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How homogeneous is the boreal forest? Characteristics and variability of old-growth forest on a *Hylocomium–Myrtillus* site type in the Pallas-Yllästunturi National Park, northern Finland

Inari Ylläsjärvi & Timo Kuuluvainen*

*Department of Forest Ecology, P.O. Box 27, FI-00014 University of Helsinki, Finland (*corresponding author's e-mail: timo.kuuluvainen@helsinki.fi)*

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An adequate understanding of an old-growth forest structure and its variability is needed for forest conservation and restoration. We studied the local scale structural variability of boreal old-growth forests on a *Hylocomium–Myrtillus* site type in the Pallas-Yllästunturi National Park in northern Finland. Principal component analysis (PCA) revealed that the main directions of structural and compositional variability were related to variables describing the total volume of coarse woody debris (CWD), volumes of living and dead *Pinus sylvestris* and volume of deciduous CWD. An average, living tree volume was 141.5 m^3 ha^{-1}, varying among the 252 sample plots from 15.3 to 442.0 m^3 ha^{-1}. The mean CWD volume was 30.0 m^3 ha^{-1} (0–99.3 m^3 ha^{-1}). Downed and standing CWD comprised on average 64.6% and 35.4% of the total CWD volume, respectively. In general, the diameter distributions of living, standing and downed dead trees followed a negative exponential shape. Our results demonstrate high variability in structure and composition of old-growth forests on a northern boreal mesic *Hylocomium–Myrtillus* site type. This natural variability should be taken into account in forest restoration and management at landscape level.

Key words: biodiversity, coarse woody debris, forest restoration, natural forest, natural range of variability, stand structure, structural heterogeneity

Introduction

Boreal forests have traditionally been considered as relatively simple and homogeneous ecosystems. However, there is increasing evidence that especially late-successional boreal forests exhibit fine-scale complex heterogeneity in their structure and dynamics (e.g. Qinghong & Hytteborn 1991, Lilja *et al*. 2006). This heterogeneity is affected by partly stochastic allogenic disturbances such as forest fires with different severities (Zackrisson 1977, Lampainen *et al*. 2004), but especially by small-scale autogenic gap disturbances (Kuuluvainen 1994). The pres-

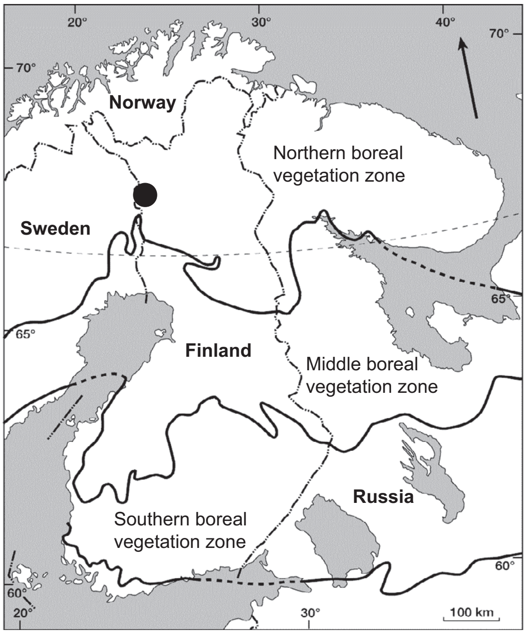

Fig. 1. Geographical location of the Pallas-Yllästunturi National Park. The borders of the vegetation zones are based on Kalela (1961) and Ahti *et al.* (1968).

ence of large living and dead trees, an abundance of decaying wood and a multi-layered tree canopy are regarded as essential structural characteristics of old boreal forests (Esseen *et al*. 1997, Kneeshaw & Gauthier 2003, Rouvinen & Kouki 2008).

Because of their complexity, the structure of a natural forest cannot be simply described, for example, as mean values; rather the aim is to define the crucial forest habitat characteristics and their limits of natural variability (Landres *et al*. 1999). This means that even on a given site type and in a given area a natural forest typically exhibits variability in structure and dynamics as a function of factors such as slope, aspect and disturbance history. However, this variability expressed at landscape scale is still poorly understood in many forest ecosystem types. This is also the case considering old-growth forests on a mesic *Hylocomium–Myrtillus* site type (*sensu* Cajander 1926) in northern Fennoscandia, although the main developmental and structural features of this important and wide-spread forest ecosystem type have been previously studied (Sirén 1955, Hyvärinen & Sepponen 1988, Wallenius *et al*. 2005, Doležal *et al*. 2006, Lilja *et al*. 2006).

It has been proposed that the natural forest can be used as a model for restoration and management of biodiversity in managed forests (Haila *et al*. 1994, Fries *et al*. 1997, 1998, Angelstam 1998, Lähde *et al*. 1999, Kuuluvainen 2002). However, an adequate landscape-level understanding of natural forest structure and its variability is needed for forest conservation and restoration. Natural variability, both spatial and temporal, has long provided ecologists insight into understanding ecological processes and the implications of ecological change (Landres *et al*. 1999). Maintaining forest structure within a natural range of variability, or restoring current conditions to that state, are possible situations that managers can face in future (Landres *et al*. 1999).

The purpose of this study was to examine the structure and its variability of old-growth forests growing on one forest site type, the mesic *Hylocomium–Myrtillus* site type in the northern boreal zone in the Pallas-Yllästunturi National Park. This area is one of the largest remnants of natural or near-natural forests in Finland (Aksenov *et al*. 1999). The specific aims of the study were to assess on one forest site type (1) the characteristics and variability of tree species composition, diameter distribution and living tree volume; and (2) the volume, quality and variability of coarse woody debris (CWD).

Material and methods

Study area

The study was carried out in northwestern Finland in the Pallas-Yllästunturi National Park (total area 1020 km^2) (Fig. 1). More specifically, the sites of sampling are located in the Ylläs–Aakenus region at altitudes of 217–386 m a.s.l. in mountainous landscape. This region is situated in the northern boreal zone (ca. 67°42´N, 24°12´E) (*sensu* Ahti *et al*. 1968), including areas that still remain in a natural state. The mean annual temperature is –1 °C. The annual precipitation is about 550 mm and the effective temperature sum (5 °C threshold) varies from 650 to 700 dd. (Vadja & Venäläinen 2003).

The forest vegetation is influenced by a considerable variability in both the bedrock and the topography. On mineral soils in the Ylläs-Aakenus region, the *Vaccinium* and *Myrtillus* site types (*sensu* Cajander 1926) are generally the dominating vegetation types and spruce (*Picea abies*) is usually the dominating tree species. *Picea*-dominated forests cover ca. 60% of the landscape. According to previous biological surveys, the forests exhibit notable structural diversity and in ca. 80% of the stands the dominating canopy trees are over 160 years old (Kuusisto 2003). Nearly 90% of the forests in the region are considered unmanaged, and they show no or few signs of logging (Kuusisto 2003). Thus, the forests can be regarded as close to their natural state because of the relatively small number of trees removed and because natural forest dynamics have prevailed for a long period of time.

Unfortunately, the forest history of the region has not been thoroughly studied. This also applies to natural disturbances, but it is generally regarded that fire and wind are the most important allogenic disturbance agents (Kuuluvainen 1994). A recent study showed that fire has been a less common disturbance in northern Finland than hitherto thought: in *Pinus sylvestris*-dominated forests the fire rotation has been ca. 350 years (Wallenius *et al.* 2008) and obviously longer in less fire-prone *Picea*-dominated forests (e.g. Hyvärinen & Sepponen 1988). Long fire rotation may also explain predominance of old-growth forest in the Ylläs-Aakenus region and indicates that small-scale autogenic disturbances play a major role in forest dynamics (Kuuluvainen 1994). However, past fires may still be an important underlying cause of structural and compositional variability of forests observed in the region (Lilja *et al.* 2006).

Site selection and data collection

The sampling of stands for data collection was based on pre-established polypore inventory lines crossing the landscape. The polypore inventory was conducted in 1999–2001 (Niemelä & Dai 2000, Niemelä *et al.* 2000, Niemelä & Kinnunen 2002). The search for stands for the polypore inventory was based on information from maps and local expertise. The stands are a representative sample of the landscape, although they do not strictly represent a random or systematic sample (Fig. 2).

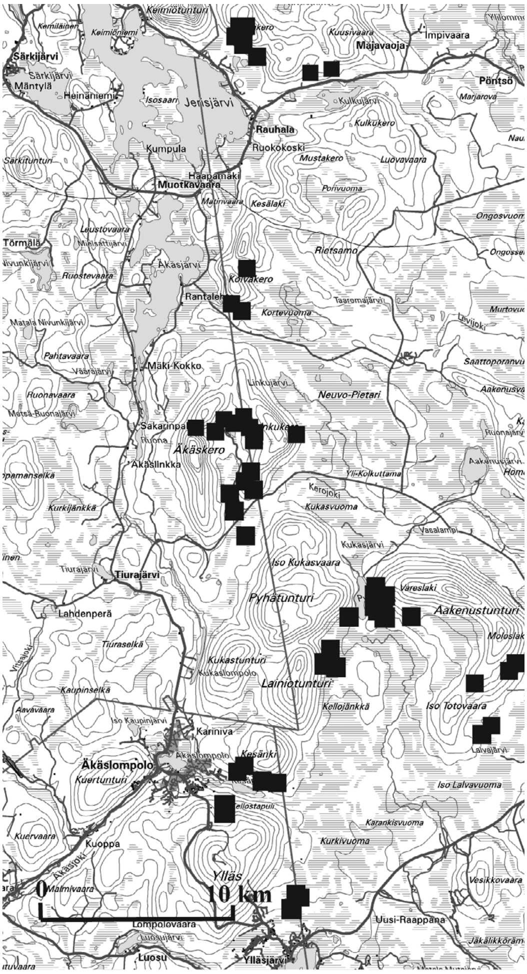

Fig. 2. Map of the study area showing the locations of the inventory lines. Reproduced with permission of the National Land Survey of Finland (224/MML/09).

The sample plots accepted for the present study fulfilled the following requirements: (1) they were located on a mesic *Hylocomium–Myrtillus* site type, and (2) no cut stumps existed on the sample plots. Data on the forest structure were collected from 252 sample plots located in 55 forest stands. Of 252 sample plots, 150 were dominated by *Picea abies* (≥ 50% of living tree volume), 51 by *Pinus sylvestris*, 21 by *Betula* spp., and 30 sample plots occurred on mixed forest stands. Typically for *Hylocomium–Myr-*

tillus site type, the understorey was dominated by mosses (*Hylocomium splendens*, *Pleurozium schreberi*), blueberry and lingonberry (*Vaccinium myrtillus* and *V. vitis-idaea*).

The measurements were conducted in 4–7 sample plots per forest stand. In each stand, the sample plots were approximately evenly distributed along the pre-established polypore inventory line using a rough step measure. As far as it was possible, the first circular plots in each stand were located in the forest stand interior to avoid potential edge effects. The number of sample plots per polypore inventory line within a forest stand varied in relation to polypore inventory line length as follows: four plots in 0–400 m lines, five plots in 400–700 m lines, six plots in 700–1000 m lines, and seven plots in > 1000 m lines.

For each sample plot the basal area (m^2 ha^{-1}) of living tree species was estimated using a relascope. All recorded living trees were further classified into five diameter (diameter at breast height; 1.3 m DBH) classes (2–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, > 40 cm), based on visual estimation. The CWD measurements were conducted on circular sample plots (radius of 9.78 m; 0.03 ha). Rapid measurements of the distance were made possible by a Vertex-measuring device, also used to measure tree heights of broken snags. CWD units originating within the plot were included in the measurements. Six categories of CWD were recorded and measured: (1) intact standing dead trees, (2) broken snags (length > 1.3 m), (3) natural stumps (length < 1.3 m), (4) uprooted downed logs, (5) downed logs broken at base, (6) pieces of downed logs or tree tops.

From each circular sample plot, all intact standing dead trees, broken snags and downed logs, with a minimum diameter of ten centimetres (10 cm) at breast height (1.3 m DBH), were measured. A height of 1.3 metres was considered the threshold between a stump and a broken snag. All stumps, pieces of downed logs and tree tops with a mid-diameter (diameter at middle point of length) of over ten centimetres (10 cm) were also included. Tree species, diameter (DBH or mid-diameter) and decay stage were recorded for each dead tree. The diameters of all trees were estimated with the accuracy of one centimetre (1 cm). Dead trees which were not possible to identify by tree species in the field because of advanced decay stage were counted as “unidentified tree species”. The height of broken snags and stumps was recorded. The length of pieces of downed logs with missing crowns or stumps was measured. A group of stems was considered as one tree if the stems were connected from their base; if not, they were counted as separate trees. The original diameter of a broken stump was roughly estimated and reported along with an estimation of the remaining volume percentage of its original volume. Downed logs which were broken into many pieces were considered as one.

Classification of CWD according to decay stage was done using a five-stage classification. The most important criterion was the hardness of the wood, which reflects its density, that is, how far the decaying process has proceeded. The hardness of wood can considerably vary in different parts of the log so the decay stage was determined according to an average, with emphasis on the basal part. The classification generated by Karjalainen and Kuuluvainen (2002) was used as a basis and further modified. This decay stage classification was used to estimate both standing and downed trees:

1. Recently dead (during the past year), phloem still fresh (no holes of bark beetles visible).
2. Phloem eaten, a knife penetrates only a few millimetres.
3. A knife penetrates up to two centimetres (2 cm). Twigs and small branches fallen down. On coniferous trees, bark is loosened or missing.
4. A knife penetrates from two to five centimetres (2–5 cm).
5. The blade of a knife can be easily pushed all the way to the wood. The log is still easily perceived. Knife penetration represents averages of several pricks per each piece of CWD.

Calculations and analysis methods

The volumes of both living trees and intact standing and downed dead trees were estimated using the volume equations of Laasasenaho (1982) for *Pinus*, *Picea* and *Betula*. Equations using both

DBH and height as independent variables were used. The equation for *Betula* was also used to estimate the volumes of other deciduous trees. Volumes of stumps and pieces of logs were calculated on the basis of their length and mid-diameter using the formula for the volume of a cylinder. The volume of stumps was included in the volume of downed dead trees.

The volume estimates for broken snags were computed using volume integrals of taper equations (Laasasenaho 1982). This method does not require information on the diameter at the snapping point of a broken snag, because the diameter at any height of a tree can be estimated with a taper function. What is needed is the DBH, snapping height and original height (height before snapping) of a tree. The height of living, standing and downed dead trees, required by the volume equations (Laasasenaho 1982), and the original height of broken snags required by volume integrals of the taper equations of Laasasenaho (1982), were estimated based on constructed regression models (Eqs. 1, 2 and 3) between tree DBH (cm) and tree height (cm).

$$\text{Height}(\textit{Picea abies}) = 134.332\text{DBH}^{0.767} \quad (1)$$
$$R^2 = 0.782, P < 0.001$$

$$\text{Height}(\textit{Pinus sylvestris}) = 140.787\text{DBH}^{0.713} \quad (2)$$
$$R^2 = 0.774, P < 0.001$$

$$\text{Height}(\textit{Betula}\text{ spp.}) = 213.795\text{DBH}^{0.584} \quad (3)$$
$$R^2 = 0.407, P < 0.001$$

The used DBH and tree height data for constructing the regression model for *Pinus* (Eq. 2) was received from the 9th National Forest Inventory (NFI). The sample tree data were from the municipalities of Kolari, Kittilä and Muonio. The sample tree data for *Picea* and *Betula* were received from earlier field measurements conducted by Tuomas Aakala in Pyhäjärvi and Pallas (unpubl. data). The regression model for *Betula* was also used to estimate the heights for other deciduous trees.

Diameter distributions of trees were constructed and density (trees ha^{-1}) calculated for living trees, standing dead trees and downed logs. The different units (such as stumps, downed logs, tree tops) of the same tree individual were counted as one tree. In the case of *Betula* and other deciduous trees, both intact standing dead trees and broken snags with tree tops were classified as standing dead trees. For conifers and unidentified tree species, only intact standing dead trees were classified as standing dead trees; broken snags (with tree tops) were classified as downed dead trees. This was justified by an assumed bias of volumes. Pieces of downed logs or tree tops without a known stump, or stumps without a known tree top, were excluded from the diameter distributions. The volume calculations of broken snags were performed using Mathematica 4.0. Other calculations were performed using MS Excel 2003.

Variability among the 46 continuous forest structure variables was reduced using Principal Component Analysis (PCA) (Appendix). PCA was used to reveal potential relationships between different variables, and clusters among sample plots. PCA is used to transform the original variables to a new set of Principal Components (PCs). The first PC explains most of the variability in the data; the second PC explains the next largest variability, and so on. PCs can be used to construct graphics to give an overview of what forest structure variables are causing differences between sample plots. At the same time they show how individual stands differ from each other in habitat characteristics. PCA gives information on: (1) the site scores of each plot, and (2) the loadings of each forest structure variable. The site scores in relation to the PCs reveal the differences between the individual sample plots. The variable loadings in relation to PCs indicate the significant role the individual variables play in causing differences in forest structure variables between sample plots. Spearman's non-parametric correlation was used to analyse the relation between e.g. total CWD volume and living tree volume. Statistical analyses were performed using SPSS™ ver. 13 and R ver. 2.4.1.

Results

Variability of forest structure

In the principal component analysis (PCA) each of the three first PCs explained more than 10% of

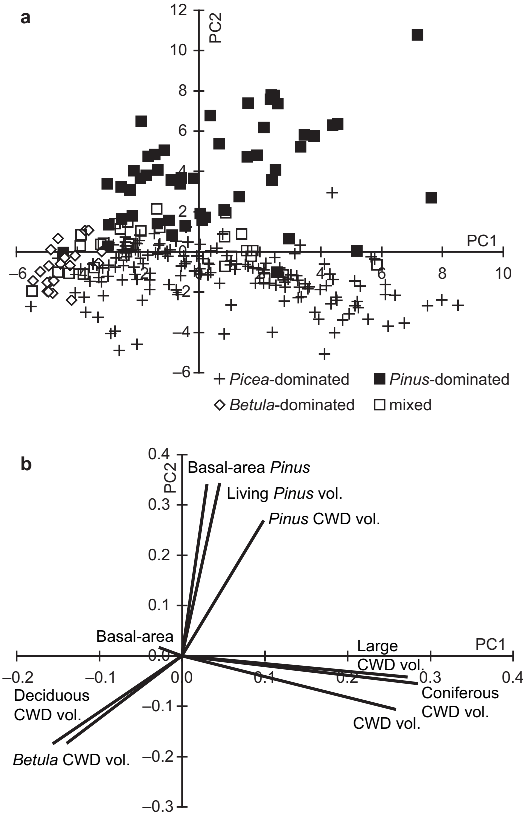

Fig. 3. (**a**) Scores of sample plots divided into tree species dominance types; *Picea*-dominated (n = 150), *Pinus*-dominated (n = 51), *Betula*-dominated (n = 21) and mixed sample plots (n = 30), and (**b**) loadings of forest habitat variables, in relation to the first two principal components axes.

the variability in the estimated variables (Table 1). Together these three components explained 47.9% of the total variability in the data. PC1 explained 23.6% of the total variability and was related positively to variables describing the amount of CWD (Fig. 3b). The volumes of coniferous CWD, large CWD (DBH ≥ 20 cm) and total CWD had the highest and positive loadings on PC1. PC2 explained 13.7% of the variability. The volumes of living and dead *Pinus* and the basal area of *Pinus* had the highest loadings on PC2 (Fig. 3b). The third component (PC3) explained 10.6% of the variability. It was positively related to the volume of deciduous CWD and basal area of living trees. PCA ordination clearly differentiated the sample plots based on the dominant tree species (PC2) (Fig. 3a and b). It also showed that *Betula*-dominated and mixed plots were missing on the right hand side of the ordination, implying that they did not attain as high CWD volumes (PC1) as found in *Picea*- and *Pinus*-dominated stands.

Table 1. Summary of principal component analysis (PCA) of 46 continuous forest structure variables. The proportion of variance in the forest structure data that is explained by the first three components is presented.

	PC1	PC2	PC3
Proportion of variance	0.236	0.137	0.106
Cumulative proportion	0.236	0.373	0.479

Living trees

The mean volume of living trees was 141.5 m^3 ha^{-1}, varying among the 252 sample plots from 15.3 to 442.0 m^3 ha^{-1} (Table 2). The mean density of living trees (DBH ≥ 2 cm) was 1144 ha^{-1}, varying among sample plots from 129 to 5371 ha^{-1}. *Picea* dominated the volumetric proportion of living trees (50.3%). *Pinus* was clearly more important on volume-basis (32.6%) than on density-basis (6.4%), indicating a relatively large mean DBH. *Betula* accounted for 15.4% of living tree volume.

On *Picea*-dominated plots, the mean living tree volume was 114.0 m^3 ha^{-1}, varying from 15.3 to 247.9 m^3 ha^{-1}. On *Pinus*-dominated sample plots the mean volume was the highest (239.4 m^3 ha^{-1}, range 95.9–442.0 m^3 ha^{-1}), whereas on *Betula*-dominated plots it was the lowest (122.1 m^3 ha^{-1}, range 47.7–178.7 m^3 ha^{-1}) (Table 2).

On mixed, *Picea*- and *Pinus*-dominated plots, the diameter distributions of *Picea* and *Betula* had a negative exponential shape, in which small trees were most abundant and the density of trees decreased with increasing diameter (Fig. 4a, b, d). However, on *Pinus*-dominated plots the diameter distribution of *Pinus* trees was unimodal, with a frequency peak at the DBH-class 20–30 cm (Fig. 4b). Also, on *Betula*-dominated plots the diameter distribution was unimodal when all the tree species were combined (Fig. 4c).

Coarse woody debris

On average, the total CWD volume (standing and downed combined) per plot was 30.0 m^3 ha^{-1}, varying strongly between the sample plots (0–99.3 m^3 ha^{-1}) (Table 3). The mean density of dead trees (standing and downed dead trees combined) was 148 trees ha^{-1} varying from 0 to 433 ha^{-1}. *Picea* dominated, accounting for 66.3% of the total CWD volume and 40.9% of the total dead tree density. The volume of dead *Betula* trees represented 16.0% of the total CWD volume, corresponding to that of the living tree volume.

The mean volume of standing dead trees was 10.6 m^3 ha^{-1}, with among-plot variability from 0 to 88.1 m^3 ha^{-1} (Table 3). The mean volume of downed logs was 19.4 m^3 ha^{-1}, varying from 0 to 91.8 m^3 ha^{-1}. On average, 35.4% of the total CWD volume was standing dead wood

Table 2. Characteristics of living tree populations by tree species as a whole (n = 252) and by tree species dominance types; *Picea*-dominated (n = 150), *Pinus*-dominated (n = 51), *Betula*-dominated (n = 21) and mixed sample plots (n = 30).

	Picea abies	*Pinus sylvestris*	*Betula* spp.	Other deciduous trees	Total
All sample plots (n = 252)					
Proportion (%)					
by volume	50.3	32.6	15.4	1.7	100
by number	56.6	6.4	34.9	2.2	100
volume (m^3 ha^{-1})					
mean	71.2	46.1	21.8	2.4	141.5
SD	41.4	81.3	22.1	6.5	68.6
trees ha^{-1}					
mean	647	73	399	25	1144
SD	599	196	511	103	808
Picea-dominated					
volume (m^3 ha^{-1})					
mean	91.0	5.7	16.0	1.3	114.0
SD	37.9	14.6	14.1	6.2	39.6
trees ha^{-1}					
mean	756	13	256	21	1047
SD	620	55	366	121	767
Pinus-dominated					
volume (m^3 ha^{-1})					
mean	40.7	184.8	12.8	1.0	239.4
SD	29.9	82.2	11.1	2.8	70.9
trees ha^{-1}					
mean	463	259	444	9	1175
SD	541	333	550	25	726
Betula-dominated					
volume (m^3 ha^{-1})					
mean	32.7	6.4	74.6	8.4	122.1
SD	19.0	13.4	19.2	6.5	35.2
trees ha^{-1}					
mean	474	12	945	50	1481
SD	489	30	495	43	716
Mixed plots					
volume (m^3 ha^{-1})					
mean	51.2	39.9	29.2	6.3	126.6
SD	22.8	29.9	18.3	8.8	43.3
trees ha^{-1}					
mean	537	95	654	56	1342
SD	550	202	698	110	1093

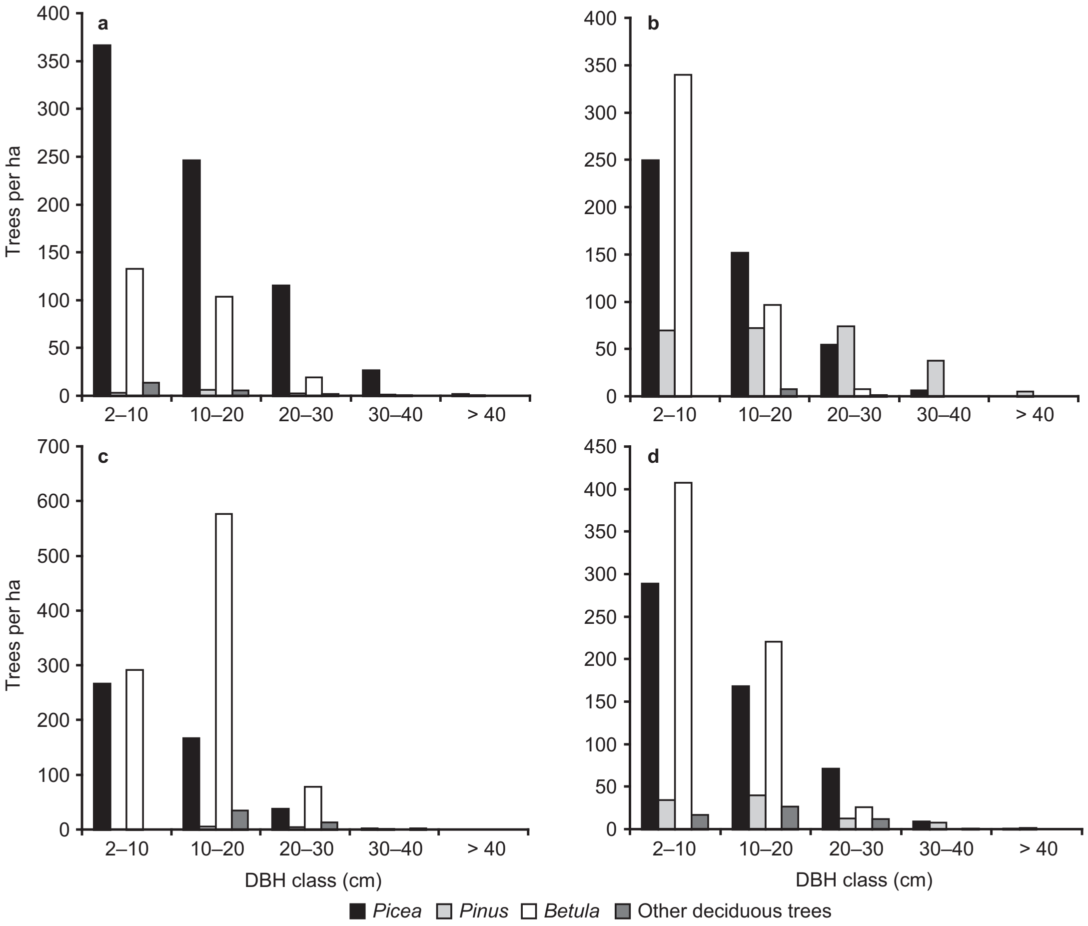

Fig. 4. Diameter class distributions of living tree species (**a**) on *Picea*-dominated plots (*n* = 150); (**b**) on *Pinus*-dominated plots (*n* = 51); (**c**) on *Betula*- dominated plots (*n* = 21); and (**d**) on mixed plots (*n* = 30).

Table 3. Volumes of total, standing and downed CWD in the sample plots as a whole (*n* = 252) and by tree species dominance types; *Picea*-dominated (*n* = 150), *Pinus*-dominated (*n* = 51), *Betula*-dominated (*n* = 21) and mixed sample plots (*n* = 30). The proportions (%) of the total CWD volume are presented in parentheses.

CWD volume	All plots	*Picea*-dominated	*Pinus*-dominated	*Betula*-dominated	Mixed
Total					
mean	30.0 (100)	34.5 (100)	28.7 (100)	12.7 (100)	22.0 (100)
min.	0.0	0.0	0.0	0.1	0.0
max.	99.3	99.3	97.1	25.6	71.5
SD	24.5	25.8	23.8	6.4	19.7
Standing					
mean	10.6 (35.4)	10.0 (29.1)	15.3(53.3)	4.2 (33.2)	10.1 (45.9)
min.	0.0	0.0	0.0	0.0	0.0
max.	88.1	64.9	88.1	10.4	45.2
SD	14.9	14.1	19.7	3.0	13.0
Downed					
mean	19.4 (64.6)	24.4 (70.9)	13.4 (46.7)	8.5 (66.8)	11.9 (54.1)
min.	0.0	0.0	0.0	0.0	0.0
max.	91.8	91.8	47.4	18.3	50.6
SD	20.5	23.1	13.6	5.2	14.3

and 64.6% downed dead wood (Table 3). On the *Picea*-dominated plots, the mean volume of CWD was highest (34.5 m^3 ha^{-1}, range 0–99.3 m^3 ha^{-1}), of which 70.9% was downed dead wood (Table 3). On the *Pinus*-dominated plots, the mean volume of CWD was 28.7 m^3 ha^{-1} (range 0–97.1 m^3 ha^{-1}), 46.7% being downed dead wood. On the *Betula*-dominated plots, the mean volume of CWD was the lowest 12.7 m^3 ha^{-1} (0.1–25.6 m^3 ha^{-1}), 66.8% being downed dead wood. The proportions of standing and downed CWD varied strongly between sample plots (from 0% to 100%).

The CWD proportion of the living tree volume was on average 21.2% (range: 0%–142.5%); on *Picea*-dominated plots the mean proportion was 30.2% (0%–142.5%), on *Pinus*-dominated 12.0% (0%–65.6%), on *Betula*-dominated 10.4% (0.3%–21.0%) and on mixed sample plots 17.4% (0%–50.2%). Total CWD volume comprised on average 17.5% of the total tree volume (171.5 m^3 ha^{-1}; living and dead wood combined), varying from 0% to 58.8% among the 252 sample plots; on the *Picea*-dominated sample plots this average proportion was 23.2%, on *Pinus*-dominated plots 10.7%, on *Betula*-dominated 9.4% and on mixed plots 14.8%, varying highly between sample plots.

Taking into account all sample plots, the dependency between dead and living tree volumes was apparent: the Spearman correlation coefficient r_S was 0.135 ($P = 0.032$). On *Picea*-dominated sample plots ($r_S = 0.226$, $P = 0.005$) and mixed sample plots ($r_S = 0.380$, $P = 0.038$) the correlation was also apparent. Conversely, on *Pinus*- or *Betula*-dominated plots we did not detect any relationship between the amount of CWD and living trees.

Based on the pooled plot data, the volume of large CWD (DBH ≥ 20 cm) was on average 20.0 m^3 ha^{-1}, representing 66.7% of the total CWD volume (Table 4). The number of large dead trees (DBH ≥ 20 cm) ha^{-1} represented 35.3% of the total dead tree density. Large dead conifers (DBH ≥ 30 cm) and large dead deciduous trees (DBH ≥ 20 cm) ha^{-1} represented 9.4% and 3.7% of the total dead tree density, respectively. The mean dead tree DBH was highest (20.5 cm) on *Pinus*-dominated plots and lowest (13.3 cm) on *Betula*-dominated plots. There were only slight differences between the *Pinus*- and *Picea*-dominated sample plots in the volume and density of large CWD. In contrast, on *Betula*-dominated sample plots, the volume of large CWD accounted for only 4.9% of the total CWD volume.

In general, the diameter distributions of standing and downed dead trees followed a pattern in which small trees were most abundant, and the density of trees decreased as diameter increased (Fig. 5). On *Picea*-dominated plots most standing dead *Picea* and *Betula* trees belonged to the smallest diameter class (DBH 10–19 cm) (Fig. 5a). The number of trees diminished with increasing DBH in all tree species except *Pinus*, which had a slightly higher number of trees in the DBH class of 20–29 cm than in the 10–19 cm class. The diameter distribution of downed dead trees followed a more or less similar pattern, although *Picea* was an exception, having more trees in the DBH class of 20–29 cm than in the 10–19 cm class (Fig. 5b). On *Pinus*-dominated plots, the number of standing *Pinus* trees diminished with increasing DBH, whereas standing *Picea* had a slightly higher number of trees in the DBH class of 20–29 cm than in the 10–19 cm

Table 4. Mean CWD diameter, volume of large dead trees (DBH ≥ 20 cm), large dead trees (DBH ≥ 20) ha^{-1}, large dead conifers (including *Picea* and *Pinus* ≥ 30 cm) ha^{-1} and large deciduous trees (including *Betula* and other deciduous trees DBH ≥ 20 cm) ha^{-1} in the sample plots as a whole (n = 252) and by tree species dominance types. The proportions (%) of total CWD volume or total number of dead trees ha^{-1} are presented in parentheses.

	All plots	*Picea*-dominated	*Pinus*-dominated	*Betula*-dominated	Mixed
Mean CWD diameter (cm)	18.7	19.3	20.5	13.3	16.1
Large dead tree volume (DBH ≥ 20 cm) (m^3 ha^{-1})	20.0 (66.7)	23.6 (68.5)	21.0 (73.4)	0.6 (4.9)	13.7 (62.1)
Large dead trees (DBH ≥ 20 cm) ha^{-1}	52.3 (35.3)	63.9 (41.5)	46.3 (41.3)	4.8 (2.5)	37.7 (25.4)
Large dead conifers (DBH ≥ 30 cm) ha^{-1}	13.9 (9.4)	15.5 (10.1)	17.6 (15.7)	0.0 (0.0)	8.9 (6.0)
Large dead deciduous trees (DBH ≥ 20 cm) ha^{-1}	5.5 (3.7)	7.5 (4.9)	2.6 (2.3)	3.2 (1.6)	2.2 (1.5)

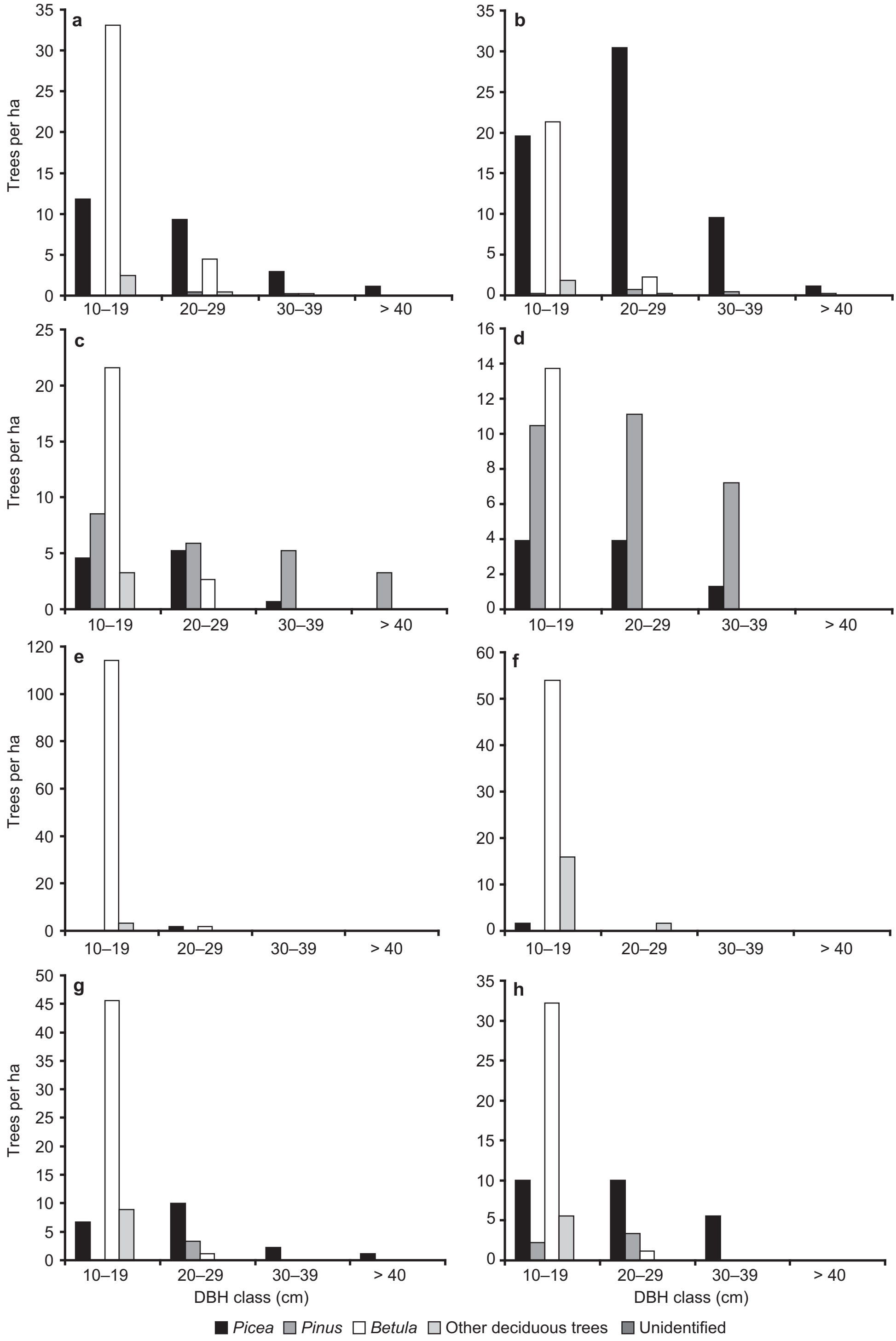

Fig. 5. Diameter class distributions of (**a**) standing dead tree species on *Picea*-dominated plots (n = 150); (**b**) downed dead tree species on *Picea*-dominated plots; (**c**) standing dead tree species on *Pinus*-dominated plots (n = 51); (**d**) downed dead tree species on *Pinus*-dominated plots; (**e**) standing dead tree species on *Betula*-dominated plots (n = 21); (**f**) downed dead tree species on *Betula*-dominated plots; (**g**) standing dead tree species on mixed plots (n = 30), and (**h**) downed dead tree species on mixed plots.

class (Fig. 5c). In downed dead tree distribution, *Pinus* had more trees in the DBH class of 20–29 cm than in the 10–19 cm class (Fig. 5d).

Taking all forms of CWD into account, the decay stage distribution of dead wood was variable, decay stage 2 being most abundant (45.0%), followed by stages 3 (20.1%), 4 (16.4%) and 5 (15.5%). Decay stage 1 (cambium still remains) was the least (3.0%) represented class. On average, downed CWD was more decayed than standing CWD. About 85.5% of standing CWD volume belonged to the first decay stages 1 and 2. In downed CWD, decay stages 2, 3, 4 and 5 were quite evenly distributed (23.9%–24.6%), while decay stage 1 accounted for less than 3% of downed CWD volume.

The decay stage distributions of different tree species were relatively similar. *Picea* and *Betula* were represented in all decay stages. Interestingly, the average *Pinus* CWD volume represented in decay stage 1 was only 0.1%. In *Picea* CWD, decay stage 2 was most abundant, consisting of 46.1% of *Picea* CWD volume. Only 3.3% of *Picea* CWD volume belonged to stage 1; the rest of the decay stages were rather evenly distributed (16.8%–17.0%). Decay stage 2 was also most abundant in *Pinus* CWD, consisting of 48.2% of the CWD volume. In *Betula* CWD, about one-third of the volume belonged to decay stages 2 (35.5%) and 3 (28.2%).

Discussion

Main directions of structural variability

Structural and compositional variability in old-growth forests on a single site type can be related to factors such as variability in past disturbance regime, time since last disturbance and topographic location (Lilja *et al*. 2006). In the studied old-growth stands on a *Hylocomium–Myrtillus* site type the main dimensions of local scale (0.03 ha) variability were related to total CWD volume, both living and dead *Pinus* volumes, and deciduous CWD volume. Variables describing these structural properties explained almost half of the total variability of the data in the PCA analysis.

The relation between deciduous CWD volume and basal area of living trees (PC3) can be thought to result from the higher mortality of *Betula* trees in denser stands with increased competition for light. The PCA ordinations indicated also that CWD volumes on *Betula*-dominated and mixed plots were not as high as on *Picea*- and *Pinus*-dominated sample plots; this was also shown by mean and maximum values of CWD volumes. This may be explained by the smaller mean DBH of dead trees on *Betula*-dominated and mixed plots, which is supported by the fact that mean densities of dead wood were somewhat similar on *Betula*-dominated and mixed sample plots as compared with those on *Picea*- and *Pinus*-dominated plots.

Living stand structure and its variability

The mean amount of living tree volume (141.5 m^3 ha^{-1}) recorded in the present study for the old-growth forest on a *Hylocomium–Myrtillus* site type agrees well with earlier the results ranging between 80 and 197 m^3 ha^{-1} on mesic site types, from more or less equal latitudes in northern boreal old-growth forests in Finland (Siitonen 1994, Sippola *et al*. 2002, Lilja *et al*. 2006).

In natural conditions in Fennoscandia, forests are composed mainly of mixtures of *Picea, Pinus* and *Betula* and species mixture varies with site type, disturbance history and successional stage (Linder *et al*. 1997, Pitkänen 1999, Axelsson & Östlund 2001, Kuuluvainen 2002). In the present study the site type and successional stage were rather similar in all the sample plots studied. Thus, the considerable variability in tree species dominance may be partly explained by disturbance history, which is unfortunately mostly unknown.

In addition to species composition, diameter distribution is considered to be a key characteristic when classifying stands according to their structure (Hasse & Ek 1981, Lähde *et al*. 1999), as it is the primary characteristic for within-stand diversity (Norokorpi *et al*. 1994, Lähde *et al*. 1995, 1999). On *Picea*-dominated plots, the diameter class distribution for dominant *Picea* followed a negative exponential shape. This pattern suggests a continuous regeneration and recruitment of new individuals (Kuuluvainen *et al*. 1998a), indicating that their proportion in the stand was stable. This conclusion was also supported by the general recognition that in non-pyrogenous spruce taiga both tree size and age distributions follow the above-mentioned pattern in the absence of severe disturbances (Dyrenkov & Manko 1991, Kuuluvainen *et al*. 1998a).

Pinus-dominated forests typically consist of different age cohorts, which form an uneven-sized stand structure (Lähde *et al*. 1994, Kuuluvainen *et al*. 2002). In the present study, the diameter class distribution on *Pinus*-dominated plots followed a negative exponential curve when all the tree species were combined. However, the dominant *Pinus* followed a unimodal diameter distribution, whereas *Picea* trees were abundant in the smallest DBH classes. This demonstrates an ingrowth of *Picea* trees into *Pinus*-dominated sample plots. This is in accordance with the study of Kuuluvainen *et al*. (2002), who showed that when a forest site has developed for a longer period of time without fire, a multi-aged understorey of *Picea* and deciduous trees emerge. If severe fires do not occur, this type of *Pinus*-dominated forest may also perpetuate itself through autogenic mortality of individual trees or small groups of trees (Rouvinen *et al*. 2002b), providing a competitive advantage to *Picea* and deciduous trees in the understorey (Kuuluvainen & Juntunen 1998, Kuuluvainen *et al*. 1998b, 2002). *Picea* possesses an excellent capacity for recuperation when released from the oppression of the overstorey (Pöntynen 1929). This may increase the probability of the development of a mixed tree species composition (Kuuluvainen *et al*. 1998b).

Betula was a notable structural component of both *Picea*-dominated and mixed plots, a feature also found by Kuuluvainen *et al*. (1998a) and Lilja *et al*. (2006). The diameter distribution of *Betula* followed a negative exponential shape on *Picea*-, *Pinus*-dominated and mixed plots, whereas on *Betula*-dominated plots it was characterized by a unimodal distribution. The high density in the smallest diameter classes indicated that gap disturbance contributes to tree species' coexistence and acts to sustain the mixed tree species composition of the forest (Grubb 1977, Denslow 1985, Kuuluvainen *et al*. 1998a, 1998b). Kuuluvainen *et al*. (1998a) suggested that *Betula*, as a pioneer species, is able to rapidly colonize favourable microsites created by treefall disturbances by producing large amounts of light wind-dispersed seeds and having a fast growth rate.

Coarse woody debris and its variability

Several studies demonstrate that old-growth forests maintain high amounts of coarse woody debris (CWD) (Siitonen 2001). This was also true in the present study, the mean volume of total CWD being 30.0 m^3 ha^{-1}. The highest average volumes of CWD were found on *Picea*-dominated (34.5 m^3 ha^{-1}), *Pinus*-dominated (28.7 m^3 ha^{-1}) and mixed plots (22.0 m^3 ha^{-1}), while the lowest average volume of CWD was found on *Betula*-dominated plots (12.7 m^3 ha^{-1}).

Previously reported average volumes of CWD in *Picea*-dominated mesic old-growth forests vary from 19 to 80 m^3 ha^{-1} in northern boreal Fennoscandia (Siitonen 2001). Separate studies report values of 32 m^3 ha^{-1} (Siitonen 1994), 19 m^3 ha^{-1} (Sippola *et al*. 1998), 17–65 m^3 ha^{-1} (Jonsson 2000) and 28 m^3 ha^{-1} (Sippola *et al*. 2002). In *Pinus*-dominated old-growth forests, the average CWD volumes vary from 20 to 70 m^3 ha^{-1} from dry to mesic site types (Siitonen 2001). Separate studies report values of 19 m^3 ha^{-1} (Sippola *et al*. 1998), 16 m^3 ha^{-1} (Sippola *et al*. 2002) and 66–120 m^3 ha^{-1} (Linder *et al*. 1997). The above-mentioned studies in general had a larger sample plot size (range = 0.01–1.0 ha) than that used in the present study (0.03 ha). Our results are in general agreement with these studies, although the documented CWD volumes are somewhat higher than those found in our study. One reason for this may be that most of the previous studies have been carried out at lower latitudes and altitudes. Our results indicate that the average volumes of CWD on *Pinus*-dominated sites seem to be comparable to those of *Picea*-dominated plots, a trend also found by Siitonen (2001).

The plot-scale variability in CWD volumes was high (0–99.3 m^3 ha^{-1}), the reason being that sample plot size considerably affects the minimum and maximum values that are obtained (Siitonen 2001). Therefore, the present results on CWD variability can be generalized to larger spatial scales only with caution. In order to obtain more reliable stand-level estimates, larger plots or transect sampling should be used. This would probably lower the variability as compared with that obtained in this study.

Direct comparisons of average CWD volumes and their variability between different studies are, however, complicated by the different scales of analysis (i.e. plot, stand, landscape) and latitudinal trends. In general, it is preferable to compare the CWD proportions of the total tree volume (living and dead wood combined) (*see* e.g. Siitonen 2001). Overall, the average proportion of CWD of the total tree volume was 17.5%, on *Picea*-dominated plots 23.2% and on *Pinus*-dominated plots 10.7%; these values are somewhat lower than the averages reported in earlier studies. According to Siitonen (2001), the average proportion of CWD in *Picea*-dominated forests varied between 18% and 40% (average 28%) and in *Pinus*-dominated forests from 18% to 37% (average 25%) without latitudinal trends. However, timberline forests are known to have lower average proportions of CWD (Sippola *et al*. 2001, 2002).

In northern Finland, Sippola *et al*. (1998) found that the volumes of living and dead wood were strongly correlated in old-growth forests. Similarly, a significant correlation was found in the present study, indicating that the productivity on the stand (as expressed by living tree volume) is an important factor affecting the amount of CWD. However, the correlation ($r_S = 0.135$, $P = 0.032$) revealed in this study was lower than the high correlation ($r_S = 0.807$, $P < 0.001$) discovered by Sippola *et al*. (1998). Furthermore, when the correlation was studied in different species dominance types, a significant relationship was found only on *Picea*-dominated and mixed sample plots. The poor correlation in the present study as compared with the high correlation obtained by Sippola *et al*. (1998) can be related to differences in the spatial scale, as Sippola *et al*. (1998) used larger sample plot size (0.5–1.0 ha) as compared with that in the present study (0.03 ha).

The proportions of standing and downed CWD of the total CWD volume varied considerably (0%–100%) among sample plots, probably because of differences in mortality and tree species composition. On average, standing and downed CWD comprised 64.6% and 35.4% of the total CWD volume, respectively. However, tree species composition affected the proportion of standing CWD, with *Picea*-dominated plots having a lower proportion (29.1%) of standing dead trees than *Pinus*-dominated (53.3%) plots. According to the review by Siitonen (2001), in *Picea*-dominated forests the average proportions of downed and standing CWD seem to be ca. 70% and 30%, whereas *Pinus*-dominated forests have a higher average proportion of standing CWD, almost 50% of the CWD volume. This is in accordance with average values reported in separate studies conducted in boreal Fennoscandia (e.g. Sippola *et al*. 1998, Jonsson 2000, Siitonen *et al*. 2000, Edman *et al*. 2007). This trend can be explained by tree species tending to have different modes of death. Most *Pinus* trees remain standing and form long-lasting intact dead kelo trees (Rouvinen *et al*. 2002b), whereas uprooting and stem breakage are typical for *Picea* (Liu & Hytteborn 1991, Siitonen *et al*. 2000, Siitonen 2001).

In addition to CWD volume, the size and decay stage variability of CWD are shown to be important for saproxylic organisms (Siitonen 2001). According to diameter distributions of CWD, trees with small diameter were clearly most abundant in the present study. However, trees with large DBH (DBH ≥ 20 cm) generally accounted for over 50% of the CWD volume, with *Betula*-dominated plots as an exception. These results are in accordance with earlier studies conducted in boreal Fennoscandia (Sippola *et al*. 1998, Siitonen *et al*. 2000, 2001). In the northern boreal zone, Sippola *et al*. (1998) reported that large trees accounted for 22% of volume in both *Picea* and *Pinus*-dominated forests. However, comparisons between different studies are complicated owing to somewhat different threshold values (DBH) between small and large logs.

Generally, the pooled diameter distributions of downed and standing dead trees followed the negative exponential shape which is considered typical of old-growth forests (e.g., Kuuluvainen *et al*. 1998a, Karjalainen & Kuuluvainen 2002, Rouvinen *et al*. 2002a). This pattern is considered to be a reflection of a similar diameter distribution of living trees in natural boreal forest stands (Linder *et al*. 1997, Kuuluvainen *et al*. 1998a, Rouvinen *et al*. 2002a). Likewise, Rouvinen *et al*. (2002b) found that diameter distributions followed the negative exponential shape among both recently dead and living trees, in a near-natural forest. This suggests that both mortality and recruitment of new individuals have been constant and relatively evenly distributed between the diameter classes (Ranius *et al*. 2004). On *Picea*-dominated sample plots, most standing dead *Picea* and *Betula* trees belonged to the smallest diameter class. This indicates that most of these trees have died as a result of competitive thinning (Kuuluvainen *et al*. 1998a). This is also supported by the relation found between the amount of deciduous CWD and basal area of living trees (PC3) in the present study, indicating a higher mortality of *Betula* trees in denser stands with increased competition for light, a central limiting resource in *Picea* stands (Schulze *et al*. 1977).

The decay stage of trees can be seen as a rough approximation of the time since tree death (Dynesius & Jonsson 1991). Thus, the distribution of CWD across decay stages can be regarded as an indicator of the temporal variability in tree mortality (Rouvinen & Kouki 2002), which in turn depends on several processes, i.e. the input of CWD, the decay rate, and the time since disturbance. In this study, CWD in decay stage 1 was most scarce (3.0% of total CWD volume), which is in accordance with the earlier findings (1.1%–3.7%; Sippola *et al*. 1998, Karjalainen & Kuuluvainen 2002). The low CWD volumes in decay stage 1 are simply due to the much shorter retention time of trees in this stage (< 1 year; *see* Material and methods) as compared with other decay stages. CWD in decay stage 2 was most abundant (45.0%), followed by decay stages 3 (20.1%), 4 (16.3%) and 5 (15.7%). By contrast, Sippola *et al*. (1998) found that in *Picea*-dominated old-growth forests, CWD was most abundant in decay stages 4 (36.5%) followed by decay stages 3 (25.8%), 2 (17.0%) and 5 (17.0%). This suggests that CWD decay stage distributions in old-growth forests exhibit considerable variability. However, comparisons between different studies on the decay stage distribution are complicated owing to a number of classification systems and the inevitably subjective assessment of the decay stage in the field. In the present study, downed CWD was on average more decayed than standing CWD, which is in accordance with earlier findings. Only the least decayed trees remain standing while CWD in more decayed stages almost exclusively occur as downed (Rouvinen & Kouki 2002).

Conclusions

Our results demonstrated that an old-growth forest on a northern boreal mesic *Hylocomium–Myrtillus* site type exhibits considerable structural and compositional variability. The composition of living tree community varied from mixed-species stands to *Picea*-, *Pinus*- and *Betula*-domination, and there was high variability in CWD amount and quality. The main directions of structural and compositional variability were related to variables describing total CWD volume, volumes of living and dead *Pinus sylvestris*, and volume of deciduous CWD. Variability is clearly an essential natural property of forest ecosystem structure at landscape scale and should be taken into account in forest restoration and management. More research is needed to improve the basic understanding of the range and causes of structural variability in primary old-growth forests, especially at broader spatial and longer time scales.

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Appendix. Forest structure variables used in PCA (Principal component analysis) (n = 252 sample plots).

	Mean ± SD		Mean ± SD
Altitude (m a.s.l.)	302.6 ± 41.2	Downed other deciduous CWD volume (m^3 ha^{-1})	0.4 ± 1.5
Total living tree volume (m^3 ha^{-1})	141.5 ± 68.6	Standing CWD volume (m^3 ha^{-1})	10.6 ± 14.9
Living *Picea* volume (m^3 ha^{-1})	71.2 ± 41.4	Standing *Picea* CWD volume (m^3 ha^{-1})	6.2 ± 12.3
Living *Pinus* volume (m^3 ha^{-1})	46.1 ± 81.3	Standing *Pinus* CWD volume (m^3 ha^{-1})	2.7 ± 10.1
Living *Betula* volume (m^3 ha^{-1})	21.8 ± 22.1	Standing *Betula* CWD volume (m^3 ha^{-1})	1.6 ± 2.9
Living other deciduous tree volume (m^3 ha^{-1})	2.4 ± 6.5	Standing other deciduous CWD volume (m^3 ha^{-1})	0.1 ± 0.6
Basal area of living trees (m^3 ha^{-1})	18.1 ± 5.4	Decay stage 1 volume (m^3 ha^{-1})	0.9 ± 3.2
Basal area of living *Picea* (m^3 ha^{-1})	10.8 ± 5.8	Decay stage 2 volume (m^3 ha^{-1})	13.5 ± 16.6
Basal area of living *Pinus* (m^3 ha^{-1})	2.5 ± 4.3	Decay stage 3 volume (m^3 ha^{-1})	6.0 ± 10.0
Basal area of living *Betula* (m^3 ha^{-1})	4.3 ± 4.3	Decay stage 4 volume (m^3 ha^{-1})	4.9 ± 8.9
Basal area of living other deciduous trees (m^3 ha^{-1})	0.4 ± 1.2	Decay stage 5 volume (m^3 ha^{-1})	4.7 ± 8.6
Living trees ha^{-1}	1144.1 ± 808.4	Coniferous CWD volume (m^3 ha^{-1})	24.7 ± 26.0
Living *Picea* density (trees ha^{-1})	647.3 ± 598.9	Deciduous CWD volume (m^3 ha^{-1})	5.3 ± 6.8
Living *Pinus* density (trees ha^{-1})	72.7 ± 195.6	Mean DBH of CWD (cm)	18.7 ± 6.9
Living *Betula* density (trees ha^{-1})	399.0 ± 510.7	Large dead trees ha^{-1} (DBH ≥ 20 cm)	52.3 ± 54.4
Living other deciduous tree density (trees ha^{-1})	25.2 ± 103.0	Small dead trees ha^{-1} (DBH = 10–19 cm)	95.9 ± 88.0
Total CWD volume (m^3 ha^{-1})	30.0 ± 24.5	Large dead conifers ha^{-1} (DBH ≥ 30 cm)	13.9 ± 22.4
Picea CWD volume (m^3 ha^{-1})	19.9 ± 25.2	Large dead deciduous trees ha^{-1} (DBH ≥ 20 cm)	5.5 ± 16.1
Pinus CWD volume (m^3 ha^{-1})	4.8 ± 13.7	Large CWD volume (DBH ≥ 20 cm) (m^3 ha^{-1})	20.0 ± 22.8
Betula CWD volume (m^3 ha^{-1})	4.8 ± 6.3	Small CWD volume (DBH = 10–19 cm) (m^3 ha^{-1})	5.1 ± 4.7
Other deciduous CWD volume (m^3 ha^{-1})	0.5 ± 1.8	Total tree (living and dead combined) volume (m^3 ha^{-1})	171.5 ± 75.6
Downed CWD volume (m^3 ha^{-1})	19.4 ± 20.5		
Downed *Picea* CWD volume (m^3 ha^{-1})	13.6 ± 21.0		
Downed *Pinus* CWD volume (m^3 ha^{-1})	2.1 ± 6.9		
Downed *Betula* CWD volume (m^3 ha^{-1})	3.3 ± 4.3		