Dissertationes Forestales 18

Ecological restoration of forests in Fennoscandia: defining reference stand structures and immediate effects of restoration

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Academic dissertation

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ABSTRACT

The first aim of this thesis was to explore the structural characteristics of near-natural forests and to quantify how human utilization has changed them. For this, we examined the stand characteristics in Norway spruce *Picea abies* (L.) Karst-dominated old-growth stands in northwestern Russia and in old Scots pine *Pinus sylvestris* L.-dominated stands in three regions from southern Finland to northwestern Russia. In the second study, we also compared stands with different degrees of human impact, from near-natural stands and stands selectively cut in the past to managed stands. Secondly, we used an experimental approach to study the short-term effects of different restorative treatments on forest structure and regeneration in managed *Picea abies* stands in southern Finland. Restorative treatments consisted of a partial cut combined with three levels of coarse woody debris retention, and a fire/no-fire treatment. In addition, we examined burned and unburned reference stands without cutting treatments. Results from near-natural *Picea abies* forests emphasize the dynamic character of old-growth forests, the variety of late-successional forest structures, and the fact that extended time periods are needed to attain certain late-successional stages with specific structural and habitat attributes, such as large-diameter deciduous trees and a variety of deadwood. The results from old *Pinus sylvestris*-dominated forests showed that human impact in the form of forest utilization and fire exclusion has strongly modified and reduced the structural complexity of stands. Consequently, small protected forest fragments in Finland may not serve as valid natural reference areas for forest restoration. However, results from the restoration experiment showed that early-successional natural stand characteristics can be restored to structurally impoverished managed *Picea* abies stands, despite a significant portion of wood volume being harvested. A variety of restoration methods is needed, due to differences in the condition of the forest when restoration is initiated and the variety of successional stages of forest structures after anthropogenic and natural disturbances.

Keywords: dead wood, disturbance dynamic, fire, near-natural stand, rehabilitation, succession

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March, 2006

Saara Lilja

LIST OF ORIGINAL ARTICLES

This thesis is a summary of the following papers, which are referred to by their Roman numerals.

I **Lilja, S**., Wallenius, T. & Kuuluvainen, T. 2006. Structural characteristics and dynamics of old *Picea abies* forests in northern boreal Fennoscandia. EcoScience 13(2): In press.

II **Lilja, S**. & Kuuluvainen, T. 2005. Stand structural characteristics of old *Pinus sylvestris*-dominated forests along a geographic and human influence gradient in boreal Fennoscandia. Silva Fennica 39: 407-428.

III **Lilja, S**., de Chantal, M., Kuuluvainen, T., Vanha-Majamaa, I. & Puttonen, P. 2005. Restoring natural characteristics in boreal Norway spruce (*Picea abies* L. Karst*)* stands with partial cutting, deadwood creation and fire: immediate treatment effects. Scandinavian Journal of Forest Research 20 (Suppl. 6): 68-78.

IV **Lilja, S**., de Chantal, M., Peterson, C, Kuuluvainen, T. Vanha-Majamaa, I. & Puttonen, P. Microsites and seedlings in managed *Picea abies* stands before and after restorative treatment with partial cutting, deadwood creation and fire. Submitted manuscript.

Saara Lilja participated in planning the reseach, was responsible for conducting the field measurements (I, III, IV) and data analysis and was the main author in all papers.

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LIST OF TERMS

Coarse woody debris (CWD): Both standing and fallen deadwood and stumps sized 5- 10 cm in diameter (Harmon et al. 1986, Siitonen 2001).

CWD treatments: Restorative treatment in which fallen wood was created within the stand by cuttings (resulting in 5, 30 or 60 m^3 ha^{-1} of CWD).

Degraded ecosystem: An ecosystem in which the ecological structure and function have been altered due to human impact. Degradation includes gradual changes that reduce the intactness of the ecosystem. For example, a managed stand in which the natural stand structure has been changed by silvicultural treatments could be seen as a degraded ecosystem (Clewell et al. 2005).

Disturbance: “Any relatively discrete event in time that disrupts an ecosystem, a community, or population structure, and that changes resources, substrate availability, or the physical environment” (White and Pickett 1985).

Ecological restoration: “The process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed” (Clewell et al. 2005); reparation of human-degraded ecosystems back to natural, near-natural or historical conditions (Hobbs and Mooney 1993, Tukia 2000, Stanturf 2005).

Forest restoration: Reparation of human-degraded managed forests by changing the dynamics and processes of forests to create near-natural structures, such as natural tree species composition or deadwood structures (Bradshaw 1997, Working Group 2003), i.e. the rehabilitation of stand structures to near-natural reference conditions.

Managed stand: A forest stand that shows distinct signs of silvicultural thinnings, with a stand structure close to even-sized.

Natural variability (range of natural variation): Means that past conditions and processes provide context and guidance for managing ecological systems today, and in addition that disturbance-driven spatial and temporal variability is a vital attribute of nearly all ecological systems (Landers et al. 1999).

Natural forest: Forest that shows no human impact or any known human influence.

Near-natural forest: Unmanaged stands that may show traces of past human impact, i.e. < 5 cut stumps per hectare (Uotila et al. 2002).

Old-growth forests: Forests that are older than some arbitrary biological age, e.g. 150 years, and in which human influence has been relatively small. In addition to old age, the presence of large living and dead trees, the abundance of decaying wood and an uneven-aged structure are essential characteristics (Esseen et al. 1997, Kneeshaw and Gauthier 2003, Spies 2004). Synonyms include ancient, antique, climax, late-successional, old, original, overmature, primary, primeval, pristine and virgin forest (Helms 2004).

Partial cutting: One type of shelterwood cutting method in which more trees are left not only for seed but also for additional growth and shelter for the new stand (Smith et al. 1997). Partial cutting (III, IV) refers to the method in which >10-cm DBH trees were cut randomly to leave a constant retention volume of standing live trees (50 m^3 ha^{-1}).

Reference stands: Natural or near-natural forest stands exhibiting traits within the range of natural variation for unmanaged forests; can be used to define restoration targets or to evaluate restoration success (Magnuson et al. 1980, Bradshaw 1987, Clewell et al.).

Rehabilitation: Re-establishing natural disturbances and structural characteristics to degraded forests (Stanturf and Madsen 2002). This means that rehabilitation is one type of restoration.

Restorative treatments: Treatments to implement ecological restoration (see Ecological restoration / Forest restoration). In the present study, these treatments consisted of partial cuttings with one of three levels of coarse woody debris (CWD; 5, 30, 60 m^3 ha^{-1}) with a constant volume of living trees (50 m^3 ha^{-1}), burned or left nonburned.

Selective logging: Any logging method in which only large and high-quality stems are harvested (Sarvas 1944). This logging method was particularly common in Finland from 1870 to 1950.

Succession, secondary succession: Temporal sequence of different ecosystem states. Secondary succession is the replacement of pre-existing vegetation following a disturbance that totally or partially disrupts the vegetation (Glenn-Lewin and van der Maarel 1992).

1. INTRODUCTION

1.1. Background

The boreal forest is a northern, circumpolar forest belt that covers 14 million km^2 (Burton et al. 2003) or about 20% of the forested regions of the world. In Fennoscandia the boreal forest accounts for a vast proportion of the total land area. Although the circumpolar Boreal Zone still has some of the last large extents of nonexploited forests in the world, some areas have been heavily exploited historically and recently managed for forestry. This is the case in most of Fennoscandia where intensive forest management, particularly over recent decades, has broadly reduced the structural complexity of forests, both at the stand and landscape levels (Kouki 1994, Esseen et al. 1997, Linder and Östlund 1998, Uotila 2004).

With increasing demands to protect biodiversity and to carry out ecosystem-based forest management (e.g. Franklin et al. 2002), the question of forest restoration has become topical in areas consisting of both managed and protected areas, and in buffer zones between these two (Working Group 2003, Kuuluvainen et al. 2005). In such areas, restoration can be seen as an important tool to maintain and complement networks of protected areas in landscapes strongly altered by human activity (Kuuluvainen et al. 2002, Hyvärinen et al. 2005). For example, in Finland restoration of protected forests, most of which are former managed forests, is in progress; by 2003 approximately 1300 ha of forests were restored. This restoration activity is often based on imitating natural disturbances to rehabilitate important stand structural characteristics (Working Group 2003, Kuuluvainen et al. 2005). In addition, new management practices that are now widely applied include the retention of living and dead trees, and setting aside habitats of special importance for biodiversity, i.e. key-habitats (Kuuluvainen 2002, Finnish…2005). These measures could also be considered as restoration in the widest sense, because they recreate the structural features of natural forests in managed forests. Such restoration operations are needed to attain a better balance between the economic, social and ecological dimensions of sustainable forestry (Fries et al. 1997, Franklin et al. 2002, Burton et al. 2003, Hyvärinen et al. 2005). However, despite the increasing concerns of biodiversity loss in Fennoscandian forests (Esseen et al. 1992, Granström 2001, Kouki et al. 2001, Siitonen 2001, Axelsson et al. 2002, Similä et al. 2002, Hyvärinen et al. 2005), restoration research is still in its infancy and we lack understanding of the ecological efficiency of restoration practices (Hyvärinen et al. 2005, Kuuluvainen et al. 2005).

1.2. Conceptual framework

The definition of ecological restoration officially adopted by the Society for Ecological Restoration states that: “Ecological restoration is the process of contributing to the recovery of an ecosystem that has been degraded, damaged, or destroyed” (Clewell et al. 2005). This definition is short, and it allows for different types of ecological restoration in dissimilar ecosystems. In this definition, the concept of degradation covers gradual changes that reduce the ecological intactness of an ecosystem (Clewell et al. 2005). In this framework, ecological restoration means the reparation of human-degraded ecosystems back to natural, near-natural or historical conditions (Jordan et al. 1987, Hobbs and Mooney 1993, Bradshaw 1997, Tukia 2000, Stanturf 2005). Thus, ecological restoration could be defined as the process of assisting the recovery and management of the function and structures of an ecosystem (Parker and Pickett 1997). At the same time it must be acknowledged that ecosystems include a range of variability in ecological processes, structures and biodiversity, as well as in regional and historical context and cultural practices (Harris and Hobbs 2001).

In forest restoration it is possible to restore part of the naturalness (rehabilitation) to an ecosystem. Complete restoration is difficult to achieve because the state of a forest ecosystem can range from natural to degraded, depending on the intensity of human influence (Stanturf and Madsen 2002). For example, rehabilitation may require altering the structure and species composition before reintroducing fire as a natural disturbance process. This emphasizes the close-to-nature or near-natural approaches to regeneration and stand management (Stanturf and Madsen 2002, Stanturf 2005). In Fennoscandia, the target of forest restoration has been to create stands with structures that are typical for natural stands (Working Group 2003). Diverse forest structures support a diversity of ecological processes that enhance species richness by providing habitat for many different species (Lämås and Fries 1995, Bradshaw 1997, Tukia 2000, Kuuluvainen et al. 2005).

The conceptual framework of restoration could be seen against a wider context containing the ecological aspects and the cultural and historical backgrounds of society. Ecological restoration activity can be related to land-use changes in urban and agricultural lands. For example, reclamation is one type of restoration in which land use changes from urban land back to forest or agricultural land. In addition, one type of ecological restoration is afforestation, in which agricultural land use changes back to forest land and the previous field becomes forest (Stanturf and Madsen 2002). Current activities in Finland seek to afforest fields back to previous herb-rich broad-leaved forest (Working Group 2003).

In the present study forest restoration is defined as the rehabilitation of structurally impoverished, managed stand structures, using natural variation of near-natural stand structures as a reference (Fig. 1). The range of natural variation in various stand characteristics can be used to set restoration targets and to evaluate restoration success (Magnuson et al. 1980, Bradshaw 1987, Clewell et al. 2005). In assessment of the natural variability of stand structures as a reference, it must be remembered that humans long influenced the forests in Fennoscandia. Thus, it is essential to evaluate the degree of human impact and the range of reference stand structures that can be found in Fennoscandian near-natural boreal forests to guide restoration activity (Objective 1, Fig. 1).

The development or succession of an ecosystem can be seen as the process represented on figure 1, which shows a gradient of stand structure from the simplest state, as in managed forests at the bottom left, towards natural variability at the top right. Rehabilitation means e.g. mimicking natural disturbances and in contrast degradation e.g. silvicultural harvesting (Fig. 1).

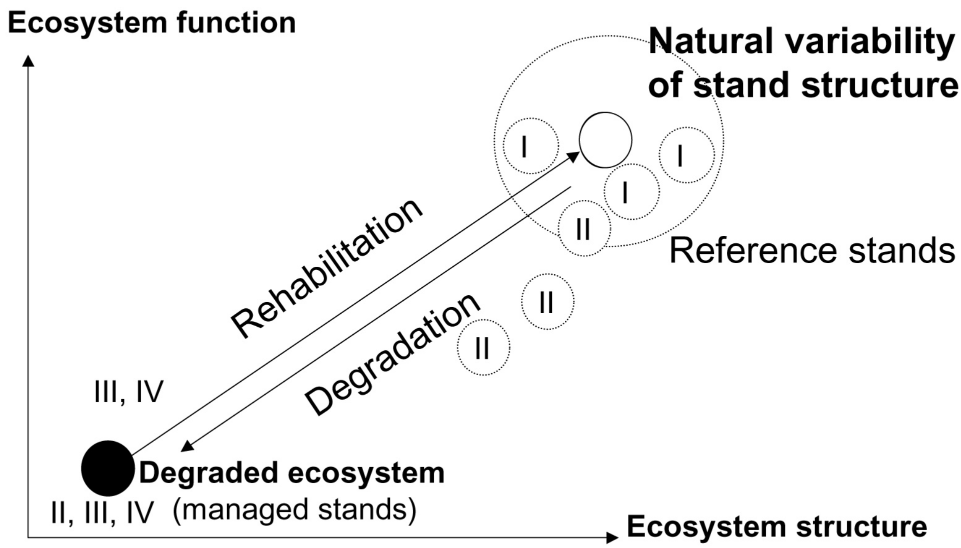

Figure 1. An illustration of the conceptual framework of this study (modified from Magnuson et al. 1980, Bradshaw 1987, Hobbs and Mooney 1993, Stanturf 2005). The change in function and structure of an ecosystem between 'degraded' (solid black circle) and 'natural' (white circle) is mainly due to disturbance and successional dynamics. Dotted circles with Roman numerals indicate studies describing the range in variability of stands for forest restoration. The conceptual 'location' of studies within this framework is indicated with Roman numerals.

1.3. Restoration in relation to disturbance and successional theory

Disturbances and subsequent successional changes are the two main driving forces of pattern, process and community composition in forest ecosystems (Attiwill 1994). In natural boreal forests, a variable set of disturbance factors, such as storms, insects and fungi, operate and interact at different space and time scales to create a wide range of structural characteristics (Bonan and Shugart 1989, Kuuluvainen 1994, Engelmark 1999). This multiscale heterogeneity is believed to be an important feature of habitat diversity. Thus it is expected that forest restoration will contribute to the maintenance of species populations by mimicking the natural dynamics of boreal forests (Attiwill 1994, Esseen et al. 1997). In Fennoscandia, forest characteristics that result from natural disturbance and successional dynamics typically include the presence of large-diameter trees (Angelstam and Arnold 1993, Syrjänen et al. 1994, Kouki et al. 2004), a high amount and diversity of deadwood (Siitonen 2001), versatile forest floor microhabitat distribution (Kuuluvainen and Laiho 2004) and multilayered canopy structures (Linder et al. 1997). These structural characteristics, which result from natural disturbances and successional development, are largely lacking in mature managed stands (Esseen et al. 1997, Kouki et al. 2001, Rouvinen et al. 2002a). Therefore, knowledge and mimicking of natural disturbances can be regarded as a prerequisite for successful forest restoration.

The practice of ecological restoration is thus closely related to our understanding of disturbance and the successional ecology of natural forests (Parker and Pickett 1997, Gayton

2001). Accordingly, natural disturbance and successional processes have been used to define forest restoration methods that will enhance natural habitat variability in forest structure (Haila 1994, Franklin et al. 2002, Kuuluvainen et al. 2002, Carey 2003). In the present study, restoration treatments are considered as disturbances that shift a stand to a particular successional stage or trajectory. Succession does not necessarily proceed as a simple linear development towards the climax stage, as suggested by Clements (1916). The present concept of succession is more diverse, wherein we recognize the importance of frequent and varying disturbances to the ecosystem during succession (Glenn-Lewin and van der Maarel 1992, Kuuluvainen 1994, Parker and Pickett 1997).

In forest restoration controlled fire can be used to create structural elements that are important for biodiversity, such as charred and decaying wood (Esseen et al. 1997, Granström 2001, Bergeron et al. 2002, Hyvärinen et al. 2005). The use of fire in restoration is needed because fire is the main large-scale natural disturbance factor in the Boreal Forest Zone (Zacrisson 1977, Esseen et al. 1997). The ecological importance of fire is evident. Fire increases stand heterogeneity and affects succession by killing trees and other organisms, thereby releasing space and nutrients (Rowe and Scotter 1973, Esseen et al. 1997). Deadwood and burned wood are important for many insects and polypore species that are fire-adapted or dependent on coarse woody debris (CWD;Muona and Rutanen 1994, Wikars 1997, 2002, Penttilä 2004, Hyvärinen et al. 2005). In Fennoscandia it was estimated that over 100 species of vascular plants, fungi, lichens and invertebrates are fire-dependent (Wikars 2004).

In Finland about 5000 (25%) of all forest-dwelling species are saproxylic, i.e. they are dependent on deadwood. Thus, the creation of deadwood has been an integral part of ecological restoration (Kouki et al. 2001, Nordlind and Östlund 2003, Gandhi et al. 2004, Hyvärinen et al. 2005). For example, an average of 60-90 m^3 ha^{-1} of CWD occurs in the natural forests of southern Finland (Siitonen 2001), while in managed stands the average volume of deadwood varies from 1.2 to 2.9 m^3 ha^{-1} only (Tomppo et al. 1999). Early-successional postfire stages with high volumes of deadwood are also suitable habitat for some species that were previously considered to be restricted to old-growth forests (Kouki et al. 2001, Similä et al. 2002, Uotila et al. 2002). However, earlysuccessional stages with large-diameter deadwood are extremely rare in managed landscapes. In the present study, one goal was to examine methods for restoration to create earlysuccessional stages with high volumes of deadwood (Stanturf and Madsen 2002).

In addition to fire, small-scale gap disturbances, such as those caused by wind, fungi and insects are especially common in old *Picea*-dominated forests (Quinghong and Hytteborn 1991, Kuuluvainen 1994, Pham et al. 2004). In old *Picea* forests, gap disturbances, old living trees and a long continuum of wood decay stages and variety of deadwood are essential for many species (e.g., Siitonen and Saaristo 2002).

Restoration of a managed stand to a fixed natural structure is not a reasonable goal, because forest structure is constantly changing through succession, i.e. there is often no final 'climax' state at the stand scale, but the climax is more of a theoretical concept (Cairns 1980, Steijlen and Zackrisson 1987). Thus, the target of forest restoration cannot be a steady state; rather, the goal of restoration should be rehabilitating lost natural structures and bringing a stand toward a more natural successional trajectory (Parker and Pickett 1997, Oliver and O´Hara 2005). In the short term, the target of forest restoration is often to improve habitat for endangered species for biodiversity goals (Dobson et al. 1997). On the other hand, restoration at the appropriate scale and in the long term, should aim at instituting and maintaining a more natural shifting mosaic of different habitats and successional stages.

1.4. Human impact on Fennoscandian forests

In forest restoration, the historical and current impact of humans on forests sets the starting point for restoration (Östlund et al. 1997, Uotila et al. 2002). This is especially true in Fennoscandian countries, where forests have been utilized for centuries. Well-documented changes include the loss of old-growth forests, simplification of tree species composition, decreases in the number of large living and dead trees and in the amount and diversity of CWD (Linder et al. 1998, Siitonen 2001, Rouvinen et al. 2002a). Due to such dramatic changes in forest structure, 46 % of endangered species in Finland are forest inhabitants (Rassi et al. 2001).

Perhaps the strongest early human impact on forests was through increased occurrence of fire (Niklasson and Granström 2000, Pitkänen et al. 2002, Wallenius et al. 2005). For example, some results have shown that the fire cycle in Norway spruce *Picea abies* (L.). Karst.-dominated stands was more than 300 years without human action (Wallenius 2002, Pitkänen et al. 2003, Wallenius et al. 2005). However, during the active period of slash-and-burn cultivation and tar burning in the 17th to 19th centuries in Finland, fire cycles were shortened in many regions down to 30-60 years (Heikinheimo 1915, Pitkänen et al. 2003). Frequent fires promoted an increased abundance of Scots pine *Pinus sylvestris* (L.) and deciduous trees, but a decreased abundance of *Picea abies* (Bradshaw 1993, Linder et al. 1997, Axelsson et al. 2002). This changed in the late 19th century when fires practically ended due to the halt in slash-and-burn cultivation and more efficient fire suppression policy (Zackrisson 1977, Niklasson and Granström 2000). Currently the lack of fires has proved to be a threat for biodiversity because deadwood and burned wood are necessary habitats for many species (eg. Wikars 2004).

The tar production period from the 16th to the 19th centuries resulted in structural changes to the forests in some regions, Scots pine being the main raw material. At that time, forests were also used for firewood collection and for grazing by domestic animals, which caused the degradation of deciduous trees and made stands more open. In Finland in the 1930s, almost half of the privately owned forest areas were still used for grazing (Tasanen 2004).

In the late 19th century, the birth of the forest industry led to an increase in the economic value of timber. This led to a period of widespread selective logging (1870-1950), when only large and high-quality stems were harvested (Sarvas 1944). This activity had already affected the characteristics of forests, depending on logging intensity.

Since World War II forests have mainly been shaped by modern forest management, using thinning, planting and clear-cut harvesting, and natural disturbance factors are being increasingly replaced by disturbances caused by forest management (Östlund et al. 1997). Forests with large old trees and abundant deadwood that historically dominated landscapes (Östlund 1993, Linder and Östlund 1998, Axelsson et al. 2002, Pennanen 2002) have been replaced by a mosaic of younger successional, even-aged and structurally impoverished stands (Fries et al. 1997, Kouki et al. 2001, Nordlind and Östlund 2003).

Due to the prolonged and ubiquitous impact of humans on forest in Fennoscandia, defining the structure, structural characteristics and variability of natural forest is challenging (e.g. Uotila 2004). However, understanding the structures of near-natural forests is needed as a reference for developing strategies and methods of restoration and, more generally, for sustainable forest management (White and Walker 1997, Franklin et al. 2002, Kuuluvainen 2002).

1.5. Forest restoration activity in practice

Forest restoration is a new and challenging research field that is still in its infancy in the Boreal Zone (Niemelä 1997, Rydgren et al. 1998, Kuuluvainen et al. 2002). Forest restoration research is challenging due to the economical, ecological, social and political aspects related to it. The target of restoration in Fennoscandia has been to increase naturalness and to protect biodiversity (e.g., Esseen et al. 1992, Kouki et al. 2001, Kuuluvainen 2002, Tukia 2000, Similä et al. 2002, Hyvärinen et al. 2005, Kuuluvainen et al. 2005). For example, in Sweden Nordlind and Östlund (2003) used 'gap restoration' and deadwood creation (clobbering, girdling, topping with explosives and inoculation of wood-rotting fungi) to restore stand structures to more 'natural' stages. In Finland, prescribed burning has been used to rehabilitate natural stand structures related to fire disturbance (Vanha-Majamaa et al. 1996, Kouki 2002). On the other hand, different natural disturbance-based management approaches, which aim to develop more sustainable forestry practices (Fries et al. 1997, Angelstam 1998, Keeley and Stephenson 2000, Gandhi et al. 2001, Bergeron et al. 2002, Franklin et al. 2002, Nordlind and Östlund 2003, Hyvärinen et al. 2005), can be regarded as restoration in its wide sense.

Local land-use history may set an essential background for restoration (Gayton 2001, Kuuluvainen et al. 2002, Ericsson et al. 2005). For example, in the USA the use of fire has been rehabilitated in dry western yellow-pine *Pinus ponderosa* (Doug. Ex. Laws.) forests because historically, before European settlements, frequent surface fires caused by indigenous peoples were an important factor affecting the ecology of these forests before settlement by Europeans (Jain and Graham 2005, Kaufman et al. 2005). In Denmark, field afforestation is regarded as one type of forest restoration (Hansen et al. 2002). These examples illustrate the wide variability in the aims of forest restoration, ranging from particular historical reference stages to complete stand naturalness (Stanturf 2005).

The first prerequisite for restoration is an adequate understanding of the natural structures and the development of ecosystems to be restored (Haila 1994, Angelstam and Petterson 1997, Esseen et al. 1997, Fries et al. 1997, Kuuluvainen et al. 2002). Fortunately, our knowledge of the structure, dynamics and processes of near-natural forests under conditions encountered in Fennoscandia has increased in recent years (e.g. Jonsson and Kruys 2001, Kuuluvainen 2002). Studies comparing the stand structure of intensively managed, selectively cut and natural forests have also been carried out (Siitonen et al. 2000, Sippola et al. 2001, Uotila et al. 2001, 2002). However, there is still a shortage of regional quantitative knowledge of structural characteristics and variability in near-natural forests and how human activities have affected them. In addition, knowledge of the effectiveness of different restoration methods is still very limited.

1.6. Scope and aims of the study

This thesis has two main goals: firstly, to define the structural characteristics and variability in near-natural stands that could be used as a reference in forest restoration and secondly, to examine what types of forest structures could be rapidly created using forest restoration. Thus, the study is based on two approaches: 1) inventories to describe the characteristics and variability in structure and composition of near-natural stands, and human impact on forest structure (I, II) and 2) studies based on an empirical restoration experiment (III, IV).

We explored the structural variability and successional pathways in near-natural old *Picea abies*-dominated sites in northwestern Russia (I). This study can be seen as defining, in part, the characteristics and range of natural variability in *Picea abies*-dominated forests (Fig. 1). We examined the near-natural stand structures in old *Pinus sylvestris*-dominated forests, and the impact of human utilization on forest structure along a geographic gradient (II). Due to the disturbance history the proportion of *Picea abies* and *Pinus sylvestris* could alternate in the same area mainly as a result of the forest fire frequency (Pitkänen and Huttunen 1999); thus it is reasonable to examine both near-natural *Pinus sylvestris* and *Picea abies* stands.

The aim of the restoration experiment was to evaluate the immediate effects of restoration on stand structural characteristics (III, IV). In mature managed *Picea abies* stands we examined different restoration treatments, using cutting and burning to rapidly restore the natural stand structural characteristics (Fig. 1).

The specific objectives of the research described in this dissertation were:

(1) to examine the structural characteristics of near-natural forests and to quantify how human utilization has changed forest stand structures in northeastern Fennoscandia (I, II) and
(2) to determine the short-term effects of restorative treatments with and without cuttings and burnings on forest structure and regeneration (III, IV).

2. MATERIAL AND METHODS

2.1. Study areas

The study was carried out in three areas in Finland and in two areas in northwestern Russia (Fig. 2).

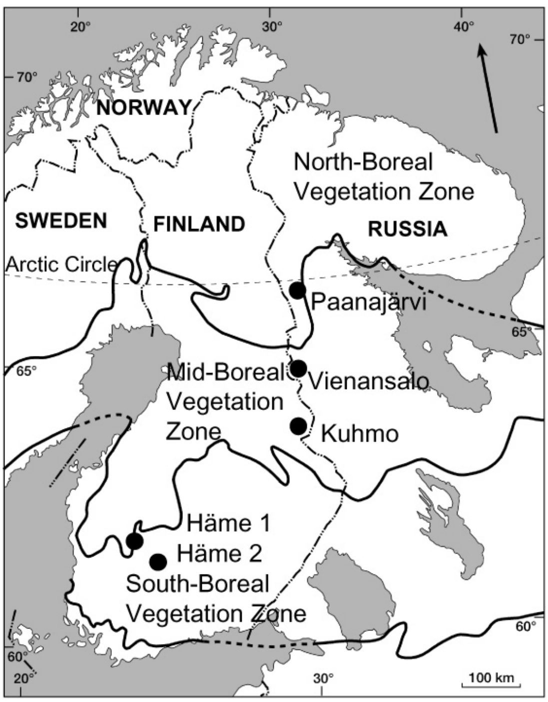

Figure 2. Study sites in Finland and northwestern Russia. Vegetation zones are according to Kalela (1961) in Finland and Ahti et al. (1968) in Russia.

One of the study areas was located in the southern Boreal Zone (III, IV), three in the mid-Boreal Vegetation Zone (II) and one in the northern Boreal Vegetation Zone near the border of the mid-Boreal Zone (I). The characteristics of the study areas are presented in Table 1.

Table 1. Characteristics of the study areas. The meteorological data are from the Atlas of Finland (1992) and Atlas Karelskoy ASSR (1989).

Study Sites	I Häme 1	Kuhmo	Vienansalo	II Paanajärvi	III &IV Häme 2
Location	62ºN, 24ºE	64ºN, 29ºE	65ºN, 30ºE	66ºN, 30ºE	61ºN, 25ºE
Altitude (m a.s.l.)	150-200	200-300	140-230	180-320	120-180
Mean annual temperature (ºC)	+3.0	+1.5	+1.0	0.0	+3.1
Mean annual precipitation (mm)	650	650	650	500-520	670
Length of growing season, days	160	145	140	125	160
Study plots	57	32	27	20	24
Stand types	Near-natural Selectively logged Managed	Near-natural Selectively logged Managed	Near-natural Selectively logged	Near-natural	Managed
Average age of the stand	188	171	198	217	80
Dominant tree species	*Pinus sylvestris*	*Pinus sylvestris*	*Pinus sylvestris*	*Picea abies*	*Picea abies*

2.1.1. History of forest utilization in the study areas

Research to define near-natural stand structures and their variability was carried out in *Picea abies*-dominated stands in the Paanajärvi area in Russia (I) and in old *Pinus sylvestris*-dominated stands in the Vienansalo area in Russia (II). In the old *Pinus sylvestris*-dominated stands the human impact on forest structure was also examined along a geographic gradient ranging from Häme (Häme 1: Fig. 2) in central Finland to Kuhmo in eastern Finland and to Vienansalo in Russia (II) (Fig. 2).

Human influence has been lowest in the Paanajärvi study area (I) compared with the other study sites. The first farmers arrived in the region in the 17th century and a village was founded on the shore of Lake Paanajärvi at the turn of the 18th and 19th centuries (Ervasti 1993). The nearest estates were located within 5-10 km from our study area. Slash-and-burn cultivation was practised until the mid-19th century in the vicinity of the village (Ervasti 1993), but recent signs of slash-and-burn cultivation were also found in the study area (Wallenius et al. 2005). Selective cuttings were initiated in the 1890s in the Paanajärvi area but no cut stumps were found in our study plots. Since World War II, human activity in the area has been minimal because villages located close to the border were evacuated during the Soviet Era (Ervasti 1993).

In all the study regions in Häme, Kuhmo and Vienansalo, past forest utilization prior to the 1950s included slash-and-burn cultivation, tar burning, cattle grazing and selective logging (II). However, both the intensity and duration of these uses varied considerably among the regions. Forest use has been longest in Häme in southern Finland, while slash-and-burn cultivation ceased more recently in the Kuhmo and Vienansalo areas (Lehtonen et al. 1996, Lehtonen and Kolström 2000). The duration of forest utilization is reflected by the settlement history. Evidence of prehistorical settlements has been found in the study regions; e.g. the ancient Sami people had small villages in the Vienansalo wilderness (Pöllä 1995). Nevertheless the last permanent settlement was established in Häme only in the mid-16th (Soininen 1957), in Kuhmo in the 17th (Keränen 1984) and in Vienansalo in the mid-18th centuries (Pöllä 1995).

In the area where the restoration experiment was initiated (in 2001) in Häme (Häme 2: Fig. 2), human effects have been prolonged (III, IV). The general features of the fire and management histories of the area are known. Slash-and-burn cultivation was widely practised in the region in the 17th and 18th centuries (Vesijaon …1995). Apparently as a consequence of this human activity, the study sites burned at intervals of about 50 years between 1600 and 1800; the last known fire occurred in the early 19th century (Tuomo H. Wallenius, unpublished data). After the mid-1850s, selective logging methods were implemented due to the increased value of sawn timber. Modern silvicultural methods, such as thinning, were introduced in the early 20th century (Vesijaon… 1995).

2.2. Sampling

2.2.1. Sampling of stand structures (I, II)

The fieldwork (I) was carried out in June 2001 in a *Picea abies*-dominated landscape in the Paanajärvi wilderness in northwestern Russia (Fig. 3). This area is one of the largest remnants of natural or near-natural *Picea*-dominated forests in Northern Europe. Systematic sampling was done in an area of about 6600 ha on a regular grid at intervals of 1 km. In the field, the locations of the sample plots were defined with the help of a global positioning system (GPS) receiver and a map. The forest ages and forest structure were measured in detail from 20 plots. The size of the study plots was 20 x 40 m. In addition, the tree age structure in a subsample of 11 plots, was studied in detail.

Sampling was carried out during three field seasons: in 1997 in Kuhmo, in 1998 in Vienansalo and in 1999 in Häme (II). The aim was to sample three stand types representing different degrees of human impact: (1) near-natural stands, (2) stands selectively cut in the past (typically in but not after the early 20th century) and (3) managed stands, which were more recently thinned according to modern stand management standards. Although these stand types were preliminarily classified in the field, the stand category was finally determined based on the measured number of cut stumps and/or stand structure according to predetermined criteria. The stands were classified as near-natural if they had no or only one cut stump per plot (< 5 cut stumps per hectare, a threshold suggested by Uotila et al. 2002) and the stand structure was typically uneven-sized. Stands classified as selectively logged had old cut stumps (≥ 5 cut stumps per hectare) from logging carried out several decades previously, but the overall stand structure was similar to that found in near-natural stands. Stands classified as managed showed clear signs of recent silvicultural thinnings and the stand structure, dominated by mature production trees, was close to even-sized, which deviated from the typically multilayered canopy of the two other stand categories. The number of sampled stands was unevenly distributed between different stand categories and regions, because sampling was done in different years in the three regions under varying conditions, and especially because old natural and managed stands were difficult to find in Häme and Kuhmo.

In all regions the same sample units, rectangular plots of 20 x 100 m, were used but they were located in the forest using somewhat different procedures, due to the different availability of potential stands and requirements of the fieldwork (II). In Häme and Kuhmo, where protected areas are often small and old managed stands are rare (as they are at the final harvest age), potential stands were sought using the stand data files of Metsähallitus (Finnish Forest and Park Service) and the Finnish Forest Research Institute, according to the following minimum requirements: (*i*) *Pinus sylvestris*-dominated forest on a volume basis, (*ii*) age of dominant trees at least 90 years and (*iii*) stand area at least 3 ha. Since such stands were rare and dispersed, they were selected in an iterative manner as the sampling progressed, based on their accessibility. This was done to make the fieldwork reasonably efficient. Another reason for this procedure was that the stand characteristics did not always conform to those in the data files, and the above-mentioned criteria had to be checked in the field each time. In Kuhmo and Häme, near-natural stands were sought in protected areas and in forests that had previously been selectively logged within the managed forests surrounding the protected areas. The location of sample plots was randomized within stands so that plots were at least 30 m from the stand edge to avoid edge effects.

Figure 3. Example of the structure of a *Picea abies*-dominated stand from the youngest age-class (110-140 yr) in the Paanajärvi wilderness.

2.2.2. Restoration experiment (III, IV)

A restoration experiment was carried out (III, IV). The experimental stands were sought for from the data files of several landowners, using the following criteria: *(i)* mature managed *Picea abies*-dominated stand, *(ii)* area of 1-3 ha and *(iii)* the site represented the *Vaccinium* site type (Cajander 1926). Restorative treatments consisted of three levels of CWD, a partial cut with a constant volume of 50 m^3 ha^{-1} of standing dispersed retention trees and a fire treatment applied in half of the stands. The CWD treatment consisted of cutting down trees and leaving them on the forest floor to create woody debris. The three levels of CWD were 5 m^3 ha^{-1} (low, corresponding to the current level of standing retention trees left on clear-cuts in Finland), 30 m^3 ha^{-1} (intermediate) and 60 m^3 ha^{-1} (high). In addition, burned and unburned reference stands without cutting treatments were included. Each treatment was replicated three times. The treatments were randomized among the stands. The restorative cuttings were conducted in February and March 2002 and the burnings in June - August 2002. The burnings were carried out using the traditional Finnish prescribed burning technique (Lemberg and Puttonen 2003; Fig. 4).

Although each stand was classified into one forest type for forestry purposes, there was clear small-scale, within-stand biotope variation. Accordingly, each stand was divided into an upland and a paludified biotope. The upland biotopes typically predominanted while the paludified biotopes covered smaller patches. Biotope mapping was preformed using tree and herb species composition and the patchiness of *Sphagnum* moss species as criteria. The

Figure 4. The burnings were carried out by using the traditional Finnish burning technique, which forms a circular burning pattern. (low-CWD-level restoration burning, plot 301)

vegetation and moisture levels of the paludified biotopes varied considerably, and consisted of patches of paludified *Vaccinium myrtillus* site type spruce swamp (Laine and Vasander 2005). Although parts of the paludified areas were drained for forestry, some patches of *Sphagnum* mosses still remained. The patches of paludified biotopes were often located in (topographical) depressions and their size varied from 0.3 to 1.8 ha.

Pretreatment inventories were done during the field season of 2001 and posttreatment inventories in autumn 2002. A detailed description of stand structure was prepared for all tree layers, including both living and dead trees (III). The diameter and height of each tree (height > 2 m) were recorded. From the 5-m buffer zone, the height and diameter at breast height of living trees (DBH >10 cm) were measured. In addition, the seedlings and their microsites and the frequency of microsite types were measured before and after restoration (IV). During the burning the climatological parameters were also measured (Table 2). Additional measurements included the location of the trees, change in soil characteristics (e.g. decrease in humus layer depth) and ground and field vegetation, but these data will be reported in separate papers not included in this thesis.

Table 2. Climatological conditions during the restoration burnings.

Treatment m^3/ha DR*	Plot numb.	Time of burning (h)	Air moisture (%)	Air (ºC)	Wind speed (m/s)	Wind direction	Burning day
Reference	334	1.5	39.5	25.1	0.2	nw	8.8.02
Reference	226	2.0	34.4	24.9	0.3	sw	11.6.02
Reference	56	2.0	29.9	26.5	1.1	se	6.6.02
	mean	1.9	34.6	25.5	0.6		
60	205	2.0	33.8	24.5	0.6	se	7.8.02
60	55	2.2	31.2	27.2	1.2	se	15.7.02
60	327	2.1	28.8	28.9	1.1	sw	18.7.02
	mean	2.1	31.2	26.9	1.0		
30	85	2.0	30.2	26.9	0.2	s	7.6.02
30	41	2.1	30.2	23.8	1.3	sw	11.6.02
30	203	2.0	31.5	21.5	0.9	e	5.6.02
	mean	2.0	30.6	24.1	0.8		
5	301	2.2	28.7	28.9	1.1	w	16.7.02
5	165	1.3	34.8	26.1	1.7	w	16.7.02
5	250	2.0	33.3	27.9	0.9	w	18.7.02
	mean	1.8	32.2	27.6	1.2		

DR*= Down retention

2.3. Measurements and computations

The forest structure was characterized by computing volumes, diameter, and species distributions of the trees (I- III). The volume of living trees of *Pinus sylvestris*, *Picea abies,* and birch *Betula* (L.) spp. was calculated using the volume equations of Laasasenaho (1982). When tree height was measured (for trees with DBH > 30 cm), equations employing both DBH and height as independent variables were used. The volume of all deciduous trees was estimated using the equations for *Betula* (I-III). The structural diversity features of living trees were summed by study region and stand type (II).

We classified deadwood into standing and fallen deadwood (I) and in the pre- and posttreatment assessments (III). The standing deadwood included standing dead trees (snags) as well as broken trunks (height > 1.3 m). Fallen deadwood (mean DBH > 5 cm) included the natural stumps (height < 1.3 m) of broken trunks, cut stumps (diameter > 10 cm, height > 20 cm), and various types of logs, such as uprooted logs (windfall), logs broken off from the base of the roots and sawn logs. The species of each piece of deadwood was identified, and its decay stage was determined using five classes: 1) tree died less than one year before sampling, cambium still fresh; 2) cambium eaten by insects, knife penetrates a few mm; 3) knife penetrates less than 2 cm; 4) knife penetrates 2-5 cm and 5) knife penetrates all the way (modified from Renvall 1995).

The tree seedlings (I, II, IV) were measured (height limits in I: 20-200 cm, II: 30-130 cm and IV: 10-200 cm. The regeneration microhabitat of seedlings was inventoried in 10 x 10 m plots (I), while in the microhabitat distribution on the forest (IV) floor was determined along the 40-m midline of the sample plot by point-recording the microhabitat class at every 0.5 m (totalling 80 recordings per plot). The microhabitat classification was: 1) even (level) ground; 2) mound (> 20-cm rise from the surrounding average ground level, including a few stones); 3) depression (< 20 cm drop from surrounding average ground level, and including a few uprooting spots); 4) deadwood-related microhabitats (deadwood included on or beside (< 15 cm) decaying wood, on or beside (< 15 cm) a stump or under a fallen crown); 5) shelter (including microsites under tree logging waste); and 6) other (including uprooting spots, exposed soil, and stone). In the present study (I-IV) used various statistical methods because the study questions and sampling schemes varied among Studies I-IV (Table 3).

Table 3. Statistical methods used in I-IV.

Study questions	Variables analysed	Methods	Used in study	Reference examples
Differences between and within regions and stand types	Total volume Proportion of deciduous trees Number of seedlings	ANOVA	I, III, IV	Uotila et al. 2001
Same as above but taking covariates into account	Total volume Proportion of deciduous trees Number of seedlings	ANCOVA and contrasts	II	Drobyshev et al. 2004
Differences between biotopes before treatments	Volume of living trees Volume of CWD	Kolmogorov-Smirnov	III	Zar 1999
Differences within regions and between restorative treatments	Volume of living trees Volume of CWD	Tukey's Studentised range test	II, III, IV	Zar 1999
Microhabitat distributions of saplings versus stand	Microsite distribution	G-test (log-likelihood test)	II, IV	Kuuluvainen and Laiho 2004
Diversity of tree diameter distributions	DBH	Shannon-Weaver	I, II	Shannon 1948

3. RESULTS

3.1. Structure and development of old *Picea abies* forests (I)

The northern *Picea abies*-dominated forests underwent significant structural and compositional changes at 110 - 300 years of age (I). Deciduous trees were an essential component throughout the range of forest succession examined, but their percentage declined with forest age. In the youngest age-class (110-140 years) the proportion of deciduous trees from the total volume comprised 26% *Betula* and 19% aspen *Populus* (L.). In the 180-240-year-old stands the proportion of *Betula* represented 14% of the volume, compared with only 5% in the oldest (> 280 years) stands.

Deadwood dynamics also reflected stand succession. The volume of logs and snags increased with forest age, but their density per hectare decreased from the youngest to the oldest age-class, due to the increasing mean tree size from the youngest to the oldest stands. In the two younger forest age-classes, *Betula* decay stage 5 predominated among dead trees, while in the oldest age-class *Picea abies* in decay stage 2 was most abundant (I; Fig. 5).
The total number of seedlings was highest in the oldest forest age-class (> 280 years) and lowest in the youngest age-class (110-140 years) (I). The microhabitat availability was significantly different from the distribution of the seedlings in microhabitats in every forest age-class ($p < 0.001$; I). 'Even ground' was the most common microhabitat class in all forest age-classes, but in the middle and oldest forest age-classes, mounds and depressions covered more of the forest floor than in the youngest age class (I).

The distribution of seedlings in microhabitats differed significantly between the middle (180-230 years) and oldest forest age-classes, and between the youngest and oldest age-classes. The occurrence of seedlings in microhabitats differed between conifers and deciduous species and among forest age-classes (I). Conifer seedlings were more common on mounds in the middle and oldest forest age-classes compared with the youngest age-class. In contrast, deciduous species seedlings were often found on mounds in the youngest and oldest forest age-classes. Availability of deadwood microhabitats was highest in the youngest and oldest forest age-classes and lowest in the middle age-class (180-230 years). However, the proportion of seedlings in deadwood microhabitats was highest in this age-class. In addition, the proportion of seedlings in deadwood-related microhabitats was higher for conifers than for deciduous seedlings in all forest age-classes.

3.2. Structure of old *Pinus sylvestris*-dominated forests along a geographical and human impact gradient (II)

3.2.1. Tree species composition

In old *Pinus sylvestris*-dominated forests the near-natural and selectively logged (in the past) stands in Häme and Kuhmo showed a significantly higher *Picea abies* proportions than stands in Vienansalo (II). In comparison, the proportions of deciduous tree volumes were higher in near-natural stands in Vienansalo compared with the near-natural stands in Häme (Fig. 6).

The *Picea abies* proportion was high in the near-natural and selectively logged stands of Häme (42% and 34% of the volume) and Kuhmo (46% and 38%, respectively), where the proportion of *Picea* was particularly pronounced in the smaller diameter classes (DBH < 25 cm). In contrast, the proportion of *Picea* was low in Vienansalo both in near-natural (10%)

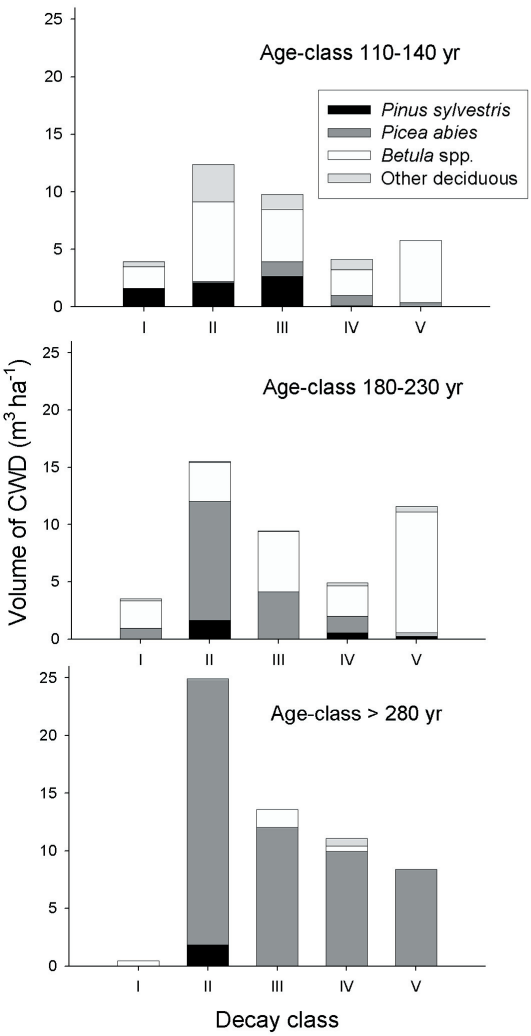

Figure 5. Volume of deadwood in different decay classes and forest age-classes (I).

and selectively logged (17%) stands. The proportion of *Picea* was even lower in the managed stands of the Kuhmo (5%) and Häme (11%) (II).

The proportion of deciduous trees in the total volume was lower in the near-natural (1%) and selectively logged (6%) stands of Häme than in those of Vienansalo (13% in both), but there was no difference between Kuhmo and Vienansalo in this respect. The lowest proportions of deciduous trees were found in the near-natural stands (1%) of Häme and in the managed stands (2%) of Kuhmo (II).

The mean proportion of *Pinus sylvestris* in near-natural and selectively logged stands was highest in Vienansalo (77% and 70% of volume, respectively), but considerably lower both in Kuhmo (44% and 51%) and in Häme (57% and 60%). This difference was most dramatic in the smallest diameter classes: in our study plots there were no *Pinus sylvestris* with a DBH-diameter smaller than 10 cm in the near-natural forests of Häme (Fig. 6).

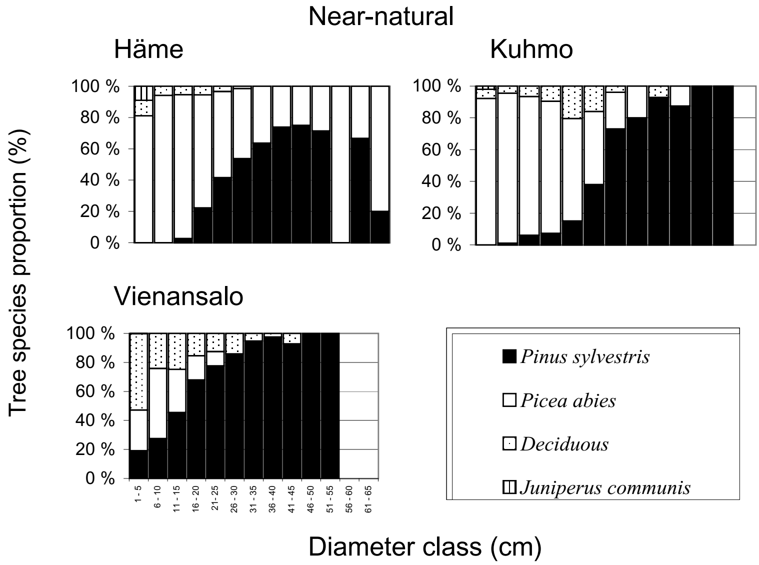

Figure 6. The proportion of volume of tree species varies among study areas in near-natural *Pinus sylvestris* -dominated stands (II).

3.2.2. Volume of living trees

Among stand types in Häme the proportion of *Picea* abies was higher in near-natural and selectively logged stands compared with managed stands, whereas in Kuhmo the proportion of deciduous trees was higher. On the other hand, in Vienansalo the tree species composition did not differ between near-natural and selectively logged stands (Fig. 7).

The near-natural stands differed significantly among the study regions in their total volumes, taking into account the effects of variation in mean stand age and length of the growing season (II). In general, the volumes decreased from Vienansalo to Kuhmo to Häme, except for deciduous trees which showed a contrasting trend. In the near-natural stands in Vienansalo and Kuhmo the volume of deciduous trees was significantly higher than in Häme, where the deciduous volume was lowest. In Kuhmo the near-natural and selectively logged stands had higher deciduous volumes and lower *Pinus sylvestris* volumes than the managed stands. In Vienansalo the near-natural and selectively logged stands did not differ (II).

Forest utilization has been most intensive in the Häme region, where the total volume in managed stands was significantly lower than that in the near-natural and selectively logged stands (II). In addition, the total volume of living trees was smaller in Häme than in Kuhmo because the managed stands were older in Kuhmo. However, there were no differences in the volumes of *Picea abies* and deciduous trees (II) between the managed stands in Häme and Kuhmo (II).

In Häme, the tree volumes were generally higher in the near-natural and selectively logged stands than in the managed stands (II). In Kuhmo, the near-natural and selectively logged stands had higher deciduous volumes and lower *Pinus sylvestris* volumes than the managed stands. In Vienansalo, the near-natural and selectively logged stands did not differ (II).

Structural diversity characteristics such as leaning and broken trunks were most common

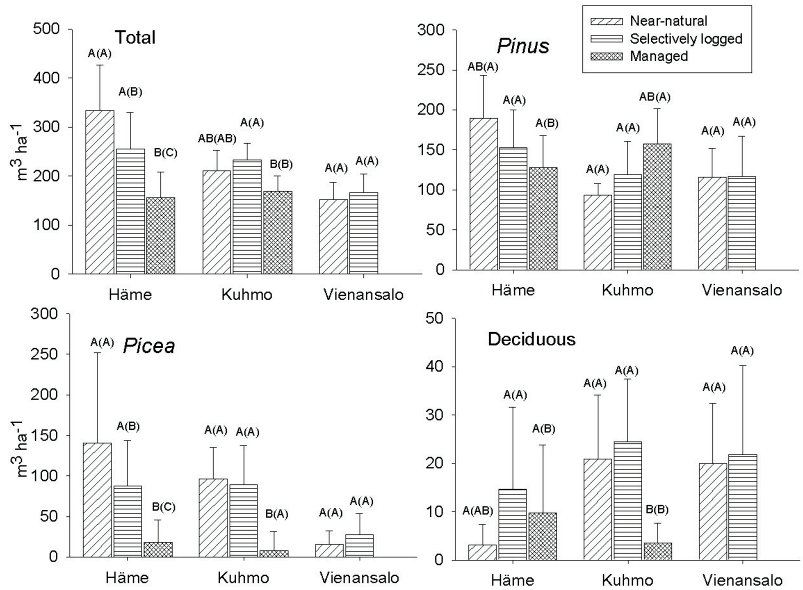

Figure 7. Volume of (a) all living trees, (b) pine, (c) spruce, and (d) deciduous trees. Columns with different letters are significantly different at the $p < 0.05$ level within regions (Tukey´s test). Letters in parentheses denote the significance test of adjusted volume (contrast analyses), in which the effect of mean age of the stand and length of the growing season are taken into account as covariates. Error bars are standard deviations (II).

in near-natural stands and in stands selectively logged in the past, and lowest in managed stands (II). However, the near-natural stands in Häme deviated from this pattern by having fewer structural diversity characteristics than managed stands in the same region.

3.2.3. Tree diameter distribution and regeneration

The pooled diameter distributions of near-natural stands and stands selectively logged in the past generally showed monotonic negative slopes, whereas trees in the managed stands exhibited bimodal patterns (II). However, there were differences in the diameter distribution among the regions, especially in the category of near-natural stands. Trees in the smallest diameter class (1-5 cm) were more abundant in the near-natural stands of Vienansalo than in the near-natural stands of Kuhmo and Häme. However, the density of large trees with DBH > 40 cm was highest in the near-natural and selectively logged stands of Häme (59 and 40 trees per hectare, respectively) and lowest in the managed stands of the same region (only one tree per hectare), but moderate in Vienansalo where 16 large trees per hectare were found in both near-natural and selectively logged stands (II).

Seedling (30-130 cm) density was highest in the near-natural and selectively logged stands in Vienansalo (II). As with total seedling number, *Pinus sylvestris* seedlings were most abundant in Vienansalo in the near-natural (3000 ha^{-1}) and selectively logged (1700 ha^{-1}) stands. No *Pinus* seedlings were observed in the near-natural stands of Häme and Kuhmo. On the other hand, the density of *Picea abies* seedlings was highest in Häme. The density of juniper *Juniperus communis* (L.) was highest in the near-natural stands of Häme and in the near-natural and selectively logged stands of Kuhmo.

The density of deciduous seedlings was highest in the near-natural (2150 ha^{-1}) and selectively logged (1630 ha^{-1}) stands of Vienansalo, followed by Kuhmo. The lowest density of the deciduous component was recorded in the managed stands of Kuhmo (500 ha^{-1}) and in the near-natural (560 ha^{-1}) stands in Häme (II).

3.3. Restoration of mature managed *Picea abies* stands: short-term effects (III, IV)

3.3.1. Description of the starting point for restoration

The pretreatment stand structure in the forest restoration sites in managed *Picea abies*-dominated stands was characterized by a bimodal pattern of pooled diameter distribution of trees in the upland biotope (III). However, in the paludified biotopes the pooled diameter distribution showed a descending slope (III). In addition, the pretreatment volume of deadwood was higher in the upland biotope than in the paludified biotope, evidently due to previous cuttings that increased the volume of large stumps and small (< 20 cm)-diameter fallen logs (III). The volume of fallen deadwood before treatments consisted mainly of logging waste: small diameter (< 20 cm) fallen logs and largediameter (> 20 cm) stumps. There were no statistical differences between stand types for the volumes of living and dead trees before treatments. However, the volume of deadwood was in some stands increased due to the wind damage in autumn 2001.

Before treatments the microsite distribution in the upland biotope was more uniform and even ground was more common than that in the paludified biotope. In contrast, the mounds and depressions in the paludified biotope, were more abundant than in the upland biotope (IV). The numbers of *Picea abies* and *Betula* seedlings were higher in the paludified biotope compared to the upland biotope. Even ground was the most common microsite for seedlings in both biotopes (IV).

3.3.2. Short-term effects of forest restoration with partial cutting and CWD creation (III, IV)

With the partial cutting treatments, we intended to change the diameter distributions towards an 'inverse J' type by cutting trees larger than 10 cm in DBH (Fig. 8 c). However, the seedlings were also damaged by the machinery, in the logging process, which caused a decrease in the number of trees below 10 cm in DBH. The amount of standing deadwood was less than 1 m^3 ha^{-1} across all CWD levels in both biotopes with CWD treatments without fire (III).

The cutting and CWD treatments significantly changed the relative abundance of microsites in the nonburned stands in both biotopes (IV). Consequent to the increase in microsites related to CWD, the proportion of microsites on even ground, mounds and depressions decreased with an increasing volume of deadwood in CWD treatments (IV). In treatments with partial cutting without fire, the effect of restoration on seedling density and microsite distribution did not significantly affect the total number of seedlings, probably because the variability in seedling density between stands was high among treatments. Instead, the proportion of seedlings in sheltered microsites increased, for all species pooled, but the

CWD-related microsites decreased in the upland biotope in the high-CWD treatment without fire. Cutting residuals and branches (mainly *Picea abies*) provides shelter for regeneration but fresh deadwood does not offer microsites for seedling establishment (IV). On a species-by-species basis, the density of *Picea abies, Betula* and other deciduous seedlings increased with low-CWD cuttings in the upland biotope, but other treatments decreased the number of seedlings (IV). In contrast, the number of *Picea abies* in the paludified biotope decreased with every treatment, whereas the number of *Betula* seedlings increased (IV). Although the number of seedlings decreased due to mortality caused by cutting damage, the microsite distribution changed and its variability increased (IV).

3.3.3. Short-term effects of forest restoration with partial cutting, CWD creation and fire (III, IV)

After the cutting and burning treatments, the number of living trees was low in both biotopes, irrespective of the CWD level. However, small-diameter trees were more abundant in the paludified biotope than in the upland biotope after the burning (Fig. 8 f). The burning of the reference stands was less intense than the burnings in stands that were cut and had more available fuel, such as fallen deadwood with dry branches and logging residuals due to cuttings. As a result, more trees survived in the burned reference stands, but the number of small-diameter trees decreased compared with the pretreatment distribution (Fig. 8 g). However, the mortality in small-diameter classes was lower in the paludified biotope than in the upland biotope (Fig. 8 h).

The use of fire reduced the volume of living trees in the upland biotope (III). There were no significant differences in living tree volumes between the CWD treatments due to variation between individual stands, especially after fire (III).The volumes of living trees were also lower after fire in the paludified biotope, although this result could not be tested statistically due to uneven burning at these sites. The living tree volumes after burning were highest with intermediate levels of CWD and lowest with high levels of CWD, a trend similar to that observed in the upland biotope (III). The different CWD treatments did not differ in the total amount of deadwood after fire in the upland biotope; however, fire increased the volume of standing deadwood ($p = 0.015$; III).

The highest amount of deadwood was formed with high levels of CWD and fire in the paludified biotopes, whereas the lowest volume was found in the unburned reference stand (III). For CWD treatments with fire, the volume of dead standing trees was highest with high levels of CWD and lowest in the burned reference stand. Overall, the reference burning areas differed from other burning sites, because the burned areas were mosaics with high amounts of unburnt area due to the lack of CWD and the high moisture content inside the covered canopy during the burning. However, the burning result in the reference burning stands promoted a good initial stage for the near-natural stand succession, because it initiated the deadwood decomposition continuum in those stands (III).

The abundance of even ground and mound microsites was lower than before burning, whereas the proportion of microsite points on or near CWD or stumps, under fallen crowns and on stones increased in treatments with cutting and fire in the intermediate- and high-CWD treatments (IV). In addition, the pre- versus posttreatment effects of partial cutting and fire on seedling density and the effects of microsite distribution on total seedling density in the upland biotope were marginally significant, although these effects were not detectable in the density of *Picea abies* and deciduous seedlings alone. Regeneration was low after fire with the intermediate- and high-CWD treatments (IV), but regeneration of *Betula* spp. was abundant after the low-CWD treatment in the upland biotope (IV). The increase in density of *Betula* spp. seedlings was high, especially with intermediate-levels of CWD, in the paludified biotopes, where the fire did not burn the entire experimental plot, such that part of the pretreatment seedling cohort survived. The seedlings regenerated mainly on even ground microsites after fire, especially in the low-CWD treatments in the upland biotopes, but also on mounds in the intermediate-CWD treatments in paludified biotopes (IV).

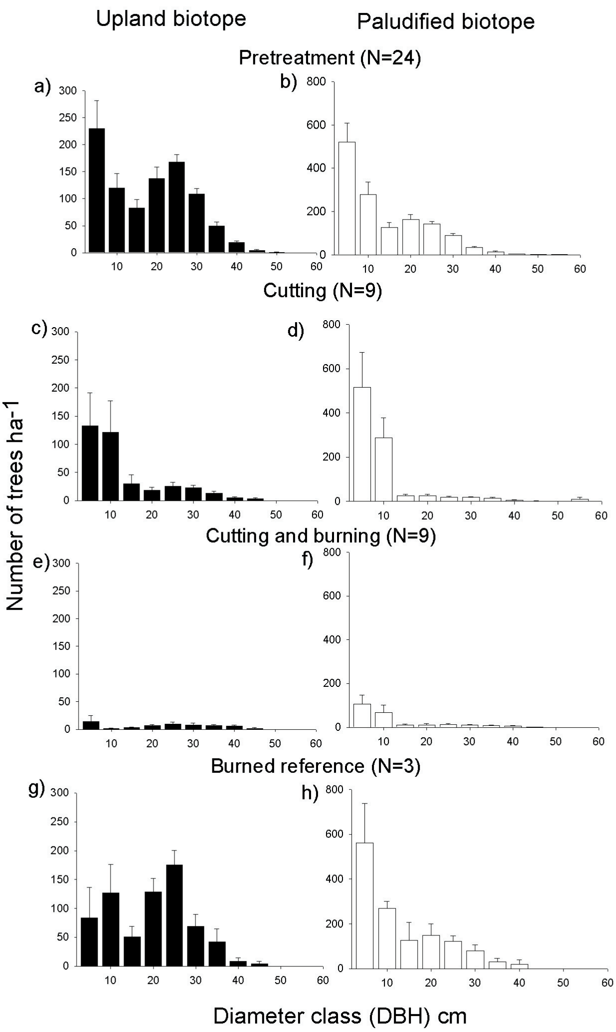

Figure 8. Diameter class distribution of living trees before and after treatments in the upland and paludified biotopes for trees taller than 2 m. Reference means that no cutting was done. Error bars depict standard deviation (III). Note the difference in the y-axis scales between biotopes.

3.4. Volume of the living trees and deadwood related to the age of the dominant cohort or time since last major disturbance

Total volume of the living trees and deadwood varied widely between near-natural *Picea abies* and *Pinus sylvestris*-dominated stands related to the age of the dominant cohort or time since last major disturbance (Fig. 9).

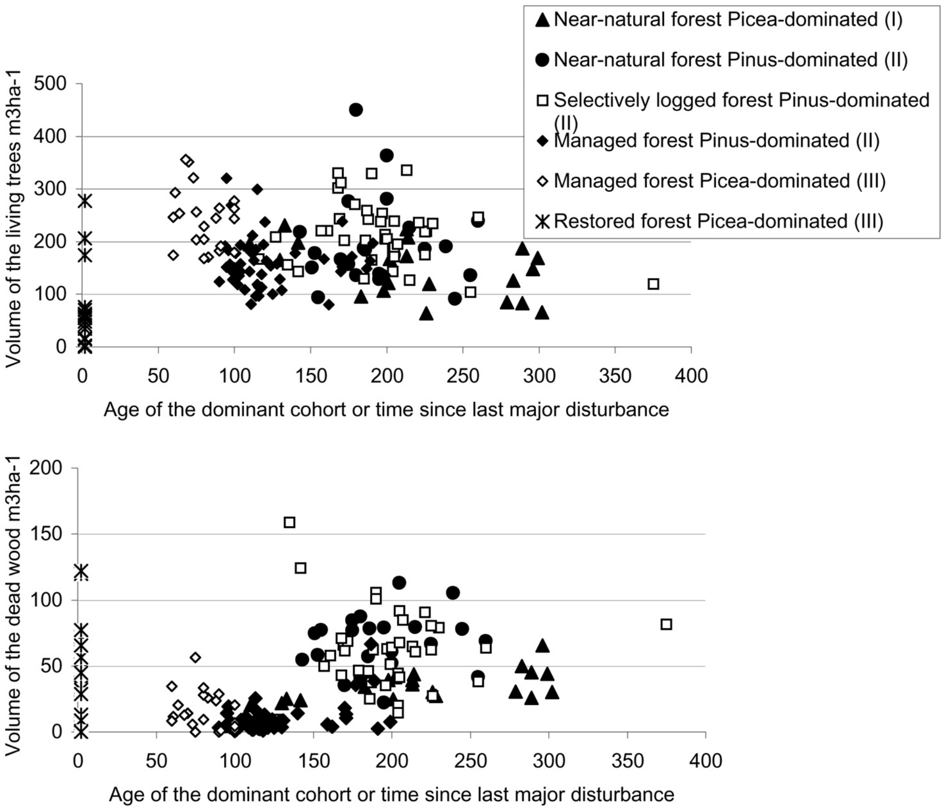

Figure 9. Volume of living trees and deadwood of the studied forests (I-III) related to the age of the dominant cohort or time since the last major disturbance. The deadwood data from *Pinus sylvestris*-dominated stands is from Rouvinen et al. 2002a. Restored forests with high volumes of living trees are reference burnings.

4. DISCUSSION

4.1. Structural characteristics of old near-natural *Picea abies* stands (I)

Here we showed that the structural characteristics of near-natural *Picea*-dominated stands changed considerably during late succession, from 110 to 300+ years of age (I). Since the stands were systematically sampled from a landscape, this also reflects the landscape-level variability in stand ages and structures. There were no recent forest fires or large wind damage areas in the sampled landscape (Wallenius et al. 2005). This suggests that forest fires were rare in our studied landscape, since 95% of the forests were older than 120 years (Wallenius et al. 2005). For comparison, an average of only 12.2 % of the forested land in Finland according to VMI 9 (Finnish forest inventory 1996-2003) is more than 120 years of age (in northern Finland 21.2%) (Finnish… 2005). Such drastic differences are clearly reflected in stand characteristics, due to the structural diversification of stands towards old age (Spies 2004).

Deciduous trees (mainly *Betula*) were frequently present in the near-natural *Picea abies*-dominated stands, but their proportion decreased with time since the previous fire. The mean proportion of deciduous trees varied in old *Picea abies*-dominated stands, from nearly 50% of the total volume in the 110-140-year-old stands to stands older than 280 years in which deciduous trees represented only 5% of the total volume (I). The occurrence of deciduous trees in old-growth *Picea abies* stands was reported (Steijlen and Zackrisson 1987, Kuuluvainen et al. 1998), but in these studies the effect of forest age was not determined (however see Sirén 1955, Linder et al. 1997). De Grandpré et al. (2000) and Lesieur et al. (2002) reported that in the absence of fire in the northeastern boreal forests of Canada, the proportion of conifers increases and that of hardwoods decreases. In the *Picea abies*-dominated stands of the present study, forest age can play an important role in biodiversity, e.g. of epiphytic flora, (Kuusinen 1996, Kouki et al. 2004), although a small proportion of deciduous trees was found in the oldest age-class (> 280 years). Overall, it appears that deciduous trees are important characteristics of near-natural *Picea* stands, but their proportion decreases with succession.

The average volume of deadwood increased from the youngest to the oldest forest age-class in stand succession (Fig. 6). Comparable results were reported from old-growth *Picea abies* forests in Russia (Syrjänen et al. 1994) and northern Sweden (Linder et al. 1997). The review by Siitonen (2001), showed that the average volume of decaying wood varies from 50 to 80 m^3 ha^{-1} in mesic *Picea*-dominated old forests in the northern Boreal Zone. Separate studies reported values such as 17-65 m^3 ha^{-1} (Jonsson 2000), 32 m^3 ha^{-1} (Siitonen 1994) and 19 m^3 ha^{-1} (Sippola et al. 1998). The present results are consistent with previous findings in that there was considerable between stand variations in deadwood. However, this study showed that much of the variation in dead wood can be explained by forest age and successional history (I).

The decay stage distribution and tree species composition of deadwood changed over the course of late forest succession (I). In the youngest age-class stands (110-140 years), *Betula* deadwood predominated in decay stage 5. In addition, small-diameter standing deadwood commonly occurred in this age-class due to self-thinning mortality. In the oldest age-class (> 280 years), decay stage 2 *Picea abies* was the predominant deadwood type (Fig. 6). Sirén (1955) also reported that recently dead *Picea* were most commonly found in 300-year-old stands, while highly decayed *Betula* logs predominated in stands under 195 years of age. The deadwood continuum of volumes and decay stages is crucial for many ecosystem processes and forest inhabitants (Harmon et al. 1986), e.g. saproxylic organisms (Siitonen 2001, Siitonen and Saaristo 2002). The deadwood succession and continuum of volumes and decay stages is probably one of the most essential characteristics of near-natural forests (I).

The present study showed that the tree diameter distributions in general decreased in *Picea abies*-dominated old-growth stands, so that small trees were most abundant and the number of trees decreased with increasing tree size (I). However, the occurrence of large-diameter (> 20 cm) trees, both deciduous and conifers, was also typical in each of the successional stages studied (I). Accordingly, old-growth (or natural) forests that have long escaped stand-replacing disturbances are described as having an uneven-aged, all-aged or multimodal tree age distribution (Lähde et al. 1991, Zackrisson et al. 1995, De Grandpré et al. 2000).

The regeneration characteristics varied among the age-classes in old-growth *Picea abies* forests (I). Tree regeneration was most abundant in the oldest stand age-class (> 280 years) in which *Betula* seedlings were the most numerous (I), probably due to more open canopy conditions and gap disturbances that allow regeneration by pioneer species and the maintenance of a mixed tree composition even in old-growth forests (Steijlen and Zackrisson 1987, Kuuluvainen et al. 1998).

The distributions of microhabitat availability and those of seedlings in microhabitats were different among the old-growth *Picea abies* stand successional stages (I). The oldest stands showed the highest proportion of mounds and depressions, which originated partly from a high volume of deadwood late in succession. The decayed logs can serve as a substrate for tree regeneration (Harmon and Franklin 1989, Kuuluvainen and Kalmari 2003) and elevated microsites are favourable to seedling establishment due to reduced competition with other vegetation (e.g. Nakashizuka 1989, Hörnberg et al. 1997). Microhabitat distributions of old *Picea abies* forests appear to change throughout stand succession, up to ages of ~300 years and probably longer. The higher proportion of mounds and depressions in the oldest age-classes has some beneficial effects on tree regeneration (I).

The results suggest that the *Picea*-dominated landscape studied represents a shifting mosaic of different successional stages (Spies and Turner 1999), in which different natural disturbances from fire to gap dynamics create the structural and functional variability at various scales (Roberts and Gilliam 1995). For example, late forest succession can proceed for long time periods without fire disturbance (e.g. Wallenius et al. 2004), during which time small-scale gap dynamics cause variation in stand structures (I). The maximum biological age of *Picea abies* is 300-400 years, because it cannot resist forest fires due to its thin bark and decays easily when it is old. The present study indicates that in northern *Picea abies* forests after a stand-replacing fire disturbance, succession to a clearly uneven-aged old-growth structure with different cohorts and great deadwood volumes lasts up to 300 years (I). Overall, we showed that the development of near-natural, old-growth, *Picea abies*-dominated stands exhibits a continuum of different structural characteristics (I). This successional variability should be taken into account in landscape-level forest restoration in which the target is to increase near-natural characteristics and biodiversity (Fig. 1).

4.2. Structure of old *Pinus sylvestris* stands in relation to human impact (II)

The tree species compositional differences between the study regions (II) evidently originated mainly from differences in previous and recent human impact. The near-natural *Pinus sylvestris*-dominated stands in the Vienansalo wilderness had higher proportions of deciduous trees than the near-natural protected forests in Kuhmo and Häme in Finland (Fig. 7). Uuttera et al. (1996) and Jantunen et al. (2002) also reported a higher proportion of deciduous trees from mature forests in Russian Karelia compared with similar forests in Finland. This difference in the proportion of deciduous trees in near-natural stands was likely the result of more recent forest fires in Russia than in Finland.

Regional differences in the proportion of deciduous trees existed in the protected forests of Finland (II); the proportion of deciduous trees was higher in the near-natural and selectively logged stands of Kuhmo than in those of Häme. Prolonged forest utilization has decreased the abundance of deciduous trees, mainly in Häme. In Kuhmo, the deciduous proportion is higher because forest management has not been as efficient as in Häme, and the historical slash-and-burn cultivation may have increased the proportion of deciduous trees more recently in eastern Finland (Lehtonen et al. 1996). The scarcity of living deciduous trees in the near-natural (protected) areas of Häme is noteworthy, since many endangered species are dependent on old deciduous trees for habitat (Kouki et al. 2004, Penttilä 2004). For example, the smaller proportion of deciduous trees is probably one reason for the larger number of endangered polypore species out of the total amount of polypores in Häme compared with Kuhmo (Penttilä 2004).

The proportion of *Picea abies* was clearly higher, especially in the small-diameter classes, in the near-natural and selectively logged stands of Häme and Kuhmo than in those in Vienansalo. This difference is evidently related to the scarcity of fires during the past 100-200 years in Finland, a situation that in the conservation areas has favoured the shade-tolerant fire-sensitive *Picea* over the shade-intolerant but fire-resistant *Pinus sylvestris* (Linder 1998, Pennanen 2002). As stand stocking increases, with increasing time since fire, the regeneration conditions deteriorate for light-demanding species, such as *Pinus sylvestris* and deciduous trees, and *Picea abies* as a shade-tolerant species gains an advantage (Pöntynen 1929, Sirén 1955, Linder et al. 1997). The decline in *Picea* following the fires could be 60-90 years in duration, although *Picea* has since benefited. This trend was also reported before the slash-and-burn period from eastern Finland (Pitkänen and Huttunen 1999). In addition, past selective logging has increased the proportion of *Picea* as a result of its superior competitive ability inside the closed forest compared with *Pinus sylvestris* (Sarvas 1944). The trend towards increase in *Picea* dominance in forest reserves was also reported in other studies (Haapanen and Siitonen 1978, Bradshaw 1993, Linder 1998, Lehtonen and Kolström 2000). Studies of unmanaged forests in North America also showed species compositional shifts due to the absence of fire (Minnich et al. 1995, De Grandpré et al. 2000, Lesieur et al. 2002). Natural tree species dynamics in protected areas has changed due to a lack of natural disturbances (Linder and Östlund 1998, Kouki et al. 2004). Consequently, the large differences (in tree species proportions and volumes) between the protected areas in Finland and the more naturally dynamic landscape in Vienansalo in Russia raise the question: To what extent do the protected areas in southern Finland provide ‘natural’ references for managed forests? The present results suggest that the history of selection of these conservation areas and the long-lasting human impact (e.g. through fire suppression) have potential consequences on the structure of these areas, which may decrease their value as ‘natural benchmarks’ for forest restoration and conservation in the area.

The *Pinus sylvestris*-dominated near-natural and selectively logged stands showed a negatively sloped diameter distribution (II) similar to that in the near-natural *Picea abies*-dominated stands (I). This pattern of diameter distribution was documented in the near-natural *Pinus sylvestris*-dominated stands in the northern and mid-Boreal Zones in Sweden (Zackrisson et al. 1995, Linder et al. 1997) and in the middle boreal zone in southern and eastern Finland (Norokorpi et al. 1994, Uotila et al. 2001, Rouvinen and Kuuluvainen 2005). In the present study, small-diameter trees in the near-natural stand category, were more abundant in Vienansalo than in Kuhmo and Häme. In addition, many of the small-diameter trees in Vienansalo were deciduous, whereas *Picea abies* predominated in the small-diameter classes in Kuhmo and Häme (Fig. 7). These differences in near-natural stands are evidently related to the factors favouring regeneration in Vienansalo in Russia, particularly more recent fires and more open stand structures, compared with Kuhmo and Häme in Finland (Pöntynen 1929, Linder et al. 1997, Lehtonen and Kolström 2000, Rouvinen et al. 2002b).

There were up to 3000 *Pinus sylvestris* seedlings per hectare in the near-natural stands of Vienansalo. In contrast, the sampled near-natural stands in Häme had no *Pinus sylvestris* or *Populus* seedlings (II). The lack of regeneration of pioneer tree species in forest reserves was also reported previously (Haapanen and Siitonen 1978, Linder 1998, Lehtonen and Kolström 2000, Kouki et al. 2004). This constitutes a major problem for the future management of conservation areas, because a large number of species are dependent on deciduous trees for their survival (Esseen et al. 1997, Kouki et al. 2004). Thus, restorative treatments in biodiversity conservation could be used to change the stand structure and increase regeneration (IV).

In Häme the near-natural stands and those selectively logged in the past had significantly more large trees than the near-natural stands in Vienansalo (II), with the length of the growing season used as a covariate in the analysis of covariance (ANCOVA). The densities of large trees (DBH > 40 cm) in *Pinus sylvestris*–dominated near-natural forests apparently vary considerably; reported densities range from 14 trees per hectare in central Sweden (Linder and Östlund 1998) up to 40 trees per hectare in Komi, Russia (Majewski et al. 1995). However, the unusually high number of large trees in Häme may also have resulted from these stands being initially selected for conservation due to their unusually large trees. Large-diameter trees are a characteristic feature of near-natural *Pinus*-dominated forests (Linder and Östlund 1998, Pennanen 2002, Spies 2004). However, anthropogenic land use has influenced the variability in numbers of large-diameter trees in near-natural stands.

Old-growth stands may be threatened by anthropogenic disturbances, but the lack of natural disturbances may also pose a threat (Spies 2004). The latter appears to be the case in the studied protected areas in Finland, which appear to have a special stand structure due to fire suppression, i.e. a high proportion of *Picea abies* and a lack of *Pinus sylvestris* and deciduous regeneration. In comparison, *Pinus sylvestris*-dominated stands in Vienansalo still contain stand structures that are due to fire disturbance, such as a high proportion of deciduous trees and an abundance of small-diameter *Pinus sylvestris* that formed layered, uneven-sized canopies (Fig. 7). Although some of the fires were ignited by humans in the Vienansalo wilderness (Lehtonen and Kolström 2000), the near-natural forest structural characteristics have been maintained (Rouvinen et al. 2002a, II). *Pinus sylvestris* is adapted to fire disturbances; e.g. old individuals have thick bark that acts as a shell against fire, and the branches are also located near the top of the trunk. Thus, the natural succession of *Pinus sylvestris*-dominated forests can be long, due to the long biological age of *Pinus sylvestris*, up to 600- 700 years. Usually only the large-diameter trees survive fire disturbances because most of the small-diameter trees are killed (Agee 1998). Lampainen et al. (2004) reported that in a *Pinus sylvestris*-dominated forest in Vienansalo, wildfire killed all trees only on 2.5% of the entire burned area and usually left most of the large trees alive.

This type of stand succession after fire could be classified as cohort dynamics (Angelstam and Kuuluvainen 2004). Cohort dynamics results in multilayered canopy structures (Linder et al. 1997, Ericsson et al. 2005, II in Vienansalo). For example, in northern Sweden multilayered *Pinus sylvestris*-dominated stands, with old individuals and characteristics such as large amounts of standing and fallen deadwood, were still common in the 19th century landscape (Östlund et al. 1997, Ericsson et al. 2005). Evidently, the potential impacts of fire suppression must be taken into account when reference stand structures in forest restoration are defined (II).

4.3. Defining reference stand structures for forest restoration (I, II)

This study showed that in defining reference stand structures for forest restoration their natural range of variability should be given special focus (Fig. 9, Moore 1999). Natural variability means ecological conditions with spatial and temporal variation, which are only "relatively unaffected by people" (Landers et al. 1999). Thus, in the present study where natural variability is defined as a target for forest restoration, only the near-natural stands in the Russian wilderness could be qualified as reference stands for forest restoration due to their low human impact (I, II, Fig. 1).

However, human-impacted old-growth stands could also have structures that are crucial for biodiversity and could act as reference structures for forest restoration (Fig. 1, Fig. 9). For example, stands selectively logged in the past in Vienansalo did not significantly differ in stand structures compared with near-natural stands (II). However, there could be differences in species composition between natural and selectively logged stands, due to differing deadwood compositions (Sippola et al. 2001, Rouvinen et al. 2002a). But the deadwood composition will change during succession in selectively logged stands because these stands will attain more old-growth characteristics with time (Deal et al. 2002). In addition, although the near-natural stands in the Häme area have stand structures that originated partly from previous indirect and direct human impact (see 4.2), these stands still have large-diameter living trees that are important for epiphytic species and later in succession for the saproxylic species that need large-diameter deadwood as a habitat (Siitonen and Saaristo 2002). Thus in defining the target for forest restoration, both reference structures and natural variability of reference stand structures can be considered (Fig. 1).

In defining reference stand structures, the quality of the reference stands or targets for restoration can be evaluated in terms of their naturalness or historical background (Stanturf 2005). Firstly, near-natural forests may have existed without human impact for hundreds of years as a result of their isolated location. For that reason, natural stand structures were studied in Paanajärvi, one of the largest natural forest areas in Fennoscandia (I). Secondly, near-natural stands with such characteristics as resulting from variable intensity and duration of human influence were studied (II). This examination of the reference structures for forest restoration, in which both natural variability of natural stands and historical human land use and degradation of stand structures were studied, shows how different stand structural characteristics could be defined, based on the successional stages and disturbance history.

The late-successional stages were studied as a reference for forest restoration (I, II), whereas early-successional stages were studied in the restoration experiment (III, IV). The natural stages of early-succession were studied because we lacked examples of natural stand structures in the early successional stages after disturbances, such as forest fires (e.g. Uotila et al. 2001, Hyvärinen et al. 2005). The reintroduction of natural disturbance factors and the rehabilitation of near-natural old-growth forest structures have been the targets of forest restoration in Fennoscandia (Tukia 2000, Kouki et al. 2001, Kuuluvainen 2002, Nordlind and Östlund 2003, Kuuluvainen et al. 2005). Due to the lack of knowledge of the natural variability in forest structures as a whole, the late-successional stages were studied as reference stands.

Forest naturalness is not a clear concept and the definition is highly variable, due to limited understanding of the natural succession of boreal forests after long-lasting human impacts (Östlund 1993, Uotila 2001). Although humans have not played a long-lasting role in the Paanajärvi wilderness, they evidently have had some influence on stand structures in that area (Wallenius et al. 2004). For example, the youngest stands studied (110-140 years) showed traces of historical use resulting from slash-and-burn cultivation (Wallenius et al. 2004). These stands were mixed *Populus tremula*, *Betula* and *Picea abies* stands with a high quantity of standing and fallen deadwood (I). Deadwood offers important substrates for species diversity (Siitonen 2001), and therefore this type of stand structure is important despite previous human impacts. This historical land use, when it was minimal, was included in the concept of natural variability (historical range of variability) (Landers et al. 1999). Nevertheless, these stands could be useful as reference stands for forest restoration because they offer close-to-nature forest structures with natural variability in their stand characteristics (see 4.1 & 4.2).

We showed that small protected forest fragments in Finland may not always serve as valid natural reference areas for forest restoration. Human impact has lasted longest in southern Finland, where only 1.2% of the forested area is protected statutority (Finnish…2005), humans have made effective use of the land, and managed fragmented forests dominate the landscape (Kouki et al. 2001). Thus, the forest structure in the small 700-4100-ha national parks in southern Finland (Kansallispuistot 1993) is far from any natural stage, due to anthropogenic influence such as firewood collection and past forest grazing by cattle (Östlund et al. 1997, Tasanen 2004). These influences, together with fire suppression, have resulted in low volumes of deciduous trees (II) and are posing a threat for biodiversity (Kouki et al. 2004, Uotila 2004). Moreover, protected areas have not had natural fire disturbance dynamics (II). The lack of fires in protected forests of Finland (Uotila et al. 2001, 2002) has increased the proportion of *Picea abies* and decreased the deciduous representation in the total volume (II). This resulted from the previous attitude that protected areas were 'natural stands' by definition, such that the target has been to preserve these untouched natural characteristics (Kansallispuistokomitea 1976, Borg and Ormio 1978) and to maintain the image of a 'primeval forest' (Kalliola 1956). Although protected areas are important habitats for many species, they probably can not serve as natural references due to the lack of disturbances and the prolonged human impact.

Near-natural stands, even when they are of the same age and have the same dominant species, can evidently vary widely in their structures due to nonconverging successional pathways as well as past and recent disturbances. In the present study, only a narrow part of the natural variability in stand structures could be reported, because the data are restricted to two studies of the reference stages (a total of 136 forest stands) in which both *Picea abies*- and *Pinus sylvestris*-dominated stands are represented; thus care should be used in interpreting and extrapolating the results (I, II).

Recently, it was shown that the majority of the protected areas with near-natural characteristics in Finland are old managed forests in which the stand structures are even-sized (Restoration … 2003, Kuuluvainen et al. 2005). Accordingly, restoration activities have been initiated in protected areas. Reference stand structures (I, II) could be classified as targets of forest restoration, but in defining reference stands the variability in near-natural stands should be considered.

4.4. Human impact on managed forests

The structure of mature/old managed *Picea abies* and *Pinus sylvestris* stands (II, III) was different than that of near-natural stands in Finland and Russia (I, II). Managed stands lacked large-diameter living trees, especially deciduous trees (II, III). Large trees were much less common in managed stands than in near-natural stands and in stands selectively logged in the past (II). Linder and Östlund (1998) also stated that in central Sweden the number of large trees with DBH > 33 cm has been reduced by about 90% since the late 1800s; in managed forests there was only one tree per hectare with DBH > 40 cm. The scarcity of large trees in managed forests is evidently due to past selective logging and more recent silvicultural measures aimed at homogenizing tree size distributions and shortening rotation ages. In near-natural forests, on the other hand, large *Pinus sylvestris* often survive fire disturbance due to their heat-insulating bark, thus forming a typical feature of *Pinus*-dominated forests (Sirén 1973, Agee 1998, Linder and Östlund 1998, Engelmark 1999, Kuuluvainen et al. 2002).

The pooled tree diameter distribution of *Picea abies*-dominated stands was bimodal in the managed stands studied (II, III) because thinning of *Pinus sylvestris*, which is practised as a standard silvicultural procedure, has modified the stand structure and decreased stand volume (Vuokila 1984, Östlund 1993). Thinning has also decreased the variability in tree diameters by favouring dominant trees of good timber quality and by removing both the largest and smallest tree individuals from stands (Nyyssönen 1950, Uuttera et al. 1996, Uotila et al. 2001, Rouvinen and Kuuluvainen 2005).

In addition, tree species composition is not as diverse in the mature managed *Picea*- and *Pinus sylvestris*-dominated stands in Finland as in the old near-natural successional stages in Russia (I, II, III). The proportion of *Pinus* in the total wood volume has increased in managed stands compared with near-natural stands and in stands selectively logged in the past (II). This is evidently due to silvicultural thinnings in managed stands, which have favoured *Pinus sylvestris* and removed *Picea abies* and deciduous trees (e.g. Linder and Östlund 1998, Maltamo et al. 2000). Finnish forest inventories show that, an average of 40% of stands have structures in which only one tree species predominates (volume share of dominant tree species > 95%) in Finland (Finnish… 2005). *Pinus sylvestris* is the dominant tree genus in all forest stands (65%), while deciduous species predominate in only 9% of forests (Finnish… 2005). This small proportion of deciduous trees in the managed landscape is most pronounced in the oldest age-classes. In Sweden, 80-100-year-old managed stands had 4% deciduous trees (Svensson 1980) in contrast to stands in Komi, northwestern Russia, where the proportion of deciduous trees during the first 100 years ranged from 30% to 70% (Angelstam and Arnold 1993). Our results are consistent with those of Uotila et al. (2001), reporting a lack of deciduous trees in managed stands.

The structural diversity characteristics of living trees were less common in managed stands than in near-natural stands and those selectively logged in the past (II). In managed stands there were only a few large-diameter trees with damaged trunks, due to thinnings and the young age of the trees. Andersson and Östlund (2004) reported that modern forest management in northern Sweden has decreased the occurrence of old conifer trees (over 160 years) by as much as one third since the 1920s. In near-natural stands and selectively logged stands, dead or broken treetops and damaged trunks were the most common type of structural characteristic (II). These structural diversity characteristics of old living trees provide habitats for specific old-growth organisms (Bond and Franklin 2002), such as saproxylic beetles (Siitonen and Saaristo 2002). In addition, there were more fire-scarred trees in the near-natural and selectively logged stands than in managed forests (II). Although fire scars are partly 'cultural legacies' from human-ignited fires (e.g. Wallenius et al. 2004), the lack of these characteristics is concrete evidence of the decrease in forest fires.

There was also a lack of deadwood types and different decay stages in the *Picea abies*-dominated managed stands in Häme (III) compared with near-natural stands in Paanajärvi, Russia (I). Naturally, wind disturbances create deadwood in forests, but the amount of deadwood was reduced because dead and fallen trees were collected for firewood and because of the fear of insect damage in managed stands (Anon. 1991). Mechanical site preparation also decreased the volume of fallen wood, because it breaks down logs (Vanha-Majamaa and Jalonen 2001, Hautala et al. 2004). Some studies suggested that more than 20 m^3 ha^{-1} of deadwood in managed stands is needed for threatened species conservation (Siitonen 2001, Penttilä 2004, Hyvärinen et al. 2005). Otherwise, the extinction of species will be inevitable in managed forest landscapes if forest restoration and conservation are not implemented (Hanski 2000, Kuuluvainen et al. 2002).

The present study showed that intrastand biotope variation and stand structures before restoration affect the results of restoration (III); the stand structures differed especially, between the two biotopes (upland and paludified) before the restorative treatments (III). The pretreatment diameter distribution was bimodal in the upland biotope, due to past thinnings, while in the paludified biotope the diameter distribution typically was negatively sloped (III). This resulted from the more abundant understorey trees in the paludified biotope (Sarkkola et al. 2003). The volume of deadwood was higher in the upland biotope than in the paludified biotope. This was in contrast to the finding of Jalonen and Vanha-Majamaa (2001) who reported that in paludified biotopes in mesic *Picea abies* stands, the volume of deadwood was higher than the average in managed stands. In the experimental study stands, the recent thinning activity increased the volume of deadwood in the upland biotope in the form of stumps and abundant logging waste such as crown tops (III). The occurrence of deadwood before restoration is of an ecological importance for saproxylic species during the succession of dead wood after restorative treatments. Thus it appears that the initial stage of the forest to be restored plays an important role in the restoration result. Previous forest management and disturbances should also be taken into consideration in the restoration planning. For example, the windfall in the autumn 2001 brought fresh deadwood to some of the selected experimental stands, which increased the volume of deadwood.

Managed *Picea*-dominated stands have low amounts of deadwood-related microsites (IV). A similar trend was also reported from *Pinus sylvestris*-dominated managed sites in southern Finland (Kuuluvainen and Laiho 2004). The present study also showed that in paludified biotopes there were more mounds and depression microsites than in upland biotopes in managed forests (IV). In contrast, the deadwood and higher proportions of mounds and depressions in near-natural old-growth forests typically occurred in the oldest age-classes (I). Hörnberg et al. (1997) reported that hummocks, which are often overgrown remnants of deadwood, typically occur in old-growth swamp forests. A long history of forest utilization in Fennoscandia, where forest stands are generally thinned 1-2 times during a rotation period, has led to remarkably low amounts of CWD (Siitonen 2001) and a decrease in microsite variability.

The rehabilitation of stand structures is challenging, because some near-natural stand structures such as large diameters of living and dead trees and variable deadwood structures, need lengthy periods to develop. All the reference ecosystems studied were old-growth, late-successional stands (I, II), because we do not have near-natural early-successional stages in the Fennoscandian managed landscape (e.g. Uotila 2004). Since our second target was to evaluate the immediate effects after forest restoration, we constructed a restoration experiment in southern Finland (III, IV).

4.5. Immediate effects of forest restoration in mature managed *Picea abies* stands (III, IV)

The restoration treatments studied were 'hybrid' in nature because the targets were both ecological and economical. The experiment was based on the *Picea abies* shelterwood logging method. In each cutting treatment, more than 100 m^3 ha^{-1} of wood (III: Table 1) was harvested for industrial purposes and 50 m^3 ha^{-1} was left as standing wood retention; the volume of fallen wood created varied among treatments. As a result of the logging treatments, the managed *Picea*-dominated stand structure changed immediately after forest restoration; the diameter distribution changed towards an inverse 'J-shape' and the canopy became more open (III: Fig. 7). These structural features were the goal because old-growth *Picea* stands have an uneven tree size distribution due to small-scale tree mortality and regeneration, i.e. gap dynamics (Sirén 1955, Kuuluvainen et al. 1998, Kneeshaw and Gauthier 2003). Historical partial cuttings were studied in Fennoscandia (e.g. Lundqvist 1993) in *Picea abies* stands where cuttings were done more than 30 years ago and the focus has been on the regeneration result. In Alaska, Deal et al. (2002) reported that it is possible to maintain old-growth characteristics in stand structure using partial cuttings, based on an evaluation of 12-96-year-old selective cuttings in western hemlock-spruce *Tsuga heterophylla* (Raf.) Sarg. -Sitka spruce *Picea sitchensis* (Bong.) Carr. stands. Their results were similar to those of II, in which the similarities between near-natural and selectively logged stands were also reported (see 4.2). The open stand structure with an abundance of deadwood that was created by the restorative treatments (III) resembles the early postdisturbance stage of natural forest development, a habitat type that is practically absent in managed forest landscapes (Uotila et al. 2001). This type of habitat, where the volume of deadwood is high (more than 20 m^3 ha^{-1}), is now known to be preferred by many species, many of which were previously considered to be strict old-growth specialists (Martikainen et al. 2000, Kouki et al. 2001, Similä et al. 2002, Hyvärinen et al. 2005). The immediate impact of forest restoration with partial cutting and deadwood creation, without fire treatment, generated different early-successional starting points with high volumes of deadwood (Siitonen 2001, Fig. 9) and the microsites related to it (IV) that are characteristic of early- and late-successional forest stages (Hörnberg et al. 1997, I).

The use of partial cuttings and fire mimics catastrophic fire disturbance (III, IV). The fire treatment increased the volume of standing deadwood, but there were differences between the CWD treatments. The live tree mortality was highest with the high-CWD (60 m^3 ha^{-1}) treatments, because the flames frequently climbed up to the canopy, using fallen trees as a 'ladder', thus killing the trees. In addition, heavy fuel loading would also generate greater fire intensity, which can cause the canopy to ignite directly without ladder fuels. With high levels of CWD, the fallen trees together with the number of small-diameter trees also promoted the spread of fire to the paludified biotopes, causing high tree mortality. The increase in the total amount of deadwood was highest in paludified biotopes with the high-CWD treatment, in which the total volume of dead wood was as high as 112 m^3 ha^{-1}. Similarly, high amounts of deadwood were reported for forests in the early stages of succession after fire (Uotila et al. 2001), as well as for forests in late-successional stages (Siitonen 2001, Fig. 9). However, since the number of standing trees was low after harvesting, the fire did not spread through the canopy, but instead several individual trees were torched. In contrast, with the low- and intermediate- CWD (5 and 30 m^3 ha^{-1}) treatments, the fire remained on the surface and caused more mortality in the upland than in the paludified biotope. Fire rarely climbed to the crown of standing trees and tree mortality occurred mainly because *Picea abies* has thin bark, which cannot prevent fire injuries, and an easily damaged superficial root system (Uggla 1958). Live tree mortality was lowest in the burned reference stand because fire propagated through the stand very slowly and left many unburned spots, especially in the paludified biotopes (III). These results suggest that the creation of fallen wood is needed in restoration with fire when the targets are intensive burning and high deadwood volume. It is also possible to regulate the severity of restoration burnings through the amount of CWD.

Restoration using fire changed the previous stand structure most effectively compared with treatments without fire (III), because it increased the volume of deadwood. In previously managed stands the formation of deadwood by natural succession may require lengthy periods, due to the generally healthy condition and appropriate growing space of trees that result from silvicultural thinnings. Moreover, dead trees can remain standing for years and the decomposition of fallen *Picea abies* logs can require as long as 100 years in Norway (Storaunet and Rolstad 2002). Thus creating fallen trees is essential to restoration. The importance of deadwood as a habitat for many species is well known (Jonsson and Kruys 2001, Siitonen 2001, Similä et al. 2002). These restoration treatments with partial cutting and fire will also probably increase tree regeneration after fire, because the shade from dead trees promotes germination and the treatments favour the expansion of even ground microsites with free growing space for seedling establishment (Vanha-Majamaa et al. 1996, Lampainen et al. 2004, IV).

Regeneration was most abundant in the paludified biotopes after the intermediate- CWD treatments (30 m^3 ha^{-1}) and fire (IV); thus the occurrence of paludified patches in the rehabilitation areas of managed stands may beneficially affect the constitution of new tree cohorts. The stand structure is naturally more uneven and regeneration more effective in the paludified areas, despite drainage or thinning (Sarkkola et al. 2003). In addition, paludified biotopes can be important refugia for some fire-sensitive species (Hörnberg et al. 1997) and act as sources of species dispersal after fire, since *Picea abies* forests and mire patches typically occur as intermingled fine-scale mosaics under the conditions countered in Fennoscandia (Jalonen and Vanha-Majamaa 2001, Wallenius et al. 2004). These small patches of paludified biotope, interspersed within a forest in drier upland biotopes, can be important for biodiversity despite their limited size, both as key habitat and refugia, at least during low- or moderate-severity fire disturbance events (Hörnberg et al. 1997, Vanha-Majamaa and Jalonen 2001, III). However, even paludified patches can clearly burn in high-severity fires, but this may occur rarely (Ohlson et al. 1997, Pitkänen et al. 2003). Traditionally, the high level of biodiversity in paludified forest biotopes has been related to the lack of disturbance, i.e. long continuity (Zackrisson 1977). However, examination of the long-term history of *Picea abies* swamp forests with high levels of biodiversity has often revealed a history of forest fires or human utilization (Hörnberg et al. 1995, Ohlson et al. 1997). In fact, it was shown that fungi species diversity in moist swamp forests does not require a very long time since disturbance, but is better correlated with the amount and high diversity of deadwood (Ohlson et al. 1997). This suggests that enhancing natural habitat structures by active restoration has great potential for biodiversity conservation within relatively short periods of time and does not require hundreds of years of succession.

The technique of restoration impacts the restoration result. We used a prescribed burning technique, also called the 'horseshoe' technique (Lemberg and Puttonen 2003, III, IV), where the ignition forms a circular burning. This pattern may cause higher tree mortality than is the case with wildfires (Saari 1923, Granström 2001). In addition, in using this technique, fire may have spread to the paludified biotopes more effectively than what can be assumed to occur with wildfires. However, with this prescribed burning technique, which has been used in forestry for silvicultural site preparation for regeneration, the goal is to have as secure and even a burn as possible (Lemberg and Puttonen 2003). Nevertheless, in all our burning treatments, patches were left unburned, and the paludified biotopes contributed most to the heterogeneity of the burning mosaic.

It is possible to develop more site-adjusted or biotope-focused restoration methods. One essential task in forest restoration is to increase and maintain biodiversity in forest stands by increasing the heterogeneity in patterns and processes (Halpern and Spies 1995, Kuuluvainen 2002, Spies 2004). However, the forest structures varied widely between within-stand biotopes (III, IV), thus maintaining a variety of structures. Oliver and O´Hara (2005) emphasized that all stands in the landscape must be taken into account in restoration, such that an appropriate mix of structures is created over time, representing the natural range of variation in stand structures. Our results indicate that, in addition to among-stand variability, within-stand small-scale biotope variability should also be taken into account in forest restoration (Fig. 9, III, IV).

The variability of living tree and deadwood volumes was high within reference and managed stands (Fig. 9) e.g. due to the variable disturbance histories and different vegetation types. Despite these differences the volume of deadwood was high in near-natural and selectively logged stands. After restoration treatments the stand structure was altered differently due to the different restoration treatments, but the volume of deadwood increased which rehabilitated more near-natural characteristics to managed forests. In the initial stage of the degraded managed stands, e.g. the age of the dominant cohort (Fig. 1, Fig. 9) is an important factor for the rehabilitation because without big-diameter trees the dead wood formation is limited.

Restorative treatments created different structures by mimicking natural disturbances (III, IV, Fig. 1, Fig. 9). Near-natural early-successional stages with open habitat and high volumes of dead-wood are especially needed (Similä et al. 2002, Hyvärinen et al. 2005). These active restorative treatments with deadwood creation and/or the use of fire add immediately to such stand structures, which may be profitable for biodiversity conservation. This type of restoration may be recommended in areas that have managed mature stand structures, e.g. in protected areas or buffer zones of protected areas (also Hyvärinen et al. 2005). However, ‘passive restoration’ through the conservation of individual old trees and other reference stand structures (see 4.1 & 4.2) can also be considered as a restoration activity.

5. CONCLUSIONS

Both old-growth *Picea abies* forests and near-natural old *Pinus sylvestris* forests exhibited a wide variety of late-successional stages that have specific structural and habitat attributes (I, II). This demonstrates that near-natural stand structures are naturally characterized by high variability in structural characteristics, caused by different disturbance histories and successional status, or possibly by past anthropogenic impact. This emphasizes that there is no single reference stage or stand structure for restoration but restoration should aim at creating a range of stand structures as part of the natural variability found in naturally dynamic boreal forest landscapes.

The results from the near-natural stands in Finland compared with those from Vienansalo indicate that it may be questionable to use small protected forest fragments surrounded by intensively managed forest as ‘natural benchmarks’ in forest restoration and nature conservation. This is because previous human land use and the lack of natural disturbances (such as fire) in the protected forests have influenced the formation of stand structures. This has caused structural and compositional changes in the protected fragments in southern Finland, e.g. the high proportion of *Picea abies* and the low volume of deciduous trees in old *Pinus sylvestris*-dominated stands (II).

In managed forests human impact in the form of forest utilization and fire exclusion has strongly modified and reduced the structural complexity. For example, large-diameter coniferous and deciduous trees, and a wide diversity of decay stages and types of deadwood, which existed in near-natural reference stands, were lacking in the managed stands. The natural variability was high in reference stand structures, due to cycles of disturbances and succession. The recreation of variable stand structures is needed, but stand structural variability as related to vegetation type and land-use history should be taken into account. For example, deadwood occurrence and future development, and the potential of deciduous tree establishment of the stand must be evaluated before the restoration treatments.

Different types of restoration treatment caused a variety of immediate restorative effects in mature managed *Picea abies* stands. Partial cutting treatments with deadwood creation, with and without fire, could be used to create structures that mimic natural early-successional stages after various disturbances, even when a significant portion of the wood volume is harvested. In addition, the burned reference treatments without cuttings added to the treatment variability, because the burning result was the most uneven (and left a burnt and unburnt mosaic). The paludified patches also sustained the living and dead tree continuum in the area, because small paludified patches within stands created a small-scale mosaic of burned and unburned patches. The restoration experiment showed that a range of within- and between- stand structures can be created by varying the deadwood retention level and by using or not using fire (III, IV).

Since natural forest landscapes contain both old-growth and early-successional forests, landscape-level restoration should include active restoration to mimic natural disturbances and consequent long-lasting succession. Restoration should be based on knowledge of natural disturbances and successional processes.

REFERENCES

Agee, J. K. 1998. Fire and pine ecosystems. In: Richardson, D. M. (ed.). Ecology and biogeography of Pinus. Cambridge University Press, Cambridge. pp. 193-218.

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in north-western Europe. Annales Botanici Fennici 5: 169-211.

Andersson, R. & Östlund, L. 2004. Spatial patterns, density changes and implications on biodiversity for trees in the boreal landscape of northern Sweden. Biological Conservation 118:443-453.

Angelstam, P. K. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. Journal of Vegetation Science 9: 593-602.

–, & Arnold, G.W. 1993. Contrasting roles of remnants in old and newly impacted landscapes: lessons for ecosystem reconstruction, In Saunders, D.A., Hobbs, R.J., Ehrlich, P.R. Nature conservation 3: Reconstruction of fragmented ecosystems. pp. 109-125. Surrey Beatty & Sons.

–, & Petterson, B. 1997. Principles of present Swedish forest biodiversity management: In: Hansson, L. (ed.) Boreal ecosystems and landscapes – structures, functions and conservation of biodiversity. Ecolological Bullulletins 46: 191-203.

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

Anon. 1991. Laki metsän sieni- ja hyönteistuhojen torjunnasta. Suomen säädöskokoelma 263/1991: 566-568 (in Finnish).

Atlas Karelskoy ASSR. 1989. Glavnoe upravlenie geogezii I kartografii pri solete ministrov SSSR. Moscow (in Russian).

Atlas of Finland. 1992. Folio 123-126. Geology. National Board of Survey and Geographical Society of Finland, Helsinki.

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

Axelsson, A.-L., Östlund, L. & Hellberg, E. 2002. Changes in mixed deciduous forests of boreal Sweden 1866-1999 based on interpretation of historical records. Landscape Ecology 17: 403-418.

Bergeron, Y., Leduc, A., Harvey, B., Gauthier, S., 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. Silva Fennica 36: 81-96.

Bond, B. J. & Franklin, J. F. 2002. Aging in Pacific Northwest forests: a selection of recent research. Tree Physiology. 22: 73-76.

Borg, P & Ormio, H. 1978. Perustiedot kansallispuistoista. Ihanteet ja käytäntö. WSOY Porvoo. 113 pp.

Bradshaw, A. D. 1987. The reclamation of derelict land and ecology of ecosystems. In Jordan, W.R., Gilpin, M.E., Aber, J.D., (eds.) Restoration Ecology. Cambidge University Press. Cambridge, U.K. pp. 53-74.

–, 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, U.K. pp. 8-14.

Bradshaw, R. H. W. 1993. Tree species dynamics and disturbance in three Swedish boreal forest stands during the last two thousand years. Journal of Vegetation Science 4:759-764.

Burton, P., Messier, C., Smith, D. W. & Adamovicz, W.L. (eds.). 2003. Toward sustainable management of the boreal forest. NRC Research Press, Ottawa, Ontario, Canada.

Cairns, J. Jr. (ed.) 1980. The recovery process in damaged ecosystems, Annales Arborescens Science, Ann Arbor, Michigan, 167 pp.

Cajander, A. K. 1926. The theory of forest types. Acta Forestalia Fennica 29: 1-108.

Carey, A.B., 2003. Biocomplexity and restoration of biodiversity in temperate coniferous

forest: inducing spatial heterogeneity with variable-density thinning. Forestry 76 (2): 127-136
Clements, F. E. 1916. Plant succession: An analysis of the development of vegetation.Carnegie Institute, Washington, D.C., 512 pp.
Clewell, A., Ricger, J., Munro, J. (eds.) 2005. Guidelines for developing and managing ecological restoration projects, 2nd edition. www.ser.org & Tucon: Society for Ecological Restoration International.
Deal, R. L. 2002. The effects of partial cutting on stand structure and growth of westernhemlock-Sitka spruce stands in southeast Alaska. Forest Ecology and Management 159:173-186.
De Grandpré, L., Morissette, J. & Guathier, S. 2000. Long-term post-fire changes in the northeastern boreal forest of Quebec. Journal of Vegetation Science 11: 791-800.
Dobson, A.P., Bradshaw, A.D. & Baker, A.J.M. 1997. Hopes for future: Restoration ecology and conservation biology. Science 277:515-522.
Drobyshev, I., Niklasson, M., Angelstam, P., & Majewski, P. 2004. Testing for anthropogenic influence on fire regime for a 600-year period in the Jaksha area, Komi Republic, East European Russia. Canadian Journal of Forest Research 34: 2027-2036.
Engelmark, O. 1999. Boreal forest disturbances. In: Walker, L. R. (ed.). Ecosystems of disturbed ground. Ecosystems of the world 16. Elsevier, Amsterdam, pp. 161-186.
Ericsson, T. S., Berglund, H. & Östlund, L. 2005. History and forest biodiversity of woodland key habitats in south boreal Sweden. Biological Conservation 122: 289-303.
Ervasti, S. 1993. Autonomisen ajan Paanajärvi. In Koutamieni, L. (ed). Paanajärven kansallispuisto. Koillissanomien Kirjapaino, Kuusamo. pp. 109-114.
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, London. pp. 252-325.
–, Ehnström, B., Ericson, L. & Sjöberg, K. 1997. Boreal forests. Ecological Bulletins 46: 16-47.
Finnish Statistical Yearbook of Forestry 2005. Peltola, A. (ed). Finnish Forest Research Institute. Helsinki.
Franklin, J. F., Species, T. A., Van Pelt, R., Carey, A. B., Thornburgh, D. A., Rae Berg, D., 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.
Fries, C., Johnsson, O., Petterson, B. & Simonsson, P. 1997. Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. Forest Ecology and Management 94: 89-103.
Gandhi, K. J.K., Spence, J. R., Langor, D., W. & Morgantini, L., E., 2001. Fire residuals as habitat reserves for epigaeic beetles (Coleoptera: Carabidae and Staphylinidae). Biological Conservation 102 (2): 131-141.
–, Spence, J. R., Langor, D., W., Morgantini, L., E. & Cryer, K. J. 2004. Harvest retention patches are insufficient as stand analogues of fire residuals for litter-dwelling beetles in norther coniferous forests. Canadian Journal of Forest Research 34:1319-1331.
Gayton, D. V. 2001. Ground work: Basic concepts of Ecological Restoration in British Columbia. SIFERP Series 3. Southern Interior Forest Extension and ResearchPartnership and SER-BC.
Glenn-Lewin, D. C. & van der Maarel, E. 1992. Patterns and processes of vegetation dynamics. In Glenn-Lewin, D. C., Peet, R. K. & Veblen, T. T. (eds.). Plant succession, theory and prediction. pp. 11-59. Chapman & Hall.
Granström, A. 2001. Fire management for Biodiversity in the European boreal forest. Scandinavian Journal of Forest Research 3:62-69.
Haapanen, A. & Siitonen, P. 1978. Kulojen esiintyminen Ulvinsalon luonnonpuistossa. Silva Fennica 12(3): 187-200.

Haila, Y. 1994. Preserving ecological diversity in boreal forests: ecological background, research, and management. Annales Zoologi Fennici 31: 203-217.
Hanski, I. 2000. Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. Annales Zoologi Fennici 37: 271-280.
Harmon, M.E., Franklin, J.F. 1989. Tree seedlings on logs in Picea-Tsuga forests of Oregon and Washington. Ecology 70: 48-59.
Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Advantage Ecological Research. 15: 133-302.
Harris, J. A. & Hobbs, R. J. 2001. Clinical practice for ecosystem health: the role of ecological restoration. Ecosystem Health vol. 7(4): 195-202.
Hautala, H., Jalonen, J., Laaka-Lindberg, S. & Vanha-Majamaa, I. 2004. Impacts of retention felling on coarse wood debris (CWD) in mature boreal spruce forests in Finland. Biological Conservation 13: 1541-1554.
Heikinheimo, O. 1915. Kaskiviljelyn vaikutus Suomen metsiin. [The influence of slash-and-burn cultivation on forests in Finland]. 260 pp (in Finnish).
Helms, J.A. 2004. Old-growth what is it? Journal of Forestry, April/May 8-12.
Hobbs, R.J. & Mooney, H. A. 1993. Restoration ecology and invasions, In Saunders, D.A., Hobbs, R.J., Ehrlich, P.R. (eds.) Nature conservation 3: Reconstruction of fragmented ecosystems. pp. 127-133. Surrey Beatty & Sons.
Hörnberg, G., Ohlson, M. & Zackrisson, O. 1995. Stand dynamics, regeneration patternsand long-term continuity in boreal old-growth Picea abies swamp-forests. Journal of Vegetation Science 6: 291-298.
–, Ohlson, M. & Zackrisson, O. 1997. Influence of bryophytes and microrelief conditions on Picea abies seed regeneration patterns in boreal old-growth swamp forest. Canadian Journal of Forest Research 27: 1015-1023.
Hyvärinen, E., Kouki, J., Martikainen, P. & Lappalainen, H. 2005. Short-term effects of controlled burning and green-tree retention on beetle (Coleoptera) assemblages in managed boreal forests. Forest Ecology and Management 212(1-3):315-332.
Jain, T.B. & Graham, R. T. 2005. Restoring dry and moist forests of the inland northwestern U. S. In Stanturf, J. A. & Madsen, P. (eds.). Restoration of boreal and temperate forests pp. 463-480. ISBN 1-56670-635-1.
Jalonen, J. & Vanha-Majamaa, I. 2001. Immediate effect of four different felling method on mature boreal spruce forest understorey vegetation in southern Finland. Forest Ecology and Management 146: 25-34.
Jantunen, J., Saarinen, K., Saarnio, S. & Marttila, O. 2002. Stand structure in pine, spruce and deciduous forests: a comparison between Finnish and Russian Karelia. Scandinavian Journal of Forest Research 17: 53-61.
Jonsson, B. G. 2000. Patterns of availability of coarse woody debris in a boreal old-growth Picea abies forests. Journal of Vegetation Science 11: 51-56.
–, & Kruys, N. (eds.) 2001. Ecology of wood debris in boreal forests. Ecological Bulletins 49.
Jordan, W.R., Giplin, M. E. & Aber, J.D. 1987. Restoration ecology: Ecological restoration as a technique for basic research. In Restoration Ecology, eds. W.R. Jordan, M.E. Giplin, & J.D. Aber, pp. 3-21. Cambridge University Press.
Kalela, A. 1961. Waldvegetationszonen Finnlands und ihre Klimatischen Paralleltypen. Arch Soc. Zool. Bot. Fenn. 16: 65-83 (in German).
Kalliola, R. 1956. Luonnonsuojelu. In: Jalava, M., Lihtonen, V., Heiskanen, V. & Sippola,H. (eds.). Metsäkirja 1. Oy Länsi-Suomen kirjapaino, Rauma. p. 597-608 (in Finnish).
Kansallispuistot 1993. Painatuskeskus, Helsinki. 78 pp. (in Finnish).
Kansallispuistokomitea 1976. kansallispuistokomitean mietintö. Komiteamietintö 1976:88.

Helsinki.
Kaufmann, M. R., Ryan, K. C., Fulé, P. Z., & Romme, W.H. 2005. Restoration of ponderosa pine forests in the interior western U.S. after logging, grazing, and fire suppression. In Stanturf, J. A. & Madsen, P. (eds.) Restoration of boreal and temperate forests 481-500 pp. ISBN 1-56670-635-1.
Keeley, J. E. & Stephenson, N. L. 2000. Restoring natural fire regimes to the Sierra Nevada in an era of global change. USDA Forest Service Proceedings RMRS-P-15: 255-265. Keränen, J. 1984. The settling of Kainuu. Studia historica Jyvskylensia 28. Keurusprint Oy, Keuruu (in Finnish with English summary).
Kneeshaw, D. & Gauthier, S. 2003. Old growth in the boreal forest: A dynamic perspective at the stand and landscape. Environmental Review 11: 1-16.
Kouki, J. 1994. Biodiversity in the Fennoscandian boreal forests: natural variation and itsmanagement. Annales Zoologici Fennici 31: 35-51.
–, 2002. Fire as a tool in restoring forest successional properties and biodiversity in managed and protected boreal forests in Finland. In Gardiner, E.S. and Breland, L.J (compiled). In Proceedings of the IUFRO Conference on Restoration of Boreal and Temperate Forests. Skov & Landskab Reports no. 11. Ministery of the Environment Danish Forest and Landscape Research Institute. 151-152.
–, Löfman, S., Martikainen, P., Rouvinen, S. & Uotila, A. 2001. Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. Scandinavian Journal of Forest Research, suppl. 3: 27-37.
–, Arnold, K. & Martikainen, P. 2004. Long-term persistence of aspen – a key host for many threatened species – is endangered in old-growth conservation areas in Finland. Journal for Nature Conservation 12: 41-52.
Kuuluvainen, T. 1994. Gap disturbance, ground microtopography, and the regenerationdynamics of boreal coniferous forests in Finland: a review. Annales Zoologi Fennici 31: 35-51.
–, T. 2002. Disturbance dynamics in boreal forests: Defining the ecological basis of restoration and management of biodiversity. Silva Fennica 36: 5-12.
–, Syrjänen, K. & Kalliola, R. 1998. Structure of a pristine Picea abies forest in northeastern Europe. Journal of Vegetation Science 9: 563-574.
–, Aapala, K., Ahlroth, P., Kuusinen, M., Lindholm, T., Sallantaus, T., Siitonen, J. & Tukia, H. 2002. Principles of ecological restoration of boreal forestedecosystems: Finland as an example. Silva Fennica 36: 409-422.
–, & Kalmari, R. 2003.Regeneration microsites on *Picea abies* seedlings in a windthow area of a boreal old-growth forest in southern Finland. Annales Botanici Fennici 40: 401-413.
–, T. & Laiho, R. 2004. Long-term forest utilization can decrease forest floor microhabitat diversity: evidence from boreal Fennoscandia. Canadian Journal of ForestReseach. 34: 303-309.
–, 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 285-298 pp. ISBN 1-56670-635-1.
Kuusinen, M. 1996. Epiphyte flora and diversity on basal trunks of six old-growth forest tree species in southern and middle boreal Finland. Lichenologist 28: 443-463.
Laasasenaho, J. 1982. Taper curve and volume function for pine, spruce and birch. Communicationes Instituti Forestalis Fenniae 108. Helsinki. 74 p.
Laine, J. & Vasander, H. 2005. Suotyypit ja niiden tunnistaminen. Metsäkirjat, Metsäkustannus Oy, Helsinki. 110 pp. (in Finnish).
Lampainen, J., Kuuluvainen, T., Wallenius, T. H., Karjalainen, L. & Vanha-Majamaa, I. 2004. Long-term forest structure and regeneration after wildfire in Russian Karelia. Journal of Vegetation Science 15: 245-256.

Landers, P.B., Morgan, P. & Swanson, F.J. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9(4): 1179-1188.
Lehtonen, H., Huttunen, P. & Zetterberg, P. 1996. Influence of man on forest fire frequency in North Karelia, Finland, as evidenced by fire scars on Scots pines. Annales Botanici Fennici 33: 257-263.
–, H. & Kolström, T. 2000. Forest fire history in Viena Karelia, Russia. Scandinavian Journal of Forest Research 15: 585-590.
Lemberg, T. & Puttonen, P. 2003. Kulottajan käsikirja. [Guide for prescribed burning]. Metsälehti kustannus, Vammalan kirjapaino Oy. pp. 113. ISBN 952-5118-41-X (in Finnish).
Lesieur, D., Gauthier, S. & Bergeron, Y. 2002. Fire frequency and vegetation dynamics for the south-central boreal forest of Quebec, Canada. Canadian Journal of Forest Research 32: 1996-2009.
Linder, P., Elfving, B. & Zackrisson, O. 1997. Stand structure and successional trends in virgin boreal forest reserves in Sweden. Forest Ecology and Management 98: 17-33.
–, P. 1998. Stand structure and successional trends in forest reserves in boreal Sweden. Doctoral dissertation, Acta Universitatis Agriculturae Sueciae, Silvestria 72. Swedish University of Agricultural Sciences, Umeå.
–, Jonsson, P. & Niklasson, M. 1998. Tree mortality after prescribed burning in an old-growth Scots pine forest in northern Sweden. Silva Fennica 32(4): 339-349.
–, & Östlund, L. 1998. Structural changes in three mid-boreal Swedish forest landscapes, 1885-1996. Biological Conservation 85: 9-19.
Lundqvist, L. 1993. Changes in the stand structure on permanent Picea abies plots managed with single-tree selection. Scandinavian Journal of Forest Research 8: 510-517.
Lähde, E., Laiho, O., Norokorpi, Y. & Saksa T. 1991. The structure of advanced virgin forests in Finland. Scandinavian Journal of Forest Research 6: 527-537.
Lämås, T. & Fries, C. 1995. Emergence of a biodiversity concept in Swedish forestrypolicy. Water, Air, Soil Pollutation 82: 57-66.
Magnuson, J.J., Regier, H. A., Christien, W. J., Sonzogi, W.C. 1980. To rehabilitate and restore Great Lakes ecosystems. In Cairns, J. (ed.) The recovery process in damaged ecosystems. Pp. 95-112. Michigan: Ann Arbor Science.
Majewski, P., Angelstam, P., Andren, H., Rosenberg, P., Swensson, J., Hermansson, J.-O. & Nilsson, S. G. 1995. Differences in the structure of the pine forest on deep sediment in pristine and managed taiga. Department of Wildlife Ecology, report 28, Swedish University of Agricultural Sciences, Uppsala.
Maltamo, M., Kangas, A., Uuttera, J., Torniainen, T. & Saramäki, J. 2000. Comparison of percentile based prediction methods and Weilbull distribution in describing the diameter distribution of heterogeneous Scots pine stands. Forest Ecology and Management 133: 263-274.
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: 199-209.
Minnich, R. A., Barbour, M.G, Burk, J. H. & Fernau, R. F. 1995. Sixty years of change in Californian conifer forests of the San Bernardino mountains. Conservation Biology 9: 902-914.
Moore, M.M., Covington, W.W. & Fulé, P. Z. 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. Ecological Applications 9(4): 1266-1277.
Muona, J. & Rutanen, I. 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forest. Annales Zoologici Fennici 31: 109-121.
Nakashizuka, T. 1989. Role of uprooting in composition and dynamics of an old-growth forest in Japan. Ecology 70: 1273-1278.
Niklasson, M & Granström, A. 2000. Numbers and sizes of fires: long-term spatially explicit

fire history in a Swedish boreal landscape. Ecology 81: 1484-1499.
Niemelä, J. 1997. Invertebrates and boreal forest management. Conservation Biology. 11: 601-610.
Nordlind, E. & Östlund, L. 2003. Retrospective comparative analysis as a tool for ecological restoration: a case study in a Swedish boreal forest. Forestry 76: 243-251.
Norokorpi, Y., Lähde, E., Laiho, O. & Saksa, T. 1994. Stand structure and diversity of virgin forests in Finland. Metsäntutkimuslaitoksen tiedonantoja 495: 54-89 (in Finnish with English summary).
Nyyssönen, A. 1950. Comparative observations on the structure and development of tended and natural pine stands. Silva Fennica 68: 1-48. (In Finnish with English summary).
Ohlson, M., Söderström, L., Hörnberg, G., Zackrisson, O. & Hermansson, J. 1997. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. Biological Conservation 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 31-59 pp. ISBN 1-56670-635-1.
Östlund, L. 1993. Exploitation and structural changes in the north Swedish boreal forest 1800-1992. Dissertation in Forest Vegetation Ecology 4. Swedish University of Agricultural Sciences Department of Forest Vegetation Ecology, Umeå.
–, Zackrisson, O. & Axelsson, A.-L. 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. Canadian Journal of Forest Research 27: 1198-1206.
Parker, V. T. & Pickett, S. T. A. 1997. Restoration as an ecosystem process: implications of the modern ecological paradigm. In Urbanska, K.M., Webb, N.R., Edward, P.J. (eds.). Restoration ecology and sustainable development. Cambridge University Press, Cambridge, UK. 397 p.
Pennanen, J. 2002. Forest age distribution under mixed-severity fire regimes – a simulation-based analysis for middle-boreal Fennoscandia. Silva Fennica 36: 213-231.
Penttilä, R. 2004. The impacts of forestry on polyporous fungi in boreal forests. PhD. Thesis. Department of Biological and Environmental Sciences Faculty of Biosciences University of Helsinki. ISBN 952-10-2095-4
Pham, A. T., de Grandpré, L., Gauthier, S. & Bergeron, Y. 2004. Gap dynamics and replacement patterns in gaps of the northern boreal forest of Quebec. Canadian Journal of Forest Research 34: 1-12.
Pitkänen, A. & Huttunen, P. 1999. A 1300-year forest fire history at a site in eastern Finland based on charcoal and pollen records in laminated lake sediment. Holocene 9: 559-567.
–, Huttunen, P., Jungner, H. & Tolonen, K. 2002. A 10 000 year local forest fire history in a dry heath forest site in eastern Finland, reconstructed from charcoal layer records of a small mire. Canadian Journal of Forest Research 32: 1875-1880. Pitkänen, A., Huttunen, P., Tolonen, K. & Jungner, H. 2003. Long-term fire frequency in the spruce-dominated forests of the Ulvinsalo strict nature reserve, Finland. Forest Ecology and Management 176: 305-319.
Pöllä, M. 1995. Changes in the ethnic composition of Viena Karelia in the 17th-19th centuries. Suomalaisen Kirjallisuuden Seuran Toimituksia 635: 1-353 (in Finnish withEnglish summary).
Pöntynen, V. 1929. Tutkimuksia kuusen esiintymisestä alikasvoksina Raja-Karjalanvaltionmailla. Acta Forestalia Fennica 35: 1-190. (In Finnish with German summary).Qinghong, L. & Hytteborn, H. 1991. Gap structure, disturbance and regeneration in primeval *Picea abies* forest. Journal of Vegetation Science 2: 391-402.
Rassi, P., Alanen, A., Kanerva, T. & Mannerkoski, I. (eds.). 2001. The 2000 red list of finnish species. The ministry of the environment, the II committee for the monitoring of threatened species in Finland. Helsinki. (In Finnish with English abstract)
Renvall, P. 1995. Community structure and dynamics of woodrotting Bacidiomycetes on

decomposing conifer trunks in northern Finland. Karstenia 35: 1-51.
Rouvinen, S., Kuuluvainen, T. & Karjalainen, L. 2002a. Coarse woody debris in old *Pinus sylvestris* dominated forests along a geographic and human impact gradient in boreal Fennoscandia. Canadian Journal of Forest Research 32: 2184-2200.
–, Kuuluvainen, T. & Siitonen, J. 2002b. Tree mortality in a Pinus sylvestris dominated boreal forest landscape in Vienansalo wilderness, eastern Fennoscandia. Silva Fennica 36: 127-145.
–, & Kuuluvainen, T. 2005. Tree diameter distributions in natural and managed old *Pinus sylvestris*-dominated forests. Forest Ecology and Management 208: 45-61.
Rowe, S. J. & Scotter, G.W. 1973. Fire in the boreal forest. Quat. Res. 3:444-464.
Rydgren, K., Hestmark, G. & Okland, R. H. 1998. Revegetation following experimental disturbance in a boreal old-growth Picea abies forest. Journal of Vegetation Science 9: 763-776.
Saari, E. 1923. Kuloista etupäässä Suomen valtionmetsiä silmällä pitäen. Tilastollinen tutkimus. [Forest fires in Finland with special reference to state forests. Statistical investigation.] Acta Forestalia Fennica 26: 1-155 (in Finnish with English summary).
Sarkkola, S., Alenius, V., Hökkä, H., Laiho, R., Päivänen, J. & Penttilä, T. 2003. Changesin structural inequality in Norway spruce stands on peatland sites after water-level drawdown. Can. J. For. Res. 33:222-231.
Sarvas, R. 1944. Tukkipuun harsintojen vaikutus Etelä-Suomen yksityismetsiin.Valtioneuvo ston kirjapaino. 255 pp. (in Finnish).
Shannon, C. E., 1948. The mathematical theory of communication. In: Shannon, C. E., Weaver, W. (eds.), The mathematical theory of communication. University of IllinoisPress, Urbana, pp. 29-125.
Siitonen, J. 1994. Decaying wood and saproxylic Coleoptera in two old spruce forests: a comparison based on two sampling methods. Annales Zoologi Fennici 31: 89-95.
–, Martikainen, P., Punttila, P. & Rauh. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. Forest Ecology and Management 128: 211-225.
–, 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49: 11-41.
–, & Saaristo, L. 2002. Habitat requirements and conservation of Pytho kolwensis, a beetle species of old-growth boreal forest. Biological Conservation 94: 211-220.
Similä, M., Kouki, J., Martikainen, P. & Uotila, A. 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. BiologicalConervation. 106, 19-27.
Sippola, A.-L., Siitonen, J. & Kallio R. 1998. Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish Lapland. Scandinavian Journal of Forest Research 13: 204-214.
–, Lehesvirta, T. & Renvall, P. 2001. Effects of selective logging on coarse woody debris and diversity of wood-inhabiting fungi in eastern Finland. Ecological 49: 243-254.
Sirén, G. 1955. The development of spruce forest on raw humus sites in northern Finland and its ecology. Acta Forestalia Fennica 62: 1-363.
–, 1973. Some remarks on fire ecology in Finnish forestry. Proceedings 13th Tall Timber Fire Ecology Conference. Tallahassee, Florida. pp. 191-208.
Smith, D. M., Larson, B. C., Kelty, M. J. & Ashton, P. Mark. S. 1997. The practice of silviculture. Applied forest ecology. John Wiley & Sons, Inc. USA. pp. 537.
Soininen, A. M. 1957. Erämaiden asuttaminen. In: Hämeen historia II. (ed.). Jutikkala, E., Aaltonen, E., Kuusanmäki, L. & Seppälä, F. Arvo A. Karisto Oy:n kirjapaino, Hämeenlinna. pp. 5-24 (in Finnish).
Spies, T.A., 2004. Ecological concepts and diversity of old-growth forests. Journal ofForestry, April/May 14-20 pp.
Stanturf. J.A. 2005. What is forest restoration? In. restoration of boreal and temperate forests.

(eds.). Stanurf, J.A. & Madsen (eds.). Integrative studies in water management and land development. CRC Press. pp. 3-11.
–, & Madsen, P. 2002. restoration concepts for temperate and boresl forests of North America and Western Europe. Plant Biosystems 136(2): 143-158.
Steijlen, I. & Zackrisson, O. 1987. Long-term regeneration dynamics and successional trends in a northern Swedish coniferous stand. Canadian Journal of Botany 65: 839-848.
Storaunet, K. O. & Rolstad, J. 2002. Time since death and fall of Norway spruce logs in old-growth and selectively cut boreal forest. Canadian Journal of Forest Research 32: 1801-1812.
Svensson, S.A. 1980. The Swedish National Forest Survey 1973-77. Swedish University of Agricultural Sciences, Department of Forest Survey. Report 30, Umeå.
Syrjänen, K., Kalliola, R., Puolasmaa, A. & Mattson, J. 1994. Landscape structure and forest dynamics in subcontinental Russian European taiga. Annales Zoologi Fennici 31: 19-34.
Tasanen, T. 2004. The history of silviculture in Finland from Mediaeval to the breaktrough of forest industry in 1870s. Metsäntutkimuslaitoksen tiedonannot 920. 443 pp. (in Finnish with abstract in English).
Tomppo, E. Henttonen, H., Korhonen, K. T., Aarnio, A., Ahola, A. & Ihanalinen, A. et al.1999. Keski-Suomen metsäkeskuksen alueen metsävarat ja niiden kehitys 1967-96. [Forest assets and their development in Central Finland 1967-96]. Metsätieteen aikakausikirja 2B/1999: 309-387 (in Finnish).
Tukia, H. 2000. Metsien ennallistamisen ekologiaa [Ecological aspects of forest restoration]. Metsähallituksen luonnonsuojelujulkaisuja, sarja A:1-65 (in Finnish).
Uggla, E. 1958. Forest fire areas in Muddus nationalpark, northern Sweden. Acta Phytogeographica Suecica 41. 116 p. (in Swedisch with English summary)
Uotila, A. 2004. Vegetation patterns in managed and semi-natural boreal forests in easternFinland and Russian Karelia. Academic dissertation. University of Joensuu, Faculty of Forestry. pp. 167. ISBN 952-458-470-0
Uotila, A., Maltamo, M., Uuttera, J. & Isomäki, A. 2001. Stand structure in semi-natural and managed forests in eastern Finland and Russian Karelia. Ecological Bulletins 49: 149-158.
Uotila, A., Kouki, J., Kontkanen, H. & Pulkkinen, P. 2002. Assessing the naturalness of boreal forests in eastern Fennoscandia. For. Ecol. Manage. 161: 257-277.
Uuttera, J., Maltamo, M. & Kuusela, K. 1996. Impact of management history on the state of forests in relation to natural forest succession. Comparative study, North Karelia, Finland vs. Republic of Karelia, Russian Federation. Forest Ecology and Management 83: 71-85.
Vanha-Majamaa, I., Tuittila, E.-S., Tonteri, T. & Suominen, R., 1996. Seedling establishment after prescribed burning of a clear cut and partially cut mesic boreal forest in southern Finland. Silva Fennica 30: 31-45.
–, I. & Jalonen, J. 2001. Green tree retention in Fennoscandian forestry.Scandinavian Journal of Forest Research 3: 79-90.
Vesijaon tutkimusalue, hoito- ja käyttösuunnitelma 1994-2003. 1995. [Plan for the management and use of forests in Vesijako research area 1994-2003].Metlan tutkimusmetsien julkaisusarja 5. Vantaa. pp. 228. ISBN 951-40-1432-4. (in Finnish).
Vuokila, Y. 1984. Harsinnan teoriaa ja käytäntöä. Finnish Forest Research Institute, Research Papers 130: 1-107 (in Finnish).
Wallenius, T. 2002. Forest age distribuition and traces of past fires in a natural boreal landscape dominated by Picea abies. Silva Fennica 36 (1): 201-211.
–, Pitkänen, A., Kuuluvainen, T., Pennanen, J. & Karttunen, H. 2005. Fire history and forest age distribution of an unmanaged *Picea abies* dominated landscape. Canadian Journal of Forest Research 35:1540-1552.
–, Kuuluvainen, T. & Vanha-Majamaa, I. 2004. Fire history in relation to site type and vegetation in Vienansalo wilderness in eastern Fennoscandia, Russia. Canadian Journal

of Forest Research 34: 1400-1409.

White, P. S. & Pickett, S.T.A. 1985. Natural disturbance and patch dynamics: Anintroduction. The ecology of natural disturbance and patch dynamics. Academic Press, Inc. pp. 3-13.

–, & Walker, J. L. 1997. Approximating nature's variation: selecting and using reference information in restoration ecology. Restoration Ecology 5: 338-349.

Wikars, L.-O. 1997. Effects of Forest Fire and the Ecology of Fire-Adapted Insects. Department of Zoology. Uppsala, Uppsala University: 35.

-, 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.

–, 2004. Brand beroende insekter – respons på tio års naturvårdsbränningar. Fauna & Flora 99(2): 28-34 (in Swedish with summary in English)

Working Group on Restoration, Restoration in Protected Areas: Report by the Working Group on restoration 2003. The Finnish Environment 618: 1-220 (in Finnish with abstract in English).

Zackrisson, O. 1977. Influence of forest fires on the North Swedish boreal forest. Oikos 29: 22-32.

–, Nilsson., M.-C., Steijlen, I. & Hörnberg, G. 1995. Regeneration pulses and climate-vegetation interactions in non-pyrogenic boreal Scots pine stands. Journal of Ecology 83: 1-15.

Zar, J. H. 1999. Biostatistical analysis. Second edition. Prentice- Hall, Englewood Cliffs, New Jersey. 718 pp.