay detection in standing trees are, for example, increment borers, acoustic tomographs, and micro-drills. Most likely, errors in assessment of tree vitality result in bias in predicting forest stand dynamics by assessing a higher probability of tree survival and higher growth rates of unhealthy trees than warranted.

The root rots caused by the pathogens *Heterobasidion* spp. and *Armillaria* spp. are considered to be the most important forest diseases in Europe (including Estonia), causing serious concern in forest management. According to State Register of the Forest Resource [4], visual estimation of decay on living standing trees shows that at least 16.8% of spruce stands and 0.3% of pine stands are affected by root rots in Estonia. Sims et al. [5] found that 17% of Scots pine and 12% of Norway spruce mortality in managed forests is directly caused by diseases, including root rots. For some wind-thrown trees, where wind-throw affected 10% of Scots pine and 26% of Norway spruce, the mortality may also indirectly be caused by root rot [6,7]. Root rot spreads in a stand by air- or soilborne propagules, creating clumps of infected trees. Neighbouring trees can be affected by soil movement via mycelia [8,9] and rhizomorphs [10], but the mycelium of *Heterobasidion* is not able to spread freely in the soil. The disease may inhibit nutrient and water flow by damaging or killing the roots, which ultimately leads to tree

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mortality and decreases in forest ecosystem health, resilience, and productivity [3,11–13]. The incidence of *Heterobasidion* root disease is higher in stands on former agricultural lands [14–17] and in stands growing in mineral soils with good water drainage and higher soil pH [18]. Managed forests are damaged by *Heterobasidion* root disease more often than unmanaged forests, as stumps created during thinning and harvesting operations provide a favourable entry point for infection with airborne fungal spores [14]. *Armillaria* root rot damage is more severe in stands with reduced soil fertility, a lower pH, and drier moisture regime [15].

The aims of this paper are (1) to study how often visually healthy trees in managed stands are infected by root diseases which cause internal decay; (2) to quantify how much the diseases influence tree growth; and (3) to assess how the incidence of a root rot in a tree depends on the former land use and on the main tree species in a stand.

2. Materials and Methods

This study was carried out in intensively managed forest stands in Southern Estonia on permanent sample plots belonging to the Estonian Network of Forest Research Plots (ENFRP). The ENFRP was started in 1995 to collect long-term empirical data from Estonian forests [19]. A large amount of different tree- and stand-level measurements have been collected, including the species, diameter at breast height, height of trees measured, evidence of damage (mechanical, wind, moose, deer, cold, resin flows, etc.), and are re-measured every five years. All studied sample plots were in high-productivity stands. Ten sample plots were in Norway spruce stands growing in *Oxalis* site type, and ten sample plots in Scots pine stands in *Rhodococcum* site type. Site type classification follows Lõhmus [20]. Using historical background maps (1894–1922), the sample plots were selected on historical forestland and on former agricultural land on an equal basis.

This study uses data of trees from 20 sample plots. The age of the studied stands was 29–95 years. On each sample plot, at least ten randomly selected visually healthy trees were studied. For decay detection, all sampled trees were drilled once at the root collar, mostly throughout the tree (up to 450 mm depth). Drillings were carried out with the non-destructive micro-drill RESISTOGRAPH® 4450-P/S which, by measuring the power consumption, allows the detection of tree density changes caused by decay [21]. In case decay occurred in a tree, up to four visually healthy neighbouring coniferous trees growing at a distance of up to five meters from the sample tree were also drilled to describe clumping of decayed trees. Altogether, 238 (113 Norway spruce and 125 Scots pine) sample trees and 34 (29 Norway spruce and 5 Scots pine) neighbouring trees were tested. The exact pathogen species causing the decay was not identified in this study. Most likely, decay was caused by *Heterobasidion* spp. and/or *Armillaria* spp., since these pathogens are the most common root rot-causing fungi in Estonia [22].

The resistograph profiles of drilled trees were analysed using the Rinntech e.K. $Decom^{TM}$ Scientific program to determine decayed trees (Figure 1). In order to detect the exact areas of decay as accurately as possible, a specific algorithm was written in $Microsoft^{(B)}$ Visual $FoxPro^{(B)}$. For every point of the drilling profile, the algorithm compares the mean value of the drilling measure five mm before and after the point. Then, it searches the maximum difference between the mean values before and after the point at two cm width ranges and establishes the area where the mean values differ from each other the most. This method identifies the decayed area more precisely than visual evaluation of the drilling profile.

To evaluate the clumping of decayed neighbouring trees, the decay mingling index—which is based on the deadwood mingling index [23] and the species mingling index [24]—was used. We calculated the decay mingling index of a reference tree with decay (Equation 1) to assess the proportion of the n nearest neighbours j of a reference tree i:

$$NM_{\rm i} = \frac{1}{n} \sum_{j=1}^{n} v_{\rm ij} \tag{1}$$

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where $v_{ij} = 1$, if the neighbouring tree also had decay 0, if the neighbouring tree was healthy

With three neighbours, for example, NM_1 holds four values: 0, 0.33, 0.67, and 1. The larger the mean index, the more neighbouring trees are decayed and the higher is the clumping of decayed trees.

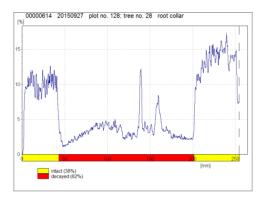


Figure 1. A resistography drilling profile of a tree with well-developed decay.

The link between decay at root collar and former land use and main tree species was tested using the general linear model with *glmer* function in R environment [25]. The occurrence of decay in a tree was considered as the function characteristic which was given binary values of 0 and 1.

To examine how decay affects tree radial growth, the growth of healthy and decayed trees was assessed. The diameters of ten trees from each species with well-developed decay were chosen from the data of the last four inventories. Drilled trees without decay and diameters similar to the diameters of trees with well-developed decay were chosen for comparison. As the number of decayed trees of Scots pine was insufficient, we included additional data from Oxalis site type for Scots pine (eight trees). To assess the statistical significance, a one-tailed t-test was used, where p-value ≤ 0.05 was considered as statistically significant.

For all drilled trees, the relative diameters of root collars were calculated to define if internally decayed trees, on average, were larger than the drilled trees. A tree was larger than the average drilled tree if its relative diameter value exceeded 1.0. All arithmetic means are presented with \pm standard deviations in this study.

3. Results

Data analysis showed well-developed decay (see Figure 1 as an example) in $8.0 \pm 2.9\%$ of visually healthy Norway spruces and in $1.6 \pm 1.4\%$ of visually healthy Scots pines. Decay was found in Norway spruce in 50–66-year-old stands and in Scots pines in 94–95-year-old stands (Table 1). The percentage of drilled trees with detected decay varied from 6.2% to 33.3% on plots where trees were damaged with root rot. According to visual evaluation, these forest stands had up to 25.2% of dead trees and 1.9–12.9% of damaged trees. On plots where no root rot was found in drilled trees, forest stands had 1.5–24.2% of dead trees and up to 20.5% of damaged trees. The overall condition of pine stands was better, as the average amount of dead trees ($5.3 \pm 5.2\%$) and damaged trees ($1.1 \pm 1.5\%$) was lower than in spruce stands ($10.4 \pm 9.5\%$ and $11.6 \pm 5.0\%$).

Norway spruces were significantly more often decayed than Scots pines (p=0.035). The relative diameter of the root collar of decayed trees was 1.08 ± 0.32 in Norway spruces and 1.16 ± 0.27 in Scots pines, showing that in both species the diameter of decayed trees was somewhat larger than the average diameter of all drilled trees.

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Plot No.	Dominant Tree Species	Stand Age (Year)	Stand Height (m)	Stand Diameter at Breast Height (cm)	Proportion of Trees with Root Rot (%)	Proportion of Dead Trees in the Stand (%)	Proportion of Visually Detected Damaged Trees in the Stand (%)
133	Norway spruce	66	24.9	25.1	33.3	9.8	12.9
128	Norway spruce	50	22.5	19.9	30.0	10.7	5.4
135	Norway spruce	55	23.9	24.1	10.0	9.2	12.8
414	Norway spruce	56	25.9	22.3	10.0	25.2	5.9
347	Scots pine	95	30.7	31.0	8.3	1.6	4.1
351	Scots pine	94	32.0	30.5	6.2	0.0	1.9

Table 1. General characteristics of plots with root rot damage in visually healthy trees.

Scots pines growing on historical forestland had $1.7\pm1.6\%$ decayed trees, and on former agricultural land there were $1.5\pm1.7\%$ decayed trees. Norway spruces growing on historical forestland had $13.1\pm5.9\%$ decayed trees and $1.9\pm1.7\%$ decayed trees in stands on former agricultural land. Norway spruce trees growing on historical forestland were significantly more often decayed than spruce growing on former agricultural land (p=0.026).

The assessment of clumping of decayed trees showed that in 60% of the cases at least one of the sampled neighbouring trees also had well-developed decay. The average decay mingling index of trees was 0.36, indicating a substantial spread of root rot in visually healthy trees. Norway spruce had more clumping $(NM_i = 0.42)$ of decayed trees than Scots pine $(NM_i = 0.13)$.

The extent of decay in Norway spruce was higher than in Scots pine; the radial proportion of decay was $61.1 \pm 16.1\%$ and $35.5 \pm 26.1\%$, respectively. Norway spruce was mostly damaged by central decay, and Scots pine by peripheral decay. The growth of visually healthy trees with root rot was 21% smaller for Norway spruce and 13% smaller for Scots pine compared to the trees without decay. Although the extent of decay in visually healthy trees was relatively large, especially in Norway spruce, and could have influenced tree growth, we did not find statistically significant differences between the diameter growth of trees with root rot and healthy trees (Norway spruce, p = 0.22; Scots pine, p = 0.09).

4. Discussion

The tree vitality assessment with resistography showed that a considerable proportion of visually healthy conifers can be infected with root diseases in Estonia. Externally healthy Norway spruce trees were decayed more frequently and heavily compared to Scots pines. The overall visual condition of spruce stands was also poorer than pine stands. Some signs, such as the proportion of dead or damaged trees, can indeed indicate disease in a stand, especially when basidiocarps of pathogenic fungi appear. In such a case, it can be assumed that some visually healthy trees are internally decayed. However, symptoms do not confirm the existence of decay in trees. In cases where the visual condition of a stand is good and no signs directly indicate disease in the stand, our results suggest that tree vitality assessment requires the internal assessment of visually healthy trees with micro-drills. Forest models are used for the assessment of timber product yields [26], but with visual assessment of disease only, the proportion of decayed trees can be underestimated and probably leads to miscalculation of tree mortality and ultimately inaccurate yield predictions (Figure 2).

Although some studies have stated that decayed trees tend to grow more slowly than healthy trees [12,27], we could not discover any significant reductions in the diameter growth of decayed trees, similarly to Oliva et al. [7]. There could be many possible reasons. We can speculate that at a certain stage of a disease or age of a tree, root disease does not influence tree growth. Another reason could be that, even if drillings at the root collar did not indicate that trees were decayed, the root system of trees may have been infected and the growth of "healthy" trees reduced (i.e., a false negative result). Wang et al. [28] showed that growth loss will significantly increase, even when only a small percentage of roots are infected by root pathogens. The study by Laarmann et al. [23] found that the probability of trees dying due to diseases in Estonia is higher in trees with a larger relative diameter at breast height.

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Our study showed that in both species the diameter of damaged trees was relatively larger than the average diameter of all drilled trees.

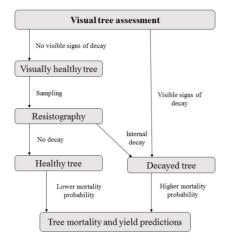


Figure 2. When assessing tree vitality only visually, tree mortality and yield predictions may be strongly under- or overestimated.

If a notable proportion of decayed trees are clumped (Figure 3), it is very likely that the stand is infected with root diseases which have spread to neighbouring trees via root contacts. Our study showed decayed trees to be considerably clumped, as in 60% of the cases at least one neighbouring trees had internal decay. In Norway spruce stands, clumping was more severe, indicating that infections through root contacts in Norway spruce stands may be more likely or trees for some reasons more susceptible to pathogens.

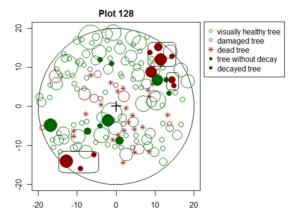


Figure 3. Clumping of decayed trees on sample plot No. 128 (x-and y-axis show distance (m) from centre).

Many studies from Europe [15–17] show that stands that are established on post-agricultural lands are highly susceptible to *Heterobasidion* root rot because the microbes in soils in arable land are

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not as diverse as in forest soils and the spread of pathogens is less well prevented. In our case, it appeared that the stands located on former agricultural land were much less damaged by diseases than the stands on historical forestland. This result draws attention to the fact that not only can forests growing on former arable lands be heavily threatened by root diseases, but also those on historical forestlands. Many stands located in historical forestland could have been infected by root rots in previous forest generations.

A notable portion of trees that have been visually assessed as healthy are actually internally damaged by root rot; therefore, visual assessment cannot be considered as a reliable method for tree vitality assessment. Rapid vitality assessment of trees with more advanced methods like resistography is the feasible way to allocate the proportion of decayed trees among visually healthy ones. The method itself may be more suitable for assessing the health condition of Norway spruce rather than Scots pine stands. In the case of spruce, decay spreads in the heartwood and may develop into butt rot without any visual symptoms. In Scots pine, the situation is different, as the decay is often limited to the roots [22] and thereby cannot be seen on the resistograph drilling profiles. If the decay has progressed to the stem of the tree, however, visual symptoms will appear in the crown. In addition, with the resistography method, two important disadvantages may appear: (1) as the radial proportion of decay was high, there remains the possibility that small-sized, incipient decay cannot be detected by microdrills; (2) decay in a tree may remain undetected due to the location of the drilling hole, as the drill may miss the rot column. The same problem occurs with increment borers [29]. Applying resistography in large-scale inventories is not easy, as the system may be a little heavy to carry and its use is somewhat time-consuming. Nevertheless, the resistograph is definitely a useful device for assessing tree internal conditions. However, a simple mobile device based on the same method as resistography could be invented in the near future.

5. Conclusions

Despite the lack of visual symptoms of internal damage, visually healthy trees in managed Norway spruce and Scots pine stands had well-developed decay on the root collar. Using resistography, we found that $8.0\pm2.9\%$ of Norway spruce and $1.6\pm1.4\%$ of Scots pine trees had decay. Norway spruces were significantly more often decayed than Scots pines. The radial proportion of decay was $61.1\pm16.1\%$ in Norway spruces and $35.5\pm26.1\%$ in Scots pines, and the decay was more present in trees with a larger diameter. A resistograph is useful for allocating the proportion of decayed trees among visually healthy ones, necessary for more accurate growth modelling. Simpler devices which are easy to carry around in forests would allow this approach to become operationally feasible.

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Author Contributions: Eneli Allikmäe, Diana Laarmann and Henn Korjus designed the study; Eneli Allikmäe did fieldwork; Eneli Allikmäe, Diana Laarmann and Henn Korjus analysed the data and wrote the paper.

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Assessment of spatial stand structure of hemiboreal conifer dominated forests according to different levels of naturalness



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Keywords: Structural index Nearest neighbourhood relationship Structural pattern Forest management

ABSTRACT

Ecosystem legacies, reflecting the management history traits, are visible in structural indicators of a forest stand. We assessed patterns of spatial forest structure by using individual tree indices based on the nearest-neighbourhood approach. Five different indices were quantified – species mingling, deadwood distribution, diameter differentiation and the uniform angle indices characterising the patterns that show the complexity and diversity of forests: the arrangement of tree dimensions, species and deadwood as well as tree positioning regularities. Managed Norway spruce (Picea abies) stands are remarkably more homogeneous in terms of occurrence and positioning of different tree species and dimensions when compared to unmanaged forests. Managed Scots pine (Pimas sylvestris) stands rarely show co-occurrence of living and dead trees and demonstrate lower dimensional variability than unmanaged stands. Trees are often quite randomly positioned; slightly regular positionings became evident in managed Norway spruce stands. Structural analysis confirm that large trees are particularly important in maintaining the structural diversity of forests. Forest management needs to integrate maintenance of important structural components and patterns into timber production for biodiversity conservation and sustainable forestry. Natural forests are indispensable source for reference structures in forest ecosystems.

1. Introduction

Forest ecosystems have significant heterogeneity in ecological quality, which depends on the level of anthropogenic influence on them. For safeguarding ecological values of forest ecosystems, 25.6% of productive forestland is protected under different conservation regimes in Estonia (Estonian Environment Agency, 2017). However, all Estonian forests have been in some way shaped by long-term human impact (Reitalu et al., 2013) and the overall coherence and ecological quality of boreal forest ecosystems tend to decline (Kuuluvainen, 2002). The reasons are mainly related to common forest management practices such as invariable forest management regimes, homogenization of the forest structure and absence of natural forest remnants (Bengtsson et al., 2000; Jögiste et al., 2017; Kuuluvainen, 2002; Löhmus and Kraut, 2010; Tikkanen et al., 2006).

The preservation of forest ecosystem complexity and diversity is often linked to forest naturalness (Eastaugh et al., 2013). Forest naturalness is a complex issue with many definitions combining adaption to the changing environment, dynamics and disturbances, and including human influence on forest ecosystems (Laarmann et al., 2009).

The most common definition is based on the comparison of a forest ecosystem's current condition to its natural state (Winter 2012). Forest stands in hemiboreal forests can span from highly artificial to naturally vigorous forest ecosystems (Roberge et al., 2008, Ranius and Roberge, 2011). The degree of naturalness of forest ecosystems varies according to natural conditions and forest management practices used, e.g. audyte et al. (2005) distinguish six classes of forest naturalness in Lithuania, ranging from the untouched virgin forest to an artificial forest. For Estonian conditions, Korjus (2002) used four classes in Estonia according to European forest classification suggested by Wulf (1998): old-growth forests, natural forests, recovering forests and managed (semi-natural) forests. The indicators of naturalness include various tree ages, sizes and species, the presence of old and large (especially deciduous) trees and broadleaved species, the presence of deadwood and its volume and decay classes, recent and historical management practices as well as many other characteristics (Liira and Sepp, 2009; Lõhmus and Kraut, 2010).

Proper understanding of the structural patterns of different forest ecosystems requires evaluating the spatial forest structure and quantifying tree composition (Maes et al., 2011). Classical forest inventory

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variables are usually insufficient for assessing structural diversity in forest ecosystems (Bouman, 2015). The tool for evaluation can be point process statistics, using individual tree indices based on a nearestneighbourhood approach (Maleki et al., 2015). Structural indices have been widely used for quantifying stand structure and heterogeneity within a forest community (for an example see: Gadow, 1993; Gadow, 1999; Hui and Hu, 2001; Kint et al., 2001; Pommerening, 2002; Gadow and Hui, 2002; Aguirre et al., 2003; Pommerening, 2006; Gadow et al., 2016; Pommerening and Uria-Diez, 2017; and many more). The aim of this study is to compare the spatial structure of managed, recovering and natural forest ecosystems based on spatially explicit structural indices calculated for each tree growing on sample plot using species mingling, deadwood mingling, deadwood distribution, diameter differentiation and uniform angle indices. The nearest-neighbourhood approach gives an opportunity to describe, assess, understand and model the comprehensive spatial structure, including spatial arrangement of tree dimensions, species, deadwood, and tree positioning regularities of different forest ecosystems. We hypothesis that natural and recovering forest stands have a more complex stand structures than managed forest stands and this is reflected in the structural indices as high natural diversity is associated with multiple tree species and sizes as well as irregular positioning of trees and the presence of deadwood (Esseen et al., 997). Structural indices may serve as naturalness indicators in the planning of treatments and assessment of forest ecosystems in the fu-

2. Methods

2.1. Sample plots

Forest stands in this study belong to the hemiboreal vegetation zone (Ahti et al., 1968). The study is based on circular sample plots that are located all over Estonia (Fig. 1) and are part of the Estonian Network of Forest Research Plots. The network was established in the year of 1995 and the sample plots have been measured repeatedly every five years in order to study different spatiotemporal patterns, silvicultural treatments, the growth and yield of Estonian forests (Kiviste et al., 2015). Approximately 100–150 permanent sample plots are measured or re-

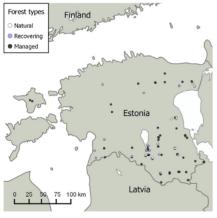


Fig. 1. Location of the sample plots in Estonia. A point may represent several sample plots located close to each other.

measured annually and the data are collected at single-tree level. The radius of sample plots varies from 15 to 30 m and depends on stand density. Sample plots belong to Oxalis, Oxalis-Rhodococum and Oxalis-Myrtillus site types according to Löhmus' (2004) classification. These sites represent mostly conifer-dominated mixed oligo-mesotrophic and mesotrophic forests on mineral soils. We sampled stands dominated by Scots pine (Pinus sylvestris) and Norway spruce (Picea abies). Information on all trees growing on the sample plots included species, diameter at breast height, vitality status (dead, damaged or visually healthy tree) and the exact geographical location of trees. Additional information related to the Estonian Network of Forest Research Plots is described in studies by Kiviste et al. (2015) and Kiviste and Hordo (2002).

First, we evaluated the ecological quality of the sampled stands in order to describe the naturalness of a forest stand using the scoring of naturalness approach by Estonian Forest Conservation Area Project (EFCAN) method (Viilma et al., 2001; Korius, 2002) which has been extensively used for describing naturalness of forest stands in Estonia. The assessment takes into account biological values (including the presence of different stand elements, especially the presence of deadwood with different volume as well as decay classes), cultural-biological values and human impact and it is a scoreboard type assessment that gives an individual naturalness score to a forest stand. Studied sample plots were grouped according to EFCAN nature value assessment scores and Korjus (2002) grouping methodology into following naturalness classes: 1) managed forests - 123 plots, 2) recovering forests - 58 plots, and 3) natural (including old-growth) forests - 31 plots; altogether 212 sample plots were under study. Typically, managed forests are relatively homogeneous stands with notable signs of human interventions - planted trees, cut stumps, homogenization in tree species composition, absence or lack of dead trees and lying deadwood as well as traces of drainage. Recovering forests may have been established by human activities (seeded, planted) or naturally regenerated and have signs of past management, yet the present human impact on forest structure is insignificant. Recovering forests have more natural elements than managed forests, such as standing dead and downed wood and different tree species are present of different ages. Recovering forests are developing towards the natural state and, with great probability, will turn into natural forest within next decades when left untouched by humans. Natural forests are naturally regenerated and have no visible signs of direct human influence; these are usually unevenaged multiple species stands with uneven spacing of trees characterizing the site type. Deadwood is very important trait of natural forests, both lying and standing dead trees are usually present in a natural

General information of the stands on the sample plots is presented in Table 1. The mean age of the stands ranged from 50 to 153 years, diameter from 20.2 to 39.3 cm, height from 20.4 to 30.3 m, basal area from 30.7 to 41.3, volume of living trees from 30.8 to 510.0 m³ ha $^{-1}$ and the volume of coarse woody debris (CWD) including standing dead trees, snags and lying deadwood from 15.3 to 85.1 m³ ha $^{-1}$.

The average number of tree species ranged from three to five species per sample plot. Scots pine, Norway spruce, birch species (Betula sp.), Norway maple (Acer platanoides), common aspen (Populus tremula), grey and black alder (Alnus incana and A. glutinosa) were the most common species present on the sample plots. The distribution of diameter at breast height (DBH) in Scots pine and Norway spruce stands shows higher proportions of smaller trees in recovering and natural forests than in managed forests, reflecting thinning practices (Fig. 2). The presence of very large trees is reflected in the DBH distribution, too.

2.2. Data analysis

For the evaluation of spatial forest structure, we used individual tree indices based on the nearest-neighbourhood approach. We took attributes associated with the arrangement of tree positions, tree species and dimensions as well as deadwood under observation. All the indices

ample plots (mean values if not stated otherwise), the mean number of tree species on the plots and the presence of more frequent tree species on the plots. Tree species PS – Scots pine spruce detailed in the state of the spruce details and the spruce details. The spruce details are species on the plots. Tree species PS – Scots pine spruce details are species on the plots. Tree species PS – Scots pine spruce details are species on the plots. The spruce details are species on the plots. The spruce species of the spruce details are species on the plots. The spruce species of the spruce spe Table 1
General characteristics of the sample ple (Pinus sylvestris), PA – Norway spruce (Pi – black alder (Ahrus glutinost), TC – sma

	Naturalness level	Stand age (years)	(vears)										
		-0											
		min	mean	max	Stand diameter (cm)	Stand height (m)	Basal area (m² ha ⁻¹)	Volume of living trees $(m^3 ha^{-1})$	Volume of CWD (m ³ ha ⁻¹)	Number of tree species	tree species		
Scots pine	Managed	35	88	153	31.1	28.8	35.1	432.8	28.9	3.3			
	Recovering	44	95	153	33.9	29.9	40.7	506.3	33.9	3.5			
	Natural	06	106	153	36.8	30.2	41.3	510.0	49.3	3.7			
Norway spruce	Managed	56	50	134	20.2	20.4	30.7	308.9	15.3	2.7			
	Recovering	45	113	177	34.4	27.9	35.7	436.1	46.6	4.3			
	Natural	118	153	178	39.3	30.3	33.0	425.9	85.1	4.9			
	Naturalness level	Presence (of tree species	Presence of tree species on sample plots (%)	(%)								
		SA	PA	В	QR	AP	PT	N	AG	TC	SC	n	FE
Scots pine	Managed	100	66	59	23		< 10	< 10	< 10	< 10	< 10	< 10	< 10
	Recovering	100	86	83	14		< 10	10	< 10	< 10	< 10	< 10	< 10
	Natural	100	100	84	11	11	21	16	< 10	0	0	0	0
Norway spruce	Managed	41	100	70	< 10		11	< 10	< 10	< 10	< 10	0	< 10
	Recovering	69	100	100	0		38	19	25	13	22	12	0
	Natural	33	100	92	0	42	28	< 10	28	33	0	22	25

were calculated at the single-tree level for all trees (reference tree). For calculations of indices, trees from the 1st and 2nd storey as well as regeneration (DBH ≥ 4 cm) were used, understorey trees were excluded. For deadwood analysis, standing dead and broken trees were additionally included. The amount of closest neighbours was four as this number is proved to be a sufficient number of neighbours (Hui and Hu, 2001; Pommerening, 2006). Indices calculated for reference trees take five values with four neighbouring trees – 0, 0.25, 0.5, 0.75 and 1 (Table 2).

Sample plot edge correction (Lilleleht et al., 2014; Pommerening and Stoyan, 2006) should be applied to the reference trees near the sample plot boundary. Such reference trees may have some neighbouring trees located outside of the plot. In this study, these reference trees were not included in the calculations of the mean values. Edge correction is needed especially in the case of small circular plots, such as those in the current study. Without applying edge correction, serious bias in spatial estimations may appear (Lilleleht et al., 2014). However, if dead trees on a sample plot are only located near the boundary, this might result in biased estimation of the deadwood mingling index. Details, examples and additional information describing used indices can be found in Table 2

Species mingling index (Gadow, 1993) characterises the variety of tree species within a group of neighbours. Low mingling indicates homogeneous and high mingling indicates heterogeneous groups of tree species. Deadwood mingling index (Laarmann et al., 2009) characterises the spatial arrangement of deadwood within a group of neighbours, showing how often the neighbouring trees of a dead reference tree are dead or alive. Low deadwood indicates a small amount of deadwood within a group and high deadwood indicates a high amount of deadwood within a group and clumping of dead trees. Deadwood distribution index, proposed in this study, characterises the spatial arrangement of deadwood within a group of neighbours, showing how often the neighbouring trees of a living reference tree are dead or alive. It is different from the initial deadwood mingling index approach where dead trees are used as the reference trees. The advantage of the deadwood distribution index is that it gives a better overview of the plot - most of the trees on a sample plot are alive and we take living trees under observation to assess their immediate vicinity. A low average value of deadwood distribution index indicates a small amount of deadwood within a group, a high value shows a high amount of deadwood within a group in the immediate vicinity of a living tree. Diameter differentiation index (Gadow, 1999) characterises the dimensional differences between trees within a group of neighbours. Low differentiation indicates a group of trees with homogeneous dimensions and a high value indicates a group of trees with heterogeneous dimensions. The uniform angle index (Gadow and Hui, 2002) characterises the positioning regularities of trees within a group of neighbours. A low index value indicates the tendency to regular positioning of trees in groups and a high index value the irregular positioning or clumping of trees in groups. Additionally, the expected mingling index (Lewandowski and Pommerening, 1997), which does not depend on the number of nearest neighbours but on species richness in the relation of the total number of plants on a sample plot, is calculated as follows:

$$EM = \sum_{i=1}^{s} \frac{N_i(N - N_i)}{N(N - 1)}$$
(1)

where EM – expected mingling index; s – the total number of species on a sample plot; N – the total number of plants on a sample plot; N_i –the number of plants of species i on a sample plot.

Data analysis was carried out in the R environment (R Core Team, 2017) version 3.3.1 using packages Rcpp, dunn.test and plotrix. To assess the differences between mean index values of different forest groups, Kruskal-Wallis nonparametric test (Kruskal and Wallis, 1952) with Dunn's multiple comparison test (Dunn, 1961) as a post hoc were performed. Confidence intervals (at 95% confidence level) for the mean

index values were calculated with bootstrap method (Efron, 1979). Wilcoxon one sample test (Wilcoxon, 1945) was used to investigate whether the index values of large trees were higher than small trees. ANOVA was used to assess the actual and expected species mingling index differences between different forest groups. The threshold for a statistically significant p-value was set to 0.05.

3. Results

The summary characteristics of Scots pine and Norway spruce dominated sample plots of managed, natural and recovering forests are presented in Table 3. For a detailed overview of the variability of the structural indices calculated for each reference tree of the given forests, the frequency distributions are presented in Fig. 3.

3.1. Scots pine stands

Stand level mean indices of species mingling and uniform angle indices do not show any statistically significant differences among different naturalness levels (K = 0.24, p = 0.89 and K = 4.78, p = 0.09, respectively). Deadwood mingling index shows that in natural forests, dead trees are significantly more often surrounded by dead trees than in recovering or managed forests (K = 7.02, p = 0.03) and deadwood distribution index indicates that the more natural is forest conditions. the more often dead trees occur on sample plots interlaced with living trees (K = 19.85, p < 0.001). The deadwood distribution index is zero on four plots meaning that deadwood has been removed from these plots during forest management operations. Statistical differences occur also between the differentiation in tree dimensions (K = 19.62, p < 0.001) - trees have remarkably more uneven dimensions in recovering and especially in natural forests compared to managed forests. Frequency distributions of deadwood mingling index shows that both in managed and recovering forests 52% of dead reference trees have all neighbouring trees alive, whereas in natural forest, the amount is smaller -43% of dead trees have all the neighbours alive. High deadwood mingling index values (0.75, 1.00) show that clumping of dead trees occurs more often in managed and natural forests (4% and 5% of the trees had signs of clumping, respectively) and less in recovering forests (2%). Deadwood distribution index shows that about 76% of the living reference trees have all living neighbours; in recovering forests the amount is 68% and in natural forests it is 57% - so, the more natural the forest conditions, the more frequently the neighbours of living trees are dead. Diameter differentiation index shows a relatively strong tendency of neighbouring trees to have uneven and very uneven dimensions under

more natural forest conditions (together 57% of the trees in managed, 72% of the trees in recovering and 83% of the trees in natural forests) and less moderately uneven, even or very even dimensions.

3.2. Norway spruce stands

Differences in stand level mean index values between different naturalness levels in Norway spruce stands show that deadwood distribution index is without significant differences among different naturalness levels (K = 0.81, p = 0.67). Deadwood mingling index shows that dead trees are more often surrounded by dead trees in managed forests than in recovering or natural forests but the differences are not statistically significant as well (K = 2.03, p = 0.36). Mean species mingling index shows that managed forests are significantly more homogeneous compared to recovering and especially to natural forests (K = 16.25, p < 0.001). Species mingling index has zero value in 11 plots that are single-species spruce stands. The dimensions of trees are remarkably more uneven in recovering and especially in natural forests compared to managed forests (K = 37.21, p < 0.001). The positioning of trees in managed forests is slightly more regular when compared to recovering and natural forests (K = 9.50, p = 0.01). The distribution of the species mingling index in Norway spruce stands shows that about 65% of the reference trees have all neighbours from the same species and the rest of the trees have at least one neighbour from a different species in managed forests. In recovering forests, the frequency of neighbours of the same species decreases to 39% and in natural forests to 38%. The distribution of the diameter differentiation index shows that neighbouring trees in managed forests have more often moderately uneven, even or very even dimensions (54% of the reference trees) than uneven and very uneven dimensions; neighbouring trees in recovering and natural forests have more often uneven and very uneven dimensions - 72% of the trees in recovering and 79% of the trees in natural forests. The uniform angle index shows again that most of the trees are randomly positioned regardless of the forest naturalness level but the more natural the forest condition is, the more the trees are positioned irregularly or very irregularly (altogether 23% of the trees in managed, 25% of the trees in recovering and 26% of the trees in natural forests). Trees were less often positioned regularly or very regularly (altogether 25% of the trees in managed, 19% of the trees in recovering and 18% of the trees in natural forests).

Comparing the actual species mingling index to expected mingling index (Fig. 4) calculated by taking into account the tree species composition, shows that the actual species mingling index is 5% lower than the expected value in average and there are no significant differences

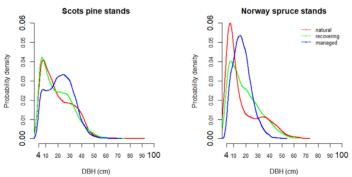
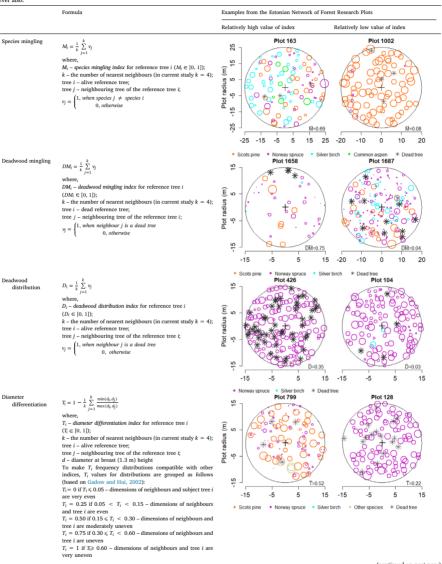


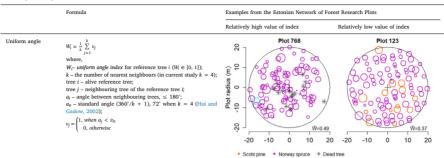
Fig. 2. Diameter (DBH) distributions in Scots pine and Norway spruce stands.

Table 2
Formulas of individual tree level indices. Examples belong to the Estonian Network of Forest Research Plots and show the mean indices of all trees calculated at a plot level also.



(continued on next page)

Table 2 (continued)



between managed, recovering and natural forests (p = 0.17).

Finally, we evaluated whether large trees (DBH \geq 40 cm) have higher structural indices values than smaller trees. We found that large trees in Scots pine stands have higher mean species mingling, deadwood distribution and diameter differentiation indices values (0.69, 0.10, 0.55, respectively) compared to smaller trees (0.41, 0.09, 0.38, respectively) and those differences are statistically significant (p = 0.001, p = 0.045, p < 0.001, respectively). Large trees in Norway spruce stands have significantly higher species mingling and diameter differentiation indices values (0.43, 0.58, respectively) than smaller trees (0.22, 0.34, respectively) and those differences are again statistically significant (p < 0.001 in terms of both indices). These results show that large trees are especially important in terms of maintaining the diversity of forests.

4. Discussion

The increased public awareness of the importance of biodiversity conservation has called for development and application of forest practices that increase stand structural complexity. Spatial forest structure strongly influences the functioning of forests (Guillemot et al., 2014), and it is crucial to preserve the most important structural elements and patterns occurring in natural forest whenever possible. We assessed the structural patterns of forest stands with different levels of naturalness in order to evaluate structural patterns inherent in natural. recovering and managed forests and to determine the impacts of forest management practices on spatial forest structure. Management has a considerable impact on forest structural diversity and this influences the overall biodiversity in Estonia (Jögiste et al., 2018). The structure of managed forests is mostly less diverse in terms of the occurrence of different tree dimensions as well as the occurrence and positioning pattern of different tree species and deadwood when compared to recovering and natural forests in our study, however, forest management and structural diversity do not necessarily conflict with each other.

The diameter differentiation index reflects the vertical structure and age structure of a stand – in natural forests, high diameter differences appear, demonstrating an uneven vertical structure and age composition. Dimensional differences in both Scots pine and Norway spruce stands showed that trees have remarkably more uneven dimensions in recovering and natural forests when compared to managed forests. This is self-explanatory since one of the main purposes of forest management is to maximize economic gain through homogenizing forest structure including evening tree dimensions (Buongiorno et al., 1994). The key how to create and maintain complexity of forests during management can be preserving large (e.g. previous-generation) trees when they exist

in a forest stand. Large trees are ecosystem legacies that could harbour many species in managed forests and be the stepping stones to larger and more continuous patches of old-growth forests (Mazurek and Zielinski, 2004). Our study showed that large trees are especially important in terms of maintaining the structural diversity of forests similarly to Pommerening and Uria-Diez (2017) – more precisely, large trees (DBH \geq 40 cm) in our study were more often surrounded with dead trees, trees with different dimensions and species than smaller trees. Another option how to preserve dimensional differences in managed forest ecosystems, still following the main idea of forest management, would be to retaining some regrowth during forest management operations and keeping seed trees in gaps and patches whenever possible. Review by Gauthier et al. (2015) suggests that the presence of natural regeneration is one factor retaining higher stand-level diversity.

Stand density controlled by thinning has been the main tool to regulate tree growth and improve timber quality (Mäkinen and Isomäki, 2004). A similar management history of forests in Estonia strongly affects tree species composition (Jõgiste et al., 2018), but the current study indicates that the impact on management to species composition is more apparent in Norway spruce stands than in Scots pine stands. The species mingling index reflects how diverse a stand is in terms of tree mingling of different tree species. Managed Norway spruce forests are significantly more homogeneous in terms of mingling of different tree species when compared to recovering forests and especially when compared to natural forests; but no statistical differences appeared in Scots pine stands. This can be explained by the historical stand regeneration strategy in Estonia, Norway spruce stands have been mostly planted and Scots pine stands also considerably sown (Jäärats, 2018); and by the fact that Norway spruce stands seem to be heavily managed by the information shown on Table 1. The occurrence of common aspen in horeal conifer stands indicates forest ecosystem naturalness levels with low-level forest management influences (e.g. Latva-Karjan naa et al., 2007). Kuuluvainen (2002) states predominance of birch species and scattered occurrence of commons aspen in Fennoscandian natural forests. Only managed spruce forests have a lower number of deciduous species in our study, especially important is the lack of hardwood species like Scots elm, small-leaved lime and common ash. Higher levels of naturalness in both Scots pine and Norway spruce forests are associated with a higher mean number of species. Particularly high is the mean number of species in natural Norway spruce stands in comparison to managed stands (almost twice as high). The mix of ecosystem services is higher among forests with more tree species (Gamfeldt et al., 2013). Therefore, it is important to sustain higher mingling of species also for ecosystem services and wood

Table 3

Means with confidence limits at 95% level of structural indices (M – species mingling, DM – deadwood mingling, D – deadwood distribution, T – diameter differentiation, W – uniform angle) for managed, recovering and natural forests. Mean values with the same superscript letter do not differ significantly at p < 0.05.

	Naturalness level	\bar{M}	DM	Ď	\bar{T}	\bar{W}
Scots pine	Managed	0.43 ^a	0.13 ^a	0.08 ^a	0.36ª	0.48 ^a
	ů.	(0.39, 0.46)	(0.09, 0.16)	(0.07, 0.09)	(0.34, 0.38)	(0.47, 0.49)
	Recovering	0.44a	0.12a	0.11b	0.41 ^b	0.49 ^a
	-	(0.41, 0.47)	(0.10, 0.15)	(0.09, 0.13)	(0.39, 0.44)	(0.48, 0.50)
	Natural	0.44 ^a	0.18 ^b	0.15 ^c	0.44 ^b	0.49 ^a
		(0.37, 0.50)	(0.14, 0.22)	(0.12, 0.17)	(0.43, 0.46)	(0.48, 0.50)
Norway spruce	Managed	0.17 ^a	0.15 ^a	0.10 ^a	0.31a	0.47 ^a
	ů.	(0.13, 0.21)	(0.11, 0.19)	(0.07, 0.12)	(0.30, 0.33)	(0.46, 0.48)
	Recovering	0.28 ^b	0.10 ^a	0.10 ^a	0.40 ^b	0.49 ^b
		(0.22, 0.34)	(0.06, 0.15)	(0.07, 0.13)	(0.37, 0.43)	(0.47, 0.50)
	Natural	0.35 ^b	0.12a	0.08 ^a	0.45 ^b	0.49 ^b
		(0.29, 0.41)	(0.06, 0.18)	(0.06, 0.11)	(0.43, 0.48)	(0.48, 0.51)

production (Vilà et al., 2007).

The presence and frequency of dead trees are important structural components of forests reflected in the deadwood distribution index. The differences between naturalness levels appeared in Scots pine stands – the less artificial the condition of the forest is, the more often dead trees occur on sample plots and are mingled with living trees. Frequency distributions of DBH show that trees with small diameters are obviously predominating in recovering and natural forests. Therefore, deadwood

distribution index may indicate self-thinning processes. In managed forests, the higher index values are related to the higher rates of tree mortality what can be a result of tree competition and natural succession processes in unthinned planted stands. It has been shown by Mäkinen and Isomäki (2004) that part of the total production of unthinned plots is lost by natural mortality. The clumping of dead trees is reflected in the deadwood mingling index which had statistically significant differences between naturalness levels in natural Scots pine

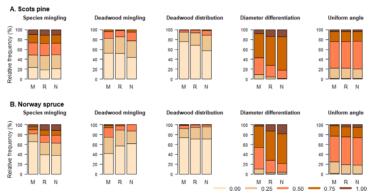


Fig. 3. Frequency distributions of trees on the sample plots according to different indices and naturalness levels (M - managed, R - recovering, N - natural).

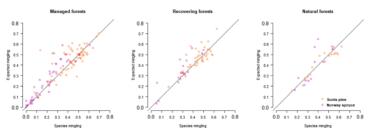


Fig. 4. Actual species mingling index compared to expected species mingling index in managed, recovering and natural forests, the lines show a plotted 1:1 reference line.

stand. The clumping of dead trees enables gap formation which is an important process in natural boreal forest ecosystems (Esseen et al., 1997). Dead trees should be preserved in managed forests, and the larger those trees are in dimensions and vary in species and decay stages the better (Blaser et al, 2013; Purahong et al., 2018), creating possible habitats for specialized species. Statistical differences did not appear between naturalness levels in Norway spruce stands as the deadwood mingling index was even higher in managed stands than in unmanaged. Deadwood frequency in a managed forest can be a result of root rot infection as the frequency distribution indicates clumping of trees and the disease spreads through root contacts. This is a serious problem for Estonian coniferous forests, especially in Norway spruce stands (Allikmäe et al., 2017).

We expected that trees growing on managed forests are positioned regularly and that the uniform angle index reflects human impact. Regardless of the naturalness level, most of the trees are randomly positioned, and Pommerening (2002) study indicates that this pattern is very common in most forests. A weak trend appeared in Norway spruce stands for trees to be positioned irregularly or very irregularly as the condition of the forests is more natural and more often regularly in managed forests; this trend does not appear in Scots pine stands.

Recovering forest stands are often relatively similar to natural forest, most of the indices did not show statistical differences between natural and recovering forest, except deadwood distribution index in Scots pines stands. Anyway, the trend was clear that the values of structural indices are mostly higher in natural forests and recovering stands could further contribute to the restoration of naturalness through active restoration/facilitation to enhance ecosystem functionality (Laarmann et al., 2013). Burning has shown to be the most effective restoration method in terms of deadwood development (Hekkala et al., 2016). However, it is important to keep in mind that this study was conducted in conifer-dominated mixed oligo-mesotrophic and mesotrophic forests of mineral soils and not directly transferable to another types of Estonian forests.

5 Conclusion

Modelling of forest ecosystems may require more detailed data than common forest inventories produce. The research of structural diversity indicators of a forest stand contributes to more comprehensive ecological planning of forest management. The research methods comprise individual tree indices based on nearest-neighbourhood approach, attributes associated with the arrangement of tree positions, tree species and dimensions of living trees as well as deadwood. The results of the study indicate that species mingling, deadwood mingling, deadwood distribution, diameter differentiation and the uniform angle indices are all useful for assessing spatial stand structure of hemiboreal conifer dominated forests according to different naturalness levels. The study confirms that structural patterns of forests according to different levels of naturalness have several differences, and large trees are important elements for sustaining structural diversity as large trees are more often surrounded with dead trees, trees with different dimensions and species than smaller trees. Maintaining structural patterns of recovering and natural forests could be beneficial in order to maintain habitats of desired species as well as the overall biodiversity, usually structural diversity is one of the main indicators showing the presence and quality of habitats of different species (Motz et al., 2010). The advantage of forest management where forest growth and yield is combined with the maintenance of important stand structural patterns will be the increase of forest naturalness level and biodiversity values.

CRediT authorship contribution statement

Eneli Põldveer: Conceptualization, Methodology, Validation, Formal analysis, Resources, Writing - original draft. Henn Korjus: Conceptualization, Methodology, Writing - original draft. Andres

Kiviste: Methodology, Resources, Writing - review & editing. Ahto Kangur: Writing - review & editing, Supervision. Teele Paluots: Resources, Writing - review & editing. Diana Laarmann: Conceptualization, Methodology, Resources, Writing - original draft, Project administration

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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III

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The structural complexity index SCI is useful for quantifying structural diversity of Estonian hemiboreal forests

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ARTICLE INFO

Spatial stand structure Stand structural heterogeneity Conservation forests Managed forests Rehabilitation forests

ABSTRACT

Comprehensive description and quantification of stand structure is needed for managing or maintaining forests as complex systems. The tree position and diameter based structural complexity index SCI was used to quantify the structural heterogeneity of forest stands in Estonia. The aims of the study were to determine if SCI is related to the conventional stand characteristics used for forest management planning and to assess the direct impact of silvicultural treatments on stand structural heterogeneity. The SCI for hemiboreal forests in Estonia ranged from 1.36 to 10.78, being highest in conservation forests on fertile sites (7.42 \pm 1.20), followed by managed forests on fertile sites (4.74 \pm 1.44), managed forests on poor sites (4.00 \pm 1.02), conservation forests on poor sites (3.85 \pm 0.87), and lowest in rehabilitation forests (2.64 \pm 0.69). The mean SCI between forest groups and site types differs significantly, except in managed and protected forests growing on poor sites. The SCI is positively associated with commonly measured stand characteristics, indicating that stand structural heterogeneity reflected in SCI is higher for older stands with larger trees, higher deadwood quantity and biomass. The results also show that species diversity promotes stand structural diversity. SCI is a promising method for providing quantitative assessments of multidimensional forest stand structure in Estonia

1. Introduction

Structural heterogeneity within a forest stand is increasingly recognized as an important characteristic when the aim is managing forests as complex systems (Messier et al., 2013). The attributes of stand structural heterogeneity include elements such as species composition, spatial position, height and diameter of individual stems, deadwood and canopy cover; containing both the number of attributes present and their relative abundance (McElhinny et al., 2005). Structural heterogeneity is known to be positively linked to forest ecological quality (Por 2002; Seidel et al., 2019). The loss in structural diversity, a common trend in actively managed forests, weakens the ability of forests to maintain biological diversity, which may have a negative effect on ecosystem resilience, especially in the context of climate change (Bradshaw et al., 2009). Resilience, the capacity of forests to maintain essential characteristics of taxonomic composition, structure, ecosystem functions, and processes in the face of disturbances, is dependent on biodiversity at multiple scales (Thompson et al., 2009). Management,

both passive and active, can increase or decrease the vulnerability of forests to climate change (Spathelf et al., 2018; Jandl et al., 2019). Climate is changing with unprecedented speed and amplitude and increasingly threatens forests; therefore, preserving forest resilience and maintaining different scales of biodiversity are important for protecting forests and the services they provide (Gauthier et al., 2015).

The variability in tree size in a stand is acknowledged as one of the key variables of structural diversity providing spatial heterogeneity (Pommerening and Särkkä, 2013). While different aspects of diversity in forests are important, the structural characteristics (the threedimensional distribution of trees) is the one attribute that could be altered directly through silvicultural activities (Seidel et al., 2019). Therefore, the combination of the spatial arrangement of trees and their dimensions is an important variable to comprehensively describe forest structure (Zenner, 2000) and it can be used, for an example, to quantitatively compare different stands (Zenner and Hibbs, 2000; Peck et al., 2014) or stand dynamics.

Trees in commercially managed Scots pine (Pinus sylvestris L.) and

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Norway spruce (Picea abies (L.) H. Karst.) forests in Estonia are less variable in structural dimensions than in unmanaged stands left to natural development (Poidver et al., 2020). The aims of this study are to determine if stand structure is related to stand conventional forest mensuration characteristics and to assess the direct impact of silvicultural treatments on stand structural heterogeneity. Stand structural heterogeneity was quantified using a structural complexity index SCI based on tree positions and diameter variations in order to distinguish how structural heterogeneity changes along forest management history and site fertility. The research hypothesis is that SCI is dependent on management history and site fertility, and that forest management directly affects forest structural heterogeneity.

2. Materials and methods

2.1. Study site and data collection

The study utilized the tree-level data collected from 852 sample plots (Fig. 1) within the Estonian Network of Forest Research Plots (ENFRP; Kiviste et al., 2015). Studied plots were assigned into three forest groups:

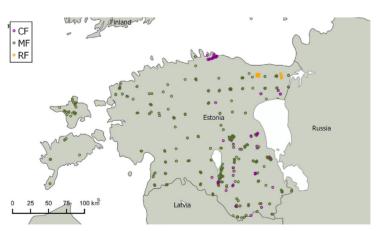
- CF conservation forests (165 plots): stands belonging to nature protection areas or woodland key habitats where forest management activities are not allowed or are strongly restricted;
- MF managed forests (622 plots): stands in commercial forests without special restrictions on forest management. Managed forests include stands with different management histories divided into: o passively managed stands (316 plots) where no major manage-
- o passively managed stands (316 plots) where no major manage ment has been present approximately for the last 20 years, and
- o actively managed stands (306 plots) where stands that have been managed during the same period, with the condition that at least 10% of the trees were felled; 125 of the 306 sample plots were thinned right before the last measurement of sample plots;
- RF rehabilitation forests (65 plots): stands in former oil-shale openmined areas that have been afforested mostly by single species; these are stands that are actively managed (see more: Laarmann et al., 2015).

The dominant tree species on the sampled plots were 53% Scots pine,

24% Norway spruce, 16% birch (silver or downy birch; Betula pendula Roth or B. pubescens Ehrh.), 5% common aspen (Populus tremula L.), < 1% black alder (Alnus glutinosa (L.) Gaertn.), < 1% grey alder (Alnus incana (L.) Moench) and < 1% European ash (Fraxinus excelsior L.). Other tree and shrub species co-occurring on the sample plots were small-leaved lime (Tilia cordata Mill.), Norway maple (Acer platanoides L.), common oak (Ouercus robur L.), Scots elm (Ulmus glabra Huds.), European white elm (Ulmus laevis Pall.), common hazel (Corylus avellana L.), rowan (Sorbus aucuparia L.), bird cherry (Prunus padus L.), common juniper (Juniperus communis L.), alder buckthorn (Frangula alnus Mill.), larch (Larix spp.), fir (Abies spp.) and willow (Salix spp). The majority of Estonian forest site types classified by the methodology of Löhmus (2004) were represented in the sample plots. Whenever needed, site types were divided into fertile and poor sites regarding the site productivity according to Löhmus (2004). Site productivity is characterized by site index which generalizes climatic, edaphic and physiographic factors of a site. Fertile site types are defined where site index (stand height at the age of 100 years) on average is 19 m or more.

All ENFRP plots are re-measured on a five-year interval. In the current study, the last measurements from 2015 to 2019 of sample plots were under observation. In addition to the last measurements of ENFRP, pre-harvest data were included in order to assess the immediate impact of silvicultural treatments on stand structural heterogeneity. All possible previous measurements following thinning were also included to monitor the dynamics of SCI.

Sample plots were circular with radii varying from 8 to 30 m, depending upon stand age, density and other stand characteristics (Kiviste et al., 2015; Laarmann et al., 2015). Data of all trees and shrubs with diameter at breast height (DBH) larger than 4 cm collected from ENFRP include species, polar coordinates (azimuth and distance from the plot centre), DBH, height of approximately every fifth tree, and vitality status – whether the tree was alive or dead. Standing dead trees and snags were considered as deadwood. Stand age was determined from increment cores extracted from dominant trees. General stand characteristics calculated on the basis of sample plots are presented in Table 1.



 $\textbf{Fig. 1.} \ \ Location \ of studied \ sample \ plots. \ \ CF-conservation \ forests, \ MF-managed \ forests, \ RF-rehabilitation \ forests.$

Table 1 General stand characteristics, mean \pm standard deviation if not stated otherwise. CF – conservation forests, MF – managed forests, RF – rehabilitation forests.

	CF	MF	RF
Stand age, years	117 ± 35	63 ± 23	31 ± 7
Stand age, years (range)	62-250	20-177	15-45
Basal area, m ² ha ⁻¹	30.2 ± 8.4	28.2 ± 7.4	18.2 ± 7.1
Stand diameter, cm	34.9 ± 9.4	23.2 ± 6.9	12.7 ± 3.9
Stand height, m	28.6 ± 6.0	23.4 ± 5.7	12.6 ± 4.4
Volume of living trees, m3 ha-1	434.6 ±	$236.2 \pm$	$145.0 \pm$
	140.4	118.2	69.1
Volume of standing deadwood, m ³ ha ⁻¹	24.5 ± 19.7	12.9 ± 17.9	1.7 ± 3.1
Stem density*, trees ha-1	$1,157 \pm 404$	$1,301 \pm 746$	$1,667 \pm$
			765
Number of different tree and shrub species*	4.4 ± 2.2	3.8 ± 1.8	2.1 ± 1.0

^{*} Includes all living and dead trees.

2.2. Data analysis

The structural complexity index SCI (Zenner, 1998) was calculated for each sample plot using collected tree-level data. The index is a three-dimensional model describing stand structural heterogeneity based on location and size information of trees within a plot. The index calculation and edge effect correction methods were performed as described in Zenner (2000); the first steps of data analysis are illustrated in Fig. 2. All the standing trees and shrubs (alive and dead) present on sample plots were used for calculating the SCI.

The stand level SCI was calculated as a ratio between the area of faceted surface (three-dimensional triangles generated by tree x and y coordinates and z coordinate according to tree DBH; denoted as SCI' in Eqs. (1) and (2)) and its projection (the sum of non-overlapping two-dimensional triangles calculated by tree x and y coordinates; illustrated in Fig. 2B, denoted as A_T in Eq. (1)). A higher SCI value for a sample plot indicates more heterogeneous stand structure, based on the area of a faceted surface compared to its projection, which depends on variation in tree sizes. For index calculation, the following equations were used:

$$SCI = \frac{SCI^*}{A_*}$$
(1)

where A_T is the sum of areas of all non-overlapping two-dimensional triangles of the sample plot generated using Delaunay triangulation routine

$$SCI^* = \sum_{i=1}^{N} \frac{1}{2} |a \times b| \tag{2}$$

where N is the number of triangles in the plot, $|a \times b|$ is the absolute value of the vector product of vectors AB and AC with coordinates $a = (x_b - x_a, y_b - y_a, z_b - z_a)$ and $b = (x_c - x_a, y_c - y_a, z_c - z_a)$, respectively.

The Kruskal-Wallis (1952) nonparametric test with Dunn's (1961) multiple comparison test as a post hoc was used in order to assess the differences in mean SCIs between multiple groups. To study the effect of forest management and site fertility on SCI considering the multiple influence of stand variables, the generalized additive model (GAM) as an extension of generalized linear models (Kobinson et al., 2011; Mehtiatalo and Lappi, 2020) was used. The priori exact parametric forms of relationships between SCI and the stand variables were not known, that is why the spline approach was used as mooth functions of the predictor variables. The GAM coefficients were obtained using penalized iteratively reweighted least squares method (Wood, 2006). The following equation was used:

$$SCI = M + F + s(A) + s(G) + s(D) + s(H) + s(100/\sqrt{N}) + s(V),$$
 (3)

where SCI – structural complexity index, M – management (actively managed stands/passively managed stands), F – site fertility (fertile sites/poor sites), A – stand age (years), G – stand basal area ($\mathbf{m}^2 \, \mathbf{h} \mathbf{a}^{-1} \mathbf{b}$, D – stand mean square diameter (cm), H – stand mean height (m), $100/\sqrt{N}$ – stand sparsity (characterises the mean distance between trees, Nilson (2005)), N – number of living trees per hectare, and V – volume of standing deadwood ($\mathbf{m}^3 \, \mathbf{h} \mathbf{a}^{-1}$). The evaluation is based on the 622 sample plots of the managed forests group.

The GAM was additionally used for modelling and visualizing the relationship between SCI and stand variables from Table 1 based on the data of all 852 sample plots. A linear model with 95% confidence limits was used (Mehtätalo and Lappi, 2020) to model and visualize the SCI trend from 1996 to 2016 based on actively managed plots on fertile sites. Data analysis was performed in the statistical software environment R (R Core Team, 2017) version 3.31 using packages tripack (Renka and Gebhardt, 2020), dumn.test (Dinno, 2017), mgcv (Wood, 2020), pracma (Borchers, 2019), ggplot2 (Wickham et al., 2020) and plotrix (Lemon et al., 2020). A significance level of p = 0.05 was used throughout the study

3. Results

The SCI on sample plots ranged from 1.36 to 10.78 (Table 2). While the minimum values of SCI mostly ranged between 1 and 2 (an exception was conservation forests on fertile sites with SCI = 3.16), the maximum values of rehabilitation forests were noticeably lower than in managed or conservation forests. The mean values of SCI decreased in the following order: conservation forests on fertile sites, managed forests on

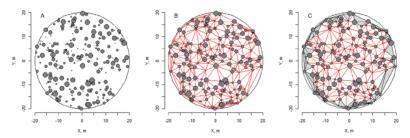


Fig. 2. Mapping the location of measured trees within a sample plot, symbol size is related to tree and shrub DBH (A); Generating network of non-overlapping triangles between a sample point (tree) and its two nearest neighbours using the Delaunay triangulation routine (B); Correcting possible edge-effects, grey triangles are omitted to avoid the situation when trees near a plot boundary may have actual nearest neighbours located outside the sample plot (C).

Table 2 SCI values in different forest groups according to the site fertility. CF – conservation forests, MF – managed forests, RF – rehabilitation forests, N – number of sample notes.

			99,999
	CF (N = 165)	MF (N = 622)	RF (N = 65)
The range of SCI			_
Fertile sites	3.16-10.22	1.86-10.78	-
Poor sites	1.99-5.90	1.72-6.77	1.36-4.15
The mean ± standard deviation	of SCI		
Fertile sites	7.42 ± 1.20	4.74 ± 1.44	-
Poor sites	3.85 ± 0.87	4.00 ± 1.22	2.64 ± 0.69

fertile sites, managed forests on poor sites, conservation forests on poor sites, rehabilitation forests.

The Kruskal-Wallis test revealed significant differences (p < 0.01) for mean SCI among forests groups (CF, MF, RF) and different site fertilities. The post hoc analysis showed that the difference was weaker between managed forests on fertile sites and conservation forests on poor sites (p = 0.02) and that no significant differences appear between managed forests on poor sites and conservation forests on poor sites (p = 0.32).

As the differences in SCI may be affected by the age of the stand in addition to the management or protection regime (Fig. 3), we adjusted the dataset by filtering out stands younger than 75 and older than 177 years in a common range in order to obtain a balanced sample of managed forests and conservation forests. This resulted in SCI of

managed forests and conservation forests that ranged from 1.86 to 10.78 (Table 3). The mean values of SCI remained in the same order, that is, highest in conservation forests on fertile sites, followed by managed forests on fertile sites, managed forests on poor sites and conservation forests on poor sites.

The results of Kruskal-Wallis test were similar after balancing; the differences in mean SCI between groups remained significant (p < 0.01), the post hoc test did not show significant differences between managed and conserved forests growing on poor sites (p = 0.20).

The relationship between SCI and stand characteristics (Table 1) showed that the measured stand variables were positively and significantly related to SCI (Fig. 3). The strongest correlation with SCI appears to be with the standing wood volume, followed by stand diameter, stand

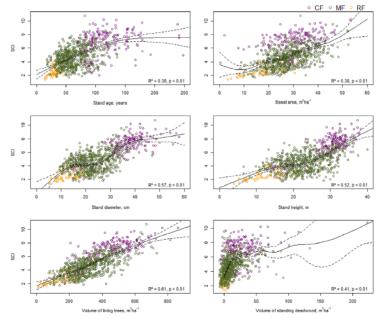


Fig. 3. The relationship between SCI and stand characteristics. CF – conservation forests, MF – managed forests, RF – rehabilitation forests. Number of sample plots – 852

Table 3

SCI values in different forest groups according to the site fertility after balancing the data. CF – conservation forests, MF – managed forests, N – number of sample plots.

	00 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	MF (N = 158)
The range of SC	I	
Fertile sites	3.16-10.22	1.86-10.78
Poor sites	1.99-5.90	2.27-6.77
The mean ± sta	ndard deviation of SCI	
Fertile sites	7.39 ± 1.21	5.55 ± 1.68
Poor sites	3.71 ± 0.85	4.28 ± 1.40

height, the volume of standing deadwood, stand age and basal area. The results indicated the following trend: the older the stand, the larger and taller were the trees and therefore also the biomass quantity; the higher value of SCI reflected an increase in structural heterogeneity within a stand

Silvicultural operations had a strong immediate impact on stand structural heterogeneity (Fig. 4); Kruskal-Wallis test showed that the SCI dropped noticeably after thinning on both, fertile (p < 0.01) and poor sites (p < 0.01). Modelling the effects of forest management and site fertility on SCI when considering the multiple influence of stand variables (using Eq. (3)) showed that both variables have an additional impact on forest structural heterogeneity; silvicultural operations negatively affected SCI (-0.14, p = 0.03) and site fertility positively (0.26, p < 0.01). Management, site fertility and stand characteristics explained 82% of SCI.

Tree and shrub species with different dimensions can occupy complementary spatial positions, therefore, we tested the difference in SCI according to the number of species present on plots. The result was a trend of increasing SCI value along with the increasing number of tree and shrub species per plot [Fig. 5). Kruskal-Wallis test shows that group means were significantly different from each other (p < 0.01), however, the post hoc analysis showed that the difference in SCI was weaker as the number of species increased (i.e., between three and four (p = 0.01), four and five (p = 0.02), and five and more than six species per plot (p = 0.04)).

The trend of SCI values immediately after the thinning over 20 years (1996 to 2016) in fertile sites indicates that forest management in Estonia may have shifted toward favouring increased structural heterogeneity (Fig. 6): the trend is statistically significant (p = 0.03).

4. Discussion

Sustainable management of hemiboreal forests requires that simplified forest structures are restored (rehabilitated, sensu Stanturf et al., 2014) to more complex conditions at spatial and temporal scales (Laarmann et al., 2013; Messier et al., 2013). The terms structural heterogeneity, complexity and diversity are often used interchangeably to indicate forest ecological quality or naturalness (Messier et al., 2013) even though all-natural forests are not necessarily structurally complex (Ehbrecht et al., 2017), A metric is needed to effectively manage forests to maintain structural heterogeneity. All structural indices provide quantifiable information about forest stand structure. Those include spatially explicit tree level indices that are based on nearest neighbourhood approaches or their further development (Gadow et al., 2002, 2015; Aguirre et al., 2003; Pommerening, 2006; Laarmann et al., 2009; Pastorella and Paletto, 2013; Pommerening et al., 2020) and stand level ones, such as SCI (Zenner, 2000; Peck et al., 2014). Our results show that SCI is a promising measure in addition to general stand characteristics for quantifying the heterogeneity of hemiboreal forests.

The average values of the index in Estonian conditions were 7.42 on fertile and 3.85 on poor conservation forests, 4.74 on fertile and 4.00 on poor managed forests, and 2.64 on rehabilitation forests. These results correspond with other European studies. For an example, the range of SCI in the study conducted by Peck et al. (2014) in conifer-dominated stands in Switzerland were 1.99 to 4.79 for even-aged and 4.33 to 7.23 for uneven-aged stands, and the average index was 2.77 for evenaged and 5.59 for uneven-aged stands. A study carried out in Norway spruce-dominated stands in Finland (Zenner et al., 2011) showed that the average index was 2.49 for even-aged and 5.49 for uneven-aged stands. Based on the current study, the SCI strongly correlates to different stand characteristics traditionally used for describing stand structure, however, SCI is not easily implemented as the index requires tree location and size information. Therefore, it may not be suitable for everyday use in forest inventory but could be used, for example, in forest audits. Nevertheless, to adequately describe forest structure and incorporate its spatial nature, it is necessary to use such indices that take into account the spatial dimensions of forest structure (Zenner and Hibbs,

Protected or natural forests in Estonia have been shaped by various stand structural elements and legacies (Jögiste et al., 2017) to have higher structural heterogeneity when compared to recovering and managed forests (Pöddveer et al., 2020). The current study confirms that thinning immediately impacts stand structural heterogeneity, and that structural heterogeneity tends to decrease as management intensity increases and increase with greater site fertility in Estonia. The average SCI between managed and conservation forests on poor sites were not statistically different. On such sites, the forest is often kept unmanaged

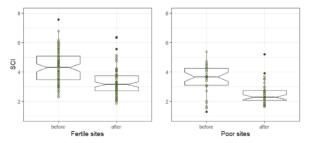


Fig. 4. SCI before and after thinning: the bottom and top of the box denote the interquartile range, black horizontal line medians, coloured dots observations and black dots outliers. Data are from the 125 sample plots belonging to actively managed stands thinned before the last measurement.

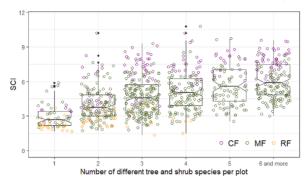


Fig. 5. SCI according to number of tree and shrub species occurring on a sample plots: the bottom and top of the box denote the interquartile range, black horizontal line medians, and black dots outliers. Coloured points are observations, added to the boxplot using jitter that adds a small amount of random variation to the location of each point to avoid overlapping. CF – conservation forests, MF – managed forests, RF – rehabilitation forests. Number of sample plots = SC.

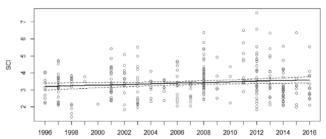


Fig. 6. The trend of SCI values immediately after the thinning. Data are from sample plots belonging to actively managed stands on fertile sites.

until clear-cutting, therefore, no differences in structural diversity appear. In contrast, there are rehabilitation forest stands that are very homogeneous at young age but may develop more heterogeneity over time. On fertile sites, the impact of silvicultural activities is clear managed forests are significantly more homogeneous than conservation forests. The SCI range in protected forests with high ecological quality could be used as a reference or baseline for assessing the suitability of management techniques to maintain or enhance stand structural heterogeneity. Our results support the position that species diversity promotes stand structural diversity. Furthermore, these results support the position that mixed forests add to heterogeneity and complexity of stand structure and species diversity. Species-diverse mixed forests potentially are more easily adapted to uncertain future change, diluting the impact of disturbance agents such as specialist pathogens (Bauhus et al., 2017) resulting in a positive effect on forest productivity (Benneter et al., 2018). It may be that thinning policies are slowly changing attitudes in forest management and that forest machine operators conducting thinning have actively promoted stand structural diversity since the 1990s in Estonia (Fig. 6). Alternatively, natural processes driven by global change could be the cause of increasing structural heterogeneity even in managed stands (Yue et al., 2016).

Structural indices should become more widely adopted as large-scale tree-level data are more available from high-resolution (spatial and temporal) remote sensing data, such as terrestrial and airborne lasers

(Lang et al., 2012; Arumãe and Lang, 2018). Such wall-to-wall remotely sensed data will allow future mapping of biodiversity, which is known to have strong correlations with forest structure (Guo et al., 2017; Bae et al., 2019) and applications in ecosystem services mapping and quantification (Oxbrough and Pinzón, 2020). More comprehensive information about forest stand structure additionally can be used to search for links between structural indices and important forest development processes (such as the patterns of regeneration and gap dynamics), and the importance of individual tree-level characteristics (e.g., large trees or damaged trees) on stand-level structural heterogeneity (Allikmäe et al., 2017).

5. Conclusions

Insight into forest stand structural heterogeneity is needed for sustainable management of boreal and hemiboreal forests. The results of this study revealed that the relatively simple stand level structural complexity index (SCI) is strongly correlated with different stand characteristics, thus providing quantitative assessments of multidimensional stand structure in Estonian forests and that stand-level SCI is a suitable approach for quantifying multidimensional stand structure in hemiboreal forests. The index showed a generally decreasing trend along management intensity and increasing site fertility. The SCI showed that the heterogeneity of stand structure depends on the number of different

tree and shrub species, indicating that species diversity promotes stand structural diversity. The disadvantage of the index is that it requires tree location and size information that are not gathered during standard ground inventory. Therefore, separate data collection requiring additional resources is needed for index calculation. In addition, the index does not directly cover certain important indicators; the composition of tree species and dead tree component - these need to be considered separately. Even though the SCI may be too costly at present for routine monitoring and inventory measurements, it may be useful for periodic audits and/or assessing the success of nature conservation objectives. and could be routinely implemented in the near future as remotelysensed structural data become routinely available, e.g., from laser scanning and machine learning.

CRediT authorship contribution statement

Eneli Poldveer: Writing - original draft, Conceptualization, Formal analysis, Methodology, Visualization. Aleksei Potapov: Writing - original draft, Formal analysis, Methodology, Visualization. Henn Korjus: Writing - review & editing, Conceptualization, Methodology, Supervision. Andres Kiviste: Writing - review & editing, Methodology, Project administration, Supervision. John A. Stanturf: Writing - review & editing, Supervision. Tauri Arumäe: Writing - review & editing, Visualization. Ahto Kangur: Writing - review & editing, Supervision. Diana Laarmann: Writing - review & editing, Conceptualization, Project administration, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Sciences

2015–2016 Master studies in natural resources management,

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2011–2015 Bachelor studies in natural resources

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2008–2011 Rakvere Gymnasium

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Professional employment:

2016-... Estonian University of Life Sciences, Institute of

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Forest structure modelling, sustainable management

of forest resources

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Training and special courses:

	8 · · · · I
2019	Publish or Perish: Preparing a High Impact Scientific
	Publication, Järvselja, Estonia
2018	Statistical Models, Tartu, Estonia
2017	Applied Spatial Statistics, Umeå, Sweden
2017	Biological Processes in the Biosphere-Atmosphere
	System, Järvselja, Estonia

Study and research visit:

2018 U	University of	Santiago de	Compostela, Spain
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Projects:	
2020-2022	Estonian Environmental Investment Centre project
	No 17283: Re-measuring of the Estonian Network
	of Forest Research Plots 2020–2021.
2020-2022	Estonian Environmental Investment Centre project
	No 17900: Publication of peer-reviewed forestry
	journals "Forestry Studies / Metsanduslikud
	Uurimused" and "Baltic Forestry".
2019-2020	Estonian Environmental Investment Centre project
	No 15710: Follow-up of naturalness restoration
	experiment in Karula National Park.
2019-2020	Estonian Environmental Investment Centre project
	No 15566: Publication of peer-reviewed forestry
	journals "Forestry Studies / Metsanduslikud
	Uurimused" and "Baltic Forestry".
2018-2020	Estonian Environmental Investment Centre project
	No 14515: Re-measuring of the Estonian Network
	of Forest Research Plots 2018–2019.
2018–2019	Estonian Environmental Investment Centre project
	No 15205: Developing Model Forest in Järvselja
	Forestry District.
2016–2017	Estonian Environmental Investment Centre project
	No 10931: Re-measuring of the Estonian Network
	of Forest Research Plots 2016.

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2011–2015 Eesti Maaülikool, metsandus- ja maaehitusinstituut,

loodusvarade kasutamine ja kaitse, bakalaureuseõpe

2008–2011 Rakvere Gümnaasium 1999–2008 Kunda Ühisgümnaasium

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metsa- ja maakorralduse ning metsatööstuse

õppetool, nooremteadur

Teadustöö suunad:

Metsa struktuuri modelleerimine, metsade

jätkusuutlik majandamine

Võõrkeelte oskus:

Inglise, soome

Täiendkoolitused:

2019	Kirjuta või koole: Kõrge tsiteeritavusega teadusartikli
	koostamine, Järvselja, Eesti
2018	Statistilised mudelid (vabavaralise programmi R
	baasil), Tartu, Eesti
2017	Rakenduslik ruumistatistika, Umeå, Sweden
2017	Bioloogilised protsessid biosfääri-atmosfääri
	süsteemis, Järvselja, Eesti

Täiendusõpe välisülikoolis:

2018	Santiago de Compostela	Ulikool, Hispaania

Projektid:	
2020–2022	SA Keskkonnainvesteeringute Keskuse projekt
	nr 17283: Metsa kasvukäigu püsiproovitükkide
	võrgustiku kordusmõõtmine 2020–2021.
2020–2022	SA Keskkonnainvesteeringute Keskuse projekt nr
	17900: Metsanduslike teadusajakirjade "Forestry
	Studies/Metsanduslikud Uurimused" ja "Baltic
	Forestry" väljaandmine.
2019–2020	SA Keskkonnainvesteeringute Keskuse projekt nr
	15710: Looduslikkuse taastamise katseala uuringu
	jätkamine Karula rahvuspargis.
2019–2020	SA Keskkonnainvesteeringute Keskuse projekt
	nr 15566: Metsandusajakirjade "Metsanduslikud
	Uurimused" ja "Baltic Forestry" väljaandmine.
2018–2020	SA Keskkonnainvesteeringute Keskuse projekt
	nr 14515: Metsa kasvukäigu püsiproovitükkide
	võrgustiku kordusmõõtmine 2018–2019.
2018–2019	SA Keskkonnainvesteeringute Keskuse projekt
	nr 15205: Metsakorraldusliku mudelala rajamine
	Järvselja Õppe- ja Katsemetskonda.
2016–2017	SA Keskkonnainvesteeringute Keskuse projekt
	nr 10931: Metsa kasvukäigu püsiproovitükkide
	võrgustiku kordusmõõtmine 2016.

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Allikmäe, E., Laarmann, D., Korjus, H. 2017. Vitality assessment of visually healthy trees in Estonia. Forests, 8 (7): 223.

Rebane, S., Jõgiste, K., Põldveer, E., Stanturf, J.A., Metslaid, M. 2019. Direct measurements of carbon exchange at forest disturbance sites: A review of results with the eddy covariance method. Scandinavian Journal of Forest Research, 34 (7): 585–597.

Korjus, H., Kiviste, A., Kangur, A., Paluots, T., Laarmann, D., Põldveer, E. 2020. Dataset on stand structural indices and forest ecosystem naturalness in hemiboreal forests. Data in Brief, 29: 105387.

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Põldveer, E., Potapov, A., Korjus, H., Kiviste, A., Stanturf, J.A., Arumäe, T., Kangur, A., Laarmann, D. 2021. The structural complexity index SCI is useful for quantifying structural diversity of Estonian hemiboreal forests. Forest Ecology and Management, 490: 119093.

Nigul, K., Padari, A., Kiviste, A., Noe, S.M.; Korjus, H., Laarmann, D., Frelich, L.E., Jõgiste, K., Stanturf, J.A., Paluots, T., Põldveer, E., Kängsepp, V., Jürgenson, H., Metslaid, M., Kangur, A. 2021. The possibility of using the Chapman-Richards and Näslund functions to model height-diameter relationships in hemiboreal old-growth forest in Estonia. Forests, 12 (184): 1–15.

Publications in other peer-reviewed journals

Korjus, H., Hordo, M., Põldveer, E. 2018. Editorial. Forestry Studies, 69: 5–6.

Peedosaar, L., Põldveer, E., Kollo, J., Kangur, A. 2019. A narrative of virtual and augmented reality in the forest sector. Forestry Studies, 70: 88–96.

VIIS VIIMAST KAITSMIST

HEIKI LILL

NOVEL APPLICATION PRINCIPLES FOR ENERGY STORAGE TECHNOLOGIES IN NEARLY ZERO ENERGY BUILDINGS ERINEVATE ENERGIA SALVESTUSTEHNOLOOGIATE UUDSED RAKENDUSPÕHIMÕTTED LIGINULLENERGIAHOONETES

Teadur Alo Allik, professor Andres Annuk

24. november 2021

PIRET RAUDSEPP

POLYPHENOLIC COMPOSITION OF RHUBARB (*RHEUM RHAPONTICUM L.*) AND BLACKCURRANT (*RIBES NIGRUM L.*), ANTIBACTERIAL AND FREE RADICAL SCAVENGING PROPERTIES OF THESE PLANTS IN COMPARISON WITH SOME OTHER FOOD PLANTS

HARILIKU RABARBERI (*RHEUM RHAPONTICUM L.*) JA MUSTA SÓSTRA (*RIBES NIGRUM L.*) POLÜFENOOLNE KOOSTIS, NENDE TAIMEDE ANTIBAKTERIAALSE TOIME JA VABADE RADIKAALIDE SIDUMISE VÕIME VÕRDLUS MÕNEDE TEISTE TOIDUTAIMEDEGA

Professor Tonu Püssa, vanemteadur Ave Kikas

10. detsember 2021

INGRID BENDER

EFFECT OF ORGANIC MANAGEMENT METHODS ON YIELD AND QUALITY OF CARROT AND ON WEEDS

MAHEVILJELUSE MEETODITE MÕJU PORGANDI SAAGILE JA KVALITEEDILE NING UMBROHTUDELE

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17. detsember 2021

LIINA SOONVALD

RESPONSE OF ROOT FUNGAL COMMUNITIES TO FERTILISATION, CROP SPECIES AND CULTIVAR

VÄETAMISE, PÓLLUKULTUURI NING SORDI MÓJU TAIMEJUURTE SEENTE KOOSLUSTELE

Professor Marika Mänd, professor Alar Astover, professor Leho Tedersoo (TÜ)
4. veebruar 2022

HELI KIRIK

MOSQUITO (DIPTERA: CULICIDAE) DIVERSITY IN THE URBAN ENVIRONMENT AND COUNTRYSIDE OF ESTONIA PISTESÄÄSKLASTE (DIPTERA: CULICIDAE) MITMEKESISUS EESTI LINNAKESKKONNAS JA LOODUSES

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