# Structure of Old *Pinus sylvestris* Dominated Forest Stands along a Geographic and Human Impact Gradient in Mid-Boreal Fennoscandia

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Stand structural characteristics were examined in old *Pinus sylvestris* dominated sites in three regions along a broad geographic and human impact gradient in mid-boreal Fennoscandia. The study regions were: 1) Häme in south-western Finland, with a long history of forest utilization, 2) Kuhmo in north-eastern Finland, with a more recent history of intensive forest utilization, and 3) Vienansalo in Russian Karelia, still characterized by a large near-natural forest landscape. Within each region the sampled sites were divided into three human impact classes: 1) near-natural stands, 2) stands selectively logged in the past, and 3) managed stands treated with thinnings. The near-natural and selectively logged stands in Häme and Kuhmo had a significantly higher *Picea* proportion compared to stands in Vienansalo. In comparison, the proportions of deciduous tree volumes were higher in near-natural stands in Vienansalo compared to near-natural stands in Häme. The pooled tree diameter distributions, both in near-natural and selectively logged stands, were descending whereas managed stands had a bimodal diameter distribution. Structural diversity characteristics such as broken trunks were most common in near-natural stands and in stands selectively logged in the past. The results demonstrate the higher structural complexity of near-natural stands and stands selectively logged in the past compared to managed stands, and highlight that old near-natural stands and stands selectively logged in the past vary widely in their structures. This obviously reflects both their natural variability but also various combinations of pre-industrial land use and human impact on fire disturbance. These factors need to be acknowledged when using "natural" forest structures as a reference in developing strategies for forest management, restoration and nature conservation.

**Keywords** disturbances, managed forest, old growth forest, restoration, stand structure
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# 1 Introduction

Disturbance and successional processes shape the structural characteristics of forest stands in time and space (Attiwill 1994, Webb 1999, Franklin et al. 2002). In natural boreal forests a variable set of disturbance factors, such as fire, storms, insects, and pathogens operate and interact on different space and time scales to create a wide range of structural heterogeneity (Kuuluvainen 1994, Engelmark 1999). This multiscale heterogeneity is believed to be an important feature of habitat diversity, thus contributing to the maintenance of species populations in naturally dynamic boreal forests (Attiwill 1994, Esseen et al. 1997).

In many parts of the boreal zone humans have utilized forests for a long time, often modifying or suppressing natural disturbance regimes. For example, in Finland the period of active slash-and-burn cultivation (1600–1900) was associated with more frequent fires (Heikinheimo 1915, Lehtonen et al. 1996). The birth of forest industry in the late 18$^{th}$ century led to a period of widespread selective logging (1870–1950), when only large and high quality stems were harvested. More recently forests are being shaped mainly by modern forest management, using thinnings and clear-cut harvesting, while natural disturbance factors are being increasingly replaced by disturbances caused by forest management.

Fire suppression, past selective logging, and more recent clear-cut harvesting together with silvicultural procedures such as thinning and planting have reduced the structural complexity of forests, both at the stand and landscape levels (Kouki 1994, Esseen et al. 1997, Linder and Östlund 1998). In Fennoscandia, perhaps the most dramatic changes have been the rapid decrease in the number of large living and dead trees and the amount of coarse woody debris (Linder et al. 1998, Rouvinen et al. 2002a). At the landscape level the forest was historically dominated by old-growth forests, as stand-replacing fires were relatively rare in Fennoscandian forests (Axelsson et al. 2002, Pennanen 2002). This matrix has now largely been replaced by a mosaic of patches of younger successional even-aged forest (Kouki et al. 2001).

The understanding of the ecology and structures of near-natural forests provides an indispensable reference for developing strategies and methods of restoration and more sustainable management of boreal forests (White and Walker 1997, Franklin et al. 2002, Kuuluvainen 2002). In general, understanding of the structure, dynamics and processes of natural forests under Fennoscandian conditions has increased in recent years (e.g. Engelmark and Hytteborn 1999, Jonsson and Kruys 2001, Korpilahti and Kuuluvainen 2002). Studies comparing managed, selectively cut, and natural forests have also been carried out (Siitonen et al. 2000, Sippola et al. 2001, Uotila et al. 2001, 2002). As a result, we have a general understanding of how natural and managed forests differ. However, we lack detailed and quantitative descriptions of the impact of humans and disturbance regimes on stand structures and their variability, using consistent methodologies and addressing both local and geographical scales.

The purpose of the present study was to quantify and compare the structural characteristics in old *Pinus sylvestris* L. dominated forest stands in three regions along a broad geographic gradient of human influence in the mid-Boreal vegetation zone in Fennoscandia. The regions selected for the study were 1) Häme in (SW) Finland, having a long history of forest utilization, 2) Kuhmo in (NE) Finland with a more recent history of forest utilization, and 3) Vienansalo in (NW) Russia, still characterized by large areas of near-natural forests. The local variation in intensity of human impact within each region was considered by dividing the plots into 1) near-natural stands, with practically no signs of human impact, 2) selectively logged stands, in which the logging has been low in intensity and completed decades ago, and 3) managed stands, which have been treated to become production forests. We wanted to quantify how the intensity and duration of human impact has affected the volume, species proportions, diameter distributions and abundance of structural diversity characteristics of trees. This study is complemented by that of Rouvinen et al. (2002a), who examined deadwood structures measured in the same sample plots.

# 2 Material and Methods

## 2.1 Study Regions

The study sites are located in three regions, in the Häme region in (southwestern) Finland, in the Kuhmo region in (northeastern) Finland, and in the Vienansalo wilderness area in Russian Karelia (Fig. 1). All three regions are located within the mid-Boreal vegetation zone, although the Häme region is in the transition zone between the mid- and southern Boreal zones (Kalela 1961, Ahti et al. 1968).

The bedrock in Häme consists of orogenic granitoids, in Kuhmo of granite and gneiss, and in Vienansalo of gneiss with a high proportion of biotite. The bedrock at all forest sites is covered with moraine and peat (Atlas Karelskoy ASSR 1989, Atlas of Finland 1992, Gorkovets et al. 2000). The climatic data and the location of the study regions are presented in Table 1.

*Pinus sylvestris* and *Picea abies* (L.) Karst. mostly dominate the forests in the Häme region. *Pinus* dominated forests are most common in the Kuhmo and Vienansalo regions, but *Picea* dominated forests also occur. The most common forest site types in the Häme region are the mesic *Vaccinium-Myrtillus* type (VMT) and the dryish *Empetrum-Vaccinium* type (EVT), *sensu* Cajander (1926), covering about 45% and 20% of the forest land area, respectively (Korhonen et al. 2000). The mesic VMT in Kuhmo covers about 30% and the dryish EVT about 60% of the forest land area (Rouvinen et al. 2002a). The VMT and EVT also dominate the landscape in the Vienansalo region (Pyykkö 1996).

**Table 1.** Locations and climatic conditions in the three geographic regions where the sampling was carried out. The meteorological data are from Atlas of Finland (1992) and Atlas Karelskoy ASSR (1989). Reproduced after Rouvinen et al. (2002a).

| | Häme | Kuhmo | Vienansalo |
|---|---|---|---|
| Location | 62°N, 24°E | 64°N, 29°E | 65°N, 30°E |
| Altitude (m.a.s.l.) | 150–200 | 200–300 | 140–230 |
| Mean annual temp. (°C) | +3 | +1.5 | +1 |
| Mean annual precipitation (mm) | 650 | 650 | 650 |
| Growing season (days) | 160 | 145 | 140 |
| Mean effective temperature sum (threshold +5 °C) | 1100 | 950 | 900 |

## 2.2 History of Forest Utilization in the Study Regions

Knowledge of forest utilization history is needed as a background for interpreting the overall human impact on the forest regions studied. In all the study regions past forest utilization prior to the 1950s included slash-and-burn cultivation, tar burning, cattle grazing and selective logging. However, both the intensity and duration of these uses varied considerably among the regions.

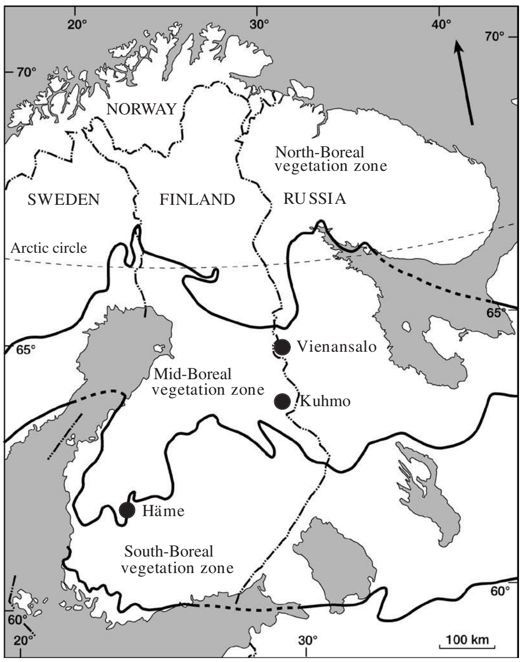


**Fig. 1.** Geographical locations of the three study regions.

The duration of forest utilization is reflected by the settlement history. Evidence of pre-historical settlements was found from the study regions, for example ancient Sami people had small villages in Vienansalo wilderness (Pöllä 1995). Nevertheless 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 Häme slash-and-burn cultivation was practiced until the early 20th century (Heikinheimo 1915). Tar was commonly burned, in Häme particularly in the 18th century (Kaila 1931, Soininen 1974). Selective logging was carried out from the mid-18th until the mid-20th centuries (Helander 1949). With the emergence of the forest industry in the late 19th century, the demand for quality timber increased and selective logging became common, in which only the most technically perfect large trees were removed. The period of selective logging has been longest and most intensive in Häme due to a higher human population density and location near the forest industry in southern Finland.

In Kuhmo slash-and-burn cultivation was practiced until the early 20th century (Heikinheimo 1915). Tar burning was also intensive in Kuhmo (Kaila 1931, Soininen 1974) and was actively practiced until the early 20th century (Helander 1949, Heikkinen 2000). Slash-and-burn cultivation and tar burning continued longer in the Kuhmo region than in the Häme region, but since the mid-19th century logging has also been essential for earning a livelihood in Kuhmo (Heikkinen 2000). Logging was selective until the 1950s, when clear-cutting became the predominant harvesting method.

In Vienansalo fishing, hunting and slash-and-burn cultivation have always been important sources of livelihood (Virtaranta 1958, 1978, Bazegskij 1998). Tar was burned for domestic use in every village (Virtaranta 1958), although large-scale tar production was not practiced in the Vienansalo region (Hautala 1956). The cut stumps left in Vienansalo demonstrate that trees have been cut selectively (Lehtonen and Kolström 2000, Karjalainen and Kuuluvainen 2002), but the cutting frequency was not as high as in Kuhmo and Häme (Gromtsev and Litinski 2003).

The number of fires in all three regions increased considerably, apparently due to human activity, in the 18th and 19th centuries (Tuominen 1990, Lehtonen et al. 1996, Lehtonen and Kolström 2000, 2002), followed by a subsequent decline. The decline in fires occurred in the Häme area in the mid-19th century (Tuominen 1990, Lehtonen and Kolström 2002), i.e. earlier than in Kuhmo and Vienansalo, where fires continued to occur until the 20th century (Haapanen and Siitonen 1978, Lehtonen and Kolström 2000, Pennanen and Kuuluvainen 2002).

Based on the available information, a general decreasing trend of overall human impact on forests is evident from Häme toward the more remote regions in Kuhmo and Vienansalo (Kalliola 1966). During recent decades in the Häme and Kuhmo regions, large areas of forest, previously impacted only by scattered selective cuttings, have been treated to become managed production forests, e.g. by using silvicultural thinnings and removal of understory *Picea abies* and deciduous trees. In contrast, there have been no silvicultural treatments in Vienansalo, and even the domestic use of wood has been very low due to the abandonment of small nearby villages during the Soviet era (Nieminen 1998, Gromtsev and Litinski 2003).

### 2.3 Sampling and Measurements

The sampling was carried out during three field seasons, in 1997 in Kuhmo, in 1998 in Vienansalo, and in 1999 in Häme. 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 the early 20th century and not treated since), and 3) managed stands, which were more recently thinned to conform to modern stand management standards. Although these stand types were preliminarily judged in the field, the stand category was finally determined based on the measured number of cut stumps (Siipilehto and Siitonen 2004) and/or stand structure according to pre-determined criteria. Stands classified as near-natural if they had no or only one cut stump per plot ($<5$ cut stumps $ha^{-1}$: Uotila et al. 2002) and the stand structure was typically uneven-sized. Stands classified as selectively logged had old cut stumps ($\geq 5$ cut stumps $ha^{-1}$) from logging carried out several decades ago, but the overall stand structure was similar to that found in near-natural stands. Stands classified as managed had clear signs of recent silvicultural thinnings and the stand structure, dominated by mature production trees, was close to even-sized, i.e. very different from the typically multi-layered canopy of the two other stand categories. The number of sampled stands was unevenly distributed between different stand categories and regions (Table 2), 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 unit, a rectangular plot of 20 m × 100 m, was used, but they were located in the forest using somewhat different procedures, due the different availability of potential stands and requirements of the field work. In Häme and Kuhmo, where protected areas are small and old managed stands are rare (as they are at the final harvest age), potential stands were searched using the stand data files of Metsähallitus (Finnish Forest and Park Service) and Finnish Forest Research Institute, according to the following minimum requirements: 1) *Pinus sylvestris* dominated forest on a volume basis, 2) dominant *Pinus* at least 90 years of age, and 3) stand area at least 3 ha. Because such stands were rare and dispersed, they were selected in an iterative manner as the sampling progressed, based on their accessibility, to make field work reasonably efficient. Another reason for this procedure was that the stand characteristics in the field did not always correspond to data files, and the above-mentioned criteria had to be checked in the field each time. In Kuhmo and Häme near-natural stands were searched from protected areas and selectively logged (in the past) and managed stands from the managed forests surrounding the protected areas. The location of sample plots were randomized within stands so that the plot was at least 30 m from stand edge to avoid edge effects.

In the Vienansalo wilderness the sampling was carried out in a continuous *Pinus* dominated forest area of 4 km × 6 km. The study area was selected using Landsat Thematic Mapper (TM) satellite imagery and the following criteria: 1) the area should be remote to minimize potential human influence, 2) the landscape should be typical of the Vienansalo area, and 3) there should be water access to the area to facilitate the transportation necessitated by the research. For sampling, five systematic 4000 m lines running east-west across the area were marked in the field. Random points were located on the lines, points were accepted if they were on firm land and the sample plot could be located within a relatively homogeneous forest patch. These random points determined the location of the sample plots (for details see Karjalainen and Kuuluvainen 2002). In Vienansalo only near-natural and selectively logged forests were found because there is no managed forest; this area is currently planned to become a national park (Gromtsev and Litinski 2003).

The Vienansalo study area was examined for fire history by Lehtonen and Kolström (2000), characteristics of coarse woody debris by Karjalainen and Kuuluvainen (2002), tree mortality dynamics by Rouvinen et al. (2002b), and tree age structures by Kuuluvainen et al. (2002). Rouvinen and Kuuluvainen (2005) compared the tree diameter distributions in Vienansalo 'natural' stands and Häme managed stands using partly the same sample tree material as in this study. This study reports a more detailed analysis of the tree diameter distributions in different stand types and geographic regions.

A total of 116 sample plots (20 × 100 m) were established in the three study regions: 57 in Häme, 32 in Kuhmo and 27 in Vienansalo (Table 2). In Häme and Kuhmo the forest site type (sensu Cajander 1926) of the sample plots, was either the mesic *Vaccinium-Myrtillus*-type (Häme 10 and Kuhmo 25 plots) or the dryish *Vaccinium-Vitis-idaea*-type (Häme 46 and Kuhmo 6 plots), which together dominate the landscape. Also dry *Calluna*-type stands included (Häme 1 and Kuhmo

**Table 2.** The number of study plots in near-natural, selectively cut, and managed stands in Häme, Kuhmo, and Vienansalo.

| | Near-natural | Selectively logged | Managed | Total |
|---|---|---|---|---|
| Häme | 4 | 8 | 45 | 57 |
| Kuhmo | 5 | 18 | 9 | 32 |
| Vienansalo | 13 | 14 | 0 | 27 |
| Total | 22 | 40 | 54 | 116 |

1 plot). In Vienansalo the plots were located on *Vaccinium-Myrtillus* (16 plots), *Empetrum-Vaccinium* (6 plots) and dry *Empetrum-Calluna* sites (5 plots) (Karjalainen and Kuuluvainen 2002). Since there were no consistent differences in stand structural characteristics among the site types in any of the study regions (analysis not shown), the data from all site types were pooled for the analyses.

For each 20×100 m sample plot, one to three dominant trees were cored at their trunk bases for stand age determination. For measurements of DBH, height, age and structural diversity of living and dead woody material, the sample plot was divided into 20 subplots of 10×10 m quadrates. All living trees (height>1.3 m) were identified for species and their diameters at breast height (DBH) were measured to an accuracy of 1 cm. The height was measured for trees with DBH>30 cm to enable reliable estimation of their volume. The number of tree saplings of each species (height 30–130 cm) was calculated, using one subplot of 2×100 m within the main sample plot.

Structural diversity features of living trees that potentially can contribute to substrate or habitat diversity for forest organisms, such as epiphytic lichens and insects, were also recorded. The following such features were registered: broken trunk, dead or broken treetop, damaged, crooked or leaning trunk, old tree with round top, large branches, nesting tree with holes, fire scars, trunk with multiple tops, trunk with polypore fruiting bodies or trunk with malformed base and offset group.

### 2.4 Data Analysis

The forest structure was characterized by computing volumes, diameter, and species distributions of the trees. The volume of living trees of *Pinus*, *Picea*, and *Betula* spp. was assessed using the volume equations of Laasasenaho (1982). When tree height was measured (for trees with DBH>30 cm), equations using both DBH and height as independent variables were used. The volume of all deciduous trees was estimated using the equations for *Betula*. Structural diversity features of living trees were summed by study regions and stand types.

The analysis of covariance (ANCOVA), where the log-transformed mean stand age (natural basis) and length of growing season were the covariates, was used to examine the differences between and within regions and stand types in living tree volume, tree species proportions, total number of structural diversity characteristics and density of tree regeneration. The analysis of covariance model was:

$$Y_{ijk} = \mu + R_i + T_j + R \times T_{ij} + \beta_1 A + \beta_2 G + E_{ijkl} \quad (1)$$

where $Y_{ijk}$ is the dependent variable, $\mu$ is the overall mean, $R_i$ is the main effect of region, $T_i$ is the main effect of stand type. $\beta$ is the coefficient for covariates. A is the age and G is the length of growing season, both as a covariates, $TI_{ij}$ is the interaction between region and study type, and $E_{ijkl}$ is the experimental error.

Contrast analyses were done for stand age and length of growing season adjusted means. Appropriate weighting of the group means was made to take into account the unbalancedness of the design. By using contrasts it was also possible to analyze different groups together, for example we did contrast analyses for near-natural stands of Häme and Kuhmo versus near-natural stands of Vienansalo. Analysis of covariance and contrasts were carried out using the GLM procedure of SAS (SAS Institute Inc. 1989).

To characterize the diversity of tree diameter distributions we used the Shannon–Weaver formula (Shannon 1948, MacArthur and MacArthur 1961, Kuuluvainen et al. 1996):

$$H' = \sum_{i=1}^{n} p_i \log_e p_i \quad (2)$$

where $p_i$ is the proportion of trees in the $i$th diameter class. The width of the diameter class was 5 cm.

# 3 Results

### 3.1 Tree diameter Distributions

The pooled DBH distribution of trees in the managed stands exhibited a bimodal pattern (Fig. 2). Both in Häme and Kuhmo the first peak in the diameter distribution was in the smallest diameter

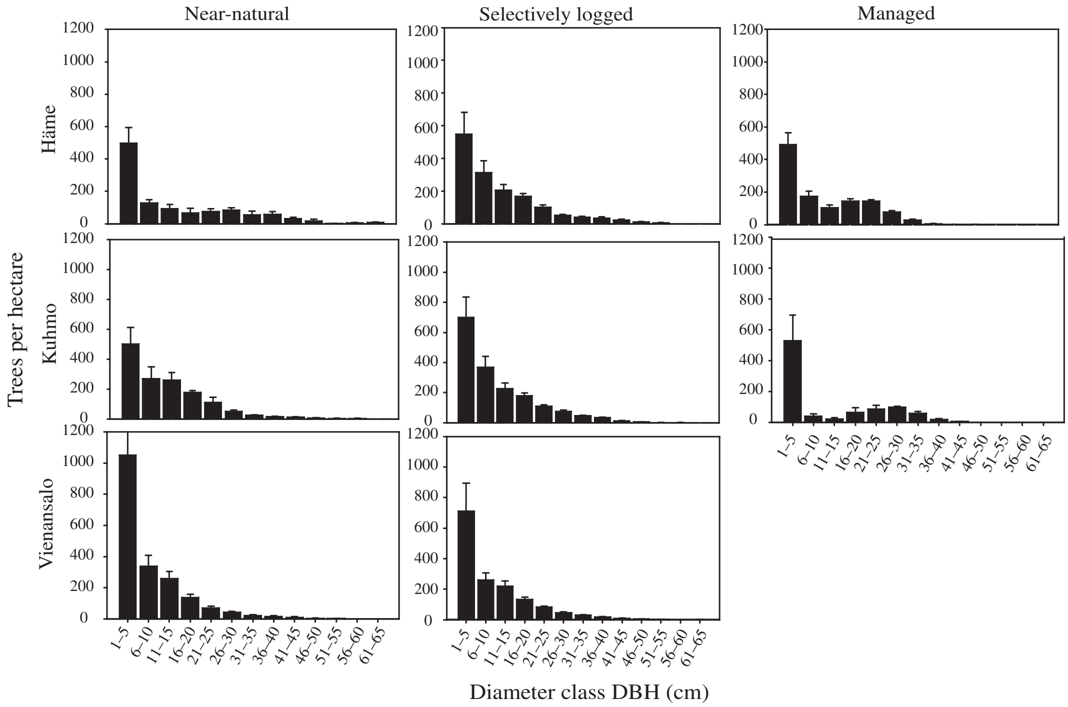


**Fig. 2.** Pooled diameter distributions of living trees (DBH > 1 cm) by stand types and geographic regions.

class (1–5 cm). The second peak in Häme was in the diameter range of 16–25 cm and in Kuhmo in the range of 16–35 cm (Fig. 2). Thus, compared to Häme, the dominant trees in the managed stands in Kuhmo displayed more large trees and a wider range of diameters. The largest trees in the managed stands of Kuhmo were in the 41–45 cm diameter class and in Häme in the 36–40 cm diameter class (Fig. 2).

In contrast to managed stands, the near-natural stands and stands selectively logged in the past generally showed a descending diameter distribution, in which small trees were most abundant and the number of trees declined with increase in tree size (Fig. 2). However, there were differences in the diameter distributions between 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 compared to Kuhmo and Häme. The diameter distribution of near-natural stands in Häme showed a weak bimodal pattern, thus deviating from the distributions detected in Kuhmo and Vienansalo. The diameter distributions in the selectively logged stands were rather similar in all three studied regions (Fig. 2).

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 $ha^{-1}$ respectively) and lowest in the managed stands of the same region (only 1 tree per hectare). The same decreasing trend in the density of large trees from near-natural to selectively logged to managed stands (30, 17 and 5 trees $ha^{-1}$, respectively) was found in Kuhmo. The densities of large trees in the near-natural and selectively logged stands of Vienansalo were similar, 16 trees $ha^{-1}$ in both, but clearly lower compared to Häme (see Table 3).

The tree diameter diversity index (Shannon–Weaver index) was highest in the near-natural stands of Häme (1.88) and lowest in the near-natural stands of Vienansalo (1.43) (Table 3). Both in Häme and Kuhmo the diversity index was highest in the near-natural stands and lowest in the managed stands.

**Table 3.** Stand structural characteristics of living trees in near-natural, selectively logged, and managed stands in the three geographic regions. Standard deviations are in parentheses.

| | Häme | | | Kuhmo | | | Vienansalo | |
|---|---|---|---|---|---|---|---|---|
| | Near-natural (N=4) | Sel. logged (N=8) | Managed (N=45) | Near-natural (N=5) | Sel. logged (N=18) | Managed (N=9) | Near-natural (N=13) | Sel. logged (N=14) |
| Total volume ($m^3$ $ha^{-1}$) | 333.3 (93.3) | 255.0 (74.8) | 155.8 (51.8) | 210.4 (41.7) | 232.8 (34.5) | 168.8 (31.6) | 151.3 (36.5) | 165.7 (38.5) |
| *Pinus sylvestris* | 189.4 (54.1) | 152.5 (47.2) | 128.2 (39.4) | 93.1 (14.8) | 118.9 (42.1) | 157.2 (44.2) | 115.8 (36.4) | 116.4 (50.5) |
| *Picea abies* | 140.7 (111.0) | 87.7 (55.9) | 17.8 (28.3) | 96.4 (38.6) | 89.4 (47.8) | 8.1 (23.4) | 15.6 (17.1) | 27.5 (25.9) |
| *Betula* spp. | 3.2 (4.2) | 12.2 (13.5) | 8.4 (12.3) | 18.5 (12.7) | 21.8 (12.6) | 3.0 (4.5) | 16.1 (10.1) | 20.0 (17.3) |
| *Populus tremula* | 0 | 2.2 (4.3) | 1.1 (5.5) | 2.0 (2.8) | 2.4 (3.3) | 0.5 (1.4) | 3.4 (5.3) | 1.6 (2.5) |
| *Salix caprea* | 0 | 0.1 (0.2) | 0.04 (0.1) | 0.3 (0.5) | 0.2 (0.7) | 0.01 (0.01) | 0.2 (0.4) | 0.1 (0.2) |
| *Sorbus aucuparia* | 0 | 0.2 (0.5) | 0.03 (0.06) | 0.02 (0.04) | 0.01 (0.03) | 0.002 (0.004) | 0 | 0 |
| Total volume of deciduous trees ($m^3$ $ha^{-1}$) | 3.2 (4.2) | 14.8 (16.9) | 9.8 (14.0) | 20.9 (13.2) | 24.5 (12.9) | 3.5 (4.1) | 19.9 (12.5) | 21.8 (18.3) |
| Deciduous tree portions (%) | 1 | 5.8 | 6.3 | 9.9 | 10.5 | 2.1 | 13.2 | 13.2 |
| Range of total volume ($m^3$ $ha^{-1}$) | 239.0–449.8 | 142.9–329.9 | 80.2–320.0 | 184.2–276.2 | 183.8–335.5 | 137.2–238.4 | 91.0–218.2 | 103.6–239.4 |
| Volume of large trees ($m^3$ $ha^{-1}$)[a] | 293.6 (112.9) | 179.9 (78.8) | 83.5 (63.3) | 127.1 (34.7) | 152.0 (33.3) | 133.5 (52.2) | 85.3 (44.8) | 103.3 (39.4) |
| Number of large trees $ha^{-1}$ (DBH > 40 cm) | 59 | 40 | 1 | 30 | 17 | 5 | 16 | 16 |
| Mean age (yrs) | 210.0 (34.6) | 175.4 (45.0) | 111.0 (13.8) | 204.0 (25.1) | 196.7 (21.6) | 179.3 (12.8) | 186.7 (35.9) | 208.3 (57.1) |
| Tree diameter diversity index (H') | 1.88 | 1.81 | 1.68 | 1.79 | 1.73 | 1.46 | 1.43 | 1.61 |
| Variance of H' | 0.001 | 0.00052 | 0.00054 | 0.00051 | 0.00046 | 0.00137 | 0.00057 | 0.00065 |

[a] *Pinus* and *Picea* DBH > 25 cm, *Betula DBH* > 20 cm, *Alnus* and *Populus DBH* > 15 cm, and *Salix* DBH > 10 cm.

### 3.2 Structural Diversity Characteristics of Living Trees

Between regions there was a significant difference in the density of structural diversity characteristics in near-natural stands, and between stand types in Kuhmo and Vienansalo (Table 4). In general, the density of structural diversity characteristics was highest in the near-natural stands, followed by stands selectively logged in the past, and lowest in managed stands (Table 4). However, the near-natural stands in Häme deviated from this pattern by having fewer structural diversity characteristics than managed stands in the same region.

The most commonly detected structural diversity characteristics in all forest classes of Häme and Kuhmo were crookedly growing, damaged or leaning trunks. The most common structural characteristics in the near-natural and selectively logged forests in Vienansalo were dead or broken treetops; fire scars were also common. Moreover, the structural diversity characteristics in Vienansalo were more evenly distributed into different characteristic categories compared to Kuhmo and especially Häme (Table 4).

### 3.3 Tree Species Composition

Although the sampled stands were selected based on their *Pinus* dominance, the between stand type and among region differences in the degree of *Pinus* dominance and abundance of other tree species merits examination. Between the study regions the mean proportion of *Pinus* was significantly different only between near-natural and selectively logged stands in Kuhmo and Vienansalo (Table 5). The mean proportion of *Pinus* 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* in the near-natural forests of Häme with a diameter smaller than 10 cm (Fig. 3). Overall, *Pinus* dominance was highest in the managed stands of Häme (82% of the volume) and Kuhmo (93%), and lowest in the near-natural stands of Kuhmo (44%).

The mean proportion of *Picea* both in near-natural and selectively logged stands differed significantly between the regions of Häme and Kuhmo, versus Vienansalo. There were no differences in the proportion of *Picea* between the stand types neither in Häme nor in Kuhmo (Table 5). *Picea* 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) (Fig. 3). In contrast, the proportion of *Picea* was low in the managed stands of the same regions (5% in Kuhmo and 11% in Häme), and also in Vienansalo both in near-natural (10%) and selectively logged (17%) stands.

The proportion of deciduous trees was significantly lower in natural and selectively logged stands of Häme than in those of Vienansalo, but there was no difference between Kuhmo and Vienansalo in this respect. In addition, the proportion of deciduous trees, mainly *Betula*, differed significantly in near-natural and selectively logged stand between Kuhmo and Häme (Table 5). The proportion of deciduous trees from total volume was highest in Vienansalo in the near-natural (13% of the volume) and selectively logged (13%) stands (Table 3). The lowest proportions of deciduous trees were found in the near-natural stands (1%) of Häme and in the managed stands (2%) of Kuhmo (Fig. 4, Table 3). However, deciduous trees were abundant in the small diameter classes (DBH < 10 cm) in the managed stands of Häme and Kuhmo (Fig. 3).

Among stand types the proportion of *Picea* was significantly different in Häme, where the proportion of *Picea* was higher in near natural and selectively logged stands compared to managed stands. In Kuhmo the proportion of deciduous trees was higher in near-natural and selectively logged stands than in managed stands. On the other hand in Vienansalo the tree species composition did not differ between near-natural and selectively logged stands.

**Table 4.** Density of structural diversity characteristics of living trees (ha$^{-1}$) in the forest types in the three geographic areas with the range in parentheses.

| Structural characteristic | Häme Near-natural (N=4) | Häme Selectively logged (N=8) | Häme Managed (N=45) | Kuhmo Near-natural (N=5) | Kuhmo Selectively logged (N=18) | Kuhmo Managed (N=9) | Vienansalo Near-natural (N=13) | Vienansalo Selectively logged (N=14) |
|---|---|---|---|---|---|---|---|---|
| Broken trunk | 0.0 (0–0) | 0.0 (0–0) | 0.0 (0–0) | 15.0 (0–40) | 7.8 (0–40) | 2.2 (0–20) | 4.6 (0–40) | 7.1 (0–25) |
| Dead or broken treetop | 8.8 (0–15) | 21.9 (5–70) | 13.6 (0–70) | 46.0 (25–85) | 53.6 (20–110) | 16.7 (0–70) | 188.5 (15–805) | 178.6 (10–1205) |
| Damaged trunk | 46.3 (20–90) | 53.1 (25–80) | 31.0 (0–100) | 77.0 (50–110) | 90.0 (35–190) | 56.1 (0–255) | 84.2 (20–190) | 41.8 (5–105) |
| Crooked trunk | 135.0 (75–160) | 176.3 (70–285) | 160.9 (10–325) | 142.0 (50–215) | 134.2 (15–380) | 31.7 (0–105) | 63.8 (10–320) | 50.4 (10–110) |
| Leaning trunk | 58.8 (30–90) | 86.9 (10–225) | 33.1 (0–135) | 115.0 (50–185) | 123.6 (10–455) | 16.1 (0–40) | 65.0 (0–275) | 62.5 (0–195) |
| Old tree with rounded crown top | 3.8 (0–5) | 8.1 (0–20) | 0.2 (0–5) | 0.0 (0–0) | 0.8 (0–10) | 0.0 (0–0) | 7.3 (0–40) | 5.4 (0–20) |
| Large branches | 7.5 (0–20) | 8.8 (0–15) | 4.2 (0–15) | 33.0 (10–60) | 18.6 (0–40) | 5.6 (0–20) | 21.5 (5–45) | 23.6 (0–75) |
| Nesting tree with holes | 0.0 (0–0) | 0.0 (0–0) | 0.2 (0–5) | 1.0 (0–5) | 0.6 (0–5) | 0.0 (0–0) | 0.4 (0–5) | 0.0 (0–0) |
| Fire scar on the trunk | 6.3 (0–25) | 21.3 (0–115) | 0.3 (0–10) | 3.0 (0–10) | 1.4 (0–10) | 0.0 (0–0) | 55.4 (0–190) | 108.2 (5–365) |
| Trunk with multiple tops | 2.5 (0–10) | 12.5 (5–35) | 7.9 (0–35) | 44.0 (35–55) | 36.9 (10–90) | 16.7 (0–50) | 48.8 (0–165) | 46.4 (5–240) |
| Trunk with polypore fruiting bodies | 3.8 (0–10) | 7.5 (0–40) | 0.7 (0–10) | 4.0 (0–10) | 8.6 (0–20) | 0.6 (0–5) | 6.9 (0–15) | 5.4 (0–15) |
| Trunk with malformed base | 2.5 (0–10) | 6.3 (0–20) | 0.6 (0–10) | 3.0 (0–5) | 5.3 (0–15) | 0.6 (0–5) | 11.2 (0–55) | 13.6 (0–45) |
| Sprouting group | 8.8 (0–35) | 40.0 (0–230) | 51.9 (0–340) | 32.0 (0–60) | 100.3 (0–310) | 57.8 (0–160) | 165.4 (15–895) | 56.4 (5–145) |
| Total | 283.8 (165–350) | 442.5 (265–825) | 304.0 (50–580) | 515.0 (315–715) | 581.7 (185–1070) | 203.9 (15–525) | 723.1 (235–1960) | 599.3 (175–2050) |

**Table 5.** Results of selected comparisons between regions and stand types with respect to total volume of living trees ($m^3$ $ha^{-1}$), species composition (% of volume), and sapling density ($ha^{-1}$). The corresponding *contrasts* are tested within an analysis of covariance (ANCOVA) model with stand age and the length of growing season as covariates. *Estimate* denotes difference between the contrasted mean values and *CI* its 95 % confidence interval. Significant *p*-values are in bold (df = 1). The abbreviations are: Na = near-natural, Se = selectively logged, Ma = managed, NaSe = near-natural and selectively logged; H = Häme, K = Kuhmo, V = Vienansalo. For example, Na(V) means near-natural stands in Vienansalo and NaSe(H+K) near-natural and selectively logged stands in Häme and Kuhmo and so on.

| Comparison | Between regions | | | | | | Between stand types | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Near-natural | | | Selectively logged | | Häme | | | Kuhmo | | | Vienansalo |
| | NaSe (H+K) *vs* NaSe (V) | Na (H) *vs* Na (V) | Na (K) *vs* Na (V) | Na (H) *vs* Na (K) | Se (H) *vs* Se (K) | Se (K) *vs* Se (V) | Na *vs* Se | Na *vs* Ma | Se *vs* Ma | Na *vs* Se | Na *vs* Ma | Se *vs* Ma | Na *vs* Se |
| Total volume | | | | | | | | | | | | | |
| Estimate | –111.7 | –210.7 | –69.8 | 140.8 | 29.3 | –68.5 | 91.0 | 210.4 | –119.3 | –20.4 | 69.5 | –90.0 | 21.7 |
| CI | [–177 –46] | [–326 –95] | [–125 –14] | [40 241] | [–48 107] | [–197 –2] | [31 151] | [151 269] | [–160 –77] | [–68 27] | [–16 155] | [–165 –14] | [–15 59] |
| *p*-value | **0.001** | **0.0004** | **0.014** | **0.006** | 0.457 | **0.001** | **0.003** | **<0.0001** | **<0.0001** | 0.400 | 0.112 | **0.020** | 0.250 |
| *Pinus* % of volume | | | | | | | | | | | | | |
| Estimate | 17.9 | 14.7 | 29.5 | 14.7 | 8.0 | 17.6 | 0.6 | –19.3 | 19.9 | –6.0 | –34.1 | 28.0 | –5.8 |
| CI | [–6 42] | [–28 57] | [8 50] | [–22 52] | [–21 37] | [2 33] | [–21 23] | [–41 2] | [4 35] | [–24 11] | [–66 –1] | [0 56] | [–19 8] |
| *p*-value | 0.149 | 0.499 | **0.005** | 0.437 | 0.584 | **0.026** | 0.953 | 0.085 | **0.012** | 0.493 | **0.038** | 0.052 | 0.411 |
| *Picea* % of volume | | | | | | | | | | | | | |
| Estimate | –30.5 | –36.7 | –34.7 | 2.0 | 3.4 | –23.7 | 4.9 | 20.0 | –15.1 | 6.3 | 17.9 | –11.6 | 4.7 |
| CI | [–50 –10] | [–71 –1] | [–51 –17] | [–28 32] | [–20 27] | [–36 –11] | [–13 23] | [2 37] | [–27 –2] | [–8 20] | [–8 44] | [–34 11] | [–6 16] |
| *p*-value | **0.002** | **0.040** | **<0.0001** | 0.894 | 0.772 | **0.0003** | 0.594 | **0.028** | **0.019** | 0.394 | 0.176 | 0.318 | 0.413 |
| Deciduous % volume | | | | | | | | | | | | | |
| Estimate | 12.6 | 22.0 | 5.1 | –16.8 | –11.5 | 6.0 | –5.5 | –0.7 | –4.8 | –0.2 | 16.1 | –16.3 | 1.0 |
| CI | [3 22] | [5 38] | [–2 13] | [–31 –2] | [–22 0] | [0 12] | [–14 3] | [–9 7] | [–10 1] | [–7 6] | [3 28] | [–27 –5] | [–4 6] |
| *p*-value | **0.009** | **0.010** | 0.207 | **0.024** | **0.045** | 0.050 | 0.207 | 0.870 | 0.112 | 0.942 | **0.012** | **0.003** | 0.688 |
| Number of saplings $ha^{-1}$ | | | | | | | | | | | | | |
| Estimate | 5630.1 | 8771.1 | 5394.0 | –3377 | –3462 | 2446.7 | –299.7 | –3276.0 | 2976.2 | –384.7 | 100.9 | –485.7 | –2562.5 |
| CI | [1384 9875] | [1279 16262] | [1772 9015] | [–9900 3146] | [–8517 1593] | [–251 5145] | [–4204 3605] | [–7348 796] | [91 5860] | [–3511 2741] | [–5612 5814] | [–5533 4561] | [–4972 –152] |
| *p*-value | **0.009** | **0.022** | **0.003** | 0.307 | 0.177 | 0.075 | 0.879 | 0.113 | **0.043** | 0.807 | 0.972 | 0.849 | **0.037** |

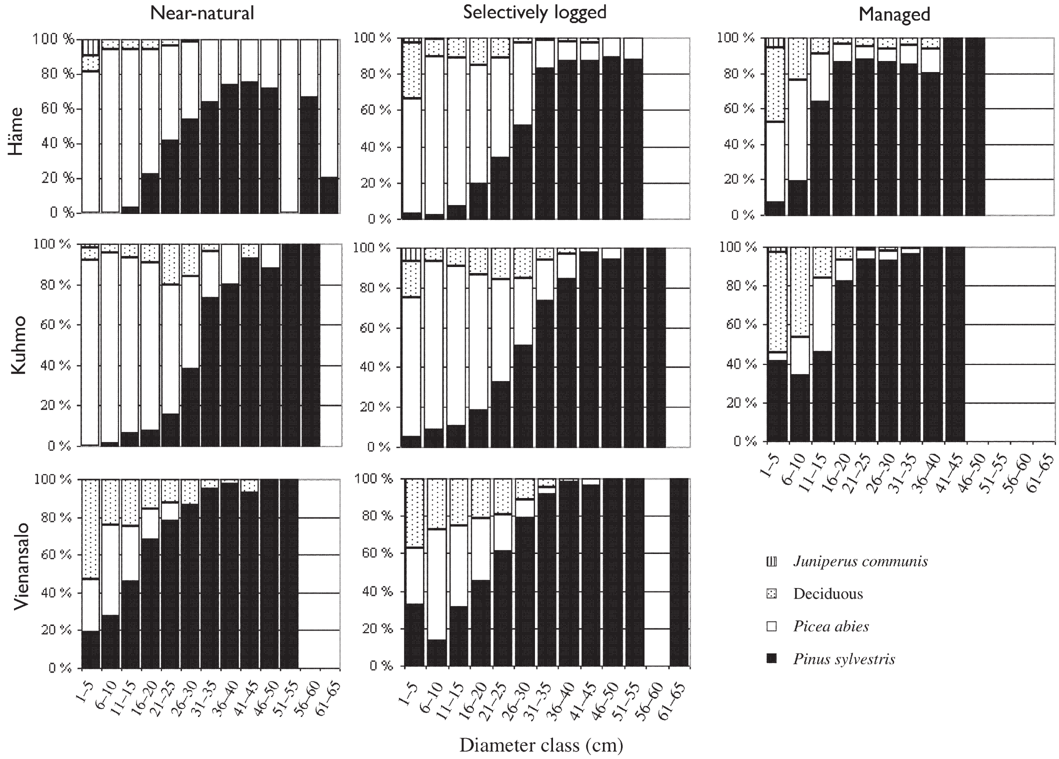


**Fig. 3.** The distribution of tree species by diameter classes in the different stand types and geographic regions.

### 3.4 Volume of Living Trees

*Between Regions*

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 growing season (Table 5). Total volume was significantly related to stand age (covariate in ANCOVA, $p=0.041$), but the length of the growing season was not. In near-natural stands the volume of *Pinus* was significantly higher in Häme compared to Kuhmo ($p=0.029$), but there were no differences between Häme and Vienansalo.

In near-natural and selectively logged stands the volume of *Picea* was significantly higher in Häme and Kuhmo, compared to Vienansalo ($p=<0.0001$, Fig. 4). There was no difference between Häme and Kuhmo regions in the volume of *Picea* between any stand types (contrast analyses not shown; Fig. 4). In general, the volumes decreased from Vienansalo to Kuhmo to Häme, except for deciduous trees where the trend was the opposite (Fig. 4).

In the near-natural stands in Vienansalo the volume of deciduous trees was significantly higher ($p=0.048$) than in Häme where the deciduous volume was the lowest. Also, in near-natural and selectively logged stands of Kuhmo the volume of deciduous were significantly higher than in Häme (contrast analyses not shown; Fig. 4). In managed stands there were no significant differences among regions in the volume of *Pinus*, *Picea* or deciduous trees.

*Between Stand Types*

When the differences among stand types within regions were examined it showed that in Häme the stand types differed in their total volumes

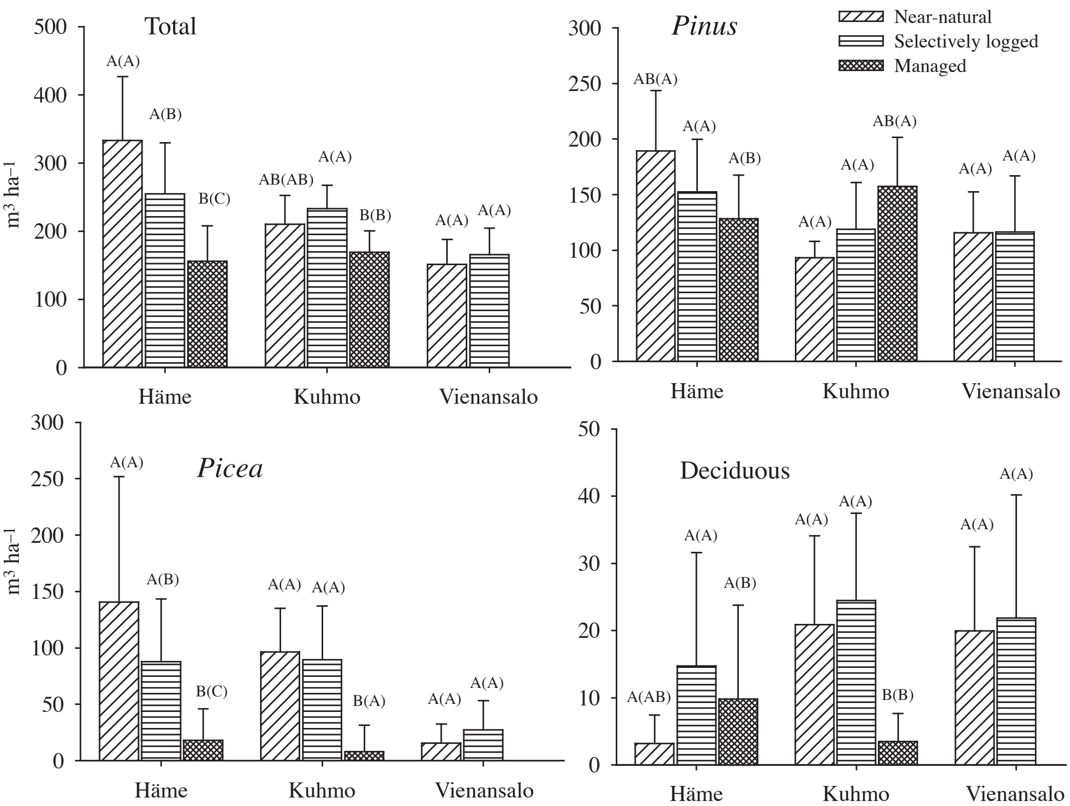


**Fig. 4.** Volume of a) all living trees, b) pine, c) spruce, and d) deciduous trees. Columns with different letters are significantly different at the $p<0.05$ level within regions (Tukey´s test). Letters in parentheses denote the significance test of adjusted volume (contrast analyses), where the effect of mean age of the stand and length of the growing season are taken into account as covariates. Error bars are standard deviations.

(Table 5) and volumes of *Picea* (Fig. 4). In Häme these volumes and volume of *Pinus* were generally significantly higher in near-natural and selectively logged stands compared to managed stands (Table 3 and Fig. 4). The deciduous volumes differed only between selectively logged and managed stands (Fig. 4).

In Kuhmo near-natural and selectively logged stands had higher volume of deciduous volumes compared to managed stands, but for *Pinus* volume the situation was the reverse (Fig. 4). The selectively logged stands had higher total volume than managed stands in Kuhmo (Table 5). In Vienansalo the near-natural and selectively cut stands did not differ from each other (Fig. 4, Table 5).

Overall, in Häme the volume of *Picea* was significantly lower in managed stands compared to that in near-natural and selectively logged stands (Fig. 4). On the other hand, in Kuhmo the volume of deciduous trees was significantly lower in managed stands compared to that in near-natural and selectively logged stands. The volume of deciduous trees was highest in the near-natural and selectively logged stands in Kuhmo and Vienansalo, and lowest in Häme (Fig. 4). The volume of deciduous trees in Häme was lowest in near-natural stands and in Kuhmo in managed stands.

**Table 6.** Number of saplings (30–130 cm) by tree species in the various forest classes from the three geographic areas. Standard deviations are in parentheses.

| | Häme | | | Kuhmo | | | Vienansalo | |
|---|---|---|---|---|---|---|---|---|
| | Near-natural (N=4) | Sel. logged (N=8) | Managed (N=45) | Near-natural (N=5) | Sel. logged (N=18) | Managed (N=9) | Near-natural (N=13) | Sel. logged (N=14) |
| Total number of saplings per hectare | 2100 (1168.3) | 1025 (941.5) | 1893.3 (2150.4) | 1850 (1887.8) | 2152.8 (1463.8) | 1388.9 (1642.2) | 5673.1 (7070.3) | 3661.7 (4118.6) |
| *Pinus sylvestris* | 0 | 12.5 (23.1) | 272.2 (548.3) | 0 | 2.8 (11.8) | 672.2 (1472.4) | 3000 (5885.4) | 1728.6 (3764.4) |
| *Picea abies* | 462.5 (143.6) | 331.3 (538.5) | 593.3 (1427.3) | 270 (175.3) | 355.6 (343.8) | 77.8 (180.5) | 342.3 (386.7) | 150 (165.3) |
| *Juniperus communis* | 1075 (810.9) | 68.8 (88.4) | 143.3 (431.9) | 580 (411.7) | 608.3 (669.8) | 127.8 (346.5) | 176.9 (345.0) | 150 (301.9) |
| *Betula* spp. | 25 (50) | 25 (26.7) | 127.8 (205.5) | 40 (41.8) | 50 (59.4) | 416.7 (1102.0) | 1007.7 (1577.3) | 328.6 (378.6) |
| *Populus tremula* | 0 | 100 (213.8) | 122.2 (269.8) | 60 (22.4) | 72.2 (144.7) | 38.9 (54.6) | 188.5 (400.1) | 146.4 (213.5) |
| *Salix caprea* | 25 (50) | 12.5 (23.1) | 205.6 (341.3) | 30 (44.7) | 13.9 (23.0) | 22.2 (26.4) | 46.2 (69.1) | 46.4 (53.6) |
| *Sorbus aucuparia* | 512.5 (434.7) | 468.8 (356.5) | 414.4 (813.4) | 870 (1408.7) | 1050 (1108.9) | 33.3 (50) | 565.4 (623.3) | 1067.9 (1207.9) |
| Total number of deciduous per hectare | 562.5 (520.2) | 612.5 (500.5) | 884.4 (1297.9) | 1000 (1475.6) | 1186.1 (1113.9) | 511.1 (1092.5) | 2153.9 (2433.3) | 1632.1 (1646.5) |

### 3.5 Regeneration

Between regions the mean density of saplings (height 30–130 cm) differed in near-natural stands of Häme and Kuhmo versus Vienansalo, and between stand types (near-natural versus selectively logged) in Vienansalo (Table 5). Sapling density was highest in the near-natural and selectively logged stands in Vienansalo: 5670 and 3660 $ha^{-1}$, respectively (Table 6). The mean sapling density in the other two regions varied from 2150 $ha^{-1}$ in the selectively logged stands of Kuhmo to 1020 $ha^{-1}$ in the selectively logged stands of Häme. As with total sapling number, *Pinus* saplings were most abundant in Vienansalo in the near-natural and selectively logged stands. No *Pinus* saplings were measured in the near-natural stands of Häme and Kuhmo. On the other hand, the density of *Picea* saplings was highest in Häme. The density of *Juniperus communis* was highest in the near-natural stands of Häme and in the near-natural and selectively logged stands of Kuhmo. The density of deciduous saplings was highest in the near-natural and selectively logged stands of Vienansalo, followed by the same forest classes in Kuhmo. The lowest density of the deciduous component was recorded in the managed stands of Kuhmo and in the near-natural and selectively logged stands in Häme (Table 6).

# 4 Discussion

### 4.1 Diameter Distributions and Structural Characteristics of Stands

The shapes of the pooled tree diameter distributions were different in managed versus near-natural and selectively logged stands. The tree diameter distributions, both in near-natural stands and in stands selectively logged in the past, were descending so that small trees were most abundant and the number of trees decreased with increasing tree size (Fig. 2). This pattern of diameter distribution has been documented in natural or near-natural *Pinus* dominated stands (Norokorpi et al. 1994, Zackrisson et al. 1995, Linder et al. 1997, Uotila et al. 2001, Rouvinen and Kuuluvainen 2005). In managed stands, the pooled diameter distributions were bimodal, evidently as a consequence of silvicultural thinnings (Fig. 2), which have also decreased the variability of tree diameters by favoring dominant trees of good timber quality and by removing both the largest and smallest tree individuals from the stand (Nyyssönen 1950, Uuttera et al. 1996, Uotila et al. 2001, Rouvinen and Kuuluvainen 2005).

In the near-natural stand category small-diameter trees were more abundant in Vienansalo compared to Kuhmo and Häme (Fig. 2). In addition, many of the small-diameter trees in Vienansalo were deciduous, whereas in Kuhmo and Häme *Picea* was dominant in the small-diameter classes (Fig. 3). These differences in near-natural stands are evidently related to factors favoring regeneration in Vienansalo in Russia, particularly more recent fires and more open stand structures, compared to Kuhmo and Häme in Finland (Pöntynen 1929, Lehtonen and Kolström 2002, Kuuluvainen et al. 2002, Rouvinen et al. 2002b).

Large trees with DBH > 40 were much more common in the near-natural stands and in stands selectively logged in the past compared to managed stands. Only one such tree per hectare was found in the managed stands of Häme and 5 in Kuhmo, while in the near-natural stands of Vienansalo there were 16 such trees per hectare. Linder and Östlund (1998) 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 a DBH > 40 cm. The scarcity of large trees in managed forests is evidently due to silvicultural measures aimed at homogenizing tree size distributions and stand structures. In near-natural forests, on the other hand, large *Pinus* often survive fire disturbances, 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). Overall, our results showed that managed forests lacked large-diameter trees, which are a characteristic feature of near-natural *Pinus* dominated forests (Linder and Östlund 1998, Pennanen 2002).

In Häme the near-natural and selectively logged stands had as many as 59 and 40 large trees with a DBH > 40 cm $ha^{-1}$, respectively, which was much more than in the near-natural stands in Vienansalo (16 $ha^{-1}$). The figures for Häme are also considerably higher than those reported in the review by Nilsson et al. (2002), suggesting that old-growth boreal forests typically have at least 20 living trees $ha^{-1}$ with a DBH > 40 cm. However, the reported densities of large trees (DBH > 40 cm) in *Pinus* dominated near-natural forests vary considerably, from 14 trees $ha^{-1}$ in central Sweden (Linder and Östlund 1998) up to 40 trees $ha^{-1}$ in Komi, Russia (Majewski et al. 1995). The unusually high number of large trees in Häme may also be because these stands were initially selected for protection due to their unusually large trees. That this is the case is also suggested by the high volume of living trees in these stands.

Structural diversity characteristics were more common in near-natural and selectively logged stands compared to managed stands. In managed stand there was a lack of large diameter trees with a damaged trunk apparently, due to thinnings and the younger age of trees (Table 3). Andersson and Östlund (2004) reported that in Sweden modern forest management has decreased the occurrence of old conifer trees (over 160 years) by as much as one third from the 1920s. In our study in near-natural stands and selectively logged stands dead or broken tree tops and damaged trunks were most common. These structural characteristics of old living trees are unique habitats for specific old-growth organisms (Bond and Franklin 2002), such as saproxylic beetles (Ranius and Jansson 2000).

There were 55 and 108 fire-scarred trees $ha^{-1}$ in the near-natural and selectively logged stands, respectively, in Vienansalo, while in the managed stands of Häme the average was less than one fire-scarred tree $ha^{-1}$ (Table 5). There were 21 fire-scarred trees $ha^{-1}$ in the selectively logged stands of Häme, which is similar to the result of Siitonen et al. (2000) who found 27 old fire-scarred living pines with a DBH > 40 $ha^{-1}$ in spruce dominated old-growth forests in (SW) Finland. Fire scars are partly cultural legacies from human ignited fires, and the decrease of these characteristics is concrete evidence of the decrease in forest fires.

### 4.2 Tree Species Composition and Volume

The proportion of *Pinus* out of the total volume was higher in the managed stands of Häme and Kuhmo compared to near-natural stands and stands selectively logged in the past in these regions (Fig. 3). This is evidently due to silvicultural thinnings in managed stands, which have favored *Pinus* and removed *Picea* and deciduous trees (e.g. Linder and Östlund 1998, Maltamo et al. 2000). On the other hand, the proportion of *Picea* was clearly higher, especially in the small diameter classes, in the near-natural and selectively logged stands of Häme and Kuhmo compared to the managed stands in these two regions. However, in Häme the proportion of *Picea* volume was significantly higher in natural and selectively logged stands compared to managed stands, but this was not the case in Kuhmo (Table 5). This difference is evidently related to the lack of fires during the past ca. 100 years in Finland, a situation that in the protection areas has favored the shade-tolerant fire-sensitive *Picea* over the shade-intolerant but fire-resistant *Pinus* (Pennanen 2002). With increasing time since fire, the regeneration conditions for light-demanding species, such as *Pinus* and deciduous trees, deteriorate, and *Picea* as a shade-tolerant species gains an advantage (Pöntynen 1929, Sirén 1955). In addition, past selective logging has increased the proportion of *Picea* because of its better competition ability inside the closed forest compared to *Pinus* (Sarvas 1944). The trend toward an increase in *Picea* dominance in forest reserves has also been reported in other studies (Haapanen and Siitonen 1978, Bradshaw 1993, Linder 1998, Lehtonen and Kolström 2002). Also studies from unmanaged forests in North America have shown species compositional shifts in the absence of fire (Minnish et al. 1995, Lesieur et al. 2002).

In the Vienansalo study sites the last fires occurred in 1941 and 1947 (Lehtonen and Kolström 2000) and there the fire-tolerant *Pinus* still had maintained a clear dominance over fire-intolerant species (see also Kuuluvainen et al. 2002). The volume of early-successional deciduous species was higher but that of *Picea* lower in Vienansalo, compared to Häme (Fig. 4). Also Jantunen et al. (2002) found that *Picea* dominated forests in Russian Karelia had a higher proportion of deciduous trees compared to similar forests in Finland. However, in our study the proportion of deciduous trees was higher, in near-natural and selectively logged stands of Kuhmo than in Häme. The scarcity of dead and living deciduous trees in near-natural (protected) areas of Häme is noteworthy as many endangered species are dependent on old deciduous trees as a habitat (Rouvinen et al. 2002a, Kouki et al. 2004).

*Juniperus*, an understory tree, was six times more abundant in the near-natural stands of Häme compared to those of Vienansalo (Table 6). High numbers of *Juniperus* in forest reserves have also been reported in Sweden (Hesselman 1935, Bradshaw and Hannon 1992). The abundance of *Juniperus* in the protected areas in Häme is probably related to the land use history of these forests. In earlier times slash-and-burn cultivation and later on commonly practiced cattle grazing in forests kept the forests relatively open, thus favoring *Juniperus* (Heikinheimo 1915, Hesselman 1935, Huttunen 1980, Bradshaw and Hannon 1992). Cattle also favored *Juniperus* and *Picea* by selectively grazing competing deciduous trees (Lampimäki 1939).

The average living tree volumes in near-natural and old selectively logged *Pinus* dominated stands, 333 and 255 $m^3\ ha^{-1}$ in Häme and 210 and 232 $m^3\ ha^{-1}$ in Kuhmo, are in agreement with some earlier results from *Pinus* dominated old-growth forests in the mid-Boreal vegetation zone. For example, Uotila et al. (2001) found 198–223 $m^3\ ha^{-1}$ of living trees in 'semi-natural' stands in eastern Fennoscandia. Östlund (1993) reported, based on an analysis of historical data, 314 $m^3\ ha^{-1}$ of living trees in old-growth *Pinus* forests in northern Sweden. In Swedish forest reserves Linder (1998) documented a mean volume of 239 $m^3\ ha^{-1}$ (ranging from 87 to 511 $m^3\ ha^{-1}$). Kardell (1998) reported an average living tree volume of 320 $m^3\ ha^{-1}$ on more productive sites which is very similar to what we found in protected areas in the Häme region.

In Häme, near-natural stands and stands selectively logged in the past had significantly higher living tree volumes compared to managed stands (Table 5). The near-natural and selectively logged stands in Häme had 2.1 and 1.6 times, and in Kuhmo 1.2 and 1.4 times more volume compared to managed stands, respectively. In Sweden Östlund (1993) also found large differences in living tree volumes between old-growth (314 $m^3$ $ha^{-1}$) and managed (156 $m^3$ $ha^{-1}$) *Pinus* dominated stands.

The higher volume of living trees in near-natural and selectively logged stands compared to managed stands was apparently due to differences in management history of the stands and older stand age (Table 3). For example, thinning, which is practiced as a standard silvicultural procedure, has modified the managed stands and decreased their volume (Vuokila 1984, Östlund 1993).

In near-natural stands the living tree volume declined significantly along the broad geographic gradient from Häme towards the more north-eastern Kuhmo and Vienansalo regions. This was true even when the effect of differences in mean stand age and length of growing season were taken into account. Thus differences in forest age and the northern, more continental and harsh climate in Vienansalo did not explain this trend. There was an over two-fold difference in average living tree volumes between Häme (333 $m^3$ $ha^{-1}$) and Vienansalo (151 $m^3$ $ha^{-1}$) (Fig. 4). These differences can be due to several reasons, including past selection criteria of protected areas (especially in Häme), differences in the occurrence of disturbances between these two regions, as well as climatic differences. First, it may well be that the small protected forest fragments in Häme are not representative of the original landscape, but were from the beginning exceptionally well-stocked areas containing large trees. It is possible that these areas were set aside for their special characteristics that conformed to the image of a 'primeval forest' (Helander 1949, Kalliola 1956). Second, in Häme the intensively utilized forests surrounding the protected areas have evidently also had an indirect impact on the protected forest e.g. by excluding fire as a disturbance factor (see Uotila et al. 2001, 2002). Finally, the more recent fire in Vienansalo (Lehtonen and Kolström 2002) may be one reason for the lower living tree volume, because recurrent fires may decrease the aboveground net primary production in boreal *Pinus sylvestis* forests (Wirth et al. 2002).

In general, the large differences in tree species proportions and volume between the protected areas in Finland and the more naturally dynamic landscape in Vienansalo in Russia raise questions to what extent the protected areas in southern Finland provide "natural" references for managed forests. Our results suggest that possibly the history of selection of these protection areas and the long-lasting human impact (e.g. fire suppression) have potential impacts on the structure of these areas as well as implications for their use as "natural benchmarks" for managed forests.

### 4.3 Regeneration

The overall density of saplings (height 30–130 cm) was nearly three times higher in the near-natural stands of Vienansalo compared to the managed stands of Häme (Table 6). Both *Pinus* and *Betula* saplings were more abundant in Vienansalo than in the managed stands of Häme and Kuhmo. As with the small-diameter trees (Fig. 3), the higher regeneration density in Vienansalo is likely to be a consequence of more recent fires and more open stand structure compared to the studied sites on the Finnish side (Kuuluvainen et al. 2002, Lehtonen and Kolström 2002).

There were up to 3000 *Pinus* saplings $ha^{-1}$ in the near-natural stands of Vienansalo. In contrast, the sampled near-natural stands in Häme had no *Pinus* or *Populus* saplings, and also less *Betula* and *Sorbus* compared to the Vienansalo stands (Table 6). The lack of regeneration of pioneer tree species in forest reserves has also been reported previously (Haapanen and Siitonen 1978, Linder 1998, Lehtonen and Kolström 2002, Kouki et al. 2004). This constitutes a major problem for the future management of protection areas because a large number of species is dependent on deciduous trees (Esseen et al. 1997, Kouki et al. 2004).

On the other hand, the near-natural stands of Häme had more *Picea* saplings than those of Vienansalo. This observation is parallel to the tree species proportions of larger trees (see Fig. 3). *Picea* is a shade-tolerant and late-successional species, which in the absence of fire is able to regenerate successfully in the forest understory and in small gaps (Sirén 1955, Bradshaw 1993, Kuuluvainen 1994).

# 5 Conclusion

The results showed that human impact in the form of forest utilization and fire exclusion has strongly modified and reduced the structural complexity of old *Pinus* dominated forests. Evidently, this can be attributed mostly to modern silviculture that has favored dominant *Pinus* trees of good timber quality and reduced the number of other tree species as well as the number of large, small, and damaged trees in managed stands. On the other hand, near-natural stands and stands selectively logged in the past often did not markedly differ in structural characteristics from each other. In *Pinus* forest restoration and management aimed at biodiversity conservation, there is a need to rehabilitate structural features, which are known to be important for biodiversity and which are now lacking from managed stands, such as large trees, trees with structural diversity characteristics, and old dying deciduous trees.

Near-natural stands and stands selectively logged in the past varied widely in their structures between the regions. This variability obviously reflects both their natural variability but also various combinations of pre-industrial land use and human impact, especially the presence or absence of fire disturbance along the examined geographic gradient. Thus, the picture is more complex than has previously been acknowledged regarding what is a “natural” forest. Finally, it may be questionable to use small protected forest fragments surrounded by intensively managed forest as “natural benchmarks” in research and when developing strategies for sustainable forest management, forest restoration and nature conservation.

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