



Long term effects of forest management on forest structure and dead wood in mature boreal forests

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ABSTRACT

The history of forestry in Fennoscandia spans five centuries, with clear-cutting being the dominant practice since the mid-20th century. This has led to a significant transformation of the forest landscape. In this study we investigated long-term effects of clear-cutting on forest structure and dead wood volumes. We established twelve pairs of spruce forest sites in southeastern Norway, each pair constituting of a mature, previously clear-cut stand and its near-natural counterpart with similar edaphic factors. The near-natural stands had 2.8 times higher volumes of dead wood and a larger proportion of dead wood in late stages of decay. The near-natural stands had on average $36.8 \pm 9.1 \text{ m}^3 \text{ ha}^{-1}$ of downed dead wood and $24.1 \pm 6.2 \text{ m}^3 \text{ ha}^{-1}$ of standing dead wood. Corresponding numbers for the previously clear-cut stands were $10.2 \pm 2.8 \text{ m}^3 \text{ ha}^{-1}$ and $11.9 \pm 3.7 \text{ m}^3 \text{ ha}^{-1}$. Forests with lower volumes of dead wood often also had lower connectivity of old spruce forests, which potentially have further negative effects on biodiversity. Furthermore, near-natural stands displayed greater tree size heterogeneity, resulting in a wider variation in light conditions. While no difference was observed in living tree volume, we found only weak evidence for higher basal area in the previously clear-cut stands, which had a higher stem density with more slender stems and shorter crowns. Our findings suggest that managed forests do not develop

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structures typical of near-natural forests before they become mature for logging. We stress the importance of a thorough site selection for studies of management effects, as forest management history may be confounded with productivity and other edaphic factors. Experimental designs like ours are vital for testing how differences in structure and deadwood volumes, driven by forest management, translate into variations in biodiversity, carbon sequestration and ecosystem functioning in future studies.

1. Introduction

The history of forestry in Fennoscandia spans over five centuries, with records of large-scale wood exports for more than 500 years (Aasetre and Bele, 2009; Åström, 1975; Holmberg, 2005; Tveite, 1964). Prior to the 1940s, the predominant practice was different types of selective cuttings. This practice increased in intensity up to the early 1900s, eventually leading to overexploitation. As a result, it left a diminished forest landscape with low timber volumes, yet still maintaining a relatively high structural heterogeneity (Lie et al., 2012). These methods were largely supplanted by stand-based forest management, with a particular emphasis on clear-cutting followed by planting. Today, most of the area of productive forest in Norway have undergone at least one cycle of clear-cutting, while a scant 1.7 % remain untouched by any forestry activities (Storaunet and Rolstad 2020). Centuries of timber harvesting has resulted in a fundamental transformation of the forest landscape, manifested by the current mosaic of even-aged stands, representing various successional stages, ranging from newly clear-cut areas to mature forests with ages between 70 and 120 years. The modern even-aged stand management with active reforestation has led to a tremendous increase in growing stocks and stand density (Breidenbach et al., 2020). However, the long-term change has had a profound impact on forest-dwelling organisms, and 48 % of species assessed as threatened on the Norwegian Red List for species (Norwegian Biodiversity Information Centre 2021a) live in forests. As many as 84 % of the threatened forest species are associated with old forest (Norwegian Biodiversity Information Centre 2021b).

Forestry affects biodiversity in various interconnected manners and across multiple temporal and spatial scales. It does so primarily by causing a lack of natural disturbance dynamics and the removal of biomass, which in turn alters structural components and spatial patterns (Esseen et al., 1997). One of the main structural components of forests is dead wood, serving as a habitat for approximately 7500 species in Fennoscandia (Esseen et al., 1997; Stokland et al., 2012). However, modern managed forests typically possess less than 10 % of the dead wood volume found in natural forests (Jonsson et al., 2016; Siitonen, 2001; Storaunet and Rolstad 2015). This diminished volume, coupled with a less diverse range of dead wood in terms of size and decay classes, represents a significant substrate loss (Jonsson et al., 2007; Stokland et al., 2012). Further, intensive logging reduces the amount of large and old trees that are typically more structurally diverse with coarse bark, holes and cavities. These are important for a diverse group of taxa, such as epiphytic lichens and bryophytes, invertebrates and birds (Hämäläinen et al., 2023; Kozák et al., 2023). Meanwhile, natural disturbance dynamics lead to multilayered tree canopies, which have a patchy distribution of trees in several age classes (Kuuluvainen, 2016). This results in small-scale structural heterogeneity and variation in light and microclimate conditions. In sum, the reduced structural and functional diversity due to intensive forestry limits the variety of habitats and substrates, negatively impacting biodiversity by providing fewer niches for different organisms.

Clear-cutting also disrupts the temporal and spatial continuity of suitable habitats and thus poses significant challenges for dispersal-limited species, which require time to colonize new forest (Moor et al., 2021; Undin et al., 2024). At larger scales, intensive forestry has led to the fragmentation of old-growth forests, resulting in loss and reduced connectivity of suitable habitats (Kuuluvainen and Gauthier, 2018). This can have negative effects on forest species dependent on

transient and patchy resources, such as dead wood, but the spatial scales at which species respond to connectivity will vary according to the environmental conditions they are adapted to (Nordén et al., 2018; Ranius et al., 2019; Southwood, 1988).

The forests that were clear-cut in 1950s and 60s are now approaching the biological stage where self-thinning has taken place, and more light is reaching the ground. At the same time, they are increasingly becoming so-called economically mature, meaning that they might be subject to another round of clear-cutting. It is important to use the opportunity to compare these old clear-cuts to forests that have not been cleared and replanted. This is of interest for understanding long-term effects of clear-cutting on biodiversity and how it is interlinked with ecosystem processes. However, stands subjected to clear-cutting, and those with less intensive harvesting, frequently differ regarding both edaphic and climatic factors. For instance, early clear-cuts were often on more productive soils or in more easily accessible areas (e.g. lower elevations, closer to settlements, or close to rivers) than less intensively harvested sites, and these factors in turn potentially affect biodiversity and ecosystem processes (Jonsson et al., 2009; Kya-schenko et al., 2019; Siitonen, 2001). For this reason, there are often several confounding factors that need to be accounted for when evaluating the effects of forest management. While it is well known that forestry structurally alters forests, few studies compare stands where other factors are kept constant, ultimately making it difficult to evaluate ecological consequences of intensive logging. Here we take a comparative approach by identifying pairs of stands with contrasting forest management history while other key variables are kept constant, effectively serving as a 'natural' experiment.

In the EcoForest project (Forestry effects on biodiversity, carbon stocks and ecological processes in mature boreal forests, RCN 320722), we have identified 12 pairs of Norway spruce (*Picea abies*; hereafter referred to as 'spruce') stands with contrasting forest management, i.e. mature previously clear-cut stands vs. "near-natural" stands with various degrees of historical selective cutting. We use this setup to test how forest management affects forest structure and availability of the key structural component dead wood - a necessity for many species-rich organism groups and proxy for biodiversity as well as important for carbon and nutrient dynamics. In this paper, we seek to test the hypotheses that, compared with near-natural stands, previously clear-cut stands: (i) have higher stand density, with higher number of stems, living basal area and volume, resulting in lower light availability and vascular plant cover; (ii) are structurally more homogeneous in terms of tree sizes and consequently light availability; and (iii) have lower volumes of standing and downed dead wood, especially in larger size classes. We further explore the differences in connectivity of older spruce forests at two spatial scales between forest management types. This is important as a fragmented landscape in addition to reduced dead wood volumes and lack of structural diversity negatively affects biodiversity. The establishment of this study system sets the stage for further studies of how forest management affects biodiversity and ecosystem processes related to carbon and nutrient cycling, as well as the linkages between these functions.

2. Materials and methods

2.1. Site description

This study was performed on 12 site pairs positioned throughout

southeastern Norway spanning 200 km in latitude and 160 km in longitude (Fig. 1). In each site, we identified a pair consisting of a previously clear-cut stand and a near-natural stand, where both shared similar topographic characteristics including slope, elevation, and aspect, as well as edaphic factors and site index. The two forest management types were both in *Picea abies*-dominated (Norway spruce) stands with an average distance of 1270 m (range: 540–3140 m; Table S1). Previously clear-cut stands were either old production forest (i.e., maturity class IV *sensu* Breidenbach et al., 2020; Viken, 2021) or mature forest (i.e., maturity class V), with a stand-age between 43 and 82 years (Table 1). Near-natural stands were defined as stands that have not been clear-cut and have limited signs of recent human influence. The stands were not subjected to drainage or fertilization, and showed no signs of commercial thinning. Further details on site selection criteria and methodologies are given in Appendix A.

There are large variations in macroscale bioclimatic variables between sites, with mean annual temperatures ranging from 0.5 to 5.4 °C (Fig. S1; Table 1). The two most southern site pairs, Halden and Marker, are in the hemiboreal zone (Bakkestuen et al., 2008) and are characterized by higher summer temperatures and longer growing seasons compared with the other site pairs. The ten other pairs are either in the south boreal (Blåfjell and Särkilampi) or the middle boreal zone. While Blåfjell also is characterized by relatively warm summers, it has higher summer precipitation than Halden and Marker and is more oceanic. Särkilampi, Braskereidfoss and Hemberget (in the upper left corner of Fig. S1) are more continental with broad annual temperature range and higher precipitation seasonality. Gullenhaugen, Øytjern, Skotjernfjell and Langvassbrenna are all higher elevation sites with short growing seasons. Lastly, Storås and Tretjerna are more intermediate in terms of bioclimatic variables (i.e. close to the centre of the PCA; Fig. S1). Apart from macroclimatic variation, the geographical placement of sites also

corresponds to differences in historical and contemporary utilization of natural resources, and thus differences in land-use and population densities (Table S1). For instance, intensive timber harvest started earlier in southern areas close to the coast (Aasetre and Bele, 2009). Further, high elevations are typically more remote, and characteristically have higher proportion of forests due to lower proportions of settlements, agricultural lands, and water bodies.

2.2. Sampling design

At each of the paired sites, we established a 15 × 15 m main plot (Fig. 2) where we registered diameter at breast height (DBH; 1.3 m) and height of all living and standing dead trees with DBH ≥ 5 cm. For living trees, height to lowest green branch was also measured. These data were used for calculating number of stems per hectare (stem density), total basal area, and volume of the living stand. Volume was calculated following Vestjordet (1967) for spruce, Brantseg (1967) for pine and Braastad (1966) for broadleaves, in line with the Norwegian National Forest Inventory (NFI) (Breidenbach et al., 2020; Viken, 2021). Top height was calculated as the average height of the two largest (DBH) trees per plot, corresponding to, based on our plot size, the 89 largest trees per hectare.

Within each plot, we established six sub-plots within the 15 × 15 m grid, based on the same predefined random positions within each plot. In case the predefined position was unsuitable due to standing or downed trees, surface stones etc., the subplot was moved to the closest representative location. At the centre of each sub-plot, temperatures at –8 cm (within soil), +2 cm (soil surface), and +15 cm (air) were registered every 15 min using TMS-4 (TOMST s.r.o, Praha, Czech Republic), starting when each plot was set-up (between 17 August 2021 and 30 June 2022). Spherical panoramas were taken at 60 cm above the ground in August 2022, using an iPhone SE, 2nd generation (Apple Inc.) with the, now discontinued, application Street View (Google LLC). Circular hemispherical images were generated as described by Arietta (2022), and binarized using the Hemispherical 2.0 plugin (Beckschäfer, 2015) for ImageJ v.1.51. These images were then used to calculate diffuse light index and leaf area index using Hemisfer 3.0 (Schleppi et al., 2007; Thimonier et al., 2010). Total cover of vascular plants was visually estimated in 1 × 1 m quadrats at each sub-plot.

Standing and downed dead wood was surveyed in a 133.33 × 15 m (0.2 ha) north-south or west-east transect, due to dead wood being sparser and less evenly distributed than live trees. Each transect was divided into five cells: four 29.6 m × 15 m cells and the 15 × 15 m main plot in the middle (Fig. 2). All standing and downed dead wood (DBH or basal diameter ≥ 5 cm) with their point of birth inside the transect were measured for diameter and length/height, and tree species, type of dead wood (e.g. man-made, uprooted or broken downed dead wood, snag, fallen tree-top), decay stage class (Viken, 2021) and other ecological variables were noted down. Details on volume calculations are given in Appendix C.

All cut stumps with a top diameter of at least 5 cm were surveyed in the 0.2 ha transects and species, top diameter, height and decay stage class were registered. Decay stage class followed the same classes as for the dead wood. More detailed information are given in Krok (2024) and Botten (2024). It is noteworthy that because of the strong interest in the forestry history, the survey of cut stumps in this study was more thorough than customary in dead wood surveys, and included also very old cut stumps completely overgrown by vegetation (Siitonen et al., 2009; Storaunet and Skarpaas, 2022). At each main plot, we collected three increment cores at breast height. In near-natural stands, Botten (2024) collected additional increment cores to date growth releases, which are defined as a 100 % increase in mean annual increments over 10-year periods before and after the event. The selection of these additional cores was done using two separate approaches. The first approach involved selecting the two largest trees at each cell corner (or one tree in main plot corners; i.e. 20 trees). The second approach involved coring

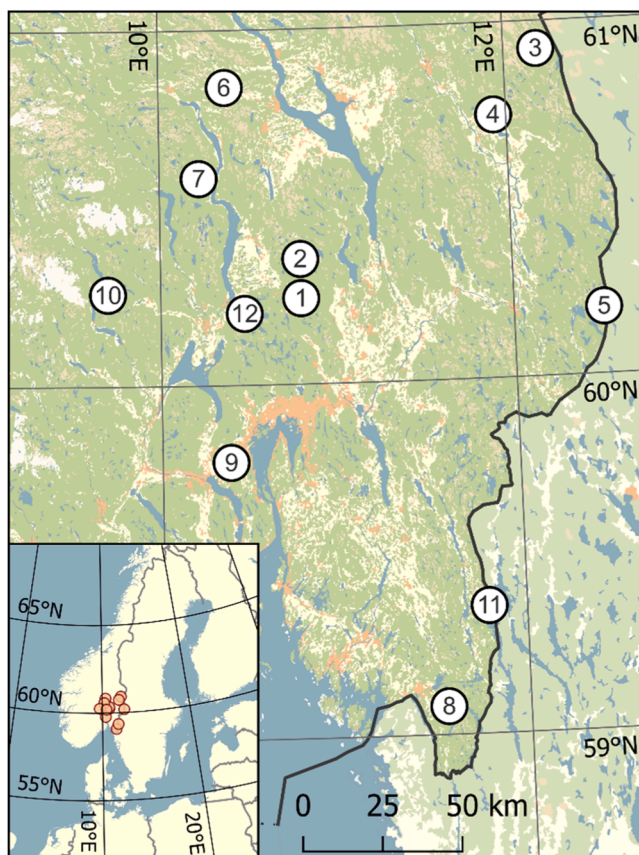


Fig. 1. Location of the twelve study sites in southeastern Norway. Numbers refer to the site names provided in Table 1.

Table 1

List of sites and their geographical position (decimal degrees [$^{\circ}$ N and $^{\circ}$ E; WGS84] and m a.s.l.) as well as mean annual temperature (MAT; $^{\circ}$ C) and mean annual precipitation (MAP; mm). Macroclimate is modeled, at a 100×100 m scale, for the period 2004–2014. Stand age is basal area-weighted breast height age (years in 2023) and oldest tree is the maximum breast height age (years) of 3–26 trees in each 15×133 m plot. Cut stumps refer to the number of cut stumps per hectare in each 15×133 m transect. Mean summer temperature ($^{\circ}$ C; June, July, August and September), growing degree days ($^{\circ}$ C; base temperature = 5) and number of days with snow (detected at 2 cm above the ground). Microclimate data are the averages of 6 sensors (TMS-4, Tomst) at each plot measuring air (15 cm), surface (2 cm) and soil (-8 cm) temperatures, for one year starting on 1 October 2022. Management types are mature previously clear-cut forests (CC) and near-natural (NN) forests. †Indicates that the plot is in a nature reserve.

No.	Site name (abbr.)	Management type	Latitude	Longitude	Elevation	MAT	MAP	Stand age	Oldest tree	Cut stumps	Summer temperature			Growing degree days			Days with snow
											Air	Surface	Soil	Air	Surface	Soil	
1	Skotjernfjell (SKO)	CC†	60.2413	10.8084	571	2.2	972	82	83	660	12.4	12.2	10.4	1005	950	698	172
		NN†	60.2422	10.7960	610	2.3	974	188	292	145	12.4	12.3	11.0	1005	964	767	164
2	Gullenhaugen (GUL)	CC	60.3700	10.7872	591	2.1	854	68	74	685	11.9	11.7	10.2	916	868	662	175
		NN†	60.3526	10.7966	668	1.9	867	130	224	370	11.9	11.7	10.1	919	867	640	170
3	Hemberget (HEM)	CC†	60.9211	12.1889	584	0.6	766	43	47	600	12.2	11.9	9.9	971	910	620	156
		NN†	60.9151	12.2065	581	0.5	764	119	191	615	12.1	11.7	9.5	959	873	567	156
4	Braskereidfoss (BRA)	CC	60.7476	11.9264	332	2.3	683	55	56	745	13.1	12.8	10.4	1148	1073	717	115
		NN	60.7398	11.9285	427	2.1	684	96	130	485	13.1	12.7	10.3	1157	1070	705	124
5	Särkilampi (SAR)	CC†	60.2005	12.5281	388	2.4	762	78	90	370	13.5	13.2	11.1	1235	1180	850	135
		NN†	60.1877	12.5080	368	2.4	761	143	177	350	13.3	13.0	11.1	1211	1131	829	141
6	Øytjern (OYT)	CC†	60.8432	10.4090	663	1.4	819	77	88	605	11.5	11.1	9.4	839	765	535	180
		NN†	60.8389	10.3812	640	1.3	818	156	213	260	11.5	11.3	9.4	844	796	534	179
7	Tretjerna (TRE)	CC	60.5773	10.2285	520	2.6	821	59	59	730	12.4	12.1	10.7	992	931	728	160
		NN†	60.5836	10.2265	472	2.7	821	143	230	125	12.4	12.1	10.4	994	924	688	164
8	Halden (HAL)	CC	59.0798	11.5595	197	5.4	1051	57	62	760	14.6	14.5	12.7	1553	1511	1198	11
		NN	59.0798	11.5465	211	5.3	1056	141	175	385	14.9	14.7	13.1	1593	1552	1261	6
9	Blåfjell (BLA)	CC†	59.7880	10.3865	322	4.8	1049	75	82	135	14.0	13.9	12.0	1315	1255	979	146
		NN†	59.7831	10.3813	264	4.8	1041	132	176	85	14.1	14.0	12.2	1378	1309	1023	129
10	Storås (STR)	CC	60.2615	9.7091	432	2.8	884	70	71	750	12.6	12.4	10.9	1024	971	751	168
		NN†	60.2591	9.7007	483	2.6	888	111	150	315	12.5	12.3	10.6	1009	953	713	164
11	Marker (MRK)	CC	59.3835	11.7590	178	4.9	960	73	75	640	14.7	14.5	12.5	1529	1487	1161	11
		NN†	59.3601	11.7900	187	4.9	971	128	186	515	14.7	14.7	12.6	1532	1516	1168	16
12	Langvassbrenna (LAN)	CC	60.2010	10.4980	548	2.6	883	69	70	690	12.3	12.1	11.0	1003	949	775	162
		NN†	60.2018	10.4738	607	2.2	868	151	255	210	12.1	11.9	10.7	971	918	737	164

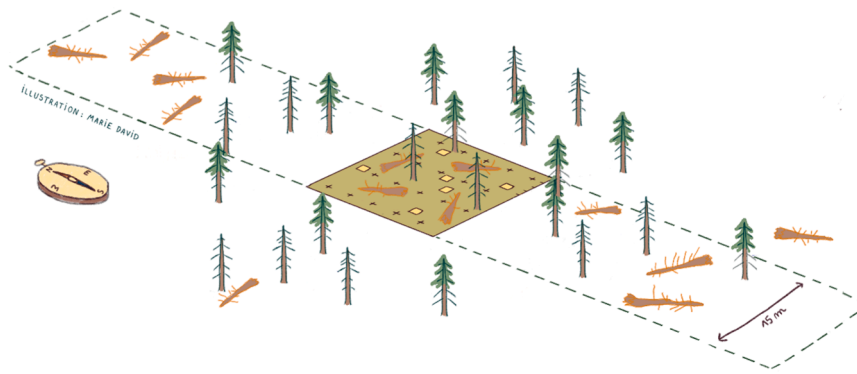


Fig. 2. Overview of sampling design. Surveys of dead wood were conducted within the 133.3×15 m transect (dashed outline). Measurements of standing trees were done in the 15×15 m central main plot. Microclimatic measurements and vegetation surveys were done in the six sub-plots (yellow). Illustration: Marie David.

1–3 additional trees, estimated to be at least 40 years older than the stump, within a 3-meter radius of each cut stump. We then estimated the age of the oldest trees and the basal area-weighted stand age (referred to as ‘stand age’ hereafter), based on all collected increment cores. For both these metrics, we used the chronological age at breast height, rather than the biological age which would take into account years of suppression below the canopy.

2.3. Environmental and landscape data

Environmental variables were generated for the time period 2004–2014 following Horvath et al. (2019); deposited at Asplund et al. (2024). Briefly, 19 standard bioclimatic variables (Fick and Hijmans, 2017; Fig. S1) were derived from monthly temperature and precipitation data from seNorge (v.2) on a 1-km grid (Lussana et al., 2018). Other variables include topographic (derived from a digital elevation model, DEM), geological (quaternary geology and bedrock), and proximity to water (distance to water bodies). All data were adapted to a 100×100 m grid using ordinary kriging in SAGA GIS v.2.3 (Conrad et al., 2015) or rasterization.

Patch connectivity was calculated using an incidence function model measuring the distance-weighted area volumes of spruce forests more than 80 years old, with weighting parameter (α) to scale the effect that distance has on dispersal (Moilanen and Nieminen, 2002; Prugh, 2009). We used the α -values 2 and 0.05, which represent expected mean dispersal of 0.5 km and 20 km, as measures of short-distance and intermediate-distance connectivity based on known relevant scales for fungi (Nordén et al., 2018), respectively. Details on calculations of connectivity are given in Appendix B.

2.4. Data analyses

Many of the standard bioclimatic variables *sensu* WorldClim (Fick and Hijmans, 2017) as well as distance to nearest coastline, elevation and growing season length show natural correlation. To understand how each site fits within this bioclimatic spectrum and determine which variables to use as covariates in further analyses, we employed principal component analysis (Fig. S1). We determined that the temperature of the warmest quarter (bioclim 10), which is closely related to the length of the growing season, is a crucial variable to include due to the significant variation between sites and its importance for many biological processes. Additionally, we aimed to incorporate another variable orthogonal to bioclim 10 in the ordination, representing a different bioclimatic aspect. The climatic oceanicity-continental gradient emerged as a suitable dimension, leading us to select bioclim 7 (temperature annual range) as a continental proxy. To test how the measured variables of forest structure and dead wood volumes differ between forest management types, we performed separate ANCOVAs for

each response variable with management type as explanatory factor and bioclim 10 and bioclim 7 as covariates. The correlation between the measured variables was tested with Spearman correlation tests. Hierarchical cluster analysis was then performed on the correlation matrix, and a dendrogram was created using the default settings (complete linkage of Euclidean distances) of the *hclust* function, which is called internally by the *heatmap* function from the stats R-package.

Microclimatic data were processed using the R package *myClim* (Man et al., 2023). All analyses were performed in R version 4.3.2 (R Core Team, 2024).

3. Results

Near-natural stands were on average twice as old as previously cut stands (stand age was 67 ± 3.3 and 137 ± 6.8 for previously clear-cut and near-natural stands, respectively; Table 1; S2). The oldest tree was 71 ± 3.9 and 200 ± 13.1 years at breast height on average in clear-cut stands and near-natural stands, respectively (Table 1; S2). Previously clear-cut stands had on average 614 ± 53.2 cut stumps ha^{-1} , which is significantly more than the 322 ± 47.6 cut stumps ha^{-1} in the near-natural stands (Table 1; S2). However, this metric represents different aspects in the forest management types. In stands that have been clear-cut, the cut stumps originate from the clear-cutting and thus represents the previous stand’s stem density. Meanwhile, in near-natural stands the cut stumps originate from selective cuttings and is a measure of cutting intensity. The vast majority of the cut stumps in both forest management types were in the latest decay class (i.e. class V; Table S3), meaning decomposed and overgrown.

There was only weak evidence ($P = 0.063$) for higher basal area in the previously clear-cut stands compared with the near-natural stands, while there was no evidence for any difference in living volume between the two management types (Fig. 3a-b; Table S2, S5). Previously clear-cut stands had on average 70 % higher stem density than near-natural stands (Fig. 3c; Table S2). There were no patterns between stand age and volume or basal area in previously clear-cut stands (Volume: $F_{1,10}=0.134$, $P = 0.896$; Basal area: $F_{1,10}=1.11$, $P = 0.293$; linear regressions) or in the near-natural stands (Volume: $F_{1,10}=-0.330$, $P = 0.749$; Basal area: $F_{1,10}=0.516$, $P = 0.617$; linear regressions). However, the relatively young previously clear-cut stand at Hemberget (43 years at breast height) had clearly lower volumes and basal area compared to the other previously clear-cut stands. Removing this outlier results in a negative relationship between stand age and volume ($F_{1,9}=-2.68$, $P = 0.025$, linear regression) but not basal area ($F_{1,9}=-0.57$, $P = 0.580$, linear regression) in previously clear-cut stands.

The top height was on average 2 m higher in near-natural stands relative to the previously clear-cut stands (Fig. 3d). Near-natural stands had higher variation in tree heights (measured as coefficient of variation; Fig. 3e), and the higher structural heterogeneity in near-natural

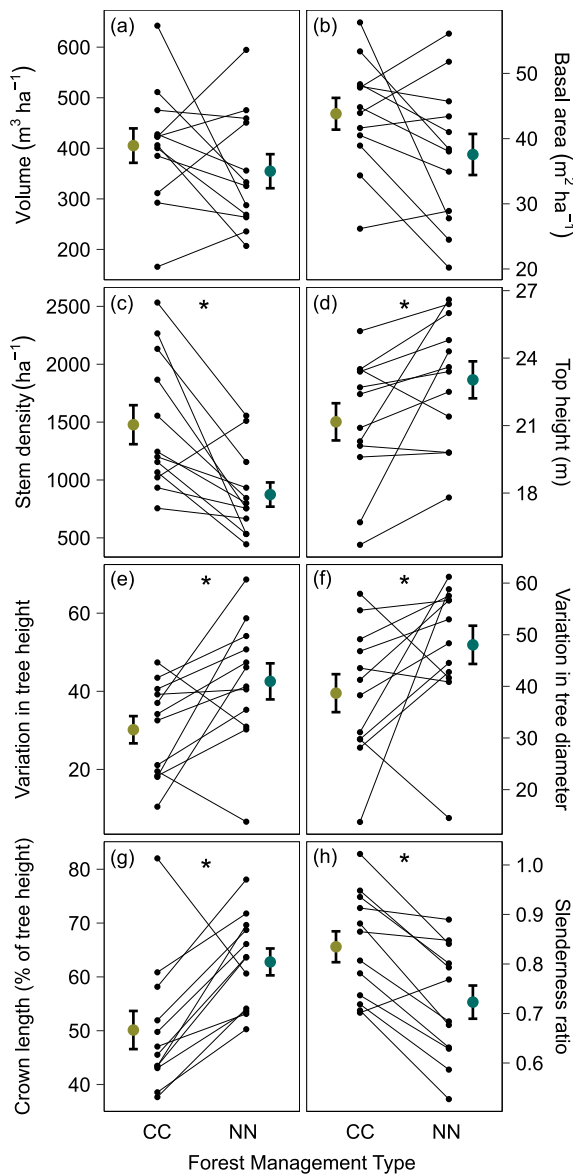


Fig. 3. (a) Volume, (b) basal area, (c) number of stems per hectare, and (d) top height, (e) variation in tree height measured as coefficient of variation, (f) variation in DBH measured as coefficient of variation, (g) crown length relative to tree height, and (h) slenderness (height to DBH ratio) of living trees measured in the 15×15 m main plot in two different management types (CC = mature previously clear-cut; NN = near natural) at twelve sites. Colored dots with error bars are means (± 1 S.E.) per management type and lines connect the values within each pair. Asterisks denote significant differences between management types.

stands was also indicated by the higher variation in tree diameters (Fig. 3f). In near-natural stands the crown length relative to the total tree height was on average 25 % longer compared with clear-cut stands (Fig. 3g). This pattern was consistent across all sites except Hemberget, where the green crown in the young previously clear-cut stand was more than 80 % of the tree height at the clear-cut stand. Noteworthy is that the Hemberget previously clear-cut stand is young and has yet not reached the threshold at which self-thinning typically occur. Trees at previously clear-cuts were on average more slender (i.e. higher relative to their diameter) than trees at near-natural stands (Fig. 3h). Diffuse light index showed no consistent pattern between management types, but the variation was 25 % higher in near-natural stands (Fig. 4a-b). The average vascular plant cover in the understory was almost twice as high

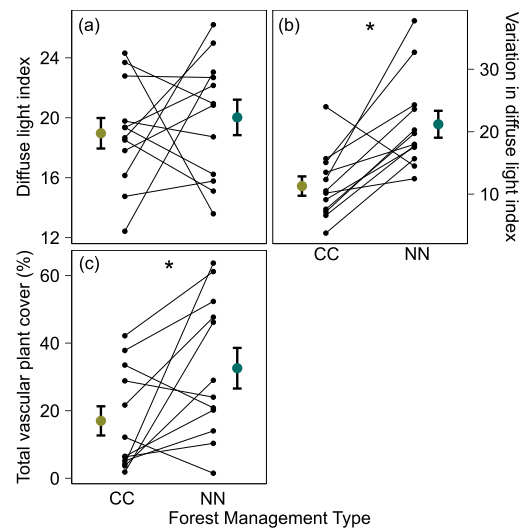


Fig. 4. (a) Diffuse light index (DLI), (b) variation in DLI measured as coefficient of variation, and (c) vascular plant cover at six sub-plots in the 15×15 m main plot in two different management types (CC = mature previously clear-cut; NN = near natural) at twelve sites. Colored dots with error bars are means (± 1 S.E.) per management type and lines connect the values within each pair. Asterisks denote significant differences between management types.

in near-natural stands compared to previously clear-cut stands (Fig. 4c). Forest management did not affect microclimatic growing degree days measured at 8 cm soil depth, at the soil surface, or 15 cm in the air (Table S2). However, there was weak evidence ($P = 0.059$) that near-natural forests had higher daily range in temperature, measured at 15 cm, in the summer months compared with the previously clear-cut stands (Table S2). There was no evidence for such patterns at the other sensor positions.

Volumes of downed dead wood were higher in each near-natural stand relative to its previously clear-cut pair (Fig. 5; Table S2; S4). Downed dead wood had an average volume of $36.8 \pm 9.1 \text{ m}^3 \text{ha}^{-1}$ in near-natural stands which is 3.6 times higher than the volume in

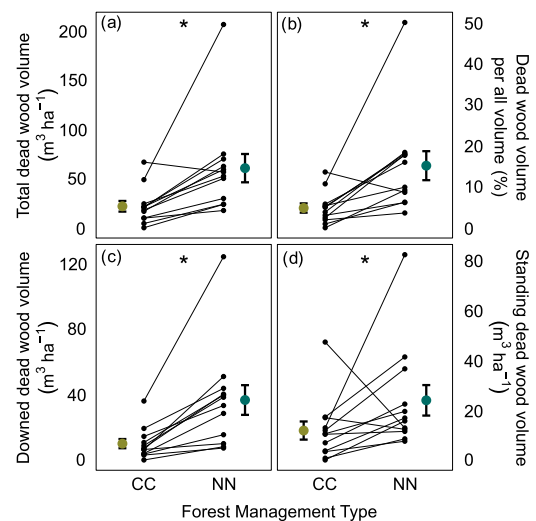


Fig. 5. (a) Total dead wood volume (standing + downed), (b) total dead wood volume relative to all volume (living + dead), (c) volume of downed dead wood, and (d) volume of standing dead wood measured in a 15×133.33 m plot in two different management types (CC = mature previously clear-cut; NN = near natural) at twelve sites. Colored dots with error bars are means (± 1 S.E.) per management type and lines connect the values within each pair. Asterisks denote significant differences between management types.

previously clear-cut stands ($10.2 \pm 2.8 \text{ m}^3 \text{ ha}^{-1}$). The near-natural stand at Tretjerna had more than twice as much downed dead wood ($124 \text{ m}^3 \text{ ha}^{-1}$) as the site with the second highest volume of downed dead wood (the near-natural stand at Braskereidfoss; $51.2 \text{ m}^3 \text{ ha}^{-1}$). Even after excluding the paired Tretjerna stands, the ratio of downed dead wood volumes between near-natural and previously clear-cut stands remained unchanged, as the previously clear-cut stand at Tretjerna also exhibited an unusually high volume ($36.2 \text{ m}^3 \text{ ha}^{-1}$). Further, there were large differences in the size distribution of downed dead wood. In previous clear-cuts, only 23 % of the total downed dead wood volume consisted of logs with a diameter above 20 cm, while for near-natural stands 84 % of the total volume consisted of logs >20 cm in diameter (Fig. S3). As such, downed dead wood in previous clear-cuts were typically broken tops of snow/ice-damaged of living trees, with the tops being naturally of smaller dimensions. By contrast, the origin of downed wood in the near-natural stands is more diverse. Both management types had most of the volume in the second and third decay class, but later decay classes were more common in near-natural stands than in the previous clear-cuts (Fig. S3a-b).

The volume of standing dead wood was twice as high in near-natural stands compared with previously clear-cut ones (24.1 ± 6.2 vs $11.9 \pm 3.7 \text{ m}^3 \text{ ha}^{-1}$; Fig. 5), with only Braskereidfoss and Storås having higher volumes in the previously clear-cut stand than in the near-natural stand. However, previous clear-cuts had on average 38 % higher density of snags than the near-natural stands (data not shown), suggesting that the snags were generally smaller and thus likely resulting from self-thinning. Total volume of dead wood was on average 15.2 ± 3.5 % of the total living and dead volume combined in near-natural stands and 4.93 ± 1.1 % in previous clear-cuts (Fig. 5b). In the near-natural stands, total dead wood volume decreased with increasing logging intensity (measured as number of cut stumps; $F_{1,10} = -2.39, P = 0.038$).

Connectivity of spruce forest ≥ 80 yrs corresponding to a mean dispersal distance of 0.5 km (i.e. $\alpha=2$; hereafter short-distance connectivity) was significantly higher at near-natural stands than in the previously clear-cut ones ($F = 6.72, P = 0.01$; Fig. 6a). However, intermediate distance connectivity (i.e. with $\alpha=0.05$, corresponding to mean dispersal distance of 20 km) did not differ between forest management types, but instead increased with elevation (Management type: $F = 0.00, P = 0.989$; Elevation: $F = 36.66, P < 0.001$; Fig. 6b).

The hierarchical clustering revealed two major clusters of variables

(Fig. 7). The first cluster comprised variables that varied within site pairs and therefore are likely linked to forest management effects. This cluster featured subclusters related to connectivity and dead wood, logging intensity, structural heterogeneity, and canopy openness. The second major cluster included variables that primarily varied on a regional scale and are less influenced by forest management. These were mostly bioclimatic and climate-dependent variables, forming subclusters describing temperature, continentality, and productivity.

A principal component analysis of forest structure, microclimate and connectivity showed a clear separation between previously clear-cut and near-natural stands along the first axis that explains most of the variation (Fig. 8). Both logging intensity and age of the oldest tree corresponded broadly to the first axis. The division between the two management types also related to two orthogonal groups of variables. First, there were variables related to structural heterogeneity and volumes of dead wood as well as short-distance connectivity, that increased towards the upper left corner of the ordination. At the extreme end of this gradient, we have the near-natural stand at Tretjerna that by far has the highest dead wood volume and the highest variation in tree heights. Less extremely on this gradient, yet noteworthy, are near-natural stands at Langvassbrenna and Braskereidfoss. Meanwhile, the near-natural stands at Halden and Marker were at the opposite end of this gradient, on par with the previously clear-cut stands in terms of both dead wood volume and structural heterogeneity. The other group of variables dividing the two management types, albeit less clearly than the first group, are those related to canopy openness (e.g. stem density, daily temperature range, crown length).

4. Discussion

Our first hypothesis that mature previously clear-cut stands are denser was partly supported as stem density was higher, while there was no clear difference in volume or basal area. The fact that volume and basal area did not evidently differ between the management types supports earlier findings that previous loggings have minor effect on volumes in mature stands, which instead are driven by productivity (Storaunet and Skarpaas, 2022). This also explains why volume and basal area were more related to larger geographical patterns and growing season length in our dataset. Surprisingly, the higher stem density in the previously clear-cut stands did not translate into lower

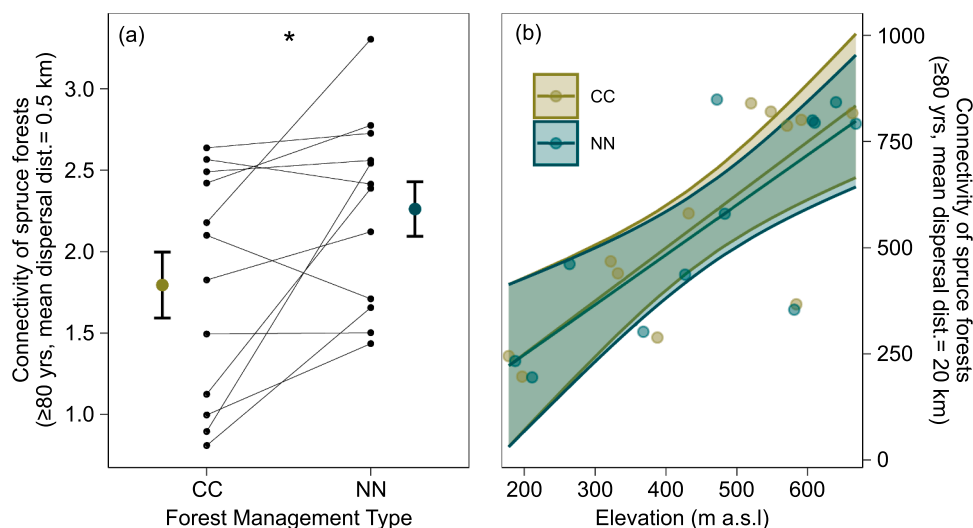


Fig. 6. Connectivity of mature and old spruce forests measured as distance-weighted volumes (in $\text{m}^3 \text{ ha}^{-1}$) of living spruce in ≥ 80 yrs old forests. Panel (a) assumes a mean dispersal distance of 0.5 km (i.e. $\alpha = 2$) and depicts the mean value (± 1 S.E.) of two different management types (CC = mature previously clear-cut; NN = near natural) at twelve paired sites. Black dots represent values for each plot and the lines connect the values within each pair. Panel (b) assumes a mean dispersal distance of 20 km (i.e. $\alpha = 0.05$) and shows the relationship with elevation per management type. Asterisks denote significant differences between management types.

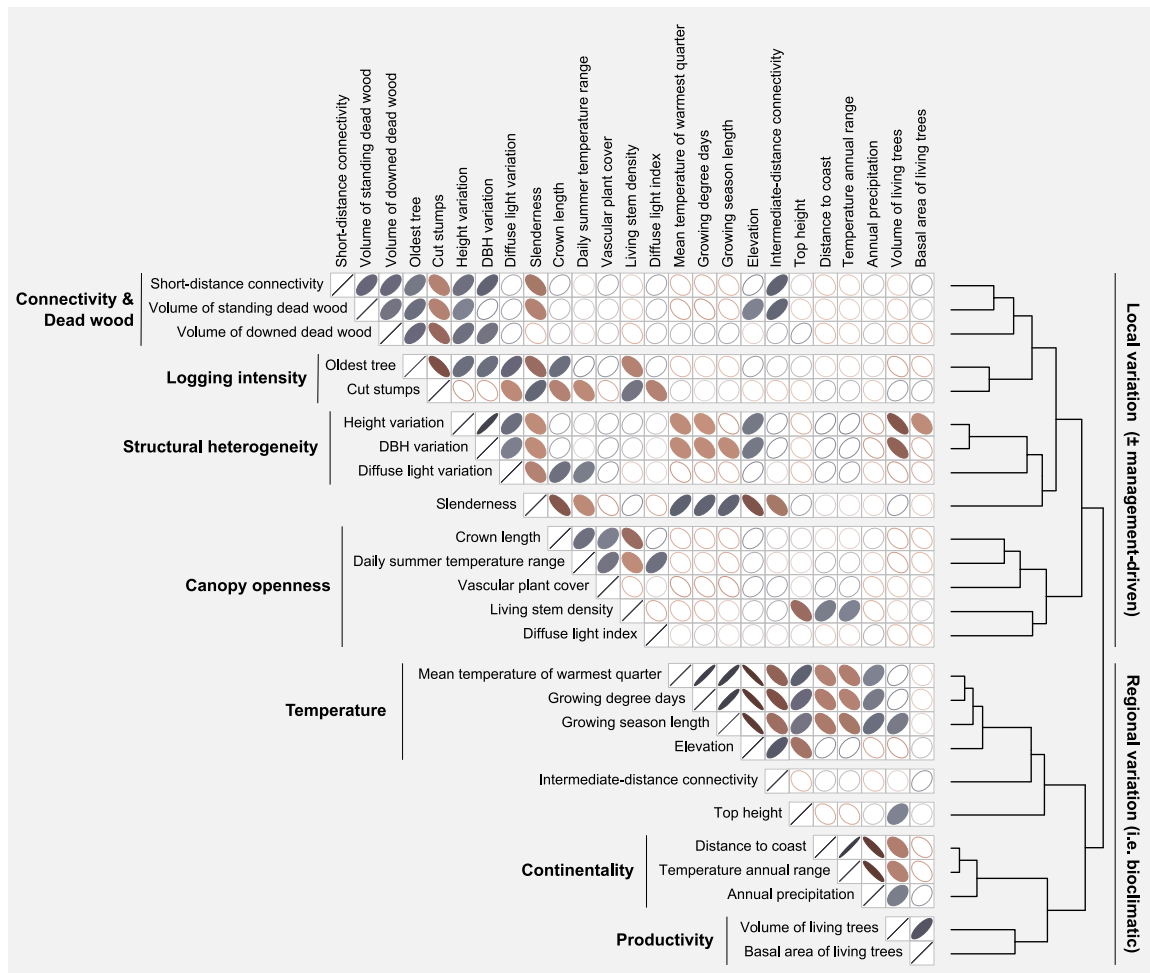


Fig. 7. Correlation matrix of measured variables. The variables are divided into two major clusters depending on whether they vary locally within site pairs (i.e. between forest management type) or whether they primarily vary on a regional scale and thus are less related to forest management type. Ellipses show strength (narrower = stronger) and direction of spearman correlations. Unfilled ellipses denote $P > 0.05$. Brown and blue colors denote negative and positive correlations, respectively, and their intensity denote the strength of the correlation.

light availability. One possible explanation is that light availability is more heterogeneous in the near natural stands, and the presence of larger trees creates a mosaic of light conditions. In such forest environments, certain areas are significantly darker, which moderates the overall average light levels. Importantly, as long as there are sufficient patches of light penetrating to the understory, the average light availability across the forest might be less critical. Indeed, understory plant diversity have been shown to be driven by light heterogeneity rather than by mean light availability (Reich et al., 2012). This could also explain the higher plant cover in our near-natural stands. Further, small gaps can be sufficient for spruce seedling survival, while shade intolerant species such as aspen, pine and birch are dependent on disturbances that create larger gaps (Messier et al., 1999).

The higher variation in light that we observed in the near-natural stands is linked to the higher heterogeneity of the tree layer (i.e. higher variation in tree heights and DBH), supporting our second hypothesis. This is anticipated considering that the regularly planted trees in the previously clear-cut stands are of the same age, resulting in unimodal size distributions. In contrast, the near-natural stands experience mortality either through selective cutting or natural growth and disturbances. Both factors remove only a part of the living stand at a time, thereby promoting a greater heterogeneity in tree size (Rouvinen and Kuuluvainen, 2005). Meanwhile, our 15×15 m plots are likely too small for representatively capturing the heterogeneity of near-natural stands with randomly occurring small gaps, suggesting that the

observed heterogeneity likely is an underestimation. Nevertheless, the higher structural heterogeneity consequently fosters greater biodiversity, as it essentially translates to a higher diversity of habitats or niches (Esseen et al., 1997; Kuuluvainen, 2002).

Near-natural stands had less slender (i.e. thicker relative to their height) and longer crowns. This could be a result of lower stand density (Wang et al., 1998), and thus lower competition, or the fact that older trees naturally are less slender (Albrecht et al., 2012). Tree slenderness is crucial in determining vulnerability to wind and snow damage as less slender trees have a lower centre of gravity and a more robust root system, enhancing stability (Lohmander and Helles, 1987; Wang et al., 1998). However, Albrecht et al. (2012) found that slenderness was not a good predictor of stability, partly due to temporal variations of confounding factors. Further, the longer crowns in near-natural stands could increase resistance to bark beetle attack through higher level of stem shading (Jakuš et al., 2011).

Our finding that near natural stands have higher volumes of dead wood than previously clear-cut stands are in line with our third hypothesis. This result supports previous studies that managed forests are deprived of dead wood (Jonsson et al., 2016; Siitonen, 2001). The dead wood volume estimates for our previously clear-cut stands ($22.1 \pm 5.4 \text{ m}^3 \text{ ha}^{-1}$) are on par with the NFI estimates of $15.5 \text{ m}^3 \text{ ha}^{-1}$ from mature managed forests, considering the large variations and that the NFI data includes all site indices and regions (Storaunet and Rolstad 2015). However, our estimates from the near-natural stands ($60.9 \pm$

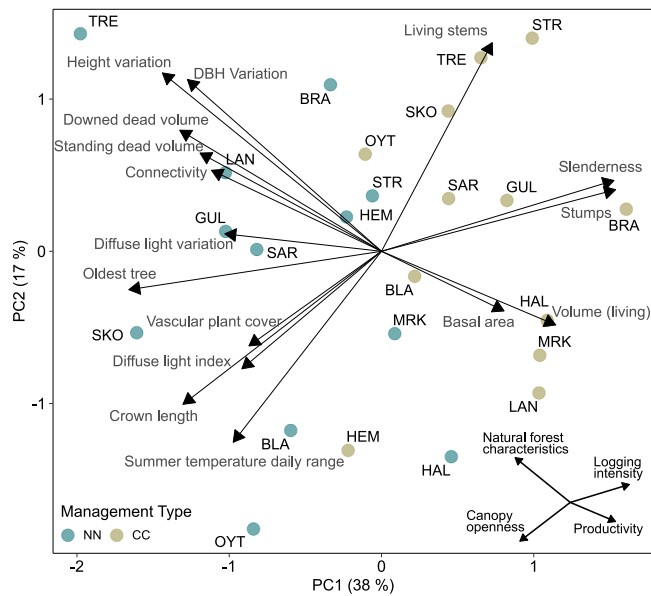


Fig. 8. Principal component analysis of measured tree structure parameters as well as microclimate and connectivity in 12 sites with two different forest management history (CC = mature previously clear-cut forests; NN = near natural forests). The insert in the lower right corner summarizes the four major gradients.

14.4 m³ ha⁻¹) are on average higher than NFI estimates for mature spruce stands that have never been clear-cut (26.3 m³ ha⁻¹). This can partly be explained with that NFI are averaged across all site indices and regions, while our study was confined to southeastern Norway with medium to high site index, and that dead wood volumes typically increase with productivity (Storaunet and Rolstad 2015; Storaunet and Skarpaas, 2022). Meanwhile, our estimates are generally lower than what is commonly found in near-natural hemiboreal to middle boreal Fennoscandian spruce forests at medium to high productivity (91 m³ ha⁻¹ in average of 62 sites; Storaunet and Skarpaas, 2022). Despite these high averages, the variation in Scandinavia is large; Nordén et al. (2018) reported values ranging from 8.7 to 143.2 m³ ha⁻¹ (average: 53.6 ± 6.5 m³ ha⁻¹) which is similar to our findings, but they specifically studied forests with high temporal continuity in the availability of spruce dead wood. Our relatively low volumes of dead wood is likely explained by the generally high numbers of cut stumps, indicating intensive historical selective cutting activity. As such, we found dead wood volumes to decrease with increasing number of stumps in our near-natural stands, in line with what Storaunet and Skarpaas (2022) report in their review of 174 non-clearcut forests across Fennoscandia. Our near-natural site in Tretjerna, which had relatively few cut stumps, clearly stands out with its exceptionally high volume of dead wood (200 m³ ha⁻¹). Additionally, Botten (2024) report frequent growth releases not associated with logging in this stand, suggesting that the near-natural site in Tretjerna is driven by gap dynamics.

The near-natural stand in Halden, and to some extent the one in Marker, showed fewer natural-forest characteristics, with low dead wood volumes and less structural heterogeneity than the other near-natural stands. These are the southernmost sites and at lowest elevations, where productivity is expected to be highest. By contrast, structural heterogeneity and dead wood volumes typically increase with productivity (Hämäläinen et al., 2024; Liira et al., 2007; Storaunet and Skarpaas, 2022). Past human influence could have been more intense in these southeastern areas, where forests are patchier in between agricultural land, explaining why our findings deviate from this general pattern. Halden had several trees with growth releases around 1920 (Botten, 2024), and relatively high density of cut stumps. However, the

majority of these stumps were from recent cuttings of suppressed trees that were left as dead wood and is thus not part of historical commercial cuttings. Marker was the near-natural stand with the second highest density of cut stumps, suggesting a high cutting intensity. Further, Hemberget was the near-natural site with highest density of cut stumps, on par with many of the previously clear-cut stands. Botten (2024) dated this cutting event to the early 1900s, and the stand was then probably quite open, although half of the cored trees were older. Interestingly, Hemberget had very low volume of downed dead wood (8.3 m³ ha⁻¹). The near-natural stand in Braskereidfoss also had a high density of cut stumps and had likely very low stem density following selective cuttings around the start of the 20th century. Since then, it has been left unmanaged and has now reached a stage where it starts to produce high volumes of downed dead wood (51.2 m³ ha⁻¹). Generally the densities of cut stumps in the previously clear-cut stands (average 614 cut stumps ha⁻¹) were high and comparable to those (688 cut stumps ha⁻¹) reported from mature or middle-aged (>50 y) spruce dominated production forest in Finland, while the densities of cut stumps in our near-natural stands were intermediate (322 cut stumps ha⁻¹) and lower than those (460 cut stumps ha⁻¹) reported for spruce dominated woodland key habitat forests in Finland (Hottola and Siitonen, 2008; Siitonen et al., 2009). Ericsson et al. (2005) reported cut stumps densities in Swedish woodland key habitats that ranged from 10 to 1200 cut stumps ha⁻¹, the lowest values representing forests considered as “untouched” prior to the cut stump survey. Most woodland key habitats in their survey had >100 cut stumps ha⁻¹.

The absence of typical natural stand characteristics in lower elevation southern sites may have negative effects on biodiversity. Additionally, the reduced connectivity (when assuming a mean dispersal distance of 20 km, i.e. $\alpha = 0.05$) of older spruce forests in these areas may further influence biodiversity negatively. This indicates habitat fragmentation and will lower the probability for species to avoid regional extinction by dispersing to nearby forests (Hanski, 1998). The response to fragmentation will, however, depend on the dispersal ability of different species, which is determined by the stability of the habitats they have adapted to (Percele et al., 2019; Southwood, 1988; Sverdrup-Thygeson et al., 2014). Interestingly, when assuming short dispersal distance (<0.5 km), connectivity was higher around near-natural stands than previously clear-cut stands, but showed no relationship with elevation. This link between forest management and connectivity highlights the importance of considering habitat quality and landscape patterns simultaneously. As such, Nordén et al. (2018) showed that connectivity was only important for the occurrence of indicator fungal species given that dead wood volumes were above a certain limit.

Although we aimed at studying mature previously clear-cut forests, we also included old production forest (i.e. maturity class IV, which are yet to reach the ‘mature’ stage as classified by the NFI) due to difficulties in finding stands that could be paired with our near-natural stands. The previously clear-cut forest at Hemberget is far too young to be called mature and had low volumes of both living trees and dead wood compared to the other previously clear-cut sites. However, it did not deviate from the other stands in terms of other measured variables. One could expect structural differences between the two forest management types to decrease as the clear-cut forests becomes overmature and eventually start to develop natural forest characteristics, but our study is not designed to evaluate the time frame for this. Eight of our twelve sites were 70 years or older, the oldest being 90 years. Still, there was no trend of increasing structural heterogeneity or volumes of dead wood with increasing age of the clear-cut stands. This suggests that at the time when previously clear-cut stands again are ready to be harvested, they have still not developed stand characteristics similar to near-natural stands. This means that although trees grow back after clear-cutting, components important for biodiversity do not readily return.

5. Conclusions

In this study, we demonstrate that mature forests that have previously been clear-cut differ in structure and deadwood volumes compared to stands that have not been clear-cut, termed "near-natural". Specifically, near-natural stands exhibit greater structural heterogeneity, with fewer yet larger trees than the previously clear-cut stands. The dead wood volumes in the near-natural stands were lower than those typically found in natural stands in other studies, likely due to a significant human influence as suggested by the high density of cut stumps. These findings are in line with what we know from previous research in Fennoscandia. In this study, however, we focus on comparing stands in pairs where other factors are kept as similar as possible. This is important because during the initial phase of clear-cutting in the mid-1900s, forests that were easily accessible and highly productive were most likely to be selected. In contrast, forests that were far from roads or rivers or on steep terrain, or those with lower productivity, often escaped clear-cutting. As a result, the two management types are generally not found under similar site conditions. Experimental designs like ours are therefore vital for testing how differences in forest management translate into variations in biodiversity, carbon storage, or processes. Thus, the establishment of this study system allows us to explore how past forest management influences present-day ecosystem processes and how these are governed by biodiversity.

CRedit authorship contribution statement

Ulrik G. Botten: Methodology, Investigation, Formal analysis. **Lisa Fagerli Lunde:** Writing – review & editing, Formal analysis. **Regine J. Krok:** Methodology, Investigation, Formal analysis. **Tone Birkemoe:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Håvard Kauserud:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Eivind Kverme Ronold:** Methodology, Investigation. **Line Nybakken:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Milda Norkute:** Writing – review & editing, Methodology, Investigation. **Karin Ulrika Jansson:** Writing – review & editing, Methodology, Investigation. **Damian P. Karlsen:** Writing – review & editing, Methodology, Investigation. **Anne Sverdrup-Thygeson:** Writing – review & editing, Methodology, Investigation. **Johan Asplund:** Writing – original draft, Formal analysis, Data curation, Conceptualization. **Inger Skrede:** Writing – review & editing, Methodology, Investigation. **Jenni Nordén:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Ine-Susanne Hopland Methlie:** Writing – review & editing, Methodology, Investigation. **Olaug Janne Kjønaas:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Sundy Maurice:** Writing – review & editing, Methodology, Investigation. **Rieke Lo Madsen:** Writing – review & editing, Methodology, Investigation, Formal analysis.

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Declaration of Competing Interest

No potential conflict of interest was reported by the authors.

Data availability

Link to data is provided in the manuscript

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2024.122315](https://doi.org/10.1016/j.foreco.2024.122315).

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