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Variation in environmental conditions, understorey species number, abundance and composition among natural and managed *Picea abies* forest stands

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Abstract

We studied four south-facing and three north-facing boreal spruce forest stands (ca. 0.1 ha each) in SE Norway with the aim of testing the hypothesis that former logging has long-term effects on boreal forest-floor vegetation. The stand series comprised unlogged natural forests and forests that were selectively or clear cut 60–70 years prior to our study. Each stand was described with respect to history of forestry impact and tree-stand structure. Environmental, species number, species abundance and species composition (vegetation gradients obtained as ordination axes) variables obtained for 25 m × 1 m plots in each stand were tested for among-stand differences.

Significant among-stand differences were found, partly related to former forest management and partly due to among-stand differences in topography. Differences among stands related to management were found for tree stand density, highest in managed stands, and for *Dryopteris expansa* agg. and *Luzula pilosa* abundances, peaking in formerly clear-cut stands. Species number (at plot or stand scales) was weakly related to former management. On southerly as well as northerly aspects, gradients in species composition were found that separated plots according to former management. Differences among stand conditioned on topography resulted in opposite patterns in the two series of stands because among southerly stands the clear cut was the least while among northerly the clear cut was the most strongly sloping. Low-inclination sites tended more strongly to be paludified and to have high *Sphagnum* cover, and to have low abundance of specific microsites with small mosses and hepatics. Vegetation gradients related to soil moisture and microtopography were found for both aspects.

A strong gradient in species composition related to tree influence at within-stand scales was found, with variation in species number. Existence of such a gradient should provide for significant biotic effects (of short or long duration) of the environmental changes that take place during forest re-growth: (1) the immediate creation of small or large tree-layer gaps by tree felling; and (2) the closing of the tree layer during the regeneration phase. Most notably, the phases at which the tree layer reaches minimum and maximum cover, respectively, may act as 'bottlenecks' for survival of forest-floor species.

We conclude that forestry impacts understorey vegetation by way of changes in tree-layer structure and, to a lesser extent, substrate availability and the local environment, during forest regrowth. The extent and duration of this impact will depend on a

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complex set of factors. Our results are consistent with the view that if maintenance of species diversity is aimed at, environmental considerations should be built into forest management practices, preferably by mimicking the natural structural dynamics of the tree layer.

Keywords: Environmental factors; Forest management; Old-growth; Ordination; Species abundance; Species composition; Species number; Spruce forest; Tree structure; Vegetation

1. Introduction

During the last 100 years, boreal forestry has undergone mechanisation and shifts from less to more intensive management regimes (Östlund et al., 1997). In the present forest landscape managed stands differ from old-growth forest in age structure and spatial patterns of the tree layer, in lower amounts of dead wood, in reduced importance of natural gap-forming processes, and in reduced structural complexity (Östlund and Linderson, 1995; Kuuluvainen et al., 1996; Östlund et al., 1997). Forest management thus impacts environmental conditions, and in turn species abundances and diversity negatively in boreal forests (Esseen et al., 1997). New forestry practices for ecological sustainability have therefore been proposed (Angelstam, 1998; Larsson and Danell, 2001). However, the new management regimes have remained largely untested (Spence, 2001). Improved knowledge of the long-term impact of older as well as new forest management strategies on species composition and species diversity, notably in the boreal forest floor, is therefore urgently needed (Simberloff, 2001).

Tree felling brings about immediate changes in vascular plant and bryophyte composition of the forest floor (Zobel, 1989; Nykvist, 1997; Jalonen and Vanha-Majamaa, 2001). However, empirical data on longer-term effects (50 years or more) are sparse and inconclusive (Halpern and Spies, 1995; Bailey et al., 1998; Reich et al., 2001). While epiphytes and epixyles are strongly affected by tree felling (Esseen et al., 1997) due to substrate extinguishment and/or intolerable microclimatic conditions (Gauslaa and Solhaug, 1996; Kruys et al., 1999), there are reasons to believe that ground vegetation is less strongly affected. Lack of knowledge also applies to the long-term impact of felling method, although selective felling is likely to affect vegetation less than clear felling (Bailey et al., 1998; Jalonen and Vanha-Majamaa, 2001) because of less drastic effects on substrate availability (Sturtevant et al., 1997; Stokland, 2001) and environmental conditions (Brais et al., 1995).

Ideally, temporal processes should be studied in permanent plots in replicated experiments (Bakker et al., 1996). Successional dynamics has, however, mostly turned out to be reliably inferred also from chronosequences, and chronosequence studies therefore represent an alternative strategy when long-term experiments are not available (Foster and Tilman, 2000). Furthermore, the complexity of interactions in the forest ecosystem calls for a broad-scoped study in which several aspects of ecosystem structure are studied in parallel (T. Økland, 1996).

In the this study, we compare present-day vegetation and environmental conditions of forest stands with 60–70-year-old tree harvests (by selective and clear cutting) and unlogged controls (natural forest stands without signs of logging). Stands were selected that lacked signs of severe natural disturbances (stormfelling, forest fires, etc.) having taken place in the last 80-year period. Our main aim is to test the hypothesis that former logging has long-term effects on boreal forest-floor vegetation, i.e. if there are differences in species richness, abundance and composition of boreal forest-floor vegetation among forest stands that can be traced back to previous timber harvesting, and/or if between-stand differences could be explained by variation in environmental factors not likely to be impacted by former logging. We tested four sets of boreal forest characteristics for among-stand differences: (i) environmental conditions and tree stand structure, (ii) single-species abundances, (iii) species number, and (iv) species composition, and made a careful assessment of the results.

2. Study area and selection of stands

2.1. Study area

The study was carried out in the National Nature Reserve Oppkuven, a forested hill 550–700 m a.s.l., of ca. 2 km^2 extent (60°07′N, 10°32′E), in Ringerike municipality, Buskerud county, ca. 40 km NNW of Oslo, Norway. Oppkuven is situated within the Krokogen lava area in the Oslo region and the bedrock consists of feltsitic intrusives and extrusives (Larsen, 1978). The terrain is broken, with steep cliffs as well as gently undulating hills. Morainic deposits are sparse. The climate is moderately humid. The annual mean temperature and precipitation (1961–1990) at 650 m a.s.l., estimated from data in Aune (1993) and Førland (1993) by correcting for altitude, were 2.9 °C and ca. 1200 mm, respectively. Oppkuven is situated in the middle boreal zone (Moen, 1998). Norway spruce (*Picea abies*) forests alternate with swamp forests and mires. Palaeoecological studies in swamp forests (Ohlson and Tryterud, 1999) indicate a 1500-year period without fire.

2.2. Selection of stands

Southerly and northerly aspects prevail in the study area. At these latitudes, environmental differences between the two aspects give rise to well-documented differences in vegetation (Heikkinen, 1991). Accordingly, we selected two series of stands that were analysed separately, one from south-facing and one from north-facing slopes. Within each series, stands were selected to represent variation in management history from natural old-growth forests without traces of logging to formerly intensively managed forests. In order to maximise comparability among stands, stands were preferred that: (1) had an age of the tree stand of 60 years or more; (2) were gently sloping (mean inclination: 8–22); (3) had uniform forest management history over a rectangular area, at least 20 m broad and 0.1 ha; (4) lacked signs of extensive natural disturbances such as windfall having taken place in the last 80 years; (5) were situated close to 650 m a.s.l.; (6) had uniform tree-layer dominance by *Picea abies* (Norway spruce); and (7) lacked species typical of sites with high nutrient content. Four south-facing stands (natural (south-Nat), minor selectively cut (south-MiSeC), major selectively cut (south-MaSeC) and formerly clear cut (south-CleC) forest) and three north-facing stands (natural (north-Nat), minor selectively cut (north-MiSeC) and formerly clear cut (north-CleC) forest) were selected. Some compromises were made with respect to the specifications: The south-Nat stand was long and irregular, occupying a south-facing grove; north-Nat consisted of a slightly convex hillslope that downward passed into an almost level slightly paludified forest; and north-CleC was situated at 550 m a.s.l.

2.3. Management history and tree stand characteristics of selected stands

A detailed study (K.O. Storaunet et al., unpublished data) was carried out in 1997 to reveal the management history and summarise the main tree-stand characteristics of the seven stands. That study included: (1) mapping and measurement with respect to height and diameter at breast height of all dead (divided into log and snag, i.e. fallen and standing dead) and living trees in all stands; (2) determination of tree age by coring at breast height and measurement of tree-ring widths (in clear-cut stands, only selected trees were cored); (3) recording of cut stumps; (4) dating of gaps, created by natural processes or by logging, by (i) inspection of age distributions; (ii) determination of major growth releases in cored trees (Dynesius and Jonsson, 1991); and (iii) recording the distribution of dead wood on decay stages (Brewer and Merritt, 1978); the time needed for cut stumps to decompose completely is ca. 100 years (Groven et al., 2002); and (5) estimation of the volume of living and dead trees (Nyyssönen, 1955; Fitje and Vestjordet, 1977).

The south-facing natural forest stand (south-Nat) had high mean tree age, large amounts of dead wood distributed on all decay classes and no cut stumps (Table 1). The stand volume has been high for the last 100-year period. In 1997, the stand was a mosaic of patches in the ageing, decay and regeneration phases. The south-MiSeC stand was subjected to a minor selective cutting around 1927. Trees up to 200 years of age were present. Logs were in intermediate stages of decay. In 1997, the stand was in the optimal/early decay phases, without large gaps and with low regeneration. The south-MaSeC stand was subjected to a major selective cutting around 1927. Most trees were

Table 1
Tree-layer characteristics of sample stands

Characteristic (unit of measurement)	South-				North-		
	Nat	MiSeC	MaSeC	CleC	Nat	MiSeC	CleC
Dated tree harvests (±2 years)	None	1927	1927	1937	None	1890–1930	1935
Tree stand; trees alive in 1997							
Number of trees, dbh >8 cm (daa^{-1})	53	58	108	133	57	52	83
Estimated volume of living trees (m^3/daa)	30.6	33.1	42.7	27.5	18.8	19.9	28.3
Mean age of trees, dbh >8 cm (years)	126	85	67	...	135	126	...
Dead wood							
Number of logs, dbh >8 cm (daa^{-1})	36	13	12	...	10	13	...
Number of snags, dbh >8 cm (daa^{-1})	12	2	11	19	10	13	5
Estimated volume of logs >8 cm (m^3/daa)	14.1	4.3	0.7	<1	2.5	2.2	<1
Estimated volume of snags >8 cm (m^3/daa)	6.8	1.8	4.5	1.1	4.4	7.9	0.3
Dead wood volume, % of volume of living trees	68	18	12	<10	37	51	<5
Cut stumps							
Number of cut stumps (daa^{-1})	0	26	36	55	0	12	58
Estimated volume removed by cutting (m^3/daa)	0	6.7	14.5	18.7	0	3.4	23.4
Removed volume, % of volume of living trees	0	20	34	68	0	17	83

daa = decares; 1 decare = 0.1 hectare = 1000 m^3.

50–70 years of age and very few logs were present. In 1997, the stand was dense, in the growth phase, without larger gaps and regenerating poorly. The south-CleC stand was clear cut around 1937 (some young trees and saplings were left uncut). In 1997, it was in the growth phase, with scattered gaps. The number of trees per unit area increased and tree dimension and abundance of dead wood decreased along the series. Standing tree volume peaked in the south-MaSeC stand.

The north-facing natural forest stand (north-Nat) had an even age distribution with tree ages (at breast height) up to 300 years, low stand volume and low number of trees per unit area (Table 1). In 1997, the stand was open, mostly in the optimal and ageing phases, with low regeneration but without large gaps. The north-MiSeC stand was subjected to multiple minor selective cuttings between 1890 and 1930. Mean tree age was high. The relatively high amounts of dead wood (snags) were caused by tree deaths after 1985 due to bark beetle infestation. In 1997, the stand was open, in the ageing (decay) phase, with large gaps and low regeneration. The north-CleC stand was clear cut around 1935, with only a few young trees and saplings left uncut. In 1997, the stand was densely stocked, in the growth phase, but also with some larger gaps.

3. Methods

3.1. Sampling

All field work was performed in 1997.

The long axis (*centreline*), in direction of the slope of each stand (39–54 m, 136 m in south-Nat), was divided into five (10 in south-Nat) segments of equal length, within each of which one *transverse line*, 20 m (9–14 m in south-Nat) long, was placed at random (but ≥3 m from the border between segments or the border of the stand). A *transverse area*, 20 m × 2 m, and an *extended transverse area*, 20 m × 6 m, was placed symmetrically around each transverse line. Twenty-five 1 m^2 plots were placed in each stand, five in each transverse area (two or three in south-Nat). Of these, 60% were placed at random and 40% according to five pre-defined special criteria (see Rydgren et al., 1999): (1) underneath the largest tree; (2) at the crown perimeter of the largest tree; (3) in the largest gap; (4) at the most distinct terrain concavity, and (5) at the most distinct terrain convexity. Every plot had one edge coinciding with the transverse line. All plots were separated by 1 m or more. Plot positions were rejected and replaced by the next available position if including (1) mire, brook or other non-forest element; (2) >25% bare rock; (3) microscale walls higher than

0.25 m; (4) boulder stones with diameter >0.25 m; (5) logs with diameter (within the plot) >0.2 m; (6) stumps with diameter at stump height >0.2 m; or (7) trees taller than 2 m rooted within the plot.

3.2. Recording of explanatory variables

Twenty-six explanatory variables, supposed to be important for the differentiation of vegetation within and between stands, were recorded for each of the 175 sample plots. Of these, 10 that were strongly correlated with other variables or contributed little to explaining variation in vegetation, were left out, leaving 16 variables in four groups (see Table 2 for methods): (1) topography and soil depth variables; (2) tree influence variables; (3) soil moisture; and (4) soil chemical and physical variables.

Tree influence indices were calculated from measurements of all 936 trees (840 *Picea abies*, 53 *Sorbus aucuparia* and 43 *Betula* spp.) higher than 2 m recorded in the seven stands, including: mapped positions of stem and crown perimeter; height (h); crown height (ch; the length along the stem from top to the point of emergence of the lowest-situated green branch whorl); diameter at breast height (dbh); crown area (ca; calculated as the area encircled by the crown perimeter), and crown cover (cc; percentage of ca covered by living phytomass).

Moisture and soil chemical and physical variables were determined in soil collected from the upper 5 cm of the humus layer, about 10 cm from the border of each plot. All samples were kept frozen until analysed. Fixed-volume samples stored in paper bags kept inside double plastic bags were used to determine moisture. Soil chemical and physical variables were determined in a second set of samples, each consisting of 5–10 subsamples, collected on 25 August 1997. Before analysis at Landbrukets analysesenter, Ås, samples were dried at 38 °C, ground and sifted (2 mm mesh width).

3.3. Recording of species abundance and species number variables

Presence/absence of all humus-dwelling vascular plant (except lignified shoots >80 cm high), bryophyte and lichen species was recorded in each of 16 m × 0.0625 m subplots within each 1 m^2 plot. A species was recorded as present if its vertical projection covered a subplot. Frequency in subplots was used as species abundance measure (Økland, 1988).

Five species number (α-diversity) variables were determined for each plot: (1) vascular plants, (2) mosses (without *Sphagnum*), (3) *Sphagnum*, (4) hepatics, and (5) lichens. The number of infrequent species, i.e. with frequency lower than the median frequency in each stand series, was also determined. Stand-scale species number was recorded as the number of species occurring in at least one of the 25 m × 1 m plots in the stand.

Nomenclature follows Lid and Lid (1994), Frisvoll et al. (1995) and Krog et al. (1994) except for: *Dryopteris expansa* agg., that may also include *D. dilatata* (Hoffm.) A. Gray and *D. carthusiana* (Vill.) Fuchs.; *Dicranum fuscescens* agg., that may also include *D. flexicaule* Brid.; the genus *Polytrichastrum* G.L.Sm., which is not recognized as distinct from *Polytrichum* Hedw.; *Lophozia ventricosa* agg., that includes *L. silvicola* Buch and that may also include *L. longiflora* (Nees) Schiffn.; and *Cladonia chlorophaea* agg., that may also include *C. cryptochlorophaea* Asah., *C. grayi* Merr. ex Sandst., *C. fimbriata* (L.) Fr., *C. merochlorophaea* Asah. and *C. pyxidata* (L.) Hoffm.

3.4. Ordination, environmental interpretation of ordination axes and derivation of species composition variables

Ordination methods were used to identify the main vegetation gradients in the data sets of 1 m^2 plots from each of south- and north-facing stands, 100 and 75 plots, respectively. The plot scores were used as species composition variables. As recommended by Økland (1990, 1996), we applied the most reliable method within each of the two main families of ordination methods, detrended correspondence analysis (DCA; Hill, 1979) and local, non-metric multidimensional scaling (LNMDS; see Minchin, 1987), in parallel.

CANOCO (ter Braak, 1987, 1990), Version 3.15 debugged according to Oksanen and Minchin (1997), was used to run DCA with detrending by segments, non-linear rescaling, and down-weighting of species with lower than median frequency (Eilertsen et al., 1990). DECODA, Version 2.01 (Minchin, 1990) was

Table 2
Explanatory variables: abbreviated code, statistical distribution, unit of measurement, range of values, and method for recording[a]

Code	Variable name	Distribution	Unit	Range	Explanation of method and comments
Inclin	Inclination	–	•	0–60	Measured, representative for the sample plot, by means of a clinometer (400° scale)
HeatI	Heat index	*		−1.29–0.87	Index of insolation, calculated according to Parker (1988), as HeatI $= \tan a_1 \cdot \cos a_2$, where a_1 is the inclination and a_2 the absolute value of the difference between the plot's aspect and SSW (225°), considered to be the most favourable aspect (Heikkinen, 1991)
RoughMe	Median terrain	*	cm	0.5–18.5	Obtained according to Nellemann and Thomsen (1994) from the average lengths of six chains, placed on the ground along the borders between subplots (25 cm apart, three chains in each direction), from which the theoretical minimum length of 100 cm were subtracted
InclMax	Maximum-inclination	•		24–100	Measured, by means of a clinometer (400° scale), as the maximum slope between two points in the sample plot, situated 10 cm apart
SoilDMe	Median soil depth	–	cm	2–100	The median of eight measurements of the distance a steel rod could be driven into the soil in fixed positions, 25 cm outside the sample plot borders
BasalAr	Basal area	–		0–40	A measure of tree density, measured at breast height by a relascope using relascope factor 1 (Fitje and Strand, 1973)
GapAvg	Gap, average	*	%	0.0–43.2	Gaps over the sample plot were measured by a convex, spherical densiometer (Lemmon, 1956; Forestry Supplier Inc.) as the percentage of visible sky. Measurements made from the mid-points of the four plot edges, with the meter directed towards the plot, were averaged to derive the variables
TreeInf	Tree influence	–		0.00–0.96	The tree influence model of Økland et al. (1999) was used: For each plot, the influence I_i of tree i was calculated as $I_i = 0.0825\ \mathrm{dbh}^{0.6} \exp(-0.248 s^{2.2}\ \mathrm{dbh}^{-1.52})$, where s (in dm) is the distance from the plot center to the center of the stem of tree i and dbh is diameter at breast height of tree i. The I_i values for all n trees that influence a particular plot are combined to a tree influence index by TreeInf $= 1 - \Pi_{i=1,\dots,n} [1 - I_i]$
LitterI	Litter index	*		0–261	Calculated according to Økland (1990, 1996) and Økland and Eilertsen (1993) as $\mathrm{LitterI}_i = \Sigma_{i=1,\dots,n} (\mathrm{d}_i/\mathrm{cr}'_i)\mathrm{cc}_i\mathrm{ca}_i\mathrm{ch}_i$, where d_i is the distance from the crown periphery to the proximal sample plot border (i.e. the side facing the stem) along the line through the plot center and the stem center for tree i, cr'_i is the crown radius of tree i, measured through the plot center, cc_i is the crown cover of tree i, ca_i is the crown area of tree i within the 1 m^2 plot, and ch_i is the length along the stem from top to the point of emergence of the lowest-situated green branch whorl (in m), respectively.
MoisMed	Soil moisture, med.	–	vol.%	48.4–84.8	The samples were collected on 19 September 1997, after a period with ample precipitation followed by two rain-free days weighed, dried at 110 °C to constant weight, and weighed The measurements were interpreted as median soil moisture (cf. Økland, 1990; Økland and Eilertsen, 1993)
LossOI	Loss on ignition	*	%	67.8–97.9	Determined by ashing ca. 1 g of sample at 550 °C in a muffle furnace
pH	pH	–		3.5–4.6	Measured in aqueous solution; one part of sample mixed with 2.5 parts of distilled water

Table 2 (*Continued*)

Code	Variable name	Distribution	Unit	Range	Explanation of method and comments
Ca	Exchangeable Ca	–	ppm	274–4305	Determined in the Jarrell Ash instrument after adding 50 cm^3 of 1 M NH_4NO_3 solution to 10 g dried soil, leaving the solution overnight, filtering and washing the sediment with 1 M NH_4NO_3 until the extract volume amounted to 250 cm^3. Element concentrations were recalculated as ppm of organic matter (from mg/kg dry sample to mg/kg organic matter, by multiplication with 100 per loss OI), as recommended by T. Økland (1988)
Mg	Exchangeable Mg	–	ppm	121–729	
N	Total N	*	%	1.54–2.66	Determined by digestion of the dried sample with H_2SO_4 in the presence of a Se catalyst in a Tecator FIA system; recorded as wt.% of organic matter
P	Total P	*	ppm	60.1–265.3	Determined by the ammonium lactate-method: one part dried sample was mixed with 20 parts of a solution 0.1 M with respect to ammonium lactate and 0.4 M with respect to acetic acid, pH was adjusted to 3.75, and P determined in the extract by a Jarrell Ash model 1100 ICP instrument

[a] Variables with right-skewed distributions, ln-transformed before analyses, are indicated by asterisk.

used to run LNMDS with the following options: dimensionality (number of axes) = 4; dissimilarity measure = percentage dissimilarity; species abundance standardised by division with species maximum (Faith et al., 1987); minimum number of starting configurations = 100, maximum number of iterations = 1000, stress reduction ratio for stopping the iteration procedure = 0.99999. Minimum stress solutions were accepted when arrived at from two or more starting configurations. The LNMDS axes were linearly rescaled in S.D. units by DCCA (using CANOCO) to enhance comparability with DCA axes, one LNMDS axis at a time used as the only constraining variable (Økland, 1990). Three species-poor south-facing plots acted as outliers in the ordination and were removed before LNMDS was re-run for the remaining 97 south-facing plots (R. Økland, 1996).

For southerly as well as northerly aspects, the four DCA axes and the four LNMDS axes were strongly correlated in pairs (Kendall's $\tau > 0.37$, $P < 0.0001$). The two ordination methods therefore identified a consistent gradient structure (R. Økland, 1996).

Ordination axes were interpreted environmentally by calculation of Kendall's non-parametric correlation coefficient τ between plot scores and explanatory variables. Kendall's τ between plot scores and species number in each of the species groups was also calculated. The eight environmentally interpreted LNMDS axes were used as species composition variables because they were mostly (slightly) more strongly correlated with explanatory variables than the DCA axes.

3.5. Statistical tests of among-stand differences

Testing was performed separately for south-facing (4 stands, 100 plots) and north-facing (3 stands, 75 plots) stands. Explanatory variables were ln-transformed (Table 2) when necessary to satisfy demands of parametric statistical methods for homoscedasticity (homogeneity of variances). Transformation of species number and composition variables was not needed. Non-parametric methods were used for species abundance variables.

Most descriptors of variation in nature are spatially structured; among others due to *spatial autocorrelation* (Legendre, 1993). When spatially autocorrelated variables recorded in discrete stands are tested for between-stand differences by standard statistical methods (all observations treated as independent), the null hypothesis of no difference between stands will be rejected too often (the test will be too liberal; Type I error) because each observation does not carry with it one full degree of freedom (Legendre et al., 1990). No method exists for estimating the real degrees of freedom of spatially autocorrelated variables except in regular grid sampling (Legendre et al., 1990; Legendre and Legendre, 1998). Our solution to this challenge was to subject all variables to descriptive semivariance analysis (Rossi et al., 1992) prior to testing. Almost all variables had spatial structure at within-stand scales (T. Økland et. al., unpublished results). Most strongly, this was the case for tree influence and species composition variables, which were spatially structured with a range of influence of the spatial process of 6–10 m. Every stand could, however, be divided into 12 or more compartments, each with plots separated from plots in other compartments by more than 10 m. The number of effectively independent observations in each stand was therefore ≥ 12 for all variables. Accordingly, the maximal effect of spatial autocorrelation on test results could be assessed by comparing P values for n (the number of plots) and $n/2$ degrees of freedom. P_n never differed from $P_{n/2}$ more than by one half order of magnitude. Thus, if $P_n < 0.01$, the “true” $P = <0.05$. We report P_n, but have adopted a conservative interpretation: $P \leq 0.001$ is referred to as strongly significant, $P \leq 0.01$ as significant, and $0.01 \leq P \leq 0.05$ as indicatively significant.

One-way ANOVA was used to test explanatory variables, species number variables and species composition variables for among-stand differences. In case of significant effects ($P < 0.01$), the Tukey–Kramer multiple comparisons test (Sokal and Rohlf, 1995) was used to test for pair-wise differences. The nonparametric Kruskal–Wallis test (Sokal and Rohlf, 1995) was used to test species abundance variables.

4. Results

4.1. Among-stand differences in explanatory variables

South-facing stands differed significantly with respect to inclination and fine-scale surface roughness; both highest in the natural forest and lowest in the formerly clear-cut stand (Table 3). Topographic variables were not significantly different among north-facing stands. Soil depth differed significantly among stands, consistently related to forest management on northerly aspects only (the formerly clear-cut stand had the shallowest soils; Table 3).

On both aspects, tree density (basal area) differed significantly among stands in a manner consistently related to forest management: lowest in the natural forests and highest in the south-MaSeC and north-CleC stands (Table 3). The three other tree influence variables, which were strongly correlated with each other ($\tau > 0.35$, $P < 0.0001$), were weakly correlated with BasalAr ($\tau < 0.18$, $P > 0.04$). The GapAvg index differed significantly among southerly stands, where gaps were larger and/or more numerous in the natural forest stand (Table 3).

The clear-cut stands deviated from the other stands with respect to soil moisture; highest in the south-facing and lowest in the north-facing clear-cut stand. Humus contents of Mg and P varied among stands in systematic manners related to forest management; in both series Mg was significantly higher in the natural forest than in all other stands and had lowest means in the formerly clear-cut stands while P was invariably higher in the formerly clear-cut stands (Table 3). The formerly clear-cut north-facing stand differed significantly from the other stands in lower loss on ignition and higher n.

4.2. Among-stand differences in species number

A total of 108 species were recorded in the 175 plots; 87 (20 vascular plant, 57 bryophyte and 10 lichen species) in the four south-facing and 86 (25, 51 and 10, of the respective groups) in the three north-facing stands. Slightly higher species numbers were recorded in the natural forest stands within each series mostly due to higher number of lichens (Fig. 1).

Among south-facing stands species number in 1 m^2 plots did not differ significantly for any species group. The number of moss species differed significantly among north-facing stands and were highest in the formerly clear-cut stand (Table 4). Indicatively significant among-stand differences in species number were found for hepatics on northerly aspects and for infrequent species on both aspects (ANOVA; southerly aspects: $F_{3,96} = 2.853$, $P = 0.042$; northerly aspects: $F_{2,72} = 3.750$, $P = 0.028$).

4.3. Among-stand differences in species abundance

Six and seven vascular plant species differed significantly in abundance among south- and north-facing

Table 3
Explanatory variables: stand medians, ANOVA tests for differences among stands (*F* statistic), and Tukey's test for between-stand contrasts[a]

Variable	South-					North-			
	Nat	MiSeC	MaSeC	CleC	*F*	Nat	MiSeC	CleC	*F*
Inclin	22 b	20 b	20 ab	11 a	6.68***	15 b	12	24	4.41*
HeatI	0.13	0.22	0.19	0.12	0.41	−0.09	−0.15	−0.29	4.48*
RoughMe	5.5 b	5.0 b	5.0 b	2.5 a	9.17****	4.5	3.5	6.0	2.61
InclMax	70 b	62 ab	50 ab	44 a	4.95**	44	45	58	2.08
SoilDMe	37.5 b	24.0 a	32.5 b	25.0 a	6.57***	40.5 b	37.5 b	19.0 a	27.40****
BasalAr	**12 a**	**18 b**	**27 c**	**22 c**	**30.23********	**13 a**	**16 b**	**18 c**	**24.78********
GapAvg	5.7 b	1.6 a	1.6 a	0.0 a	6.28***	15.3	3.1	2.6	3.00
TreeInf	0.20	0.35	0.54	0.28	2.19	0.16	0.29	0.20	1.05
LitterI	59	192	199	266	3.70*	62	221	282	1.34
MoisMed	71.8 ab	69.1 a	69.3 ab	74.8 b	5.90**	76.5 b	76.0 b	69.9 a	16.51****
LossOI	95.2	94.3	93.9	94.8	1.60	97.2 b	96.3 b	92.4 a	59.49****
pH	3.8	3.8	3.9	3.9	2.56	3.8	3.8	3.9	3.98*
Ca	2303	2019	1812	1556	2.60	2187	1483	1732	3.93*
Mg	**328 b**	**266 a**	**261 a**	**233 a**	**11.61********	**447 b**	**320 a**	**270 a**	**37.81********
N	1.98	2.01	2.02	2.03	0.66	1.83 a	1.71 a	2.00 b	8.41***
P	107.0 a	115.2 a	111.8 a	147.7 b	17.58****	130.7 b	107.0 a	173.4[c]	39.39****

Codes and measurement units are given in Table 2. Tests were made separately for south- and north-facing series of stands. Variables with concordant, significant, patterns of variation within the two stand series are indicated by bold-face letters. Significance probabilities are based on the assumption that all observations are statistically independent (d.f. = 3 and 93 for the south-facing and d.f. = 2 and 72 for the north-facing stands).

[a] Different letters indicates differences not significant at the $P < 0.05$ level.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

**** $P < 0.0001$.

stands, respectively (Table 5). Consistent, at least indicatively significant patterns over stand series were found for *Vaccinium vitis-idaea*, which peaked in the natural forest stands and *D. expansa* and *Luzula pilosa* which were most abundant in the formerly clear-cut stands. Two species, *Cornus suecica* and *Rubus chamaemorus*, were restricted to the two north-facing stands least affected by forestry.

Table 4
Species number variables (1 m^2 plots): stand medians, ANOVA tests for differences among stands (*F* statistic), and Tukey's test for between-stand contrasts[a]

Variable	South-					North-			
	Nat	MiSeC	MaSeC	CleC	*F*	Nat	MiSeC	CleC	*F*
Vascular plants	5	5	5	6	0.33	6	6	5	0.19
Mosses	7	6	6	6	1.41	7 a	7 a	9 b	11.53****
Sphagnum	0	0	0	1		1	1	0	
Hepatics	4	4	4	2	1.82	3	4	4	4.71*
Lichens	1	0	0	0		0	0	0	

Tests were made separately for south- and north-facing series of stands. Significance probabilities are based on the assumption that all observations are statistically independent (d.f. = 3 and 93 for the south-facing and d.f. = 2 and 72 for the north-facing stands). Tests were not made for *Sphagnum* and lichens because of the many plots devoid of species of these groups.

[a] Different letters indicate differences not significant at the $P < 0.05$ level.

* $P < 0.05$.

**** $P < 0.001$.

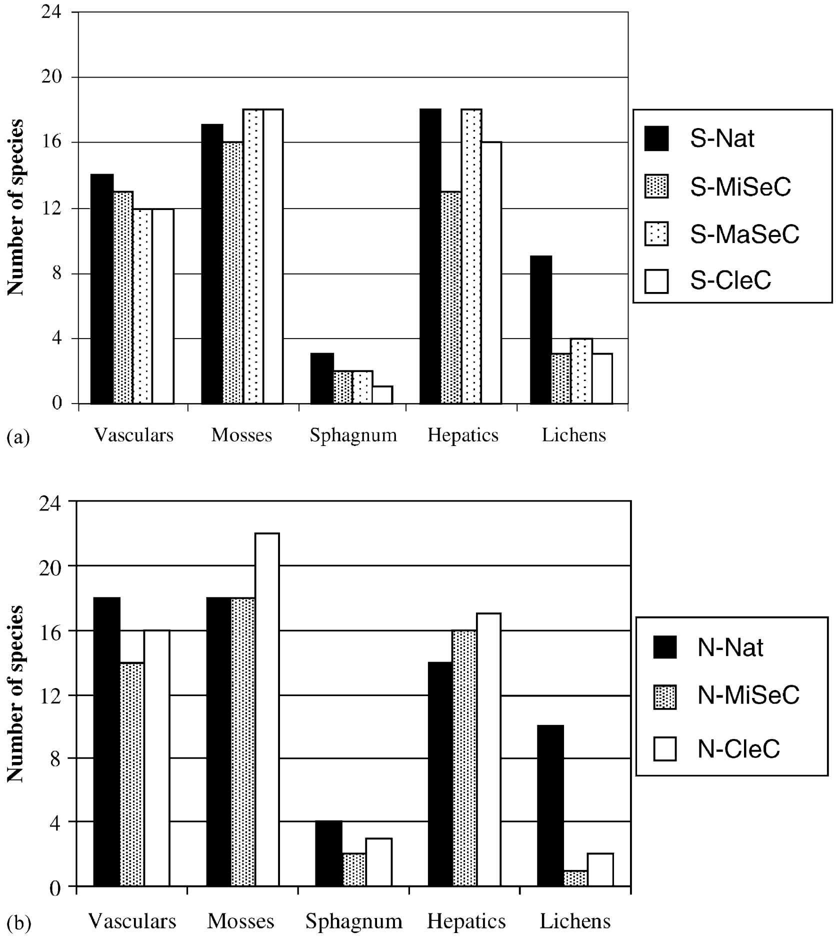

Fig. 1. Total number of species in each taxonomic group observed in the 25 × 1 m^2 plots in each of (a) the four south-facing stands, and (b) the three north-facing stands.

Nine and 21 bryophyte and lichen species differed significantly in abundance among south- and north-facing stands, respectively (Table 5). Significant and consistent patterns over stand series were found for *Dicranum majus* and *Calypogeia muellerana*, that peaked in selectively cut stands. *Brachythecium reflexum*, *Sphagnum girgensohnii* and *Chiloscyphus profundus* increased in abundance from natural to formerly clear-cut stands in both series (among-stand differences were significant in one) while the opposite pattern was observed for *Sphagnum russowii* and *Cladonia chlorophaea* agg. Opposite patterns in the two stand series (with peak abundance in the S-Nat and N-CleC stands) were observed for *Tetraphis pellucida* and *Barbilophozia attenuata* (both significant) and *Pohlia nutans* (significant on southerly and infrequent on northerly aspects).

4.4. Environmental interpretation of, and variation in, species number along ordination axes, and among-stand differences in species composition variables

Four species composition variables (LNMDS axes; vegetation gradients), interpretable in terms of explanatory variables and/or forest management history (Table 6), were obtained for each data set. They made up four pairs, each with one south- and one north-facing gradient with more or less similar environmental basis: (a) gradients related to *soil moisture* that

Table 5

Species abundances: stand constancy percentage, mean subplot frequency given as index and the results of Kruskal–Wallis test for differences among stands (*H* statistic) for species occurring in five or more plots in at least one stand series

Species	South-					North-			
	Nat	MiSeC	MaSeC	CleC	*H*	Nat	MiSeC	CleC	H
Picea abies	36^{2}	16^{3}	52^{4}	60^{2}	11.17^{*}	44^{2}	60^{2}	36^{5}	1.73
Sorbus aucuparia	80^{4}	96^{5}	84^{4}	76^{4}	4.63	44^{2}	76^{3}	76^{4}	10.78^{**}
Vaccinium myrtillus	100^{15}	100^{14}	100^{12}	80^{14}	13.92^{**}	96^{15}	100^{16}	100^{16}	0.92
Vaccinium vitis-idaea	**52^{6}**	**20^{6}**	**20^{3}**	**28^{8}**	**8.06^{*}**	**64^{10}**	**12^{7}**	**4^{13}**	**26.64^{****}**
Cornus suecica	0	0	0	0		52^{13}	84^{10}	0	29.14^{****}
***Dryopteris expansa* agg.**	**8^{2}**	**56^{3}**	**76^{4}**	**80^{5}**	**15.09^{**}**	**4^{1}**	**40^{4}**	**80^{6}**	**32.22^{****}**
Gymnocarpium dryopteris	0	0	0	8		0	0	28^{1}	15.19^{***}
Lycopodium annotinum	4^{2}	16^{4}	44^{4}	16^{3}	13.25^{**}	36^{3}	48^{7}	24^{3}	4.96
Maianthemum bifolium	28^{5}	36^{2}	24^{3}	28^{3}	0.60	24^{2}	12^{2}	36^{6}	5.11
Rubus chamamorus	0	0	0	0		40^{10}	8^{2}	0	17.18^{***}
Trientalis europaea	44^{6}	40^{5}	12^{4}	52^{10}	12.41^{**}	44^{2}	64^{6}	56^{6}	5.07
Deschampsia flexuosa	92^{13}	92^{14}	88^{9}	76^{14}	12.70^{**}	88^{14}	100^{16}	100^{12}	12.34^{**}
Luzula pilosa	**0**	**4^{2}**	**0**	**32^{2}**	**21.51^{****}**	**0**	**4^{5}**	**20^{2}**	**7.21^{*}**
Brachythecium populeum	0	0	0	0		0	0	24^{6}	12.84^{**}
Brachythecium reflexum	32^{3}	36^{3}	20^{3}	48^{6}	5.84	44^{6}	28^{4}	80^{7}	16.70^{***}
Brachythecium starkei	0	0	4^{1}	28^{4}	18.58^{***}	8^{2}	12^{2}	0	2.99
Dicranum fuscescens	88^{9}	68^{6}	88^{6}	76^{3}	17.48^{***}	40^{7}	28^{4}	68^{4}	6.99^{*}
Dicranum majus	**48^{8}**	**76^{8}**	**48^{5}**	**24^{4}**	**17.02^{***}**	**76^{10}**	**88^{12}**	**60^{5}**	**17.59^{***}**
Dicranum montanum	12^{4}	16^{2}	12^{2}	0	3.95	4	0	12	
Dicranum scoparium	92^{13}	100^{10}	100^{10}	92^{11}	2.89	100^{12}	96^{9}	100^{15}	16.30^{**}
Hylocomiastrum umbratum	28^{7}	20^{5}	8^{3}	28^{3}	4.17	36^{9}	48^{5}	84^{10}	16.85^{***}
Hylocomium splendens	20^{6}	24^{7}	0	4^{1}	10.09^{*}	52^{5}	28^{4}	28^{4}	3.56
Plagiothecium denticulatum	4^{2}	4^{10}	12^{2}	12^{1}	1.97	12^{2}	8^{3}	36^{3}	7.72^{*}
Plagiothecium laetum	88^{8}	80^{7}	92^{6}	92^{7}	1.78	68^{5}	88^{4}	100^{8}	16.01^{***}
Pleurozium schreberi	48^{9}	56^{8}	48^{5}	48^{6}	1.44	92^{13}	92^{10}	84^{9}	8.75^{*}
Pohlia nutans	44^{3}	0	4^{1}	4^{1}	29.10^{****}	0	0	12	
Polytrichum commune	4^{5}	12^{11}	4^{9}	8^{11}	1.77	16^{4}	28^{2}	12^{1}	2.45
Polytrichum formosum	88^{10}	64^{11}	76^{10}	76^{8}	2.86	48^{6}	88^{12}	84^{9}	17.96^{***}
Polytrichum strictum	0	0	0	0		20^{3}	0	0	10.56^{**}
Ptilium crista-castrensis	0	0	0	0		12^{2}	24^{4}	12^{6}	1.75
Rhytidiadelphus loreus	4	0	8	4		32^{9}	84^{9}	12^{10}	25.51^{****}
Rhytidiadelphus subpinnatus	0	4	0	4		0	4^{3}	44^{8}	22.14^{****}
Tetraphis pellucida	68^{4}	16^{2}	40^{3}	28^{2}	17.50^{***}	4^{2}	12^{2}	40^{2}	11.25^{**}
Sphagnum capillifolium	0	0	0	0		36^{6}	0	0	20.08^{****}
Sphagnum girgensohnii	4^{15}	20^{14}	28^{9}	60^{7}	15.91^{**}	4^{1}	16^{9}	16^{8}	2.48
Sphagnum quinquefarium	8	4	4	0		20^{8}	72^{9}	32^{2}	19.38^{***}
Sphagnum russowii	8	0	0	0		24^{7}	0	4^{6}	9.86^{**}
Barbilophozia attenuata	64^{4}	36^{3}	48^{3}	16^{1}	15.46^{**}	0	4^{2}	36^{2}	16.52^{***}
Barbilophozia floerkei	36^{5}	40^{4}	32^{3}	28^{4}	1.05	80^{7}	80^{8}	20^{5}	22.63^{****}
Barbilophozia lycopodioides	80^{9}	80^{7}	56^{6}	80^{8}	7.62	100^{13}	96^{10}	100^{11}	8.78^{*}
Calypogeia integristipula	36^{2}	20^{2}	28^{2}	16^{2}	3.74	12^{3}	8^{2}	20^{2}	1.55
Calypogeia muelleriana	0	0	28^{4}	0	22.32^{****}	4^{1}	44^{6}	8^{7}	15.89^{***}
Cephalozia bicuspidata	0	4^{1}	28^{4}	8^{2}	13.54^{**}	12^{2}	28^{4}	28^{4}	2.48
Cephalozia lunulifolia	48^{3}	28^{2}	44^{3}	16^{3}	8.43^{*}	8^{1}	8^{5}	28^{3}	5.27
Chiloscyphus profundus	52^{4}	60^{4}	80^{4}	72^{6}	7.54	24^{2}	68^{4}	96^{8}	39.89^{****}
Lophozia obtusa	8^{3}	0	4^{1}	12^{2}	3.56	16^{3}	8^{2}	52^{6}	16.53^{***}
Lophozia ventricosa agg.	60^{3}	44^{3}	52^{2}	40^{4}	3.02	36^{3}	12^{2}	64^{5}	15.34^{***}
Ptilidium ciliare	24^{3}	20^{4}	0	16^{4}	6.30	28^{3}	4^{2}	4^{3}	8.81^{*}

Table 5 (*Continued*)

Species	South-					North-			
	Nat	MiSeC	MaSeC	CleC	*H*	Nat	MiSeC	CleC	H
Ptilidium pulcherrimum	20^2	16^3	12^7	8^1	1.80	24^1	8^4	32^1	3.61
Cladonia chlorophaea agg.	60^4	12^1	28^2	24^3	16.95^{***}	16^4	0	4^1	5.64
Cladonia coniocraea	44^4	8^2	28^2	20^1	11.63^{**}	32^1	8^2	24^2	4.06

Species with concordant, at least indicatively significant patterns of abundance differences within both stand series are indicated by bold-face letters. Significance probabilities are based on the assumption that all observations are statistically independent (d.f. = 3 and 93 for the south-facing and d.f. = 2 and 72 for the north-facing stands).

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

**** $P < 0.0001$.

Table 6

Separate LNMDS ordinations of 97 south-facing and 75 north-facing 1 m^2 sample plots: length (compositional turnover in S.D. units) of ordination axes; Kendall rank correlations between sample plot scores and explanatory variables (shown for the most strongly correlated variables only) and species number variables; and ecological interpretation of gradients in vegetation

LNMDS axis	Gradient length	Correlated environmental variables				Correlated species/number variables		Ecological interpretation
South-facing stands ($n = 97$)								
S1	2.30	TreeInf	-0.492^{****}	MoisMed	0.271^{***}	Mosses	0.450^{****}	Related to variation in tree influence and, to some extent, soil moisture as related to tree influence on fine and intermediate scales
		GapAvg	0.415^{****}	Ca	-0.246^{***}	VascPl	0.438^{****}	
		LitterI	-0.335^{***}	N	0.187^{**}	*Sphagnum*	0.261^{**}	Runs from dry and dark sites below trees and sites in very dense forest to sites in gaps between trees in more open forest, with higher soil moisture and higher incoming radiation
		BasalAr	-0.284^{***}	LossOI	-0.141^{*}	Hepatics	0.194^{**}	
S2	1.92	InclMax	0.382^{****}	RoughMe	0.216^{**}	Hepat	0.538^{****}	Related to variation in microtopography, on very fine scales
		LitterI	-0.252^{***}	LossOI	-0.210^{**}	Lichens	0.434^{****}	Runs from even forest-floor sites to uneven sites with small pockets (such as steep ledges, microsites adjacent to dead wood, underneath stones, peat, disturbed substrates, etc.)
		Inclin	0.223^{**}	TreeInf	-0.194^{**}	Mosses	0.286^{***}	
S3	1.94	Ca	-0.392^{****}	Ph	0.262^{***}	*Sphagnum*	0.498^{****}	Related to variation in soil moisture on a broader scale than the variation due to tree influence
		MoisMed	0.364^{****}	BasalAr	0.217^{**}	VascPl	0.187^{*}	Runs from dry to moist (paludified) sites, the latter dominated by *Sphagnum* spp.
		Mg	-0.321^{****}			Hepatics	0.161^{*}	The opposite signs of correlations with Ca and pH indicate no relationship with soil nutrient status
S4	1.56	P	0.318^{****}	MoisMed	0.144^{*}	None		Separates formerly clear-cut stands from selectively cut and natural stands (Fig. 2c)

Table 6 (*Continued*)

LNMDS axis	Gradient length	Correlated environmental variables				Correlated species/number variables		Ecological interpretation
		TreeInf	-0.151^{*}					Correlation with P unlikely to represent a cause of the vegetation gradient due to incongruent patterns of spatial variation (T. Økland et al., unpublished results)
North-facing stands ($n = 75$)								
N1	2.33	MoisMed	0.571^{****}	GapAvg	0.258^{**}	*Sphagnum*	0.525^{****}	Related to variation in soil moisture on several scales
		SoilDMe	0.346^{****}	HeatI	0.250^{**}	Lichens	-0.291^{**}	Runs from dry sites to moist paludified sites with high importance of *Sphagnum* spp.
		LossOI	0.331^{****}	Mg	0.232^{**}			Corresponds to the third gradient on south-facing aspects
		Ca	-0.329^{****}	InclMax	-0.213^{**}			
		P	-0.305^{***}	TreeInf	-0.204^{*}			
		Inclin	-0.280^{***}					
N2	2.26	Ca	-0.378^{****}	TreeInf	-0.235^{**}	Hepatics	0.449^{****}	Separates the natural forest stand from managed stands (Fig. 2d)
		BasalAr	0.336^{****}	Inclin	0.222^{**}	Mosses	0.404^{****}	Related to tree-stand density
		LossOI	-0.334^{****}	LitterI	-0.188^{*}	VascPl	0.301^{**}	Runs from natural forest via selectively cut stands to formerly clear-cut stands
		SoilDMe	-0.324^{****}	GapAvg	0.186^{*}	Lichens	-0.226^{*}	Corresponds partly to the fourth gradient on south-facing aspects
		Ph	0.305^{***}	RoughMe	0.171^{*}			The opposite signs of correlations with Ca and pH indicate no relationship with soil nutrient status
		Mg	-0.303^{***}	InclMax	0.156^{*}			
		HeatI	-0.268^{***}					
N3	1.60	P	0.382^{****}	GapAvg	0.164^{*}	Mosses	0.384^{****}	Weakly related to variation in microtopography, on fine scales
		RoughMe	0.266^{**}	Mg	0.164^{*}			Correlation with P unlikely to represent a cause of the vegetation gradient due to incongruent patterns of spatial variation (T. Økland et al., unpublished results)
		LitterI	-0.197^{*}					
								Corresponds partly to the second gradient on south-facing aspects
N4	1.57	LitterI	-0.418^{****}	RoughMe	0.169^{*}	Lichens	0.408^{****}	Due to variation in tree influence; on fine scales
		TreeInf	-0.357^{****}	SoilDMe	-0.167^{*}	Hepatics	0.341^{***}	Runs from dark sites below trees to sites in gaps between trees
		GapAvg	0.310^{***}			VascPl	0.246^{**}	Corresponds partly to the first gradient on south-facing aspects

Significance probabilities are based on the assumption that all observations are statistically independent.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

**** $P < 0.0001$.

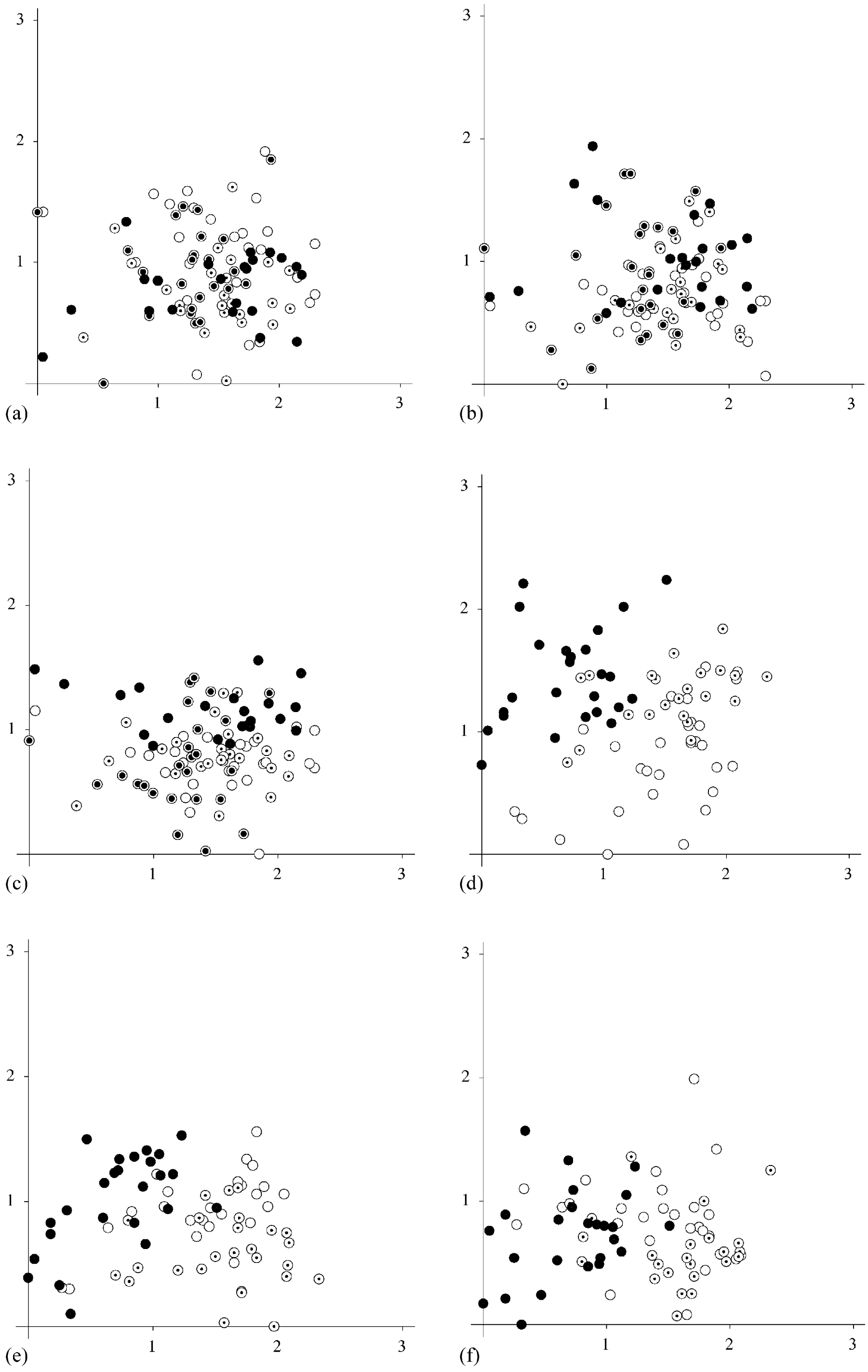

Fig. 2. LNMDS ordination of (a–c) 97 plots from south-facing stands (three outliers removed); (a) axes 1 (horizontal) and 2; (b) axes 1 (horizontal) and 3; and (c) axes 1 (horizontal) and 4 (stand affiliation is indicated by symbol: open ring: south-Nat, ring with small dot: south-MiSeC, ring with large dot: south-MaSeC, dot: south-CleC); and of 75 plots from north-facing stands; (d) axes 1 (horizontal) and 2; (e) axes 1 (horizontal) and 3; and (f) axes 1 (horizontal) and 4 (stand affiliation is indicated by symbol: open ring: north-Nat, ring with dot: north-MiSeC, dot: north-CleC). All axes rescaled in S.D. units.

Table 7
LNMDS ordination scores for plots: stand medians, ANOVA tests for differences among stands (F statistic), and Tukey's test for between-stand contrasts[a]

Axis	South-					North-			
	Nat	MiSeC	MaSeC	CleC	F	Nat	MiSeC	CleC	F
LNMDS 1	1.53	1.49	1.23	1.46	1.971	1.42 b	1.59 b	0.71 a	27.458****
LNMDS 2	1.10 b	0.74 a	0.94 ab	0.80 a	4.901**	**0.71 a**	**1.30 b**	**1.45 b**	**29.976******
LNMDS 3	**0.70 a**	**0.73 a**	**0.91 ab**	**1.02 b**	**4.067****	0.92 b	0.59 a	1.10 b	10.477***
LNMDS 4	**0.73 a**	**0.80 a**	**0.74 a**	**1.16 b**	**11.943******	0.87	0.61	0.73	3.287*

Interpretations of axes are provided in Table 6. Tests were made separately for south- and north-facing series of stands. Axes with significant differences among stands and stands means more or less monotonously related to forest management intensity are indicated by bold-face letters. Significance probabilities are based on the assumption that all observations are statistically independent (d.f. = 3 and 93 for the south-facing and d.f. = 2 and 72 for the north-facing stands).

[a] Different letters indicates differences not significant at the $P < 0.05$ level.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

**** $P < 0.0001$.

separated paludified sites dominated by *Sphagnum* spp. from non-paludified sites appeared as the first axis on northerly and the third axis on southerly aspects; (b) gradients related to *tree influence* on scales up to 8–14 m, from below trees and/or in dense forests to gaps between trees, appeared as the first axis on southerly and the fourth axis on northerly aspects; (c) gradients related to *microtopography*, strongly so for the second axis on southerly (with spatial structure on scales < 2 m (T. Økland et al., unpublished results)) and less strongly so for the third axis on northerly aspects; and (d) gradients from natural forest via selectively cut to clear-cut stands (Fig. 2c–d), related to different explanatory variables on southerly and northerly aspects (Table 6), appeared as the second axis on northerly and the fourth on southerly aspects.

Significant among-stand differences of plot positions along the gradients related to soil moisture and microtopography were observed in both stand series (Fig. 2, Table 7), although with opposite relationships to forest management. S-CleC and N-Nat made up the *Sphagnum*-rich extremes along gradients related to soil moisture, while plots rich in bryophytes and lichens typical of sites with uneven microtopography were best represented in S-Nat and N-CleC. Significant among-stand differences were also observed along one gradient with less clear environmental interpretation in both stand series (Table 7).

Species number for several groups varied significantly along gradients. Most notably the number of species in all groups except lichens increased significantly with decreasing tree influence along LNMDS 1 on southerly aspects, while vascular plants, hepatics and lichens increased with decreasing tree influence along LNMDS 4 on northerly aspects.

5. Discussion

5.1. Interpretation of differences in tree-layer characteristics, environmental variables, species number, species abundances and species composition among stands

We recognise two main patterns for the analysed characteristics: (1) significant among-stand differences consistently related to former forest management; and (2) topographically based differences among stands. In addition, there are several characteristics that do not fit into any of these patterns.

5.1.1. Differences consistently related to former forest management

The most distinct differences among stands, consistently related to former forest management, are observed for stand-scale tree-layer structural characteristics (number of trees per unit area, amount and size distribution of dead wood, and number/size of gaps) and basal area, which expresses tree density on scales broader than the zone of influence of single trees (Table 7; Økland et al., 2001, T. Økland et al., unpublished results). Regardless of aspect, natural forests have a more open tree layer than forests subjected to timber harvesting 60–70 years ago. The distinctive structural features of old-growth as compared to managed coniferous forests accord with results of other studies (Kuuluvainen et al., 1996; Östlund et al., 1997).

On both aspects humus concentrations of Mg are highest in the natural forests stands, while P has the opposite pattern with maximum in the formerly clear-cut stands. Although nutrients are released by clear cutting, especially if the slash is not removed (Nykvist and Rosén, 1985; Olsson and Staaf, 1995), effects of the contents of nutrients in humus that can still be traced 60 years after logging are unlikely to occur (cf. van Ohne, 1992, but see Zobel, 1989) and reasons other than former forestry are likely to be responsible.

Two species, *L. pilosa* and *D. expansa,* are significantly more abundant in the formerly clear-cut stands. Most likely, these species established in open forest shortly after tree harvesting (Nykvist, 1997). These species have a large, long-lived soil propagule bank (Rydgren and Hestmark, 1997). Germination and establishment are likely to be due to the opening of the tree layer and logging disturbance, favoured by a subhumid climate (Rydgren and Hestmark, 1997).

One vegetation gradient for northerly and one for southerly aspects (the second and the fourth, respectively) separate stands according to former forest management. We interpret the second axes for northerly aspects as a partial response to environmental factors not properly represented among the explanatory variables. Plots from two large gaps with shallow soil in the formerly clear-cut north-facing stand occupy the high-score end of this gradient. Easy access to soil nutrients is indicated by the occurrence of species typical of more nutrient-rich soils, like *Gymnocarpium dryopteris* and *Rhytidiadelphus subpinnatus* (Økland and Eilertsen, 1993; T. Økland, 1996). These plots contrast the plots from the sparsely stocked ridge in the natural forest stand, with high abundance of species with optima in pine forests, such as *Vaccinium vitis-idaea* and *Ptilidium ciliare* (Økland and Eilertsen, 1993). Nevertheless, the high correlation of this gradient with tree density may indicate a partial, direct relationship with former forest management. The fourth gradient for southerly aspects emphasise the distinctive species composition of the clear-cut stand.

5.1.2. Topographically based differences among stands

The formerly clear-cut stands are deviant within each series, in opposite ways. While the south-facing is less sloping, the north-facing stand is more strongly sloping than the other stands in the respective series. Differences in topography give rise to patterns of variation inversely related to forest management history in the two stand series.

The more level stands (S-CleC, N-Nat and N-MiSeC) have higher average soil moisture and higher importance of *Sphagnum*-dominated, paludified patches because more strongly sloping sites tend to be better drained (Økland, 1989). The rougher microtopography of strongly sloping sites partly explains the peaking of abundance of several pocket species (Økland et al., 2001), i.e. small mosses, hepatics and lichens, in the more strongly sloping clear-cut north-facing and natural south-facing stands. Furthermore, the preference of species such as *Tetraphis pellucida*, *Barbilophozia attenuata*, *Cephalozia lunulifolia*, *Lophozia ventricosa* agg. and *Cladonia* spp., for the natural southerly stand is likely to be strengthened by these species' preferences for dead wood in various stages of decomposition (Frisvoll and Prestø, 1997), the abundance of which is enhanced by the absence of management (Green and Peterken, 1997; Stokland, 2001), and by the contribution of dead wood to a varied, rough surface (Schaetzl et al., 1989, Kuuluvainen, 1994).

5.2. The strong variation in species composition related to tree influence and identification of critical factors for development of species diversity after logging

The strong gradients in species composition, associated with significant decrease in species number from gaps and open forest to below trees and in dense stands (most notably on southerly aspects) clearly demonstrate the importance of tree-layer properties for the vegetation of the understorey. Similar results are obtained in other studies of boreal coniferous forests (Økland and Eilertsen, 1993; T. Økland, 1996; Økland et al., 1999). This indicates that, at least when climatic humidity is low or moderate, many species find establishment and survival difficult on the dark, dry sites below trees and in very dense spruce forest with high litterfall accompanied by a thick litter layer (cf. Tarkhova and Ipatov, 1975; Busby et al., 1978). This is also likely to account for the difference in understorey species composition and/or species number between thinned and unthinned coniferous forest stands observed by Bailey et al. (1998) and Thomas et al. (2000).

We find important differences between south- and north-facing stands with respect to which environmental gradients are the most important for differentiation of the vegetation. Whereas variation in vegetation related to tree influence is most important on south-facing stands, variation related to soil moisture is most important on north-facing stands. Higher importance of variation in soil moisture on north-facing stands and, hence, larger paludified area, reflects the more humid local climate of north-facing slopes (Økland, 1989).

Our results indicate that north-facing stands remain more open than south-facing stands for a longer period following forest management, most likely due to differences in rates of natural regeneration and tree growth rates (Hannerz and Hånell, 1997). Furthermore, north-facing sites below trees are less dry, allowing more species to establish and survive there than in comparable, south-facing sites. Tree-layer structure therefore exerts a stronger influence on vegetation in south-facing stands, by stronger effects of litter, radiation and temperature and by modifying soil moisture conditions.

Some studies of logging effects on coniferous forest understorey vegetation indicate that the total long-term effects on understorey species are small (Halpern and Spies, 1995; Bailey et al., 1998; Reich et al., 2001). This will be the case if the understorey species composition rapidly adjusts to the prevailing site conditions (Halpern and Spies, 1995; Bailey et al., 1998), or if many species are resilient to periods of unfavourable conditions (Lezberg et al., 1999). However, there are also indications, in our and other studies, of differences between south- and north-facing stands, among species (Jules, 1998; Lezberg et al., 2001) and among regions (Olsson and Staaf, 1995).

The strong relation we observe between tree influence, understorey species composition and species number, should provide for significant biotic effects (of short or long duration) of the environmental changes that take place during forest re-growth: (1) the immediate creation of gaps by tree felling; and (2) the closing of the tree layer during the regeneration phase. Most notably, the phases at which the tree layer reaches minimum and maximum cover, respectively, should be expected to act as 'bottlenecks' for survival of forest-floor species; the first by imposing rapid and thorough environmental change, the second by providing long-term presence of environmental conditions that are unfavourable for most species (Nihlgård, 1970; Meier et al., 1995; Jules, 1998; Lezberg et al., 2001). We will address the changes that take place during the two critical phases.

Immediately after logging, the radiation to the forest floor and the vertical temperature amplitude in the uppermost soil layers increase (Bjor, 1965). The vertical transport of soil water depends on variation in temperature (Bjor, 1965), the vertical soil water gradient becomes stronger and the diurnal range of variation in soil moisture greater in a recently clear-cut stand than in old-growth forest stands. This may, however, be counteracted by the rise of the groundwater table often following clear cutting due to disappearance of tree transpiration (Zobel, 1993). Thus, while water supply to deeply rooted species may increase after clear cutting, vascular plants with shallow roots and bryophytes and lichens without roots or equivalent functional parts may experience increased drought and temperature stress, especially on warm summer days. Several species, e.g. the most abundant forest-floor species, cannot survive under such conditions (Busby et al., 1978; Nykvist, 1997) and the cover as well as species number of bryophytes and forest vascular plants decrease (Nykvist, 1997; Jalonen and Vanha-Majamaa, 2001) while other species temporarily increase in abundance (Bergstedt and Milberg, 2001). Furthermore, regional factors are likely to be important determinants of drought-stress severity in the first, critical phase after clear cutting. In the relatively humid climate of the Oppkuven area, the summer drought stress on clear-cut sites is probably insufficient to exterminate most local populations, leaving local centres of species dispersal also within clear-cut sites (Brumelis and Carleton, 1989). Under climatically drier conditions, the extinction probability of most species is likely to be higher than in Oppkuven.

Within a given area, this first bottleneck after logging will be narrower for a given species when it occurs on south- and west-facing than on north- and east-facing slopes, due to higher radiation, higher temperatures and thus lower minimum soil moisture content, resulting in higher drought stress. However, the number of species that will have their abundance reduced in this first critical phase after clear cutting, will also depend on the relative frequency of drought-tolerant species, which is expected to be higher on south-facing sites.

Changes in tree-layer structure during forest regrowth have strong effects on the development of understorey vegetation. This is evident from the strong gradient in vegetation in south-facing stands in Oppkuven from below trees and dense forest stands to between trees and more open stands, from the increase in the number of species in most species groups along this gradient, and from the strong negative effects of a dense, homogenous tree layer in the regeneration phase on the abundance of several understorey species (Nihlgård, 1970; Nykvist, 1997; Bailey et al., 1998; Lezberg et al., 2001). The magnitude of negative responses in the second critical phase is expected to depend on climatic and local topographic conditions (Olsson and Staaf, 1995). Towards a more humid climate the tree influence gradient becomes less strong, due to sufficient supply of water for species to establish and survive even below trees (T. Økland, 1996) and due to lower maximum tree densities. In Oppkuven, this is seen at the local scale by lower tree density and lower importance of the tree influence gradient in north-facing than in south-facing stands. This suggests that the second bottleneck is in general less narrow on north-facing aspects. Further amelioration of bottleneck effects may have been brought about by natural regeneration, which is patchy (Liu and Hytteborn, 1991), locally occurs at low rates (Nilson and Lundqvist, 2001) and thus contributes to a varied gap structure (Kuuluvainen et al., 1996).

Topographic conditions are also likely to influence the magnitude of fine-scale effects in the second critical phase. In sites with a rough surface and strong variation in species composition related to microtopography, a larger number of bryophyte species are likely to be sufficiently abundant to survive the critical period.

Distance from potential source populations is an important factor affecting re-establishment of forest-floor species in secondary forests (Brunet and von Oheimb, 1998; Grashof-Bokdam and Geertsema, 1998), interacting with the species' mechanisms of dispersal. In the Oppkuven area, relatively small formerly clear cut, selectively cut and natural forest stand patches make up a fine-grained mosaic that facilitates re-establishment of species after clear cutting to an extent that few differences in species diversity exist between stands that may be traced back to the critical phases after clear cutting (Kouki et al., 2001).

Our results do not reveal clearly stronger effects of clear cutting than of selective cutting on species number. We interpret this most likely to be due to the less extreme conditions during the critical phases in the studied area than in many other areas and to the small areas that were clear cut. The stronger and longer-lasting effects on tree layer structure brought about by clear cutting than by selective cutting (Fries et al., 1997) are likely, in general, to be reflected in the magnitude of effects on understorey vegetation.

We find few significant differences in species number and single-species abundances among stands that can be ascribed to former forest management. Nevertheless, our results point to two key factors on within-stand scales of major importance for building a forestry management regime that balances production and biodiversity preservation: (1) the tree layer is regenerated in a way that favours development of a forest stand with a gap structure close to that of a natural forest (Linder et al., 1997), and (2) environmental considerations are built into the management regime by adaptation to variation in the local site conditions and maintenance of fine-scale environmental heterogeneity.

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