Eesti Maaülikool
Estonian University of Life Sciences

MONITORING AND EVALUATION OF FOREST ECOSYSTEM RESTORATION

METSAÖKOSÜSTEEMI TAASTAMISE
SEIRE JA ANALÜÜS

DIANA LAARMANN

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

Väitekiri
filosoofiadoktori kraadi taotlemiseks metsanduse erialal

Tartu 2014

Eesti Maaülikooli doktoritööd

Doctoral Thesis of the Estonian University of Life Sciences

Eesti Maaülikool
Estonian University of Life Sciences

MONITORING AND EVALUATION OF FOREST ECOSYSTEM RESTORATION

METSAÖKOSÜSTEEMI TAASTAMISE
SEIRE JA ANALÜÜS

DIANA LAARMANN

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

Väitekiri
filosoofiadoktori kraadi taotlemiseks metsanduse erialal

Tartu 2014

Institute of Forestry and Rural Engineering
Estonian University of Life Sciences

According to verdict No 196 of July 14, 2014, the Doctoral Committee of the Agricultural and Natural Sciences of the Estonian University of Life Sciences has accepted the thesis for the defence of the degree of Doctor of Philosophy in Forestry.

Opponent: **Prof. Ioan Vasile Abrudan, PhD**
Transilvania University of Brasov

Supervisors: **Henn Korjus, PhD**
Institute of Forestry and Rural Engineering
Estonian University of Life Sciences

John A. Stanturf, PhD
Center for Forest Disturbance Science
Southern Research Station, USDA Forest Service

Defence of the thesis:
Estonian University of Life Sciences, room 2A1, Kreutzwaldi 5, Tartu on August 29, 2014, at 10:00.

The English language was edited by John A. Stanturf and the Estonian by Moonika Kuusk.

Publication of this thesis is granted by the Estonian University of Life Sciences and the Doctoral School of Earth Sciences and Ecology created under the auspices of European Social Fund.

European Union
European Social Fund

Investing in your future

ISSN 2382-7076
ISBN 978-9949-536-42-9 (trükis)
ISBN 978-9949-536-43-6 (pdf)

CONTENTS

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 **Laarmann, D**., Korjus, H., Sims, A., Stanturf, J.A., Kiviste, A., Köster, K. 2009. Analysis of forest naturalness and tree mortality patterns in Estonia. Forest Ecology and Management 258S: S187-S195.

II **Laarmann, D.**, Korjus, H., Sims, A., Kangur, A., Stanturf, J.A. 2013. Initial effects of restoring natural forest structures in Estonia. Forest Ecology and Management 304: 303-311.

III **Laarmann, D.**, Korjus, H., Sims, A., Kangur, A., Kiviste, A., Stanturf, J.A. 2014. Evaluation of afforestation development and natural colonization on a reclaimed mine site. Restoration Ecology [Submitted].

IV Sims, A., Kiviste, A., Hordo, M., **Laarmann, D**., Gadow, K.v. 2009. Estimating tree survival: a study based on the Estonian Forest Research Plots Network. Annales Botanici Fennici 46 (4): 336-352.

The contributions from the authors to the papers are as follows:

	I	II	III	IV
Original idea	**DL**, HK	**DL**, HK	**DL**, HK, AK, JS	AK, AS
Study design	**DL**, HK, AK	**DL**, HK	**All**	**All**
Data collection	**DL**	**DL**	**DL**	**All**
Data analysis	**DL**, AS, HK, AK	**DL**, HK, AS	**DL**, HK, AS	AK, AS
Preparation of manuscript	**All**	**All**	**All**	**All**

AK – Andres Kiviste; AS – Allan Sims; **DL – Diana Laarmann**; HK – Henn Korjus; JS – John A. Stanturf; All - all authors of the paper.

ABBREVIATIONS

C	Control plot
CM	Cause of mortality
CMDI	Diversity index of mortality causes
CWD	Coarse woody debris
DBH	Diameter at breast height
DM_i	Deadwood mingling index
DS	Relative diameter
DW	Deadwood input
ENFRP	The Estonian Network of Forest Research Plots
FNR	Forest naturalness restoration plots
G	Gap cutting
GAM	Generalized Additive Model
GB	Gap cutting and overburning
GDW	Gap cutting with deadwood input
ISA	Indicator Species Analysis
MRPP	Multiple Response Permutation Procedure
NMS	Non-metric Multidimensional Scaling
PCA	Principal Component Analysis
PMR	Post-mining reclamation plots
PSP	Permanent sample plot
RDV5	The average recent deadwood volume for the last 5-year period

1. INTRODUCTION

Modern forestry is shifting from timber production towards the service of a broader set of resource values and aims to find the balance between conservation and management objectives of a forest ecosystem (Korjus, 2009). Silvicultural systems for timber production have caused fundamental changes in ecosystem structure and function associated with anthropogenic alterations of natural disturbance regimes (Esseen *et al.*, 1992; Kuuluvainen, 2009). Increasingly, forest management is based on understanding of processes of natural disturbances, their effects for stand and landscape composition and structure, considering that this enables managers to reduce the negative impacts of timber harvest on biodiversity and thereafter maintain ecological functions (Attiwill, 1994).

Ecological restoration as a research area has developed rapidly over the past few decades (Harris *et al.*, 2006; Hobbs *et al.*, 2011). The objective of ecological restoration is to re-create a self-supporting ecosystem which existed previously and is resilient to contingent damage (Urbanska *et al.*, 1997) and to maintain the system in a desirable state or moving away from an undesirable state. Forest restoration is widely practiced in North America (Stanturf *et al.*, 2009; Bolton and D'Amato, 2011; Humber and Hermanutz, 2011; White *et al.*, 2011), Australia (Grant *et al.,* 2007), and in Europe, particularly in Finland (Kuuluvainen *et al.*, 2005), the United Kingdom (Hancock *et al.*, 2009), and Sweden (Olsson and Jonsson, 2010). Forest restoration not only aims for stand re-establishment, but to initiate natural processes and foster natural structures and species composition (Stanturf and Madsen, 2002; Vanha-Majamaa *et al.*, 2007; Stanturf *et al.*, 2014).

Restoration is activity which can improve conservation efforts in protected areas in order to enhance quality and quantity, to improve connectivity between fragmented areas and create buffer zones between protected and managed forest areas (Kuuluvainen *et al.*, 2002). For example, the need for restoration in protected areas in Sweden is 3-11% of protected areas (Angelstam and Andersson, 2001). In 2003 in Finland, the need was 38,600 ha (3.7% of protected forests) (Similä and Junninen, 2012). Key processes in practical restoration include identifying and dealing with processes leading to degradation, determining realistic goals and measures of success, developing methods for implementing the goals and integrating them into planning and management strategies, and monitoring the restoration and assessing its success (Hobbs and Norton, 1996).

Traditionally a natural/historical reference system has been used for setting restoration goals in ecological restoration despite the difficulty of assessing how natural a forest would be without anthropogenic disturbances (Stanturf *et al.*, 2004). Forest naturalness (Korjus, 2009; Winter, 2012; McRoberts *et al.*, 2012) is widely used to describe the anthropogenic influence level and management status of a forest ecosystem. Natural forests are dynamic and versatile ecosystems with their characteristic components, processes, and functions relatively little studied. Passive nature conservation of disturbed forests does not ensure sustainable biodiversity protection as natural rehabilitation processes may be slow, fragmented or still indirectly heavily influenced by humans. Active nature restoration activities may have unexpected results. The results of restoration effort can be evaluated by predicted ecosystem development trajectories or classified as historic, hybrid and novel ecosystems (Hobbs *et al.*, 2009).

Assessment of ecosystem structural properties and characteristics is needed to understand restoration success and supported processes (Bradshaw, 1987). For assessing restoration success, it is important to focus on the current state and dynamics of the degraded ecosystem besides to the reference ecosystem (Cortina *et al.*, 2006). Restoration is an important tool for enhancing conservation values in protected and productive landscapes, which is a key component for the development of sustainable land-management systems (Hobbs and Norton, 1996). Knowledge of forest disturbance and successional processes is relevant for developing ecologically sustainable forest management strategies (Kuuluvainen, 2002) including restoration of ecosystem functions. Emulating natural disturbance regimes that result in more diverse forest structure and composition provides the main conceptual framework for alternative management approaches varying from continuous cover forestry to biodiversity restoration (Stanturf, 2005; Pommerening and Murphy, 2004; Suffling and Perera, 2004; Kangur *et al.*, 2005; Toivanen *et al.*, 2014).

Deadwood formation is an important indicator of forest naturalness (Rouvinen *et al.*, 2002; Debeljak, 2006) and also an indicator of restoration success. Disturbance events cause mortality and result in continuous input of deadwood (coarse woody debris) in a forest stand. Deadwood has immediate and complex effects on the microsite environment experienced by surviving or newly germinating seedlings. Blocking the sun can reduce drought stress and increase seedling survival on sandy sites while reducing growth by shading on other sites where water is not limiting. Deadwood may also physically hinder the ability of herbivores to eat seedlings. During decay process deadwood can become a seedbed for germination that may differ from surrounding soils in temperature, water holding capacity, and penetrability for roots. Coarse woody debris dynamics (decay class, position in the stand) depend on dead tree species and cause of mortality (Taylor and MacLean, 2007; Köster *et al.*, 2009).

Tree competition, insect and herbivore activity and delayed disturbance effects (e.g., erosion of mineral soil, ageing or decomposition of biological legacy components) and other processes usually direct tree mortality and regeneration in a stand. Modelling tree mortality or survival is essential for individual tree based forest simulation models. These models provide support and tools for planning of restoration activities.

Restoration of forest ecosystems has been applied in Estonia on abandoned oil-shale mining areas since 1960 (Kaar, 2010) and also on nature conservation areas as experiments (Korjus, 2005; **II**). More suitable tree species for post-mining site reclamation have been studied by Kuznetsova (2011), afforestation of former agricultural land by Jõgiste *et al.* (2005), Uri *et al.* (2009), Tullus (2010), and Aosaar (2012), and characteristics of understorey vegetation by Tullus (2013).

The current thesis synthesizes different aspects and components of forest restoration. Assessment of forest naturalness as an aim for classical restoration has been carried out in Estonia. Amount and spatial distribution of deadwood as one of indicator of forest naturalness has been assessed (**I**). Factors influencing tree mortality (**I**) and tree survival probability (**IV**) have been studied. Effects of rehabilitation on biodiversity and stand structure (**II**) and success of reclamation (**III**) are important results for planning future restoration activities and forest management.

2. REVIEW OF LITERATURE

2.1. Concept of ecological restoration for forest ecosystems

"Ecological restoration is the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed" (SER, 2004). Forest restoration is done in the context of ecological and social conditions and restoration is seen as symmetric with degradation: an undisturbed natural forest can be degraded and a degraded forest can be restored to natural or historical conditions (Stanturf, 2005). Restoration actions attempt to guide the trajectory toward desired targets more quickly than would occur spontaneously (Fischer and Fischer, 2006).

Restoration will be used in a broad sense, incorporating reclamation, rehabilitation, ecological restoration and forest landscape restoration (van Diggelen *et al.*, 2001; Stanturf *et al.*, 2014). A definition of targets depends on the level ambition and desired endpoint. Ecological restoration has the ambitious goal of restoring to a previous situation or historic target (Harris and van Diggelen, 2006). This includes re-establishment of former functions and characteristics of species, communities and structure (Grootjans *et al.*, 2001).

Rehabilitation consists of the reintroduction of certain ecosystem functions (Wali, 1992) including aspects of naturalness by using techniques that promote natural stand structure, species composition or disturbance regimes (Bradshaw, 2002; Stanturf, 2005) and focuses on the dynamic processes that drive structural and compositional patterns (Stanturf *et al.*, 2014). This can be used to complement conservation efforts on protected areas to enhance habitat quality and quantity, to improve connectivity between fragmented areas and to create buffer zones between reserved and managed forest areas (Kuuluvainen *et al.*, 2002). Rehabilitation would make the landscape more natural, but it would not necessarily result in a significant increase of biodiversity (van Diggelen *et al.*, 2001). Also restored ecosystem may have different structure and composition than the historical ecosystem (Stanturf *et al.*, 2014).

Reclamation consists of attempts to restore productive functions and avoid soil erosion in highly disturbed sites (Stanturf *et al.*, 2014). This starts at “point zero” (Hüttl and Weber, 2001) “making the land fit for cultivation” (Bradshaw, 1997) and it’s commonly used in the context of mined land and restoring degraded farmland. Reclamation refers to restoration of forest conditions on highly disturbed sites and may require stabilization, fertilization and other measures in addition to afforestation or natural invasion. Primarily focuses on revegetation without regard for nativeness of species or structural diversity. With continuing intervention over time, the forest condition may move closer to a natural endpoint (Stanturf, 2005). The endpoint may be a less diverse natural forest than existed pre-mining or a mixed species plantation of native or exotic species.

Restoration ecology, a subdiscipline of ecology, is an integrated science, bound up with other disciplines for example, conservation biology, disturbance ecology, forestry, invasion biology, landscape ecology *etc.* (Walker *et al.*, 2006; van Andel and Grootjans, 2006). Young (2000) has said that “the long-term future of conservation biology is restoration ecology”. Restoration ecology is focused on biodiversity at the species and community levels, ecosystem health and integrity, resilience and sociological issues as well (Walker *et al.*, 2006).

When considering ways to restore a habitat, landscape or ecosystem, we must address question about why, where, how, what and when (Harris and van Diggelen, 2006). Guidelines have been created for helping decision makers to answer these questions (Hobbs and Norton, 1996; Clewell and Aronson, 2007; Jõgiste *et al.*, 2008). Conceptual planning identifies a number of key processes: (1) the need for restoration, (2) realistic goals, (3) easily observable measures of success, (4) practical techniques for implementing restoration goals, (5) monitor key system variables.

A fundamental starting point for any restoration scheme is to define both the starting conditions and the target ecosystem or endpoint (Hobbs and Norton, 1996; Clewell and Aronson, 2007). Usually the target or endpoint refers to a natural and/or historic ecosystem. Restoration success is evaluated by comparing measurement trajectories from starting point and any other point of time with target values.

2.2. Naturalness of forest ecosystems

Natural and/or historic reference systems can be applied in forest ecosystem restoration by assessing the naturalness of an ecosystem.

Forest naturalness is a complex issue converging forest dynamics, disturbances at different scales, adaptation to changing environment, and human influence (Harris and van Diggelen, 2006). Even without anthropogenic disturbances it is difficult to specify what constitutes a natural forest in a given place and time (Stanturf *et al.*, 2004). Naturalness is a continuous variable, where forest stands span a gradient from mainly artificial forest through semi-natural to naturally dynamic forest (Roberge *et al.*, 2008).

Ecological understanding of natural systems has progressed from the Clementsian notion of "steady-state" or "climax" ecosystems, essentially without disturbance, to today's recognition that disturbances structure ecosystems (Clements, 1936). The natural disturbance regime may be characterized by gap-dynamics where mortality of large trees allows for replacement by younger trees (Frelich, 2002), defined by Borman and Likens (1994) as a "shifting mosaic steady state." Alternatively other ecosystems are characterized by relatively frequent stand-replacement disturbances (Oliver and O'Hara, 2005). In many areas it may be unrealistic to define natural vegetation for a site and often several communities could be "natural" vegetation for any given site at any given time. The similarity of a current ecosystem state to its natural state defines its naturalness (Winter, 2012) also naturalness can be assessed by quantifying the level of human influence to a forest ecosystem (Uotila *et al.*, 2002). Nevertheless, it is often possible to separate between managed and unmanaged forests for only a limited interval following a disturbance or management intervention. As managers attempt to emulate natural disturbances in their interventions by adopting principles of "ecological forestry" (Franklin *et al.*, 2007) "continuous cover forestry" (Gadow *et al.*, 2002), "nature-based silviculture" (Larsen, 1995) or "close-to nature silviculture" (Duncker *et al.*, 2012), definitions of naturalness as being the opposite of anthropogenic disturbances become even more problematic.

Despite the difficulty of defining naturalness, it is an accepted concept in European forest management and nature conservation and an ability to assess forest naturalness is important for practical forest management and conservation decisions (Šaudyte *et al.*, 2005; McRoberts *et al.*, 2012).

Forest naturalness is related to forest structural diversity and also occurrence of indicator species in the forest (Winter, 2012). Naturalness indicators are deadwood volume, deadwood decay classes, sizes of the largest trees, native tree species composition, canopy closure, specific epiphytic lichens, mosses, and herb layer species as well as other characteristics (Korjus, 2002; Bartha *et al.*, 2006; Liira and Sepp, 2009).

Tree mortality as a natural process generates a constant flow of deadwood in forest ecosystems (Jonsson *et al.*, 2005), and becomes a major structural ecosystem component (Franklin *et al.*, 2002). Deadwood is important for maintenance of biodiversity especially in regenerating stands (Franklin *et al.*, 1987).

2.3. Concept of novel ecosystem

The novel ecosystem concept was raised by Milton (2003) who characterized landscape changes by anthropogenic drivers that resulted in new species composition that was atypical for natural biome as an emerging ecosystem. Hobbs *et al.* (2006, 2009) characterized as novel ecosystems those resulting from introduction of invasive species, enrichment of soil fertility, land degradation and environmental change, or combinations of these. It is important that the new ecosystem is independent from continuing human intervention and that it is impossible to return to the historical condition because of crossed thresholds (Figure 2.1) (Hallett *et al.*, 2013). Thresholds are the result of a sudden discontinuous change in ecosystem functions and status (Harris *et al.*, 2013). Hybrid and novel ecosystems differ from natural or historical ecosystems in their abiotic and biotic characteristics. Abiotic changes often facilitate new species colonization or species loss (Mascaro *et al.*, 2013). A threshold can keep a new ecosystem in a novel state despite attempts to drive its abiotic and biotic characteristics back to the historical ecosystem. Hybrid ecosystems can be returned to natural ecosystems by restoration treatments.

The underlying concept (Stanturf *et al.*, 2014) determines the restoration goal and this determines the way to get to this goal (Harms *et al.*, 1993). Katz (2000) stated that if a restored system has been created and managed by anthropogenic technology, then it is no longer a natural system. This follows from the definition that forests without any human intervention are natural and seems to answer the question whether humans part of nature or outside of nature in the negative. This means that most of the world's forests are not natural, in the sense that they have been influenced by human activities. Several in the literature talk about human-dominated forests (Noble and Dirzo, 1997; Vitousek *et al.*, 1997; Messerli *et al.*, 2000; Nagendra, 2007) relatedly, the concept of "novel ecosystems" is based on knowing that past and present ecosystems differ in composition and/or function, as a result of climate and land use change (Lindenmayer *et al.*, 2008; Hobbs *et al.*, 2009). Therefore, it would appear that semi-natural forests would be the only feasible goal of restoration.

Historical ecosystems have been used as reference ecosystems, but this is a moving target and what we consider as historical ecosystems today were new ecosystem long ago (Mascaro *et al.*, 2013). Novel ecosystems of today may be a reference ecosystem in the future and may be preferable to any historical ecosystem, for example, emergent assemblages are better able to respond to ongoing environmental change (Hallett *et al.*, 2013).

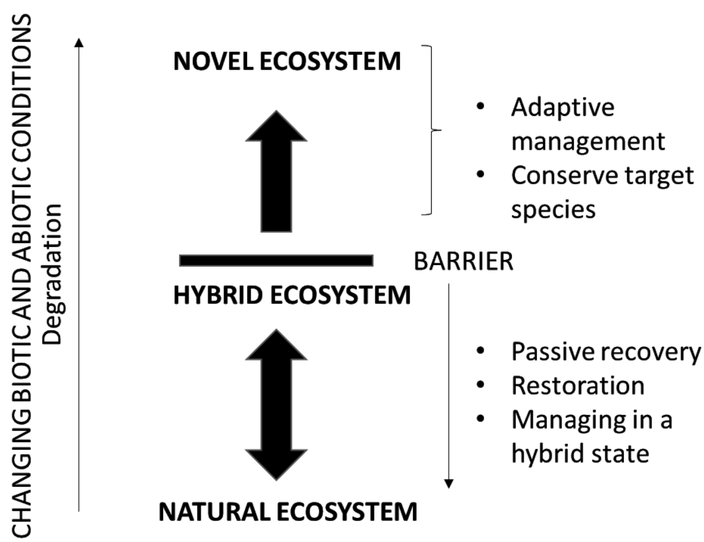


Figure 2.1. Three different types of ecosystems under changing abiotic and biotic alterations. From Hobbs *et al.*, 2009 and Hulvey *et al.*, 2013. Natural ecosystems might be natural or historical. Hybrid ecosystems differ from natural/historical with the changed abiotic condition and biotic composition; moving from hybrid to natural is possible due to restoration. Novel ecosystems are changed irreversibly from natural ecosystems and have passed a threshold (barrier) so that it is impossible to return back to the natural state. Shown in this figure are some management options.

2.4. Research on forest restoration activities

Boreal and temperate forest ecosystems have been the main focus of restoration research (Burton and Macdonald, 2011), including Europe (Lõhmus, 2005; Halme *et al.*, 2013). Forest restoration is connected to many other forest research issues, e.g. improvement of forest health, reduction of fire risk, soil erosion control, restoration of culturally important forest types, and multiple uses of forests. Most of the restoration experiments and research in Nordic countries have been carried out in Finland. Many protected areas have been used heavily, such that they lack elements and processes that are common for natural forest ecosystems (Lõhmus *et al.*, 2005). For planning of restoration activity it is important to know the (natural) history, species composition, and disturbance regime of the area.

Controlled burning is an activity mostly associated with forest ecosystem restoration in Scandinavia and the Baltics where fire is not an acceptable forest management practice. Fire regime has been altered heavily by fire prevention and suppression in forest ecosystems; for example in Finland, the average fire interval in pine forests in the 17h century was 50 years (Wallenius *et al.,* 2007), but nowadays forest fires rare. Nevertheless, controlled burning and/or partial harvesting, which are more acceptable restoration activity in Finland, increased the number of bark beetles in spruce forest, especially when both had been combined (Toivanen *et al.*, 2009), although after seven years no effect on ground beetles was found (Toivanen *et al.*, 2014). Burning affects polypores negatively in the short-term in pine forests, but after 13 years species richness tended to be higher (Penttilä *et al.*, 2013). Greater amounts of dead wood increased the average number of common polypores in pine and spruce forests, but not rare or threatened species (Pasanen *et al.*, 2014). Controlled burning combined with dead wood creation (a unique type of dead wood) have strong effects on diversity of wood-inhabiting fungi (Olsson and Jonsson, 2010; Berglund *et al.*, 2011). Number of birch seedlings increased in spruce forest after a burning treatment, whereas spruce seedlings increased after partial harvesting (Vanha-Majamaa *et al.*, 2007). Seedling and sapling densities increased in harvest gaps (Bolton and D'Amato, 2011). Pine seedling establishment was almost 10 times higher on burnt ground (Hancock *et al.*, 2009). After fire or harvesting, early successional species appeared in the understorey (Vanha-Majamaa *et al.*, 2007). Such species represent ruderal species and decline with time;

ruderality was significant only in the first year (Pywell *et al.*, 2003), but at the beginning they suppress the abundance of typical forest species by competition.

Deadwood input as a restoration activity usually serves restoration goals. Deadwood monitoring (evaluation and addition) after restoration is less investigated in forest ecosystems (Burton and Mcdonald, 2011). After deadwood input, tree mortality caused by bark beetles at forest edges surrounding a restoration plot was relatively low (Eriksson *et al.*, 2006). Level of deadwood volume had no effect on beetle species richness (Vanha-Majamaa *et al.*, 2007). Created logs do not fully mimic natural logs as habitat for polypores (Komonen *et al.*, 2014). Due to restoration treatments beetle species can find many habitats. Decaying wood is a variable substrate for hundreds of different species of beetles (Esseen *et al.*, 1992; Siitonen, 2001). The main factors determining species composition on a dead tree are tree species, diameter, stage of decay (Jonsell *et al.*, 1998), and quality of the trunk- snag, log or stump (Berg *et al.*, 1994; Nilsson, 1997). The amount (Martikainen *et al.*, 2000) and diversity (Similä *et al.*, 2003) of deadwood are crucial for many species; different parts of dead trees also offer different kinds of habitat. Different insect species favour different kinds of fruiting polypore bodies on decaying trees, determined by tree size, height above the ground, moisture content, and stage of decomposition (Komonen *et al.*, 2000). A high number of species of beetles are attracted to and depend on burned wood (Niklasson and Drakenberg, 2001; Niemelä *et al.*, 2007) and numerous fire-specialists are included in national red lists of rare and endangered species (Muona and Rutanen, 1994; Wikars, 2002).

Gap treatment as a small-scale disturbance plays an important role for determining species composition and stand structure (Kuuluvainen, 1994; Frelich, 2002). Development of some old conifer forest is mainly driven by gap formation by a continuous series of small-scale mortality events (Caron *et al.*, 2009). Small gaps caused by the death of one or several trees increase local scale variation in microtopography, which affect understory and recruitment (Pickett and White, 1985). Gap size and canopy openness are primary factors for density of seedlings (Zhu *et al.*, 2003) and understory vegetation growth (McGuire *et al.*, 2001). In a study in Finland, Kuuluvainen (1994) concluded that gaps with diameter from 15 to 20 meters have good seedling establishment in the middle of gap, but not near the edges.

The immediate effect of gap cutting in a boreal spruce forest was that bryophytes and vascular plant species richness and cover decreased 1-year after treatment (Jalonen and Vanha-Majamaa, 2001). The amount of beetles was highest one year after treatment (Koivula and Niemelä, 2003) and species richness was higher in larger gaps with diameter 56 m (Klimaszewski *et al.*, 2008). Opposite results appeared in deciduous forest, where herbs species richness and abundance increased significantly (Falk *et al.*, 2008). Creating gaps with added deadwood is more common practice in management, because managed forest have a low amount of different quality of deadwood (Kuuluvainen, 2002b) and combining the two activities will create more varied habitat for more species. Gap expansion (Kneeshaw and Bergeron, 1998) is probable from natural disturbance following artificial gap creation (Köster *et al.*, 2009).

Many ecological studies cover the early stages of stand development, e.g. on oil-shale quarry rehabilitation in Estonia (Kuznetsova and Mandre, 2006; Ostonen *et al.*, 2006; Kuznetsova *et al.*, 2010, 2011), but there is lack of studies covering longer time-periods. Hüttl and Bradshaw (2001) pointed out that long-term research is needed to better understand the processes directing successional development of post-mine sites. Soil factors are under-represented in restoration approaches with an objective of forest diversification, improving forest health. Fire is rarely used in northern Europe to promote forest regeneration and diversification, mine reclamation, or old-field recovery. Also pests, pathogens, herbivory and predation are ignored. There is lacking of a true ecosystem-based approach in these studies. Research should have more focus on restoration of the ecological processes underlying ecosystem structure and function (Stanturf *et al.*, 2001).

3. AIMS OF THE STUDY

Ecological restoration aims to return the degraded system to conditions where ecosystem structure, function and processes are regained (Bradshaw, 1997). Planning of restoration treatments should be based on adequate data and prediction models. Long-term monitoring and evaluation of restoration areas provides scientific knowledge on the effects and success of restoration activities. This thesis synthesizes several studies of forest ecosystem restoration in Estonia.

The aims of the thesis are:

1. To develop naturalness and structural indicators in forest ecosystems (**I**);
2. To analyze the effects of restoration treatments for biodiversity and stand development in managed forest ecosystems (**II**);
3. To analyze the success of reclamation on post-mining restoration site (**III**);
4. To determine factors influencing tree survival/mortality in forest stands (**IV**).

The main hypotheses of the study were:

1. Multiple causes of tree mortality and dispersed spatial distribution of dead trees are relevant indicators of forest naturalness;
2. Restoration treatments accelerate development of natural forest structures;
3. Gap cutting, dead wood input and overburning treatments have different effects on forest structure, deadwood flow and species composition in forest ecosystems;
4. Novel ecosystems on oil-shale post-mining restoration sites (by spontaneous succession or afforestation) develop towards to common forest types but their abiotic and biotic compositions remain remarkably different for several decades.

4. MATERIALS AND METHODS

4.1. Study area

Three different datasets have been used in current thesis. These datasets are available in ForMIS system (http://formis.emu.ee/sampplot/) and registered also in Noltfox database (http://noltfox.metla.fi/).

4.1.1. Estonian Network of Forest Research Plots (ENFRP)

The Estonian Network of Forest Research Plots (ENFRP) provided forest permanent sample plot measurement data for papers **I** and **IV**. The network is located all over Estonia (Figure 4.1) and was established (first round of measurements) from 1995 to 2004. Sample plots are re-measured at five-year intervals (Kiviste and Hordo, 2003). At present, a total of 693 permanent sample plots are included in the network, 650 of which are already re-measured twice and 247 plots three times.

Assessment of naturalness and spatial distribution of deadwood (**I**) based on 294 sample pots (data from 43,848 trees) and 236 plots with 31,097 trees has been used to estimate tree survival probability (**IV**).

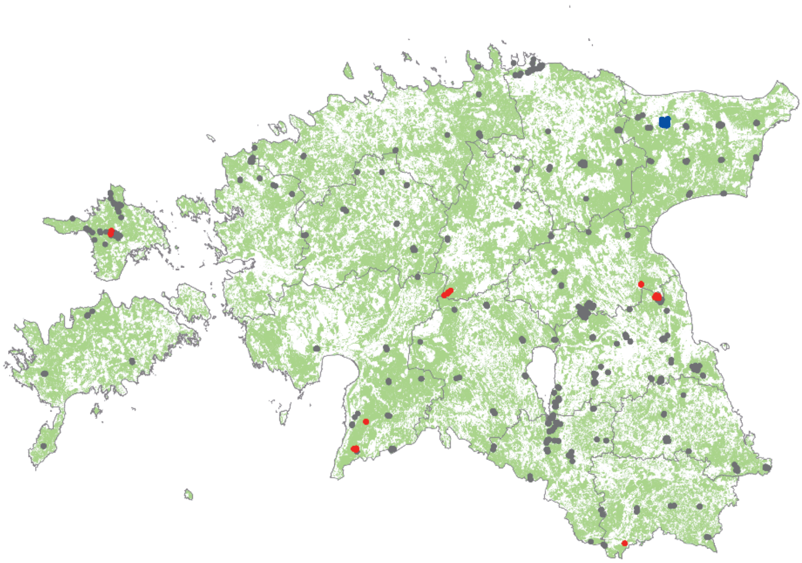


Figure 4.1. Location of the study plots in Estonia. Grey dots denote The Estonian Network of Forest Research plots (**I**, **IV**), red forest naturalness restoration plots **(II)** and blue dots denote post-mining reclamation plots in Aidu quarry (**III**). Green area indicates forests in Estonia.

4.1.2. Forest naturalness restoration plots (FNR)

The study (**II**) was connected to the LIFE-Nature project „Protection of priority forest habitat types in Estonia", where one of the purposes was nature restoration on seven nature protected areas with low levels of naturalness and diversity. Restoration treatments were implemented on planted, 30-60 years old, pure coniferous stands that were normally or densely stocked and growing on mineral soils. Altogether 350 ha in seven protection areas in Estonia were measured according to management design (Figure 4.1). Fifty restoration areas with permanent sample plots (PSP) were established in 2004. 27 PSP are on areas where treatments have been carried out and 23 PSP are control plots on areas without manipulation (Table 4.1). Plots were established before treatments in 2004, re-measured after treatments in 2005 and then re-measured after three years in 2008.

Table 4.1. Distribution of permanent sample plots by treatment. DW - dead wood input, G - gap cutting, GB - gap cutting and over burning; GDW - gap cutting with dead wood input, C – control plot.

Nature protection area/ landscape reserve	No of plots	C	DW	G	GDW	GB
Kääpa	6	2				4
Laiksaare	3	1			2	
Laulaste	10	5			5	
Leigri	4	2	2			
Mõisamõtsa	3	1		2		
Padakõrve	15	8		2	5	
Saarjõe	9	4			5	
Total	**50**	**23**	**2**	**4**	**17**	**4**

4.1.3. Post-mining reclamation plots (PMR)

The study was carried out at Aidu quarry in northeast part of Estonia (59°15'N; 27°42'E), where excavation of oil-shale in opencast mining was started 1974 (Figure 4.2). The reforestation began on opencast mining area (area 30 km^2) in 1981 (Kaar, 2010). Scots pine (*Pinus sylvestris* L.) 2-year-old seedlings were used. During oil-shale mining the ground and surface water were continuously extracted. Mining and water extraction was stopped in 2012. Over the next few years, the water table will gradually rise. For evaluation of post-mining reclamation success in the past, and monitoring the effect of changing water regime in the future, 60 survey plots have been established in 2011 in stands with ages of 12-33 years (Figure 4.2).

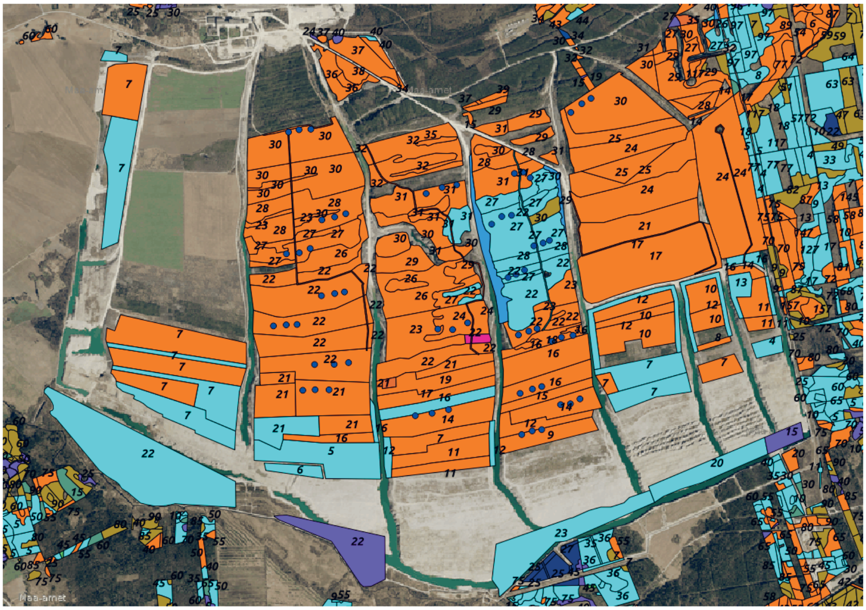


Figure 4.2. Network of post-mining reclamation plots in Aidu quarry, orange areas are Scots pine stands, light blue areas are silver birch stands. Blue dots are permanent sample plots. Number on each compartment shows the age of forest stand. (Base map: Maa-amet, 2014)

4.2. Data collection

4.2.1. Field measurements on permanent sample plots (PSP)

The methodology from ENFRP (Kiviste and Hordo, 2002) for monitoring stands was used for all studies (**I**; **II**; **III**; **IV**). Permanent sample plots were circular with a radius from 15 to 30 m, depending on the forest density and age. On each plot the azimuth and distance from plot center to each tree was recorded along with its diameter at breast height (DBH) and defects. For every fifth tree and also for dominant and single species, tree height and height to crown base were measured. In young stands (**III**) many trees were below 1.3 meter (6 plots) and the height was measured from all trees and DBH if it was possible. Measurement records were available for living trees (upper-, mid-, understory and shrub layer trees), dead trees (standing, downed and broken trees) and fresh stumps.

The need to determine reasons of tree death came up during the course of the work and was addressed with paper **IV**. The causal agent responsible for tree death was identified with the help of observed symptoms and other signs indicating the occurrence of the causing factor. The cause of mortality (CM) of each tree was determined every tree that had been alive at the time of the previous measurement but was dead at the last measurement (**I**; **II**). For each sampling period, the mortality rate was calculated as the number of trees that died, expressed as a percent of the number of trees living at the beginning of the period. Annual mortality is the number of dead trees in an interval divided by the number of years in the period. Different causal agents were grouped into density-dependent and density-independent factors. One of the most important density-dependent effects was competition among individual trees including unspecified causes of mortality for suppressed trees. Density-independent mortality was identified more precisely by causal agents: a) wind; b) game; c) insects; d) fungi and diseases; e) other.

Natural regeneration establishment was recorded in study **II** for the first time on the third inventory. Five 25 m^2 subplots were established in each PSP, one in the center of the PSP and the other four were located 10 meters from plot center in cardinal directions. All seedlings were counted by tree species and the two tallest seedlings of each species were selected for height measurement.

Naturalness was estimated in each PSP (**I**) using a method that incorporates both quantitative and qualitative scoring (Korjus, 2002). Different anthropogenic influences in a forest stand determine the level of naturalness.

4.2.2. Biodiversity assessment

In study **II**, all inventories were carried out before, immediately after, and three years after treatments by species-specific experts. Data on understory vegetation were surveyed on each PSP using a step-line intercept method (Jõgiste *et al.*, 2008). A 25 m^2 quadrat was located from center of a PSP in the north direction; after each step a 10 x 10 cm square was described, resulting in total 100 squares. Lichens were inventoried on selected living and dead trees, tree roots and stumps. Beetle diversity was inventoried with flight-intercept traps. 18 traps were set together on all PSPs. Beetles were collected six times during the vegetation period.

The majority of the beetles caught were identified to the species level. Beetle diversity was not inventoried on control plots because they were too close to the treatment plots.

In paper **III** biodiversity is inventoried on the ground vegetation layer. Vegetation sampling plots were connected to the PSP; from the center of each PSP, 5 meters to north, east, south and west plots of 1 x 1 m were established, where all seedlings, vascular plant species and all bryophytes were recorded by Braun-Blanquet scale. Altogether 240 subplots were described.

4.2.3. Soil sampling

Local soil conditions were characterized in each plot in study **III**. The humus layer and topsoil layer thickness was measured by the re-bar method at 13 points. Stoniness for each plot was calculated using the model of Laarmann *et al.* (2011). Topsoil samples were taken from each plot to a depth of 10 cm and analyzed in the Laboratory of Biochemistry of the Estonian University of Life Sciences. Total nitrogen and carbon content of oven-dried samples were determined by the dry combustion method on a varioMaX CNS elemental analyzer (ELEMENTAR, Germany). Soil organic carbon was determined with Tjurin's method (Vorobjova, 1998), pH values were determined by extraction using potassium chloride, and the concentrations of potassium and phosphorus was extracted in ammonium lactate and measured by flow injection analysis (Ruzicka and Hansen, 1981) and available potassium was measured with a flame photometer (FiaStar5000, Relingen, Germany). Soil texture was classified into three categories: clay (1- <0.002 mm), silt (2-0.002 – 0.063 mm) and sand (0.063 – 2 mm).

4.3. Data analysis

The logistic function was used for estimating tree survival (**IV**) and to model mortality of individual trees (**I**). Goodness-of–model-fit was determined by examining percent concordant values, which indicate overall model quality through the association of predicted probabilities and observed responses. The higher the predicted event probability of the larger response variable, the greater the percent concordant value will be.

The spatial distribution of deadwood in a stand can be evaluated by the pattern of mingling of dead and live stems (**I**). Deadwood mingling is defined as the proportion of the *n* nearest neighbours that are also dead trees (Figure 3 in **I**). In paper **I** a deadwood mingling index (DM_i) was developed using the species mingling formula proposed by Gadow (1993) for a group with four nearest neighbours of a dead reference tree *i*:

$$DM_i = \frac{1}{4}\sum_{j=1}^{4} v_j$$

with (1)

$$v_j = \begin{cases} 1 \text{ , when the neighbour j is dead tree} \\ 0 \text{ , when the neighbour j is living tree} \end{cases}$$

With four neighbours, DM_i can assume five different values: 0, 0.25, 0.50, 0.75 and 1. The mingling index value of 1 indicates that all neighbouring trees of a dead tree are also dead trees; conversely a mingling value of 0 indicates that all neighbouring trees are alive. The distribution of all reference trees or average DM_i can be used as a surrogate for deadwood clumping in a stand.

Diversity index of mortality reasons (CMDI) was adopted from Shannon (1948) H' index for the estimation of diversity in an ecosystem. CMDI can be calculated by the formula (**I**):

$$CMDI = -\sum_{i=1}^{S} p_i \cdot \ln(p_i) \tag{2}$$

S = number of CM; p_i = proportion of the CM ($p_i = N_i/N$); N_i= number of dead trees because of CM_i; N = total number of dead trees.

Species richness (**II**; **III**) was set to the average number of different species per plot sampled for the vascular plants, bryophytes, lichens and beetles; this variable is expected to have the Poisson distribution and significance analyzed with SAS procedure GLIMMIX (Freund and Littell, 2002).

Species and communities data (**II**; **III**) were analyzed using different ordination techniques with the PC-ORD software ver.6. (McCune and Grace, 2002). Non-metric multidimensional scaling (NMS) was used to ordinate understorey data in study **III**. NMS is an ordination technique based on ranked similarities of species composition suitable for community data that may not be normally distributed or fit assumptions of linear relationships among variables.

Principal Component Analysis (PCA) was used for tracking changes in forest composition over time (**II**) and for ordination of environmental parameters of the reclamation research area (**III**). Stand parameters were logarithmically transformed if needed. Randomization test showed suitability for PCA.

The significance of grouping factors was tested (**II**; **III**) using Multiple Response Permutation Procedure (MRPP). MRPP is a nonparametric procedure that tests the hypothesis of no difference in compositional similarity among two or more groups (McCune and Mefford, 1999).

Indicator species analysis (ISA) was performed to find out indicator species for different treatments (**II**). Indicator species are species that are used as ecological indicators of environmental conditions or environmental changes (De Caceres *et al.*, 2010). Indicator values were tested for statistical significance using Monte Carlo simulation tests.

To compare measured data with forest inventory data (**III**), a generalized additive model (GAM) estimation method was used (Hastie and Tibshirani, 1990).

The level of statistical significance was set at $p<0.05$.

5. RESULTS

5.1. Deadwood flow as an indicator of forest naturalness

The flow of deadwood characterises natural processes within a forest ecosystem. The dimensions of dead trees, amount and steadiness of the flow are related to forest naturalness. Paper **I** shows that forest naturalness can be assessed by qualitative scoring and the naturalness score is significantly different in managed and semi-natural forests (t-test, $p<0.001$); naturalness score was 8 in managed forests and 24 in semi-natural forests. The forest naturalness score is correlated to the diversity of tree mortality causes (Table 4 in **I**) which shows that tree mortality is more diverse in semi-natural forests than in managed forests. Diverse tree mortality causes refer to more constant flow of deadwood in semi-natural forests.

The amount of deadwood formation also indicates forest naturalness. The recent deadwood volume (RDV5) was different in managed and semi-natural forests (Figure 5.1). Deadwood accumulated twice as quickly in semi-natural forests (2.5 m^3 $ha^{-1}yr^{-1}$) than in managed forests (1.1 m^3 $ha^{-1}yr^{-1}$) according to the study **I**. There is correlation between RDV5 and tree mortality causes and deadwood mingling value (Table 4 in **I**).

Standing dead trees were more dispersed within a forest stand in semi-natural stands in comparison with managed stands (Figure 10 in **I**).

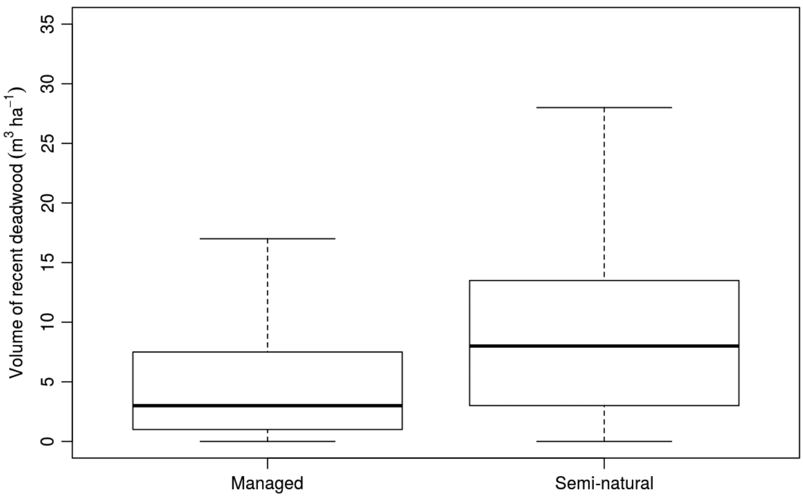


Figure 5.1. Comparison of the volume of recent deadwood in managed and semi-natural stands (**I**). The upper and lower boundaries of the boxes are the 75 and 25 percentiles, the horizontal line within the box is the median and the error bars show the 10^{th} and 90^{th} percentiles.

5.2. Restoration effects on a forest ecosystem

5.2.1. Effects on forest stand structure

More diverse stand structure is often an aim for forest ecosystem restoration. Gaps, different tree mingling patterns, deadwood, trees of different sizes and species provide more habitats for different species. From the paper **II**, stand structure was changed by different naturalness restoration treatments between pre-treatment and subsequent years ($F=6.18$, $p<0.001$) (Figure 3 in **II**). The number of living trees on most of the plots was reduced by gap cuttings (treatments G, GB, GDW) and the amount of deadwood increased to 67 m^3 ha^{-1} on plots (treatments DW and GDW). Pre-treatment stands were structurally quite even and similar to each other and three years after treatments stand structure has changed as well as herb, moss, lichen, and beetle composition and tree regeneration.

5.2.2. Effects on biodiversity

Restoration treatments can change species abundance and composition in an ecosystem. Different species groups react differently as well as different treatments may have diverse effects. From the paper **II**, herb species richness was affected by changes in light conditions; due to gap formation (G, GDW, GB treatments) richness was increased ($F=6.94$, $p<0.001$). The greatest change was in the G treatment, an average of 4.25 species were added. Richness of mosses and lichens was not significantly affected in any treatment. Richness of beetles increased over time ($p<0.001$) (Figure 1 in **II**).

Effects on species composition three years after treatment become evident in MRPP analysis (Table 5.1). Significant differences between treatments were in composition of herbs ($p<0.001$, $A=0.07$), mosses ($p=0.04$, $A=0.03$), lichens ($p<0.001$, $A=0.03$) and beetles ($p<0.001$, $A=0.14$). In pairwise comparisons (Table 5.1), herb species composition in treatment GB was significantly different from control plots ($T=-7.87$, $p<0.001$) and the rest of the treatments. Also moss composition in the treatment GB differed from the other treatments ($p<0.05$) except from the treatment DW ($p=0.12$). Lichen composition was different for all treatments and control plot except in treatment GDW ($p=0.44$). Beetle composition was shown only for treatments and a clear pattern was not detected.

5.2.3. Effects on tree regeneration

Abundance of natural regeneration was significantly different by treatments and by seedling species three years after treatment ($p<0.05$). The treatment GB increased the number of pine seedlings (Figure 2 in **II**). Treatments GB and GDW increased the number of birch seedlings and G increased number of spruce seedlings. The number of other trees, mainly aspen and oak did not differ among treatments.

Table 5.1. Multi-response permutation procedure analysis between treatments (G-gap cutting, DW-deadwood input, GDW-gap cutting with deadwood input, GB-gap cutting and overburning, C-control plot) in herbs (H), mosses (M), lichens (L) and beetles (B) three years after treatment (**II**). Shown are only significant differences (p<0.05).

	G	DW	GDW	GB	C
G					
DW	L; B				
GDW	L	L; B			
GB	H; M; L	H; L	H; M; L; B		
C	L	L		H; M; L	

5.2.4. Effects on deadwood flow

Forest naturalness restoration treatments should initiate conditions for constant deadwood flow in a forest ecosystem. At the same time, treatment reduces the immediate effects of deadwood formation. Tree mortality during first three years after treatment was 1.6% with treatment DW, 3.9% with treatment G, 4.7% with treatment GDW, and 6.7% on control plots. Sample plots with treatment GB, where gap size was significantly larger than on sample plots with treatment G or GDW, had no any dead trees during this three-year period. Amount of coarse woody debris (CWD) was significantly different in treatment plots (11.3 m^3 ha^{-1}) than in control plots (0.16 m^3 ha^{-1}) ($F=7.99$, $p=0.006$).

Relative diameter (DS) of tree describes tree survival better than absolute diameter (Table 7 in **IV**). Growth-dependent CM, wind and insects showed different behaviour related to DS in semi-natural, managed forests, and restoration plots (Figure 5.2). The share of growth-dependent mortality was lower in the treated plots than in managed forests while the share of wind CM increased with the treatments.

The assessment of causes of tree mortality revealed the treatments have an effect on tree mortality caused by tree competition ($p=0.001$) and by other reasons ($p=0.023$); the remaining CM had no significant relations with treatments. Tree mortality was highest in control plots (2.2% yr^{-1}). Average annual mortality on the gap alone (1.3%) and gap with deadwood (1.6%) was higher than the treatment of added deadwood (0.5%).

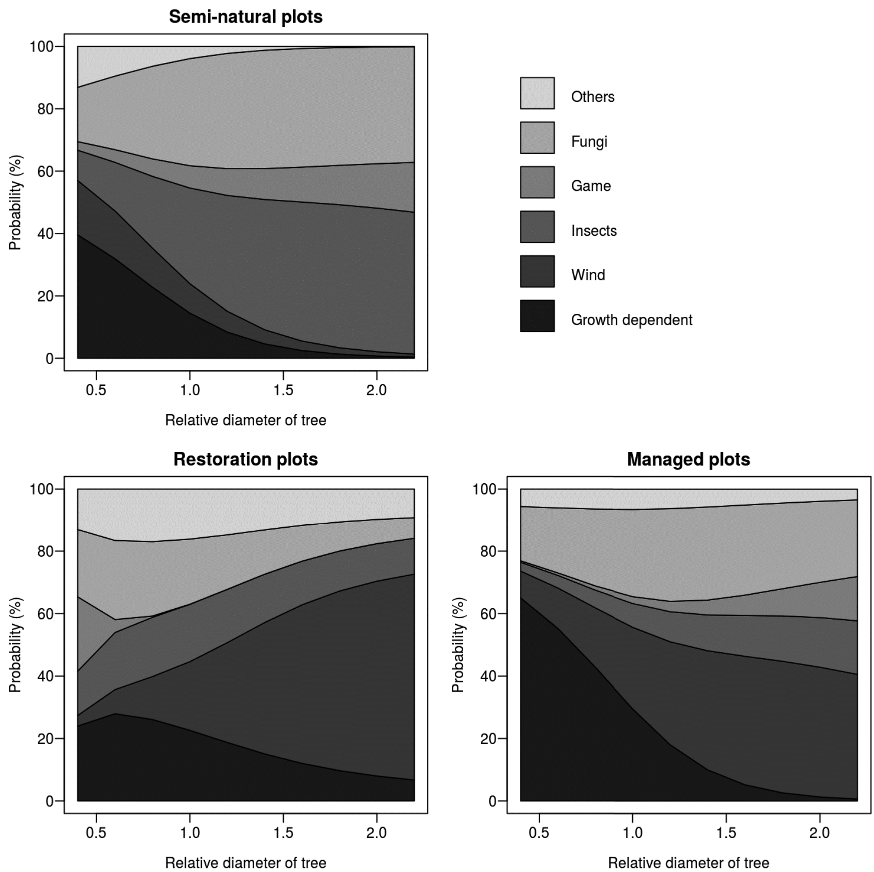


Figure 5.2. Probability of mortality causes for individual trees depending from relative tree diameter in semi-natural forests, managed forests and restoration plots (**I; II**).

5.3. Evaluating restoration success

5.3.1. Soil properties

The soil formation over the 33 years in the oil-shale post-mining restoration site in Aidu has created a suitable environment for forest development. The increase in soil nitrogen was statistically significant ($p<0.001$) over the years (Figure 5.3). Also phosphorus content ($p<0.001$) and organic carbon content ($p=0.05$) increased. Soil pH was higher in young pine stands and soil acidity increased with age ($p<0.001$). Total carbon and potassium content did not depend on age ($p>0.05$) (Figure 2 in **III**).

Comparing content results from the mining site with soil of regular forest types, then nitrogen (0.11%), potassium (86 mg kg^{-1}) and organic carbon (4.7%) content were similar to soil in *Hepatica* type forests (respectively by Lõhmus (1973) 0.07-0.2%, 10-120 mg kg^{-1}, 2.6-9.1%). Total carbon (9.2%), phosphorus (25 mg kg^{-1}) and soil acidity (7.55), on the other hand, were similar to soil in *Calamagrostis* type forests (C-8.4%, P-19-50 mg kg^{-1}, pH 6-7.5).

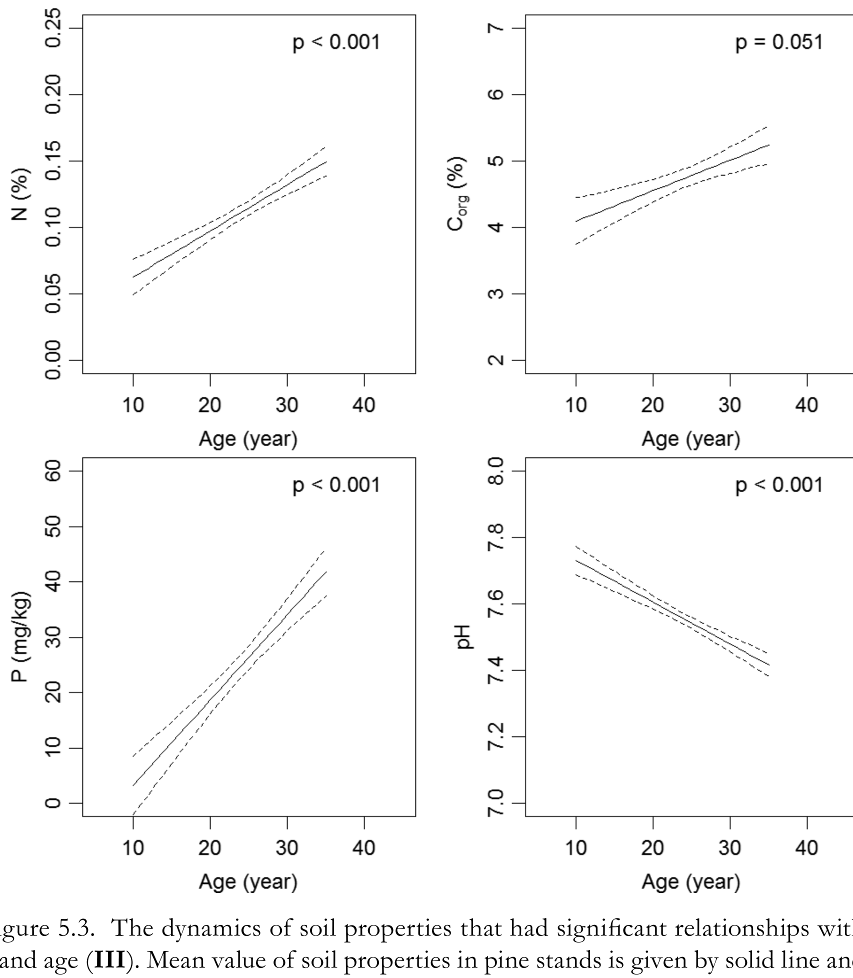


Figure 5.3. The dynamics of soil properties that had significant relationships with stand age (**III**). Mean value of soil properties in pine stands is given by solid line and 95% confidence limits by the dashed lines.

5.3.2. Vegetation composition

Three protected herbaceous species were found in the afforested post-mining area in Aidu (*Epipactis helleborine*, *Goodyera repens* and *Dactylorhiza* *fuchsii*), also two hemerophobic species (*Orthilia secunda* and *Monotropa hypopitys*). Understory species richness increased significantly ($p<0.001$) with stand age. The greatest increase was in the forest species group (Figure 4 in **III**). Meadow and forest/meadow species groups also increased, with the meadow group increasing more than the forest/meadow group.

In matching species to site types by indicator species, two-thirds of vascular species on the area were not characteristic to site types of similar bedrock condition (Figure 5.4, Table S1 in **III**). More forest species are indicators of *Hepatica* site type than to other types.

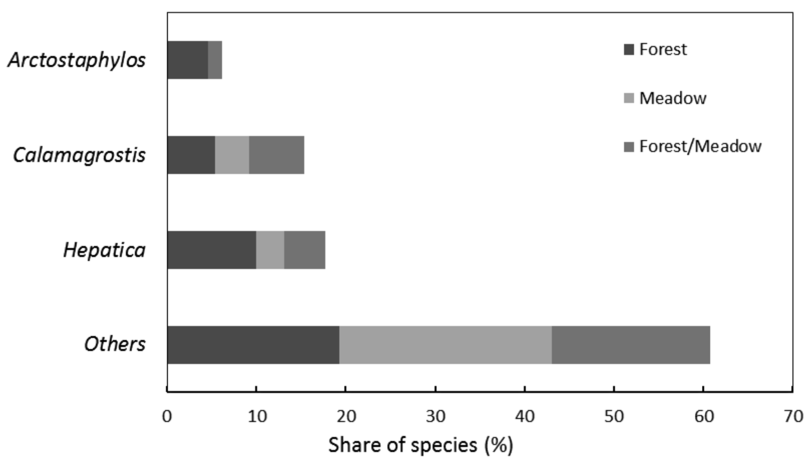


Figure 5.4. Distribution of all the understory species into forest site type and habitat preference group (**III**).

5.3.3. Stand development

Despite that pine was used for afforestation in Aidu, birch colonized naturally some areas. The thickness of the mineral soil layer was significantly different ($p<0.001$), with the average soil depth in pine stands 6.7 cm and in birch stands 37.6 cm (Figure 1 in **III**). Stand height and mean stand diameter were significantly ($p<0.001$) different in pine and birch stands (Table 1 in **III**). Height and diameter in pine stands showed strong relationships with stand age. Data of tree height and diameter were not significantly different from *Hepatica* type forest ($p=0.146$, Figure 5.5) and was significantly different from alvar forests ($p<0.001$, Figure 5 in **III**).

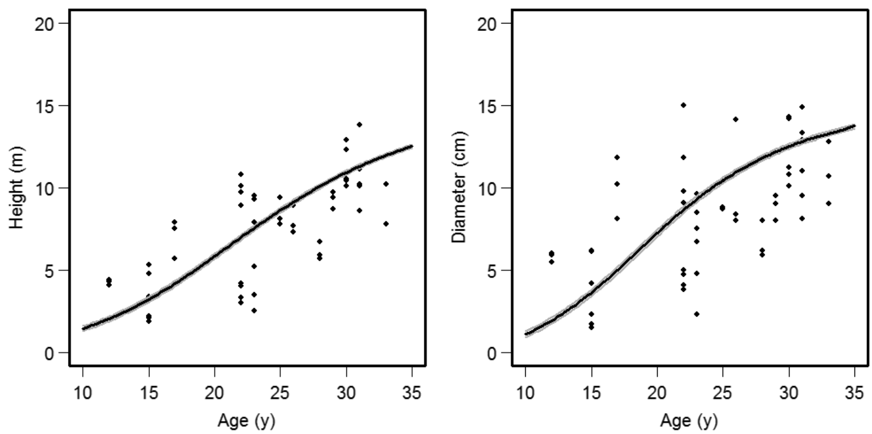


Figure 5.5. Relationship of stand height and diameter with stand age on pine plots (dots) and *Hepatica* type forest (solid line) (**III**).

5.3.4. Evaluation of novel ecosystem

Restoration of post-mining site in Aidu raised a question about novel ecosystem development in these sites. Distinguishing novel ecosystem from natural or hybrid ecosystems is based on three main criteria: irreversibility, species composition, and development of a self-organizing community.

Irreversibility is the most important criteria. Restoration of post-mining site faces completely altered substrate conditions at the beginning and usually it is not possible to restore historical or natural conditions of soil and substrate. The properties of soil may have similarities to several forest site types, if any, and usually different soil variables refer to different site types.

Species composition is also the important criteria. New species arrival, not common earlier to the site, may compensate losses in biodiversity or in functions of an ecosystem. Compositional mix of understory species (dry and wet site habitat species, poor and fertile site characteristic species) results from changed abiotic conditions and spontaneous succession of understory species (Table S1 in **III**).

The third criterion is a self-organizing community, without further human intervention needed. Tree species composition is affected by human activity (planted pine) and further by spontaneous colonization by birch. There were differences in almost all measured variables between birch and pine stands (Table 1 in **III**), which provide different habitat for understory species and increase diversity of the area.

Restoration of post-mining sites often leads to development of novel ecosystems. Their functions and composition may be valuable and serve restoration goals. Novel ecosystems on post-mining sites are dynamic; changing completely by disturbances or management activities and their development is not easily predictable. Long-term monitoring and evaluation of restoration of post-mining sites should be linked with planning and implementation of further management activities on these areas. In certain cases, spontaneous succession should be considered in restoration of oil shale post-mining sites as an alternative to common afforestation practice, especially if these sites are small, surrounded by natural vegetation, and there is no specific production goal or time limit for restoration.

6. DISCUSSION

The aim of forest restoration in Estonia is afforestation on abandoned areas (**III**) and restoration of natural structures, processes, and habitat for diverse species (**II**). Due to increasing anthropogenic land use, biodiversity has decreased, old-growth features declined, and natural disturbance regime depressed. Establishment of restoration goals is site and situation dependent and is challenged over timing (Burton and Macdonald, 2011); this is difficult because of the heterogeneity and dynamics of forest ecosystems. Clear objectives are important for monitoring progress and success of restoration activities. A question that should arise in a study evaluating restoration treatments is whether the cost of intervention is worthwhile; that is, would natural revegetation processes be sufficient to develop desirable conditions quickly enough to meet social goals? To answer this question requires a non-intervention treatment in the study design. Restoration activities may need repeated treatments to obtain self-sustaining ecosystems and to meet the desired objectives. Choosing a reference ecosystem for ecological restoration is complicated because of changed condition (Hallett *et al.*, 2013); it is easier to achieve success when the goal is to restore some degree of function or some of the species than to achieve complete restoration (Hobbs, 2007). In forest restoration, a restoration goal at given place may be a fully functional natural ecosystem instead of a human managed forest stand. In the Estonian case, historic reference ecosystems are not always available because of long-term human influence to ecosystems and lack of knowledge, as well as natural ecosystems dynamics and the present may not be similar to the past. A good indicator for restoration evaluation and goal-setting may be the level of naturalness of an ecosystem.

Naturalness can be assessed by different ways (McRoberts *et al.*, 2012); through signs of management, species composition, stand structure, deadwood, *etc.* and altogether in qualitative scoring as in paper **I**. The amount of deadwood, dispersed standing dead trees, and diversity of mortality causes are related to forest naturalness (**I**). The abundance of deadwood is dependent on disturbance severity and frequency (Franklin *et al.*, 1987) and amount of deadwood is an important indicator of forest ecosystem quality (Jonsson and Jonsell, 1999; Kohv and Liira, 2005; Liira *et al.*, 2007). Semi-natural forests have larger amounts of deadwood than managed forest (**I**); in managed forests it was 5.4 $m^3\,ha^{-1}$ and in semi-natural forests, deadwood was 12.3 m^3 ha^{-1}. Similar results have been found in southern Finland where the mean volume of standing deadwood was 2.7 m^3 ha^{-1} in forests available for wood production and in mature forests, standing deadwood was 14.5 m^3 ha^{-1} (Tomppo *et al.*, 2011). Forest naturalness cannot be explained only by the amount of deadwood and tree survival rates, but deadwood spatial and size distributions and variety of the causes of mortality are good indicators of forest naturalness (**I**; Laarmann, 2007).

Disturbances are important processes for maintaining community and landscape biodiversity in boreal ecosystems (Bonan and Shugart, 1989; Attiwill, 1994; Kuuluvainen, 2002a). Disturbances have strong control over the species composition and structure of forests (Frelich, 2002). In boreal forests, natural disturbance regimes range from succession following stand-replacing disturbances, such as severe fires and wind-storms, to small-scale dynamics associated with gaps in the canopy created by the loss of individual trees (Angelstam and Kuuluvainen, 2004). Non-fire disturbance events, particularly those caused by insects and disease, tend to be skewed towards the low-severity end of the disturbance spectrum, causing tree mortality in gaps and small patches with little understory or soil damage (Kneeshaw and Bergeron, 1998). Opening up the tree canopy often results in increased abundance of understory species (Jentsch *et al.*, 2002). Changes in disturbance regimes (because of management or climate change) can affect forest health in indirect and unexpected ways (Messerli *et al.*, 2000). Restoring natural forest composition and structure in forests can create healthy forests (Crow, 2014).

Anthropogenic disturbances such as clearcut logging, thinning, and selective cutting of trees impact the species diversity and composition of populations (Aavik *et al.*, 2009). Forest management does not mean a direct threat to species diversity; its amplitude depends on its characteristics and can be positive or negative (Voolma and Õunap, 2006). Small-scale environmental heterogeneity may support higher species richness (Wilson, 2000). These impacts could be negative or positive: understorey species richness in previously clearcut managed forest has been shown to be lower (Qian *et al.*, 1997; Jalonen and Vanha-Majamaa, 2001), similar (Okland *et al.*, 2003; Moora *et al.*, 2007) or higher (Zobel, 1989; Scheller and Mladenoff, 2002; Aavik *et al.*, 2009) than in old-growth unmanaged forests. Management influences spatial structure of vegetation. Multi-layers (Lorimer *et al.*, 2001; Fraver and White, 2005) and canopy gaps (Attiwill, 1994; Moora *et al.*, 2007) in old-growth forest stands due to presence of mosaic light conditions may create differences in the spatial structure of vegetation, which gives different local conditions compared to even-aged stands regenerated after clear-cutting. Different species groups reacted differently and different treatments had diverse effects in study **II**. The richness of herbs, mosses, lichens and beetles increased after treatments. Control areas stayed quite similar over time. Beetles have the most dynamic reaction to the changing conditions in forest ecosystems, which makes them one of the most valuable markers in the research of biological diversity (**II**; Süda, 2009). Decaying wood is a variable substrate for hundreds of different species of beetles (Esseen *et al.*, 1992; Siitonen, 2001). The main factors determining species composition in a dead tree are tree species, tree diameter, stage of decay (Jonsell *et al.*, 1998) and quality of the trunk- snag, log or stump (Berg *et al.*, 1994; Nilsson, 1997), amount (Martikainen *et al.*, 2000) and diversity (Similä *et al.*, 2003) of dead wood are crucial for many species and different part of dead trees also offer different kind of habitats. On the treatment with the added deadwood the debris had decomposed enough to create habitat for some new species (**II**). Beetle diversity increased after treatments from 0.5 (Shannon index, Table 2 in **II**) to 3.4 showing remarkable immediate effect of treatments.

Gap cutting may emulate the effect of natural small-scale disturbance by mortality of single trees or groups of trees. Retaining compositional and structural attributes induces increased growth rates in residual trees (Gendreau-Berthiaume *et al.*, 2012). Gap cuttings accompanied by creating deadwood increased the amount of CWD to 67 m^3 ha^{-1} (**II**). This was similar to Siitonen (2001), who stated that CWD in natural forest in Finland ranges from 60 to 90 m^3 ha^{-1} while in managed forests the range is only 2 to 10 m^3 ha^{-1}. Tree survival or mortality depends significantly on relative diameter of trees (**I**; **IV**). CM showed different patterns in semi-natural, managed forests and on restoration plots. Deadwood input and heterogeneity increased after treatment; pre-treatment stands were quite even in structure and composition (**II**). Determining the cause of tree death is often difficult and in future studies the process-based multiple-reason method (Figure 11 in **I**) may be more useful.

The gap creation with overburning treatment differed significantly from control plots in each species group. Fire treatments are not allowed as restoration activity in Estonia anymore. For experimental purposes, a low intensity overburning was conducted on the Kääpa Nature reserve area. The purpose of the fire treatment was to recreate features of natural forest that have disappeared because of fire suppression. Two vascular plants, two bryophytes, three lichens, and 12 beetle species were identified as indicator species to the GB treatment (Table 4 in **II**). Different studies have also shown that wildfire provides opportunity for fire-adapted and fire-dependent species to develop in closed-canopy stands (Wikars, 2002; Junninen *et al.*, 2008; Ruokolainen and Salo, 2009). Natural regeneration is often difficult to achieve on pine stands. On dry sandy soils is the problem with thick litter layer and on moderately wet sandy soils the difficulty is due to abundant understorey vegetation cover or thick raw humus layers. GB treatments created conditions for successful Scots pine regeneration, reduced competition and increased light availability.

When a forested landscape has been heavily degraded by human activity, it may not be possible to return to historical or natural conditions. In post-mining sites the inability to easily achieve ecological restoration goals is due to the radical difference in physiochemical and biological features of these sites as compared to historical environments. The degree of degradation is so severe that novel ecosystems develop (Hobbs *et al.*, 2006; Mascaro *et al.*, 2013). In Aidu plots in this study a suitable environment for forest development was formed (Figure 5.5) but the composition of soil was unlike natural soil due to the mixing of extraction waste from mining (Toomik and Liblik, 1998). Properties of soil showed (**III**) that some variables (N, K, organic C) were more similar to one type of forest soil and others (total C, P and pH) were more similar to a different type of forest soil. Species composition of the canopy is known to influence soil variables as a result of litter type (Prescott, 2002). Falling litter is a source of soil organic matter rich in carbon but poor in nitrogen (Reintam *et al.*, 2002). Deep rooting grasses play an important role in humus accumulation (Reintam *et al.*, 2002). Soil pH (higher in clearcut and young stands) and P (higher in mid-aged and old-growth stands) content affect also the variation in community composition (Aavik *et al.*, 2009). Soil nitrate content was higher in young stands (Moora *et al.*, 2007).

One advantage of active restoration is usually that there is a faster formation of continuous vegetation cover than a passive approach that relies on spontaneous succession (Prach and Hobbs, 2008). Active restoration has helped to create a more natural landscape after mining (Toomik and Liblik, 1998). After extreme ecosystem change on mine-sites, reclamation managers often plant fast-growing plants regardless of their origin to ensure that protective environmental service is restored (Richardson *et al.*, 2010). In the current study, planting Scots pine was the aim because it was a common reforestation practice on mined land and for commercial purposes (**III**; Kaar, 2002).

Novel ecosystems and cultural ecosystem services are not tied to historical species assemblage and they can reflect people's preference for nature that may not include historical ecosystems (Perring *et al.*, 2013); they do not fall along the gradient from old-growth to degraded forests (Lindenmayer *et al.*, 2008). Novel ecosystem management depends on the specific management goal and decisions focus on what to value and when to intervene in these ecosystems. Precaution is an important element of novel ecosystem management (Hallett *et al.*, 2013). A feature of novel ecosystems is new combinations of species assemblages that has not occurred previously in a given place (Hobbs *et al.*, 2006). The study **III** results indicate that ground vegetation includes species of broad amplitude; dry and wet site, poor and fertile site-specific habitats species are represented. If we look at the vegetation of the ground layer then it is spontaneous and is not influenced by seeding or sowing. Pines in the overstory layer were planted, but birch came spontaneously. Colonization ability of species is important in the early stages of development of a restored community (Pywell *et al.*, 2003). Such species represent ruderal species and decline with the time, because ruderality was significant only in the first year (Pywell *et al.*, 2003), but at the beginning they suppress the abundance of typical forest species by competition. We found a combination of meadow and forest species, but also ruderal species and pioneer species were represented. Share of forest species increased as the stands aged, but the number of meadow and forest/meadow species also increased with age (Figure 5 in **III**). Sites of spontaneous succession may act as habitat for endangered species, while reclaimed sites offer habitat for common species with broad amplitude (Prach *et al.*, 2011). Also novel ecosystems may be more diverse than natural communities and may offer suitable habitat for threatened and protected species (Richardson *et al.*, 2010). This supports our findings in Aidu site where three protected species were growing there. The natural value of spontaneously colonized sites is higher than planted sites (Hodačovà and Prach, 2003; Pensa *et al.*, 2004) and it is more probable when the disturbed site is small and surrounded by natural vegetation (Prach and Pyšek, 2001). Novel ecosystems on post-mining sites are dynamic, changing completely by disturbances or management activities and their development is not easily predictable, and nevertheless their functions and composition may be valuable and serve restoration goals.

7. CONCLUSIONS

Knowledge from ecological studies (**I**; **II**; **III**; **IV**) supports forest management policies aiming to increase the value and functions of commercially managed forests and to restore naturalness in protected forests. Forest restoration is changing traditional forestry practices to more individualized approaches. New methods, experiments and models provide scientific background for data assessment and design of restoration activities. Long-term monitoring and evaluation should be an integral part of any restoration project as it serves for planning and implementation of further management activities on these areas and at new sites.

Based on the results of this thesis, the general conclusions are:

- Deadwood quantity and spatial distribution as well as tree mortality rate and causes are reliable indicators of forest naturalness. Deadwood mingling index and diversity index of mortality reasons as new proposed variables improve the assessment of forest naturalness and clarify the effects of recent disturbances.

- Tree mortality in a stand is caused by specific agents or by the complex effect of several mortality agents and it is different in semi-natural and managed forest. Determining the cause for a tree death is often difficult; therefore it is sensible to use a process-based multiple-reason method for determining the factors of mortality for a single tree.

- Survival probability of a tree is dependent on the specific mortality agent and relative size of the tree in a stand.

- Restoration pre-treatment stands are often homogeneous even-aged monocultures on fertile sites; rehabilitation treatments (gap cuttings, overburning and addition of deadwood) increase their structural heterogeneity and promote differentiation of microclimatic conditions and therefore species richness and abundance increase after treatments.

- In a gap treatment, the ratio between the gap diameter and the surrounding stand height determines the light availability inside the gap; the larger this ratio is, the greater likelihood of seedling recruitment and successful establishment of light demanding species.

- Species groups respond differently to treatments: understory vegetation diversity increases in gaps with burning, lichen diversity in gaps without burning, and bryophyte diversity with the addition of dead wood. Increased beetle abundance and greater species diversity is a direct effect of changed light conditions inside the canopy. Gaps with overburning have the greatest recruitment of tree seedlings.

- Multiple treatments create stand heterogeneity and can increase biodiversity more than one homogenous application of a single treatment.

- It is not possible to restore historical or natural ecosystems on reclaimed mined areas by simple afforestation. Soil formation and properties and the vegetation on reclaimed sites is different from soils and vegetation on common forest sites, hence this leads to development of novel ecosystems.

- Spontaneous succession should be considered in forest restoration as an alternative to afforestation practice, especially if reclamation sites are small, surrounded by natural vegetation, and there is no specific production goal or time limit for restoration.

REFERENCES

Aavik, T., Püssa, K., Roosaluste, E., Moora, M. 2009. Vegetation change in boreonemoral forest during succession – trends in species composition, richness and differentiation diversity. Annales Botanici Fennici 46: 326-335.

Angelstam, P., Andersson, L. 2001. Estimates of the needs for forest reserves in Sweden. Scandinavian Journal of Forest Research 16 (S3): 38-51.

Angelstam, P., Kuuluvainen, T. 2004. Boreal forest disturbance regimes, successional dynamics and landscape structures: a European perspective. Ecological Bulletins 51: 117-136.

Aosaar, J. 2012. The development and biomass production of grey alder stand on abandoned agricultural land in relation to nitrogen and carbon dynamics. A Thesis for applying for the degree of Doctor of Philosophy in Forestry. Tartu.

Attiwill, P.M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management 63: 247-300.

Bartha, D., Ódor, P., Horváth, T., Timár, G., Kenderes, K., Standovár, T., Bölöni, J., Szmorad, F., Bodonczi, L., Aszalós, R. 2006. Relationship of tree stand heterogeneity and forest naturalness. Acta Silvatica & Lignaria Hungarica 2: 7-22.

Berg, Ǻ. Ehnström, B., Gustavsson, L., Hallingback, T., Jonsell, M., Weslien, J. 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. Conservation Biology 8: 718-731.

Berglund, H., Jönsson, M.T., Penttilä, R., Vanha-Majamaa, I. 2011. The effects of burning and dead-wood creation on the diversity of pioneer wood-inhabiting fungi in managed boreal spruce forest. Forest Ecology and Management 261: 1293-1305.

Bolton, N.W., D'Amato, A.W. 2011. Regeneration responses to gap size and coarse woody debris within natural disturbance-based silvicultural systems in northeastern Minnesota, USA. Forest Ecology and Management 262: 1215-1222.

Bonan, G.B., Shugart, H.H. 1989. Environmental factors and ecological processes in boreal forests. Annual Review of Ecology and Systematics 20: 1-28.

Borman, F.H., Likens, G.E. 1994. Pattern and Process: in a Forested Ecosystem. Springer-Verlag, New York.

Bradshaw, A.D. 1987. The reclamation of derelict land and the ecology of ecosystems. In: Jordan, W.R., Gilpin, M.E., Aber, J.D. (Eds.) Restoration ecology: A Synthetic Approach to Ecological Research. Cambridge University Press, Cambridge, pp. 53-74.

Bradshaw, A.D. 1997. What do we mean by restoration? In: Urbanska, K.M., Webb, N.R., Edwards, P.J. (Eds.) Restoration ecology and sustainable development. Cambridge University Press, Cambridge, pp. 8-14.

Bradshaw, A.D. 2002. Introduction and philosophy. In: Perrow, M.R., Davy, A.J. (Eds.) Handbook of Ecological Restoration. Cambridge University Press, Cambridge, pp. 3-9.

Burton, P.J., Macdonald, S.E. 2011. The restorative imperative: assessing objectives, approaches and challenges to restoring naturalness in forests. Silva Fennica 45 (5): 843-863.

Burton, P.J. 2014. Considerations for monitoring and evaluating forest restoration. Journal of Sustainable Forestry 33 (S1): S149-S160.

Caron, M.N., Kneeshaw, D.D., De Grandpre, L., Kauhanen, H., Kuuluvainen, T. 2009. Canopy gap characteristics and disturbance dynamics in old-growth *Picea abies* stands in Northern Fennoscandia: is the forest in quasi-equilibrium? Annales Botanici Fennici 46 (4): 251-262.

Clements, F.E. 1936. Nature and structure of the climax. The Journal of Ecology 24 (1): 252-284.

Clewell, A.F., Aronson, J. 2007. Ecological restoration: Principles, values and structure of an emerging profession. Island Press.

Crow, T.R. 2014. Functional restoration: from concept to practice. Journal of Sustainable Forestry 33 (S1): S3-S14.

De Caceres, M., Legendre, P., Moretti, M. 2010. Improving indicator species analysis by combining groups of sites. Oikos 119: 1674-1684.

Debeljak, M. 2006. Coarse woody debris in virgin and managed forest. Ecological Indicators 6: 733-742.

Duncker, P.S., Barreiro, S.M., Hengeveld, G.M., Lind, T., Mason, W.L., Ambrozy, S., Spiecker, H. 2012. Classification of forest management approaches: a new conceptual framework and its applicability to European forestry. Ecology and Society 17 (4): 51.

Eriksson, M., Lilja, S., Roininen, H. 2006. Dead wood creation and restoration burning: implications for bark beetles and beetle induced tree deaths. Forest Ecology and Management 231: 205-213.

Esseen, P.A., Ehnström, B., Ericson, L., Sjöberg, K. 1992. Boreal forests - the focal habitats of Fennoscandia. In: Hansson, L. (Ed.) Ecological principles of nature conservation. Elsevier, pp. 252-325.

Falk, K.J., Burke, D.M., Elliott, K.A., Holmes, S.B. 2008. Effects of single-tree and group selection harvesting on the diversity and abundance of spring forest herbs in deciduous forests in southwestern Ontario. Forest Ecology and Management 255: 2486-2494.

Fischer, A., Fischer, H. 2006. Restoration of forests. In: van Andel, J., Aronson, J. (Eds.) Restoration Ecology. Blackwell Publishing, pp.124-140.

Franklin, J.F., Shugart, H.H., Harmon, M.E. 1987. Tree death as an ecological process. BioScience 37 (8): 550-556.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155: 399-423.

Franklin, J.F., Mitchell, R.J., Palik, B.J. 2007. Natural disturbance and stand development principles for ecological forestry. Newtown Square, PA, U.S. Department of Agriculture, Forest Service, Northern Research Station. General Technical Report NRS-19.

Fraver, S., White A. 2005. Disturbance dynamics of old-growth *Picea rubens* forest of northern Maine. Journal of Vegetation Science 16: 597-610.

Frelich, L.E. 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. Cambridge University Press, Cambridge.

Freund, R.J., Littell, R.C. 2000. SAS System for Regression. SAS Institute, Cary, NC.

Gadow, K.v. 1993. Zur Bestandesbeschreibung in der Forsteinrichtung. Forst und Holz 48 (21): 602-606. [in German].

Gadow, K.v., Nagel, N., Saborowski, J. (Eds.). 2002. Continuous Cover Forestry – Assessment, Analysis, Scenarios. Managing Forest Ecosystems, vol. 4. Kluwer Academic Publishers, Dordrecht Boston London.

Gendreau-Berthiaume, B., Kneeshaw, D.D., Harvey, B.D. 2012. Effects of partial cutting and partial disturbance by wind and insects on stand composition, structure and growth in boreal mixedwoods. Forestry 85 (4): 551-565.

Grant, C.D., Norman, M.A., Smith, M.A. 2007. Fire and silvicultural management of restored bauxite mines in western Australia. Restoration Ecology 15 (S4): S127-S136.

Grootjans, A.P., Everts, H., Bruin, K., Fresco, L. 2001. Restoration of wet dune slacks on the Dutch Wadden sea islands: recolonization after large-scale sod cutting. Restoration Ecology 9: 137-146.

Hallett, L.M., Standish, R.J., Hulvey, K.B., Gardener, M.R., Suding, K.N., Starzomski, B.M., Murphy, S.D., Harris, J.A. 2013. Towards a conceptual framework for novel ecosystems. In: Hobbs, R.J., Higgs, E.S., Hall, C.M. (Eds.) Novel Ecosystems: Intervening in the New Ecological World Order. Wiley-Blackwell, pp. 16-28.

Halme, P. Allane, K.A., Auniņš, A., Bradshaw, R.H.W., Brūmelis, G., Čada, V., Clear, J.L., Eriksson, A., Hannon, G., Hyvärinen, E., Ikauniece, S., Iršėnaitė, R., Jonsson, G.B., Junninen, K., Kareksela, S., Komonen, A., Kotiaho, J.S., Kouki, J., Kuuluvainen, T., Mazziotta, A., Mönkkönen, M., Nyholm, K., Olděn, A., Shorohova, E., Strange, N., Toivanen, T., Vanha-Majamaa, I., Wallenius, T., Ylisirniö, A., Zin, E. 2013. Challenges of ecological restoration: lessons from forests in northern Europe. Biological Conservation 167: 248-256.

Hancock, M.H., Summers, R.W., Amphlett, A., Willi, J. 2009. Testing prescribed fire as a tool to promote Scots pine *Pinus sylvestris* regeneration. European Journal of Forest Research 128: 319-333.

Harms, B. Knaapen, J.P., Rademakers, J.G. 1993. Landscape planning for nature restoration: comparing regional scenarios. In: Vos, C.C., Opdam, P. (Eds.) Landscape Ecology of a Stressed Environment. Chapman and Hall, London, pp. 197-218.

Harris, J.A., van Diggelen, R. 2006. Ecological restoration as a project for global society. In: van Andel, J., Aronson, J. (Eds.) Restoration Ecology. Blackwell Publishing, pp. 3-15.

Harris, J.A., Hobbs, R.J., Higgs, E., Aronson, J. 2006. Ecological restoration and global climate change. Restoration Ecology 14 (2): 170-176.

Harris, J.A., Murphy, S.D., Nelson, C.R., Perring, M.P., Tognetti, P.M. 2013. Characterizing novel ecosystems: challenges for measurement. In: Hobbs, R.J., Higgs, E.S., Hall, C.M. (Eds.) Novel Ecosystems: Intervening in the New Ecological World Order. Wiley-Blackwell, pp. 192-204.

Hastie, T.J., Tibshirani, R.J. 1990. Generalized Additive Models. Chapman & Hall. CRC.

Hobbs, R.J., Norton, D.A. 1996. Towards a conceptual framework for restoration ecology. Restoration Ecology 4: 93-110.

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladeres, F., Vilà, M., Zamora, R., Zobel, M. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15: 1-7.

Hobbs, R.J. 2007. Setting effective and realistic restoration goals: key direction for research. Restoration Ecology 15 (2): 354-357.

Hobbs, R.J., Higgs, E., Harris, J.A. 2009. Novel ecosystems: implications for conservation and restoration. Trends in Ecology & Evolution 24 (11): 599-605.

Hobbs R.J., Hallett, L.M., Ehrlich, P.R., Mooney, H.A. 2011. Intervention ecology: applying ecological science in the twenty-first century. BioScience 61 (6): 442-450.

Hodačovà, D., Prach, K. 2003. Spoil heaps from brown coal mining: technical reclamation versus spontaneous regevegetation. Restoration Ecology 11 (3): 385-391.

Humber, J.M. Hermanutz, L. 2011. Impacts of non-native plant and animal invaders on gap regeneration in a protected boreal forest. Biological Invasions 13 (10): 2361-2377.

Hulvey, K.B., Standish, R.J., Hallett, L.M., Starzomski, B.M., Murphy, S.D., Nelson, C.R., Gardener, M.R., Kennedy, P.L., Seastedt, T.R., Suding, K.N. 2013. Incorporating novel ecosystems into management frameworks. In: Hobbs, R.J., Higgs, E.S., Hall, C.M. (Eds.) Novel Ecosystems: Intervening in the New Ecological World Order. Wiley-Blackwell, pp. 157-171.

Hüttl, R.F., Weber, E. 2001. Forest ecosystem development in post-mining landscapes: a case study of the Lusatian lignite district. Naturwissenschaften 88: 322-329.

Hüttl, R.F., Bradshaw, A. 2001. Ecology of post-mining landscapes. Restoration Ecology 9 (4): 339-340.

Jalonen, J., Vanha-Majamaa, I. 2001. Immediate effects of four different felling methods on mature boreal spruce forest understorey vegetation in southern Finland. Forest Ecology and Management 146: 25-34.

Jentsch, A., Beierkuhnlein, C., White, P. 2002. Scale, the dynamic stability of forest ecosystems, and the persistence of biodiversity. Silva Fennica 36: 393-400.

Jonsell, M. Weslien, J., Ehnström, B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity Conservation 7: 749-764.

Jonsson, B.G., Jonsell, M. 1999. Exploring potential biodiversity indicators in boreal forests. Biodiversity & Conservation 8: 1417-1433.

Jonsson, B.G., Kruys, N., Ranius, T. 2005. Ecology of species living on dead wood – lessons for dead wood management. Silva Fennica Monigraphs 39 (2): 289-309.

Junninen, K., Kouki, J., Renvall, P. 2008. Restoration of natural legacies of fire in European boreal forests: as experimental approach to the effects on wooddecaying fungi. Canadian Journal of Forest Research 38: 202-215.

Jõgiste, K., Kuuba, R., Viilma, K., Korjus, H., Kiviste, A., Kalda, A., Parmasto, E., Jüriado, I., Lõhmus, P., Õunap, H. 2008. Metsade looduslikkuse taastamine. Tartu. [In Estonian].

Jõgiste, K., Vares, A., Uri, V., Tullus, H. 2005. Baltic afforestation. In: Stanturf, J.A., Madsen, P. (Eds.). Restoration of boreal and temperate forests. CRC Press Inc, pp. 225-234.

Kaar, E. 2002. Coniferous trees on exhausted oil shale opencast mines. Forestry Studies XXXVI: 120-125.

Kaar, E. 2010. Afforestation of flattened oil shale quarries. In: Kaar, E., Kiviste, K. (Eds.). Mining and rehabilitation in Estonia. Tartu, Eesti Maaülikool, pp. 129-154. [in Estonian with English summary].

Kangur, A., Korjus, H., Jõgiste, K. Kiviste, A. 2005. A conceptual model of forest stand development based on permanent sample-plot data in Estonia. Scandinavian Journal of Forest Research 20 (S6): 94-101.

Katz, E. 2000. Another look at restoration: technology and artificial nature. In: Gobster, P.H., Hull, R.B. (Eds.) Restoring Nature: Perspectives From The Social Sciences And Humanities. Island Press, Washington D.C., U.S.A., pp. 37-48.

Kiviste, A., Hordo, M. 2002. Network of permanent forest growth plots in Estonia. Forestry Studies 37: 43-58. [in Estonian with English summary].

Kiviste, A., Hordo, M. 2003. The network of permanent sample plots for forest growth modeling in Estonia. In: Markevica, A., Lypsik, A., Leep, R. (Eds.) Research for Rural development 2003. International Scientific Conference Proceedings, Jelgava, pp. 174-177.

Klimaszewski, J., Langor, D.W., Work, T.T., Hammond, J.H.E., Savard, K. 2008. Smaller and more numerous harvesting gaps emulate natural forest disturbances: a biodiversity test case using rove beetles (*Coleoptera, Staphylinidae*). Diversity and Distributions 14: 969-982.

Kneeshaw, D.D., Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southern boreal forest. Ecology 79: 783-794.

Kohv, K., Liira, J. 2005. Anthropogenic effects on vegetation structure of the boreal forest in Estonia. Scandinavian Journal of Forest Research 20 (S6): 122-134.

Koivula, M., Niemelä, J. 2003. Gap felling as a forest harvesting method in boreal forests: responses of carabid beetles (Coleoptera, Carabidae). Ecography 26: 179-187.

Komonen, A., Penttilä, R., Lindgren, M., Hanksi, I. 2000. Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. Oikos 90: 119-126.

Komonen, A., Halme, P., Jäntti, M., Koskela, T., Kotiaho, J.S., Toivanen, T. 2014. Created substrates do not fully mimic natural substrates in restoration: the occurrence of polypores on spruce logs. Silva Fennica 48 (1): 1-12.

Korjus, H. 2002. Inventorying natural values in forest stands. Forestry Studies 37: 59-71. [In Estonian with English summary].

Korjus, H. 2005. Monitoring of nature restoration areas. Forestry Studies 43: 49-57. [In Estonian with English summary].

Korjus, H. 2009. Approaches to forest design in Estonia. A Thesis for applying for the degree of Doctor of Philosophy in Forestry. Tartu.

Kuuluvainen, T. 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. Annales Zoologici Fennici 31: 35-51.

Kuuluvainen, T. 2002a. Disturbance dynamics in boreal forests: defining the ecological basis of restoration and management biodiversity. Silva Fennica 36: 5-11.

Kuuluvainen, T. 2002b. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fennica 36: 97-125.

Kuuluvainen, T. Aapala, K. Ahlroth, P., Kuusinen, M., Lindholm, T., Sallantaus, T., Siitonen, J., Tukia, H. 2002. Principles of ecological restoration of boreal forested ecosystems: Finland as an example. Silva Fennica 36: 409-422.

Kuuluvainen, T., Tukia, H., Aapala, K. 2005. Ecological restoration of forested ecosystems in Finland. In: Stanturf, J.A., Madsen, P. (Eds.) Restoration of Boreal and Temperate Forests. CRC Press, pp. 285-298.

Kuuluvainen, T. 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in northern Europe: The complexity challenge. Ambio 38 (6): 309-315.

Kuznetsova, T., Mandre, M. 2006. Chemical and morphological indication of the state of lodgepole pine and scots pine in restored oil shale opencast mining areas in Estonia. Oil Shale 23 (4): 366-384.

Kuznetsova, T., Mandre, M., Klõšeiko, J., Pärn, H. 2010. A comparison of the growth of Scots pine (Pinus sylvestris L.) in a reclaimed oil shale post-mining area and in a Calluna site in Estonia. Environmental Monitoring and Assessment 166: 257-265.

Kuznetsova, T. 2011. Plantations of native and introduced tree species in the reclamation of oil shale post-mining areas. A Thesis for applying for the degree of Doctor of Philosophy in Forestry. Tartu.

Kuznetsova, T., Tilk, M., Pärn, H., Lukjanova, A., Mandre, M. 2011. Growth, aboveground biomass and nutrient concentration of young Scots pine and lodgepole pine in oil shale post-mining landscapes in Estonia. Environmental Monitoring and Assessment 183: 341-350.

Köster, K., Voolma, K., Jõgiste, K., Metslaid, M., Laarmann, D. 2009. Assessment of tree mortality after windthrow using photo-derived data. Annales Botanici Fennici 46: 291-298.

Laarmann, D. 2007. Individual tree mortality in relationship with naturalness of forest stands on the permanent sample plot data. MSc thesis. Estonian University of Life Sciences. [in Estonian with English summary].

Laarmann, D., Sims, A., Korjus, H., Kiviste, A., Kangur, A. 2011. Forest ecosystem restoration microhabitat pattern analysis on abandoned oil-shale mining areas in Estonia. SER Europe Knowledge Base on Ecological Restoration in Europe. http: //www.ser.org/europe/. Society of Ecological Restoration International.

Larsen, J.B. 1995. Ecological stability of forests and sustainable silviculture. Forest Ecology and Management 129: 25-30.

Liira, J., Sepp, T., Parrest, O. 2007. The forest structure and ecosystem quality in conditions of anthropogenic disturbance along productivity gradient. Forest Ecology and Management 250: 34-46.

Liira, J., Sepp. T. 2009. Indicators of structural and habitat natural quality in boreo-nemoral forests along the management gradient. Annales Botanici Fennici 46: 308-325.

Lindenmayer, D.B., Fischer, J., Felton, A., Crane, M., Michael, D., Macgregor, C., Montague-Drake, R., Manning, A., Hobbs, R.J. 2008. Novel ecosystems resulting from landscape transformation create dilemmas for modern conservation practice. Conservation Letters 1 (3): 129-135.

Lorimer, C.G., Dahir, S.E., Nordheim, E.V. 2001. Tree mortality rates and longevity in mature and old-growth hemlock-hardwood forests. Journal of Ecology 89: 960-971.

Lõhmus, E. 1973. Eesti NSV metsade tüpoloogiline analüüs. Väitekiri põllumajandusteaduste kandidaadi teadusliku kraadi taotlemiseks. Tartu. [in Estonian].

Lõhmus, A. 2005. Restoration of naturalness of forests: aims and results. In: Sammul, M., Lõhmus, A. (Eds.) Year-book of the Estonian Naturalists' Society – Ecological Restoration 83: 113-141. [in Estonian with English summary].

Lõhmus, A., Lõhmus, P., Remm, J., Vellak, K. 2005. Old-growth structural elements in a strict reserve and commercial forest landscape in Estonia. Forest Ecology and Management 216: 201-215.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L., Rauh, J. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation 94 (2): 199-209.

Mascaro, J., Harris, J.A., Lach, L., Thompson, A., Perring, M.P., Richardson, D.M., Ellis, E.C. 2013. Origins of the novel ecosystems concept. In: Hobbs, R.J., Higgs, E.S., Hall, C.M. (Eds.) Novel Ecosystems: Intervening in the New Ecological World Order. Wiley-Blackwell, pp. 45-57.

McCune, B., Mefford, M.J. 1999. PC-ORD. Multivariate Analysis of Ecological Data. MjM Software Design, Gleneden Beach, Oregon, USA.

McCune, B., Grace, J.B. 2002. Analysis of Ecological Communities. MjM Software, Gleneden Beach, Oregon, USA.

McGuire, J.P., Mitchell, R.J., Moser, E.B., Pecot, S.D., Gjerstad, D.H., Hedman, C.W. 2001. Gaps in a gappy forest: plant resources, longleaf pine regeneration, and understory response to tree removal in longleaf pine savannas. Canadian Journal of Forest Research 31: 765-778.

McRoberts, R.E., Winter, S., Chirici, G., LaPoint, E. 2012. Assessing forest naturalness. Forest Science 58 (3): 294-309.

Messerli, B., Grosjean, M., Hofer, T., Nunez, L., Pfister, C. 2000. From nature-dominated to human-dominated environmental changes. Quaternary Science Reviews 19: 459-479.

Milton, S.J. 2003. Emerging ecosystems – a washing stone for ecologists, economists and sociologists? South African Journal of Science 99: 404-406.

Moora, M. Daniell, T., Kalle, H., Liira, J., Püssa, K., Roosaluste, E., Öpik, M., Wheatley, R., Zobel, M. 2007. Spatial pattern and species richness of boreonemoral forest understorey and its determinants – a comparison of differently managed forests. Forest Ecology and Management 250: 64-70.

Muona, J., Rutanen, I. 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forest. Annales Botanici Fennici 31: 109-121.

Nagendra, H. 2007. Drivers of reforestation in human-dominated forests. Proceedings of the National Academy of Sciences of the United States of America 104 (39): 15218-15223.

Niemelä, J., Koivula, M., Kotze, D.J. 2007. The effects of forestry on carabid beetles (Coleoptera: Carabidae) in boreal forest. Journal of Insect Conservation 11: 5-18.

Niklasson, M., Drakenberg, B. 2001. A 600-year tree-ring history from Norra Kvills National Park, southern Sweden: implications for conservation strategies in the hemiboreal zone. Biological Conservation 101: 63-71.

Nilsson, T. 1997. Survival and habitat preferences of adult *Bolitophagus reticulates.* Ecological Entomology 22: 82-89.

Noble, I.R., Dirzo, R. 1997. Forests as human-dominated ecosystems. Science 277: 522-525.

Okland, R.H., Rydgren, K., Okland, T. 2003. Plant species composition of boreal spruce swamp forests: closed doors and windows of opportunity. Ecology 84: 1909-1919.

Oliver, C.D., O'Hara, K.L. 2005. Effects of restoration at the stand level. In: Stanturf, J.A., Madsen, P. (Eds.) Restoration of boreal and temperate forests. CRC Press, pp. 31-59.

Olsson, J., Jonsson, B.G. 2010. Restoration fire and wood-inhabiting fungi in a Swedish *Pinus sylvestris* forest. Forest Ecology and Management 259: 1971-1980

Ostonen, I., Lõhmus, K., Alama, S., Truu, J., Kaar, E., Vares, A., Uri, V., Kurvits, V. 2006. Morphological adaptations of fine roots in scots pine (Pinus sylvestris L.), silver birch (Betula pendula roth.) and black alder (Alnus glutinosa (L.) Gaertn.) stands in recultivated areas of oil shale mining and semicoke hills. Oil Shale 23 (2): 187-202.

Pasanen, H., Junninen, K., Kouki, J. 2014. Restoring dead wood in forests diversifies wood-decaying fungal assemblages but does not quickly benefit red-listed species. Forest Ecology and Management 312: 92-100.

Pensa, M., Sellin, A., Luud, A., Valgma, I. 2004. An analysis of vegetation restoration on opencast oil shale mines in Estonia. Restoration Ecology 12 (2): 200-206.

Penttilä, R., Junninen, K., Punttila, P., Siitonen, J. 2013. Effects of forest restoration by fire on polypores depend strongly on time since disturbance – A case study from Finland based on a 23-year monitoring period. Forest Ecology and Management 310: 508-516.

Perring, M.P., Manning, P., Hobbs, R.J., Lugo, A.E., Ramalho, C.E., Standish, R.J. 2013. Novel urban ecosystems and ecosystem services. In: Hobbs, R.J., Higgs, E.S., Hall, C.M. (Eds.) Novel Ecosystems: Intervening in the New Ecological World Order. Wiley-Blackwell, pp. 310-325.

Pickett, S.T.A., White, P.S. 1985. Patch dynamics: A synthesis. In: Pickett, S.T.A., White, P.S. (Eds.) The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Pommerening, A., Murphy, S.T. 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. Forestry 77 (1): 27-44.

Prach, K., Hobbs, R.J. 2008. Spontaneous succession versus technical reclamation in the restoration of disturbed sites. Restoration Ecology 16 (3): 363-366.

Prach, K., Pyšek, P. 2001. Using spontaneous succession for restoration of human-disturbed habitats: experience from Central Europe. Ecological Engineering 17: 55-62.

Prach, K., Rehounkova, K., Rehounek, I., Konvalinkova, P. 2011. Ecological restoration of central European mining sites: a summary of a multi-site analysis. Landscape Research 36 (2): 263-268.

Prescott, C.E. 2002. The influence of the forest canopy on nutrient cycling. Tree Physiology 22: 1193-1200.

Pywell, R.F., Bullock, J.M., Roy, D.B., Warman, L., Walker, K.J., Rothery, P. 2003. Plant traits as predictors of performance in ecological restoration. Journal of Applied Ecology 40: 65-77.

Qian, H., Klinka, K., Sivak, B. 1997. Diversity of the understorey vascular vegetation in 40 year-old old-growth forest stands on Vancouver Island, British Columbia. Journal of Vegetation Science 8: 773-780.

Reintam, L., Kaar, E., Rooma, I. 2002. Development of soil organic matter under pine on quarry detritus of open-cast oil-shale mining. Forest Ecology and Management 171: 191-198.

Richardson, P.J., Lundholm, J.T., Larson, D.W. 2010. Natural analogues of degraded ecosystems enhance conservation and reconstruction in extreme environments. Ecological Applications 20: 728-740.

Roberge, J.M., Angelstam, P., Villard, M.A. 2008. Specialised woodpeckers and naturalness in hemiboreal forests – deriving quantitative targets for conservation planning. Biological Conservation 141: 997-1012.

Rouvinen, S., Kuuluvainen, T., Siitonen, J. 2002. Tree mortality in a *Pinus sylvestris* dominated boreal forest landscape in Vienansalo wilderness, eastern Fennoscandia. Silva Fennica 36 (1): 127-145.

Ruokolainen, L., Salo, K. 2009. The effect of fire intensity on vegetation succession on a sub-xeric heath during 10 years after wildfire. Annales Botanici Fennici 46: 30-42.

Ruzicka, J., Hansen, E.H. 1981. Flow Injection Analysis. John Wiley and Sons, New York.

Šaudyte, S., Karazija, S., Belova, O. 2005. An approach to assessment of naturalness for forest stands in Lithuania. Baltic Forestry 11 (1): 39-45.

Scheller, R.M., Mladenoff, D.J. 2002. Understorey species patterns and diversity in old-growth and managed northern hardwood forests. Ecological Applications 12: 1329-1343.

Shannon, C.E. 1948. The mathematical theory of communication. In: Shannon, C.E., Weaver, W. (Eds.) The Mathematical Theory of Communication. University of Illinois Press, Urbana, pp. 3-91.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49: 11-41.

SER. 2004. The SER International Primer on Ecological Restoration. Society for Ecological Restoration International Science & Policy Working Group. www.ser.org.

Similä, M., Kouki, J., Martikainen, P. 2003. Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. Forest Ecology and Management 174: 365-381.

Similä, M., Junninen, K. 2012. Ecological restoration and management in boreal forests – best practices from Finland. Metsähallitus, Vantaa.

Stanturf, J.A., Schoenholtz, S.H., Schweitzer, C.J., Shepard, J.P. 2001. Achieving restoration success: myths in bottomland hardwood forests. Restoration Ecology 9 (2): 189-200.

Stanturf, J.A., Madsen, P. 2002. Restoration concepts for temperate and boreal forest of North America and Western Europe. Plant Biosystems 136: 143-158.

Stanturf, J.A., Madsen, P., Gardiner, E.S. 2004. Silviculture for restoration of degraded temperate and boreal forests. In: Kangur, A., Kivastik, S. (Eds.) Proceedings of the International Conference on Natural Disturbances and Ecosystem-Based Forest Management, May 27-29, Tartu, Estonia, pp. 1-3.

Stanturf, J.A. 2005. What is forest restoration? In: Stanturf, J.A., Madsen, P. (Eds.) Restoration of boreal and temperate forests. CRC Press, pp. 3-11.

Stanturf, J.A., Gardiner, E.S., Shepard, J.P., Schweitzer, C.J., Portwood, C.J., Dorris Jr, L.C. 2009. Restoration of bottomland hardwood forests across a treatment intensity gradient. Forest Ecology and Management 257: 1803-1814.

Stanturf, J.A., Palik, B.J., Williams, M.I., Dumroese, R.K., Madsen, P. 2014. Forest restoration paradigms. Journal of Sustainable Forestry 33 (S1): S161-S194.

Suffling, R., Perera, A.H. 2004. Characterizing natural forest disturbance regimes: concepts and approaches. In: Perera, A.H., Buse, L.J., Weber, M.G. (Eds.) Emulating Natural Forest Landscape Disturbances: Concepts and Applications, Columbia University Press, New York, pp. 43–54.

Süda, I. 2009. New woodland beetle species (Coleoptera) in Estonian fauna. Forestry Studies 50: 98-114. [In Estonian with English summary].

Taylor, S.L., MacLean, D.A. 2007. Spatiotemporal patterns of mortality in declining balsam fir and spruce stands. Forest Ecology and Management 253: 188-201.

Toivanen, T., Liikanen, V., Kotiaho, J.S. 2009. Effects of forest restoration treatments on the abundance of bark beetles in Norway spruce forests of southern Finland. Forest Ecology and Management 257: 117-125.

Toivanen, T., Heikkilä, T., Koivula, M.J. 2014. Emulating natural disturbances in boreal Norway spruce forests: Effects on ground beetles (Coleoptera, Carabidae). Forest Ecology and Management 314: 64-74.

Tomppo, E., Heikkinen, J. Henttonen, H.M., Ihalainen, A., Katila, M., Mäkelä, H., Tuomainen, T., Vainikainen, N. 2011. Designing and Conducting a Forest Inventory – case: 9th National Forest Inventory of Finland. Springer.

Toomik, A., Liblik, V. 1998. Oil shale mining and processing impact on landscapes in north-east Estonia. Landscape and Urban Planning 41: 285-292.

Tullus, A. 2010. Tree growth and the factors affecting it in young hybrid aspen plantations. A Thesis for applying for the degree of Doctor of Philosophy in Forestry. Tartu.

Tullus, T. 2013. Understorey vegetation and factors affecting it in young deciduous forest plantations on former agricultural land. A Thesis for applying for the degree of Doctor of Philosophy in Forestry. Tartu.

Urbanska, K.M., Webb, N.R., Edwards, P.J. 1997. Why restoration? In: Urbanska, K.M., Webb, N.R., Edwards, P.J. (Eds.) Restoration Ecology and Sustainable Development. University Press, pp. 3-7.

Uri, V., Lõhmus, K., Kiviste, A., Aosaar, J. 2009, The dynamics of biomass production in relation to foliar and root traits in a grey alder (*Alnus incana* (L.) Moench) plantation on abandoned agricultural land. Forestry 82 (1): 61-74.

Uotila, A., Kouki, J., Kontkanen, H., Pulkkinen, P. 2002. Assessing the naturalness of boreal forests in eastern Fennoscandia. Forest Ecology and Management 161: 257-277.

Van Andel, J., Grootjans, A.P. 2006. Concepts in restoration ecology. In: van Andel, J., Aronson, J. (Eds.) Restoration Ecology. Blackwell Publishing, pp. 16-28.

Van Diggelen, R., Grootjans, A.P., Harris, J.A. 2001. Ecological restoration: state of the art of state of the science? Restoration Ecology 9: 115-118.

Vanha-Majamaa, I., Lilja, S., Ryömä, R., Kotiaho, J.S., Laaka-Lindberg, S., Lindberg, H., Puttonen, P., Tamminen, P., Toivanen, T., Kuuluvainen, T. 2007. Rehabilitating boreal forest structure and species composition in Finland through logging, dead wood creation and fire: The EVO experiment. Forest Ecology and Management 250: 77-88.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M. 1997. Human Domination of Earth's Ecosystems. Science 277: 494-499.

Voolma, K., Õunap, H. 2006. Diversity and abundance of insects and some other arthropods in unmanaged and managed forests. Forestry Studies 44: 95-111. [in Estonian with English summary].

Vorobjova, L.A. 1998. Khimitcheskaja analis potchv: utchebnik. Ist. Moskovskovo Universiteta.

Wali, M.K. 1992. Ecosystem rehabilitation: Ecosystem analysis and synthesis. SPB Academic Publishing, The Hague.

Walker, L.R., Walker, J., del Moral, R. 2006. Forging a new alliance between succession and restoration. In: Walker, L.R., Walker, J., Hobbs, R.J. (Eds.) Linking Restoration and Ecological Succession. Springer, New York, pp. 1-18.

Wallenius, T.H., Lilja, S., Kuuluvainen, T. 2007. Fire history and tree compostion in managed *Picea abies* stands in southern Finland: Implications for restoration. Forest Ecology and Management 250: 89-95.

White, C.A., Perrakis, D.D.B., Kafka, V.G., Ennis, T. 2011. Burning at the edge: integrating biophysical and eco-sultural fire processes in Canada's parks and protected areas. Fire Ecology 7 (1): 74-105.

Wikars, L.O. 2002. Dependence on fire in wood-living insects: An experiment with burned and unburned spruce and birch logs. Journal of Insect Conservation 6: 1-12.

Wilson, S.D. 2000. Heterogeneity, diversity and scale in plant communities. In: Hutchings, M.J., John, E.A., Stewart, A.J. (Eds.) Ecological Consequences of Habitat Heterogeneity. Blackwell Science, Oxford, pp. 53-69.

Winter, S. 2012. Forest naturalness assessment as a component of biodiversity monitoring and conservation management. Forestry 85 (2): 293-304.

Zhu, J., Matsuzaki, T., Lee, F., Gonda, Y. 2003. Effect of gap size created by thinning on seedling emergency, survival and establishment in a coastal pine forest. Forest Ecology and Management 182: 339-354.

Zobel, M. 1989. Secondary forest succession in Järvselja, southeastern Estonia: changes in field layer vegetation. Annales Botanici Fennici 26: 171-182.

Young, T.P. 2000. Restoration ecology and conservation biology. Biological Conservation 92: 73-83.

SUMMARY IN ESTONIAN

METSAÖKOSÜSTEEMI TAASTAMISE SEIRE JA ANALÜÜS

Sissejuhatus

Tänapäeval arvestatakse metsade majandamisel puidutootmise kõrval üha enam ka teiste metsakasutuse viiside ja väärtustega, mis tähendab sageli seda, et eesmärgist lähtuvalt tuleb leida tasakaal metsaökosüsteemi kaitsmise ja majandamise vahel. Üldiselt on intensiivne metsade majandamine põhjustanud metsade struktuuri ja liigilise koosseisu lihtsustumist ning muutnud looduslike häiringute dünaamikat. Maailmas pööratakse järjest enam tähelepanu nii inimeste kui ka kliimast tingitud muutustele ökosüsteemides ja nende muutuste komplekssele mõjule, et tagada olemasolevate funktsioonide ja väärtuste säilimine ka muutunud tingimuste korral. Seetõttu tuleks eelkõige kaitsealustes metsades jälgida ja taastada metsade looduslikku funktsionaalsust. Metsi oskuslikult majandades saab vähendada majandamisvõtete negatiivset mõju elurikkusele ja säilitada metsaökosüsteemide looduslikke funktsioone.

Ökoloogiline taastamine kui tegevusvaldkond on viimase paarikümne aasta jooksul kiiresti arenenud, taastamistegevused on praktikas laialdaselt kasutusel kogu maailmas. Ökoloogilise taastamise eesmärk on kiirendada muudetud, rikutud või hävitatud ökosüsteemides loodusliku taastumise protsesse. Metsaökosüsteemide taastamise eesmärk pole mitte ainult taasmetsastamine, vaid ka looduslike protsesside kiirendamine ja taaskäivitamine, looduslike struktuurielementide olemasolu tagamine ning soovitud liikide vajadustest tingitud elupaikade struktuuri ja funktsionaalsuse taastamine. Metsaökosüsteemi taastamist võib vaadata erinevatest aspektidest: kaevandamisega rikutud alade taasmetsastamine, metsa häiringurežiimi taastamine, loodusmetsade struktuurikomponentide tekitamine madala loodusväärtusega aladele ning aladele, kus loodusliku taastumise protsess on väga aeglane.

Looduslik ökosüsteem on taastamistegevusele eesmärkide seadmisel eeskujuks. Looduslikud metsad on mitmekesised nii puude ruumilise paiknemise, vanuselise ja liigilise koosseisu kui ka seal elavate erinevate organismide poolest. Surnud puit on nii jalalseisva kui ka lamapuiduna üheks loodusmetsade hindamise oluliseks indikaatoriks. Looduslikkuse hindamine on kompleksne ülesanne, mis hõlmab nii puistudünaamika, häiringute kui ka keskkonnamuutuste ja inimmõjude hindamist. Metsaökosüsteemide looduslikkus on pidev tunnus, kus äärmusteks on ühelt poolt „puupõllud“ ja teiselt poolt inimtegevusest puutumata ürgmetsad.

Doktoritöös käsitletakse ja analüüsitakse metsade taastamise erinevaid aspekte ja komponente. Doktoritöö eesmärkideks oli: 1) uurida puistute looduslikkuse indikaatoreid ning hinnata puistute looduslikkust (**I**), 2) määrata puistus üksikpuu suremist mõjutavad faktorid (**IV**), 3) analüüsida looduslikkuse taastamise võtete mõju puistu dünaamikale ja elurikkusele majandatud metsades (**II**), 4) analüüsida kaevandamisjärgsel taasmetsastamisel tekkinud ökosüsteemi (**III**). Töös püstitati järgmised hüpoteesid: 1) puude suremise põhjuste mitmekesisuse ning surnud puude paiknemise järgi puistus saab paremini hinnata puistu looduslikkust, 2) taastamisvõtted kiirendavad looduslike struktuurielementide lisandumist puistusse, 3) erinevad taastamisvõtted avaldavad erinevat mõju puistu struktuurile, surnud puidu voole ja liigilisele mitmekesisusele, 4) aastakümnete jooksul peale kaevandamisjärgset taasmetsastamist on välja arenenud uudne ökosüsteem.

Materjal ja metoodika

Doktoritöös kasutati kolme andmekogu (joonis 4.1): 1) Eesti metsa kasvukäigu püsiproovitükkide andmed (**I**; **IV**), 2) metsade looduslikkuse taastamise katsealade andmed (**II**), 3) taasmetsastatud Aidu põlevkivikarjääri püsiproovialade andmed (**III**).

Eesti metsa kasvukäigu püsiproovitükkide võrgustik koosneb 693 proovitükist üle Eesti; esimesed proovitükkide mõõtmised algasid 1995. aastal ning 5-aastase intervalliga mõõtmine jätkub seniajani. Metsade looduslikkuse taastamise 50 katseala rajas 2004. aastal Eesti Metsakaitsealade Võrgustik (EMKAV). Taastamisvõtetena kasutati häilu raiumist (G), lamapuidu tekitamist (DW), häilu raiumist koos lamapuidu jätmisega (GDW) ning häilu raiumist ja ülepõletamist (GB). 23 proovitükki jäeti kontrollaladeks (C). Inventuurid tehti enne taastamisvõtete tegemist, üks aasta pärast võtteid ning neli aastat pärast võtete tegemist. Aidu põlevkivikarjääri hakati kaevandamise järel järk-järgult metsastama hariliku männiga (*Pinus sylvestris* L.) 1981. aastal.

Taasmetsastatud Aidu karjääri rajati 2011. aastal püsiproovitükkide võrgustik (60 proovitükki), et jälgida taasmetsastamise tulemusi ning ökosüsteemi arengut erivanuselistes puistutes karjääri sulgemise järel.

Puistute looduslikkust uuriti 294 püsiproovitükil üle Eesti (**I**). Looduslikkuse hindamise metoodika põhineb Eesti Metsakaitsealade Võrgustiku projekti käigus koostatud puistu loodusväärtuste, kultuurilis-bioloogiliste väärtuste ning negatiivsete inimmõjude hindamismeetodil, punktiskoori järgi saab määrata puistute looduslikkuse seisundit (joonis 4 artiklis **I**).

Kõikide proovitükkide (640 tk) puistu mõõtmistel kasutati Eesti metsa kasvukäigu püsiproovitükkide metoodikat. Puistu struktuuri ning seisukorra kirjeldamiseks mõõdeti igal proovitükil kõikidel puudel diameeter, mudelpuudel kõrgus, määrati puude suremise põhjused nendel puudel, mis olid eelmisel mõõtmisel elus olnud ning viimase viie aasta jooksul surnud (**I**; **II**). Puude suremise põhjuste mitmekesisuse uurimiseks koostati suremise põhjuste mitmekesisuse indeks (CMDI), mis annab hinnangu suremise põhjuste mitmekesisusele puistus (valem 3 artiklis **I**). Surnud puude ruumilise paiknemise uurimiseks arendati välja surnud puude ruumilise paiknemise indeks (DMi), mis põhineb surnud puule nelja lähima naaberpuu seisukorral (surnud või elus) (valem 4 artiklis **I**). Kui DMi väärtus on 1, siis on kõik neli naaberpuud surnud, kui DMi väärtus on 0, siis on naaberpuud elus. Selle meetodi järgi saab hinnata, kas surnud puud on puistus hajutatult või kobaras koos.

Puu ellujäämistõenäosuse hindamisel kasutati 31 097 puu andmeid 236 proovitükilt (**IV**). Ellujäämistõenäosuse arvutamiseks sõltuvalt üksikpuu tunnustest kasutati logistilist regressiooni (valem 20 artiklis **IV**).

Liigilise mitmekesisuse inventeerimisel kasutati metsade looduslikkuse taastamise juhendit, kõik liigiinventuurid tegid vastava eriala spetsialistid. Alustaimestiku liigilise mitmekesisuse määramiseks kasutati 100 sammu meetodit 25 m^2 suurusel püsialal (**II**) ning nelja 1 m^2 suurust püsiprooviala (**III**). Määrati kõikide liikide esinemine ning katvus. Samblike seire viidi läbi selleks valitud püsiseirepuudel (elusad, surnud, kännud) (**II**). Määrati liikide esinemine ning ohtrus. Putukate seirel kasutati 18 akenpüünist, mida tühjendati juunist septembrini (kuus korda), ning määrati kõik püünistes olevad liigid ning isendite arv (**II**).

Liigirikkuse analüüsimisel kasutati programmi SAS protseduuri GLIMMIX. Liigilise mitmekesisuse hindamiseks kasutati Shannoni indeksit. Indikaatorliikide analüüsiga leiti erinevatele taastamisvõtetele indikaatorliigid, kasutades selleks programmi PC-ORD. Indikaatorväärtuste olulisuse hindamiseks tehti Monte Carlo test. Puistustruktuuri muutuse hindamiseks läbi aja (**II**) ning taasmetsastatud ja loodusliku arenguga puistute ordineerimiseks mõõdetud parameetrite järgi (**III**) kasutati peakomponentanalüüsi (PCA). Statistilist olulisust testiti mitmese reaktsiooni permutatsiooni protseduuriga (MRPP). Usaldusnivoo kõikide analüüside korral oli $p < 0,05$.

Tulemused ja järeldused

Looduslikkuse hindamisel selgus, et majandatud metsa ning looduslikus seisundis metsa punktiskoorid erinevad statistiliselt üksteisest oluliselt (vastavad keskmised 8 ja 24). Surnud puidu kogus, ruumiline jaotus, samuti suremise kiirus ja põhjused on tihedas seoses puistu looduslikkusega (**I**). Surnud puidu maht looduslikus seisundis ja majandatud metsas erinevad üksteisest oluliselt (joonis 5.1). Puude suremise hindamine võimaldab paremini aru saada metsaökosüsteemi struktuurist ja seal toimivatest protsessidest (**I**). Seeläbi kogutakse infot puistu tootlikkuse, elurikkuse ja tervisliku olukorra kohta. Puistus põhjustab puude suremist kas mõni kindel häiringuagent või erinevate häiringuagentide koosmõju. Üksikpuude suremise põhjuste hindamine ja analüüsimine on vajalik metsade inventeerimisel ja korraldamisel. Puu ellujäämine sõltub kõige enam puu suhtelisest diameetrist puistus (**IV**) ning puu suremise põhjused erinevat tüüpi puistutes on erinevad (joonis 5.2). Suremise põhjuste mitmekesisus on suurem looduslikus seisundis puistutes ning samuti on surnud puude paiknemine sellises puistus rohkem hajutatud (**I**), töös väljatöötatud indeksid pakuvad võimalusi paremini hinnata puistu looduslikkust ja seejuures eristada puistus toimunud hiljutisi häiringuid.

Puistu struktuuri mitmekesisemaks muutmine ning looduslike elementide lisamine on sageli metsaökosüsteemide looduslikkuse taastamise eesmärkideks. Häilud, puude paiknemise mitmekesine muster, surnud puud, erineva suurusega puud ja erinevad liigid pakuvad elupaiku paljudele teistele liikidele. Looduslikkuse taastamisvõtetega muudeti puistustruktuuri võrreldes taastamiseelse seisundiga oluliselt (joonis 3 artiklis **II**). Kui eelnevalt olid puistud ühetaolised ning sarnased, siis pärast võtteid struktuur mitmekesistus, näiteks surnud puidu maht suurenes võtete DW ja GDW korral kuni 67 m^3 ha^{-1} (**II**). Taastamisvõtted avaldasid erinevatele liigirühmadele erinevat mõju. Häilu suuruse ja puistu kõrguse suhtarv määrab häilus olevad valgustingimused: kui suhtarvu väärtus on üks või suurem, siis on seal arvukam looduslik uuendus ja edukas valgusnõudlike liikide esinemine. Loodusliku uuenduse arvukus oli kõrgeim pindalalt suuremas häilus ning taastamisvõtte GB korral (**II**). Rohttaimede liigirikkus ja mitmekesisus suurenesid võtete G, GDW ja GB korral. Sammalde ja samblike keskmine liigirikkus peale võtteid ei muutunud, kuid sammalde mitmekesisuse indeks erines võtete vahel oluliselt (tabel 2 artiklis **II**) ning võtete järel suurenes enim võtte DW korral. Samblike mitmekesisus erines kontrollalade ja võtete vahel, mitmekesisuse indeks suurenes enim võtte G korral, võtte GB korral mitmekesisus vähenes. Kontrollaladest eristub kõige rohkem võte GB rohttaimede, sammalde ja samblike puhul (tabel 5.1). Mardikaliste suurenenud arvukus ja liigiline mitmekesisus on puistu valgustingimuste muutuse ning elupaikade lisandumise (joonis 1 artiklis **II**) otsene tulemus. Võrreldes ühe taastamisvõtte rakendamisega suurendab erinevate taastamisvõtete üheaegne kasutamine puistu heterogeensust ja tänu sellele suureneb ka elurikkus.

Metsade looduslikkuse taastamise võtete mõju elurikkusele (**II**) ja kaevandamisjärgse taastamise edukuse hindamine (**III**) annavad vajalikud teadmised planeerimaks erinevaid taastamisvõtteid ning metsade majandamist. Kaevandamisjärgse taasmetsastamise eesmärk on taastada ökosüsteemide kaevandamiseelne olukord (**III**). Üldjuhul on võimatu taastada minevikus olnud seisundit, sest kaevandamisega on kasvupinnast täielikult muudetud ning tihtipeale areneb seal välja hoopis uudne ökosüsteem. Taastamisedukuse hindamine põhineb mullanäitajate dünaamika, liigilise mitmekesisuse, taimkatte struktuuri ja ökoloogiliste protsesside uurimisel. Endiste kaevandamisalade mullad erinevad tüüpilistest metsamuldadest ja seetõttu on seal taimestiku arenguks tekkinud teistsugused tingimused (joonis 5.3). Samuti erinevad sealsed taimekooslused tüüpilistest metsas esinevatest kooslustest (joonis 5.4, tabel S1 artiklis **III**). Puistu takseernäitajad on sarnaseimad sinilille kasvukohatüübi puistute takseernäitajatega (joonis 5.5). Ala looduslikule arengule jätmine võib taastamisel olla oluline alternatiiv metsaistutamisele, eriti juhul, kui rikutud ala on väike ja ümbritsetud loodusliku taimkattega ning kui alale pole määratud soovitavat eesmärki ning taastumise tähtaega.

Edasised uurimissuunad

Doktoritöö raames tehtud uuringud on kavandatud jätkuma pikemaajalise uurimisprogrammi osana. Metsade taastamise võtete ning ökosüsteemi taastumise mõjude uurimine on pikaajaline protsess, mis vajab katsealade edasist jälgimist ning annab infot edasisteks praktilisteks tegevusteks metsade majandamisel. Looduslike metsaökosüsteemide dünaamika kui taastamise eesmärgi kirjeldamine on muutuvate kliimatingimuste korral suhteliselt keeruline ülesanne. Seetõttu on kavas jätkata looduslike metsaökosüsteemide uuringuid püsiproovitükkidel ning katsealade võrgustikku laiendada ka põlismetsa tunnustega puistutesse.

ACKNOWLEDGEMENTS

I would like to express my greatest thanks to my supervisor Henn Korjus for his guidance, support and encouragement in my studies through Bachelor's, Master's and PhD years. Thank you very much!

I am very grateful to my supervisor John Stanturf who made me believe that my research area is very important worldwide and significant for Estonia, as well. Beside our student-supervisor relationship our families have become close. I am very touched that Eileen and John have treated me and my family as we were their family. I will always remember their warmth and kindness. Thank you for everything!

My deepest thanks belong to Professor Andres Kiviste who suggested that I enter the Master's studies when I was a Bachelor's student in the distance learning programme and the Master's programme was the only short step towards PhD studies. Thank you for your confidence in me with project management. You were always there when I needed some advice or technical skills.

I would like to thank all my colleagues at the Department of Forest Management and fellow students who have helped me in fieldwork during the years and given me valuable comments and advice. Special thanks to Allan who has showed me that statistics can be easy, Ahto who has taught me patience, and Maris and Andres for our long discussions over a cup of coffee.

I would like to thank all people who have been involved in my fieldwork. I am thankful to Ilmar Süda, Ede Leppik, Liis Kasari, Krista Takkis, Hedi Pedajas and others who carried out specific species inventories.

Kõige suurem tänu Jaanile, kes on olnud mulle alati suurimaks toeks; toredatele lastele – Gretele ja Kris Gregorile, kes on pidanud leppima sellega, et olen tihti olnud kodust eemal. Suured tänusõnad emale toetuse ja õpetuse eest, et võetud kohustused tuleb alati täita. Siiani jõudmine võttis aega 14 pikka aastat, aga on seda väärt!

The studies in this thesis were financially supported by grants from the Estonian Environmental Investment Centre, the Estonian Research Council, the Environmental Board, Metsahoiu Sihtasutus, OÜ Eesti Metsakeskus and the Estonian University of Life Sciences.

I

ORIGINAL PUBLICATIONS

Laarmann, D., Korjus, H., Sims, A.,
Stanturf, J.A., Kiviste, A., Köster, K. 2009.
Analysis of forest naturalness and tree mortality patterns in Estonia.
Forest Ecology and Management 258S: S187-S195.

Forest Ecology and Management 258S (2009) S187–S195

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Analysis of forest naturalness and tree mortality patterns in Estonia

Diana Laarmann [a,*], Henn Korjus [a], Allan Sims [a], John A. Stanturf [b], Andres Kiviste [a], Kajar Köster [a]

[a] *Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Kreutzwaldi 5, Tartu, Estonia*
[b] *Southern Research Station, US Forest Service, Green Street 320, Athens, GA 30602, USA*

ARTICLE INFO

Article history:
Received 13 February 2009
Received in revised form 26 June 2009
Accepted 2 July 2009

Keywords:
Deadwood
Forest disturbance
Forest naturalness
Mingling
Tree mortality

ABSTRACT

New methods for evaluating structural properties of stands and individual tree mortality within forests are needed to enhance biodiversity assessment in forest inventories. One approach is to assess the degree of naturalness in a forest. We assessed forest naturalness by examining patterns and causes of mortality and deadwood amount and spatial distribution as indicators of naturalness, or degree of anthropogenic disturbance. This study is based on 5-year interval measurement using 294 permanent samples plots from a forest growth network in Estonia. The average annual mortality was 1.3% from stem number counting 29% of Scots pine, 27% of silver and downy birch and 20% of Norway spruce. Most common reasons for the individual tree death were growth-dependent reasons (45%), fungi (23%) and wind damage (16%). Modelling showed that relative diameter of a tree in a stand is significantly related to mortality probability. Modelling the reasons of tree death showed that with increasing relative diameter there was a greater probability that mortality was caused by wind or damage from game (mostly moose (*Alces alces* L.)), insect or fungi and a lower probability that mortality was due to competition between trees. Use of structural variable such as deadwood mingling, which was based on the neighbouring trees, improved the assessment of forest naturalness and helped to distinguish recent disturbances. A comparison of deadwood mingling and nature value scores in managed and semi-natural forests showed that dead trees were more dispersed and the naturalness score was higher in semi-natural forest stands. The nature score was significantly correlated with the diversity of mortality causes indicating that mortality causes are more diverse in semi-natural stands. Mean values and distribution of the deadwood mingling index in managed and semi-natural forests were not significantly different. In middle-aged semi-natural forests, mortality is spatially more random than in managed forests, thus there is no evidence of gap formation yet.

1. Introduction

Forests in Baltic countries are structurally diverse, often with complex structures (Nilson, 1996). Factors that have contributed to this structural diversity include infrequent management intervention, reliance on natural regeneration methods, as well as great variation in site conditions within stands, even in commercial forests (Jõgiste, 1998). New methods for evaluating structural properties of ecosystems and mortality within forests are needed to enhance biodiversity assessment in forest inventories (Lee et al., 2000). Increasingly, the importance of stand dynamics and resulting structural properties are recognized in forest management and modelling (Ozolincius et al., 2005; Kint et al., 2004; Gadow, 1993) and environmental planning (Pommerening, 2006). One approach is to assess the degree of naturalness in a forest but naturalness is difficult to objectively evaluate in routine forest inventories and therefore is often omitted or very simplified methods are used (McElhinny et al., 2005).

Forest "naturalness" is a complex issue converging forest dynamics, disturbances at different scales, adaptation to changing environment and human influence. Stanturf et al. (2004) stated that even without anthropogenic disturbances it is difficult to specify what constitutes a natural forest in a given place and time. Sprugel (1991) explained that in some regions an equilibrium may exist in which patchy disturbance is balanced with regrowth, but in others equilibrium may be impossible. Where equilibrium does not exist, defining "natural" vegetation becomes much more challenging, because the vegetation would not be stable over long periods even without man's influence. Ecosystems in a steady state (climax ecosystems) are still continuously dynamic and changing due to gap formation caused by the mortality of large trees. Borman and Likens (1994) defined this as a "shifting-mosaic steady state" ecosystem. In many areas it may be unrealistic to define natural vegetation for a site and often several communities could be "natural" vegetation for any given site at any given time. In regions characterized by infrequent or only fine-scale disturbance,

* Corresponding author. Fax: +372 7313156.
E-mail address: diana.laarmann@emu.ee (D. Laarmann).

0378-1127/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2009.07.014

naturalness can be assessed by quantifying the level of human influence to a forest ecosystem. Uotila et al. (2002) define the level of naturalness as the extent to which human influence has affected the current forest structure. Nevertheless, it is often possible to distinguish between managed and unmanaged forests for only a limited interval following a disturbance or management intervention. As managers attempt to emulate natural disturbances in their interventions by adopting principles of "ecological forestry" (Franklin et al., 2007) "continuous cover forestry" (Gadow et al., 2002) or "nature-based silviculture" (Larsen, 1995), definitions of naturalness as being the opposite of anthropogenic disturbances become even more problematic. Despite the difficulty of defining naturalness, it is an accepted concept in European forest management and nature conservation and an ability to assess forest naturalness is important for forest management and conservation decisions (Šaudyte et al., 2005).

In this study we used a random selection of commercially managed forests between 10 and 170 years of age in Estonia. We examined the usefulness of individual tree mortality and composition and structure of deadwood for evaluation of forest naturalness and biodiversity value at the stand level, with application for forest inventory methods. Our rationale was that because of the relatively undisturbed nature of forests in Estonia, mortality and deadwood were useful for operationally defining "naturalness". Individual tree death and replacement (fine-scale disturbance) as a process guarantees vitality and dynamics of forest ecosystems. Its main features are altered forest structure and release of additional resources for the remaining trees and other organisms (Köster et al., 2005). The process of tree mortality is critical for understanding forest stand dynamics (Juknys et al., 2006; Ozolincius et al., 2005; Monserud and Sterba, 1999) and a likely indicator of naturalness (Debeljak, 2006; Rouvinen et al., 2002). Assessment of individual tree mortality permits evaluation of stand development stage and the level of human influence. Deadwood structure includes both the variety and condition of individuals such as snags and logs and their spatial arrangement. These attributes change during stand development and the amount and structure of deadwood is another indicator of the level of human disturbance, i.e., the amount of material that has been removed in harvests.

There are different ways to categorize causes of tree death. One possibility is to distinguish between abiotic and biotic factors (Franklin et al., 1987; Rouvinen et al., 2002). Abiotic factors are fire, wind, flooding, snow breakage etc. Biotic causes of tree mortality are diseases, insects, mechanical imbalance, old age etc. Another possibility is to group tree mortality into density-dependent (Greenwood and Weisberg, 2008) and density-independent factors (Franklin et al., 2002; Ozolincius et al., 2005). Density-dependent tree mortality is due to competition among individuals (self-thinning mortality) and density-independent mortality is due to other agents.

Our specific hypotheses were that (a) multiple causes (processes) for individual tree mortality are a good indicator of naturalness in a forest stand; (b) the spatial distribution of dead trees within a stand is a good indicator of naturalness, specifically in middle-aged semi-natural forests, dead trees are not clumped together as they would be in a managed forest; (c) deadwood properties (distribution by size, spectrum of mortality causes, species composition) may be used to detect recent forest disturbances in a stand; and (d) trees with smaller relative diameter are more likely than larger trees to have died because of tree competition.

2. Material and methods

2.1. Estonian forest growth network

Estonia is situated in the hemiboreal vegetation zone (Ahti et al., 1968) and covers a broad range of biogeographical conditions. The climate varies from maritime to continental. Average annual precipitation increases from west to east within a range of 600–700 mm. Mean temperature of the warmest month (July) ranges from 16.3 to 17.4 °C; and the coldest month (February) from −2.0 to −7.4 °C.

We used 5-year interval measurement data provided by the Estonian forest growth network permanent research plots. This network was established during the period 1995–2004 and covers all of Estonia (Kiviste et al., 2003). Since 1999, the network of forest research plots has been extended using the sample grid of the ICP Forest level I monitoring plots (Karoles et al., 2000) to place the centers of plot groups. The plot locations in the field were selected randomly on a map and represent the most common forest types and age groups in Estonia. The method of establishing the plots is mainly based on the experience of the Finnish Forest Research Institute (Gustavsen et al., 1988). Data on 98,106 trees from 680 sample plots had been recorded in the database until 2008.

Generally the permanent sample plots were circular with a radius of 15, 20, 25 or 30 m. The size depended on the forest density and age, and as a rule every plot had at least 100 trees in the upper-storey. On each plot the azimuth and distance from plot centre to each tree was recorded along with its diameter at breast height (DBH) and defects. For every fifth tree and also for dominant

Fig. 1. Geographic location of study areas (black dots). Grey area indicates forests in Estonia.

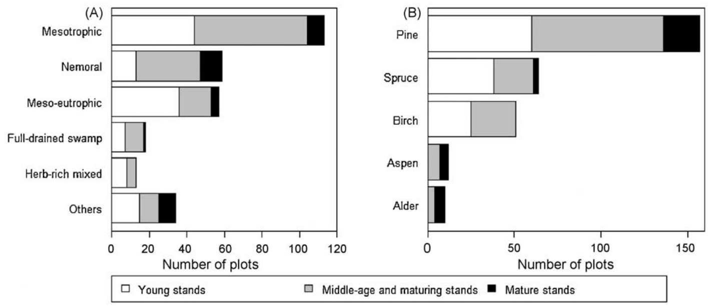


Fig. 2. Distribution of plots by groups of forest site types (A) and main tree species (B). The site type "others" includes alvar, bog moss, heath, paludified and fen forests. Age classes are appropriate to the dominant species (e.g., mature pine stands are considerably older than mature alder stands).

and rare tree species, tree height and height to crown base were measured. (Kiviste and Hordo, 2003).

Relative tree diameters were calculated for each measured tree, where relative diameter is defined as the ratio of an individual tree's diameter to the mean diameter of the stand (Eid and Tuhus, 2001). A relative tree diameter value <1.0 indicates a tree smaller than the stand average tree. Measurement records were available for living trees (upper-, mid-, under-storey and shrub layer trees), dead trees (standing, downed, and broken trees) and fresh stumps.

This study was based on 294 sample plots (Fig. 1) and the data from 43,848 trees. Species composition of the sampled trees was 42% Scots pine (*Pinus sylvestris* L.), 25% Norway spruce (*Picea abies* (L.) Karst.), 21% birch (*Betula pendula* Roth. and *Betula pubescens* Ehrh.) and 12% of several deciduous species. Fig. 2 presents distributions of permanent sample plots analyzed in this study by forest site types, dominant species and stand development classes. Distribution of plots by stand age and dominant species is presented in Table 1.

2.2. Analysis of patterns of individual tree mortality

For each sampling period, mortality rate was calculated as the number of trees that died, expressed as a percent of the number of trees living at the beginning of the period. Annual mortality is the number of dead trees in an interval divided by the number of years in the period.

The cause of the mortality (CM) of each dead tree was categorized into density-dependent and density-independent factors. One of the most important density-dependent effects is competition among individual trees including unspecified causes of mortality for suppressed trees. Density-independent mortality was identified more precisely:

a) Wind damage, including wind throw and stem breakage;
b) Game damage, mainly by moose peeling the bark from spruce and pine leading to death of trees;
c) Insect attacks, mainly bark beetle (*Ips sp.*) as primary or secondary causes;
d) Fungi and disease, mainly root rot, heart rot, canker and other pathogens as primary or secondary causes;
e) Other, including flooding, frost or unknown reasons.

The logistic function (Eq 1) (Freund and Littell, 2000) was used to model mortality of individual trees due to the causes considered with each dead tree being an observation, as

$$\mathrm{logit}(p) = \ln\frac{p}{1-p} \tag{1}$$

where p is probability of CM (e.g., wind).

The logit-transformation rendered CM into a dependent variable with a normal distribution, which can be analyzed with methods of regression and variance analysis:

$$\mathrm{Logit}(p) = f(x) \tag{2}$$

where $f(x)$ is a linear function of the vector x of measurement variables.

Goodness of model fit was determined by examining percent concordant values which indicate overall model quality through the association of predicted probabilities and observed responses. The higher the predicted event probability of the larger response variable, the greater the percent concordant value will be.

Diversity index of mortality reasons (CMDI) was adopted from Shannon (1948) H' index for the estimation of diversity in an ecosystem. CMDI can be calculated by the formula:

$$\mathrm{CMDI} = -\sum_{i=1}^{S} p_i \ln(p_i) \tag{3}$$

S = number of CM; p_i = proportion of the CM ($p_i = N_i/N$); N_i = number of dead trees because of $\mathrm{CM_i}$; N = total number of dead trees.

2.3. Deadwood mingling

The spatial distribution of deadwood in a stand can be evaluated by the pattern of mingling of dead and live stems. Deadwood mingling is defined as the proportion of the n nearest

Table 1
Distribution of sample plots by main species and age classes.

Age	Alder	Aspen	Birch	Pine	Spruce
5–14	1				1
15–24			10	18	12
25–34	7	1	18	28	26
35–44	1	4	12	12	14
45–54	1	7	11	26	5
55–64				18	1
65–74				16	2
75–84				16	2
85–94				6	1
95–104				10	
105–114				2	
115–124				3	
135–144				1	
165–174				1	

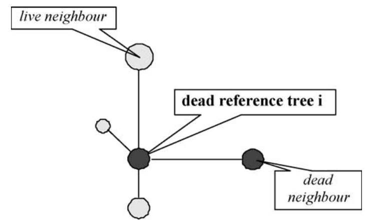


Fig. 3. Structure variable—deadwood mingling for reference tree and four of its nearest neighbours. The mingling index value DM_i is 0.25 in this example.

neighbours that are also dead trees (Fig. 3). We developed a deadwood mingling index (DM_i) using the species mingling formula proposed by Gadow (1993) for a group with four nearest neighbours of a dead reference tree *i*:

$$DM_i = \frac{1}{4}\sum_{j=1}^{4} v_j$$

with

$$v_j = \begin{cases} 1, \text{when the neighbour j is dead tree} \\ 0, \text{when the neighbour j is living tree} \end{cases} \qquad (4)$$

With four neighbours, DM_i can assume five different values: 0, 0.25, 0.50, 0.75 and 1. The mingling index value of 1 indicates that all neighbouring trees of a dead tree are also dead trees; conversely a mingling value of 0 indicates that all neighbouring trees are alive. The distribution of all reference trees or average DM_i can be used as a surrogate for deadwood clumping in a stand. We calculated the DM_i for each plot and tested for homogeneity of variances in deadwood mingling of each category of forest using the Fligner–Killeen test implemented with the R statistical software.

Edge effects should be considered in calculating the mingling index. One way is to consider a buffer zone around the edge of the plot, with a buffer width equal to the distance to the fourth nearest neighbour. This method has been shown to reduce bias effectively in a comparison of several edge correction techniques (Pommerening and Stoyan, 2006). In the case of deadwood mingling, edge effects cannot be effectively adjusted afterwards because there are usually just few dead trees on a plot.

2.4. Nature value assessment

Nature value assessment has been included in sample plot measurements since 2006 using a method that incorporates both quantitative and qualitative scoring (Korjus, 2002). The method is based on evaluating specific stand and landscape attributes to arrive at a score that is compared to a scoreboard (Fig. 4).

Naturalness was measured as different levels of anthropogenic influence in a forest stand. Forests were classified as old-growth, natural, recovering, or commercial forests, depending on the signs of management activities. As most forests in Estonia have been managed or influenced by humans to some degree, by "old-growth" we meant that the remnants have not been managed for at least 200 years. According to the special full-scale inventory of present and possible forest conservation areas (Viilma et al., 2001) there are several hundred hectares of such "old-growth" still existing in Estonia. Natural forest included uneven-aged forests of natural origin with a composition characteristic of the site. Natural forest can bear traces of earlier cuttings but these must have no effect on the present structure of the stand. There is also some downed dead wood in different stages of decomposition in such stands. Recovering forest has come into existence as a result of

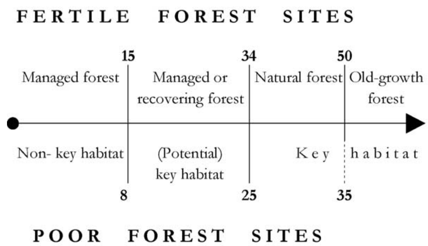


Fig. 4. The scale for evaluating forest naturalness by the method of nature value assessment (Korjus, 2002). Numbers represent total scores of nature value for distinguishing different levels of naturalness and key habitats. For example, on poor forest sites the margin between natural forests and recovering forests is 25 points; on fertile sites the margin between non-key habitats and potential key habitats is 15 points.

human activities, bears numerous traces of earlier cuttings but their effect on the present structure of the stand is insignificant such that the stand would develop into a natural forest in 20–30 years if left untouched. Standing and downed dead wood is present in various amounts in a recovering forest. Compared to a classification for Lithuania (Šaudyte et al., 2005), our recovering forests match their semi-natural forests and the natural forests are the same for both classifications. Managed forests have evidence of cuttings with a strong effect on the species composition and structure of the stand; there is very little or no downed dead wood.

For our sample plots, all old-growth forests, natural forests and recovering forests were regarded as semi-natural forests in the analysis. Of the sample plots, 32 were classified as semi-natural and 262 as managed forests. Large-scale disturbances (at least 15% of trees died within last 5-year) were present on 13 sample plots, all in managed forests.

3. Results

A total of 2493 trees died during the study period from 2001 to 2007. Of the dead trees, 29% were pine, 27% birch, and 20% spruce. The average annual tree mortality rate was 1.3% based on the initial stem numbers. Grey alder (*Alnus incana* (L.) Moench) had the highest mortality rate (4.3%) and pine and spruce had the lowest (0.9%) (Table 2).

Data analysis showed that the main CM was competition (45%) between trees. Scots pine, birch and aspen (*Populus tremula* L.), were the most influenced by tree competition and spruce was the least (Fig. 5). Fungi and diseases was the second commonest CM, accounting for 30% of grey and black alder (*Alnus glutinosa* (L.) Gaertn.) mortality. Wind (wind throw and storm breakage) was the third commonest CM (19%). Spruce was the most influenced (more than 40% of dead trees) and pine the least influenced (10%).

Table 2
Annual mortality rates (% from stem number per year) by tree species and stand development class.

Tree species	Stand development class		
	Young stands	Middle-aged and maturing stands	Mature stands
Scots pine	1.21	0.55	0.48
Norway spruce	1.05	0.97	0.84
Black alder	1.52	1.80	1.43
Birch	1.54	2.05	1.28
Aspen	0.95	2.90	–
Grey alder	–	3.74	5.06

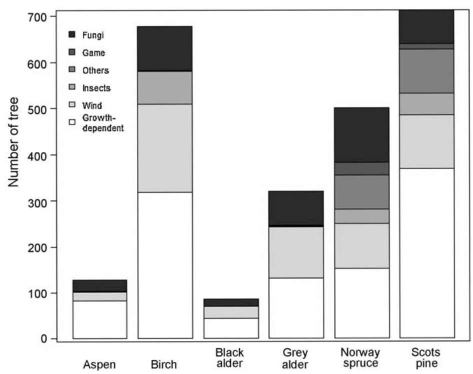


Fig. 5. Distribution of dead trees by causes of mortality (CM) and tree species.

The best relationship between CM and tree size was with relative tree diameter. Growth-dependent causes, wind and insects are showing different behavior related to relative diameter in semi-natural and managed forests (Fig. 6). Growth-dependent causes and wind were relatively less important reasons and insects a more important reason for individual tree mortality in semi-natural stands (Fig. 7). Logistic regression modelling (Table 3) showed that trees with lower relative diameters were more likely to die because of tree competition. Larger relative diameter trees were more likely to die because of wind damage and from game (mostly moose) and insect damage. However there seemed to be no relationship between relative diameter and mortality caused by fungi and diseases. The relationships between causes of mortality and relative diameter differed among species. We found significant relationships between relative diameter and mortality probability for all CM for Scots pine (p-value < 0.001); fungi (p-value < 0.001) and growth-dependent (p-value < 0.001) CM for Norway spruce; and fungi (p-value < 0.001), growth-dependent (p-value < 0.001) and wind (p-value < 0.001) CM for birch trees.

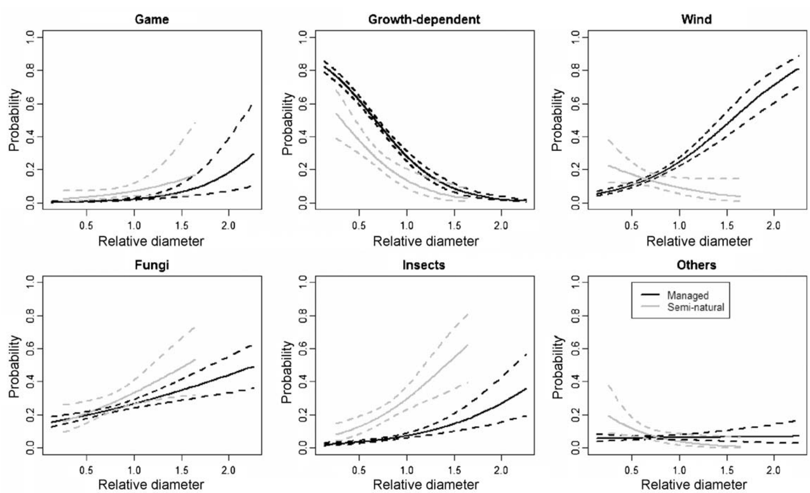


Fig. 6. Predicted probability (%) of different CM (solid line) with 95% confidence limits (dashed lines) depending on relative diameter in managed and semi-natural stands.

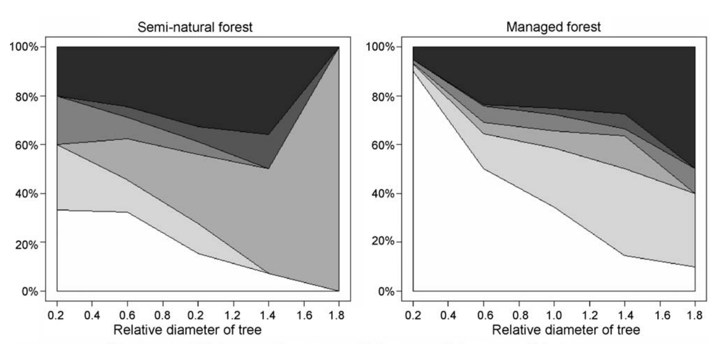


Fig. 7. Probability (%) of CM for individual trees depending from relative tree diameter in semi-natural and managed forests.

Table 3
Results of logistic regression for probability of individual tree mortality on relative diameter of tree (Dr) by different reasons.

Reason for individual tree mortality	Parameter	Estimate	Standard error	Pr > Chi-Square	Percent concordant
Fungi	Intercept	−1.8179	0.1327	<.0001	56.3
	Dr	0.8435	0.1654	<.0001	
Game	Intercept	−5.7174	0.4048	<.0001	69.1
	Dr	2.1289	0.4081	<.0001	
Insects	Intercept	−3.9417	0.2201	<.0001	65.1
	Dr	1.7507	0.2439	<.0001	
Wind	Intercept	−2.9240	0.1579	<.0001	64.6
	Dr	1.6984	0.1854	<.0001	
Growth-dependent	Intercept	1.8309	0.1331	<.0001	69.0
	Dr	−2.8806	0.1855	<.0001	

The average recent deadwood volume (RDV5) for the last 5-year period for all stands was 6.1 $m^3\,ha^{-1}$. The highest average RDV5 was found in aspen stands (15.3 $m^3\,ha^{-1}$), the lowest in black alder stands (1.0 $m^3\,ha^{-1}$) (Fig. 8). The average RDV5 was significantly lower (p-value < 0.001) in managed forests (5.4 $m^3\,ha^{-1}$) than in semi-natural forests (12.3 $m^3\,ha^{-1}$) (Fig. 9). RDV5 is correlated to the number of mortality causes and deadwood mingling (Table 4).

A comparison of deadwood mingling and nature value scores in managed and semi-natural forests showed that dead trees were more dispersed (Fligner–Killeen test, p-value < 0.001) and the naturalness score was higher in semi-natural forest stands (t-test, p-value < 0.001) (Fig. 10). The nature score was significantly correlated with the diversity index of mortality causes (CMDI), indicating that CM are more diverse in semi-natural stands (Table 4). Mean values and distribution of the deadwood mingling index (DM_i) in managed and semi-natural forests (Table 5) were not significantly different. In middle-aged semi-natural forests, mortality is spatially more random than in managed forests, thus there is no evidence of gap formation. Gap formation, however, should be more characteristic of older stands.

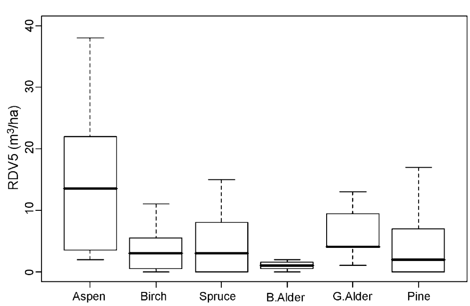


Fig. 8. Amount of recent deadwood volume (RDV5) in stands dominated by different species.

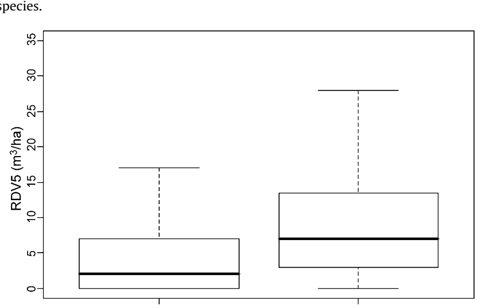


Fig. 9. Comparison of the volume of recent deadwood (RDV5) in managed and semi-natural stands.

4. Discussion

There are many different definitions of forest naturalness (Lee et al., 2000). A true "natural" forest can be defined as an idealized virgin forest condition that is not influenced by large-scale, systematic human activity (Bradshaw, 2005). Accumulation of large standing and downed deadwood and complex structural properties are often important indicators in these definitions (Kneeshaw and Burton, 1998). However, most definitions of "old-growth" include the premise that recent large-scale forest disturbances are absent (Rubin et al., 2006), which is challenged by some authors (e.g., Oliver and O'Hara, 2005). As recent disturbances are almost always present at the landscape level, we expected a variety of tree mortality patterns even on landscapes dominated by old-forests. Managed forests usually have an even distribution of stands in different developmental stages (age classes) except that old over-mature forests are generally lacking in managed landscapes. Often a mosaic of stands in different stages of forest development is desirable for biodiversity considerations, which also can be characteristic of unmanaged forests.

In the real world "naturalness" is almost impossible to define quantitatively. A bare landscape destroyed by natural large-scale

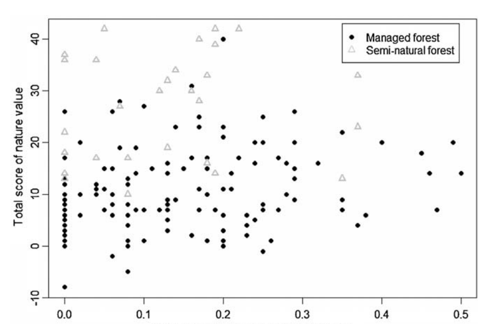


Fig. 10. Deadwood mingling and score of nature value in managed and semi-natural stands.

Table 4
Spearman correlation matrix of mean deadwood mingling index (DM*i*), nature value score, diversity index of mortality causes (CMDI), number of mortality causes (CM) and recent deadwood volume (RDV5) on sample plot data (values in bold are significantly different from zero).

	Mean DM*i*	Nature score	CMDI	Number of CM	RDV5
Mean DM*i*	1.000				
Nature score	0.182	1.000			
CMDI	**0.194**	**0.471**	1.000		
Number of CM	**0.331**	**0.423**	**0.914**	1.000	
RDV5	**0.630**	0.291	**0.469**	**0.661**	1.000

Table 5
Mean values and distribution of the deadwood mingling index (DM*i*) in managed and semi-natural forests.

Forest class	Mean value of DM*i*	Percent of trees with corresponding DM*i* value				
		0.00	0.25	0.50	0.75	1.00
Managed forests	0.220	44.23	31.55	17.32	5.91	1.00
Without large disturbance	0.196	48.28	30.78	15.63	4.77	0.54
With large disturbance	0.291	31.86	33.89	22.47	9.39	2.39
Semi-natural forests	0.199	49.82	30.26	13.28	3.69	2.95

disturbance may be more natural than a beautiful planted forest with high biodiversity value. We can only use surrogates to define a degree of naturalness. We hypothesized that multiple causes of tree mortality indicated naturalness of a stand. Our analysis results showed that the number of reasons for mortality was not directly connected to the number of processes leading to tree death. Our experience was that determining with certainty the reason or reasons a tree dies is often difficult. Visible or detectable evidence for a cause of mortality was present for some trees but also several trees died without any indication of the cause. Tree death is generally the result of complex interactions among multiple factors (Franklin et al., 1987; Manion, 1981). In future studies, better results may be obtained by not constraining mortality to be caused by a single reason but rather to use a process-based multiple-reason method (Fig. 11).

Modelling the CM showed that with increasing relative diameter there was a higher probability for tree mortality to be caused by wind, insect or fungi damage and a lower probability for tree mortality to be due to growth-dependent causes. The survival probability of a tree was dependent on its relative diameter in the stand (Laarmann, 2007). Usually forest growth and yield models use data representing past forest dynamics. The applications of these models in simulating the future growth and development of a stand assume that future conditions will be similar to the past (Garcia-Gonzalo, 2007). Because changing growth conditions that influence the resilience of trees may lead to increased mortality, therefore the actual changes in forest growth conditions can bias judgments made about the nature value of a forest.

Several studies (e.g. Neumann and Starlinger, 2001) have found that forest naturalness is not correlated with tree species composition or stand diversity. It can be true also in relation to the amount and distribution of deadwood. Debeljak (2006) found that there is a considerable difference in deadwood quantity between managed and virgin forests in European temperate forests. Several studies (Liira et al., 2007; Kohv and Liira, 2005; Jonsson and Jonsell, 1999; Ohlson et al., 1997) found that the amount of deadwood is an important indicator of forest ecosystem quality in boreal and hemiboreal zone. Individual tree mortality in natural forests of a *Pinus*-dominated landscape in a wilderness area in Fennoscandia was characterized by a continuous flow of local-scale autogenic mortality of individual trees or small groups of trees (Rouvinen et al., 2002). Rouvinen et al. (2002) found deadwood accumulation levels of $1.8\,m^3\,ha^{-1}\,yr^{-1}$ in the old-growth forest in Eastern Fennoscandia. In our study, deadwood accumulated twice as quickly in forests that were left for natural development (semi-natural forests; $2.5\,m^3\,ha^{-1}\,yr^{-1}$) than in

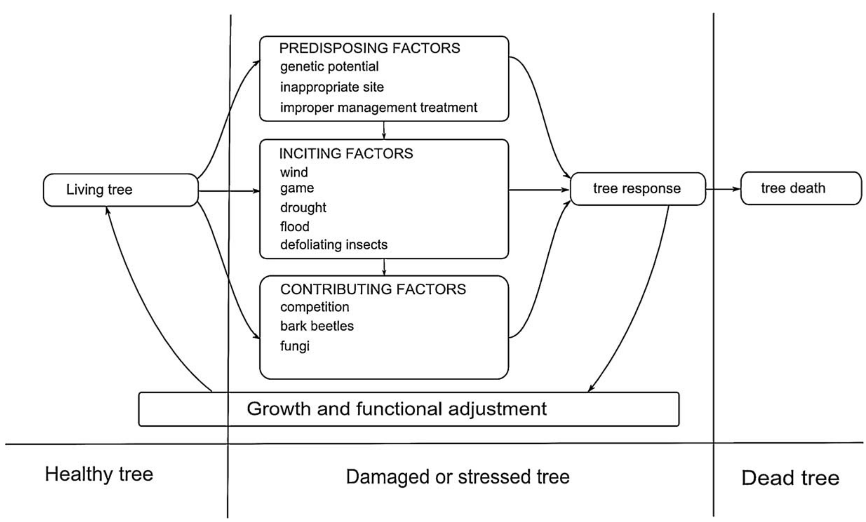


Fig. 11. Principal scheme of a process-based method for determining multiple causes for individual tree mortality; revised from Franklin et al. (1987); terminology after Manion (1981). Predisposing factors are generally static or non-changing factors. Inciting factors are short in duration and may be physical or biological in nature; these generally produce a drastic damage. The contributing factors produce noticeable symptoms and sign on the weakened tree.

managed forests (1.1 m^3 ha^{-1} yr^{-1}). This difference may indicate that deadwood accumulation is more intensive in semi-natural forests than in old-growth climax forests.

Our results indicate that forest naturalness cannot be explained only by the amount of dead trees or by tree survival rates in a stand. Laarmann (2007) estimated that approximately 40% of forest stand naturalness in Estonia can be described with structural and qualitative properties of dead trees (how and where trees died). Therefore deadwood quantity itself is not a good indicator of forest naturalness. Better indicators are deadwood spatial and size distributions and the variety of CM.

Kint et al. (2003) compared nearest neighbour indices with other method and concluded that these indices are suitable for quantifying forest structure characteristics. Kint (2005) showed that the clustered spatial pattern that followed large disturbances will develop to a regular spatial point pattern in young Scots pine stands because of self-thinning and competition with other species. The deadwood mingling variable we used was acceptable for distinguishing the clumping of dead trees that indicated recent disturbances and for characterizing deadwood spatial pattern. Patches of clumped dead trees in a stand often indicate recent forest disturbance and, in this case, the quantity of deadwood may not indicate forest naturalness. Our study showed that variation of deadwood mingling is characteristic of both managed and semi-natural forests in the Baltic countries. However, higher values of deadwood mingling indicate recent disturbances in forest stands.

The current study showed that assessment of forest naturalness can be improved with analysis of tree mortality patterns. Deadwood quantity and spatial distribution, recent mortality rate and causes of mortality together are good indicators of forest naturalness and should be useful in assessing and conserving biodiversity. Assessment and analysis of causes for individual tree mortality remains a challenge for applications in forest inventory and conservation planning.

Acknowledgements

We thank Prof. Klaus von Gadow and Prof. Kalev Jõgiste for their help in preparing the manuscript. This study was supported by the Estonian State Forest Management Centre, the Environmental Investment Centre Foundation and the Estonian Ministry of Education and Science grant SF0170014s08.

References

Ahti, T., Hämet-Ahti, L., Jalas, J., 1968. Vegetation zones and their sections in northwestern Europe. Ann. Bot. Fenn. 5, 169–211.
Borman, F.H., Likens, G.E., 1994. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York, Inc, p. 253.
Bradshaw, R.H.W., 2005. What is a natural forest? In: Stanturf, J.A., Madsen, P. (Eds.), Restoration of Boreal and Temperate Forests. CRC Press, pp. 15–30.
Debeljak, M., 2006. Coarse woody debris in virgin and managed forest. Ecol. Indic. 6, 733–742.
Eid, T., Tuhus, E., 2001. Models for individual tree mortality in Norway. Forest Ecol. Manag. 154, 69–84.
Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process. BioScience 37 (8), 550–556.
Franklin, J.F., Spies, T.A., Pelt, R.V., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecol. Manag. 155, 399–423.
Franklin, J.F., Mitchell, R.J., Palik, B.J., 2007. Natural disturbance and stand development principles for ecological forestry. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. General Technical Report NRS-19; 44 p.
Freund, R.J., Littell, R.C., 2000. SAS System for Regression. SAS Institute, Cary, NC.
Gadow, K.v., 1993. Zur Bestandesbeschreibung in der Forsteinrichtung. Forst und Holz 48 (21), 602–606 (in German).
Gadow, K.v., Nagel, N., Saborowski, J. (Eds.), 2002. Continuous Cover Forestry—Assessment, Analysis, Scenarios. Managing Forest Ecosystems, vol. 4. Kluwer Academic Publishers, Dordrecht Boston London.
Garcia-Gonzalo, J., 2007. Effects of management on timber production and carbon stock in a boreal forest ecosystem under changing climate: a model based approach. Dissertationes Forestales 42. University of Joensuu, Faculty of Forest Sciences.
Greenwood, D.L., Weisberg, P.J., 2008. Density-dependent tree mortality in pinyon-juniper woodlands. Forest Ecol. Manag. 255, 2129–2137.
Gustavsen, H.G., Roiko-Jokela, P., Varmola, M., 1988. Kivennäismaiden talousmetsien pysyvät (INKA ja TINKA) kokeet. Suunnitelmat, mittausmenetelmät ja ainestojen rakenteet. Metsäntutkimuslaitoksen Tiedonantoja 292. Helsinki. (in Finnish).
Jonsson, B.G., Jonsell, M., 1999. Exploring potential biodiversity indicators in boreal forests. Biodivers. Conserv. 8, 1417–1433.
Jõgiste, K., 1998. Productivity of mixed stands of Norway spruce and birch affected by population dynamics: a model analysis. Ecol. Model. 106, 77–91.
Juknys, R., Vencloviene, J., Jurkonis, N., Bartkevicius, E., Sepetiene, J., 2006. Relation between individual tree mortality and tree characteristics in a polluted and non-polluted environment. Environ. Monitor. Assess. 121, 519–542.
Karoles, K., Õunap, H., Pilt, E., Terasmaa, T., Kivits, H., 2000. Forest condition in Estonia 1988-1999, defoliation and forest damages on Level I sample points. Air pollution and forests in industrial areas of north-east Estonia. Forest. Stud. XXXIII, 209–216.
Kint, V., 2005. Structural development in ageing Scots pine stands. Forest Ecol. Manag. 124, 237–250.
Kint, V., De Vulf, R., Lust, N., 2004. Evaluation of sampling methods for the estimation of structural indices in forest stands. Ecol. Model. 180, 461–476.
Kint, V., Van Meirvenne, M., Nachtergale, L., Geudens, G., Lust, N., 2003. Spatial methods for quantifying forest stand structure development: a comparison between nearest neighbour indices and variogram analysis. Forest Sci. 49 (1), 36–49.
Kiviste, A., Hordo, M., 2003. The network of permanent sample plots for forest growth modeling in Estonia. In: Markevica, A., Lypsik, A., Leep, R. (Eds.), Research for Rural development 2003, International Scientific Conference Proceedings, Jelgava, pp. 174–177.
Kiviste, A., Nilson, A., Hordo, M., Merenäkk, M., 2003. Diameter distribution models and height-diameter equations for Estonian forests. In: Amaro, A., Reed, D., Soares, P. (Eds.), Modelling Forest Systems. CABI Publishing, pp. 169–179.
Kneeshaw, D.J., Burton, P.J., 1998. Assessment of functional old-growth status: a case study in the sub-boreal spruce zone of British Columbia, Canada. Nat. Area. J. 18, 293–308.
Kohv, K., Liira, J., 2005. Anthropogenic effects on vegetation structure of the boreal forest in Estonia. Scand. J. Forest Res. 20 (Suppl. 6), 122–134.
Korjus, H., 2002. Puistu loodusväärtuse inventeerimine (Inventorying natural values in forest stands). Metsanduslikud Uurimused/Forest. Stud. 37, 59–71 In Estonian with English summary.
Köster, K., Jõgiste, K., Tukia, H., Niklasson, M., Möls, T., 2005. Variation and ecological characteristics of coarse woody debris in Lahemaa and Karula National Parks, Estonia. Scand. J. Forest Res. 20 (Suppl. 6), 102–111.
Laarmann, D., 2007. Puude suremus ja seosed puistute looduslikkusega metsa kasvukäigu püsiproovitükkide andmetel (Individual tree mortality in relationship with naturalness of forest stands on the permanent sample plot data). M. Sc. Thesis. Estonian University of Life Sciences, Institute of Forestry and Rural Engineering. (In Estonian with English summary).
Larsen, J.B., 1995. Ecological stability of forests and sustainable silviculture. Forest Ecol. Manag. 73, 85–96.
Lee, P., Hanus, S., Grover, B., 2000. Criteria for estimating old growth in boreal mixedwoods from standard timber inventory data. Forest Ecol. Manag. 129, 25–30.
Liira, J., Sepp, T., Parrest, O., 2007. The forest structure and ecosystem quality in conditions of anthropogenic disturbance along productivity gradient. Forest Ecol. Manag. 250, 34–46.
Manion, P.D., 1981. Tree Disease Concepts. Prentice-Hall, New Jersey.
McElhinny, C., Gibbons, P., Brack, C., Bauhus, J., 2005. Forest and woodland stand structural complexity: its definition and measurement. Forest Ecol. Manag. 218, 1–24.
Monserud, R.A., Sterba, H., 1999. Modeling individual tree mortality for Austrian forest species. Forest Ecol. Manag. 113, 109–123.
Neumann, M., Starlinger, F., 2001. The significance of different indices for stand structure and diversity in forests. Forest Ecol. Manag. 145, 91–106.
Nilson, A., 1996. Role of environmental values in forest management planning in the Baltic countries, European Forest Institute, EFI Proceedings, vol. 13, 23–34.
Ohlson, M., Söderstom, L., Hörnberg, G., Zackrisson, O., Hermansson, J., 1997. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. Biol. Conserv. 81, 221–231.
Oliver, C.D., O'Hara, K.L., 2005. Effects of restoration at the stand level. In: Stanturf, J.A., Madsen, P. (Eds.), Restoration of Boreal and Temperate Forests. CRC Press, pp. 31–59.
Ozolincius, R., Miksys, V., Stakenas, V., 2005. Growth-independent mortality of Lithuanian forest tree species. Scand. J. Forest Res. 20 (Suppl. 6), 153–160.
Pommerening, A., 2006. Evaluating structural indices by reversing forest structural analysis. Forest Ecol. Manag. 224, 266–277.
Pommerening, A., Stoyan, D., 2006. Edge-correction needs in estimating indices of spatial forest structure. Can. J. Forest Res. 36, 1723–1739.
Rouvinen, S., Kuuluvainen, T., Siitonen, J., 2002. Tree mortality in a *Pinus sylvestris* dominated boreal forest landscape in Vienansalo wilderness, eastern Fennoscandia. Silva Fenn. 36 (1), 127–145.

Rubin, B.D., Manion, P.D., Faber-Langendoen, D., 2006. Diameter distributions and structural sustainability in forests. Forest Ecol. Manag. 222, 427–438.
Shannon, C.E., 1948. The mathematical theory of communication. In: Shannon, C.E., Weaver, W. (Eds.), The Mathematical Theory of Communication, University of Illinois Press, Urbana, pp. 3–91.
Sprugel, D.G., 1991. Disturbance, equilibrium, and environmental variability - what is natural vegetation in a changing environment. Biol. Conserv. 58, 1–18.
Stanturf, J.A., Madsen, P., Gardiner, E.S., 2004.In: Silviculture for restoration of degraded temperate and boreal forests, Meeting the challenge: Silvicultural Research in a Changing World, IUFRO Division 1 Conference, Montpellier, France, 14–18 June 2004.
Šaudyte, S., Karazija, S., Belova, O., 2005. An approach to assessment of naturalness for forest stands in Lithuania. Baltic Forest. 11 (1), 39–45.
Uotila, A., Kouki, J., Kontkanen, H., Pulkkinen, P., 2002. Assessing the naturalness of boreal forests in eastern Fennoscandia. Forest Ecol. Manag. 161, 257–277.
Viilma, K., Öövel, L., Tamm, U., Tomson, P., Amos, T., Ostonen, I., Sørensen, P., Kuuba, R., 2001. Estonian Forest Conservation Area Network. Final report of the Estonian Forest Conservation Area Network Project. Triip Grupp. Tartu.

II

Laarmann, D., Korjus, H., Sims, A., Kangur, A., Stanturf, J.A. 2013.
Initial effects of restoring natural forest structures in Estonia.
Forest Ecology and Management 304: 303-311.

Forest Ecology and Management 304 (2013) 303–311

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Full length article

Initial effects of restoring natural forest structures in Estonia

Diana Laarmann[a,*], Henn Korjus[a], Allan Sims[a], Ahto Kangur[a], John A. Stanturf[b]

[a] Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Kreutzwaldi 5, Tartu 51014, Estonia
[b] Center for Forest Disturbance Science, US Forest Service, 320 Green Street, Athens, GA 30602, USA

ARTICLE INFO

Article history:
Received 30 October 2012
Received in revised form 8 May 2013
Accepted 10 May 2013

Keywords:
Forest restoration
Gaps
Hemiboreal forest
Protected forests
Rehabilitation

ABSTRACT

The legacy of structural homogenization due to forest management for commercial products is a loss of biodiversity. A common policy in many European countries is to increase forest diversity by converting managed forests to more natural conditions. The aim of this study was to provide an early evaluation of the effectiveness of different restoration treatments to rehabilitate managed stands in order to increase their naturalness. Restoration treatments were imposed on 30–60 years old conifer plantations including gap creation with and without added deadwood, added deadwood without gaps, gaps plus overburning, and controls. We sampled stand structure, understory vegetation and beetles before and after treatments on 50 circular permanent plots. Diversity of different groups responded differently to treatments with understory vegetation diversity increasing the most in gaps with burning, lichens in gaps without burning and bryophytes with the addition of dead wood. Increased beetle abundance and greater species diversity was a direct effect of changed light conditions inside the canopy. Gaps with overburning had the greatest recruitment of tree seedlings. Stands that were homogeneous pre-treatment increased in heterogeneity in structural conditions and microclimatic conditions after treatments and therefore richness and abundance of different species groups increased.

1. Introduction

Ecological restoration aims to return degraded ecosystems to an idealized natural state as before anthropogenic intervention, with similar species diversity, composition and structure (SERI, 2004; Stanturf and Madsen, 2002). Rehabilitation of a degraded forest stand aims to restore naturalness in terms of stand structure, species composition or disturbance regimes (Bradshaw, 2002; Stanturf, 2005). Rehabilitation at the landscape scale can be used to complement conservation efforts in protected areas in order to enhance habitat quality and quantity, to improve connectivity between fragmented areas and to create buffer zones between reserved and managed forest areas (Kuuluvainen et al., 2002).

The ultimate goal of restoration is to create a self-maintaining ecosystem that is resilient to perturbation without further assistance (Urbanska et al., 1997). Integrated approaches are suggested to measure restoration success including examining vegetation characteristics, species diversity and ecosystem processes (Ruiz-Jaen and Mitchell Aide, 2005). The main aim of restoring forest naturalness is to initiate natural processes in forests that have been heavily influenced by human manipulation, to monitor these processes going forward, including monitoring of important interrelated processes of stand regeneration, small-scale disturbances and tree mortality (Kuuluvainen, 2002; Beatty and Owen, 2005). Intervention at the stand regeneration phase can be the basis for diversification and dynamics of forests (Vodde et al., 2011). Small and large disturbances generate different possibilities and scales for successional development. Tree mortality, for example is a natural process with many causes and high spatiotemporal variability (Laarmann et al., 2009). Gap formation in natural and semi-natural forests is dependent on mortality processes that also add deadwood structure to forests. Quality of coarse woody debris is a key structural component of unmanaged forests and plays an extremely important role in ecosystem function and biodiversity conservation (Lilja-Rothsten et al., 2008; Köster et al., 2009).

One common effect of forest management to produce commercial products is structural homogenization and compositional simplification over time (Halpern and Spies, 1995). The legacy of such landscape homogenization is a loss of biodiversity; forest policy in many European countries has been to increase forest diversity by converting managed forests to more natural states (Fries et al., 1997; Lõhmus et al., 2005). In Estonia, it can be seen as reversing the trend in forest management from cultivated, even-age coniferous forests of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) toward more complex structures that include special attention to spatial and quality properties of deadwood in forest stands (Laarmann et al., 2009; Lõhmus and Kraut, 2010; Paal et al., 2011; Liira et al., 2011).

* Corresponding author. Fax: +372 7313156.
E-mail address: diana.laarmann@emu.ee (D. Laarmann).

0378-1127/$ - see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.foreco.2013.05.022

Ensuring the sustainable dynamics processes for sustaining or steadily increasing forest biodiversity and structural complexity may be expected from either allowing natural disturbance processes to operate (Franklin et al., 1997; Kangur et al., 2005; Shorohova et al., 2009) or by attempting to emulate disturbance processes by management intervention (North and Keeton, 2008; Long, 2009) although, management actions may never fully mimic natural disturbance regimes (Lindenmayer and Franklin, 2002). Restoration involves rehabilitating stands using a set of silvicultural treatments to speed up the development of structural complexity including thinning, creating snags or cavities, enhancing recruitment of woody debris and where necessary under-planting with desired species. Forest stands with high spatial heterogeneity (indicated by a large number of gaps) are typically a result of continuous moderate-intensity canopy disturbances (Lerzman and Fall, 1998; Bradshaw et al., 2011). Many non-traditional approaches can be taken in thinning for designing multispecies and multi-storeyed stands that mimic such a moderate-intensity disturbance regime (Coates and Burton, 1997; Fulé et al., 2005; Keeton, 2006; Vanha-Majamaa et al., 2007; Felton et al., 2010).

The aim of this study was to examine the early effects of treatments that targeted restoring naturalness in Estonian hemiboreal protected forests. Study questions we addressed were: (1) what were the initial effects of restoration treatments on biological diversity and (2) were there significant differences on assemblages of understory and beetle diversity and abundance of deadwood between restoration treatments? To address these questions we focused on detection of small changes at an early stage after restoration treatments.

2. Materials and methods

2.1. Study design

The study was carried out in Estonia (lat. 58–259N, long. 26–209E), which is situated in the hemiboreal vegetation zone (Ahti et al., 1968). The climate varies from maritime to continental. Annual average precipitation ranges from 600 to 700 mm. Mean temperature ranges from 16.3 to 17.4 °C in July and from −2.0 to −7.4 °C in February. Forests cover 51% of the land area of the country and the terrain is flat. Forests under some form of protection are 26% of the total forest area; about half of them are situated in nature protection areas (Yearbook, 2010).

The study was connected to the LIFE-Nature project "Protection of priority forest habitat types in Estonia" where one of the purposes was naturalness restoration on recently designated protected areas that had a low-level of naturalness and diversity. Stands requiring restoration that were selected included plantations, middle-aged (30–60 years old), normally or densely stocked, pure coniferous (*P. sylvestris* or *P. abies*) stands growing on mineral soils. Restoration treatments were implemented altogether on 350 ha in seven nature protection areas in Estonia according to existing management plans. For monitoring the restoration process, in 2004 50 permanent sample plots (PSPs) were established in 23 forest stands with total area of 78.1 ha (Korjus, 2005).

The 50 restoration treatment plots were divided into 27 with interventions and 23 without interventions designated as control plots (Table 1). Plots were established before treatments, re-measured after treatments and then re-measured after 3 years. In the 27 forest stands studied there was at least one treated plot and one control plot. Four stands had two treated plots and one stand had three treated plots.

The primary treatment was to create gaps (72–1463 m^2) by removing overstory trees; gaps were defined as an opening in the forest canopy extending vertically through all layers down to 2 m above ground (Brokaw, 1982). Our treatments were a single gap (G) with four installations; a gap with added dead wood (GDW) with 17 installations; and four installations with low intensity fire from burning branches and needles at the end of summer within a gap (GB). Intentional burning in the forest is usually not allowed in Estonia, even for research purposes. Other treatments included two installations with added dead wood but no overstory manipulation (DW) and 23 controls with no manipulation (C).

The PSP were established as a circular layout with a radius ranging between 15 and 25 m. The PSP radius varied depending on forest density and age structure, following the rule that every plot needed to include at least 100 main canopy trees before treatment. On each plot before treatment the tree coordinates were determined by measuring azimuth and distance from plot cente. Diameter at breast height (DBH) of each tree larger than 4 cm was measured. For every fifth tree the total height and height to crown base were measured.

Mortality was calculated for the 3 year period after treatments. The cause of mortality of each dead tree was categorized into (a) density dependent mortality; (b) wind damage; (c) game damage; (d) insect attacks; (e) fungi and diseases; (f) others (Laarmann et al., 2009).

Regeneration establishment was recorded in newly established measurement plots on each treatment plot in 2008. Five 25 m^2 subplots were established on each treatment plot. Subplots included one in the center of the treatment plot and the other four subplots were each located 10 m from the plot center in cardinal directions. All seedlings in each subplot were counted by tree species and the two tallest seedlings of each species were selected for height measurement.

We used a crown shape model (Lang and Kurvits, 2007) to reconstruct crowns for gap size estimation. Based on the methods of Green (1996) we used sixteen distance/direction coordinates as a polygon to estimate the gap area, which is more accurate (Zhu et al., 2009) than the widely used method of Brokaw (1982).

Biodiversity in a given area is usually evaluated through surveys of species richness in different taxonomic groups (Terradas et al., 2003; Liira and Sepp, 2009). Data on understory vegetation were collected before, immediately after and 3 years after treatments. Herbaceous species and mosses were surveyed using a step-line intercept method (Jõgiste et al., 2008). On each PSP a permanent quadrate (5 × 5 m) was located 4 m from the center of the PSP in the north direction. Within the quadrate, species were recorded on step-line, where after each step a 10 × 10 cm square was described, resulting in total 100 squares. Lichens were inventoried on selected host material before treatment and measured 1 and 3 year after treatments (Jõgiste et al., 2008). Lichens sampling was done on: (1) 5 randomly selected main canopy trees (dominating tree species), (2) all trees from co-dominating tree species on the plot, (3) five standing dead trees or/and snags (diameter > 10 cm), (4) from three different fallen logs and (5) from three different decaying stumps and root mound.

Beetle diversity was inventoried with flight-intercept traps on the treatment areas. Beetle diversity was not monitored on control plots as forest stands are quite small (1–2 ha) in Estonia and control plots are close to treatment plots. Therefore any treatment in a stand influences beetle fauna also on control plot and control plot does not represent an area without treatment. In total 22 traps were set out and beetles were collected six times (every 2 weeks) during the summer of the pre-treatment year and in years one and three after treatment. 82% of the all beetles collected were identified to the species level.

2.2. Data analysis

Biodiversity was calculated using the coverage data per species and the total coverage by species group using Shannon–Wiener

Table 1
Distribution of plots by treatment. DW – dead wood input, G – gap cutting, GB – gap cutting and over burning; GDW – gap cutting with dead wood inclusion.

Treatment	No of plots	Deadwood input (m^3 ha^{-1})		Gap size (m^2)		Stand age (year)		Basal area (m^2 ha^{-1})	
		Min	Max	Min	Max	Min	Max	Min	Max
DW	2	7	12	–	–	50	100	31	41
G	4	–	–	119	225	30	45	19	28
GDW	17	1	67	72	404	30	60	22	38
GB	4	–	–	933	1463	50	50	1	5
C	23	–	–	–	–	30	100	20	47

index. Species richness was set to the average number of different species per plot sampled for the herbs, mosses, lichens and beetles, this variable is expected to have the Poisson distribution.

Thus, we used two different procedures for analysis of variance (ANOVA). With unbalanced data, as our data were, it is more appropriate to use the SAS procedure GLM for analysis instead of the procedure ANOVA (Littell et al., 2002). The procedure GLM was used for species diversity. A repeated measures ANOVA was conducted to determine the effects of treatment and time (2004–2008) on Shannon indexes of the herbs, mosses, lichens and beetles. Every species group was analyzed separately.

For species richness analysis we used the SAS procedure GLIMMIX, because it allows having data with the Poisson distribution. For analyzing significance of year effect for every treatment a statement CONTRAST in the procedure GLIMMIX was used.

We used Multiple Response Permutation Procedure (MRPP) to test for differences in species composition among treatments in 2008 (3 years post-treatment) with PC-ORD ver. 6 (McCune and Mefford, 2010). MRPP is a nonparametric procedure that tests the hypothesis of no difference in compositional similarity among two or more groups. MRPP gives a *p*-value based on the probability that the observed within group distance is smaller than could have occurred by chance. Measure of effect size is provided by the value *A* which describes the within group homogeneity.

We used Indicator Species Analysis (ISA) for the 2008 measurement to test for differences of species by treatments. Indicator species are species that are used as ecological indicators of environmental conditions or environmental changes (De Caceres et al., 2010). ISA produces indicator values for each species in each treatment, based on the standards of a perfect indicator, which based on relative frequency and abundance of a given species. Indicator values were tested for statistical significance using Monte Carlo simulation tests (1000 runs). Indicator species were identified from additional species that appeared between 2004 and 2008.

For tracking changes in forest composition over time in the treatment plots we used principal components analysis (PCA in PC-ORD v.6.0, McCune and Mefford, 2010). Stand parameters used were basal area (m^2 ha^{-1}), mean height of trees (m), species richness and diversity indices for each species group; gap size (m^2), diameter of gap (m), ratio between diameter of gap and stand mean height, coarse woody debris (m^3 ha^{-1}), number of dead trees and cause of mortality, which were logarithmically transformed.

3. Results

Among the 50 plots, we identified a total of 138 vascular plant and bryophytes species in 2004–2008; of these, there were 94 herbs, 7 shrubs and 37 mosses. Moss species *Hylocomium splendens* and *Pleurozium schreberi* were present in 91–100% of plots and vascular plants *Deschampsia flexuosa* and *Melampyrum pratense* were present in all treatments in 2008. Over all treatment plots there were 79 lichen species, including rare and threatened species in Estonia *Biatora botryosa*, *Calicium pinastri, Cladonia incrassata*, *Cladonia norvegica*, *Micarea hedlundii*, *Placynthiella dasaea*, and *Trapelia coarctata* (Lilleleht, 1998; Randlane and Saag, 1999; Randlane et al., 2008). A total of 512 beetle species were found during 2004–2008: 145 species in 2004, 340 species in 2005, and 365 species in 2008.

Herb species richness (Fig. 1) was affected significantly by changes in light conditions with gap formation increasing richness (G + GB + GDW treatments together, $F = 6.94$, $p < 0.001$; GDW treatment alone, $F = 4.76$, $p = 0.01$). However, we did not find significant changes between the years in single treatments except GDW (G, $p = 0.37$; DW, $p = 0.73$; GB, $p = 0.11$) or on control plots ($p = 0.63$), but the biggest change was in the G treatment where an average of 4.25 species was added. Richness of mosses and lichens was not significantly affected in any treatment. The average richness of mosses was 4.74 in 2004 and 5.46 three years later and the average richness of lichens was 5.6 and 6.2 respectively. Richness of beetles increased over time, since a response in any treatment affects other treatments due to the small stand size ($p < 0.001$).

Shannon indexes of herbs, mosses and lichens were significantly dependent upon treatments ($p < 0.003$) (Table 2). Shannon index of herbs increased the most in the gap with burning treatment (GB), and decreased in the added deadwood treatment (DW). The smallest change was on the control plots. The deadwood and gap with burning treatments positively affected Shannon index of mosses, while the gap alone (G) treatment affected moss that negatively. Changes in Shannon index of lichens were higher in the gap alone and gap with added deadwood treatments but decreased in the gap with burning treatment. Shannon index of beetles was different among years ($p = 0.01$, $f = 8.16$), but did not show any differences among the treatments. Interaction between time and treatment was not significant for any variable.

Differences in effects of composition 3 years after treatments are shown by MRPP analysis (Table 3). We found significant differences among treatments for herbs ($p < 0.001$, $A = 0.07$), mosses ($p = 0.04$, $A = 0.03$), lichens ($p < 0.001$, $A = 0.03$) and beetles ($p < 0.001$, $A = 0.14$). In pairwise comparisons, herb species in the gap with burning treatment (GB) was significantly different from control ($T = -7.87$, $p < 0.001$) and the rest of the treatments. Moss composition in the GB treatment was different from the other treatments ($p < 0.05$) except from the DW treatment ($p = 0.12$). Lichens were similar in control and GDW treatment ($p = 0.44$); in all the other treatments lichens were different. Beetles differed between deadwood and gap, deadwood and gap with added deadwood; and between gap with burning and gap with added deadwood.

Indicator species analysis (ISA) for the year 2008 presented seven herbaceous species, 1 moss, 8 lichen species and 28 insect species as indicators (Table 4). Indicator species in 2008 were not the same as in the pre-treatment measurement in 2004.

The ISA revealed some beetle species specific to some treatments; species such as *Cardiophorus ruficollis*, *Mycetochara flavipes*, *Ochthebius minimus*, *Tomoxia bucephala*, *Cis comptus, Sericoderus lateralis,* which were present on burned sites (Süda and Voolma, 2007). *Hylobius abietis*, *Hylastes brunneus*, *Scolytus ratzeburgi* were present close to fresh cutting (DW) sites (Voolma et al., 2003). A new indicator species in Estonia was recorded for treatment DW, *Malthinus facialis* (Süda, 2009).

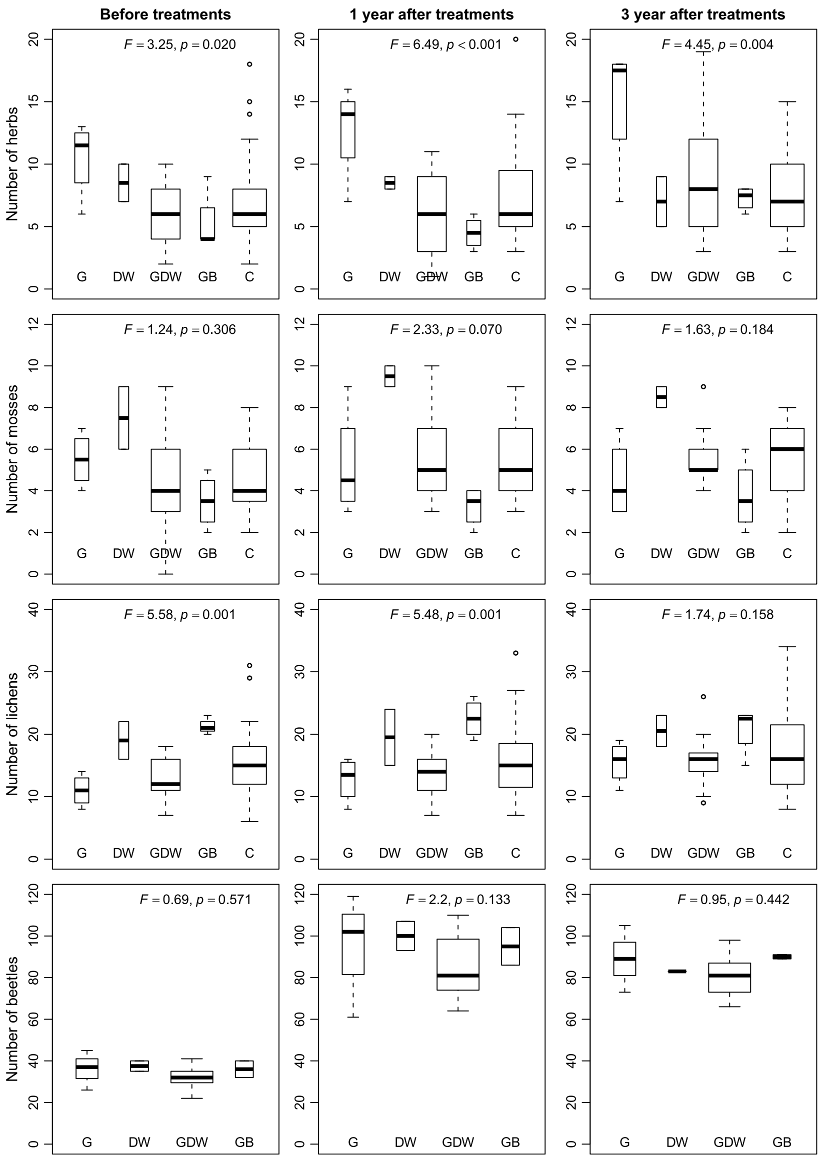


Fig. 1. The average species richness of vascular plants, mosses, lichens and beetles per plot in the treatment categories before the treatments, 1 year after the treatments and 3 years after the treatments. Treatment categories: G, gap cutting; DW, deadwood input; GDW, gap cutting with deadwood input; GB, gap cutting and overburning; C, control plots. Values of ANOVA test are presented. The upper and lower boundaries of the boxes are the 75th and 25th percentiles, the horizontal line within the box is the median and the error bars show the 10th to 90th percentiles. Width of box depends on number of plots.

Table 2
Dynamics of mean Shannon diversity index in species groups by treatments (G – gap cutting, DW – deadwood input, GDW – gap cutting with deadwood input, GB – gap cutting and overburning, C – control plots). Bold values indicate p-values lower the threshold value 0.05 (significant).

Attribute and year	Treatment					ANOVA results			
	G	DW	GDW	GB	C	Treatment		Time	
						F	*P*	*F*	*P*
Herbs						5.31	**<0.001**	2.829	0.06
2004	1.852	1.616	1.179	0.987	1.365				
2005	2.060	1.610	1.210	1.025	1.476				
2008	2.199	1.368	1.521	1.535	1.521				
Mosses						4.29	**<0.003**	3.05	0.05
2004	1.189	1.398	0.952	0.789	0.984				
2005	1.059	1.574	1.126	0.731	1.140				
2008	1.105	1.615	1.149	0.998	1.144				
Lichens						5.59	**<0.001**	1.22	0.30
2004	1.167	1.527	1.356	1.947	1.475				
2005	1.233	1.502	1.419	2.048	1.522				
2008	1.486	1.648	1.571	1.859	1.564				
Beetles						2.64	0.14	8.16	**0.01**
2004	0.966	0.499	0.487	0.867	–				
2005	2.486	2.933	2.688	3.399	–				
2008	3.010	3.438	3.066	3.247	–				

Table 3
Multi-response permutation procedure analysis between treatments (G – gap cutting, DW – deadwood input, GDW – gap cutting with deadwood input, GB – gap cutting and overburning, C – control plots) in species groups 3 years after treatment (H-herbs; M-mosses; L-lichens; B-beetles).

	G	DW	GDW	GB	C
G					
DW	L**; B***				
GDW	L*	L***; B*			
GB	H**; M*; L***	H*; L***	H***; M**; L***; B**		
C	L**	L**		H***; M**; L***	

* Significance code 0.05.
** Significance code 0.01.
*** Significance code 0.001.

The treatments reduced the number of living trees on all plots and increased the amount of dead wood on plots receiving added deadwood (DW and GWD). We found differences in the distribution of seedling species and their abundances between treatments (X^2; $p < 0.05$). The abundance of *Pinus* seedlings increased on the gap and burned plots (GB) (Fig. 2). Treatments GB and GDW increased the number of *Betula* seedlings and G increased number of *Picea* seedlings. The number of other trees, mainly *Populus tremula* and *Quercus robur* did not differ among treatments.

Comparing stand structure from before and 3 years after treatment (2004 vs. 2008) shows different patterns on treatment plots (Fig. 3). Control plots were excluded in this analysis because we did not find any significant changes between years. The PCA results indicated that five statistically significant ($p = 0.001$) axes were available for interpretation, which explained 79% of the variation in the data. The first principal component (PC1) was strongly related to density of stand while PC2 was related to attributes of dead wood; the others components described together 30% of structural variation.

We found significant changes between pre-treatment and subsequent years ($F = 6.18$; $p < 0.001$). Pre-treatment stands were structurally quite even and similar to each other; after treatment stand structure changed and this initiated changes in herb, moss, lichens and beetle composition as well as in tree regeneration.

The variables with the strongest correlation with the first axis were gap size ($r = -0.92$; $p < 0.001$), diameter of gap ($r = -0.92$; $p < 0.001$), removed basal area ($r = -0.91$; $p < 0.001$), ratio of gap and stand mean height ($r = -0.91$; $p < 0.001$), number of seedlings ($r = -0.65$; $p = 0.001$), and basal area ($r = 0.58$; $p < 0.04$). The second axis correlated best with number of dead trees per hectare ($r = -0.64$; $p < 0.001$), number of reasons for tree mortality ($r = -0.62$; $p < 0.001$), amount of coarse woody debris ($r = -0.55$; $p < 0.001$), richness of mosses ($r = -0.61$; $p = 0.03$) and richness of herbs ($r = -0.52$; $p = 0.02$).

Three years after treatment there was no clear effect on mortality. Tree mortality during the 3 years after treatment was highest on control plots, 6.7% (over the 3 year period). Mortality on the gap alone (3.9%) and gap with added deadwood treatments (4.7%) was higher than the treatment of added deadwood (1.6). Plots receiving the gap plus burning treatment had significantly larger gaps than were produced for the gap or gap with added deadwood treatments (G or GDW) but had no dead trees during this 3-year period.

4. Discussion

Managing disturbances by manipulative treatments is part of the process of restoring natural disturbance regimes that have been disrupted by human intervention (Stanturf, 2004). A challenge for forest managers is to develop and implement management practices that restore stand structural complexity and compositional diversity (Lindenmayer and Franklin, 2002). It is possible to imitate gap dynamics, which is one of the typical disturbance regimes in hemi-boreal forests (Shorohova et al., 2009). Canopy gaps are created by death of one or more trees naturally or by management (thinning, selective cutting); gaps are critical in community dynamics, species coexistence and regeneration of many types of forests (Liu and Hytteborn, 1991; Gray and Spies, 1996). Deadwood contributes to stand structural complexity and creating different sizes of slowly dying and dead wood is another important tool for restoring the natural characteristics of managed forests (Siitonen, 2001). To maintain biodiversity and ecosystem processes in managed forests different individual structures are needed such as standing dead trees, logs and coarse woody debris on forest floor, and large dimension deadwood in different decay stages (Lindenmayer and Franklin, 2002). Spatial variability of deadwood distribution in a stand is caused by different mechanisms of individual tree death (e.g., insect attack, fungi, competition); spatial variability of deadwood is one of the characteristics of natural/semi-natural stands (Laarmann et al., 2009).

Table 4
Indicator species analysis of vascular plant (V) and mosses (M), lichens (L) and beetles (B) for 3 years after treatment (G – gap cutting, DW – deadwood input, GDW – gap cutting with deadwood input, GB – gap cutting and overburning) based on relative frequency and abundance of a given species.

Species	Group	Treatment	*P*	Indicator value	% Of plots in given group where given species is present				
					G	DW	GDW	GB	C
Miarus sp.	B	G	0.001	100	100	–	–	–	n/a
Alosterna tabacicolor	B	G	0.029	80	100	–	82	–	n/a
Anthribus nebulosus	B	G	0.010	79	100	–	27	–	n/a
Liodopria serricornis	B	G	0.022	73	100	–	45	–	n/a
Leptura melanura	B	G	0.035	73	100	100	91	100	n/a
Meligethes sp.	B	G	0.009	70	100	–	91	50	n/a
Amara brunnea	B	G	0.029	67	67	–	–	–	n/a
Phyllobius argentatus	B	G	0.029	67	67	–	–	–	n/a
Caenocara affinis	B	G	0.033	67	67	–	–	–	n/a
Anemone nemorosa	V	G	0.022	55	75	–	6	–	17
Fragaria vesca	V	G	0.014	48	75	–	–	25	9
Deschampsia cespitosa	V	G	0.044	45	50	–	6	–	–
Cladonia coniocraea	L	G	0.015	17	50	19	25	32	15
Hypogymnia tubulosa	L	G	0.030	9	18	–	6	8	3
Hylobius abietis	B	DW	0.012	100	–	100	–	–	n/a
Malthinus facialis	B	DW	0.012	100	–	100	–	–	n/a
Myzia oblongoguttata	B	DW	0.012	100	–	100	–	–	n/a
Hylastes brunneus	B	DW	0.020	89	–	100	18	–	n/a
Scolytus ratzeburgi	B	DW	0.043	67	–	100	–	50	n/a
Athous subfuscus	B	DW	0.009	50	100	100	100	100	n/a
Melampyrum sp.	V	DW	0.042	50	–	50	–	–	–
Lycopodium annotinum	V	DW	0.042	50	–	50	–	–	–
Trapeliopsis flexuosa	L	DW	0.035	7	4	14	2	4	2
Agathidium sp.	B	GDW	0.031	52	100	50	100	100	n/a
Dimerella pineti	L	GDW	0.026	15	7	5	28	–	21
Carex ericetorum	V	GB	0.001	100	–	–	–	100	–
Cardiophorus ruficollis	B	GB	0.014	100	–	–	–	100	n/a
Cryptolestes corticinus	B	GB	0.014	100	–	–	–	100	n/a
Mycetochara flavipes	B	GB	0.014	100	–	–	–	100	n/a
Ochthebius minimus	B	GB	0.014	100	–	–	–	100	n/a
Orthotomicus suturalis	B	GB	0.014	100	–	–	–	100	n/a
Prosternon tessellatum	B	GB	0.014	100	–	–	–	100	n/a
Rhagonycha elongata	B	GB	0.014	100	–	–	–	100	n/a
Tomoxia bucephala	B	GB	0.014	97	33	–	–	100	n/a
Hydroporinae	B	GB	0.007	93	–	–	27	100	n/a
Anidorus nigrinus	B	GB	0.040	92	–	50	18	100	n/a
Cis comptus	B	GB	0.039	75	33	–	–	100	n/a
Sericoderus lateralis	B	GB	0.049	73	33	50	9	100	n/a
Epilobium angustifolium	V	GB	0.011	70	75	–	29	100	9
Funaria hygrometrica	M	GB	0.011	49	–	–	6	50	–
Dicranum polysetum	M	GB	0.034	45	50	100	76	100	74
Lecanora phaeostigma	L	GB	0.001	27	–	–	2	32	6
Evernia prunastri	L	GB	0.003	11	–	–	–	12	1
Hypocenomyce scalaris	L	GB	0.027	9	4	5	4	20	5

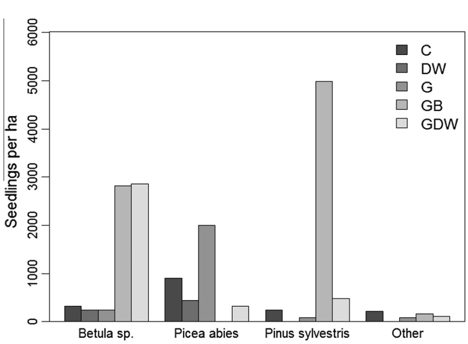


Fig. 2. Number of tree seedlings in 2008, 3 years after the treatments on gap cutting (G), deadwood input (DW), gap cutting with deadwood input (GDW), gap cutting and overburning (GB), control plots (C).

This study was initiated to provide an early evaluation of the effectiveness of different restoration treatments to rehabilitate managed stands in order to increase their naturalness. The study was conducted in previously managed forest that had recently been brought under nature protection status. Since this protection status was only developed during the last decade, managers are interested to know the possible suitable actions for conservation management purposes. The studied areas were located in the buffer zones around core natural areas and thus were not under strict protection. Although these are managed areas, the management actions allowed are to enhance biodiversity development and as such are different from management of commercial forests. Several earlier studies (Fries et al., 1997; Carey and Curtis, 1996; Kuuluvainen et al., 2002) guided the choice of restoration treatments used in this study and therefore the results should be of value not only for buffer zone management but also for increasing naturalness in commercial forests.

The treatments in this study intended to mimic natural wind disturbance that is typical of boreonemoral forests (Shorohova et al., 2009). The effects on understory diversity should follow a similar pattern as after windthrow. An increase in variation of light intensity after cutting treatments and intensive dead wood inclusion generates suitable habitats for shade-dependent species under

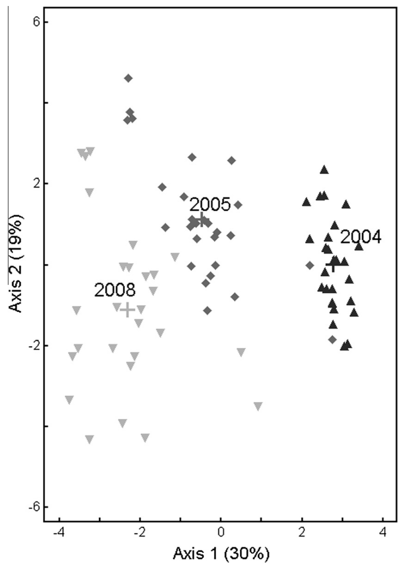


Fig. 3. Ordination of structural characteristics according to the Principal Component Analysis. Plots described by symbols: plots before treatments are indicated with triangles, 1 year after treatments with diamonds, 3 year after treatment with reverse triangles. Centroids of each year are indicated by crosses.

the shade of fallen tree trunks (Lilja-Rothsten et al., 2008). The relationship between the gap diameter and the height of the surrounding stand determines the light availability inside the gap. If the relationship is close to one or larger (i.e., the gap is as wide as the height of surrounding trees or wider) there is greater recruitment and successful establishment of light demanding species. On the other hand, understory vegetation establishment is favoured by the variability of diffuse light (Moora et al., 2007).

Several authors reported higher understory species diversity in recently cut areas as compared with that in old-growth stands (Zobel, 1993; Pykäla, 2004; Aavik et al., 2009; Moora et al., 2007) but some studies indicated that felling methods may result in a decrease in species richness in the short-term (Jalonen and Vanha-Majamaa, 2001). Our results indicate that gap and deadwood treatments (G, GDW, and DW) did not influence herbaceous species richness in comparison to control plots. But at the same time the change in species composition after treatments is illustrated by the results of indicator species analysis. Stands with gap cuttings were characterized by common pioneer species such as *Epilobium angustifolium* and light-demanding species such as *Deschampsia cespitosa*, *Fragaria vesca*, and *Carex ericetorum*. Similar results were found among bryophytes.

The gap plus burn treatment (GB), however, differed significantly from control plots for all species groups. Other studies with burning treatments showed similar results, for example Vanha-Majamaa et al. (2007) and Glasgow and Matlack (2007) where there were clear differences in understory vegetation between the biotype classes after burning treatments.

Compared to species groups on control areas, only the lichen group differed among G and DW treatments. Surprisingly the species groups were fairly similar on control plots and on treatment GDW, although this may be due to the higher variation on sample plots in the GDW treatment. Previous studies (Schimmel and Granström, 1996; Wikars, 2002; Junninen et al., 2008; Parro et al., 2009; Ruokolainen and Salo, 2009) have also shown that wildfire provides an opportunity for fire-dependent and fire-adapted species to develop in previously closed-canopy stands.

The current study results present a preliminary response to the restorative treatments, but give some confidence that creating gaps and increasing dead wood along with over burning can direct and restore rapid development of structural diversity in formerly managed forests. A conceptual scheme of the temporal trajectory of treatment effects is presented in Fig. 4. The more intensive treatments (gap cutting and burning) show an initial decline in complexity but more move rapidly towards greater complexity than the less manipulative treatments (control and added deadwood alone). This conceptual response should be interpreted in light of the differential response of the several taxonomic groups to different treatments (i.e., lichens respond to one treatment, bryophytes to another, vascular plant to another, etc.). This suggests multiple treatments and an emphasis on creating stand heterogeneity can increase biodiversity more than one homogenous application of a single treatment. Nevertheless, the conceptual diagram can be used as hypotheses to be tested in subsequent monitoring of the PSPs.

Our results indicate that deadwood input and heterogeneity increases after treatments in a stand. Similar results are reported from an on-going experimental research project (EVO) in Finland (Lilja et al., 2005; Vanha-Majamaa et al., 2007) and from simulation modelling for restoration of old-growth structural features in hardwood forests in Northern America (Choi et al., 2007). Although, we did not analyze spatial patterns and arrangement effects of deadwood inclusion in this study, the Laarmann et al. (2009) results indicated that in stand structural complexity the dead wood attributes are able to describe 40% of the variation. It is crucial to follow the enlargement of the gap size, since there is clear evidence of gap enlargement due to trees dying or being disturbed by wind on the gap edges. For example, Köster et al. (2009) reported that in Norway spruce stands the highest deadwood creation along forest edges appeared 3 years after the disturbance.

Natural regeneration of stands dominated by Scots pine is often difficult. On dry sandy soils the problem is the thick litter and raw humus layers that develop; on moderately wet or wet sandy soils the difficulty is due to abundant understory vegetation cover or

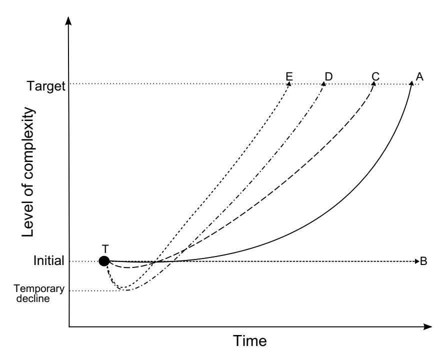


Fig. 4. Conceptual scheme of temporal trajectory of treatment effects in conifer even-aged stands: different pathways from initial level to targeted level of forest stand complexity. Some destructive treatments have temporary decline effect after that stand complexity increases more rapidly than with constructive treatments. Treatments: (A) no treatment (natural development of stand); (B) continuation of previous management regime for timber production; (C) deadwood input; (D) gap cutting; and (E) gap cutting with overburning.

thick raw humus (or peat) layers. Gap cutting and overburning treatments create conditions for successful Scots pine natural regeneration by partial soil scarification, reduced competition and increased light availability. Occurrence of successful natural regeneration allows rapid development of treated stands towards a multispecies uneven- aged stand (Hanewinkel and Pretzsch, 2000). Our results support the positive effect for Scots pine regeneration from gap cutting treatment with over burning. In comparison, the birch species abundance was higher on treatments with over burning and gaps with deadwood input. Norway spruce natural regeneration was most abundant on the treatment of gap alone. We were not able to distinguish between the individual impacts of over burning or gap creation and this needs further study. There was no notable browsing by herbivores on newly established tree regeneration on sample plots. Still, this must be monitored further because browsing may increase in the future and affect the course of stand development and understory development.

Several studies have reported increased richness of beetle species in moderately managed stands, where storm damage has been partly salvaged (Duelli et al., 2002; Ehnström, 2001). The increased abundance was due to freshly cut stumps and added deadwood that released terpenes which acted as a strong attractant for some of the beetle species. On the other hand, the insect abundance and greater species diversity was a direct effect of changed light and temperature conditions inside the canopy. Beetle monitoring is especially valuable and proper to evaluate changes on restoration areas because of beetle species and habitat richness, fast life cycle, distribution patterns and variety of monitoring methods available. Even as the species dependent on freshly cut materials moved away, there was an increase in the species dependent on fungi and dead wood. On the treatment with the added dead wood (stem parts, stumps, snags) the debris had decomposed enough to create a habitat for some new species (e.g. *Hylastes cunicularius*, *Monochamus urussovii*, and *Pityogenes chalcographus*) although their abundance was not as high as the abundance of species moving in right after treatment.

Gap cuttings in the current study presented a clear positive effect on the abundance and diversity of insects. Although older stands are expected to provide more habitat variability and therefore host more rare species, rare or threatened species were found in the current study after only 3 years post-treatment. Studied forest stands were rather small (1–2 ha) and, most likely, treatments influenced insect fauna on larger areas than these stands. Treatment areas and control areas are not physically isolated from each other and therefore it was not possible to distinguish beetle diversity between them. In future, some new control plots in similar stands should be established outside the treatment influence area. Continued study will be necessary to determine if there will be changes of insect fauna in the future.

Presence and abundance of insect species depends not only on forest management activities but rises and falls according to favourability of weather and habitat conditions. The year-to-year effect is sometimes a stronger signal than treatment effects. Our study results nevertheless indicate significantly high species diversity and species abundance shortly after the treatments. It is important to continuously monitor insect species abundance and diversity in the future to determine the long-term effect of restoration treatments on insect diversity..

5. Management implications

Forest management does not mean a direct threat to species diversity; the effect of management interventions can be positive or negative, depending upon the nature and intensity of treatments (Voolma and Õunap, 2006). Knowledge from ecological studies of natural and managed forests has helped to assess and redesign forest management policies, both to increase diversity in commercially managed forests and also in restoring naturalness to such stands now managed for nature protection.

Our study covered only the first 3 years of development after restoration treatments, which obviously limits our interpretations for management of protected areas. Nevertheless the early indications from our study are that the rehabilitation techniques we used (single gap cutting, gap cutting with dead wood input, gap cutting with over burning, and dead wood input alone) positively affected general structural heterogeneity but also species diversity. These changes were evident also in the dynamics of different species groups (vascular plant, bryophytes and beetles) in comparison to pre-treatment conditions.

Recruitment processes for coarse woody debris and tree seedling regeneration have been successfully reinitiated at a higher level and hopefully will increase the general level of biodiversity to an even higher level than it was before treatments. In selecting restorative measures it is important to base actions on the natural disturbance regime for a particular forest site. The gap creation treatment with over burning resulted in high site-specific species diversity and also produced good results for seedling establishment. Prescribed burning, however, is not allowed in Estonia; our results suggest this ban should be re-considered for restoration measures. These preliminary results underscore the importance of continuous systematic monitoring for evaluating the restoration actions as an investment but even more as an assessment of forest naturalness dynamics. This study underscores the importance of systematic monitoring for conservation management.

Acknowledgements

The research reported here was supported by the Estonian Ministry of Education and Research (Project No. SF0170014s08) and by the Estonian Science Foundation (Grant No. 8496) and Estonian Environmental Investment Centre. We thank the Environmental Board, Estonia, and fieldwork staff for their input and two anonymous reviewers for valuable comments to the manuscript.

References

Aavik, T., Püssa, K., Roosaluste, E., Moora, M., 2009. Vegetation change in boreonemoral forest during succession – trends in species composition, richness and differentiation diversity. Annales Botanici Fennici 46, 326–335.

Ahti, T., Hämet-Ahti, L., Jalas, L., 1968. Vegetation zones and their sections in northwestern Europe. Annales Botanici Fennici 5, 169–211.

Beatty, S.W., Owen, B.S., 2005. Incorporating disturbance into forest restoration. In: Stanturf, J.A., Madsen, P. (Eds.), Restoration of Boreal and Temperate Forests. CRC Press, pp. 61–76.

Bradshaw, A.D., 2002. Introduction and philosophy. In: Perrow, M.R., Davy, A.J. (Eds.), Handbook of Ecological Restoration. Cambridge University Press, pp. 3–9.

Bradshaw, R.H.W., Josefsson, T., Clear, J.L., Peterken, G.F., 2011. The structure and reproduction of the virgin forest: a review of Eustace Jones (1945). Scandinavian Journal of Forest Research 26 (Suppl. 10), 45–53.

Brokaw, N.V.L., 1982. The definition of treefall gap and its effect on measures of forest dynamics. Biotropica 14 (2), 158–160.

Carey, A.B., Curtis, R.O., 1996. Conservation of biodiversity: a useful paradigm for forest ecosystem management. Wildlife Society Bulletin 24, 610–620.

Choi, J., Lorimer, C.G., Vanderwerker, J.M., 2007. A simulation of the development and restoration of old-growth structural features in northern hardwoods. Forest Ecology and Management 249, 204–220.

Coates, K.D., Burton, P.J., 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. Forest Ecology and Management 99, 334–354.

De Caceres, M., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. Oikos 119, 1674–1684.

Duelli, P., Obrist, M.K., Wermelinger, B., 2002. Windthrow-induced changes in faunistic biodiversity in alpine spruce forests. Forest Snow and Landscape Research 77, 117–131.

Ehnström, B., 2001. Leaving dead wood for insects in boreal forests – suggestions for the future. Scandinavian Journal of Forest Research 16 (3), 91–98.

Felton, A., Lindbladh, M., Brunet, J., Fritz, Ö., 2010. Replacing coniferous monocultures with mixed-species production stands: An assessment of the potential benefits for forest biodiversity in northern Europe. Forest Ecology and Management 260, 939–947.

Franklin, J.F., Berg, D.R., Thornburgh, D.A., Tappeiner, J.C., 1997. Alternative silvicultural approaches to timber harvesting: Variable retention harvest systems. In: Kohm, K.A., Franklin, J.F. (Eds.), Creating a forestry for the 21st century: The science of ecosystem management. Island Press, pp. 111–139.
Fries, C., Johansson, O., Pettersson, B., Simonsson, P., 1997. Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. Forest Ecology and Management 94, 89–103.
Fulé, P.Z., Laughlin, D.C., Covington, W.W., 2005. Pine-oak forest dynamics 5 years after ecological restoration treatments, Arizona, USA. Forest Ecology and Management 218, 129–145.
Glasgow, L.S., Matlack, G.R., 2007. Prescribed burning and understory composition in a temperate deciduous forest, Ohio, USA. Forest Ecology and Management 238, 54–64.
Gray, A.N., Spies, T.A., 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. Journal of Ecology 84, 635–645.
Green, P.T., 1996. Canopy gaps in rain forest on Christmas Island, Indian Ocean: size distribution and methods of measurement. Journal of Tropical Ecology 12 (3), 427–434.
Halpern, C.B., Spies, T.A., 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications 5 (4), 913–934.
Hanewinkel, M., Pretzsch, H., 2000. Modelling the conversion from even-aged to uneven-aged stands of Norway spruce (*Picea abies* L. Karst) with a distance-dependent growth simulator. Forest Ecology and Management 134, 55–70.
Jalonen, J., Vanha-Majamaa, I., 2001. Immediate effects of four different felling methods on mature boreal spruce forest understory vegetation in southern Finland. Forest Ecology and Management 146, 25–34.
Jõgiste, K., Kuuba, R., Viilma, K., Korjus, H., Kiviste, A., Kalda, A., Parmasto, E., Jüriado, I., Lõhmus, P., Õunap, H., 2008. Nature restoration of forests. Tartu. [In Estonian].
Junninen, K., Kouki, J., Renvall, P., 2008. Restoration of natural legacies of fire in European boreal forests: an experimental approach to the effects on wood-decaying fungi. Canadian Journal of Forest Research 38, 202–215.
Kangur, A., Korjus, H., Jõgiste, K., Kiviste, A., 2005. A conceptual model of forest stand development based on permanent sample-plot data in Estonia. Scandinavian Journal of Forest Research 20, 94–101.
Keeton, W.S., 2006. Managing for late-successional old-growth characteristics in northern hardwood-conifer forests. Forest Ecology and Management 235, 129–142.
Korjus, H., 2005. Monitoring of nature restoration areas. Forestry Studies 43, 49–57 (in Estonian with English summary).
Köster, K., Voolma, K., Jõgiste, K., Metslaid, M., Laarmann, D., 2009. Assessment of tree mortality after windthrow using photo-derived data. Annales Botanici Fennici 46 (4), 291–298.
Kuuluvainen, T., 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fennica 36 (1), 97–125.
Kuuluvainen, T., Aapala, K., Ahlroth, P., Kuusinen, M., Lindholm, T., Sallantaus, T., Siitonen, J., Tukia, H., 2002. Principles of ecological restoration of boreal forested ecosystems: Finland as an example. Silva Fennica 36 (1), 409–422.
Laarmann, D., Korjus, H., Sims, A., Stanturf, J.A., Kiviste, A., Köster, K., 2009. Analysis of forest naturalness and tree mortality patterns in Estonia. Forest Ecology and Management 258S, S187–S195.
Lang, M., Kurvits, V., 2007. Restoration of tree crown shape for canopy cover estimation. Forestry Studies 46, 23–34.
Lerzman, K., Fall, A., 1998. From forest stands to landscapes: spatial scales and the roles of disturbance. In: Peterson, D.L., Parker, V.T. (Eds.), Ecological Scale: Theory and Applications. Columbia University Press, pp. 339–367.
Liira, J., Sepp, T., 2009. Indicators of structural and habitat natural quality in boreo-nemoral forests along the management gradient. Annales Botanici Fennici 46, 308–325.
Liira, J., Sepp, T., Kohv, K., 2011. The ecology of tree regeneration in mature and old forests: combined knowledge for sustainable forest management. Journal of Forest Research 16 (3), 184–193.
Lilja, S., De Chantal, M., Kuuluvainen, T., Vanha-Majamaa, I., Puttonen, P., 2005. Restoring natural characteristics in managed Norway spruce [*Picea abies* (L.) Karst.] stands with partial cutting, dead wood creation and fire: immediate treatment effects. Scandinavian Journal of Forest Research 20 (6), 68–78.
Lilja-Rothsten, S., De Chantal, M., Peterson, C., Kuuluvainen, T., Vanha-Majamaa, I., Puttonen, P., 2008. Microsites before and after restoration in managed Picea abies stands in southern Finland: effects of fire and partial cutting with dead wood creation. Silva Fennica 42 (2), 165–176.
Lilleleht, V., 1998. Red Data Book of Estonia. Threatened Fungi, Plants and Animals. Tallinn, Eesti Teaduste Akadeemia Looduskaitse Komisjon (in Estonian).
Lindenmayer, D.B., Franklin, J.F., 2002. Conserving Forest Biodiversity: a comprehensive multiscaled approach. Island Press, Washington, Covelo, London.
Littell, R.C., Stroup, W.W., Freund, R.J., 2002. SAS for linear models. SAS Institute Inc., Cary, NC.
Liu, Q., Hytteborn, H., 1991. Gap structure, disturbance and regeneration in a primeval *Picea abies* forest. Journal of Vegetation Science 2 (3), 391–402.
Lõhmus, A., Kraut, A., 2010. Stand structure of hemiboreal old-growth forests: Characteristic features, variation among site types, and a comparison with FSC-certified mature stands in Estonia. Forest Ecology and Management 260, 155–165.
Lõhmus, A., Lõhmus, P., Remm, J., Vellak, K., 2005. Old-growth structural elements in a strict reserve and commercial forest landscape in Estonia. Forest Ecology and Management 216, 201–215.
Long, J.N., 2009. Emulating natural disturbance regimes as a basis for forest management: a North American view. Forest Ecology and Management 257, 1868–1873.
McCune, B., Mefford, M.J., 2010. PC-ORD. Multivariate Analysis of Ecological Data. MjM Software Design, Gleneden Beach, Oregon, USA.
Moora, M., Daniell, T., Kalle, H., Liira, J., Püssa, K., Roosaluste, E., Öpik, M., Wheatley, R., Zobel, M., 2007. Spatial pattern and species richness of boreonemoral forest understorey and its determinants – a comparison of differently managed forests. Forest Ecology and Management 250, 64–70.
North, M.P., Keeton, W.S., 2008. Emulating natural disturbance regimes: an emerging approach for sustainable forest management. In: Lafortezza, R., Chen, J., Sanesi, G., Crow, T.R. (Eds.), Patterns and Processes in Forest Landscapes – Multiple Use and Sustainable Management. Springer, pp. 341–372.
Paal, J., Turb, M., Köster, T., Rajandu, E., Liira, J., 2011. Forest land-use history affects the species composition and soil properties of old-aged hillock forests in Estonia. Journal of Forest Research 16 (3), 244–252.
Parro, K., Köster, K., Jõgiste, K., Vodde, F., 2009. Vegetation dynamics in a fire damaged forest area: the response of major ground vegetation species. Baltic Forestry 15 (2), 206–215.
Pykälä, J., 2004. Immediate increase in plant species richness after clear-cutting boreal herb-rich forest. Applied Vegetation Science 7, 29–34.
Randlane, T., Saag, A., 1999. Second checklist of lichenized, lichenicolous and allied fungi of Estonia. Folia Cryptogamica Estonica 35, 1–132.
Randlane, T., Jüriado, I., Suija, A., Lõhmus, P., Leppik, E., 2008. Lichens in the new red list of Estonia. Folia Cryptogamica Estonica 44, 113–120.
Ruiz-Jaen, M.C., Mitchell Aide, T., 2005. Restoration success: how is it being measured. Restoration Ecology 13 (3), 569–577.
Ruokolainen, L., Salo, K., 2009. The effect of fire intensity on vegetation succession on a sub-xeric heath during 10 years after wildfire. Annales Botanici Fennici 46, 30–42.
Schimmel, J., Granström, A., 1996. Fire severity and vegetation response in the boreal Swedish forest. Ecology 77 (5), 1436–1450.
SERI (Society for Ecological Restoration International Science & Policy Working Group), 2004. *The SER International Primer on Ecological Restoration*. www.ser.org & Tucson: Society for Ecological Restoration International. (http://www.ser.org/pdf/primer3.pdf> (accessed 06.08.12).
Shorohova, E., Kuuluvainen, T., Kangur, A., Jõgiste, K., 2009. Natural stand structures, disturbance regimes and successional dynamics in the Eurasian boreal forests: a review with special reference to Russian studies. Annals of Forest Science 66 (2), 1–20.
Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisma: Fennoscandian boreal forests as an example. Ecological Bulletins 49, 11–41.
Stanturf, J.A., 2004. Disturbance dynamics of forested ecosystems. Transactions of the Faculty of Forestry, Estonian Agricultural University 37, 7–12.
Stanturf, J.A., 2005. What is forest restoration? In: Stanturf, J.A., Madsen, P. (Eds.), Restoration of Boreal and Temperate Forests. CRC Press, pp. 3–11.
Stanturf, J.A., Madsen, P., 2002. Restoration concepts for temperate and boreal forests of North America and Western Europe. Plant Biosystems 136 (2), 143–158.
Süda, I., 2009. New woodland beetle species (Coleoptera) in Estonian fauna. Forestry Studies 50, 98–114 (in Estonian with English summary).
Süda, I., Voolma, K., 2007. Diversity and abundance of Coleoptera in burnt forests of north-eastern Estonia: the first year after fire. Forestry Studies 47, 117–130 (in Estonian with English summary).
Terradas, J., Salvador, R., Vayreda, J., Lloret, F., 2003. Maximal species richness: an empirical approach for evaluating woody plant forest biodiversity. Forest Ecology and Management 189, 241–249.
Urbanska, K.M., Webb, N.R., Edwards, P.J., 1997. Why restoration? In: Urbanska, K.M., Webb, N.R., Edwards, P.J. (Eds.), Restoration Ecology and Sustainable Development. University Press, pp. 3–7.
Vanha-Majamaa, I., Lilja, S., Ryömä, R., Kotiaho, J.S., Laaka-Lindberg, S., Lindberg, H., Puttonen, P., Tamminen, P., Toivanen, T., Kuuluvainen, T., 2007. Rehabilitating boreal forest structure and species composition in Finland through logging, dead wood creation and fire: the EVO experiment. Forest Ecology and Management 250, 77–88.
Vodde, F., Jõgiste, K., Kubota, Y., Kuuluvainen, T., Köster, K., Lukjanova, A., Metslaid, M., Yoshida, T., 2011. The influence of storm-induced microsites to tree regeneration patterns in boreal and hemiboreal forest: a review. Journal of Forest Research 17, 155–167.
Voolma, K., Õunap, H., 2006. Diversity and abundance of insects and some other arthropods in unmanaged and managed forests. Forestry Studies 44, 95–111 (in Estonian with English summary).
Voolma, L., Õunap, H., Süda, I., Sibul, I., 2003. The diversity and abundance of Coleoptera in intensively managed pine forests and clearings. Forestry Studies XXXVIII, 85–102 (in Estonian with English summary).
Wikars, L., 2002. Dependence on fire in wood-living insects: an experiment with burned and unburned spruce and birch logs. Journal of Insect Conservation 6, 1–12.
Yearbook. 2010. Yearbook of the forest 2009. Keskkonnateabe Keskus. Tartu (in Estonian).
Zhu, J., Yan, Q., Sun, Y., Zhang, J., 2009. A new calculation method to estimate forest gap size. Frontiers of Forestry in China 4 (3), 276–282.
Zobel, M., 1993. Changes in pine forest communities after clear-cutting: a comparison of two edaphic gradients. Annales Botanici Fennici 30, 131–137.

III

Laarmann, D., Korjus, H., Sims, A.,
Kangur, A., Kiviste, A., Stanturf, J.A. 2014.
Evaluation of afforestation development and
natural colonization on a reclaimed mine site.
Restoration Ecology [Submitted].

Evaluation of afforestation development and natural colonization on a reclaimed mine site

Keywords: afforestation, long-term monitoring plot, oil-shale, reclamation, Scots pine, silver birch .

Manuscript category: Research paper

Diana Laarmann*[a], Henn Korjus[a], Allan Sims[a], Ahto Kangur[ab], Andres Kiviste[a], John Stanturf[b]

[a] Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Kreutzwaldi 5, Tartu, Estonia

[b] Center for Forest Disturbance Science, Southern Research Station, US Forest Service, Green Street 320, Athens, GA 30602, USA

* diana.laarmann@emu.ee tel/fax: +3727313156

Abstract

Post-mining restoration sites often develop novel ecosystems as soil conditions are completely new and ecosystem assemblage can be spontaneous even on afforested sites. This study presents results from long-term monitoring and evaluation of an afforested oil-shale quarry in Estonia. The study is based on chronosequence data of soil and vegetation and comparisons are made to similar forest site-types used in forest management in Estonia. After site reclamation, soil development lowered pH and increased N, K and organic C content in soil to levels similar to the common *Hepatica* forest site-type but P, total C and pH were more similar to the *Calamagrostis* forest site-type. Vegetation of the restoration area differed from that on common forest sites; forest stand development was similar to the *Hepatica* forest-type. A variety of species were present that are representive of dry and wet sites, as well as infertile and fertile sites. It appears that novel ecosystems may be developing on post-mining reclaimed land in Northeast Estonia and may require adaptations to typical forest management regimes that have been based on site-types. Monitoring and evaluation gives an opportunity to plan further management activities on these areas.

Keywords: afforestation, long-term monitoring plot, oil-shale, reclamation, Scots pine, Silver birch.

Introduction

Ecological restoration of exhausted surface mining sites aims to direct their development towards a long-term sustainable ecosystem (Lamb & Gilmour 2003) and to return the degraded system to pre-mining conditions where ecosystem structure, function and processes are regained (Bradshaw 1997). Afforestation can play a key role in harmonizing long-term reclamation (*sensu* Stanturf 2005) of the ecosystem by restoring productivity, biological diversity, and ecological integrity on such degraded areas (Kaar 2002).

Classical ecological restoration actions follow the principle of moving an undesired ecosystem state towards the desired, pre-disturbance state that existed historically (Perring et al. 2013). Although, this can be valid up to certain extent in degraded agricultural, forest or pastoral lands, it is hardly applicable to post-mining sites (Doley & Audet 2013). In post-mining sites the inability to achieve complete ecological restoration goals is due to the radical difference in physiochemical and biological characteristics of these sites as compared to historical environments. The degree of change caused by anthropogenic disturbance is often so severe, that novel ecosystems develop (Hobbs et al. 2006; Mascaro et al. 2013), where combinations but also relative abundance of species arise that have not occurred previously in a given site. Novel ecosystems result from introduction of invasive species, changes in soil fertility and physical condition, land degradation, environmental change or combinations of these; thresholds are surpassed such that restoration of previous or historical conditions are precluded (Hobbs et al. 2009). Novelty is not necessarily undesirable, however, as species adaptation to anthropogenic disturbances may set novel ecosystems on a trajectory toward a more favorable end-state, compared to historical conditions (Hallett et al. 2013).

Oil-shale mining has been carried out in Northeast Estonia since 1916 (Kaar et al. 1971). In opencast mining areas, the quaternary sediments and bedrock layers are removed to the depth of the oil-shale sediment layer, generally 5-35 meters. After commercial extraction is no longer feasible, the area is abandoned from mining and a new artificial structure of rocks (waste heaps) and terrain is formed (Toomik & Liblik 1998). Most of the surface mining sites were located in former woodlands and the goal was to restore them as such. Although the forest ecosystem was destroyed and surface and underground water regimes extensively altered, reclamation of abandoned mining areas dominated by calcareous detritus has been carried out since 1960 (Kaar 2010) and comprises an area of 13,000 ha.

Many ecological studies cover the early stages of stand development on oil-shale quarry reclamation in Estonia (Ostonen et al. 2006; Kuznetsova et al. 2011), but there is lack of studies covering longer time-periods. Lack of monitoring and evaluation is a common failing in restoration practice (Burton 2014; Mascia et al. 2014) and long-term research is needed to better understand the processes directing successional development of post-mining sites (Hüttl & Bradshaw 2001). Despite a lack of pre-mining data on such sites, it is possible to evaluate the success of restoration treatments by relying on a chronosequence of treated stands to examine developmental trends over time (Foster & Tilman 2000; Stem et al. 2005; Hutto & Belote 2013).

We set out to examine reclamation on former oil-shale mined sites in Northeast Estonia, to see how attempts at restoration that began in the 1960s fared and to compare the forest stands that resulted to native forests on similar sites. Because site and stand factors recover at different rates, we examined stand composition and structure, ground flora diversity, and development of soil physical and chemical properties over time. An early failure of the reclamation treatment (planted conifers) and subsequent recolonization by *Betula* in one area provided an opportunity to examine whether we had a "counterfactual" treatment (Ferraro 2009), that is, a "no-treatment" or natural succession treatment (Mascia et al. 2014; Prach & Pyšek 2001). A caveat is the failure with pine afforestation may have had some impact on the soil and site conditions and there may be also the issue of time. Pines could have died due to a poor chemical condition in the soil. It is also possible that the planting did something positive (e.g. mycorrhizal inoculation) that allowed *Betula* colonization.

Material and methods

Study area

The study was carried out on Aidu quarry (total area is 30 km^2) in northeast of Estonia in the hemiboreal vegetation zone (59°30'N; 27°07'E). The Estonian climate varies from maritime to continental. Average annual precipitation is 707 mm, recorded at the Jõhvi weather station close to the study area. Average annual temperature is 23.2˚C (ranging from -6.5˚C in February to 16.7˚C in July) (Tarand et al. 2013). The pre-mining land use on this area was mainly commercial woodland but also wetland and small-scale agriculture (Kaar 2010). The average thickness of soil in the woodland was 25 cm before the mining (Leedu 2010). The primary soils were *Eutro-Histic* C*leysol* with peat thickness 25 cm and pH 5.6 and a *Calcaric Luvisol* with soil thickness of 22-27 cm, pH 5.6-6.7, and plant available phosphorus of 1.4 mg/100 g and potassium 4.2 mg/100 g (Leedu 2010). The excavation of oil-shale in Aidu opencast quarry started in 1974 and was finished in 2012. The extent of the oil-shale sediment layer was 0.5 m-1.5 m, occurring at a depth of 5 m on the north of the mined area and dipping to 30 m in the south. After reclamation, including leveling of the waste materials, the elevation of the area is between 41 – 59 m above mean sea level. Since 1981, the area has been afforested mostly (86%) with Scots pine (*Pinus sylvestris* L.). Bareroot seedlings were planted at an initial density of 5,000-6,700 plants per hectare (Korjus et al. 2007; Kaar 2010).

Experimental design

The study design used a chronosequence approach; plots were randomly located within stands 12-33 years-old. A total of 60 monitoring plots were established in 2011 to examine differences in characteristics at three levels: 1) forest stand at tree level (stand structure and species composition); 2) ground layer vegetation (moss, grass and shrub layer species and their abundance); 3) soil (structure, texture, organic layer development, pH, and concentrations of K, P, N, organic C and total C). All monitoring plots were established in stands initially planted to Scots pine. On eight sample plots the pine seedlings had died within a few years of planting and were replaced spontaneously by silver birch (*Betula pendula* Roth.) that seeded in naturally. The other 52 monitoring plots are dominated by Scots pine. Three monitoring plots were established in every stand in order to estimate variation in the stand.

Sampling methods

We used the methodology of the Estonian Forest Research Plots Network (Sims et al. 2009) for design of the monitoring plots. Plots were circular with a radius of 15 m. On each plot the azimuth and distance from plot center to each tree (both live and dead) were recorded and damage on each tree was noted; diameter at breast height (1.3 m; DBH) was measured on stems on 54 plots that had attained sufficient height. In young stands (6 plots) there were many trees below 1.3 m in height and we measured height for every tree and DBH wherever possible. For every fifth tree in all plots, total height and height to crown base were also measured. We took tree cores from at least 5 trees in every stand to determine age of average trees.

Ground layer vegetation was sampled in subplots located within the monitoring plots. Subplots were placed 5 m north, east, south and west from the plot center. On these 1 x 1 m plots all woody plant, vascular plants and bryophytes were recorded following the Braun-Blanquet scale. Nomenclature and designation as forest, meadow or forest/meadow vegetation groups follows Ingerpuu and Vellak (1998) for bryophytes and Leht (2010) for vascular plants. Understory plants were divided into four groups by degree of anthropogenic impact or hemeroby. We used Kukk & Kull (2005) classification defining the ability of a species to survive and develop on habitats with a specified level of tolerance to anthropogenic impact: anthropophytes tolerate strong, apophytes moderate, hemeradiaphores little and hemerophobics no anthropogenic impact. Altogether 240 vegetation subplots were described.

In each plot, soil conditions were characterized. The depth to rock was measured by the re-bar method, where a metal rod was inserted at 13 points per plot, through the surface soil until impeded by the unconsolidated rock. The depth of the organic layer and surface mineral soil was recorded at each point.

A composite mineral soil sample (to a depth of 10 cm) was taken from each plot, air dried and analyzed. Total nitrogen and carbon content were determined by dry combustion method on a varioMaX CNS elemental analyzer. Soil organic carbon was determined with Tjurin's method (Vorobjova 1998), the pH values were determined by extraction using potassium chloride, the concentrations of available phosphorus was extracted in ammonium lactate and measured by flow injection analysis and available potassium was measured with a flame photometer (Ruzicka & Hansen 1981).

Data analysis

Species richness and Shannon-Wiener diversity index were estimated for all plots using PC-ORD ver.6 software. Species richness was defined as number of different species per plot. Soil, stand and understory data were ordinated using Detrended Correspondence Analysis (DCA). If the length of a variable's variation gradient was relatively short (<2SD), then Principal Component Analysis (PCA) was used. Differences among the stands of the two main tree species (pine and birch) were tested using the Multi-Response Permutation Procedure (MRPP).

For ordination of understory data we used Non-Metric Multidimensional Scaling (NMS) for pine stands; there was insufficient age variation in the birch stands to examine understory development over time. NMS is an ordination technique based on ranked similarities of species compostion suitable for community data that may not be normally distributed or fit assumptions of linear relationships among variables. We used the Sorensen distance measure with a log transformation on species abundances. We used the "autopilot" option on "slow and thorough" and a Monte Carlo randomisation test was applied on the stress scores. Pearson correlations with ordination axes for all quantitative variables were calculated separately for each.

For comparing soil variables and understory species composition we used data from forest site-types that have similar bedrock conditions to the study area; the site-types were *Hepatica*, *Arctostaphylos*, and *Calamagrostis*. Indicator species of these three site-types were taken from the literature (Lõhmus 2006; Paal et al. 2009). For comparing tree height and diameter with regular forest types, we used forest inventory data from the database of the Estonian Forest Registry. From the database we selected 2140 managed Scots pine stands from *Hepatica* (1111 stands), *Arctostaphylos* (973 stands) and *Calamagrostis* (64 stands) forest site-types (Lõhmus 2006), with stand mean age ranging from 1 to 39 years.

A generalized additive model (GAM) estimation method was used for comparing monitoring plot data with forest inventory data (Hastie & Tibshirani 1990). Based on forest inventory data a diameter model was created:

$$D = s(A) + s(H) \qquad (1)$$

where D is stand quadratic mean diameter, A is stand mean age, H is stand mean height and s() is a spline function in GAM.

The quadratic mean diameter for sample plots was estimated with the model and a paired t-test used to test for differences between measured and estimated diameters at a significance level $p<0.05$.

Results

Stands and site characteristics

Site development of spontaneously regenerated birch stands differs from afforested pine stands. The thickness of the surface mineral soil layer was significantly different ($p<0.001$) and thicker under the birch stands; the average soil depth in pine stands was 6.7 ± 0.6 cm and in birch stands was 37.61 ± 3.0 cm (Table 1). According to the PCA, birch stands are clearly and significantly (MRPP; $t=-11.75$; $p<0.001$) different from pine stands in the ordination plot (Fig. 1). The first ordination axis most closely represented a gradient of fine soil thickness ($r=0.92$, $p<0.001$), from a very thin soil layer on the left side of the diagram to a thicker layer on the right. The gradient went in the opposite direction for stoniness and pH level. The second ordination axis represented a gradient of stand age, with younger stands at the top of the diagram and older stands at the bottom ($r=-0.86$, $p<0.001$).

The increase in soil nitrogen (N) in pine stands over 33 years was statistically significant ($p<0.001$) (Fig. 2), but still remains lower than the nitrogen level of birch stands (Table 1). The soil phosphorus (P) level increased significantly ($p<0.001$) with stand age, reaching up to 40 mg/kg and the mean P level differed significantly between pine and birch stands ($p<0.001$). Soil pH was higher in young pine stands and soil acidity increased with age ($p<0.001$). We did not find significant differences between total carbon ($p=0.317$) or potassium ($p=0.176$) content among stands of different ages (Fig. 2).

Vegetation

All together we found 98 herbaceous plants, 32 bryophyte and 11 woody species. Most of these herbaceous species tolerate moderate anthropogenic impact (Kukk & Kull 2005), and two species tolerate strong anthropogenic impact (*Tragopogon pratensis* (on 2 plots) and *Melilotus albus* (81% of plots)). There were two hemerophobic species *Orthilia secunda* (54% of plots) and *Monotropa hypopitys* (on 2 plots). There were three protected herbaceous species: *Epipactis helleborine* (on 3 plots), *Goodyera repens* (on 3 plots) and *Dactylorhiza fuchsii* (on 2 plots). Our results showed that occurrence and cover of species increased with stand age. The average species richness of herbs on pine plots was 13 and 10 on the birch plots ($p=0.05$).The highest species richness (32 species) occurred on a 32 year-old pine plot. Moss richness was almost three times higher on pine plots than on birch plots ($p=0.001$). The average cover of herbs was significantly greater ($p<0.001$) on birch plots (59%) than pine plots (27%). The moss cover showed an opposite result, with cover on pine plots four times higher than birch plots ($p=0.001$). Pine and birch stands differentiated by herbaceous species composition (MRPP, $t=-17.71$, $p<0.001$), but they did not differ by Shannon index ($p=0.29$). Herbs species composition (Shannon index) is different by age on pine stands ($F=14.88$, p<0.001), but did not differ on birch stands (p=0.11). Pine and birch stands differed by moss composition (MRPP, t=-11.86, p<0.001) and by moss diversity index (p<0.001); the average Shannon index on pine stands is 0.55±0.1 and on birch stands 0.11±0.02. The Shannon index differed by age on pine stands (F=10.34, p=0.002), but did not differ on birch stands (p=0.31).

In matching species to site-types by indicator species, 68% of vascular species on the plots were not characteristic of the site-types based on similarity of bedrock condition (Fig. 3, Table 1 in Appendix S1). More species were indicators of the *Hepatica* site-type than the other types.

The best solution of NMS in the analysis of the composition of understory species in pine stands was 3-dimensional (final stress 15.9, number of iterations 92). Three axes described 78% of the variance (Axis 1, 23% and Axis 2, 35%). The variation of the data along the first axis is mainly determined by stand age (r=0.79,p<0.001); also significant were the relation with stand height (0.56, p<0.001) and coverage of vascular plants (r=-0.53, p<0.001). The gradient directed along the second ordination axis was mainly related to stand basal area (r=0.64, p<0.001), soil organic layer (r=0.55, p<0.001), pH (r=-0.46, p=0.001), Shannon index of moss (r=-0.43, p=0.002) and stoniness (r=-0.32, p=0.02). All species groups scattered along the first axis, while the positive side of Axis 2 represented more forest species and the bottom side contained more meadow species. Species richness increased significantly with stand age (Fig. 4). The greatest increase was in the forest species group. Meadow species richness was higher than forest/meadow species richness. Height and diameter in pine stands showed strong relationships with stand age (Fig. 5). Data of tree height and diameter were not significantly different from the *Hepatica*-type forest (t=-1.474, p=0.146) and was significantly different from the *Arctostaphylos* (t=-3.10; p<0.001) and the *Calamagrostis* (t=-6.70; p<0.001) site-types.

Discussion

Monitoring and evaluation of restoration sites is generally limited by duration (5 years or less) and often pre-mining conditions are replaced with reference ecosystems as a baseline to guide restoration or to assess success (Anderson & Dugger 1998). One way to overcome these limitations is the chronosequence approach where space is substituted for time (Hutto & Belote 2013). Our study used a quasi-experimental design lacking a true control (Anderson & Dugger 1998; Stem et al. 2005) to evaluate reclamation of spent mined lands in Northeast Estonia. The substrate (calcareous shale) differs considerably from many reclamation studies (Hüttl 1998; Wiegleb & Felinks 2001; Mudrák et al. 2010) on more acidic material, for example coal mines. Nevertheless, the reclamation approach that began in former Soviet times followed a simple revegetation paradigm (Stanturf et al. 2014) and focused on establishing a forest cover using *Pinus sylvestris*, a species that was easy to propagate, establish, and for which markets existed for the wood. The extensive use of Scots pine in afforestation of exhausted mining sites is due to its usually successful survival and establishment under these harsh conditions (Kaar 2002). Nevertheless, young trees on this stony substrate may die as a result of frost heaving in winter or drought in summer.

One question that should arise in a study evaluating restoration treatments is whether the cost of intervention is worthwhile; that is, would natural revegetation processes be sufficient to develop desirable conditions quickly enough to meet social goals? For example, reliance on natural recolonization has been successful in some quarry reclamations (Prach & Pyšek 2001). To answer this question requires a non-intervention (counterfactual or true control) treatment on a similarly degraded site in the study design. Our study lacked a true counterfactual, but the silver birch that colonized some areas after failure of the planted Scots pine may have provided such a non-intervention treatment. This would be true only if the substrate was the same, providing a common starting point. We could not meet this criterion in our study because there were differences in almost all measured variables between birch and pine stands. Species composition of the canopy is known to influence soil variables as a result of litter type (Prescott 2002) and some differences could result from stand and soil development over time. Indeed, pH decreased in our stands in relation to age, from a pH of 8.0 in the initial post-mining stage (Kuznetsova et al. 2011). To be sure, we compared pine and birch stands of similar age (Table 1); we found large differences between pine and birch stands in terms of relatively slow-changing physical characteristics such as fine soil thickness, stoniness, and texture. More labile chemical characteristics closely related to organic matter inputs such as thickness of the organic layer, organic C percentage and total N percentage also differed between the two overstory types, indicating that spontaneous succession (colonization by birch) has a different pathway from afforestation (planted pine).

One advantage of active restoration is usually there is a faster formation of continuous vegetation cover than a passive approach that relies on spontaneous succession (Prach & Hobbs 2008). If a goal is to restore productivity, as it was in the Soviet era when reclamation began, then afforestation is a preferred approach. Reclaimed mined land may present heterogeneous substrate conditions, however, and relying on a single planted species is risky if the planted species is not adapted to all site conditions. Risks include lower growth, higher mortality, and greater potential for disease or invasive species (Martinez-Ruiz et al. 2007). At the Aidu quarry, early mortality of the planted Scots pine in some areas resulted in colonization by birch; there is no guarantee, however, that the birch will achieve commercial size and other species better adapted to site conditions may have been planted that would better achieve restoration goals. Nontheless, continuous cover was obtained and a diverse understory developed, different from that under pine; which may meet current goals of biodiversity restoration. In some case, spontaneous succession may be preferable, especially in smaller disturbed sites surrounded by natural vegetation that provides a seed source and if there is no specific species composition or productivity goal. Another advantage of the passive approach may be that spontaneous succession results in a more natural condition, which may be more important than future productivity of the disturbed site (Prach & Hobbs 2008; Hodačovà & Prach 2003). Nevertheless, we found three protected species in the pine stands many sites offer unique environments for threatened and endangered species, and Prach et al. (2011) point out that sites of spontaneous succession may act as habitat for endangered species, while active restoration of reclaimed sites may favor common species with broad amplitudes over species with narrow habitat requirements.

The goal for restoration is never just increasing the total number of species (Prach & Hobbs 2008) as alien and ruderal species are often undesirable (they can change ecosystem structure and function) and forest and meadow species are more desirable in forest ecosystem restoration. We found a combination of meadow and forest species, but also ruderal species and pioneer species were represented. Dynamics of meadow, forest/meadow and forest species are expected to shift in favour of forest species through time (Verheyen et al. 2003; Soo et al. 2009). Although we found that the share of forest species is increasing due to increasing number of forest species, nevertheless the number of meadow and forest/meadow species is also increasing. This is suprising since meadow species should be declining with increasing stand age. The diversity of site conditions was apparent; when considering the preferences for dry and wet habitats, then species specific to both habitat types were present as well as species characteristic of both poor and fertile site types.

The goal of reclamation is to restore a stable ecosystem and this can be achieved if soil functionality is restored (Chodak et al. 2009). Soil formation depends on initial conditions; commonly there is an extremely low organic matter component, which affects fertility, biological activity, and moisture relations and can suppress germination and growth of seedlings. In our study, soil organic carbon content significantly increased with stand age but total carbon had no correlation with stand age because of the mineral carbon content of the rocks and detritus. Weathering of oil-shale and calcareous detritus gradually releases nutrients and topsoil thickness increases with stand age (Kaar et al. 1971). Our results show strong relationship among stand age and soil properties (pH, nitrogen content and phosphorus concentration), whereas pH decreased and P and N increased with stand age. Soil variables such as pH, organic carbon and phosphate levels, and water holding capacity influence species composition but it is not always clear how this influences vegetation colonization (Wiegleb & Felinks 2001). Bodlak et al. (2012) pointed out that soil organic carbon provides information on the quality of the reclaimed post-mining area. Broadleaf litter contains more nutrients and decomposes faster than conifer litter and this strongly influenced the nature of ground vegetation.

A common outcome of post-mining restoration is a novel ecosystem that is characterized by new species combinations resulting from human intervention, but not depending on continuing human activity (Hobbs et al. 2006). Novel ecosystems may be more diverse than natural communities and may offer suitable habitat for threatened and protected species (Richardson et al. 2010). We evaluated whether the ecosystems that develop on restored mined land in Northeast Estonia represent novel communites by comparing them to common forest conditions based on representative Scots pine site-types. We compared the soil conditions of three site-types found on similar bedrock to our study sites and then compared indicator understory vegetation common to the three sites-types. The N, K and organic carbon levels in soil are significantly similar to those found in soil of the *Hepatica* site-type, whereas P, total C and pH levels in soil are more similar to the *Calamagrostis* site-type. Soil development and nutrient levels in reclaimed mined land differ from soils of certain forest site-types and therefore formed unique conditions for vegetation development. The vegetation community is also distinctively different from vegetation on common forest site-types. Pine growth on the reclaimed sites is typical of the *Hepatica* site-type (Fig.5) and significantly different from the other site-types. Similarly, more understory species are indicators of the *Hepatica* site-type than the other types.

On balance, we suggest that indeed, novel ecosystems are developing on post-mining reclaimed land in Northeast Estonia and may require adaptations to typical forest management regimes that are based on site-types. Long-term monitoring of a novel ecosystem is important in order to study restoration pathways and determine if additional restoration measures are to be taken if the outcome is not desirable (e.g., low structural diversity on stand level, alien species invasion, etc.) (Laarmann et al. 2013). Long-term monitoring also provides feedback and information for better planning of restoration activities at new sites.

Implications for practice

Restoration of post-mining sites often leads to development of novel ecosystems. Their functions and composition may be valuable and serve restoration goals.

Novel ecosystems on post-mining sites are dynamic, changing completely by disturbances or management activities and their development is not easily predicted.

Long-term monitoring and evaluation of restoration of post-mining sites should be linked with planning and implementation of further management activities on these areas.

In certain cases, spontaneous succession should be considered in restoration of oil-shale post-mining sites as alternative to common afforestation practice, especially if these sites are small, surrounded by natural vegetation and there is no specific production goal or time limit for restoration.

Acknowledgements

This study was supported by the Estonian Environmental Investment Centre and by the Estonian Research Council (ETF8890, IUT21-04). We thank fieldwork and technical staff for their input.

References

Anderson, D.H., and B.D. Dugger. 1998. A conceptual basis for evaluating restoration success. Pages 111-121 in K.G. Wadsworth, editor. Transactions of the 63rd North American Wildlife and Natural Resources Conference. Wildlife Management Institute, Washington, DC.

Bodlák, L., Křováková, K., Kobesová, M., Brom, J., Št'astný, J., and E. Pecharová. 2012. SOC content – An appropriate tool for evaluating the soil quality in a reclaimed post-mining landscape. Ecological Engineering **43**: 53-59.

Bradshaw, A.D. 1997. What do we mean by restoration? Pages 8-14 in K.M. Urbanska, N.R. Webb and P.J. Edwards, editors. Restoration ecology and sustainable development. Cambridge University Press, Cambridge.

Burton, P.J. 2014. Considerations for monitoring and evaluating forest restoration. Journal of Sustainable Forestry **33**: S149-S160 .

Chodak, M., Pietrzykowski, M., and M. Niklinska. 2009. Development of microbial properties in a chronosequence of sandy mine soils. Applied Soil Ecology **41**: 259-268.

Doley, D., P. Audet. 2013 Adopting novel ecosystems as suitable rehabilitation alternatives for former mine sites. Ecological Processes **2**: 22.

Ferraro, P.J. 2009. Counterfactual thinking and impact evaluation in environmental policy. Pages 75-84 in M. Birnbaum and P. Mickwitz, editors. Environmental program and policy evaluation: Addressing methodological challenges. New Directions for Evaluation, 122.

Foster, B.L., and D.Tilman. 2000. Dynamic and static views of succession: Testing the descriptive power of the chronosequence approach. Plant Ecologt **146**: 1-10.

Hallett, L. M., Standish, R.J., Hulvey, K.B., Gardener, M.R., Suding, K.N., Starzomski, B.M., Murphy, S.D., and J.A. Harris. 2013. Towards conceptual framework for novel ecosystems. Pages 16-28 in R.J. Hobbs, E.S. Higgsand C.M. Hall, editors . Novel Ecosystems: intervening in the new ecological world order. Wiley-Blackwell.

Hastie, T.J., and R.J. Tibshirani. 1990. Generalized Additive Models. Chapman & Hall/CRC.

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vila, M., Zamora, R., and M. Zobel. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography **15**: 1-17.

Hobbs, R.J., Higgs, E., and J.A. Harris. 2009. Novel ecosystems: implications for conservation and restoration. Trends in Ecology and Evolution **24** (11): 599-605.

Hodačovà, D., and K. Prach. 2003. Spoil heaps from brown coal mining: technical reclamation versus spontaneous revegetation. Restoration Ecology **11** (3): 385-391.

Hutto, R.L., and R.T. Belote. 2013. Distinguishing four types of monitoring based on the questions they address. Forest Ecology and Management **289**: 183-189.

Hüttl, R.F. 1998. Ecology of post strip-mining landscapes in Lusatia, Germany. Environmental Science and Policy **1**: 129-135.

Hüttl, R.F., and A. Bradshaw. 2001. Ecology of post-mining landscapes. Restoration Ecology **9** (4): 339-340.

Ingerpuu, N. and K. Vellak. 1998. Eesti sammalde määraja. Eesti Loodusfoto, Tartu.

Kaar, E., Lainoja, L., Luik, H., Raid, L., and M. Vaus. 1971. Reclamation of the oil shale mines. Valgus, Tallinn. [in Estonian].

Kaar, E. 2002. Coniferous trees on exhausted oil shale opencast mines. Forestry Studies **XXXVI**: 120-125.

Kaar, E. 2010. Afforestation of flattened oil shale quarries. Pages 129-154 in E. Kaar and K. Kiviste, editors. Mining and rehabilitation in Estonia. Eesti Maaülikool, Tartu.[in Estonian with English summary].

Korjus, H., Sims, A., Kangur, A., Kaar, E., and A. Kiviste. 2007. Forest growth dynamics on abandoned oil shale quarries on the basis of permanent plot data. Miškininkystė **1** (61): 24-29.

Kukk, T., and T. Kull. 2005. Atlas of the Estonian Flora. Institute of Agricultural And Environmental Sciences of the Estonian University of Life Sciences. Tartu.

Kuznetsova, T., Lukjanova, A., Mandre, M., and K. Lõhmus. 2011. Aboveground biomass and nutrient accumulation dynamics in young black alder, silver birch and Scots pine plantations on reclaimed oil shale mining areas in Estonia. Forest Ecology and Management **262**: 56-64.

Laarmann, D., Korjus, H., Sims, A., Kangur, A., and J.A. Stanturf. 2013. Initial effects of restoring natural forest structures in Estonia. Forest Ecology and Management **304**: 303-311.

Lamb, D., and D. Gilmour. 2003. Rehabilitation and Restoration of Degraded Forests. IUCN, Gland, Switzerland and Cambridge, UK and WWF, Gland, Switzerland.

Leedu, E. 2010. Agricultural reclamation of open cast oil shale mines. Pages 219-254 in E. Kaar and K. Kiviste, editors. Mining and rehabilitation in Estonia. Eesti Maaülikool, Tartu.[in Estonian with English summary].

Leht, M. 2010. Eesti taimede määraja. Eesti Loodusfoto, Tartu.

Lõhmus, E. 2006. Eesti metsakasvukohatüübid. Eesti Loodusfoto, Tartu.

Mascaro, J., Harris, J.A., Lach, L., Thompson, A., Perring, M.P., Richardson, D.M., and E. Ellis. 2013. Origins of the novel ecosystems concept. Pages 45-57 in R.J. Hobbs, E.S. Higgs and C.M. Hall, editors. Novel ecosystems: intervening in the new ecological world order. Wiley & Sons, Chichester.

Mascia, M.B., Pailler, S., Thieme, M.L., Rowe, A., Bottrill, M.C., Danielsen, F., Geldmann, J., Naidoo, R., Pullin, A.S., and N.D. Burgess. 2014. Commonalities and complementarities among approaches to conservation monitoring and evaluation. Biological Conservation **169**: 258-267.

Martinez-Ruiz, C., Fernandez-Santos, B., Putwain, P.D., and M.J. Fernandez-Gomez. 2007. Natural and man-induced revegetation on mining wastes: changes in the floristic composition during early succession. Ecological Engineering **30**: 286-294.

Mudrák, O., Frouz, J., and V.Velichová. 2010. Understory vegetation in reclaimed and unreclaimed post-mining forest stands. Ecological Engineering **36**: 783-790.

Ostonen, I., Lõhmus, K., Alama, S., Truu, J., Kaar, E., Vares, A., Uri, V., and V. Kurvits. 2006. Morphological adaptations of fine roots in scots pine (*Pinus sylvestris* L.), silver birch (*Betula pendula* Roth.) and black alder (*Alnus glutinosa* (L.) Gaertn.) stands in recultivated areas of oil shale mining and semicoke hills. Oil Shale **23** (2): 187-202.

Paal, J., Rajandu, E., and I. Rooma. 2009. Alvar forests of Harjumaa district. Forestry studies 50: 42-67. [in Estonian with English summary].

Perring, M.P., Standish, R.J., and R.J. Hobbs. 2013. Incorporating novelty and novel ecosystems into restoration planning and practice in the 21st century. Ecological Processes **2**: 18.

Prach, K., and P. Pyšek. 2001. Using spontaneous succession for restoration of human-disturbed habitats: Experience from Central Europe. Ecological Engineering **17**: 55-62.

Prach, K., and R.J. Hobbs. 2008. Spontaneous succession versus technical reclamation in the restoration of disturbed sites. Restoration Ecology **16** (3): 363-366.

Prach, K., Rehounkova, K., Rehounek, I., and P. Konvalinkova. 2011. Ecological Restoration of central European mining sites: a summary of a multi-site analysis. Landscape Research **36** (2): 263-268.

Prescott, C.E. 2002.The influence of the forest canopy on nutrient cycling. Tree Physiology **22**: 1193-1200.

Richardson, T.J., Lundholm, J.T., and D.W. Larson. 2010. Natural analogues of degraded ecosystems enhance conservation and reconstruction in extreme environments. Ecological Applications **20** (3): 728-740.

Ruzicka, J., and E.H. Hansen. 1981. Flow Injection Analysis. John Wiley and Sons, New York.

Sims, A., Kiviste, A., Hordo, M., Laarmann, D., and K.v. Gadow. 2009. Estimating tree survival: a study based on the Estonian Forest Research Plots Network. Annales Botanici Fennici **46** (4): 336-352.

Soo, T. Tullus, A., Tullus, H., and E. Roosaluste. 2009. Floristic diversity responses in young hybrid aspen plantations to land-use history and site preparation treatments. Forest Ecology and Management **257**: 858-867.

Stanturf, J.A. 2005. What is forest restoration? Pages 3-11 in J.A. Stanturf and P. Madsen, editors. Restoration of boreal and temperate forests. CRC Press.

Stanturf, J.A., Palik, B.J., Williams, M.I., Dumroese, R.K., and P. Madsen. 2014. Forest restoration paradigms. Journal of Sustainable Forestry **33**: S161-S194.

Stem, C., Margoluis, R., Salafsky, N., and M. Brown. 2005. Monitoring and evaluation in conservation: a review of trends and approaches. Conservation Biology **19** (2): 295-309.

Tarand, A., Jaagus, J., and A. Kallis. 2013. Eesti kliima minevikus ja tänapäeval. Tartu Ülikooli Kirjastus. [in Estonian].

Toomik, A., and V. Liblik. 1998. Oil shale mining and processing impact on landscapes in north-east Estonia. Landscape and Urban Planning **41**: 285-292.

Verheyen, K., Guntenspergen, G.R., Biesbrouck, B., and M. Hermy. 2003. An integrated analysis of the effects of past land use on forest herb colonization at the landscape scale. Journal of Ecology **91**: 731-742.

Vorobjova, L.A. 1998. Khimitcheskaja analis potchv: utchebnik. Ist. Moskovskovo Universiteta.

Wiegleb, G., and B. Felinks. 2001. Primary succession in post-mining landscapes of Lower Lusatia – chance or necessity. Ecological Engineering **17**: 199-217.

Tables

Table 1. Summary of measured environmental variables in two types of forest stands, mean values and standard errors (in parentheses) are presented (p values are for comparison between all pine and birch stands * 0.05, ** 0.01, *** 0.001).

Variable	All pine stands		Pine stands 22-26 years		Birch stands 22-26 years		*p*
Soil properties							
Fine soil thickness (cm)	6.3	(0.6)	6.2	(1.2)	38.5	(2.4)	***
Organic layer thickness (cm)	1.4	(0.1)	1.5	(0.2)	3.1	(0.3)	***
C total (%)	9.22	(0.46)	8.50	(0.82)	6.14	(0.73)	**
C organic (%)	4.74	(0.15)	4.38	(0.22)	5.96	(0.71)	**
N total (%)	0.11	(0.01)	0.10	(0.01)	0.22	(0.03)	***
K available (mg kg^{-1})	86.47	(3.00)	86.01	(5.44)	77.94	(5.17)	
P available (mg kg^{-1})	24.91	(2.48)	24.23	(4.58)	67.23	(11.8)	***
pH_{KCl}	7.55	(0.02)	7.58	(0.03)	7.02	(0.12)	***
Sand, 2-0.05 mm (%)	55	(1.5)	58	(2.3)	70	(2.2)	***
Silt, 0.05-0.002 mm (%)	32	(1.2)	29	(1.8)	20	(1.8)	***
Clay, <0.002 mm (%)	13	(0.4)	13	(0.7)	10	(0.6)	**
Stoniness (%)	69	(0.7)	69	(1.0)	34	(2.6)	***
Vegetation							
Herb richness	13	(0.7)	12	(0.9)	10	(0.7)	*
Mosses richness	4	(0.3)	3.5	(0.4)	2	(0.3)	**
Herb cover (%)	26	(2.0)	27	(3.2)	59	(6.0)	***
Moss cover (%)	39	(3.5)	39	(6.2)	9	(3.2)	**
Herb diversity by Shannon	0.84	(0.06)	0.71	(0.08)	1.00	(0.10)	

Moss diversity by Shannon	0.55	(0.04)	0.48	(0.07)	0.11	(0.06)	***
Stand characteristics							
Share of deciduous species (%)	10	(1.9)	9	(3.9)	99	(0.8)	***
Stand height (m)	7.5	(0.4)	7.1	(0.6)	15.3	(0.9)	***
Mean stand diameter (cm)	8.5	(0.5)	8.1	(0.8)	13.3	(0.8)	***
Basal area (m^2 ha^{-1})	13.0	(1.1)	12.5	(1.8)	16.6	(1.1)	
No. of trees (ha^{-1})	2304	(114)	2500	(182)	1350	(284)	**
No. of dead trees (ha^{-1})	26	(7)	14	(7)	158	(35)	***

Figure legends

Figure 1. Ordination of plots by soil and stand variables. PC1 (37% of variance, p=0.001) and PC2 (16% of variance, p=0.001). The cut-off for vectors is R^2 of 0.5. Dec = share of deciduous trees in stand, Fsoil = topsoil layer thickness, P = phosphorus, Height = mean stand height, Diameter = mean stand diameter, Osoil = soil organic layer thickness, Age = stand age, Moss = mean richness of bryophytes, Stone = stoniness, pH = pH_{KCl}. Stands are represented by symbols: triangles = pine stands, circles = birch stands.

Figure 2. The dynamics of soil properties. Each dot represents one pine plot, mean value of pine plots is given by solid line and 95% confidence limits by the dashed lines.

Figure 3. Distribution of all understory species according to forest site type and habitat preference group.

Figure 4. Relationship between stand age and species richness of understory species in pine stands.

Figure 5. Relationship of stand height and diameter with stand age. Dots are plots in the current study, lines show trends by forest type using the GAM model.

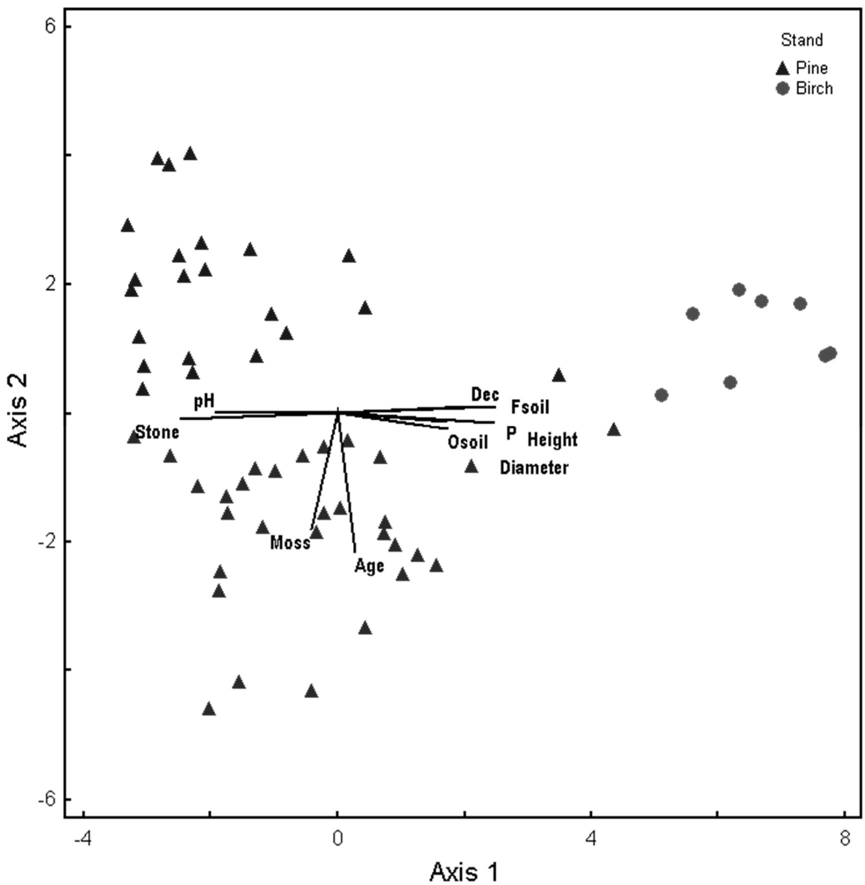

Stand
Pine
Birch
Axis 2
Axis 1
6
2
-2
-6
-4
0
4
8
pH
Stone
Dec
Fsoil
Osoil
P
Height
Diameter
Moss
Age

Figure 1.

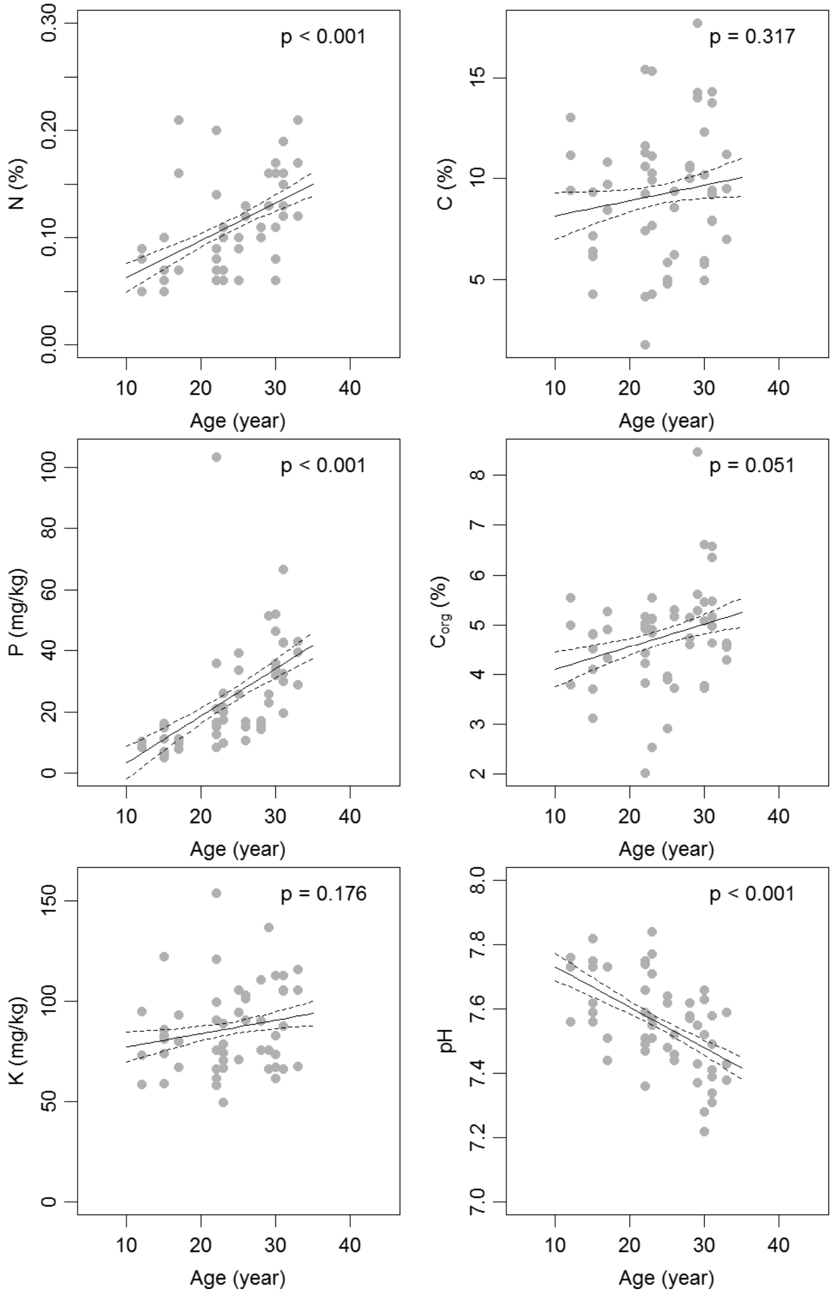

p < 0.001
N (%)
Age (year)
p = 0.317
C (%)
Age (year)
p < 0.001
P (mg/kg)
Age (year)
p = 0.051
C org (%)
Age (year)
p = 0.176
K (mg/kg)
Age (year)
p < 0.001
pH
Age (year)

Figure 2.

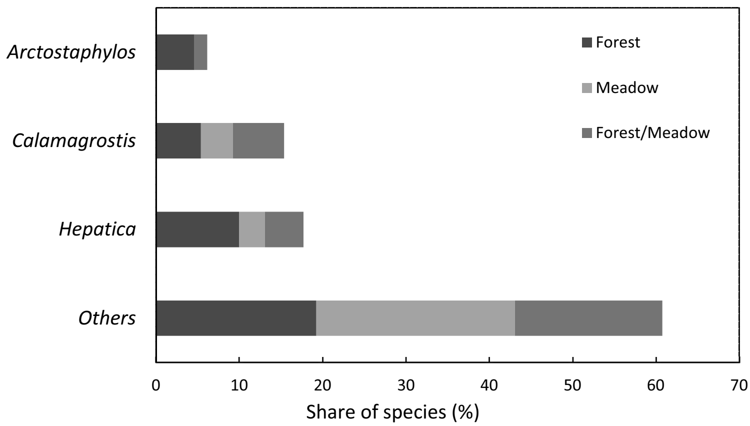

Arctostaphylos
Calamagrostis
Hepatica
Others
Forest
Meadow
Forest/Meadow
0
10
20
30
40
50
60
70
Share of species (%)

Figure 3.

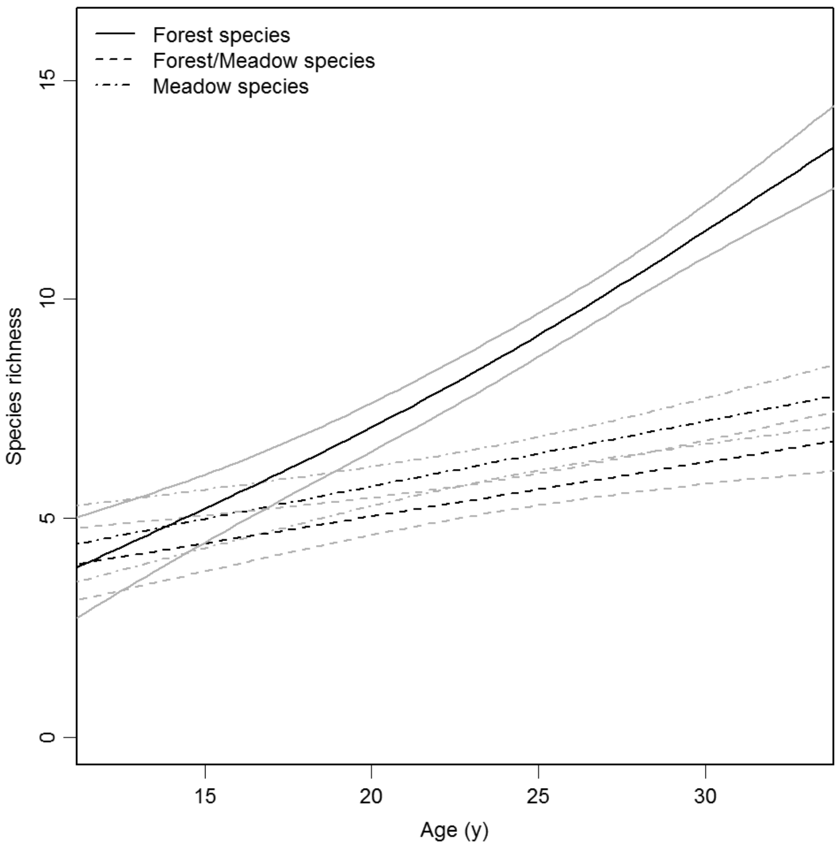
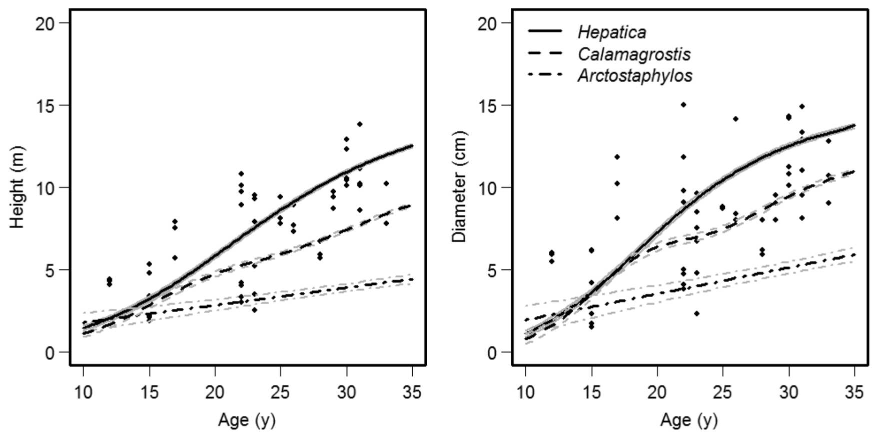

Forest species
Forest/Meadow species
Meadow species
Species richness
0
5
10
15
15
20
25
30
Age (y)

Figure 4.



Height (m)
Age (y)
Diameter (cm)
Age (y)
Hepatica
Calamagrostis
Arctostaphylos

Figure 5.

Electronic Supplementary Material 1

Table S1. Species list. Common habitat type is designated as F-forest, M-meadow and FM forest/meadow species; Forest site type (by Lõhmus 2006) is shown as H-*Hepatica* type, A-*Arctostaphylos*, C-*Calamagrostis* site type; dynamics are indicated as A-ascending with stand age (cover and abundance increased), D-decreasing, S-same with age; stands are identified as P-pine, B-birch, PB-species occur in both stands; * - single occurrence.

	In literature		Our study	
Taxon	Common habitat type	Indicator species of forest site type	Dynamics	Stand
Vascular plants				
Achillea millefolium	M	H	S	P
Agrostis capillaris	FM	H	A	PB
Agrostis stolonifera	FM		S	P
Alchemilla sp	FM		A	P*
Anthriscus sylvestris	FM	C	A	B*
Anthyllis vulneraria	M		A	P*
Arabis hirsuta	M		A	P*
Artemisia campestris	M		A	P
Artemisia vulgaris	M		S	P
Brachypodium pinnatum	FM	C/A	A	P*
Briza sp	FM	C	A	P*
Calamagrostis arundinacea	F	H/C/A	A	PB
Calamagrostis canescens	F		A	PB
Calamagrostis epigeios	FM		D	PB
Carduus crispus	FM		D	P
Carex hirta	F		A	P
Carex ornithopoda	FM		A	P
Carex panicea	FM		A	P
Carex tomentosa	FM		A	P*
Carex vaginata	F		A	P
Carlina vulgaris	M		A	P*
Centaurea jacea	M		A	P*
Centaurea scabiosa	M		A	P*
Cerastium fontanum	M		S	P
Cirsium arvense	M		S	PB
Cirsium heterophyllum	FM		A	B*

Cirsium oleraceum	F		S	B
Dactylorhiza fuchsii	F		A	P
Dactylis glomerata	M	H	A	P
Danthonia decumbens	FM		A	B*
Deschampsia cespitosa	FM	H	S	P
Elymus caninus	FM		A	B*
Epilobium angustifolium	FM		S	PB
Epilobium montanum	F		D	B
Epipactis helleborine	F		S	P
Equisetum pratense	FM		A	PB
Equisetum sylvaticum	F		A	P*
Erigeron acris	FM		A	P
Festuca ovina	FM	C/A	S	P
Festuca pratensis	FM		A	P
Festuca rubra	FM	H/C	A	P
Fragaria vesca	F	H/C/A	S	PB
Galeopsis pubescens	F		S	B
Galium album	M	C	S	P
Geranium robertianum	M	C	A	B*
Geum rivale	FM	H	A	B*
Goodyera repens	F		A	P
Helictotrichon pratense	FM	C	A	P*
Hieracium umbellatum	FM		A	P
Knautia arvensis	M	C	A	P*
Lathyrus pratensis	M		A	P
Leontodon autumnalis	M		S	P
Leontodon hispidus	M		D	P*
Leucanthemum vulgare	M		S	P
Linum catharticum	M		A	P*
Lotus corniculatus	M		A	P
Luzula pallidula	M		A	P*
Luzula pilosa	F	H	A	P
Lysimachia vulgaris	F		A	P*
Medicago lupulina	M		S	P
Melilotus albus	M		S	P
Melica nutans	F	H/C/A	A	P
Moehringia trinervia	F		A	PB
Monotropa hypopitys	F		A	P
Mycelis muralis	F	H	A	PB
Ophioglossum vulgatum	M		A	P
Orthilia secunda	F	H	A	PB
Pilosella officinarum	FM		S	PB
Plantago lanceolata	M		A	P*
Poa angustifolia	FM	C	A	PB
Poa compressa	M		S	P
Poa pratensis	M	H	A	PB

Polygala amarella	M		S	P
Potentilla anserina	M		A	P*
Potentilla erecta	FM		A	P
Prunella vulgaris	FM	H	S	P
Pyrola rotundifolia	F		A	P
Ranunculus acris	FM	H	A	P
Rubus idaeus	F		S	PB
Rubus saxatilis	F	H/C/A	A	P*
Scirpus sylvaticus	F		A	B*
Sesleria caerulea	FM	C/A	A	P*
Solanum dulcamara	F		A	B*
Solidago virgaurea	FM		A	P
Sonchus arvensis	M		A	B*
Taraxacum sp.	M	H	S	P
Tragopogon pratensis	M		A	P
Trifolium aureum	M		A	P*
Trifolium meedium	FM		S	P
Trifolium pratense	M		A	P
Tussilago farfara	M		S	PB
Urtica dioica	F		S	B
Veronica officinalis	F	H	A	P
Vicia cracca	M	C	A	P
Vicia sepium	FM		S	P
Vicia tetrasperma	M		A	P
Viola canina	F	H	S	P
Viola mirabilis	F		A	P*
Bryophytes				
Amblystegium serpens	F		A	PB
Amblystegium subtile	F		S	P
Barbula convoluta	F		S	P
Brachythecium glareosum	FM		A	P*
Brachythecium salebrosum	F		S	PB
Bryum algovicum	M		A	P*
Bryum bimum	FM		A	P*
Bryum caespiticium	FM		A	P*
Bryum imbricatum	F		A	P*
Calliergonella cuspidata	FM		A	P
Campylium sommerfeltii	F		A	PB
Ceratodon purpureus	F		A	P*
Cirriphyllum piliferum	F	H	S	P
Climacium dendriides	F		S	P
Ctenidium molluscum	M		A	P*
Dicranum polysetum	F	C	A	P*
Fissidens adianthoides	F		A	P
Hedwigia ciliata	M		A	P*
Hylocomium splendens	F	H/C/A	S	P
Mnium marginatum	FM		A	P
Orthotrichum speciosum	F		A	PB

Plagiomnium affine	F		S	PB
Plagiochila asplenioides	F	H	A	P
Plagiomnium undulatum	F		A	P*
Pylaisia polyantha	F		A	P*
Rhizomnium punctatum	F		A	P*
Rhodobryum roseum	F		A	P
Rhytidiadelphus squarrosus	M	C	A	P
Rhytidiadelphus triquetrus	F	H/C/A	A	P
Sanionia uncinata	F		A	P
Thuidium tamariscinum	F		A	P
Tortula ruralis	F		S	P

IV

Sims, A., Kiviste, A., Hordo, M., **Laarmann, D.,** Gadow, K.v. 2009.
Estimating tree survival: a study based on the
Estonian Forest Research Plots Network.
Annales Botanici Fennici 46 (4): 336-352.

Ann. Bot. Fennici 46: 336–352 ISSN 0003-3847 (print) ISSN 1797-2442 (online)
Helsinki 31 August 2009

Estimating tree survival: a study based on the Estonian Forest Research Plots Network

Allan Sims[1], Andres Kiviste[1,*], Maris Hordo[1], Diana Laarmann[1] & Klaus von Gadow[2]

[1)] *Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Kreutzwaldi 5, 51014 Tartu, Estonia (*corresponding author's e-mail: andres.kiviste@emu.ee)*
[2)] *Burkhardt Institute, Faculty of Forestry, Georg August University, Büsgenweg 5, D-37077 Göttingen, Germany*

Received 1 Sep. 2008, revised version received 23 Feb. 2009, accepted 25 Feb. 2009

Sims, A., Kiviste, A., Hordo, M., Laarmann, D. & Gadow, K. v. 2009: Estimating tree survival: a study based on the Estonian Forest Research Plots Network. — *Ann. Bot. Fennici* 46: 336–352.

Tree survival, as affected by tree and stand variables, was studied using the Estonian database of permanent forest research plots. The tree survival was examined on the basis of remeasurements during the period 1995–2004, covering the most common forest types and all age groups. In this study, the influence of 35 tree and stand variables on tree survival probability was analyzed using the data of 31 097 trees from 236 research plots. For estimating individual tree survival probability, a logistic model using the logit-transformation was applied. Tree relative height had the greatest effect on tree survival. However, different factors were included into the logistic model for different development stages: tree relative height, tree relative diameter, relative basal area of larger trees and relative sparsity of a stand for young stands; tree relative height, relative basal area of larger trees and stand density for middle-aged and maturing stands; and tree relative height and stand density for mature and overmature stands. The models can be used as preliminary sub-components for elaboration of a new individual tree based growth simulator.

Key words: forest growth, logistic regression, generalized linear mixed model, mortality, survival probability, tree and stand variables

Introduction

Tree mortality is a key factor influencing forest dynamics, and estimating tree survival therefore requires special attention (Yang *et al.* 2003). The accuracy of growth models depends largely on the accuracy of estimating tree survival. The main purpose of survival research is to understand how and why tree mortality occurs. This information is essential for developing strategies of forest management (Hamilton & Edwards 1976). Modelling tree survival is not a trivial task. In her overview Hawkes (2000) highlighted the main problems associated with such models:

Lack of long-term observations. Mortality may be caused by different biotic and abiotic factors which become relevant at different points in time. As a result, the probability of tree survival is usually rather fluctuating and irregular (Gadow 1987).

Improper use of models. Models of tree survival that have been developed on a specific data set and with specific assumptions, should not be used outside the range of their validity. Mortality patterns may differ substantially between different tree species (Dale *et al*. 1985).

Influence of human activity. Human activity is an important factor to natural which complements natural processes and complicates model prediction. It is hard to estimate the effects future management activity, because even in the case of well-defined cutting rules it is difficult to forecast the impact of the real cutting performance in terms of its weight and quality.

According to Vanclay (1994), the causes of tree mortality may be divided into three major groups:

Catastrophic: Large-scale mortality of trees, caused by storms, game damage, insect-pests, flooding or other extraordinary events.

Anthropogenic: Tree mortality caused mostly by harvesting operations, but also by industrial pollution or changes in water tables.

Regular: Tree mortality caused by tree age and competition, but also by pests and diseases and unfavourable weather conditions (storm, drought or flooding).

Catastrophic and anthropogenic mortality are hard to predict and the modeling of such processes requires long-term measurement series on permanent sample plots. Such data are lacking and for this reason, the present study deals only with modeling regular mortality.

A number of models were used to estimate tree survival, including the linear (Moser 1972, Leak & Graber 1976, West 1981), Weibull (Somers *et al*. 1980, Kouba 1989), gamma-distribution (Kobe & Coates 1997), exponential (Moser 1972), Richards (Buford & Hafley 1985), and Gompertz function (Kofman & Kuzmichev 1981). The logistic function has been used mostly for estimating individual tree survival (*see* for example, Hamilton & Edwards 1976, Monserud 1976, Buchman 1979, Hamilton 1986, Vanclay 1991, Vanclay 1995, Dursky 1997, Murphy & Graney 1998, Albert 1999, Monserud & Sterba 1999, Eid & Tuhus 2001, Yao *et al*. 2001, Hynynen *et al*. 2002, Soares & Tomé 2003, Yang *et al*. 2003, Diéguez-Aranda *et al*. 2005). The majority of the more recent survival models have been concentrating on the individual tree level (Mabvurira & Miina 2002). One reason is that the single tree level seems to allow more specific estimates in uneven-aged, species rich forests. In tree survival studies (Hynynen *et al*. 2002, Alenius *et al*. 2003) multilevel logistic regression models for hierarchically structured data are becoming more common.

Until recently, the research covering tree survival in Estonia has not been very extensive. Noteworthy is the model for estimating mortality on the stand level by Jõgiste (1998) and the research by Nilson (2006) about the relation between number of trees and mean stand diameter. Models for estimating individual tree survival are still lacking in Estonia. Only recently it has been possible to use the data from the network of permanent forest growth plots, which covers entire Estonia. Thus, the objective of the present study is to identify from that database variables which influence tree survival. We will present a first attempt to model individual tree survival in Estonia.

Our specific hypotheses were that (i) different sets of driving variables influence tree survival at different stand development stages; (ii) at the tree level, variables of relative size (e.g. ratio of tree and stand diameter) describe tree survival better than variables of absolute size; (iii) at the stand level, variables of maximum density influence survival the most; and (iv) shade-tolerant tree species are more vital than light-demanding, and fast growing species have lower rates of survival.

Factors influencing tree survival

In modeling tree survival, a variety of variables have been considered. Hamilton (1986) classified the factors that affect tree survival into four groups: tree size, tree competition status in the stand, tree viability and stand density. In the present analysis, the main factors that influenced tree survival in other studies, are considered. For that purpose, more than 20 logistic models of tree survival and mortality were analyzed. The logistic models for estimating tree survival can be presented in the following general form:

$$P=\left(1+e^{-f(X)}\right)^{-1}=\frac{1}{1+e^{-f(X)}}=\frac{e^{f(X)}}{1+e^{f(X)}} \qquad (1)$$

where P is the probability of tree survival, $(1 - P)$ is the probability of tree mortality, and $f(X)$ is the function (mostly linear) of diverse influencing factors (Vanclay 1994). Several authors have used Eq. 1 for different tree species, where every species has a specific set of coefficients (Hamilton 1986, Vanclay 1991, Monserud & Sterba 1999, Eid & Tuhus 2001, Hynynen *et al*. 2002). Factors, influencing mortality may be regarded at the single tree or stand level. The most frequently used variables are listed in Table 1.

Material and methods

Data set

The network of permanent forest growth research plots, established during the period 1995–2004 and covering entire Estonia was used in the present study. The first forest growth research plots of the network were established in the nemoral forests and mesotrophic forests of central Estonia in 1995–1996 and in the heath forests of northern Estonia in 1997–1998 (Kiviste & Hordo 2002). Since 1999, the network of forest research plots has been extended, representing the most common forest types and age groups in Estonia. For extension of the network of forest research plots, sample grid of International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (Karoles *et al*. 2000) was used for placement centres of plot groups. The plot locations in the field were selected randomly on a map.

Generally, the permanent forest growth plots are circular with radii of 15, 20, 25 or 30 meters. The plot size depends on the forest age and density, such that, as a rule, on every plot there are at least 100 trees of the upper tree storey. Trees of the second storey and shrub layer were measured in a smaller concentric circle with a radius of eight (at plot radius 15 m) or 10 meters (at plot radius more than 15 m). On each plot, the polar-coordinates (azimuth and distance from the plot centre), the diameter at breast height, and defects were assessed for each tree. The tree height and height to crown base were measured in every fifth tree and also on dominant and rare tree species. The height to the first dry branch of old coniferous trees was also assessed (*see* Kiviste & Hordo 2002 for more details).

In 2004, the network consisted of 730 of permanent forest growth plots. The tree coordinates and breast height diameters of 101 311 living trees were measured. The total tree height and the height to crown base was assessed on 33 045 trees. During 2000–2004, altogether 380 sample plots were re-measured. It was then found, that of 49 814 trees measured during the previous survey, 4658 trees (9.4%) had been harvested and 2883 trees (5.8%) had died (broken or fallen down) during the period between the two measurements.

During the period between the measurements, trees were harvested on 134 plots; 130 of these were excluded from the analysis because the condition of the trees at the time of harvest was not known. Fourteen plots, where the period between the measurements was not exactly five years, were also excluded from the analysis. Thus, the data set used in the present study contains 31 097 trees from 236 plots. Their locations are shown in Fig. 1.

Figure 2 presents distributions of permanent sample plots analyzed in this study by forest site types, dominant species and stand development stages. Most plots are located in the nemoral and mesotrophic forest types. The site type ’others’ includes alvar, transition bog, and fen forests. Pine stands are more represented than stands with other tree species. The alder forests include four black alder plots and five grey alder plots. Almost all groups by site type and by main species include stands of all development stages. Regarding stand age, it appears that the distribution of plots is quite balanced between the ages of 20 and 80 years (Fig. 3). Four plots stocked with pine forests have an age of 150 years or more.

Variables investigated

The list of variables which are assumed to influence tree survival and their statistical characteristics are presented in Table 2. The majority of the variables are continuous (age, height, diameter, etc.), but there are also some nominal variables (storey, tree species, forest site type) and binary variables as a transformation of nominal variables (tree species indicator, sign of moose damage, etc.) in the data set. The investigated data set was hierarchical, some of the variables were appointed at tree level (storey, tree species, tree diameter, tree height, etc.) and others at plot level (dominant tree species, forest site type, age of the first storey, mean diameter, mean height, etc.).

Table 1. Most frequently used tree and stand variables for estimating tree survival.

Individual tree		Forest stand	
Tree status	Source	Stand variable	Source
Tree diameter at breast height (*D*)	Monserud (1976), Hamilton & Edwards (1976), Hamilton (1986), Vanclay (1991), Dursky (1997), Monserud & Sterba (1999), Eid & Tuhus (2001), Yao *et al.* (2001), Mabvurira & Miina (2002), Hynynen *et al.* (2002), Soares & Tomé (2003), Yang *et al.* (2003)	Stand basal area	Hamilton & Edwards (1976), Hamilton (1986), Vanclay (1991), Eid & Tuhus (2001), Yao *et al.* (2001), Hynynen *et al.* (2002), Yang *et al.* (2003), Diéguez-Aranda *et al.* (2005)
Tree relative diameter (the ratio of tree diameter and stand mean diameter)	Hamilton (1986), Eid & Tuhus (2001), Mabvurira & Miina (2002)	Stand dominant height	Palahi & Grau (2003), Diéguez-Aranda *et al.* (2005)
The estimated tree diameter increment for a specified time	Monserud (1976), Hamilton (1986), Vanclay (1991), Yao *et al.* (2001), Yang *et al.* (2003)	Stand age	Hynynen *et al.* (2002), Diéguez-Aranda *et al.* (2005)
Tree height	Hamilton & Edwards (1976), Dursky (1997), Palahi & Grau (2003)	Stand mean diameter	Hamilton (1986), Eid & Tuhus (2001), Mabvurira & Miina (2002)
Tree age	Hynynen *et al.* (2002)	Relative proportion of tree species in stand (measured interms of basal area, volume or number of trees)	Yao *et al.* (2001), Eid & Tuhus (2001)
Relative length of tree crown	Hamilton & Edwards (1976), Monserud & Sterba (1999)	Stand site quality	Dursky (1997), Eid & Tuhus (2001), Yao *et al.* (2001), Mabvurira & Miina (2002)
The sum of basal area of larger trees (BAL index)	Vanclay (1991), Monserud & Sterba (1999), Eid & Tuhus (2001), Hynynen *et al.* (2002), Palahi & Grau (2003)	Number of trees per ha	Eid & Tuhus (2001), Soares & Tomé (2003), Diéguez-Aranda *et al.* (2005)
The sum of basal area of larger broadleaf trees	Yang *et al.* (2003)		
Tree defects caused by game, insects or some other damages	Hamilton & Edwards (1976)		

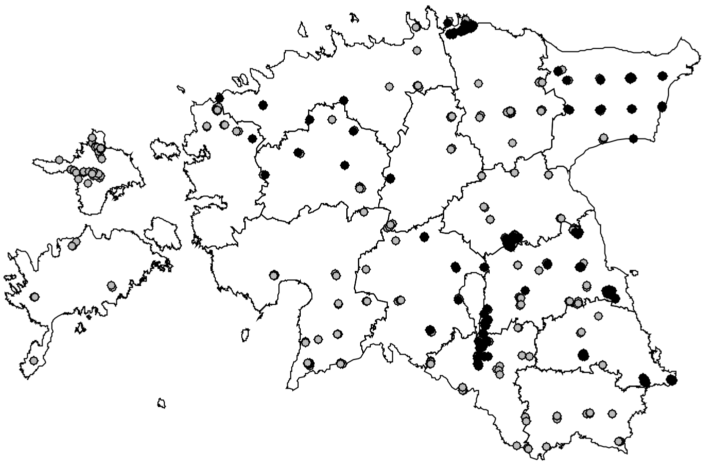


Fig. 1. Location of re-measured permanent sample plots in Estonia. Points in the map indicate locations of 3–6 permanent sample plots. Black dots = plots used in this study, grey dots = other plots in the network.

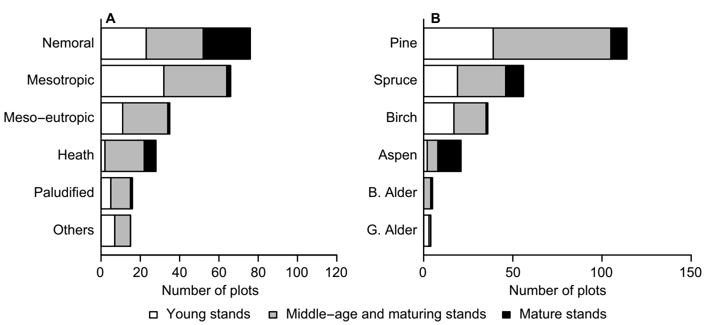


Fig. 2. Distribution of plots by groups of (**A**) forest site types and (**B**) main tree species.

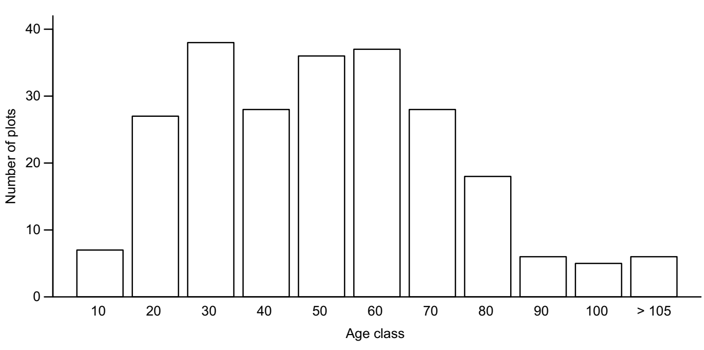


Fig. 3. Distribution of plots by age classes.

The tree storey (RIN) was defined during the field assessment according to the rules of a forest survey. The majority of trees on plots were assigned to the I storey (81.9%). Altogether 17.3% of the trees belong to the second storey (II storey), but substantially less trees were measured from the regeneration and shrub layer (respectively, 0.6% and 0.2%). In some plots, the second story (II storey) and the regeneration trees and the shrub layer were measured in the smaller concentric circle. In some sample plots, the small regeneration and shrub layer trees were not measured at all.

Almost one half of the trees (46.8%) were

Table 2. Variables influencing tree survival and their descriptive characteristics.

Variable code	Description	Unit	Type	Level	Observ. no.	Mean	Min	Max	SD
Tree Level									
RIN	Storey		Nominal	Tree	31097				
PL	Tree species		Nominal	Tree	31097				
D	Breast height diameter	cm	Continuous	Tree	31097	14.5	1.0	74.0	8.0
DS	Relative tree diameter (D/D1)		Continuous	Tree	31097	0.866	0.048	3.91	0.345
H	Tree height	m	Continuous	Tree	9226	16.3	2.0	37.1	7.1
HS	Relative tree height (H/H1)		Continuous	Tree	9226	0.868	0.083	1.79	0.223
KUDS	Relative tree diameter for spruce		Continuous	Tree	31097	0.154	0	3.91	0.355
HNLS	Tree height (calculated)	m	Continuous	Tree	31097	14.8	1.2	37.5	6.3
HNLSS	Relative calculated height (HNLS/H1)		Continuous	Tree	31097	0.868	0.083	1.79	0.223
HV	Height of crown base	m	Continuous	Tree	7807	8.9	0.1	30.3	5.6
SHV	Relative height of crown base (HV/H)		Continuous	Tree	7807	0.526	0.01	0.986	0.185
BAL	Basal area of larger trees	m^2 ha^{-1}	Continuous	Tree	31097	17.5	0	56.0	9.7
BALS	Relative basal area of larger trees (BAL/Gtot)		Continuous	Tree	31097	0.682	0	1.000	0.276
HEG5	Competition index in 5 m radius by Hegyi		Continuous	Tree	31097	4.3	0	194.5	8.2
HEGH	Competition index in 0.4H1 radius by Hegyi		Continuous	Tree	31097	4.3	0	193.7	7.3
PKAHJ	Moose damage		Binary	Tree	31097	0.050	0	1	
RIK	Other damage		Binary	Tree	31097				
Stand Level									
KKTR	Class of forest site type		Nominal	Plot	236				
A1	Age of 1st storey	year	Continuous	Plot	236	53.6	10	230	27.4
N1	Number of trees in 1st storey	1 ha^{-1}	Continuous	Plot	236	1582	143	9372	1737
G1	Basal area of 1st storey trees	m^2 ha^{-1}	Continuous	Plot	236	22.2	4.2	44.5	6.9
D1	Breast height diameter of the 1st storey	cm	Continuous	Plot	236	18.2	4.1	41.1	8.3
H1	Height of the 1st storey	m	Continuous	Plot	236	18.2	3.9	35.2	7.0
M1	Volume of the 1st storey	m^3 ha^{-1}	Continuous	Plot	236	210	19	745	109
T1	Relative density of the 1st storey		Continuous	Plot	236	0.61	0.08	1.53	0.27
L1	Sparseness of the 1st storey	m	Continuous	Plot	236	3.42	1.03	8.36	1.42
VG	Stand development stage		Nominal	Plot	236				
NOOR	Young stand		Binary	Plot	236	0.339	0	1	
KESK	Middle-aged stand		Binary	Plot	236	0.517	0	1	
VANA	Mature stand		Binary	Plot	236	0.144	0	1	
H100	Site index	m	Continuous	Plot	236	26.4	13.1	40.5	5.9
LTJ	Self-thinning sparseness by Tjurin	m	Continuous	Plot	236	2.59	0.76	5.45	1.05
TTJ	Relative sparseness by Tjurin		Continuous	Plot	236	0.77	0.33	1.19	0.14
PIIRT	Limit density by relative density		Binary	Plot	236	0.076	0	1	
PIIRTJ	Limit density by sparseness		Binary	Plot	236	0.064	0	1	

pines, 23.3% were spruces, 18% birches, 3.9% were aspens and 5.1% were alders.

Tree height (H) was measured on 29.7% of trees and the height to crown base (HV) on 25.1% of all trees. To estimate the height of all trees, Nilson's diameter/height relations were used (Kiviste *et al*. 2003). These relations were applied separately to every combination of tree species and storey of each plot (tree cohort). A two-parameter diameter/height regression is being used, when more than five trees per tree cohort were measured

$$\mathrm{HNLS} = \frac{H_\mathrm{C}}{1-b\left[1-\left(\frac{D_\mathrm{C}}{D}\right)^c\right]} \quad (2)$$

where D is the tree breast-height diameter; D_C is the mean square diameter of the respective tree cohort; b and H_C are parameters of the diameter-height regression, calculated from sample trees; c is a parameter which depends on the tree species (listed in Table 3). The variable H_C represents the mean height of the tree cohort.

When between 1 and 5 trees of each tree cohort were measured on a plot, the following one-parametric diameter-height relation was used

$$\mathrm{HNLS} = \frac{H_\mathrm{C}}{1-\left(a-0.0056D_\mathrm{C}\right)\left[1-\left(\frac{D_\mathrm{C}}{D}\right)^c\right]}$$
$$H_\mathrm{C} = \frac{1}{N}\sum_{i=1}^{N}\left(H_i\left\{1-\left(a-0.0056D_\mathrm{C}\right)\left[1-\left(\frac{D_\mathrm{C}}{D_i}\right)^c\right]\right\}\right) \quad (3)$$

where D is the tree breast height diameter; D_C is the mean square diameter of the respective tree cohort; a and c are parameters which depend on the tree species (listed in Table 3); H_i and D_i are sample tree height and diameter respectively.

The diameter/height relation (Eq. 3) was also used in the case of a tree cohort where the heights were not measured. This was the case, for example, in rare tree species which occurred on a particular plot. The mean height H_C of a tree cohort was calculated with the formula

$$H_\mathrm{C} = 1.3 + k_1\left[1-\exp\left(-k_2 D_\mathrm{C}\right)\right]^{k_3} \quad (4)$$

where D_C is the mean square diameter of the tree cohort, and k_1, k_2 and k_3 are species-specific parameters (Table 3).

Relative tree diameter (DS), relative tree height (HS), basal area of larger trees (BAL), relative basal area of larger trees (BALS) and Hegyi competition indices (HEG5 and HEGH) were the investigated variables characterizing individual tree competitive status. Four of these (DS, HS, BAL and BALS) do not require known tree positions and it is relatively easy to calculate them. The relative tree diameter (DS) is calculated as

$$\mathrm{DS} = D/D_1 \quad (5)$$

where D is the tree diameter and D_1 is the mean square diameter of the first storey trees. The relative tree height is calculated as follows

$$\mathrm{HS} = H/H_1 \quad (6)$$

where H is the tree height and H_1 is the mean height of the first storey, weighted by the species-specific basal areas. The BAL index is calculated as basal area of trees having a diameter larger than the diameter of the reference tree. The relative basal area (BALS) is equal to the BAL index divided by the basal area of all trees in the plot.

Tree position coordinates and tree-size data are used to define a competition index which requires that the tree positions are known. An example of such a position-dependent quantity is the Hegyi (1974) competition index (HEG5), which is calculated as follows:

$$\mathrm{HEG}_5 = \sum_i \frac{D_i}{DL_i^2} \quad (7)$$

Table 3. The parameters of the diameter/height relationship for different tree species (Kiviste *et al.* 2003).

Species	a	c	k_1	k_2	k_3
Pine	0.369	1.31	92.4	0.0110	1.0437
Spruce	0.394	1.47	72.7	0.0171	1.112
Birch	0.359	1.38	45.0	0.0320	1.038
Aspen	0.359	1.38	44.6	0.0387	1.290
Other	0.359	1.38	31.0	0.0529	1.144

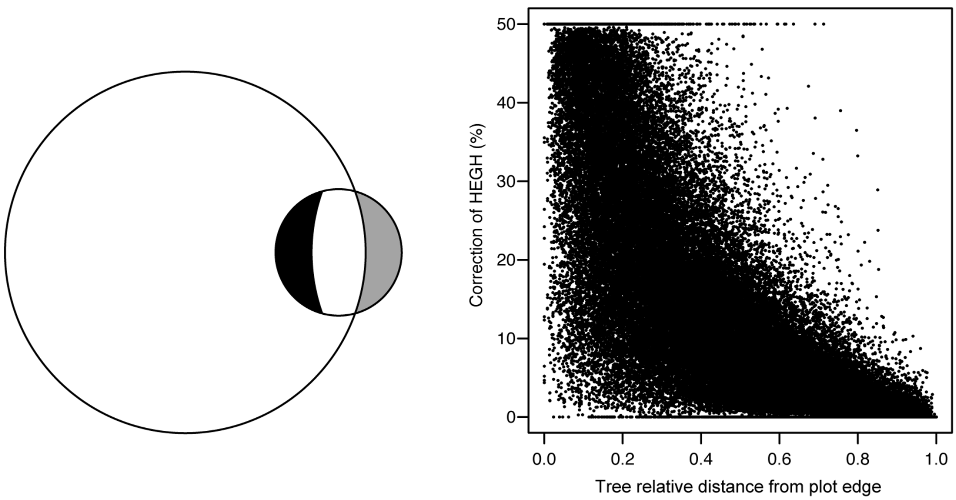


Fig. 4. Left-hand-side panel: adjustment of competition index by Hegyi. The section remaining outside the sample plot (grey) is compensated by considering the section of the same size inside the plot (black). Right-hand-side panel: correction of the edge effect of competition index by Hegyi.

where D is the diameter at breast height of the reference tree (cm); D_i is the diameter at breast height of the competitor tree (cm); L_i is the distance between the reference tree and the competitor tree ($L_i \leq 5$m).

When a tree is located near the external edge of the sample plot, Eq. 7 produces a systematic underestimate, because the influence of neighbouring trees outside the sample plot (light grey area in the Fig. 4 left) are not considered. To compensate for this lack of information, the light grey area was mirrored inside the plot (dark grey area in Fig. 4).

The relative amount of the corrections of the Hegyi index of the trees that are near the plot edges are shown in Fig. 4 (right-hand-side panel). Near the sample plot edge, the value of the competition index is increasing considerably, due to the adjustment.

The value of the Hegyi index depends on stand density and the radius of the influence zone. Thus, a fixed radius (e.g. HEG_5 = 5 m) does not always make sense. For this reason, Hegyi's competition index (HEGH) was also calculated, using an influence zone radius which was equal to 40% of the mean tree height in the first storey.

At the sample plot level, the investigated measurement variables of the first storey were stand age (A_1), density (N_1), basal area (G_1), mean square diameter (D_1), mean height (H_1), stem volume (M_1), and relative density (T_1). To calculate the stem volume of each tree, the volume equation by Ozolins (2002) was used. Stand volume (M_1) was calculated as the sum of the first storey tree stem volumes per hectare.

The site index (H_{100}, average height of dominant species at reference-age 100 years) was calculated according to the current age and height of the dominant tree species using the model developed by Nilson (1999) which is an approximation of Orlov's tables (Krigul 1969).

In the Estonian forestry practice, relative density is widely used. For tree cohorts with a mean height over 5 m, relative density (T_C) was calculated as follows

$$T_C = \frac{M_C}{a_0 + a_1 H_C + a_2 H_C^2 + a_3 H_C^3} \qquad (8)$$

where M_C is the volume of the cohort trees ($\text{m}^3\ \text{ha}^{-1}$), and H_C is the mean height of the cohort trees (m). Parameters a_0, a_1, a_2, a_3 are listed in Table 4.

In the case of the mean height being less than 5 m, the relative density (T_C) was calculated according to the National Forest Inventory Instruction (SMI 1999) based on tree cohort height (H_C) and density (N_C). In the case of pine cohorts with a height of less than 5 meters, the relative density was calculated with Eq. 9 and in the case of other tree species with Eq. 10.

$$T_C = \frac{N_C}{5610 H_C^{-0.154}} \quad (9)$$

$$T_C = \frac{N_C}{0.2966 H_C^4 - 8.9075 H_C^3 + 105.48 H_C^2 - 603.85 H_C + 3633} \quad (10)$$

The relative density for the first storey is calculated as the sum of the relative densities of the first storey tree cohorts. As indicator of high relative density, a binary variable PIIRT was used. PIIRT assumes a value of 1 if T_C is greater or equal to 1, otherwise it equals 0.

In addition to traditional stand variables, the stand sparsity (L_1), recommended by Nilson (2006), was also used in the present study:

$$L_1 = \frac{100}{\sqrt{N_1}} \quad (11)$$

where N_1 is the number of trees of the first storey per hectare. L_1 is an estimate of the average distance between trees, assuming a rectangular distribution of tree positions. A. Nilson (pers. comm.) calculated the self-thinning standard (LTJ), based on Tyurin's growth and yield tables of normal forest (Krigul 1969).

$$\mathrm{LTJ} = k_4 + k_5 D_1 + k_6 D_1 H_{100} + k_7 H_{100} \quad (12)$$

where D_1 is the mean square diameter of the first storey trees (cm); H_{100} is the site index; k_4, k_5, k_6, k_7 are species-specific parameters (listed in Table 4).

Analogically to the relative density calculated by the self-thinning model (Eq. 12), the relative sparsity of a stand (TTJ) may be calculated as follows

$$\mathrm{TTJ} = \mathrm{LTJ}/L_1 \quad (13)$$

We assume that if the value of the relative sparsity (Eq. 13) is greater than 1, then the stand has exceeded the self-thinning line which will result in greatly increased mortality of trees. As an indicator of crossing of the self-thinning line, a binary variable PIIRTJ was used. PIIRTJ assumes a value of 1 if TTJ is greater or equal to 1, otherwise it equals 0.

According to a conceptual model of forest stand development based on the study of the Estonian long-term permanent sample plot data (Kangur *et al*. 2005), stand dynamics can be divided into four stages: stand initiation, stem exclusion, demographic transition and old multi-aged. These stages are characterised by different ecological processes. In this study, we have the data from after the stand initiation stage, thus we determined three different stand development stages (VG) according to dominant species and stand age (Table 5), which is common practice in Estonian forest management.

Methods

In the present study, the dependent variable is EJ, which defines the probability that a tree will survive during the next 5-year period. The value of EJ was set equal to 1, if the tree was still alive after five years, and 0 if it was not. Thus, the probability of tree mortality is equal to

$$\mathrm{VL} = 1 - \mathrm{EJ} \quad (14)$$

Table 4. The species-specific parameters of the relative density model $T_c = M_c/(a_0 + a_1H_c + a_2H_c^2 + a_3H_c^3)$ developed on the basis of Tretyakov's standard tables (Krigul 1969) and of the self thinning model LTJ = $k_4 + k_5D_1 + k_6D_1H_{100} + k_7H_{100}$ developed on the basis of Tjurin's growth and yield tables (Krigul 1969).

Species	a_0	a_1	a_2	a_3	k_4	k_5	k_6	k_7
Pine	–30.595	16.631	0.0254	0	–0.00437	0.1834	–0.00216	0.008641
Spruce	–7.988	9.279	0.3473	0	0.1807	0.1556	–0.00181	0.003598
Birch	15.344	0	0.7411	–0.0087	0.4083	0.1822	–0.00151	0.00671
Aspen	–18.758	8.385	0.3233	0	0.02032	0.1991	–0.00277	0.01046
Other	–11.713	8.474	0.2767	0	0.3867	0.1878	–0.00277	0.0000325

where EJ is the survival probability and VL is the mortality probability. One advantage of modeling the survival probability EJ is that it can be treated as a Markovian process so that the survival probability over a period of N years is given by the Nth power of the annual probability of survival (Vanclay 1994: p. 178).

Simple linear functions are not suitable for modeling survival because they may give predictions of the survival probability outside the feasible range (0, 1). For modeling a variate which follows a binomial distribution, a logistic model may be used where the dependent variable is logit-transformed as follows:

$$\mathrm{logit(EJ)} = \ln[\mathrm{EJ}/(1 - \mathrm{EJ})] \tag{15}$$

Through logit-transformation the dependent variable is transformed into a variate with a normal distribution, which can be analyzed using logistic regression:

$$\mathrm{logit(EJ)} = f(\boldsymbol{X}) \tag{16}$$

where $f(\boldsymbol{X})$ is a linear function of the vector $\boldsymbol{X}$ of measurement variables.

The inverse of the logit-transformation (Eq. 15) is the model that we are using to predict tree survival probability:

$$\mathrm{EJ} = e^{f(X)}/[1 + e^{f(X)}] \tag{17}$$

where $f(X)$ is the equation of a logistic regression.

In logistic regression analysis, the *deviance* (also called as *log-likelihood statistic*) is used to characterize goodness of fit, calculated by logarithmic likelihood. The *likelihood-ratio test* helps to estimate the influence of new arguments, added into the model. The likelihood ratio follows a χ^2 distribution $\chi^2(p)$; where p is the number of parameters, which allows estimation of the statistical significance of added arguments (Dobson 2002). To select the best subset of variables the score statistic was calculated for every single tree variable for ranking single tree influence on survival using PROC LOGISTIC (Freund & Littell 2000) in SAS. The *score statistic* is asymptotically equivalent to the likelihood-ratio test statistic but avoids the need to compute maximum-likelihood estimates (Schaid *et al* 2002).

In the case of the traditional linear regression analysis (with the assumption of a normal distribution of residuals) to characterize the goodness of fit of a model, the root mean square error or coefficient of determination (R^2) are being used (Dobson 2002). By analogy with R^2 for ordinary regression, the generalized R^2 was used which represent the proportional improvement in the log-likelihood function due to the terms in the model of interest as compared with the minimal model (Dobson 2002, Shtatland *et al*. 2002).

$$R^2 = 1 - \frac{\log L(M) - p - 1}{\log L(0) - 1} \tag{18}$$

where $\log L(M)$ is the maximized log-likelihood for the fitted model with number of parameters p; $\log L(0)$ is the “null” model containing only the intercept term.

The SAS LOGISTIC procedure presents two different definitions of generalized coefficients of determination. One has been developed by Cox and Snell (1989: pp. 208–209), the other is an adjusted one by Nagelkerke (1991). In this study the coefficient of determination defined by Eq. 18 was used because Shtatland *et al* (2002) has shown that it has a number of important

Table 5. Age criteria by dominant tree species for stand development stages (VG).

Species	Young stands (NOOR)	Middle-age and maturing stands (KESK)	Mature and over-mature stands (VANA)
Pine	< 50	50–99	≥ 100
Spruce	< 40	40–79	≥ 80
Birch, black alder	< 35	35–69	≥ 70
Aspen	< 25	25–49	≥ 50
Grey alder	< 15	15–29	≥ 30

Table 6. Characteristics of survival probability by storey.

Layer	Number of trees	Number of sample plots	Proportion of spruce (%)	Number of surviving trees	Survival probability (%)	95% CL of survival probability		Survival probability at DS = 0.5 (%)	95% CL of survival probability (DS = 0.5)	
						Lower	Upper		Lower	Upper
1st storey	25477	236	13.5	23654	92.8	92.5	93.2	79.2	78.1	80.3
2nd storey	5380	154	68.3	4927	91.6	90.8	92.3	91.9	91.1	92.5
Regeneration	178	14	74.7	160	89.9	84.5	93.5	92.3	85.3	96.1
Shrub layer	62	5	27.4	37	59.7	47.1	71.0	60.5	45.3	73.9

advantages over the coefficients of determination of Cox and Snell (1989) and Nagelkerke (1991).

For the logistic ANOVA, the procedure GENMOD of the SAS software (Littell *et al* 2002) was used for analysing the tree cohort influence. For multilevel analysis of tree and stand variable influences the generalized linear methods (SAS procedure GLIMMIX) (Schabenberger 2005) and the R function **lmer** (Crawley 2007) were used. The SAS procedure GLIMMIX fits statistical models to data with correlations or non-constant variability and where the response is not necessarily normally distributed. Function **lmer** is used for fitting mixed-effects models in R (package lme4). Both allow analysing a a response variable with a binomial distribution and logit transformation. However, the SAS procedure GLIMMIX implements a restricted pseudo-likelihood (RPL) method whereas a restricted maximum likelihood (RML) method is used in the R function **lmer**.

Results and discussion

Tree survival probability dependence on tree storey

In the present study, four storeys were separately identified on the analyzed sample plots — the first storey (1), the second storey (2), the regeneration (J) and shrub layer trees (A). The results show that the survival probability of the trees which belong to the first storey is higher than that of trees in other storeys (*see* Table 6). The difference in survival probabilities is statistically significant between the first and the second storeys and between the first storey and the regeneration.

We assume that the difference of the survival probability in the storeys in the stand is largely caused by the differences in the relative diameter. To evaluate that assumption, a model of logistic covariance analysis was applied using the procedure GENMOD of SAS

$$\mathrm{logit}(\mathrm{EJ}_{ij}) = \mu + \tau_i + (\beta + \delta_i)\mathrm{DS}, \quad (19)$$

where EJ_{ij} is the survival probability of a tree in the ith storey and the jth relative diameter; logit() is the logit-transformation (15); μ is the model intercept; τ_i is the influence of the storey to the intercept; β is the slope of the regression line between the logit-transformation and the relative tree diameter DS; δ_i is the influence of ith storey on the slope of the regression line; DS is the ratio between the tree diameter and the first storey mean squared diameter.

Table 6 presents survival probabilities, calculated with Eq. 19 and their confidence limits for different storeys. These results are interesting because of the differences in the viability of the suppressed trees in the different layers. The value of the relative diameter DS was set to 0.5 at each layer. In the case of the suppressed trees in the second storey and regeneration layer, the tree survival was found to be substantially higher than the viability of the trees in the first storey (where DS was also equal 0.5). Much less viable were the shrub layer trees. The relatively high viability of the regeneration and second storey trees is probably due to the fact that spruce, a shade-tolerant tree species, is very prominent in these storeys, and is found here in greater proportions than in the first storey and in the shrub layer.

In many sample plots the smaller understorey trees (trees of the second storey, and of the regeneration and shrub layer) were either not present at all, were measured within a smaller circle, or were not measured at all. Therefore, only the trees from the first storey are considered in the following analysis.

Tree survival probability depending on a single variable

At first, the influence of each variable on tree survival was investigated individually without considering the influence of other variables. The influences were assessed separately for the entire data set as well as for the data sets of the three stand development stages (young, middle-aged, mature).

Table 7 presents the score statistics on different data sets, characterizing the influence of the measurement variable X in the logistic regression formula

$$\mathrm{logit}(\mathrm{EJ}) = \mu + \beta X, \tag{20}$$

where EJ is the survival probability; logit() is the logit-transformation; X is the measurement observation; μ, β are parameters of the regression equation.

The results in Table 7 show that for the entire dataset and also on separate data sets of all stand development stages, the tree survival probability EJ depended most on the relative height of a tree HNLSS. As mentioned before, the tree heights which were not measured were calculated using a specific diameter/height relationship. For the total database, the second most important variable was the tree relative diameter DS. But in middle-aged and older stands this variable was not in the first triple. The third most important variable in the total data set was BALS (the ratio between the relative basal area of larger trees and the stand basal area).

Table 7. Variables, influencing tree survival probability the most. The numbers in the table represent score statistics of differences between intercept only and intercept with variable.

Variable	All data	Young stands	Middle-aged and maturing stands	Mature and overmature stands
HNLSS	1881	640	1166	109
DS	1300	435	810	73
BALS	1099	403	620	70
HEGH	907	247	920	85
D	859	188	800	88
HEG5	776	187	932	82
BAL	725	435	249	74
HNLS	606	88	610	60

Considering the total data set, effective variables were also both Hegyi competition indices (HEGH and HEG5) and then the tree height H, the tree diameter D and the basal area of larger trees BAL. Stand variables (both versions of relative density and quality class) and tree species were clearly less important than the measured variables which characterize the relative state of a tree. From the practical viewpoint, the tree diameter D and the tree relative diameter DS are explanatory variables which can be used in distance-independent forest-growth models. Therefore, these variables are often preferred to competition indices which require known tree positions.

The influence of the height to crown base and of the relative height of crown base on the tree survival probability was analyzed for sample tree data sets where the height to crown base was measured and the spruce trees were left out. The results show that in young and middle-aged stands, the influence of the height to crown base on the tree survival probability was less than the influence of the other variables listed in Table 7. Old stands were an exception; there, the influence of relative and absolute height to crown base on mortality was clearly higher than the influence of other variables.

Tree survival probability dependence on several variables

Tree survival probability EJ was modeled with the two-level mixed model

$$\begin{aligned}\operatorname{logit}\left(\mathrm{EJ}_{ij}\right) &= \beta_{0j} + \beta_1 X_{1ij} + \beta_2 X_{2ij} + \ldots \\ &\quad + \beta_m X_{mj} + \beta_{m+1} X_{m+1j} + \ldots\end{aligned} \tag{21}$$

where EJ_{ij} is the tree survival probability; logit() is the logit transformation (Eq. 15), β_{0j} is the random intercept ($\beta_{0j} = \beta_0 + u_j$;$u_j \sim \mathrm{N}(0, \sigma_u^2)$, i is the tree number; j is the plot number; X_{1ij}, X_{2ij} are tree level variables; X_{mj}, X_{m+1j} are stand level variables; β_0, β_1, β_2, β_m, β_{m+1}, ... are model parameters.

Taking a great number of arguments into the model may be justified in the case of a random sample, such as a forest inventory, where all elements of a population have the same probability to be part of the sample. Unfortunately, the selection of stands in the Estonian forest research plot network was not entirely random, which is also revealed in the distribution histograms in Figs 2 and 3. That is why the principle of developing a model which is as parsimonious as possible (Burkhart 2003) was followed in this study.

The selected variables (Table 2) were divided into three groups: vertical size variables (HNLS, HNLSS, H_1, etc.), horizontal size variables (D, DS, D_1, etc.) and competition variables (BALS, BAL, HEG5, HEGH, etc.). Variables of relative size (relative diameter, relative height) could be handled as size group variables as well as competition group variables. However, in this study relative size variables were handled as size group variables, because we assume that they are indicative of the amount of resources needed for tree survival. For selecting variables into the multiple model, an ordered list of score statistics was calculated for all variable combinations using the LOGISTIC procedure. However, not all variable combinations on top of the list of score statistics were biologically interpretable and with statistically significant parameter estimates. For multilevel logistic modeling with a random intercept (Eq. 21) we selected one tree level variable from each group, a stand level competition variable, and the tree species as regressors (HNLSS, DS, BALS, TTJ, KUDS, PL). The results of this multilevel logistic modelling on different data sets are presented in Table 8.

Table 8 presents two sets of results of multilevel logistic modelling, one obtained with the SAS procedure GLIMMIX and the other with the R function **lmer**. Both procedures use different methods for parameter estimation. Nevertheless, both methods established the same set of significant variables and produced similar parameter estimates which is somewhat reassuring. All terms in the model are biologically sound: tree survival (EJ) is increasing with increasing relative height (HNLSS) and decreasing with increasing competition status (BALS, TTJ). Considering the effect of different tree species, spruce survival was significantly higher and grey alder survival significantly lower than other tree species for all development stages. This can be explained by the shade tolerance of spruce and the short life of grey alder. Significance of variable KUDS for old stands indicates a relatively lower survival of bigger spruces because of wind- and fungi damages (Laarmann 2007).

Conclusions

Tree mortality is a key factor in the understanding of forest dynamics. The accuracy and relevance of a growth model depends on the accuracy of predicting tree survival. The present study has shown which tree and stand variables affect tree survival probability most in Estonian forests.

Tree survival was analyzed using a data set which includes 31 097 trees from 236 research plots, measured twice during 1995–2004. During the 5-year period between measurements, altogether 2319 trees (or 7.5%) had died (dead standing, broken or fallen).

The survival probabilities, presented in Table 6 are interesting because of the differences in the viability of the suppressed trees in the different layers. In the case of the suppressed trees in the

Table 8. Results of generalized linear mixed modeling with PROC GLIMMIX (SAS) and function lmer (R) for Eq. 21.

Regressor		All data		Young stands		Middle-aged and maturing stands		Mature and overmature stands	
Coefficients of model with GLIMMIX									
		Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept		2.1624	0.4232	4.8111	0.9713	–1.2635	0.4227	10.2931	2.2789
HNLSS		4.3433	0.2559	4.5473	0.6140	4.6567	0.5607	3.4531	1.1361
DS				–1.7344	0.7159	1.7057	0.3859		
BALS		–1.8928	0.2319	–4.1013	0.7873			–2.3698	0.8679
TTJ		–2.1976	0.2510	–1.7800	0.3975	–1.8281	0.3929	–9.9323	1.8795
KUDS								–3.8111	1.7460
PL	Aspen	–1.3529	0.1125	–1.3610	0.1885	–1.4853	0.1609	–1.1760	0.5093
	Birch	0.0796	0.0871	0.0317	0.1583	0.0179	0.1261	–0.1850	0.4064
	Spruce	0.2272	0.1032	0.2561	0.1470	0.3762	0.1732	1.7442	1.7761
	B. alder	–0.1938	0.2058	–0.6747	0.2605	1.0037	0.5192	–1.6863	0.9211
	G. alder	–1.9203	0.1083	–1.5491	0.2054	–2.2703	0.1403	–2.6151	0.4481
Type III Tests of Fixed Effects									
		F	Den df	*F*	Den df	*F*	Den df	*F*	Den df
HNLSS		288.06	24906	54.85	8718	68.99	14203	9.24	1969
DS				5.87	8718	19.53	14203		
BALS		66.63	24906	27.14	8718			7.46	1969
TTJ		76.66	234	20.05	78	120	21.65	27.93	32
KUDS								4.76	1969
PL		94.40	374	25.95	138	173	71.49	7.42	53
Coefficients of model with lmer									
		Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept		1.9623	0.6442	4.7740	1.2959	–0.7766	0.7268	8.9933	2.3692
HNLSS		5.3326	0.3016	4.8669	0.8782	4.8496	0.6391	3.5957	1.0692
DS				–1.0344	0.9549	1.8207	0.4109		
BALS		–1.6489	0.2420	–3.8207	0.8970			–2.2355	0.8047
TTJ		–2.8763	0.6070	–2.8202	1.0808	–2.4132	0.7999	–8.4635	2.1181
KUDS								–3.5764	1.6793
PL	Aspen	–0.8172	0.1998	–0.6762	0.3882	–0.9910	0.2642	–1.1893	0.5332
	Birch	0.1714	0.1479	0.4230	0.2951	0.1042	0.1910	–0.3125	0.4440
	Spruce	0.4109	0.1701	0.7031	0.2699	0.3845	0.2434	1.6453	1.7147
	B. alder	–0.2659	0.2540	–0.6531	0.3643	1.0362	0.5261	–2.0163	0.8827
	G. alder	–2.0647	0.1924	–1.5209	0.3300	–2.6542	0.2577	–2.5840	0.5444
Fit statistics									
logLik		–4856		–1692		–2752		–363.1	
Deviance		9712		3384		5505		726	
R^2		0.168		0.189		0.168		0.084	

second storey and regeneration layer, the tree survival was found to be substantially higher than the viability of the trees in the first storey (for a given value of DS = 0.5).

The logistic form was used for modeling tree survival probability. The influence of 35 tree and stand measurement variables (Table 2) to tree survival probability was estimated using the score statistics of a logistic regression.

The research of separate single variables revealed that the mortality of trees is mostly influenced by tree measurement variables (presented in decreasing order of score statistic, Table 7): tree calculated relative height HNLSS, tree relative diameter DS, relative basal area of larger trees BALS, Hegyi competition index HEGH in a circle with radius $0.4H_1$, tree diameter D, Hegyi competition index HEG5 in a circle with a 5-m radius, basal area of larger trees BAL and tree height H. The study revealed that it is useful to divide the total data set into three development stages defined by dominant tree species and age: young, middle-aged and maturing, mature and very old stands. In each of these categories, different influencing factors turned out to be dominant.

The obtained results improve our knowledge of Estonian forest stand dynamics. It is possible to apply the proposed models in forest simulation studies as a preliminary approximation of a tree mortality component. The development of flexible simulators, which complement existing yield-tables, will significantly improve decision-making in practical forest management.

Acknowledgements

The establishment of the network of permanent forest research plots was supported by the Estonian State Forest Management Centre and the Centre of Environmental Investments. The study was supported by The Ministry of Education and Research (project SF0170014s08).

References

Albert, M. 1999: *Analyse der eingriffsbedingten Strukturveränderung und Durchforstungsmodellierung in Mischbeständen*. — Ph.D. thesis, Universität Göttingen. Hainholz-Verlag.

Alenius, V., Hökkä, H., Salminen, H. & Jutras, S. 2003: Evaluating estimation methods for logistic regression in modelling individual-tree mortality. — In: Amaro, A., Reed, D. & Soares, P. (eds.), *Modelling forest systems*: 225–236. CAB International, Wallingford, UK.

Buchman, R. G. 1979: Mortality functions — In: *A generalized forest growth projection system applied to the Lakes States region*: 47–55. Gen. Tech. Rep. NC-49, USDA For. Serv. N. Cent. Res. Stn.

Buford, M. A. & Hafley, W. L. 1985: Modeling probability of individual tree mortality. — *Forest Science* 31: 331–341.

Burkhart, H. E. 2003: Suggestions for choosing an appropriate level or modelling forest stands. — In: Amaro, A., Reed, D. & Soares, P. (eds.) *Modelling forest systems*: 3–10. CAB International, Wallingford, UK.

Crawley, M. J. 2007: *The R book*. — John Wiley & Sons Ltd.

Cox, D. R. & Snell, E. J. 1989: *The analysis of binary data*, 2nd ed. — Chapman and Hall, London, UK.

Dale, V. H., Doyle, T. W. & Shugart, H. H. 1985: A comparision of tree growth models. — *Ecological Modelling* 29: 145–189.

Diéguez-Aranda, U., Castedo-Dorado, F., Álvarez-Gonzàles, J. G. & Rodriguez-Soalleiro, R. 2005: Modelling mortality of Scots pine (*Pinus sylvestris* L.) plantations in the northwest of Spain. — *European Journal of Forest Research* 124: 143–153.

Dobson, A. J. 2002. *An introduction to generalized linear models*. — Chapman and Hall, London, UK.

Dursky, J. 1997: Modellierung der Absterbeprozesse in Rein- und Mischbeständen aus Fichte und Buche. — *Allgemeine Forst- und Jagdzeitung* 168: 131–134.

Eid, T. & Tuhus, E. 2001: Models for individual tree mortality in Norway. — *Forest Ecology and Management* 154: 69–84.

Freund, R. J. & Littell, R. C. 2000: *SAS system for regression*. — SAS Institute Inc., Cary, NC.

Gadow, K. v. 1987: *Untersuchungen zur Konstruktion von Wuchsmodellen für schnellwüchsige Plantagenbaumarten*. — Research Report 77, Ludwig-Maximilians-University, München.

Hamilton, D. A. 1986: A logistic model of mortality in thinned and unthinned mixed conifer stands of Northern Idaho. — *Forest Science* 32: 989–1000.

Hamilton, D. A. Jr. & Edwards, B. M. 1976: *Modeling the probability of individual tree mortality*. — USDA For. Serv. Pap. INT-185.

Hawkes, C. 2000: Woody plant mortality algorithms: description, problems and progress. — *Ecological Modelling* 126: 225–248.

Hegyi F. 1974: A simulation model for managing jackpine stands. — In: Fries, J. (ed.), *Growth models for tree and stand simulation, Proc. IUFRO meeting S4.01.04, Royal College of Forestry, Stockolm*: 74–90. Royal College of Forestry, Stockolm.

Hynynen, J., Ojansuu, R., Hökka, H., Siipilehto, J., Salminen, H. & Haapala, P. 2002: Models for predicting stand development in MELA System. — *Metsäntutkimuslaitoksen Tiedonantoja* 835: 1–116.

Jõgiste, K. 1998: Productivity of mixed stands of Norway spruce and birch affected by population dynamics. A model analysis. — *Ecological Modelling* 106: 71–79.

Kangur, A., Korjus, H., Jõgiste, K., Kiviste, A. 2005: A conceptual model of forest stand development based on permanent sample-plot data in Estonia. — *Scandinavian Journal of Forest Research* 20(Suppl 6): 94–101.

Karoles, K., Õunap, H., Pilt, E., Terasmaa, T. & Kivits, H. 2000: Forest conditions in Estonia 1988–99, defoliation and forest damages on Level I sample points. Air pollution and forests in industrial areas of north-east Estonia. — *Metsanduslikud Uurimused/Forestry Studies* XXXIII: 209–216.

Kiviste, A. & Hordo, M. 2002: Eesti metsa kasvukäigu püsiproovitükkide võrgustik. [Network of permanent forest growth plots in Estonia] — *Metsanduslikud Uurimused/Forestry Studies* XXXVII: 43–58. [In Estonian with English summary].

Kiviste, A., Nilson, A., Hordo, M. & Merenäkk, M. 2003: Diameter distribution models and height-diameter equations for Estonian forests. — In: Amaro, A., Reed, D. & Soares, P. (eds.), *Modelling forest systems*: 169–179. CAB International, Wallingford, UK.

Kobe, R. K. & Coates, K. D. 1997: Models of sapling mortality as a function of growth to charatherize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. — *Canadian Journal of Forest Research* 27: 227–236.

Kofman, G. B. & Kuzmichev, V. V. [Кофман Г. Б. & Кузьмичев В. В.] 1981: [Application Gompertz function for mortality dynamics study] — In: Terskov, I. A. [Терсков, И. А.] (eds.), *Issledovaniya dinamiki rosta organizmov*: 108–122. Nauka, Novosibirsk. [In Russian].

Kouba, J. 1989: The theory of an estimate of the development of calamities and of management of the process of forest adjustment to normal forest. — *Lesnictvi* 35: 925–944.

Krigul, T. 1969: *Metsataksaatori teatmik*. — Estonian Agricultural Academy, Tartu.

Laarmann, D. 2007: *Puude suremus ja seosed puistute looduslikkusega metsa kasvukäigu püsiproovitükkide andmetel* [*Individual tree mortality in relationship with naturalness of forest stands on the permanent sample plot data*]. — M.Sc. thesis, Estonian University of Life Sciences, Institute of Forestry and Rural Engineering, Tartu. [In Estonian with English summary].

Leak, W. B & Graber, R. E. 1976: Seedling input, death and growth in uneven-aged northern hardwoods. — *Canadian Journal of Forest Research* 6: 368–374.

Littell, R. C., Stroup, W. W. & Freund, R. J. 2002: *SAS for linear models*. — SAS Institute Inc., Cary, NC.

Mabvurira, D. & Miina, J. 2002: Individual-tree growth and mortality models for Eucalyptus grandis (Hill) Maiden plantations in Zimbabwe. — *Forest Ecology and Management* 161: 231–245.

Monserud, R. A. & Sterba, H. 1999: Modelling individual tree mortality for Austrian forest species. — *Forest Ecology and Management* 113: 109–123.

Monserud, R. A. 1976: Simulation of forest tree mortality — *Forest Science* 22: 438–444.

Moser, J. W. 1972: Dynamics of an even-aged forest stands. — *Forest Science* 15: 183–188.

Murphy, P. A. & Graney, D. L. 1998: Individual-tree basal area growth, survival, and total height models for upland hardwoods in Boston mountains of Arkansas. — *Southern Journal of Applied Forestry* 22: 184–192.

Nagelkerke, N. J. D. 1991: A note on a general definition of the coefficient of determination. — *Biometrika* 78: 691–692.

Nilson, A. 1999. Pidev metsakorraldus — mis see on. — *EPMÜ Metsandusteaduskonna Toimetised* 32: 4–13.

Nilson, A. 2006: Modeling dependence between the number of trees and mean tree diameter of stands, stand density and stand sparsity. — In: Cieszewski, C. J. & Strub, M. (eds.), *Second International Conference on Forest Measurement and Quantitative Methods and Management & the 2004 Southern Mensurationists Meeting 15–18 June 2004 Hot Springs, Arkansas USA*: 74–94. University of Georgia, Athens, USA.

Ozolins, R. 2002: Forest stand assortment structure analysis using mathematical modelling — *Metsanduslikud Uurimused/Forestry Studies* XXXVII: 33–42

Palahi, M. & Grau, J. M. 2003: Preliminary site index model and individual-tree growth and mortality models for black pine (*Pinus nigra* Arn.) in Catalonia (Spain). — *Investigación Agraria: Sistemas y Recursos Forestales* 12: 137–148.

Schabenberger, O. 2005: Introducing the GLIMMIX Procedure for Generalized Linear Mixed — In: *SAS Institute Inc. Proceedings of the Thirtieth Annuals SAS Users International Conference, Cary, NC, USA*, available at www2.sas.com/proceedings/sugi30/196-30.pdf

Schaid, D. J., Rowland, C. M., Tines, D. E., Jacobson, R. M. & Poland, G. A. 2002: Score tests for association between traits and haplotypes when linkage phase is ambiguous. — *American Journal of Human Genetics* 70: 425–434.

Shtatland, E. S., Kleinman, K. & Cain, E. M. 2002: One more time about R^2 measures of fit in logistic regression. — In: *SAS Conference Proceedings: NESUG 2002 September 29–October 2, 2002, Buffalo, New York*, available at www.nesug.org/Proceedings/nesug02/st/st004.pdf.

SMI 1999: *Statistilise metsainventeerimise välitööde juhend*. — OÜ Eesti Metsakorralduskeskus, Tallinn.

Soares, P. & Tomé, M. 2003: An individual tree growth model for *Eucalyptus globulus* in Portugal. — In: Amaro, A., Reed, D. & Soares, P. (eds.), *Modelling forest systems*: 97–110. CAB International, Wallingford.

Somers, G. L., Oderwald, R. C., Harris, W. R. & Langdon, O. G. 1980: Predicting mortality with a Weibull function. — *Forest Science* 26: 291–300.

Vanclay, J. K. 1991: Mortality functions for north Queensland rainforests. — *Journal of Tropical Forest Science* 4: 15–36.

Vanclay, J. K. 1994: *Modelling forest growth and yield. Applications to mixed tropical forests*. — CAB International, Wallingford.

Vanclay, J. K. 1995: Growth models for tropical forests: a synthesis of models and methods. — *Forest Science* 41: 15–36.

West, P. W. 1981: Simulation of diameter growth and mortality in regrowth eucalypt forest of southern Tasmania. — *Forest Science* 27: 603–616.

Yang, Y., Titus, S. J. & Huang, S. 2003: Modeling individual tree mortality for white spruce in Alberta. — *Ecological Modelling* 163: 209–222.

Yao, X., Titus, S. J. & Donald, S. E. 2001: A generalized logistic model of individual tree mortality for aspen, white spruce and lodgepole pine in Alberta mixedwood forests. — *Canadian Journal of Forest Research* 31: 283–291.

CURRICULUM VITAE

First name:	Diana
Surname:	Laarmann
Citizenship:	Estonian
Date of Birth:	25.01.1974
Address:	Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Kreutzwaldi 5, 51014 Tartu, Estonia
Telephone:	+372 7313 151
E-mail:	diana.laarmann@emu.ee

Education:

2007-2014	PhD studies in forestry, Institute of Forestry and Rural Engineering, Estonian University of Life Sciences
2005-2007	Master studies in forestry (forest management), Institute of Forestry and Rural Engineering, Estonian University of Life Sciences
2000-2005	Bachelor studies in natural resources management (*cum laude*), Institute of Forestry and Rural Engineering, Estonian Agricultural University
1986-1992	Ülenurme Secondary School
1981-1986	Tartu 14. Secondary School

Professional employment:

Since 2010	Estonian University of Life Sciences, Institute of Forestry and Rural Engineering, Department of Forest Management, Researcher
2006-2010	Estonian University of Life Sciences, Institute of Forestry and Rural Engineering, Department of Forest Management, Project manager

Academic degree:

2007 MSc in forestry (forest management) for the thesis: "Individual tree mortality in relationship with naturalness of forest stands on the permanent sample plot data" (Estonian University of Life Sciences)

Research interests: Forest management, nature conservation, ecological restoration

Foreign languages: English, Russian

Training and special courses:

2012 Study and research visit, professional upgrading at Center for Forest Disturbance Science, Southern Research Station, USDA Forest Service (USA)

2011 PhD course "Forest restoration in theory and in practice" (Sweden)

2009 Study and research visit, professional upgrading at Center for Forest Disturbance Science, Southern Research Station, USDA Forest Service (USA)

2008 PhD course "Ecology, silviculture and economics of multi-functional forestry" (Denmark, Sweden, Estonia)

2006 MSc course "Integrating innovation and entrepreneurship research in higher forestry education" (Slovakia)

Projects:

2014 – 2019 Institutional Research Funding: "The carbon dynamics in Estonian forests affected by sustainable management". Investigator.

2014 – 2015 Environmental Investment Centre (EIC) project: "Follow up of naturalness restoration experiment in Karula National Park". Principal investigator.

2013 – 2016 Baseline financed project: "The impact of land-related decisions on the use of land, forest and water resources". Investigator.

2013 – 2014 EIC project: "Evaluation of forest naturalness restoration areas". Principal investigator.

2011 – 2012	EIC project: "Researching dynamics of forest ecosystem in reclaimed oil shale quarries". Principal investigator.
2011 – 2012	EIC project: "Identifying forest stand disturbances using dendrochronological methods". Investigator.
2010 – 2012	Estonian Science Foundation grant: "Microsites and other ecological factors influencing natural regeneration in disturbance areas". Investigator.
2008 – 2013	Target financed project: "The effect of changing climate on forest disturbance regimes in temperate and boreal zone". Investigator.
2008 – 2010	EIC project: "Monitoring of forest area and cuttings by remote sensing methods". Investigator.
2008 – 2009	The Environmental Board project: "Re-measurement of forest naturalness restoration areas". Principal investigator.
2006 – 2015	EIC project: "Re-measuring of the Estonian network of forest monitoring plots". Principal investigator.

ELULOOKIRJELDUS

Eesnimi:	Diana
Perekonnanimi:	Laarmann
Kodakondsus:	Eesti
Sünniaeg:	25.01.1974
Aadress:	Metsandus- ja maaehitusinstituut, Eesti Maaülikool, Kreutzwaldi 5, 51014 Tartu, Eesti
Telefon:	+372 7313 151
E-post:	diana.laarmann@emu.ee

Haridus:

2007-2014	Eesti Maaülikool, metsandus- ja maaehitusinstituut, metsandus, doktoriõpe
2005-2007	Eesti Maaülikool, metsandus- ja maaehitusinstituut, metsamajandus, magistriõpe
2000-2005	Eesti Põllumajandusülikool, metsandusteaduskond, loodusvarade kasutamine ja kaitse, bakalaureuseõpe, *cum laude*
1986-1992	Ülenurme Keskkool
1981-1986	Tartu 14. Keskkool

Teenistuskäik:

Alates 2010	Eesti Maaülikool, metsandus- ja maaehitusinstituut, metsakorralduse osakond, teadur
2006-2010	Eesti Maaülikool, metsandus- ja maaehitusinstituut, metsakorralduse osakond, projektijuht

Teaduskraad:

2007	Eesti Maaülikool, metsateaduse magister metsakorralduse erialal, magistritöö teemal: "Puude suremus ja seosed puistute looduslikkusega metsa kasvukäigu püsiproovitükkide andmetel"

Teadustöö põhisuunad: metsakorraldus, looduskaitse, metsade taastamine

Võõrkeelte oskus: inglise, vene

Täiendkoolitus:

2012	Õppe- ja teadusvisiit, erialane täiendamine, Ameerika Ühendriikide Metsateenistus, Metsahäiringute Uurimiskeskus, Athens, USA
2011	Doktorikursus "Forest restoration in theory and in practice" (Rootsi)
2009	Õppe- ja teadusvisiit, erialane täiendamine, Ameerika Ühendriikide Metsateenistus, Metsahäiringute Uurimiskeskus, Athens, USA
2008	Doktorikursus "Ecology, silviculture and economics of multi-functional forestry" (Taani, Rootsi, Eesti)
2006	Magistrikursus "Integrating innovation and entrepreneurship research in higher forestry education "(Slovakkia)

Projektid:

2014 – 2019	Institutsionaalne grant: "Eesti metsade süsiniku dünaamika ja jätkusuutlik majandamine". Täitja.
2014 – 2015	SA Keskkonnainvesteeringute Keskuse (KIK) projekt: "Looduslikkuse taastamise katseala uuringu jätkamine Karula rahvuspargis". Põhitäitja.
2013 – 2016	Baasfinantseeritav teadusteema: "Maaga seotud otsuste mõju maa-, metsa- ja veeressursside kasutamisele". Täitja.
2013 – 2014	KIK projekt: "Metsade looduslikkuse taastamise tulemuslikkuse hindamine". Põhitäitja.
2011 – 2012	KIK projekt: "Taasmetsastatud põlevkivikarjääride ökosüsteemide dünaamika uurimine". Põhitäitja

2011 – 2012	KIK projekt: "Puistus toimunud häiringute tuvastamine dendrokronoloogiliste meetoditega". Täitja.
2010 – 2012	Eesti Teadusfondi grant: "Mikroreljeefi ja ökoloogiliste faktorite mõju puurinde looduslikule uuendusele häiringualadel". Täitja.
2008 – 2013	Sihtfinantseeritav teema: "Muutuvate kliimatingimuste mõju boreaalse ja parasvöötme metsade häiringurežiimile". Täitja.
2008 – 2010	KIK projekt: "Metsade pindala muutumise ja raiete jälgimine kaugseire meetoditega". Täitja.
2008 – 2009	Riiklik Looduskaitsekeskuse projekt: "Metsa puistuandmete kordusseire metsa taastamise 50 püsiseirealal". Põhitäitja.
2006 – 2015	KIK projekt: "Metsa kasvukäigu püsiproovitükkide võrgustiku kordusmõõtmine". Põhitäitja.

LIST OF PUBLICATIONS

Publication indexed in the Thomson Reuters Web of Science database

Laarmann, D., Korjus, H., Sims, A., Kangur, A., Kiviste, A., Stanturf, J.A. 2014. Evaluation of afforestation development and natural colonization on a reclaimed mine site. Restoration Ecology (manuscript, submitted).

Laarmann, D., Korjus, H., Sims, A., Kangur, A., Stanturf, J.A. 2013. Initial effects of restoring natural forest structures in Estonia. Forest Ecology and Management 304: 303 - 311.

Laarmann, D., Korjus, H., Sims, A., Stanturf, J.A., Kiviste, A., Köster, K. 2009. Analysis of forest naturalness and tree mortality patterns in Estonia. Forest Ecology and Management 258S: S187 - S195.

Köster, K., Voolma, K., Jõgiste, K., Metslaid, M., **Laarmann, D**. 2009. Assessment of tree mortality after windthrow using photo-derived data. Annales Botanici Fennici 46 (4): 291 - 298.

Sims, A., Kiviste, A., Hordo, M., **Laarmann, D**., Gadow, K.v. 2009. Estimating tree survival: a study based on the Estonian Forest Research Plots Network. Annales Botanici Fennici 46 (4): 336 - 352.

Publication in other peer-reviewed research journals

Mändma, R., **Laarmann, D**., Sims, A., Korjus, H. 2014. Assessment of tree mortality on the Estonian Network of Forest Research Plots. Forestry Studies (manuscript, submitted).

Kiviste, A., Hordo, M., Kangur, A., Kardakov, A., Korjus, H., **Laarmann, D**., Lilleleht, A., Metslaid, S., Sims, A. 2014. Monitoring and evaluating forest dynamics: the Estonian Network of Forest Research Plots. Forest Ecosystems (manuscript, submitted).

Korjus, H., **Laarmann, D**., Kiviste, A. 2012. Analysis of the Estonian Forest Conservation Area Network. Journal of Environmental Science and Engineering B1 (6): 779 - 788.

Articles in proceedings in a book or in a collection

Laarmann, D., Korjus, H., Pärn, P., Sims, A., Kangur, A. 2012. Forest ecosystem response to changing water regime in exhausted opencast oil shale quarry in Aidu, Estonia. Extended abstract 8th European Conference on Ecological Restoration, Ceské Budejovice, Czech Republic. SER Europe Knowledge Base (http://chapter.ser.org/europe), 4 pp.

Kiviste, A., Sims, A., **Laarmann, D**., Hordo, M., Lilleleht, A., Kangur, A., Korjus, H. 2012. The Estonian Permanent Forest Plots Network. Forest Observational Studies: 97 - 108. Beijing Forestry University

Korjus, H., **Laarmann, D**. 2011. Analysis of the Estonian Forest Conservation Area Network. Extended abstract 7th European Conference on Ecological Restoration, Avignon, France. SER Europe Knowledge Base (http://chapter.ser.org/europe), 4 pp.

Laarmann, D., Sims, A., Korjus, H., Kiviste, A., Kangur, A. 2011. Forest ecosystem restoration microhabitat pattern analysis on abandoned oil-shale mining areas in Estonia. Extended abstract 7th European Conference on Ecological Restoration, Avignon, France. SER Europe Knowledge Base (http://chapter.ser.org/europe), 4 pp.

Published meeting abstracts

Laarmann, D., Korjus, H. 2013. Initial effects of restoring natural forest structures in Estonia. In: Book of abstracts: 5th World Conference on Ecological Restoration, Reflections on the Past, Directions for the Future, October 6-11, 2013, Madison, Wisconsin, USA. Madison, USA: Society for Ecological Restoration, 2013, 224 - 224.

Laarmann, D., Korjus, H., Sims, A., Kangur, A., Kiviste, A. 2013. Taastuva metsaökosüsteemi uurimine seoses kiiresti muutuvate keskkonnatingimustega ammendatud Aidu põlevkivikarjääris. XII Eesti Ökoloogiakonverents, Tartu, 18-19. oktoober 2013. Tartu.

Nigul, K., **Laarmann, D**., Kangur, A., Kiviste, A., Jõgiste, K., Frelich, L.E. 2013. An analysis of forest ecosystem structural variation in Scots pine dominated stands: A methodological consideration based on the Estonian Network of Forest Research Plots. 98th Annual Ecological Society of America Meeting: Sustainable pathways: learning from the past and shaping the future, August 4-9, 2013, Minneapolis, USA, 2013, 97-97.

Nigul, K., Frelich E.L., **Laarmann, D**., Jõgiste, K., Kiviste, A., Kangur, A. 2013. An analysis of forest ecosystem structural variation in Scots pine dominated stands: a methodological consideration based on the Estonian Network of Forest Research Plots. In: Book of abstracts: 56th Symposium of the International Association for Vegetation Science, Vegetation Patterns and their Underlying Processes, June 26–30, 2013, Tartu Estonia. (Eds.) Püssa, K., Kalamees, R., Hallop, K. Tartu, 2013, 173 - 173.

Mändma, R., **Laarmann, D**., Korjus, H. 2013. Assessment of tree mortality in managed and unmanaged forest stands in Estonia. In: Book of abstracts: 56th Symposium of the International Association for Vegetation Science, Vegetation Patterns and their Underlying Processes, June 26–30, 2013, Tartu Estonia. (Eds.) Püssa, K., Kalamees, R., Hallop, K. Tartu, 2013, 148 - 148.

Laarmann, D., Krumm, L., Hordo, M., Korjus, H. 2012. Biological diversity of Calamagrostis type alvar forests in Estonia. In: Book of abstracts: 2nd International Conference on Biodiversity in Forest Ecosystems & Landscapes, University College Cork, Ireland, August 27-31, 2012. Cork, Ireland: UCC, 2012, 70 - 70.

Laarmann, D., Korjus, H. 2012. Effects of treatments in restoration of natural forest structures in Estonia. In: Book of abstracts: 2nd International Conference on Biodiversity in Forest Ecosystems & Landscapes, University College Cork, Ireland, August 27-31, 2012. Cork, Ireland: UCC, 2012, 74 - 74.

Laarmann, D., Kangur, A., Sims, A., Korjus, H., Kiviste, A. 2012. Forest ecosystems respond to changing water regime in Aidu exhausted opencast oil shale quarry in Estonia. In: Programme and Abstract Book:

The 8th European Conference on Ecological Restoration, September 9-14, 2012, České Budějovice, Czech Republic, Near-natural Restoration. České Budějovice: SER Europe, 2012, 97 - 98.

Kiviste, A., Sims, A., Hordo, M., **Laarmann, D**., Korjus, H., Gadow, K.v. 2011. Modelling tree survival based on Estonian forest research plots network data. In: ICFFI News: Ecosystem Design for Multiple Services – with an emphasis on Eurasian Boreal Forests, St. Peterburg State Forest Technical University, 9-11.11.11. (Eds.) Chubinsky, M., Gadow, K.v.. International Centre of Forestry and Forest Industries, St. Petersburg State Forest Technical Univer, 2011, (13), 59 - 59.

Korjus, H., **Laarmann, D**., Leemets, J. 2010. Analysis of the Estonian forest conservation area network. In: Ecological restoration and sustainable development - Establishing links across frontiers. Conference programme abstract book: 7th SER European Conference on Ecological Restoration, August 23-27, 2010, Avignon France. (Ed.) Dutoit, T. Avignon: Universite d'Avignon et des Pays de Vaucluse, 2010, 139 - 139.

Laarmann, D., Korjus, H., Sims, A., Kangur, A. 2010. Forest ecosystem restoration patterns on abandoned oil-shale mining areas in Estonia. In: Ecological restoration and sustainable development - Establishing links across frontiers. Conference programme abstract book: 7th SER European Conference on Ecological Restoration, August 23-27, 2010, Avignon France. (Ed.) Dutoit, T. Avignon: Universite d'Avignon et des Pays de Vaucluse, 2010, 141 - 141.

Laarmann, D., Korjus, H., Sims, A. 2010. Nature restoration areas in Estonian forests: monitoring of dynamics. In: Northern Primeval Forests: Ecology, Conservation & Management, Sundsvall, Sweden, August 9-13, 2010. Sundsvall: Mid Sweden University, 2010, 143 - 143.

Laarmann, D., Korjus, H. 2009. Nature restoration areas in Estonian forests: monitoring of dynamics. In: 19th Conference of the Society for Ecological Restoration International: SERI 2009 World Conference on Ecological Restoration: Making Change in a Changing World; Perth, Western Australia, August 23-27, 2009. (Ed.) Dixon, K. Perth, 2009, 100 - 100.

Laarmann, D., Korjus, H., Sims, A., Kangur, A. 2009. Forest ecosystem restoration patterns on abandoned oil-shale mining areas in Estonia. In: 19th Conference of the Society for Ecological Restoration International: SERI 2009 World Conference on Ecological Restoration: Making Change in a Changing World; Perth, Western Australia, August 23-27, 2009. (Ed.) Dixon, K. Perth, 2009, 173 - 173.

Laarmann, D., Korjus, H. 2008. Biodiversity assessment through individual tree mortality analysis on permanent sample plot data in Estonia. In: Book of abstracts: 1nd International Conference on Biodiversity in Forest Ecosystems & Landscapes, Thompson Rivers University, Kamloops, BC, Canada, August 5-8, 2008. Kamloops, 2008, 32 - 32.

Laarmann, D., Korjus, H. 2007. Nature restoration areas in Estonian forests: monitoring of dynamics. In: Proceedings of the IUFRO Conference on Forest Landscape Restoration: International Conference on Forest Landscape Restoration. Seoul, South Korea. May 14-19, 2007. (Ed.) Stanturf, J., 2007, 231 - 232.

Popular-scientific publications

Kangur, A., **Laarmann, D**., Hordo, M., Sims, A., Korjus, H., Lilleleht, A., Kiviste, A. 2013. Kasvukäigu püsiproovitükkide väärtus puistu kasvu kirjeldamisel. Eesti Mets 4: 42-48.

VIIS VIIMAST KAITSMIST

ANTS-HANNES VIIRA

STRUCTURAL ADJUSTMENT OF ESTONIAN AGRICULTURE – THE ROLE OF INSTITUTIONAL CHANGES AND SOCIOECONOMIC FACTORS OF FARM GROWTH, DECLINE AND EXIT
EESTI PÕLLUMAJANDUSE STRUKTURAALNE KOHANEMINE – INSTITUTSIONAALSETE MUUTUSTE JA PÕLLUMAJANDUSETTEVÕTETE KASVU, KAHANEMIST NING TEGEVUSE LÕPETAMIST MÕJUTAVATE SOTSIAALMAJANDUSLIKE TEGURITE OSA
Professor **Rando Värnik**, dotsent **Reet Põldaru**
5. juuni 2014

MONIKA SUŠKEVIČS

KNOWLEDGE, LEARNING AND LEGITIMACY IN MULTI-LEVEL PARTICIPATORY ECOLOGICAL NETWORK GOVERNANCE
KAASAMISPROTSESSIDE TÕHUSUS JA TULEMUSLIKKUS ÖKOLOOGILISE VÕRGUSTIKU PLANEERIMISEL NING RAKENDAMISEL MITMETASANDILISES VALITSEMISMUDELIS
Professor **Mart Külvik**, vanemteadur **Aivar Leito**
16. juuni 2014

MARKO KASS

EFFECT OF CRUDE GLYCEROL FEEDING ON FEED INTAKE, LACTATIONAL PERFORMANCE AND METABOLIC STATUS OF DAIRY COWS
TOORGLÜTSEROOLI SÖÖTMISE MÕJU LÜPSILEHMADE SÖÖMUSELE, PIIMAJÕUDLUSELE JA AINEVAHETUSLIKULE SEISUNDILE
Prof. Emer. **Olav Kärt**, Dr. **David Richard Arney**
26. juuni 2014

KATRIT KARUS

EFFECTS OF MACROPHYTES, FISH AND METAZOOPLANKTON ON A MICROBIAL FOOD WEB
VEETAIMESTIKU, KALADE JA METAZOOPLANKTONI MÕJU MIKROOBSELE TOIDUAHELALE
Vanemteadur **Priit Zingel**
28. august 2014

KAIRE LANNO

LONG-TERM CHANGES IN THE ESTONIAN FLORA AND MEASURES FOR CONSERVATION
PIKAAJALISED MUUTUSED EESTI TAIMESTIKUS JA FLOORA KAITSMISEKS SOBIVAD LOODUSKAITSEMEETMED
Vanemteadur **Marek Sammul**
28. august 2014

ISSN 2382-7076
ISBN 978-9949-536-42-9 (trükis)
ISBN 978-9949-536-43-6 (pdf)

roheline trükis

Trükitud taastoodetud paberile looduslike trükivärvidega © Ecoprint