

Differences in Stand Characteristics Between Brook-Side Key Habitats and Managed Forests in Southern Finland

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Preservation of small habitat patches termed as "woodland key habitats" or "especially important habitats" in the Finnish Forest Act has become an integral part of biodiversityoriented forest management. Forest Act habitats belong to particular habitat types defined in the act, and they are supposed to have natural-like stand characteristics. However, very little is known about the actual stand structure in the designated habitats. Our aim was to compare stand characteristics between brook-side key habitats and comparable managed forests as controls. Seven study areas were selected from four regions across southern Finland. Within each study area ten key habitats and ten controls (140 stands) were randomly selected. Living and dead trees and cut stumps were measured in each stand within a 0.2 ha plot. The average degree of previous cutting was significantly lower whereas the volume of dead wood, volume of deciduous trees, and stand diversity were each significantly higher in key habitats than controls. The average volume of dead wood was 11.7 m³ha⁻¹ in key habitats and 6.5 m³ha⁻¹ in controls. However, there was considerable variation among individual stands, and a large part of key habitats could not be distinguished from randomly selected control stands with respect to stand characteristics. The preservation of natural brook channels with their immediate surroundings is undoubtedly important for maintaining aquatic and semiaquatic biodiversity. Nevertheless, when complementing the forest conservation network in the future, main emphasis in selecting potentially valuable stands should be placed on important structural features such as dead wood and old trees.

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1 Introduction

Preservation of small habitat patches called as "woodland key habitats" or "especially important habitats" in the Finnish Forest Act has become an integral part of biodiversity-oriented forest management in Finland and other Nordic as well as Baltic countries although the definitions, legal status etc. vary between the countries (Nitare and Norén 1992, Aasaaren and Sverdrup-Thygeson 1994, Gundersen and Rolstad 1998, Norén et al. 2002, Prieditis 2002, Andersson et al. 2003, Gjerde et al. 2004). The term key habitat was coined in Sweden in 1990 (see Norén et al. 2002) and introduced to a wider audience in 1992 in a special issue of Svensk Botanisk Tidskrift dedicated to the preservation of boreal forest in Sweden. According to the Swedish definition, a key habitat is a patch where red-listed species are found or are likely to occur (Nitare and Norén 1992, Norén et al. 2002). The concept is grounded on two assumptions. Firstly, red-listed species do not occur evenly or randomly in the forest landscape but instead are concentrated into certain sites. Secondly, key habitats can be identified based on their structural features and indicator species, whereas direct observations of red-listed species are not needed.

The idea was adopted in Finland in the early 1990's and revised to suit the local conditions (Aapala et al. 1994). The key habitat concept and a general recommendation to preserve key habitats were included in the management guide-lines for private forests for the first time in 1994 (Luonnonläheinen metsänhoito 1994). Some 30

different key habitat types were separated and described (Meriluoto 1995, Soininen 1996, Meriluoto and Soininen 1998). A part of these types obtained a legal status when the Finnish forest legislation was revised and became into force in 1997. The aim of the new Forest Act (Metsälaki 1996) was to promote economically, ecologically and socially sustainable management and use of forests so that they yield a good and sustainable harvest at the same time as their biological diversity is preserved. Hence, preservation of biodiversity was placed on a par with sustainable wood production.

Seven main types (each actually consisting of several subtypes, such as different forest or mire site types, or other habitat types) of key habitats were defined in the Forest Act and termed "especially important habitats" (Table 1). All of these are topographically, edaphically or hydrologically particular places. Furthermore, to qualify as an especially important habitat, the site has to meet three criteria: it has to be natural or natural-like, clearly distinguishable from its surroundings, and generally small in size.

In addition to the especially important habitats, the preservation of which is enacted in the forest legislation, another category of key habitats has been identified and termed as "other valuable habitats". These are sites that either belong to the habitat types defined in the Forest Act but do not quite fulfil the criteria of naturalness, or they belong to other habitat types (e.g. old deciduous forest) than those defined in the Forest Act. The preservation of other valuable habitats is not enacted in the forest legislation, but has been

Table 1. Especially important habitat types according to the Finnish Forest Act (Metsälaki 1093/1996). Translation from Finnish by the authors.

¹⁾ Immediate surroundings of springs, brooks, permanent channels of trickling water, and small ponds

Herb/grass birch-spruce mires, fern-rich spruce mires, thin-peated herb-rich spruce forests, and rich fens^{a)} to the south of the county of Lapland

³⁾ Patches of herb-rich forest^{b)}

⁴⁾ Small mineral-soil islets in undrained mires

⁵⁾ Ravines and gorges

⁶⁾ Steep cliffs and the forest at the immediate feet of them

Sands, rocky outcrops, stone soils, boulder fields, sparsely forested mires and shore marshes that are less productive than barren heath forests^{b)}

^{a)} See Eurola et al. (1984) for the Finnish classification of mires.

^{b)} See Tonteri (1994) for the site type classes.

recommended in the guidelines for good forest management (Hyvän metsänhoidon suositukset 2001, 2006), and is thereby based on voluntary decisions of landowners.

After the enforcement of the new Forest Act, a large-scale mapping project of the especially important habitats was carried out in 1998-2004, and it encompassed nearly all the private forests (total area 15.5 million ha). Similar surveys were carried out in state and company forests. According to the inventories, the total area of especially important habitats is ca. 60000 ha corresponding to 0.5% of the land area in private forests, 43000 ha (0.9%) in state forests, and 11000 ha (0.6%)in company forests (Yrjönen 2004). The total number of especially important habitats in private forests is ca. 100000 and their mean size is 0.6 ha. The other valuable habitats were not systematically searched for in the mapping project. Nevertheless, their total area found in private forests was 67000 ha. Thus, the total area of all key habitats was slightly over 1% of the total forestry land area, i.e. in the order of magnitude of 250000 ha. Brook-side forests are the most common key habitat type constituting ca. one third of the total area of especially important habitats.

In the mapping project, the especially important habitats were identified on the basis of their characteristic features. These comprehended 1) topographic, edaphic and hydrological features of the habitat, 2) naturalness of the habitat, 3) stand structure and vegetation, and 4) occurrence of indicator species (Soininen 1997). Indicator species were vascular plants and bryophytes with more or less strict habitat requirements and which typically occur in the focal habitats. Different set of species was listed for each habitat type. In practice, the indicator species were mainly used for identifying the edaphically outstanding habitat types, herb-rich forests patches, rich mires, and rich fens.

Stand characteristics that could be used in evaluating the naturalness of especially important habitats were outlined in the fieldwork guide of the mapping project (Soininen 1997). These included the occurrence of dead and decaying standing and fallen trees, variable age and size distribution, and admixture of several tree species. On the contrary, regular stand structure due to thinnings, even age and size distribution, small amount of dead wood, and fresh or clearly visible signs of logging indicated lack of naturalness. However, no quantitative limits with respect to stand characteristics were set to especially important habitats, and exact measurements were not made in the mapping project. Hence, relatively little is known about the quality (in terms of stand characteristics) of the especially important habitats. It is not known how natural they are, and how much they differ from average managed forests.

The aim of this study was to quantitatively assess the stand characteristics in brook-side key habitats which constitute the most important type of especially important habitats in terms of total area and timber volume. The primary interest was in those stand characteristics that had been used to evaluate the naturalness of stands: degree of previous cutting, volume of dead wood, and diversity of living stand. Brook-side key habitats were compared with randomly selected managed forests belonging to similar site types and development classes. Possible regional differences in the quality of key habitats within southern Finland were also of interest. This study is a part of a larger project assessing stand structure and species diversity in different types of key habitats (see Siitonen et al. 2006, Hottola and Siitonen 2008).

2 Material and Methods

2.1 Study Areas and Sites

We hypothesized that the quality of key habitats may vary between the forest vegetation zones (see Ahti et al. 1968) and, within each vegetation zone, between different parts of southern Finland depending on the west-east location. Factors that could cause regional differences in the quality of key habitats include both biogeographical factors and differences in land-use history (see e.g. Lihtonen 1949, Kalliola 1966, Rouvinen et al. 2002, Tasanen 2004). Forests in southwestern Finland have the longest management history, whereas intensive forest management started relatively late in the easternmost Finland, in North Karelia and Kainuu. This could be reflected in the amount, quality and spatial configuration of



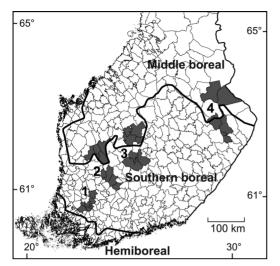


Fig. 1. Location of the seven study areas in southern and middle boreal vegetation zones in southern Finland. Regions: 1=southwestern Finland, 2=Pirkanmaa, 3=Central Finland, 4=North Karelia.

valuable habitats in the present, mainly managed landscape.

To cover the west-east gradient in land-use history, four regions were selected along the border between the southern and middle boreal zones from southwestern Finland to northern Karelia. The four regions were further divided into southern and middle boreal study areas except for southwestern Finland which belongs entirely to the southern boreal zone, making a total of seven study areas (Fig. 1). The study areas were selected within the Forestry Centres Lounais-Suomi, Pirkanmaa, Keski-Suomi and Pohjois-Karjala.

We distinguished two forest categories: especially important Forest Act habitats in brook-side forests (referred to hereinafter as brook sides or key habitats) and ordinary managed forests which served as controls (hereinafter controls). In each study area, ten brook sides and ten controls were randomly selected, making a total of 140 sites. In order to reduce the ecological gradients among the study sites, and to make the samples of key habitats and controls comparable, the study sites had to meet the following criteria: 1) site type at least mesic *Myrtillus* type (Cajander 1926) (subxeric and less fertile sites were excluded), 2) development class 3 or 4, i.e. advanced thinning stand or mature stand, 3) age of dominating trees at least 50 years, 4) dominating tree species Norway spruce (*Picea abies* [L.] Karst.) or deciduous tree, i.e. Scots pine (*Pinus sylvestris* [L.]) dominated stands were excluded, and 5) stand area at least 0.2 ha. In southern Finland, 56% of the especially important habitats in brooksides fulfil these criteria (data obtained from the Forestry Development Centre Tapio).

The database of the mapping project of especially important habitats in private forests (see introduction) constituted the sampling frame for brook sides. This database includes all the especially important habitats that were found in the mapping project within each study area. Forest management plan databases were used for selecting control sites. The forest management plans cover ca. 60% of the area of private forests in southern Finland which means that the sampling frame for controls was comprehensive too.

All the stands fulfilling the above criteria within each study area were extracted from the databases making a total of ca. 500 potential brook-side key habitats and 3000 control sites. This work was done at the Forestry Development Centre Tapio. The sites were then allotted into a random order. The first thirty brook sides as well as controls were assigned as possible study sites. A signed consent for the study was asked from the landowners by mail, including a cover letter explaining the purpose and inventory methods of the study. The local Forestry Centres took care of the contacts to landowners. About half of the owners replied and agreed to the study thus leaving some fifteen possible sites of each forest category per each study area. The ten study sites were then established in their allotted order. Some sites had to be rejected and replaced with the next site since they had been recently clear-cut or heavily thinned, in the case of especially important habitats thus obviously violating the Forest Act.

2.2 Measurements of Stand Characteristics

Part of the stand characteristics, including stand area, forest site type, development class and age of dominating trees, were obtained from the habitat-mapping and forest-management plan databases. In each study site a rectangular 0.2 ha (20 m \times 100 m) sample plot was established. The plot was divided into five 20 m \times 20 m cells. Since most of the brook sides were narrow and small in size, the sample plot had to be located parallel with the brook in most cases. If the stand was crooked in shape or less than 100 m long, the sample plot was broken along the borders of the cells to follow the brook, and in some cases one or two cells were placed besides the other cells. In the control stands that were generally larger, the sample plot was placed in the middle of the stand at a random direction.

The logging history, i.e. the degree of previous cutting, of each stand was assessed by counting the number of cut stumps ≥ 10 cm in diameter within the sample plot. Even very old (approximately 50–100 years) cut stumps which looked like moss hummocks but had a centre of rotten wood were counted. Cut stumps were separated from natural stumps based on their uniform height, evenly cut surface, and lack of trunk remains next to the stump. Tree species, decay class, and diameter in 10-cm classes (10–19 cm, 20–29 cm etc.) of each stump were measured.

Living and dead trees were measured on the sample plots. Tree species and diameter at breast height (DBH) were measured for a minimum of one hundred living trees with a minimum DBH of 5 cm within each plot. We measured as many 20 m \times 20 m cells (in the order first, third, fifth, second and fourth) as were needed to attain the minimum number of tallied trees. The heights of 32–84 (average 52) sample trees were measured within each plot, depending on the number of tree species and variation in diameter.

All dead standing or fallen trunks with DBH ≥ 10 cm and pieces of trunks with a diameter ≥ 10 cm at the basal end of the trunk and length ≥ 1.3 m were measured on the sample plots. A dead tree was included in the plot if the germination point was inside the plot. Thus, fallen trees that extended partly outside the plot were measured entirely, while fallen trees projecting onto the plot from outside were not measured. For pieces of trunks (cut bolts, logging-residue tops etc.), the location of the basal end determined whether they belonged to the plot. We recorded tree species, DBH of entire trunks or basal diameter of pieces of trunks, decay class, and quality (see

below). Heights of broken snags and lengths of pieces of logs, cut bolts, and logging-residue tops were measured.

The decay class and quality of dead trees were described using the same classifications as those applied in the Finnish National Forest Inventory. Five classes were used to describe the stage of decomposition: I) hard, a knife penetrates by pushing only a few millimetres into the wood; II) relatively hard, knife penetrates 1–2 cm; III) relatively soft, knife penetrates 3-5 cm, IV) soft throughout, V) very soft, can be moulded by hand. Eight categories were used to describe the quality of dead trees: 0) unknown (usually for very decayed logs); 1) entire dead standing trees; 2) broken snags with at least 1/3 of the upper part of the stem broken off, height at least 1.3 m; 3) uprooted; 4) broken logs; 5) cut stumps; 6) cut bolts; 7) logging-residue tops.

Some data were also recorded from the neighbouring stands of key habitats. A map of each study site was drawn in the field showing the boundaries of adjacent stands. Development class of each adjacent stand was determined using six classes: 0) open areas other than forestry land (fields, waters etc.), 1) recently clear-cut or with seed trees, shelterwood or retention trees, open or average height of seedling stand <1.3 m; 2) advanced seedling stand with average height ≥ 1.3 m but average diameter <8 cm; 3) young thinning stand with average diameter ≈ 1.6 cm; 4) advanced thinning stand with average diameter <5) mature.

2.3 Calculations

The basal area of cut stumps was calculated based on the number of stumps and the mid-point of each 10-cm diameter class (e.g. 15 cm in the class 10–19 cm). The basal area of cut stumps combines both the number and size of stumps, and is therefore directly related to the past cutting intensity of stand (Siitonen et al. 2000).

Volume calculation of both living and dead trees was made by KPL program (Heinonen 1994). The volume of entire trees was calculated using volume equations based on tree species, DBH and height (Laasasenaho 1982). The volume of pieces of dead trees was calculated by means of taper curve functions (Laasasenaho 1982) based on the sample tree data, and on the basal diameter and length of each piece.

For this study, the volume of dead wood (coarse woody debris, CWD) per ha was calculated in a similar way as in the National Forest Inventory in which only those parts of dead trees that are ≥ 10 cm in diameter in the thinnest end and ≥ 1.3 m in height or length are measured and included in the volume. Thus, the volume of entire dead trees was calculated up to the point in which the stem diameter falls below 10 cm. (Note that the volumes reported in Hottola and Siitonen [2008], which is based on the same sample plots, were larger because the minimum diameter was ≥ 5 cm, and also the volumes of natural and cut stumps were included in the dead-wood volume.)

Since both the number of tree species present and variation in size distribution were used in evaluating the naturalness of stands in the mapping project of especially important habitats, we combined these two variables into one index describing stand diversity (Siitonen et al. 2000). Diversity of living stand was calculated as the number of different types of trees present in each sample plot, i.e. as the number of combinations formed by different tree species and 10-cm diameter classes (5-9 cm, 10-19 cm, 20-29 cm etc.). Diversity of dead wood was calculated in a similar way, as the number of combinations formed by tree species, qualities (entire dead standing trees, broken snags, logs), decay classes, and 10-cm diameter classes (Siitonen et al. 2000). Cut bolts and logging-residue tops on the ground were included in logs, cut stumps were ignored.

2.4 Statistical Analyses

Factorial ANOVA without or with covariates was used to test whether variables describing the naturalness of stand differed between key habitats and controls. The three dependent variables of main interest were 1) the basal area of cut stumps describing the logging history, 2) volume of dead wood, and 3) diversity of living stand. Kolmogorov-Smirnov statistics with a Lilliefors significance level was used for checking normality of the distributions, and Levene's test for checking the homogeneity of variances of the above dependent variables. The distribution of dead-wood volume was strongly right-skewed, and therefore the variable was log-transformed before analyses. The basic model consisted of three explanatory variables: 1) forest category was considered as a fixed factor with two levels (key habitats vs. controls), 2) vegetation zone as a fixed factor with two levels (southern vs. middle boreal zone), and 3) west-east region also as a fixed factor with four levels (the four forestry centres). The factors and interactions among them were included into the model. It was particularly hypothesized that interaction between forest category and vegetation zone could be plausible. Key habitats in the middle boreal zone could be, on average, less affected by previous cutting than key habitats in the southern boreal zone even if managed control stands did not differ between the vegetation zones. Tukey's HSD post hoc tests were used for comparing differences between the four regions.

In addition to the above explanatory variables (factors), several other stand variables can affect the volume of dead wood and diversity of living stand. Therefore, the effects of site type, stand age, proportion of deciduous trees, and degree of cutting which all differed between the brook sides and controls were also taken into account. Site type was added into the model as a fixed factor with three levels (herb rich, herb-rich heathland and mesic sites), whereas the stand age, proportion of deciduous trees (arc-sin transformed), and basal area of cut stumps were included as covariates. We started with a full model containing all the factors, their interactions and covariates, and then simplified the model by leaving out nonsignificant explanatory terms step by step. The goodness of alternative models was evaluated on the basis of r^2 , adjusted r^2 , and the significance of individual explanatory variables.

Differences between brook sides and controls in other stand characteristics than the three aforementioned variables were tested in a more simple way since there were no a priori reasons to assume differences between or interactions among forest categories, vegetation zones, or regions in most of the stand variables. Moreover, several stand variables had non-normal distributions which could not be normalized using transformations. Therefore, we compared the ranked values of stand characteristics between the pooled brook sides (n=70) and controls (n=70) using the non-parametric Mann-Whitney test. All the above analyses were performed with the SPSS 16.0 statistical package.

The variation in stand characteristics among brook-side and control sites was further explored with principal component analysis (PCA) which is a useful method to study and illustrate how intercorrelated variables contribute to the total variation in data (see e.g. Legendre and Legendre 1998). PCA was performed in the statistical programming environment R (version 2.2.0, Ihaka and Gentleman 1996) with the package vegan (J. Oksanen, http://cran.r-project.org) using unweighted linear regression and unweighted singular value decomposition. Twenty stand variables were included in the analysis and scaled to unit variance: hence all the variables were given equal weight. Principal components were derived from a correlation matrix.

3 Results

The average stand area was 0.7 ha (0.2–2.5 ha) in brook-side key habitats and 1.7 ha (0.3–7.6 ha) in controls. The site type was, on average, more rich in brook sides than in controls: 23% of the brook sides were herb-rich sites, 48% herb-rich heathland forests (*Oxalis-Myrtillus* type), and 29% mesic heathland forests (*Myrtillus* type). The respective figures for controls were 3% herb-rich, 28% Oxalis-Myrtillus type and 69% Myrtillus type.

3.1 Stand Characteristics Indicating Naturalness in Key Habitats vs. Controls

The average basal area of cut stumps was significantly lower in brook sides than controls (Fig. 2A, Table 2). However, there was considerable variation in logging history among individual sites with the number of cut stumps varying from 20 to >1000 per ha, and the basal area of stumps from <1 to about 50 m² ha⁻¹ in both brook sides and controls. The basal area of stumps differed signifi-

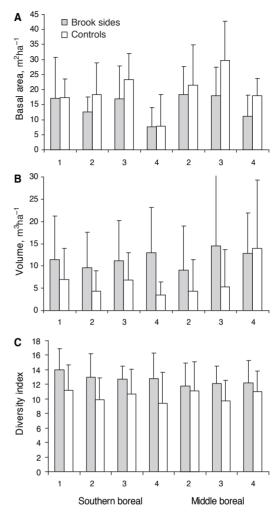


Fig. 2. Basal area of cut stumps (A), volume of dead wood (B), and diversity of living stand (C) in brook-side key habitats and control sites. Each column is the average of 10 plots; the bars represent the standard deviations. Numbers at the x-axis indicate the four study regions (see Fig. 1).

cantly (p=0.026) between the forest vegetation zones but, contrary to the expectation, middle boreal sites had more stumps $(19.4 \pm 11.2 \text{ m}^2 \text{ha}^{-1})$ than southern boreal sites $(15.8 \pm 10.0 \text{ m}^2 \text{ha}^{-1})$. The west-east regions also differed from each other, the only significant (p<0.001) difference, however, being between Keski-Suomi with the highest basal area of stumps (22.0±11.4)

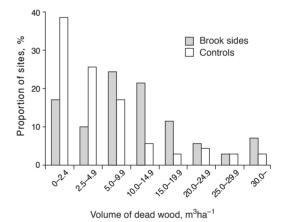
Source	Basal area of cut stumps, $m^2 ha^{-1}$				Volume of dead wood, $m^3 ha^{-1}$				Diversity of living stand				
	df	Type III SS	MS	F	р	Type III SS	MS	F	р	Type III SS	MS	F	р
Forest category	1	1019	1019	10.9	0.001	2.48	2.48	14.9	0.000	157	157	15.5	0.000
Vegetation zone	1	476	467	5.1	0.026	0.00	0.00	0.0	0.931	0.3	0.3	0.0	0.863
Region	3	1803	601	6.4	0.000	0.81	0.27	1.6	0.186	21	7	0.7	0.548
Category × zone	1	11	11	0.1	0.734	0.04	0.04	0.3	0.609	15	15	1.5	0.230
Category × region	3	231	77	0.8	0.486	0.11	0.04	0.2	0.883	0.9	0.3	0.0	0.993
Zone × region	2	4	2	0.0	0.978	0.59	0.30	1.8	0.173	9	4	0.4	0.654
Category \times zone \times region	2	78	39	0.4	0.662	0.52	0.26	1.6	0.212	12	6	0.6	0.548
Error	126	11741	94			21.00	0.17			1272	10		

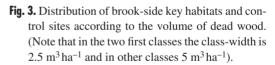
Table 2. ANOVA table for differences in stand variables describing naturalness between brook-side key habitats and control sites (forest category), southern and middle boreal forest vegetation zones, and the four study regions (cf. Fig. 1). Log-transformed volume of dead wood was used in testing.

m²ha⁻¹) and Pohjois-Karjala with the lowest one (12.6±8.3 m²ha⁻¹). None of the interactions between the main factors was significant (Table 2). The decay-class distribution of cut stumps did not differ between brook sides and controls (for the average number of cut stumps per ha in the five decay classes, χ^2 =6.81, df=3, p>0.1), hence there was no evidence of key habitats being left unmanaged for a longer time than controls.

The average volume of dead wood was significantly higher in brook sides $(11.7 \text{ m}^3 \text{ha}^{-1})$ than controls (6.5 m^3ha^{-1}) (Fig. 2B, Table 2). The volume of dead wood varied from 0 to 55 m³ ha⁻¹ in brook sides, and from 0 to 42 m^3ha^{-1} in controls. The volume distribution of dead wood among stands was strongly right-skewed and differed between the two forest categories: in over half of the brook sides (57%) dead wood amounted to 5-20 m³ ha⁻¹ whereas in two thirds of the controls (64%) the volume was less than 5 m³ha⁻¹ (Fig. 3). The median volume of dead wood was 9.2 m³ha⁻¹ in brook sides and 3.2 m³ha⁻¹ in controls. The volume did not differ significantly between the vegetation zones or between the westeast regions. None of the interactions between the main factors was significant (Table 2).

The average diversity of living stand was also significantly higher in brook sides than controls (Fig. 2C, Table 2). Diversity index varied among sites from 7 to 20 in brook sides, and from 3 to 18 in controls. Stand diversity did not differ sig-





nificantly between the southern boreal and middle boreal zones or between the west-east regions. None of the interactions between the main factors was significant (Table 2).

The average volume of dead wood was significantly higher in brook sides than controls even after controlling for the differences in site type, stand age and logging intensity between the two forest categories (Table 3). The volume of dead wood increased significantly with stand age, and

Table 3. ANOVA table for differences in the volume of dead wood (log-transformed) and diversity of living stand
between brook-side key habitats and control sites (forest category) when controlling for the site type, stand
age and logging intensity. Stand age: age of the dominating trees; cut stumps: basal area of cut stumps,
m ² ha ⁻¹ ; deciduous trees: proportion of deciduous trees of the living stand (not included in the model for
dead wood).

Source		Volun	ne of dead we	ood, m ³ ha	Diversity of living stand						
	df	Type III SS	MS	F	р	df	Type III SS	MS	F	р	
Forest category	1	1.12	1.12	7.6	0.007	1	33.66	33.66	4.3	0.040	
Site type	2	0.62	0.31	2.1	0.129	2	22.12	11.06	1.4	0.246	
Stand age	1	1.43	1.43	9.7	0.002	1	46.19	46.19	5.9	0.016	
Deciduous trees	-	-	-	-	-	1	33.56	33.56	4.3	0.040	
Cut stumps	1	1.16	1.16	7.9	0.006	1	111.98	111.98	14.4	0.000	
Error	133	19.68	0.15			132					
	R	$^{2}=0.237$				R	² =0.285				

decreased significantly with increasing logging intensity. Similarly, stand diversity was significantly higher in brook sides than controls even after controlling for the other stand variables (Table 3). The diversity of living stand increased significantly with stand age and proportion of deciduous trees, and decreased significantly with increasing logging intensity. Site type was not a significant explanatory variable but it was retained in the models because it improved the adjusted r^2 .

3.2 Differences in Other Stand Characteristics

Considering live-stand characteristics, the main difference between brook sides and controls was in the amount and species composition of deciduous trees (Table 4). The average volumes of birch, grey alder, black alder (which was only found in the southern boreal study areas) and other deciduous trees were each significantly higher, whereas the volume of pine was significantly lower in brook sides than controls. Particularly the volume of alder (Alnus spp.) differed considerably between the forest categories being almost ten times as high in brook sides (18 m³ha⁻¹) as controls (2 m³ha⁻¹). The numbers of large spruces and deciduous trees were each about twice as high in brook sides as controls. The average stand age and stand density were rather similar in the two forest categories. Brook sides and controls did not differ significantly from each other with respect to the basal area, total stand volume, volume of spruce and volume of aspen.

Besides the total volume of dead wood, the treespecies composition and diversity of dead wood also differed significantly between the two forest categories (Table 4). The volumes of all other tree species than pine and aspen were each significantly higher in brook sides than controls. The average pooled volume of dead alder was almost ten times as high in brook sides (2.0 m³ha⁻¹) as controls $(0.3 \text{ m}^3 \text{ha}^{-1})$, and also the average volume of other deciduous trees was about six times as high in brook sides (0.6 m³ha⁻¹) as controls $(0.1 \text{ m}^3 \text{ ha}^{-1})$. The numbers of both large dead coniferous and deciduous trees were low and did not differ between the two forest categories. The decay-class distribution and diameter distribution of dead wood differed to some extent between the categories (Fig. 4). The proportion of freshly dead, hard wood belonging to decay classes 1 and 2 was slightly higher in brook sides (68%) than in controls (61%). The proportion of dead wood belonging to the diameter classes 10-19 cm and 20–29 cm was clearly higher in brook sides (78%) than controls (62%). Consequently, the difference in the volume of large-diameter dead wood with the minimum diameter of 30 cm did not differ between brook sides (2.5 m³ha⁻¹) and controls $(2.4 \text{ m}^3 \text{ha}^{-1})$. The proportion of uprooted trees (out of the pooled volume of dead wood) was clearly higher in brook sides (36%) than controls

Table 4. Differences between brook-side key habitats and control stands in different live-stand and dead-wood characteristics. In the first two columns, the averages of all stands ± SD in each forest category are given. Note that testing is not based on the averages ± SDs but on ranked values and Mann-Whitney non-parametric test.

Variables	Variable abbreviation	Brook sides (n=70) $\overline{x} \pm SD$	Controls (n=70) $\overline{x} \pm SD$	Z	р
Living-stand variables					
Age of dominating trees	AgeDomin	84 ± 16	90 ± 17	-2.1	0.037
No. of stems (≥ 5 cm) ha ⁻¹	NoStemLiv	1171 ± 485	1014 ± 525	-2.5	0.013
Basal area, m ² ha ⁻¹	BasAreaLiv	29 ± 7	29 ± 7	-0.3	0.736
Total volume, m ³ ha ⁻¹		279 ± 97	295 ± 97	-1.0	0.303
– Norway spruce (Picea abies)	VLivSpruce	197 ± 105	208 ± 96	-0.4	0.703
- Scots pine (Pinus sylvestris)	VLivPine	17 ± 22	51 ± 53	-3.9	0.000
– birches (<i>Betula</i> spp.) ^{a)}	VLivBirch	38 ± 34	27 ± 41	-3.0	0.002
- trembling aspen (Populus tremula)	VLivAspen	8 ± 19	6±18	-1.3	0.179
– grey alder (Alnus incana)	VLivAinc	12 ± 23	1.0 ± 2.5	-5.3	0.000
– black alder (A. glutinosa)	VLivAglu	6 ± 18	1.1 ± 8.1	-2.3	0.023
– other deciduous ^{b)}	VLivOdec	2 ± 6	0.7 ± 2.3	-4.5	0.000
Large <i>P. abies</i> (DBH \ge 40 cm) ha ⁻¹		18 ± 25	10 ± 20	-2.1	0.032
Large <i>P. sylvestris</i> (DBH \ge 40 cm) ha ⁻¹		0.7 ± 2.7	3.1 ± 9.0	-2.0	0.041
Large deciduous (DBH \ge 30 cm) ha ⁻¹		14 ± 21	7 ± 15	-2.6	0.010
Diversity of living stand	DivLiv	12.7 ± 2.9	10.4 ± 3.3	-4.0	0.000
Dead-wood variables					
No. of stems (D \ge 10 cm) ha ⁻¹		88 ± 82	41 ± 42	-4.4	0.000
No. of cut stumps (D \ge 10 cm) ha ⁻¹		353 ± 232	528 ± 277		
Basal area of cut stumps, m ² ha ⁻¹	BasAreaStump	14.5 ± 9.6	20.3 ± 10.8	-3.5	0.001
Total volume, m ³ ha ⁻¹		11.7 ± 10.3	6.5 ± 8.5	-4.0	0.000
– Norway spruce (Picea abies)	VDeadSpruce	6.3 ± 7.9	2.5 ± 3.9	-3.0	0.003
- Scots pine (Pinus sylvestris)	VDeadPine	0.8 ± 1.9	1.8 ± 4.6	-0.4	0.703
– birches (Betula spp.)	VDeadBirch	1.7 ± 3.1	0.9 ± 1.8	-3.1	0.002
- trembling aspen (Populus tremula)	VDeadAspen	0.2 ± 0.7	0.8 ± 3.1	-0.1	0.934
– grey alder (Alnus incana)	VDeadAinc	1.7 ± 3.7	0.3 ± 0.6	-3.7	0.000
– black alder (A. glutinosa)	VDeadAglu	0.3 ± 1.3	-	-2.7	0.007
– other deciduous ^{b)}	VDeadOdec	0.6 ± 2.8	0.1 ± 0.4	-2.3	0.022
Large coniferous (DBH ≥ 40 cm) ha ⁻¹		0.1 ± 0.6	0.2 ± 1.3	-0.6	0.555
Large deciduous (DBH \ge 30 cm) ha ⁻¹		0.6 ± 2.0	0.6 ± 1.8	-0.3	0.797
Diversity of dead wood	DivDead	10.4 ± 6.8	6.3 ± 5.4	-4.1	0.000

a) Betula pendula and B. pubescens
 b) Mainly consisting of Salix caprea and Sorbus aucuparia

(22%) and, correspondingly, the proportion of broken logs was higher in controls (30%) than brook sides (18%).

In the PCA ordination of the stand variables, the first two principal components explained only 17.4% and 12.9%, respectively, of the total variation in the data. The forest categories were considerably overlapping in this ordination space although part of the brook sides (about 15 sites) were located more to the bottom right than most control sites (Fig. 5A). Regarding the stand variables, there was no clear grouping of correlated variables (Fig. 5B). Vectors pointing in the same direction in the ordination space indicate positively correlated variables, vectors pointing in opposite directions negatively correlated, and perpendicular vectors uncorrelated variables. The first main direction of variation in the data - approximately from the bottom left to the top right - can be interpreted to describe a naturalness gradient. The diversity of dead wood (as well as total volume of dead wood and number of dead stems not shown in the figure) and the diversity of living stand increased to the opposite direction

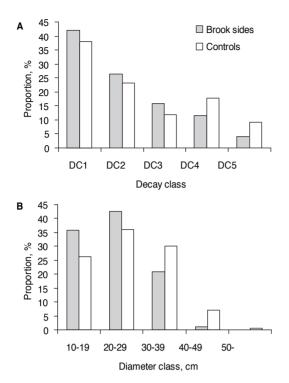


Fig. 4. Decay-class distribution (A) and diameter-class distribution (B) of dead wood in brook-side key habitats and control sites.

(top right) than the basal area of cut stumps. The second main direction of variation – approximately from the top left to the bottom right – can be interpreted to reflect mainly a site-type gradient, possibly also a successional gradient. Stand age, volume of living spruces and volume of living pines increased to the opposite direction (top left) than the volume of living alders and birches. This direction of variation separated best brook sides from controls, and it was not correlated with the naturalness gradient.

3.3 Surroundings of Brook-Side Key Habitats

Over half (51.2%) of the stands adjoining brook sides consisted of either mature forest or recently regenerated stands. This proportion was over twice as high as the proportion of the respective development classes (24.6%) in the private forests in southern Finland according to the National Forest Inventory.

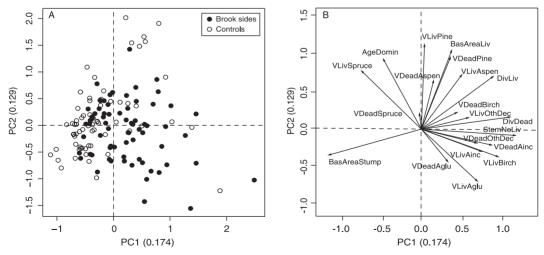


Fig. 5. Location of the brook-side key habitats and control sites (A), and relationships between the stand variables (B) in the ordination space determined by the first two principal components (PC1 and PC2). Abbreviations for the stand variables are given in Table 4.

4 Discussion

4.1 Logging History in Key Habitats

The number and basal area of cut stumps are among the most straightforward measures of naturalness. Cut stumps have been used for assessing the degree of naturalness of stands in several recent studies (Siitonen et al. 2000, Storaunet et al. 2000, 2005, Rouvinen et al. 2002, 2005, Uotila et al. 2002, Lilja and Kuuluvainen 2005). Based on stumps, none of the brook-side key habitats was natural in the strictest sense, without any signs of logging. However, this was to be expected as it is highly unlikely that totally untreated stands - even small patches - could be found in ordinary managed forests at productive sites in southern Finland. On the contrary, even old-growth forests within protected areas usually bear some signs of past selective logging (Siitonen et al. 2000, Rouvinen et al. 2002, 2005, Uotila et al. 2002). The lowest number of cut stumps in a key habitat was 20 ha⁻¹. Only 10 key habitats (about 15%) had less than 100 stumps per hectare. Our results are consistent with the results by Ericsson et al. (2005) who found that most of the studied key habitats in central Sweden had >100 cut stumps per hectare. Of the control stands, only three (about 4%) had less than 100 cut stumps per ha.

4.2 Important Structural Features in Key Habitats and Controls

Dead wood is a structural element which has been frequently used in identifying potentially important habitats. The average volume of dead wood was considerably higher in key habitats than in average managed forests where the volume is 2.5 m³ha⁻¹ in southern Finland according to the 9th National Forest Inventory (Ihalainen and Siitonen 2006). However, the volume varies according to age class and site type, being the highest in mature forests and fertile sites. In managed herb-rich and mesic sites belonging to the age class 101-140 years, the average volumes are 7.0 and 5.1 m³ha⁻¹ (Ihalainen and Siitonen 2006), i.e. close to the average volume in our control sites. In contrast, the volumes have been shown to vary from about 90 to 140 m³ha⁻¹ in old natural forests in fertile sites, according to both empirical studies and modelling results (Siitonen 2001, Ranius et al. 2004). In other words, the volume of dead wood is of an order of magnitude larger in comparable types of natural forest than in brookside key habitats.

The decay-class distribution and diameter distribution indicated that most of the dead wood in brook sides originates from relatively recent mortality of mainly small-diameter trees. The decay-class distribution was essentially similar in brook sides and controls indicating that key habitats did not have a better continuity of dead wood than control sites. Furthermore, the volumes and numbers of large-diameter dead coniferous and deciduous trees did not differ between the forest categories. Large-diameter dead trees in mid and advanced decay stages are the most important types of dead wood for both red-listed species (e.g. Jonsell et al. 1998) and the overall diversity of saproxylic species (Dahlberg and Stokland 2004).

As pointed out by Kotiaho et al. (2006), the volume distribution of dead wood among stands is generally very skewed to the right which means that most of the stands contain only little dead wood whereas a few stands can contain large amounts. In such a situation the average volume is not the most informative measure of the ecological value of stands. The right-skewed distribution is pronounced also in the present data. The stand-level volume and continuity of dead wood are significant factors for saproxylic species, and particularly for threatened species (e.g. Penttilä et al. 2004, Stokland and Kauserud 2004, Junninen and Kouki 2006, Hottola and Siitonen 2008). A total of 11 brook sides (about 15%) and seven controls (10%) had at least 20 m³ha⁻¹ of dead wood. This means that despite the low average volume in managed forests, about every tenth old stand has a relatively high volume of dead wood.

According to the results of the mapping project of especially important habitats (Yrjönen 2004), the average volume of dead wood in brook sides was $8.3 \text{ m}^3 \text{ha}^{-1}$, and the median was $5.0 \text{ m}^3 \text{ha}^{-1}$ (Kotiaho and Selonen 2006). However, in the mapping project the volumes were not measured but estimated, and it is evident that the reported volumes are gross underestimates (Kotiaho and Selonen 2006). In Sweden, a detailed inventory of dead wood was conducted as a part of the Biodiversity Monitoring Programme based on a sample of ca. 500 key habitats of different types over the whole country (see Jönsson and Jonsson 2007). The average volume was $19.5 \text{ m}^3 \text{ ha}^{-1}$; the considerably higher volume in Sweden than in Finland may be partly due to differences in recording, but a more likely explanation follows from differences in key habitat definitions and selection criteria between the countries. In Sweden old-growth coniferous forests constitute a large part of the key habitats, and the amount, diversity and continuity of dead wood have been important selection criteria (Norén et al. 2002).

The average diversity of living stand was higher in brook sides than controls because of two main reasons: lower degree of thinning resulting in more varied diameter distribution, and a higher abundance of deciduous trees. The average numbers of both large-diameter spruces and deciduous trees were about twice as high in brook sides than controls which may be of importance for e.g. epiphytic lichens and for future recruitment of large dead trees.

Contrary to our expectations, there were no major regional differences in the volume of dead wood or stand diversity among the study areas. Thus, within southern Finland, key habitats were not structurally more valuable in regions with relatively short management history than in regions with longer management history.

4.3 Surroundings and Preservation of Key Habitats

Key habitats were about twice as often surrounded by either mature forest or recently clear-cut forest than could be expected on the basis of the ageclass distribution of private forests in southern Finland. This implies that key habitats are or have recently been located within larger patches of mature forest, possibly in the properties of such landowners who have managed their forests less intensively than average. However, if the mature forest surrounding key habitats will be cut, the actual habitat area will be reduced and isolation and edge effects will increase (Aune et al. 2005). Habitat patches smaller than 1 ha surrounded by clear-cut forest can not maintain interior forest conditions (Jönsson et al. 2007).

The aim of the present study was not to assess the preservation of especially important habitats in logging. Nevertheless, of the 70 first randomly selected brook sides, eight (about 11%) had been recently treated with clear-cutting, intensive thinning or excavating the brook channel. As the aim is to preserve key habitats, this is an alarming observation for two reasons: Firstly, the sample is not necessarily representative as regards treatment since only sites for which permission from the landowner (probably indicating a positive attitude towards the preservation of key habitats) was obtained were visited. Secondly, the mapping of especially important habitats took place only recently (1998-2004) which means that the loss of the study sites had occurred during a period of the last five years. It is possible that loss of sites will continue in the future as mature stands adjoining the key habitats will be treated with regeneration cutting. These results concerning cutting are consistent with those presented by Pykälä (2006, 2007). He revisited about 50 key habitats that had been delimitated in the habitat mapping project (see introduction) in Lohja municipality, southern Finland. Of the especially important habitats on forestland, 7% had been clear cut after their delimitation, and selective cutting had occurred in additional 29% of the habitats.

4.4 Practical Implications and Conclusions

Our results show that brook-side key habitats were, on average, more natural and to some degree better in quality than randomly selected control sites in managed forest. However, individual stands varied considerably. The brook-side key habitats appear to consist of widely variable habitat types with probably equally variable biodiversity values, and a large part of them could not be distinguished from ordinary managed forests with respect to stand characteristics. The main distinguishing feature between the forest categories was thus the natural brook channel in the key habitat sites. As forestry has changed the natural state of most small waters (because of cleaning for stream floating, ditching, skidding trails etc.) preservation of natural brook channels with their immediate surroundings is undoubtedly important for maintaining aquatic and semiaquatic biodiversity connected to the brook itself. However, at present it is doubtful whether brook-side key habitats are particularly important sites for those species groups which are dependent on living or dead trees – i.e. for species groups constituting the main part of threatened forest species.

Presuming that key habitats will be excluded from management their stand structure will develop towards natural following different successional trajectories. The amount of important structural features, such as old and large living trees and coarse dead wood, will increase. Because of the edge effects, mortality of trees in these relatively small habitat patches will probably be high (Jönsson et al. 2007), and the volume of dead wood should increase rapidly. However, selective cutting and even felling of individual trees (which are both allowed in especially important habitats) will effectively slow down the formation of structural features important for biodiversity such as dead wood and large old trees (Pykälä et al. 2006, Pykälä 2007). For this reason, it would be important to exclude key habitats from forest management.

The criteria of Finnish Forest Act for designating especially important habitats and the practical mapping of them have been mainly based on the permanent structural features of habitats, and have given less weight to stand characteristics. In principle, this selection strategy implies that the most important ecological gradients are covered (successional gradient being the main exception), and that the selected habitats represent a wide variety of site types. When complementing the forest conservation network in the future, main emphasis in selecting sites should be placed on stand structure. Stands possessing important structural features such as dead wood, overmature trees etc. should be prioritized, and proper selection criteria should be developed.

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References

- Aapala, K., Alanen, A., Heikkilä, R., Heikkinen, R., Husa, J. Kostamo, J., Lindholm, T. & Schneider, H. 1994. Avainbiotooppien tunnistaminen. [Identification of key habitats]. Avainbiotooppien määrittämistyöryhmän muistio. Metsäkeskus Tapio ja vesi- ja ympäristöhallitus, Helsinki. 21 p. (In Finnish).
- Aasaaren, O. & Sverdrup-Thygeson, A. 1994. Nøkkelbiotoper i skogen. [Woodland key habitats]. Norskog, Oslo. 24 p. (In Norwegian).
- Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. Annales Botanici Fennici 5: 169–211.
- Andersson, L., Martverk, R., Kürtvik, M., Palo, A. & Varblane, A. 2003. Woodland key habitat inventory in Estonia 1999–2002. Regio Publishing, Tartu. 112 + 80 p.
- Aune, K., Jonsson, B.G. & Moen, J. 2005. Isolation effects among woodland key habitats in Sweden: Is forest policy promoting fragmentation? Biological Conservation 124(1): 89–95.
- Cajander, A.K. 1926. The theory of forest types. Acta Forestalia Fennica 29(3). 108 p.
- Dahlberg, A. & Stokland, J. 2004. Vedlevande arters krav på substrat – sammanställning och analys an 3600 arter. Skogstryrelsen, Rapport 7/2004. Jönköping. 75 p. (In Swedish).
- Ericsson, T.S., Berglund, H. & Östlund, L. 2005. History and forest biodiversity of woodland key habitats in south boreal Sweden. Biological Conservation 122(2): 289–303.
- Eurola, S., Hicks, S. & Kaakinen, E. 1984. Key to Finnish mire types. In: Moore, P. D. (ed.). European mires. Academic Press, London. p. 11–117.
- Gjerde, I., Sætersdal, M., Rolstad, J., Blom, H.H. & Stotaunet, K.O. 2004. Fine-scale diversity and

rarity hotspots in northern forests. Conservation Biology 18(4): 1032–1042.

- Gunderssen, V. & Rolstad, J. 1998. Nøkkelbiotoper i skog. En vurdering av nøkkelbiotoper som forvaltningstiltak for bevaring av biologisk mangfold i skog. [Woodland key habitats. Evaluation of key habitats as a management measure for the preservation of forest biodiversity]. Norsk institutt for skogforskning, Ås. Oppdragsrapport nr. 5/98. 61 p. (In Norwegian).
- Heinonen, J. 1994. Koealojen puu- ja puustotunnusten laskentaohjelma KPL. Käyttöohje. [KPL programme for the computation of tree and stand characteristics. Users guide]. Metsäntutkimuslaitoksen tiedonantoja 504. 79 p. (In Finnish).
- Hottola, J. & Siitonen, J. 2008. Polypore diversity in brook-side woodland key habitats and managed forests in southern Finland. Biodiversity and Conservation 17: 2559–2577.
- Hyvän metsänhoidon suositukset. 2001. [Guidelines for good forest management]. Metsätalouden kehittämiskeskus Tapio. Helsinki. 95 p. (In Finnish). ISBN 952-9891-76-8.
- Hyvän metsänhoidon suositukset. 2006. [Guidelines for good forest management]. Metsätalouden kehittämiskeskus Tapio, Helsinki. 100 p. (In Finnish). ISBN 10-952-5118-85-1.
- Ihaka, R. & Gentleman, R. 1996. R: a language for data analysis and graphics. Journal of Computational and Graphical Statistics 5: 299–314.
- Ihalainen, A. & Siitonen, J. 2006. Lahopuuston määrä talousmetsissä ja suojelualueilla VMI9:n tulosten perusteella. [The volume of dead wood in managed forests and protected areas according to the results of NFI9]. In: Horne, P., Koskela, T., Kuusinen, M., Otsamo, A. & Syrjänen, K. METSOn jäljillä. Etelä-Suomen monimuotoisuusohjelman tutkimusraportti. Maa- ja metsätalousministeriö, ympäristöministeriö, Metsäntutkimuslaitos ja Suomen ympäristökeskus, Helsinki. p. 78–79. (In Finnish). ISBN 952-453-289-1.
- Jonsell, M., Weslien, J. & Ehnström, B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation 7(6): 749–764.
- Jönsson, M. & Jonsson, B.G. 2007. Assessing coarse woody debris in Swedish woodland key habitats: Implications for conservation and management. Forest Ecology and Management 242(2–3): 363–373.

- , Fraver, S., Jonsson, B.G., Dynesius, M., Rydgård, P. & Esseen, P.-A. 2007. Eighteen years of tree mortality and structural changes in an experimentally fragmented Norway spruce forest. Forest Ecology and Management 242(2–3): 306–313.
- Junninen, K. & Kouki, J. 2006. Are woodland key habitats in Finland hotspots for polypores (Basidiomycota)? Scandinavian Journal of Forest Research 21(1): 32–40.
- Kalliola, R. 1966. The reduction of the area of forests in natural condition in Finland in the light of some maps based upon national forest inventories. Annales Botanici Fennici 3: 442–448.
- Kotiaho, J.S. & Selonen, V.A. O. 2006. Metsälain erityisen tärkeiden elinympäristöjen kartoituksen laadun ja luotettavuuden analyysi. Analysis of the quality and reliability of the survey on habitats of special importance defined in the Forest Act. Suomen ympäristö 29/2006. 65 p. (In Finnish with English summary). ISBN 952-11-2321-4.
- , Kouki, J. & Punttila, P. 2006. Ongelmakohtia kuolleen puun ylläpidossa nykyisissä metsäekosysteemeissä. [Problems in maintaining dead wood in current forest ecosystems]. In: Horne, P., Koskela, T., Kuusinen, M., Otsamo, A. & Syrjänen, K. METSOn jäljillä. Etelä-Suomen monimuotoisuusohjelman tutkimusraportti. Maa- ja metsätalousministeriö, ympäristöministeriö, Metsäntutkimuslaitos ja Suomen ympäristökeskus, Helsinki. p. 78–79. (In Finnish). ISBN 952-453-289-1.
- Laasasenaho, J. 1982. Taper curve and volume functions for pine, spruce and birch. Communicationes Instituti Forestalis Fenniae 108. 79 p.
- Legendre, P. & Legendre, L. 1998. Numerical ecology. 2nd English edition. Elsevier, Amsterdam. 353 p.
- Lihtonen, V. 1949. Piirteitä valtion metsätaloudesta. [Features of the state forestry]. Silva Fennica 66. 46 p. (In Finnish).
- Lilja, S. & Kuuluvainen, T. 2005. Structure of old Pinus sylvestris dominated forest stands along a geographic and human impact gradient in mid-boreal Fennoscandia. Silva Fennica 39(3): 407–428.
- Luonnonläheinen metsänhoito. 1994. Metsänhoitosuositukset. [Natural forest management. Forest management recommendations]. Metsäkeskus Tapion julkaisu 6/1994. 22 p. (In Finnish). ISBN 952-9891-03-2.
- Meriluoto, M. 1995. Metsäluonnon arvokkaat elinympäristöt. Tunnistaminen ja hoitosuosituksia. [Valuable habitats in forests. Identification and

management recommendations]. Metsäkeskus Tapion julkaisuja 12/1995. 32 p. (In Finnish). ISBN 952-9891-12-1.

- & Soininen, T. 1998. Metsäluonnon arvokkaat elinympäristöt. [Valuable habitats in forests]. Metsälehti Kustannus & Tapio, Helsinki. 192 p. (In Finnish). ISBN 952-5118-12-6.
- Metsälaki 1996. [Forest Act]. Suomen säädöskokoelma 1093/96.
- Nitare, J. & Norén, M. 1992. Nyckelbiotoper kartläggs i nytt projekt vid Skogsstyrelsen. Woodland keyhabitats of rare and endangered species will be mapped in a new project of the Swedish National Board of Forestry. Svensk Botanisk Tidskrift 86: 219–226. (In Swedish with English summary).
- Norén, M., Nitare, J., Larsson, A., Hultgren, B. & Bergengren, I. 2002. Handbok för inventering av nyckelbiotoper. [A handbook for the inventory of key habitats]. Skogsstyrelsen, Jönköping. 105 p. (In Swedish).
- Penttilä, R., Siitonen, J. & Kuusinen, M. 2004. Polypore diversity in managed and old-growth boreal Picea abies forests in southern Finland. Biological Conservation 117(3): 271–283.
- Prieditis, N. 2002. Evaluation of frameworks and conservation system of Latvian forests. Biodiversity and Conservation 11(8): 1361–1375.
- Pykälä, J. 2007a. Implementation of Forest Act habitats in Finland: Does it protect the right habitats for threatened species? Forest Ecology and Management 242(2–3): 281–287.
- 2007b. Metsälain erityisen tärkeät elinympäristöt ja luonnon monimuotoisuus – esimerkkinä Lohja. Suomen ympäristö 32. 57 p. ISBN 978-952-11-2823-3.
- , Heikkinen, R.K., Toivonen, H. & Jääskeläinen, K. 2006. Importance of Forest Act habitats to epiphytic lichens in Finnish managed forests. Forest Ecology and Management 223(1–3): 84–92.
- Ranius, T., Jonsson, B.G. & Kruys, N. 2004. Modeling dead wood in Fennoscandian old-growth forests dominated by Norway spruce. Canadian Journal of Forest Research 34(5): 1025–1034.
- Rassi, P., Alanen, A., Kanerva, T. & Mannerkoski, I. (eds.). 2001. The 2000 Red List of Finnish species. Ministry of the Environment & Finnish Environment Institute, Helsinki. 432 p. (In Finnish with English summary). ISBN 951-37-3594-X.
- Rouvinen, S., Kuuluvainen, T. & Karjalainen, L. 2002. Coarse woody debris in old Pinus sylvestris domi-

nated forests along a geographic and human impact gradient in boreal Fennoscandia. Canadian Journal of Forest Research 32(12): 2184–2200.

- , Rautiainen, A. & Kouki, J. 2005. A relation between historical forest use and current dead woody material in a boreal protected old-growth forest in Finland. Silva Fennica 39(1): 21–36.
- Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49: 11–41.
- , Martikainen, P., Punttila, P. & Rauh, J. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. Forest Ecology and Management 128(3): 211–225.
- , Hottola, J., Lommi, S. & Mattila, J. 2006. Metsälakipuronvarsien ja verrokkitalousmetsien puuston rakenne ja lajisto. [Stand structure and species composition in brook-side Forest Act habitats and managed control forests]. In: Horne, P., Koskela, T., Kuusinen, M., Otsamo, A. & Syrjänen, K. (eds.). METSOn jäljillä. Etelä-Suomen metsien monimuotoisuusohjelman tutkimusraportti. Maaja metsätalousministeriö, ympäristöministeriö, Metsäntutkimuslaitos ja Suomen ympäristökeskus, Helsinki. p. 78–79. (In Finnish). ISBN 952-453-289-1.
- Soininen, T. 1996. Talousmetsien avainbiotooppien tunnistaminen. Maastotyöohje, kokeiluversio.
 [Identification of key habitats in managed forests. Fieldwork guide, test version]. Suomen ympäristökeskuksen moniste 27. 109 p. (In Finnish).
- 1997. Avainbiotooppiselvitysprojekti 1996. Maastotyöopas. [Key habitat mapping project 1996. Fiedwork guide]. Metsätalouden kehittämiskeskus Tapio, Helsinki. 50 p.
- Stokland, J. & Kauserud, H. 2004. Phellinus nigrolimitatus – a wood-decomposing fungus highly influenced by forestry. Forest Ecology and Management 187(2–3): 333–343.
- , Eriksen, R., Tomter, S.M., Korhonen, K., Tomppo, E., Rajaniemi, S., Söderberg, U., Toet, H. & Riis-Nielsen, T. 2003. Forest biodiversity indicators in the Nordic countries. Status based on national forest inventories. TemaNord 2003:514. 108 p.
- Storaunet, K.O., Rolstad, J. & Groven, R. 2000. Reconstructing 100–150 years of logging history in coastal spruce forest (Picea abies) with special conservation values in Central Norway. Scandina-

vian Journal of Forest Research 15(6): 591–604.

- , Rolstad, J., Gjerde, I. & Gundersen, V.S. 2005. Historical logging, productivity, and structural characteristics of boreal coniferous forests in Norway. Silva Fennica 39(3): 429–442.
- Sverdrup-Thygeson, A. 2002. Key habitats in the Norwegian production forest: a case study. Scandinavian Journal of Forest Research 17(2): 166–178.
- Tasanen, T. 2004. The history of silviculture in Finland from the Mediaeval to the breakthrough of the forest industry in the 1870s. Metsäntutkimuslaitoksen tiedonantoja 920. 443 p. (In Finnish with English summary). ISBN 951-40-1920-2.
- Tonteri, T. 1994. Species richness of boreal understorey forest vegetation in relation to site type and successional factors. Annales Zoologici Fennici 31(1): 53–60.
- Uotila, A., Kouki, J., Kontkanen, P. & Pulkkinen, P. 2002. Assessing the naturalness of boreal forests in eastern Fennoscandia. Forest Ecology and Management 161(1–3): 257–277.
- Yrjönen, K. 2004. Metsälain erityisen tärkeät elinympäristöt. Kartoitus yksityismetsissä 1998–2004. Loppuraportti. [Especially important habitats as defined in the Forest Act. Survey in private forests in 1998–2004. Final report]. Maa- ja metsätalousministeriö, MMM:n julkaisuja 9/2004. 60 p. (In Finnish). ISBN 952-453-178-X.

Total of 57 references