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The direct and indirect effects of management on boreal forest structure and field layer vegetation

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Department of Botany, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

I Kohv, K. & Liira, J. 2005. Anthropogenic effects on vegetation structure of the boreal forest in Estonia. Scand. J. Forest. Res. 20(S6): 122–134.

II Liira, J. & Kohv, K. 2010. Stand characteristics and biodiversity indicators along the productivity gradient in boreal forests: Defining a critical set of indicators for the monitoring of habitat nature quality. Plant Biosyst. 144(1): 211–220.

III Liira, J. Sepp, T. & Kohv, K. 2011. The ecology of tree regeneration in mature and old forests: combined knowledge for sustainable forest management. J. For. Res. – Jpn. 16(3): 184–193.

IV Kohv, K., Zobel, M. & Liira, J. (submitted). Productivity affects the driver-specific resilience of the forest understory community. Oikos

Author's contribution to the papers

	Paper I	Paper II	Paper III	Paper IV
Original idea	*	*		*
Study design	*	*	*	*
Data collection	*	*	*	*
Data analyses	*	*		*
Manuscript preparation	*	*	*	*

1 INTRODUCTION

In the last century, global biodiversity has been changing at an unprecedented rate in response to human-induced changes in the environment (Foley et al. 2005). Over centuries of land use intensification, forest area has decreased in Europe (Grigg 1987), and most of the existing forest land is covered by secondary and modified stands, while only a few remnants of old-growth forests remain (Linder & Östlund 1998). The implementation of sustainable forest management systems consisting of a combination of strictly protected forest reserves and forests managed using "close to nature" silvicultural methods has been seen as one solution to halt the decline in forest biodiversity (Lähde et al. 1999; Peterken 1999; Larsen & Nielsen 2007). This has provided ground for the concept of forest naturalness, which combines information about habitat biodiversity and the integrity of ecosystem functions (Anderson 1991; Uotila et al. 2002; Winter 2012).

Many management-sensitive structural and compositional characteristics have been listed as indicators for the monitoring or detection of the near-natural status of forests (Trass et al. 1999; Lindenmayer et al. 2000). Each evaluation is usually limited by resource constraints (Ejrnaes et al. 2002), and therefore environmental agencies need an optimized and low-cost method with easy-to-apply indicators (Balmford et al. 2005; Ejrnaes et al. 2008). Rational and diagnostic indicators should be (Dale & Beyeler 2001): I) correlated to both biodiversity and management/disturbance activities; II) easy to detect and evaluate; III) informative over a wide range of environmental conditions, forest types and geographical regions; IV) subjected to rigorous testing of statistical predictive power.

Physical structures of forest like dead wood, big living trees are widely used indicators as they are characterized by relatively high inertia, are easy to measure and there is also enough scientific knowledge to link specific structures to species groups (Lindenmayer et al. 2000). For example, number of studies have shown clear linkage between characteristics of dead wood and diversity of polypores, lichens and insects (Bobiec et al 2005). Many suggested structural indicators and their threshold values are specific to a particular forest site type, i.e. dependent on soil conditions, community composition and natural disturbance regimes (Uotila et al. 2002; Lõhmus & Kraut 2010). However there have been a few studies in which potential confounding factors have been measured and analysed simultaneously (Jacquemyn et al. 2003; Aparicio et al. 2008).

Compositional indicators are more difficult to measure and interpret mainly because of their dynamic character and high variation in feedback to different drivers (Lindenmayer et al. 2000). As habitat quality is taxon or guild specific and determined by a multi-factorial environmental complex, the sensitivity to management disturbances also varies between species groups and habitat types (Jonsson & Jonsell 1999). Before using compositional indicator, it is crucial to define the complex of ecological factors that determine its variability and dynamics.

One of the compositional indicators used is composition of forest field layer (Winter 2012). Forest field layer community provides multiple ecosystem services for humans, controls forest natural regeneration, provides habitat for wildlife and has critical role in the nutrient cycling (Messier et al. 1998; Nilsson & Wardle 2005; Royo & Carson 2006). The practical importance of field layer plant community (herbs and dwarf shrubs) relays in the fact that it is used for classification of the forest site types (e.g. Cajander 1926). The effects of single environmental factors on field layer vegetation are frequently recognized (Hart & Chen 2006; Barbier et al. 2008). For example it is widely accepted that light availability and its spatio-temporal variation are the most influential factors determining species composition and the abundance of individual species in a forest (Kembel & Dale 2006; Sepp & Liira 2009). Soil conditions and other substrate-related natural conditions determine the formation of field layer vegetation and their responses to environmental changes (Peet et al. 2003; Peppler-Lisbach & Kleyer 2009; Van Couwenberghe et al. 2011). Human generated disturbances dominate in contemporary forest landscape (Bengtsson et al. 2000), and therefore, there has also been discussion about the relative role of forest management in determining forest plant community composition (Nieppola 1992; Pitkänen 2000; Hart & Chen 2008). For instance, it has been shown that the field layer in boreal forests may exhibit high resilience towards direct disturbances, because their composition only reacts to logging intensity when cutting rates exceed 80–95% (Bergstedt & Milberg 2001; Jalonen & Vanha-Majamaa 2001), while intermediate-intensity thinning treatments or other medium-level disturbances are mostly confined to changes in species coverage (De Grandpre et al. 2011).

The evaluation of the relative importance of anthropogenic vs natural processes to the plant community is complicated by two problems: I) the collinearity of effects, i.e. anthropogenic effects are frequently intermixed with natural changes in a stand (Moora et al. 2007; Bartels & Chen 2010); II) in the long-term, the direct causal effect of anthropogenic disturbances is overridden by indirect effects, such as changed resource levels and their heterogeneity (Økland et al. 2003; Reich et al. 2012). The indirect effects of human disturbances are usually long lasting, much longer than the time for which the direct effect of the disturbance itself can be recognised in the field (Jantunen et al. 2001; Paal et al. 2011). Such a combination of direct and indirect causal relationships and natural processes can be partly avoided by: I) targeting only mature stands in which major species arrivals and population adaptations have already occurred; II) by the parallel observation of all potentially affected characteristics and layers.

The following are the main questions the thesis seeks to answer:

1) Which structural and compositional characteristics of boreal forests are sensitive to forest management practices in boreal forest landscapes?
2) How much do observed relationships and indicators vary along the forest productivity gradient characterised by forest site types?
3) What would be a statistically reliable diagnostic set of indicators for the evaluation of forest "naturalness" over the range of boreal forest site types?
4) How is the pattern of natural recruitment correlated with the multitude of factors in mature and old boreal and hemiboreal forests?
5) How resilient is community composition of forest field layer to the multitude of direct and indirect anthropogenic factors in boreal forest stands?

The theses are compiled from four papers: **paper I** represents the study using the "landscape window" method to estimate the anthropogenic effects on forests of the *Rhodococcum* forest site type at various ages; **paper II** focuses on the responses of various structural and compositional characteristics to anthropogenic disturbance and within stand conditions along the productivity gradient in mature and old boreal forests; **paper III** specifically analyses tree recruitment variations in response to ecological factors along the productivity gradient in mature and old boreal and boreonemoral forest site types; **paper IV** is about forest field layer resilience along the productivity gradient in mature and old boreal forests.

II MATERIALS AND METHODS

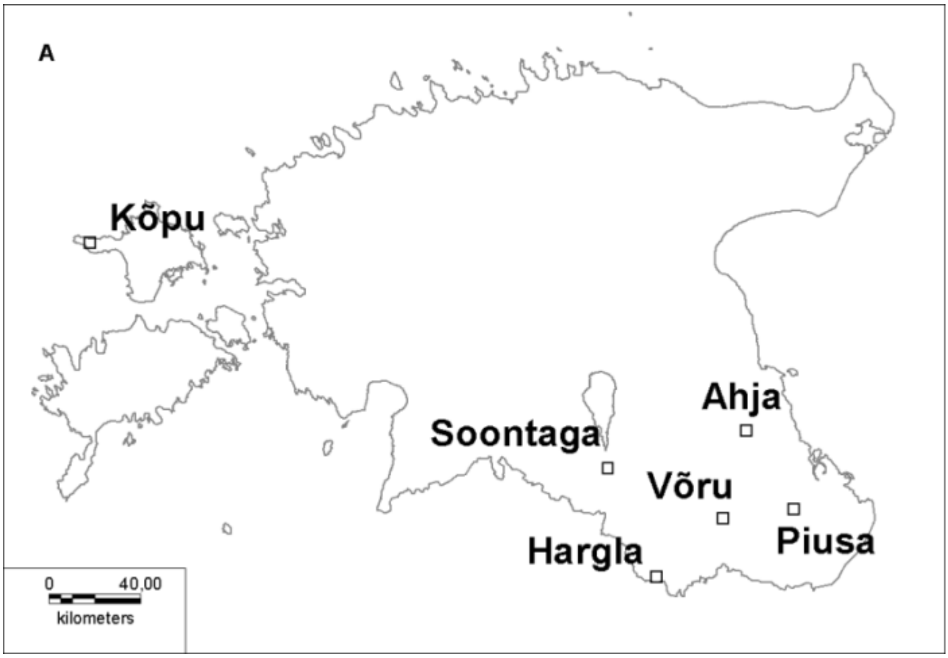
2.1. Study area

The Baltic region, including Estonia, represents a transitional zone of silvicultural traditions between Western Europe, which has historically been intensively managed, and North-Western Russia, which is still rich in old-growth forests (Angelstam et al. 1995; Carlsson & Lazdinis 2004). Estonia also represents a biogeographic ecotone between northern boreal and temperate nemoral forests, belonging to the hemi-boreal vegetation zone (Ahti et al. 1968). The average annual precipitation varies by around 650 mm per year, and average temperatures in July are about 17°C, and in February around –5°C (Aunap et al. 2004).

Most of the papers (see Table 1 for greater detail) addressed boreal forests on sandy acidic mineral soils in Estonia (Lõhmus 1984; Paal 2007). Only **paper III** used data from two boreonemoral site types (*Hepatica* and *Aegopodium*). Estonian boreal forests are mostly Scots pine (*Pinus sylvestris*) or Norway spruce (*Picea abies*) dominated forests, with Silver birch (*Betula pendula*) and aspen (*Populus tremula*) as occasional sub-dominants. The stand volume of these forest site types varies between ca 165–190 m^3/ha in the *Calluna-Cladonia*, 250–350 m^3/ha the *Rhodococcum,* 250–400 m^3/ha in the *Myrtillus* and 400–800 m^3/ha in the *Oxalis* site type (Lõhmus 1984). These forests comprise more than 30% of Estonian forested land (Adermann 2008). The commonly applied management cycle of these forests typically involves clear-cutting at the age of about 80–100(120) years, natural regeneration (sometimes sowing or planting), and two or three thinnings at approximately 20-year intervals.

2.2. Sampling design

In **paper I** we used the stratified sampling scheme based on 5*5 km landscape windows (Figure 1) dominated by poor dry podzols suitable for *Vaccinium vitis-idaea* (*Rhodococcum)* site type forests (Table 1 in **paper I**). In these landscapes we randomly selected a set of 25–30 sites. The sampling sites were selected according to the presence of the *Vaccinium vitis-idaea* site type forest and a distance of at least 100 m from the nearest neighbouring site. Altogether, forest structure was described in 6 landscapes at 174 sites (our compiled version of the field questionnaire was based on Angelstam & Dönz-Breuss 2004).



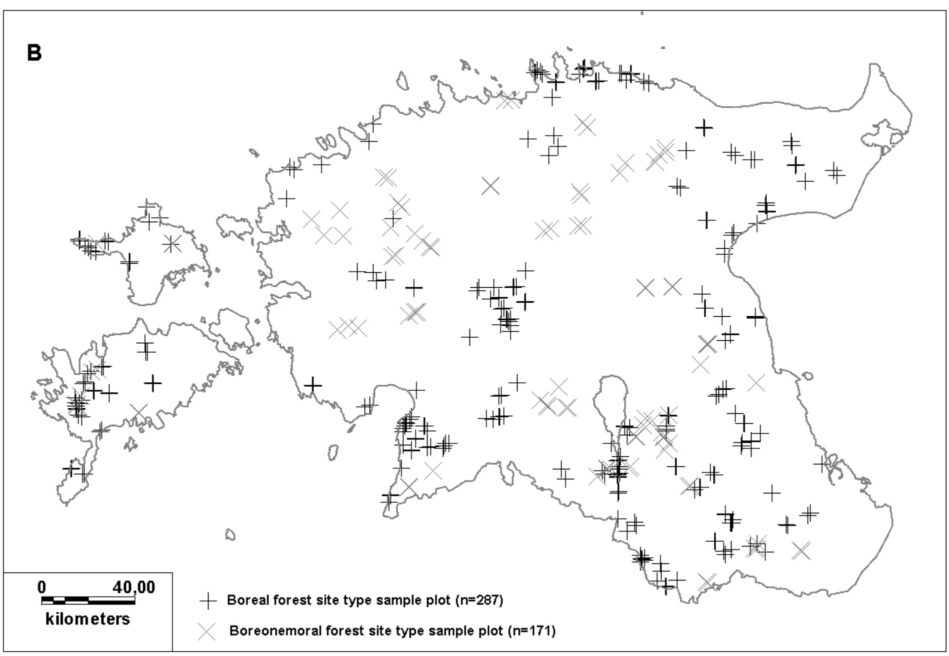


Figure 1. **A** – the location of 5*5 km forest landscapes used in **paper I**, in each landscape 25–30 random sample points were described. **B** – the location of sample points used in **paper II, III, IV**.

For **paper II, III, IV**, we intended to minimise the regional effect caused by the use of landscape window and effects related to forest age (forest succession). In these **papers** we used a stratified sampling scheme in order to maximise the estimation of anthropogenic disturbance effect and minimize the confounding effects of spatial autocorrelation, large-scale heterogeneity in the environment and biogeography (Liira et al. 2007; Liira & Sepp 2009). For that purpose, we positioned pairs (max distance 5 km) of forest study sites evenly over the entire distribution area of each forest site type in Estonia (Figure 1 and Table 1). A pair of stands was planned with aim to cover as wide management intensity gradient as possible. The studied stands were limited to the minimum values of 1 ha area and stand age of 75 years. The management and disturbance history of stands was verified using data from the State Forest Management Centre (http://www.rmk.ee), interviews with local foresters and the map of the Forest Key Habitat Network (Andersson et al. 2003).

Table 1. Distribution of sampled points among different site types in different studies.

Site type/ No of samples	Paper I	Paper II	Paper III	Paper IV
Cladonia-Calluna (boreal)		66	66	56
Rhodococcum (boreal)	174	95	95	95
Myrtillus (boreal)		91	91	90
Oxalis (boreal)				35
Hepatica (boreonemoral)			83	
Aegopodium (boreonemoral)			88	

Although the design of the sampling was changed for **paper II, III, IV**, the methodology used to describe forest structure and understory vegetation was only slightly optimized using the experience from **paper I**. In each study site, we recorded the state of more than 50 characteristics of forest structure and species composition. From the centre of a study site, we recorded the basal area of each tree species in three diameter classes: DBH=8–40 cm, 41–80 cm and >80 cm, using the Bitterlich relascope; we characterized stem diameter diversity as the number of trunk diameter classes, and described the vertical structure of the stand canopy by visually estimating the cover of the coniferous and deciduous foliar layer. We measured the quantity of standing dead trees and broken-top snags (DBH > 8 cm) using the Bitterlich relascope. We estimated the basal area of lying dead trees (logs) using a methodology that emulates the Bitterlich relascope – searching for and counting logs longer than 1.3 m with a diameter greater than 8 cm, 15 cm and 40 cm in concentric circles around the central point with a radius of 0–5 m, 5–10 m and 10–30 m respectively. We recorded the presence of various stand structural features, such as wind-thrown, wind-broken or specially-shaped trees and the decay classes of dead wood (early, medium or late decay). We described understory composition (shrubs and tree saplings) in a circle (r= 5.6 m, i.e. 100 m²) by estimating shrub layer coverage percentages and tree saplings counts by species (DBH<8 cm and height between 1.3 m and 25% of stand height).

Within study sites (r=30 m), we located one 4x4 m plot (**paper I**) or ten randomly scattered 2x2 m plots (**paper II, III, IV**) to characterize the composition of the herb layer by cover-abundance classes (1–<1%; 2–<5%; 3<25%; 4–<50%; 5–<75%; 6–<100%), moss-lichen layer coverage and canopy closure above. We also recorded the presence of widely-accepted and easily-recognizable forest biodiversity indicators such as long epiphytic lichens *Usnea spp*., *Bryoria spp.*, ground lichen *Peltigera spp*., macrofungi on living and dead wood, large insect holes (diameter classes 5–10 mm and >10 mm), ant nests and any signs of woodpecker activity. Some of the registered structural characteristics and indicators appeared very infrequently in the study sites, and were not used later.

2.3. Management intensity index

In **paper I** we used information from State Forest Management Centre databases to calculate the management intensity index (MI) as the sum of the presence/absence of various documented silvicultural activities, weighted by their proportional area in a 60-m-radius circle around the sampling point. The value of MI was 0 if no cutting operations was done and 4 if the whole area was clear cut. Because the detailed management and disturbance history of a stand was frequently only available for the last 20 years and was not available for private forests, we developed the indicator-based quantified estimate of the direct anthropogenic disturbances as an index of management intensity (**paper II, III, IV**). The latter index considers the region- and community-specific spectrum of disturbances, and avoids the potential assessment bias based on single trait estimation (e.g. the number of cut stumps). This was called the Management Intensity Index (MI), because the majority of features considered are related to forest management in Estonia. The index can be interpreted as the quantified judgment of an expert, assessing the disturbance rate by pooling the presence of various visible signs of anthropogenic disturbance. These signs, recorded from maps, databases and during stand inventories, are: cut stumps, piles of logs, forest tracks, roads, neighbouring clear-cut areas, ditches, garbage, fences, soil mechanical damage etc. Signs were recorded within two distance intervals – in a study site (r=0–30 m) and in a buffer zone (r=30–60 m). Each sign of anthropogenic activities received a score describing its proportional effect (1 – weak, 2 – strong), and these were double weighted for a radius zone of 0–30 m. The management intensity index (MI) is the sum of these weighted scores. The MI is equal to zero if there are no signs of any disturbances within a radius of 60 m, and can reach a value of 50 in the case of a clear-cut area with soil damage, trash pollution, intersecting ditches and roads, and surrounded by neighbouring arable fields or buildings. In our study sites inside larger forested areas, we observed the maximum value of MI=19.

2.4. Statistical analyses

The overview of the statistical methods used in various papers is found in Table 2. In **paper I, II, III**, General Linear Model (GLM) analysis in the Statistica ver. 8.0 statistical package was applied to test the response pattern of numerical forest structural and compositional characteristics to various factors. The inclusion of collinear factors was avoided by including only less inter-correlated characteristics in the model. The tested factors and drivers can be classified into several groups according to their roles in the model or in the ecosystem:

(1) natural confounder variables causing expected variability in data – site productivity (site type in **paper II, III**), natural succession (stand age in **paper I, II, IV**) and geographical location (geographical coordinates in **paper II**);
(2) direct effects of management as an index of the intensity of anthropogenic disturbance (MI) (**paper I, II, III, IV**);
(3) indirect effects of management (**paper II, III, IV**):
    (3a) via changed average light availability (stand closure, coverage of foliage layer from 1.3–4 and 4–10 meters, coverage of shrub layer, basal area of trees, basal area of spruce);
    (3b) via altered light resource heterogeneity (the variation coefficient of closure inside the site, the number of tree, tree sapling and shrub species, and the proportion of boreal deciduous trees in a stand as a factor describing seasonal variation and the compositional heterogeneity of litter);
    (3c) via the directly or indirectly management controlled amount of lying dead wood
(4) characteristics of small-scale (within stand) natural variation such as soil and ground layer conditions (thickness of organic soil layer (A0), thickness of soil humus layer (A1), the cover of moss layer), which can sometimes be disturbed by management, but which were little influenced by anthropogenic activities in the observed forests.

A two-directional stepwise selection of variables was applied in analyses, until the best parsimonious models were reached. Where necessary, the log-transformation or the arcsine of square-root transformation were applied to attain the normal distribution of residuals. In **paper II**, Generalized Linear Model

(GLIM) analysis was used on binomial (presence/absence data) structural features with similar model structures.

We described compositional variation (beta-diversity) within and between communities. In **paper II** we applied the index of relative richness to measure the homogeneity (or saturation) of the herb layer within the study site (r=30 m forest stand), calculating it as the average proportion of herb layer species richness in 2x2 m plots relative to the total number of herb layer species in a stand (Zobel & Liira 1997). In **paper IV** we used a combined methodology to estimate the relative importance of factors causing the variation in field layer composition allowing non-linear relationships. For that purpose, we used PC-Ord 6.0 to calculate the compositional dissimilarity of field layer vegetation reciprocally among all sites within each forest site type in terms of Sørensen distance (belonging to the family of dissimilarity measures by Dice, Hellinger and Bray Curtis; McCune & Mefford 1999). Analogously to the dissimilarity estimate, we calculated the contrast for each anthropogenic, structural or environmental factor reciprocally among all study sites within the same site type. The contrast of each stand attribute was standardized into proportional units using the average value of the two sites, which were compared. In the next step of the analyses, multi-factorial General Linear Model (GLM) analysis in the Statistica ver. 8.0 was used to fit a multi-factorial model explaining the compositional variation, which was measured as the dissimilarity among two sites. The data on compositional dissimilarity were used as a response variable, and a two-way stepwise and the best subset selection of variables was applied to find the optimal parsimonious model (based on adjusted R^2 and Mallow Cp parameters). Models were built within each forest site type. In **paper IV** we used the relative abundance of each species, by multiplying species average abundance in plots (rescaled 0...100%) by its frequency in plots (0…100%) and scaled it back to the score range of 0–100.

In **paper I**, direct gradient analyses (CCA) were used in CANOCO for Windows ver. 4.5 (Ter Braak & Šmilauer 2002) to estimate the relationship between field layer composition and environmental variables. Indicator species analyses were also used to define compositional indicators in the herb layer community (PC-ORD ver. 4.0) in **paper I**. In **paper I** and **IV** we excluded species represented in less than three study sites prior to the analyses.

To identify the diagnostic set of forest indicators that can be used to recognize the old-aged stand in near-natural status we used Generalized Linear Model (GLIM) analysis in **paper I** and **II**. For that purpose, we pre-classified stands into two groups (near-natural stands and human-disturbed stands) based on stand age (100 years) and management intensity indexes (one weak disturbance was allowed).

Tabel 2. Statistical methods used in different studies.

Statistical method	Paper I	Paper II	Paper III	Paper IV
Regression analysis	X			
Generalized Linear Model (GLIM)	X	X		
General Linear Model (GLM)		X	X	X
Ordination (CCA)	X			X
Indicator species analyses	X			

III RESULTS

3.1. The effect of geographic location, site type and forest age on forest stands

In **paper II**, geographical location, interpreted as a confounding factor in this study, showed a significant effect on 24 characteristics out of the total of 35 characteristics tested (Table 1 in **paper II**). The effect corresponded with the gradient from maritime to inland (**paper II**).

Forest site type was a significant factor for 30 forest characteristics out of the 35 that were tested (**paper II**). The tested structural and compositional forest characteristics showed a uniform positive correlation to the productivity rank of the forest site type. Only in the case of a few characteristics is the correlative trend with productivity negative – the coverage of ground layer lichens (mostly *Cladonia* spp.)and the variation coefficient of tree canopy closure tend to increase toward low productivity forests (the *Cladonia*-*Calluna* site type). It is important to note that the statistically significant increase in the values of different forest characteristics described as forest site type based homogenous groups is often trait-specific (Figure 2). Average values of forest characteristics in different site types are presented in Table 1 in **paper IV**.

In **paper I** we showed that there is a very strong negative relationship between stand age and management intensity, and the more natural *Rhodococcum* site type forests have a minimum age limit of between 50 and 80 years (Figure 1 in **paper I**). If minimum stand age was set at 75 (**paper II**, **IV**), it remained a statistically significant explanatory variable for many characteristics. In **paper II** 16 forest characteristics out of 35 were dependent on stand age (Tables 1 and 2 in **paper II**). Stand age was mostly associated with those structural traits or biodiversity indicators that are related to trees or shrubs, while the characteristics of forest floor vegetation do not correlate with stand age (Tables 1 and 2 in **paper II**). In general, older stands have a larger number of tree species, a higher proportion of spruce, basal area of large trees (DBH> 40 cm) and dead wood. The stand canopy has a denser second tree layer and understory (foliar layers 4–10 m and 1–4 m) in older forests. The only negative correlation between stand age and forest structure was observed in the basal area of small diameter trees (DBH=8–40 cm). Old forests also have a higher occurrence probability of dead branches, wind-throw and wind-break of trees, and also a higher relative incidence rate of biodiversity indicators, such as indicator lichens on trees, insect holes (d>10 mm) on trunks and signs of woodpecker activity.

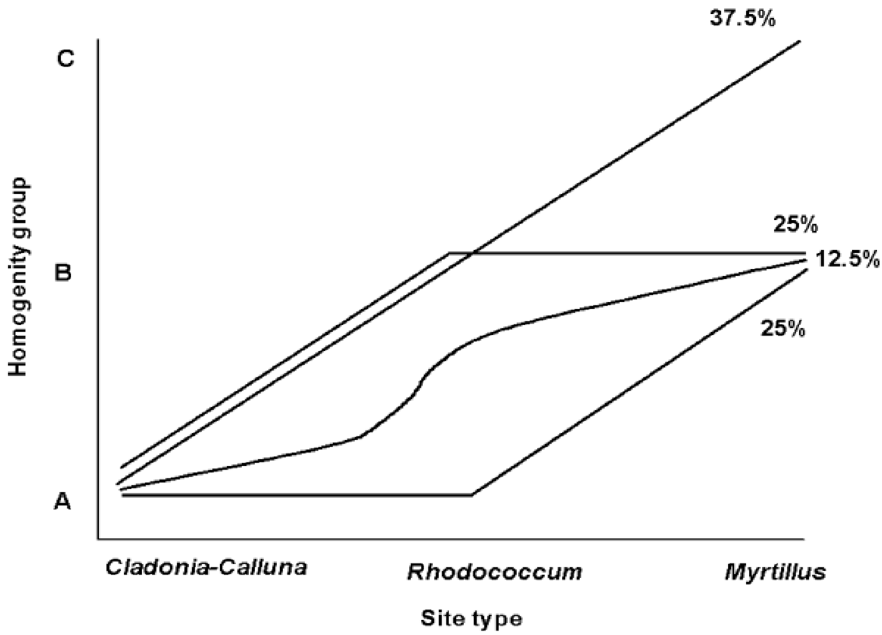


Figure 2. The pattern of statistically significant increase of stand characteristics (n=16) related with tree and shrub layer (based on ranks (a, b and c in increasing order) among homogeneity groups of average values tested with GLM analysis in Paper II).

3.2. The direct effect of management on forest stands

The direct anthropogenic impact measured through visible signs of management (management intensity index) was a significant predictor for 24 forest characteristics (**paper II**). It usually had a significant negative effect on the forest structure and compositional characteristics of trees and the shrub layer (see also Table 2 in **paper I**).

Most evidently, management reduced the total basal area of a stand, particularly of large trees, and also the number of diameter classes present in a stand. Managed boreal forests are usually dominated by Scots pine and have lower tree species richness. Management activity predicted a decrease in the amount and diversity of dead wood and the closure of the stand canopy, as well as the coverage of the lower tree layers. It also reduces the probability of the occurrence of wind-throw or wind-break trees, specially-shaped trees, fruit bodies of fungi on trees, indicator lichens, as well as signs of insects and woodpeckers.

3.3. The indirect effects of management on forest stands

The indirect effects of forest management are reflected in forest regeneration composition and abundance and in field layer vegetation (see **paper II**, **III**, **IV**). Indirect effects appear through site type specific changes in stand density, tree species composition, the availability of dead wood as substrate, but most of all in the reduction of stand closure and the coverage of understory layers (the second layer and shrubs).

In **paper II** we showed that although management did not have a direct effect on field layer vegetation, the variability of light conditions and average light availability had significant effect on field layer composition. The greater openness facilitated herb layer coverage and suppressed graminoids. These changes also reduced the total number of herb species in a stand, but did not affect small-scale species richness, therefore increasing the homogeneity of the herb layer.

3.4. Factors affecting forest regeneration along the productivity gradient

In **paper II** (see also **paper I**) we showed that management intensity did not have a direct effect on sapling species richness. In **paper III** we analysed the indirect effects of management on forest saplings, and found an analogy with field layer community.

The most common microhabitat for tree regeneration was undisturbed vegetation, and the only considerable alternative substrate for tree regeneration was dead wood, but only in spruce forests (Table 1 in **paper III**). Seedling frequency and the number of seedling species were strongly related to productivity. Boreal forest site types lacked several deciduous tree species in the field layer, and seedling frequency was also considerably lower than that of more productive boreonemoral forests (Table 2 in **paper III**). Spruce seedlings were most common in all site types other than the *Cladonia-Calluna* site type. Only rowan (*Sorbus aucuparia*) seedlings were as frequent as spruce, particularly in productive site types. The ubiquity of oak (*Quercus robur*) across forest site types was surprising: it was equally frequent everywhere, but it also possessed the highest local importance among seedlings in low-productivity boreal forests.

The GLM model on the number of saplings (Table 3 in **paper III**) revealed that there were significant differences in sapling abundance between forest site types, and that sapling abundance was positively correlated with tree species richness, variation in canopy closure and the amount of lying dead wood, hinting at the impact of microhabitat availability. The model showed the common suppressing effect of spruce density on the number of saplings, and in boreal forests this suppression was enhanced by the large number of young trees in the stand (Figure 2 in **paper III**). On the ground, abundant moss cover and the presence of a thick organic horizon layer also had positive effects on sapling abundance in a stand. Several other factors that were considered to be potential predictors, such as the average closure of the canopy and the presence of wind-thrown or wind-broken trees, did not prove to be significant in the model.

In the GLM analysis on sapling species richness, we first took into account the number of saplings in the sample, expecting a standard relationship between sample size and species richness. The model confirmed that site type was one of the most important factors (Table 3 in **paper III**, see also **paper II**). Sapling richness is significantly and positively correlated with the species richness of the tree layer (Figure 3 in **paper III**). Competitive intensity from herbs and the dense moss layer proves to be a forest site type specific interaction – only in boreonemoral forests did the mosses facilitate the species richness of saplings, while the herb layer proved to be a dominant suppressing competitor. Finally, we also found that the species richness of saplings decreased in proportion to the amount of lying wood in a stand (Figure 3 in **paper III**).

3.5. Factors affecting field layer composition along the productivity gradient

GLM analyses for each site type described a relatively similar proportion of the total variation in field layer compositional dissimilarity: 26.7% (adjusted R^2) in the *Cladonia-Calluna* site type, 26.5% in the *Rhodococcum* site type, 13.7% in the *Myrtillus* site type and 27.1% in *Oxalis* site type. General factors such as management intensity and age were significant in all site types, but their relative importance was small in all site types, being highest in the *Cladonia-Calluna* site type. The direct effect of management intensity was only observed in the *Cladonia-Calluna* site type and in the most productive *Oxalis* site type. In both site types, the relationship was non-linear, indicating that the dissimilarity increase of field layer composition occurs at widely varying management intensities (Table 2 in **paper IV**).

The forest structural and compositional characteristics determining light availability and light spatio-temporal heterogeneity were the most important significant explanatory variables in the *Cladonia-Calluna* and *Oxalis* site types (Figure 3). The pooled effect of characteristics describing light availability described 11.5% of the compositional variation of the field layer in the *Cladonia-Calluna* site type, 12.7% in the *Oxalis* site type and 5.8% and 4.7% respectively in the *Rhodococcum* and *Myrtillus* site types. Of these characteristics, shrub cover was the most common influential factor, being important in all site types. The effect of general light availability described by canopy closure and other lower canopy layers on the compositional dissimilarity of the field layer increased along the productivity gradient. The effect of canopy closure was complemented by the second foliar layer (4–10 m) only in the

Myrtillus site type. The effect of stand density, described by various sub-indices of the basal area of trees, was also a significant factor determining field layer composition in all site types. In general, the contrast in the basal area of small (DBH 8–40cm) and large (DBH >40cm) diameter trees among stands predicts increasing dissimilarity in field layer composition (Figure 1 in **paper IV**).

A group of variables describing the potential heterogeneity of light conditions in a stand (variation of closure within the stand, the species richness of trees, tree saplings and shrubs, and the proportion of boreal deciduous trees) had the strongest effect on field layer dissimilarity in the *Oxalis* (7.9%) and *Cladonia-Calluna* (7.6%) site types, while a weaker but significant effect was observed in the *Rhodococcum* (0.8%) and *Myrtillus* (1.4%) site types. Of site heterogeneity variables, the contrast of the species richness of the shrub layer was the most common and the most influential predictor of field layer compositional dissimilarity in all site types. This dissimilarity-increasing effect was only evident at large contrast in shrub richness estimates between stands. The temporal heterogeneity in light conditions described by the contrast in the proportion of *Betula* and *Populus* trees caused higher compositional dissimilarity in the *Cladonia-Calluna* site type (Figure 1 in **paper IV**). Within stands, the variation in canopy closure was a significant variable that made the field layer community more homogeneous in the *Cladonia-Calluna* site type.

The complex of soil and ground layer conditions, which was not affected by management, proved to be a relatively significant predictor of field layer composition in all forest site types. It was particularly important in the *Rhodococcum* site type, explaining 19.2% of variance. Of ground layer characteristics, the moss cover and the thickness of the organic layer (A0) were the most common revealing factors. Combining the effect profiles of these two organic-rich structures above mineral soils, the greater contrast in this 'organic blanket' predicts larger field-layer dissimilarity, particularly in the ground layer dominated communities of the *Cladonia-Calluna* site type. In forests of intermediate productivity, the *Rhodococcum* and *Myrtillus* site types, the saturating effect of moss cover contrast is supported by the effect of A0 layer contrast (Figure 1 in **paper IV**). The contrast in the quantity of lying dead wood predicts a significant effect on field layer compositional dissimilarity in all site types, except for the *Rhodococcum* site type. In extreme productivity site types (the *Cladonia-Calluna* and *Oxalis* site type), the relationship was positive, indicating increasing compositional dissimilarity along the increasing contrast in dead wood amounts. In the intermediate the *Myrtillus* site type, the relationship was negatively linear, suggesting a more similar field layer composition in forests with a great contrast in amounts of dead wood (Figure 1 in **paper IV**). The effect of the contrast in the thickness of the humus layer (A1) was significant in the *Rhodococcum* and *Myrtillus* site types. The models predicted that compositional dissimilarity increases along the A1 thickness contrast in the *Myrtillus* site type. In the *Rhodococcum* site type, the response is hump-shaped (Figure 1 in **paper IV**).

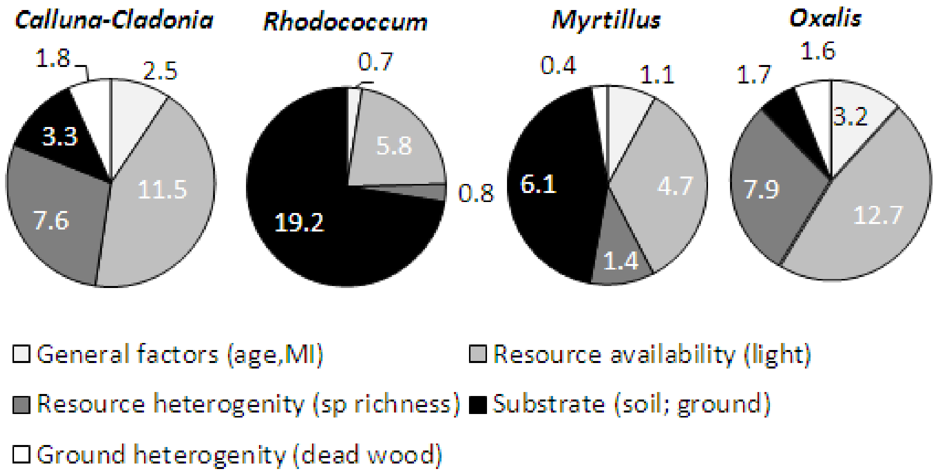


Figure 3. The relative importance of factor groups in the compositional variation of the field layer, based on GLM model partial determination coefficient (η^2) (GLM model in **paper IV**).

3.6. Optimised indicator set for determining forest near-naturalness

In **paper II** the optimised set of forest indicators was able to classify correctly 65% of pre-defined near-natural forest stands and 86% of stands with anthropogenic disturbances (Table 3 in **paper II**). In **paper I** (the model applied only to the *Rhodococcum* site type), where all successional stages were represented, the model classified correctly 75% and 96% respectively (Table 3 in **paper I**). In both studies, only a few studied features from the long list of potential and responding characteristics turned out to be statistically informative for the recognition of near-natural forests. In **paper II** the results of the analysis suggest that a minimal set of 'positive' indicators used to assess the forest's habitat quality in Estonia over a range of boreal forest site types consists of the amount (basal area) of standing dead wood, the presence of specially shaped trees and signs of woodpecker activity. The proportion of deciduous trees in a stand is informative only in the *Myrtillus* site type. Boreal forests seem to have a higher rate of anthropogenic perturbation if there is an abundance of forest herb *Melampyrum pratensis*, i.e. it is a 'negative' indicator of stand nature quality.

IV DISCUSSION

4.1. General factors determining the variability of boreal forests

In the analysis of boreal forests (**paper I, II**) we found that even in surveys with very restricted sampling to detect only management effects, many structural features and biodiversity indicators were affected by generic factors including stand age and geographic location. In addition, most of the forest characteristics have a specific correlation with site productivity described through forest site type. This supports the view that structural indicators should be interpreted specifically to site type conditions (**paper II**) (Lõhmus & Kraut 2010).

Successional young stands on the contemporary forest landscape are usually created by management operations and rarely by natural disturbances, and thus the effects of management and stand age lead to analogous response values of many forest characteristics (**paper I**, **II**) (Sturtevant et al. 1997; Ekbom et al. 2006). For example, 14 out of 16 stand characteristics that were positively correlated with stand age were negatively related to management intensity. The absence of young stands with low management intensity index values (**paper I**) suggests that Estonian dry boreal forest landscapes (dominated by the Rhodococcum site type) lack natural regeneration dynamics, e.g. patch dynamics caused by stand replacing disturbances. This is supported by the fact that we observed a very low proportion of deciduous pioneer tree species in the tree canopy (**paper I**), which was not explained by stand age and silvicultural operations during the last 20 years. This is probably the result of a long-term management history that has suppressed deciduous tree species due to their lower economic value and traditional salvage loggings after disturbances.

4.2. The direct effect of management on boreal forest structure and composition

The direct effect of forest management leads stands toward simplification through the reduction of structural complexity and tree species richness. The observed pattern was clear in our studies covering the whole successional range of *Rhodococcum* forest landscapes (**paper I**), and it was also consistent along the soil productivity gradient in the studied mature boreal forests on sandy soils (**paper II**). The same has been noted in productive broad-leaved forests in Estonia (Meier et al. 2005) and in several studies in other regions (Siitonen et al. 2000; Uotila et al. 2002; Köster et al. 2005). We also showed that the direct impact of management on natural forest regeneration and field layer composition cannot be observed in mature forests, but it is evident through the indirect effects of management on substrate and critical resources (**paper II**, **III**, **IV**).

4.3. The indirect effects of management on forest regeneration along the productivity gradient

It has been noted by Angelstam et al. (1995) that the enhancement of natural regeneration in stands may be the most cost-effective way to obtain a species-rich stand. The success of this approach depends on seed source availability, but also on management practices supporting the establishment and growth of saplings. Our study confirmed that tree regeneration is very site type specific (Kuuluvainen 1994) and is affected by a complex of factors, of which stand structure is most likely controlled by silvicultural operations such as thinning (**paper III**).

As expected, the higher rate of tree regeneration estimated as seedling frequency was found in productive habitats, and the abundance-corrected richness of saplings was also higher in productive and species-rich boreonemoral stands. Many tree seedlings in boreonemoral stands belong to various late-successional tree species, and they are ready to use the ''window of opportunity'' to support stand development into a multispecies late-successional forest (Lieffers et al. 1999; Lõhmus & Kraut 2010). In boreal forests, seed sources were limited to a few species preserved in the stand during forest management. In boreal forests, management in younger stands was probably also historically more intensive, and excluded most of the deciduous trees from stands (**paper I**). It was, however, surprising to note that oak was a species that could in near future enrich all types of forests, even dry boreal ones.

Earlier studies on specific forest types have shown that there are different facilitating or suppressing interactions between tree saplings and understory vegetation (Jäderlund et al. 1997; Hanssen 2003). We found that field and ground layer communities affect sapling abundance and diversity, as equal competitors and their effects on sapling richness were forest-type specific. In boreal forests, sapling species richness was positively correlated with herb layer cover and negatively with moss layer cover, and vice versa in boreonemoral forests (**paper III**). Many studies have indicated the importance of dead wood, microrelief and other specific ground structures for the establishment of tree seedlings (Kuuluvainen 1994). Our studies did not confirm this, as we showed that the majority of the regeneration occurs in undisturbed field layer vegetation. The only considerable alternative were lying dead tree trunks, which are a specific regeneration substrate in spruce-related stands (Svoboda et al. 2010).

Management to enhance natural tree regeneration should be based on knowledge about the maintenance of the biodiversity of forest herb layer communities, because tree saplings belong to the same ecological niche as herb layer plants. The optimal set of conditions can be achieved by including forest-type-specific cutting methods and through the generation of optimal small-area gaps of light, thereby avoiding the creation of intensive competition by light-demanding plants but nevertheless providing suitable microclimatic and microhabitat conditions for successful tree seedling germination and the growth of saplings.

4.4. The indirect effects of management on field layer composition along the productivity gradient

In **paper IV** we showed that direct management has only weak or insignificant effects on species richness and turnover (Aubin et al. 2007, see also **paper II**). One reason for the high resilience of the field layer to disturbances in intermediately productive forests (the *Rhodococcum* and *Myrtillus* site type) may be the abundant occurrence of dwarf shrub species from genus *Calluna*, *Empetrum* and *Vaccinium*, which are long-living and remarkably resistant to different types of small disturbances (Hart& Chen 2006; Hautala et al. 2005).

The indirect effects of forest management operate through changed canopy structure, which is associated with changes in the availability and spatio-temporal distribution of light. Our results confirmed the fact that the availability of light is an important driver of field layer composition (Bartemucci et al. 2006; Tinya et al. 2009). Along the productivity gradient, the importance of different factor-complexes changed non-linearly, particularly concerning light conditions, but also ground conditions.

The overall effect of light conditions did not depend only on the mono-factorial effect of the average level of light, but it was revealed through a complex effect of several hierarchically-ordered stand characteristics that determine the level and spatio-temporal structure of light availability at the level of the field layer (**paper III**). Our study supported the specific view that light availability for the field layer is instantaneously controlled by the shrub and understory tree layer (Messier et al. 1998), but this effect was only strong in forests at the extremes of the productivity gradient, and was less evident in intermediate productive types. In contrast, in the intermediate productivity *Myrtillus* forests, where the shrub layer was mostly absent, or in the *Rhodococcum* site type, where re-growth consisted mostly of spruce, only large changes in the forest's second layer and undergrowth had an effect on the composition of the field layer.

We would like to note that at each productivity level, field layer composition had different drivers because of different limiting factors. The effects of the spatio-temporal heterogeneity of light availability were related to somewhat different processes along the productivity gradient. In the *Cladonia-Calluna* site type forests, a small increase in canopy closure and the presence of spruce exert a homogenizing effect on the field layer, because moderate shade (Semchenko et al. 2012) and the occurrence of deciduous trees (*Betula pendula, Populus tremuloides)* increases resource heterogeneity, particularly temporal light variation, because light is available in early spring, when soil moisture is not limiting, and shade is only provided in the dry period. In the highly productive the *Oxalis* site type, the presence of a dense coniferous canopy creates permanently shaded conditions for the field layer, whereas even a minor increase in light availability results in a strong response in field layer composition.

Instead of the effects of light resources, in intermediate-productivity forests the ground layer and soil surface properties had a more prominent role in determining the composition of the field layer. In these site types, the thick soil organic horizon (A0) and abundant moss cover 'isolate' herbaceous plant roots from the mineral soil (particularly the *Rhodococcum* site type) at the seedling stage, and the presence or absence of an 'organic blanket' cause apparent differences in field layer composition (Zobel et al. 2000; Mallik 2003; Hautala et al. 2005). In some of the forest site types, the 'organic blanket' effect of thick organic layers was relaxed by the presence of lying dead wood (Kirchner et al. 2011).

4.5. Indicators of forest naturalness

Compared to the length of the list of structural and compositional characteristics that is widely used in assessments and monitoring systems (Larsson 2001; Andersson et al. 2003), the statistically-supported set of indicators of ecosystem naturalness appeared to be much shorter (**paper I, II**) (Liira et al. 2007). One reason for this may be the choice of the analytical method – the assessment of near-natural status takes a different analytical path than the estimation of the correlations between management and forest characteristics. In many studies, the latter has been selected as a sufficient step in the search for indicators. The evaluation of the predictive power of potential indicators should, however, be tested. Another reason for such shortening can be explained by the rarity of many widely accepted indicators of old-growth forests (e.g. very big trees), which can be treated as stochastic components in contemporary forest land, and therefore do not carry sufficient diagnostic power for contemporary forests (Lindenmayer et al. 2000; Büchs 2003).

Our studies of different site types have shown that the different structural characteristics of a forest should be combined to obtain an efficient set of indicators that would recognize the naturalness of a forest on contemporary forest landscapes (**paper I, II**). All of our suggested indicators (the amount of standing dead wood, the presence of specially-shaped trees, signs of woodpecker activity and the proportion of deciduous trees in the *Myrtillus* site type) for determining the naturalness of mature boreal forests are commonly used forest structural characteristics and biodiversity indicators, they are easy to recognize, have low observer bias, are robust to measure and have a low cost of estimation. It is clear that the extension of the list of independent indicators and the inclusion of the estimate of management intensity will only improve the evaluation.

V CONCLUSIONS

1) One must take into account the collinearity and confounding effects of different factors when analyzing the effect of management operations, because most of the structural elements do not respond linearly to the increase in site productivity and are simultaneously affected positively by stand age and negatively by management activities.
2) The effects of direct management on mature forests are mostly confounded by trees and shrubs. Forest structural and compositional characteristics that are significantly negatively affected by direct management operations are: large-diameter trees (DBH>40cm) and diameter classes, the proportion of spruce and deciduous trees, the amount of coarse woody debris of various stages, tree canopy closure and coverage of lower canopy layers.
3) Only a fraction of indicators that are negatively affected by management appear to be statistically significant for the assessment of the naturalness of mature boreal forests: the amount of standing dead wood, the proportion of deciduous trees in the *Myrtillus* site type, the presence of specially shaped trees and signs of woodpeckers.
4) Indirect forest management mainly affects tree regeneration and field layer composition through manipulated canopy structure and composition, which determines light availability and heterogeneity, but also the availability of dead wood, as the regeneration niche is important. Indirect effects have a greater influence in site types that suffer stress, either because of an excess or a deficit of light.
5) Sustainable forest management in Estonia should focus on the stand scale and on the maintenance of different structural features, particularly dead wood, old trees, and deciduous tree species. To enhance compositional diversity through field layer (natural regeneration), the management should be site type specific in diversifying stand structure. On the landscape scale, forest management and nature conservation should begin to emphasise the importance of natural regeneration with deciduous tree species after stand-replacing disturbances.

VI SUMMARY

During the last century, the biodiversity of boreal forests has been reported to be increasingly endangered. The main reasons for this in boreal forests are related to the intensification of silvicultural practices and the decline of old forests with continuous disturbance histories. One way to deal with this problem is to establish strict forest reserves together with forests with changed management practices, thereby making it possible to maintain and restore the naturalness of managed forests. To do this we need to understand what structural and compositional elements of the forest community are directly affected by silviculture, and whether these effects are uniform over an array of different forest site types.

In this thesis we sought answers to the following questions:

1) Which structural and compositional characteristics of boreal forests are directly sensitive to forest management practices in the boreal forest landscape?
2) How much do observed relationships and indicators vary along the forest productivity gradient characterised by forest site types?
3) What would be a statistically reliable diagnostic set of indicators for the evaluation of forest "naturalness" over the range of boreal forest site types?
4) How is the pattern of natural recruitment correlated with the multitude of factors in matured or old boreal and hemiboreal forests?
5) How resilient is the composition of the forest field layer community to the multitude of direct and indirect anthropogenic factors in boreal forest stands?

Our study area comprised the whole of Estonia, which is situated in the hemiboreal vegetation zone. Most of the papers addressed boreal forest site types on sandy mineral soils (*Cladonia-Calluna, Rhodococcum, Myrtillus, Oxalis* site type). The commonly applied management cycle of these forests typically involves clear-cutting at the age of about 80–100(120) years, natural regeneration (sometimes sowing or planting), and two or three thinnings at approximately 20-year intervals. In the first study we used landscape window based sampling, but we later developed it to a more random stratified sampling scheme with a minimum age limit of 75 years, covering the whole of Estonia. Data from a total of 632 sample points were used. The main statistical methods used for the statistical analyses were the General Linear Model and Generalized Linear Model analyses.

Our results suggest that as expected, site type (productivity) determines the amount and variability of most of the structural and compositional characteristics of a forest. The majority of structural elements do not, however, increase linearly on a productivity gradient. Therefore a site type specific approach is needed when interpreting structural indicators on a wider scale, because a significant part of the variability between forest stands is caused by differences in productivity and not by management intensity.

The effect of direct management in mature forests is mostly confounded by trees and shrubs. Forests' structural and compositional characteristics that are significantly negatively affected by direct management operations are: large-diameter trees (DBH>40cm) and diameter classes, the proportion of spruce and deciduous trees, the amount of coarse woody debris of various stages, tree canopy closure and the coverage of lower canopy layers. It is important to notice that only a fraction of forest characteristics affected negatively by management appear to be statistically significant for the assessment of the natural quality of mature boreal forests over a range of site types. In our case, when examining the three most common boreal forest site types (the *Calluna-Cladonia, Rhodococcum and Myrtillus* site type), the significant predictors were: the amount of standing dead wood, the proportion of deciduous wood in the *Myrtillus* site type trees, the presence of specially shaped trees and signs of woodpeckers.

Indirect forest management mainly affects tree regeneration and field layer composition through manipulated canopy structure and composition, which determines light availability and heterogeneity, but also the availability of dead wood, as the regeneration niche is important. The reaction of forest field layer composition to the indirect effects of forest management disturbances varies along the productivity gradient. Light conditions represent the dominant factor complex explaining the compositional variation of the field layer vegetation in habitat types with low and high productivity, while in intermediate productivity conditions, natural heterogeneity, such as upper soil layers and ground layer conditions, are the most important determinants.

Sustainable forest management in Estonian boreal forests should focus on the stand scale and on the maintenance of different structural features, particularly dead wood, old trees and deciduous tree species, and to enhance compositional diversity through field layer (natural regeneration), management should be site type specific in diversifying stand structure. At the landscape scale, forest management and nature conservation should begin to emphasize the importance of natural regeneration with deciduous tree species after stand-replacing disturbances.

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KOKKUVÕTE

Majandamise otsene ja kaudne mõju boreaalsete metsade struktuurile ja alustaimestikule

Viimase sajandi jooksul on hakatud boreaalsete metsade elurikkuse ohustatuse pärast järjest rohkem muret tundma. Peamised elurikkuse ohustatuse põhjusteks on vanade loodusmetsade vähenemine ja metsamajanduse intensiivistumine. Ühe lahendusena nähakse ökoloogiliste võrgustike loomist, kus majandamisest kõrvale jäetavate looduslähedaste metsade vahel paiknevad metsad, kus majandamistegevus säilitab või vajadusel taastab looduslikele metsadele iseloomulikke elemente, nagu näiteks suured vanad puud ja surnud puit. Selleks, et määratleda praktikas kõige looduslähedasemas seisundis olevaid metsasid või hinnata majandatavate metsade looduslähedust, kasutatakse indikaatoritena metsa struktuuri, liigilist koosseisu ja funktsionaalsust kirjeldavaid indikaatoreid. Indikaatorite väärtuste alusel järelduste tegemiseks peame mõistma, kuidas erinevad struktuursed ja koosseisulised indikaatorid on metsamajandamisest mõjutatud ja kas indikaatorite reaktsioon on sarnane ka erinevate kasvukohatüüpide (produktiivsustasemete) lõikes.

Käesolevate teeside eesmärgiks oli uurida, millised boreaalsete kasvukohatüüpide struktuurilised ja koosseisulised tunnused on metsamajandusest kõige enam mõjutatud ning kuidas see muutub erinevates kasvukohatüüpides. Koosseisulistest karakteristikutest uurisime detailsemalt puude järelkasvu ja metsa puhma- ja rohurinde koosseisu tundlikkust metsamajandamisest tingitud muutustele.

Teeside aluseks olevad uuringud keskendusid liivastel muldadel kasvavatele okaspuumetsadele sambliku, kanarbiku, pohla, mustika ja jänesekapsa kasvukohatüüpides. Järelkasvu uuringus olid kaasatud sinilille ja naadi kasvukohatüübi metsad. Esimeses uuringus keskendusime kitsamalt pohla kasvukohatüübi metsadele ja see põhines maastikulisel valimil. Välitööd toimusid kuuel 25 ruutkilomeetri suurusel maastikul. Igal alal kirjeldati 25–30 juhuslikku, üksteisest vähemalt 100 m kaugusel asuvat punkti pohla kasvukohatüübi metsades. Kirjeldatud puistud esindasid nii suktsessioonilist kui majandusintensiivsuse gradienti. Järgnevates uuringutes hõlmasime juba suuremat hulka kasvukohatüüpe (produktiivsusgradient) ja keskendusime ainult küpsetele ja vanadele metsadele (puistu vanus vähemalt 75 aastat). Sellega püüdsime minimeerida suktsessioonilisest vanusest tulenevaid mõjusid. Ruumilise autokorrelatsiooni vältimiseks loobusime maastikutasandil eelvalikust ja paigutasime proovipunktide paarid juhuslikult kogu kasvukohatüübi levikualale üle Eesti. Proovipunktide paar esindas võimalikult laia majandusintensiivsuse gradienti konkreetses piirkonnas. Kõikides proovipunktides kirjeldasime üle viiekümne metsa struktuuri ja koosseisu kirjeldavat näitajat. Kokku kirjeldasime erinevate uuringute raames metsa struktuuri ja alustaimestikku 632 punktis. Andmeid analüüsiti peamiselt üldise lineaarse mudeli ja üldistatud lineaarsete mudelite meetodiga ning alustaimestiku puhul kasutati ka ordinatsioonianalüüsi meetodeid.

Meie esimene uuring, mis keskendus kitsamalt pohla kasvukohatüübi metsadele näitas, et metsade vanus ja majandamise intensiivsus olid tugevalt negatiivselt korreleeritud. Kuigi järgmistes uuringutes kasutasime vanuse alampiiri (75 aastat) ja vanuse tähtsus struktuursete ja koosseisuliste indikaatorite kirjeldamisel vähenes, jäi see statistiliselt siiski oluliseks. See tulemus rõhutas veelgi vajadust pöörata majandamise mõjude uurimisel tähelepanu vanuse ja majandamise mõju omavahelisele seotusele. Nagu eeldasime, mõjutas kasvukohatüüp oluliselt erinevate struktuursete tunnuste väärtusi ja varieerumise ulatust. Oluline on siinkohal märkida, et erinevad struktuursed tunnused käitusid produktiivsuse suurenemisel erinevalt ja ei suurenenud alati lineaarselt. See viitab vajadusele arvestada kasvukohatüübipõhiste lävenditega, kui erinevaid struktuurseid elemente kasutatakse metsade loodusläheduse indikaatoritena.

Metsamajandamise otsesed mõjud olid enamasti seotud puu- ja põõsarindega. Metsakoosluse struktuurilised ja koosseisulised elemendid, mis olid statistiliselt usaldusväärselt majandamisest negatiivselt mõjutatud, olid järgmised: suurediameetriliste puude ja diameetriklasside arv, kuuse ja lehtpuude osakaal puistus, erinevas laguastmes lamapuidu kogus ning puistu erinevate rinnete liituvus. Huvitav oli, et ainult väike osa majandamisest oluliselt mõjutatud tunnustest olid statistiliselt olulised metsade loodusläheduse prognoosimise mudelis. Sambliku, kanarbiku, pohla ja mustika kasvukohatüüpide looduslähedasi metsi tundis kõige paremini ära tunnustekompleks, kuhu kuulusid: seisva surnud puidu kogus, lehtpuude osakaal mustika kasvukohatüübis, erilise võrakujuga puude hulk ja rähnide tegevusjälgede esinemine ning negatiivse tunnusena (positiivselt seotud häiringutega) jäi mudelisse *Melampyrum pratensise* ohtruse suurenemine, mis oli seega iseloomulik inimtegevusest rohkem mõjutatud metsadele. Nimetatud tunnustekompleks ennustas õigesti 65% looduslähedastest metsadest ja 86% inimtegevusest rohkem mõjutatud metsadest.

Meie uuritavates metsades mõjutas majandustegevus metsa alustaimestikku vaid kaudselt, eelkõige puistu vertikaalse struktuuri ja liigilise koosseisu kaudu, mis määrab alustaimestikuni jõudva valguse hulga ja omadused ning selle varieerumise ajas ja ruumis. Lisaks avaldub majandamise mõju lamapuidu koguse kaudu, mis väljendub konkurentsivaba substraadi olemasolus nii puuliikide kui teiste taimede jaoks. Alustaimestiku koosseisu reaktsioon kaudsetele majandusmõjudele oli erinevates kasvukohatüüpides väga varieeruv. Valgustingimusi kujundavate faktorite kompleks oli domineeriv alustaimestiku koosseisu muutuste selgitamisel kõige madalama produktiivsusega sambliku ja kanarbiku kasvukohatüübis ning kõige viljakamas jänesekapsa kasvukohatüübis. Mõlemas kasvukohatüübis on vastavalt kas valgustingimuste üleküllus või nappus ja sellest tulenevalt on alustaimestik pidevas valgusstressi seisundis ning ka väike muutus valgustingimustes toob endaga kaasa alustaimestiku koosseisu muutumise. Samas suhteliselt optimaalsete valgustingimustega keskmise produktiivsusega pohla ja mustika kasvukohatüübis on kõige olulisemateks taimestiku koosseisu määravateks teguriteks kõdu- ja huumushorisondi paksus.

Loodussõbralik metsamajandus Eesti liivastel muldadel levinud okaspuumetsades peab puistu tasandil pöörama rohkem tähelepanu surnud puidu, vanade puude ja lehtpuude säilitamisele. Alustaimestiku mitmekesisuse säilitamiseks peab erinevates kasvukohatüüpides kasutama erinevaid majandamisvõtteid, et suurendada puistute ruumilist varieeruvust. Maastiku tasandil peab senisest enam väärtustama looduslike häiringute järgsete suktsessioonifaaside olemasolu.

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