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Long term effects of clearcutting on litterfall and understory vegetation in boreal spruce forests in Norway

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ABSTRACT

Boreal forests capture and store substantial amounts of carbon in a global perspective, and the soil is especially important acting like a long-term reservoir of captured atmospheric CO₂. Most of the soil carbon originates from plant litter, shed or withered plant material, added to the forest floor and accumulated. Here, we quantify relative aboveground litter input from trees, and standing understory biomass, as well as carbon and nitrogen concentrations in different litter sources in pairs of mature clear-cuts harvested around the 1950s and near-natural stands in bilberry-spruce forests. The study is based on litter collection with litter-traps and understory biomass harvesting in nine pairs of clear-cuts and near-natural stands in south-central Norway. Our results indicate that there is more understory biomass and potentially higher inputs of aboveground understory litter in near-natural stands, especially driven by bilberry. This study provides enhanced knowledge on effects of intensive forestry practices on understory vegetation in a longer time-perspective, as well as direct measurements of carbon and nitrogen concentrations among fractions of aboveground tree litter and understory functional groups. By now there is accessible and extensive data on standing tree biomass in Norwegian forest ecosystems, but only limited empirical data on litter fluxes and concentrations of C and N from specific litter sources. More research covering long-term clearcutting effects on litterfall in boreal forests is crucial for enhancing our understanding of global carbon-flux mechanisms, as these forests cover vast areas and are profoundly affected by intensive forestry.

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Introduction

Boreal forests are the world's largest terrestrial biome covering large areas in the northern hemisphere. These ecosystems play a major role in the global carbon (C) cycle, and potentially holds the biggest terrestrial C-stocks on earth (Bradshaw & Warkentin, 2015). Soils represent the main C-reservoir in boreal forests, and it has been estimated that as much as 80% of the C in terrestrial ecosystems is found there (Bartlett et al., 2020; Scharlemann et al., 2014). Carbon is sequestered in the soil through photosynthesis where CO₂ is absorbed from the atmosphere by plants, and eventually leaves are shed or the plant withers, and dead organic material containing C and N is added to the soil. Partly decomposed organic material accumulates like litter or humus in the absence of major disturbances, due to the slower heterotrophic respiration rates in boreal forests (Crowther et al., 2019). The C-storage structure and capacity however, differs between forests worldwide (Clemmensen et al., 2013). Tropical and boreal forests store most of the world's forest carbon (87%), though having different C-storage structures, where C in tropical forests to a higher degree is stored in the living biomass (Pan et al., 2011). Because of these properties, aboveground litterfall is smaller in boreal forests than in tropical forests (Zhang et al., 2014), but soil organic carbon stocks are larger.

The biggest input of organic matter to the forest floor is litter (Akselsson et al., 2005) and at a global level accumulated litter represents 5% of the world's forest C-stocks (Pan et al., 2011). Pan et al. (2011) found evidence for litter accumulation contributing to C-sequestration with about "20% of the total C sink in boreal forests" from 1990 to 2007. The quantity of C that builds up in the soils is regulated by plant primary productivity and rate of litter input, and litter decomposition rates deciding loss of C through respiration. Addition of litter to the forest floor is linking living plants and the belowground subsystem, and the rate of CO₂-release to the atmosphere through soil-respiration is driven by an intricate interaction between climate, plant-traits and litter quality, and the decomposer community. We do not fully understand these mechanisms and how they interact (Bradford et al., 2016, 2017), but interestingly Joly et al. (2017) observed a significant effect of canopy density and plant litter traits on decomposition-rates across European forests, while macroclimatic conditions only had minor effects.

Plant species worldwide have developed different strategies and traits to adapt to their local growth conditions. The trait composition of a plant is driven by its plant economic strategy, how the plant is allocating its energy to survive and reproduce in its habitat. Litter quality is determined by a set of functional traits (e.g. lignin:N, C:N, pH, leaf area and leaf dry-mass) that normally varies between different functional groups (Freschet et al., 2010). Decomposition rates vary greatly among different types of litter in similar abiotic conditions, and typically tends to be slower among species with high lignin and/or low carbohydrate-contents (Hilli et al., 2010). For example, litter from evergreen species in general have lower decomposition rates than deciduous species (Hensgens et al., 2020; Joly et al., 2017), and according to Cornwell et al. (2008) woody deciduous species decompose 60% faster than woody evergreens on a global level. These litter-traits accounts for the whole plant, both above and belowground (Freschet et al., 2010, 2013), implying that resource conservative plants, like evergreen coniferous trees, will add more recalcitrant litter to the forest floor, likely resulting in decreased soil fertility by time due to negative feedback-mechanisms, and possibly an increase in soil C-stocks (Bardgett & Wardle, 2010).

Understory litter quantity and quality will reflect the understory species composition. In a typical understory community eudicot species, like forbs and dwarf shrubs, will decompose faster than graminoids, bryophytes and ferns (Cornwell et al., 2008), and likely show varying litter production rates. The relative proportion of standing biomass across different functional groups is therefore highly relevant for understanding how litter input may determine soil C stocks. Additionally, understory biomass varies quantitatively and qualitatively with resource- and light availability, that might be affected by forestry. It is reasonable to believe that intensive forestry regulates understory standing biomass, and potentially understory litter inputs.

Approximately 40% of the Norwegian mainland is covered by forest, and this is where we find the largest national stores of carbon (Bartlett et al., 2020). Norwegian forests have been selectively logged for centuries before the extensive stand-based harvesting started dominating around the 1940s (Storaunet & Rolstad, 2020). There was a shift from closed canopy logging, where the canopy remains intact, to open canopy practices like clearcutting where all trees in a stand are removed and an open site remains. Clearcutting is a major disturbance altering

ecosystem processes, and typically results in more homogenous and denser stands because of domination by even-aged trees. Today, the productive forest in Norway is extensively harvested through clearcutting (~91%) (Bartlett et al., 2020) and Norwegian forest landscapes are dominated by a mosaic of even-aged stands. But, even though intensive forestry alters ecosystems, it may be unrealistic to presume less intensive forest management in the future due to increasing demands of timber, and the use of production-forests as a political climate change mitigation measure.

Ameray et al. (2021) and Mayer et al. (2020) summarized current research on forest management strategies and carbon-dynamics in forest biomes. Both reviews concluded that intensive forestry management, like clear-cut harvesting, resulted in reduced soil carbon storage compared to old-growth forest conservation. When comparing different silvicultural treatments Ameray et al. (2021) concluded that clear-cuts have decreased C-sequestration rates and lower C-storages than partially cut stands. Partial cutting implies less disturbance and allows for more structurally diverse plant-communities with higher aboveground C-storage capacity, and potentially higher understory litter production. When only considering C-fluxes, future forest management should avoid disturbances of the soil (output of C) and ensure high productivity in terms of optimizing soil C-sequestration (input of C) (Jandl et al., 2007).

Several studies have investigated different aspects of short-term succession after clearcutting (For example; Atlegrim & Sjöberg, 1996; Økland et al., 2016; Tonteri et al., 2016), however, the opportunity to study long term clearcutting impacts on boreal spruce-forests has arisen only quite recently, as the first extensive clearcuts are starting to mature. In contrast to clear-cuts, old natural forests typically have more light open gaps and a more heterogenous canopy structure. Further, clearcut forests may have an altered field microclimate and changed competition-advantages both among plant-species and in the soil microfauna. Understory resource availability like sunlight, throughfall and nutrient-content, is likely indirectly affected by overstory canopy properties.

Majasalmi & Rautiainen (2020) conducted a study to improve our knowledge on the relationship between understory vegetation and structural canopy properties, like leaf area index (LAI) and canopy cover. They found evidence for understory composition being related to the structural

properties of the tree canopy. Ground species like bryophytes and lichens were not affected by canopy density, however, upper understory species like dwarf shrubs, graminoids, herbs and pteridophytes were less present in denser spruce dominated forests, with high LAI and canopy cover (Majasalmi & Rautiainen, 2020). Their findings are supported by Landuyt et al. (2020) that found evidence for understory biomass being driven by local forest attributes like light-availability and quantity of evergreen species.

In this thesis, we explored modern forestry effects on aboveground litter input from trees and understory vegetation biomass in boreal forest ecosystems in South-central Norway. We did this by comparing nine paired plots of near-natural NN and clear-cut CC stands. Near-natural plots have never been impacted by clearcutting but might have been selectively logged at different intensities, whereas clear-cut plots have gone through one rotation period of clearcutting in the 1950s.

We used this study system to test the following hypotheses: clearcutting results in (1) less understory vegetation biomass, which we attribute this to higher basal area as a proxy for lower understory light availability, and (2) higher aboveground litter input from trees. Further, we explore how different functional groups in the understory contributes to litter input across the two forest types, and carbon and nitrogen litter concentrations.

Materials and methods

Site description

The study was conducted in Norway spruce (*Picea abies* (L.) Karst.) forests in southcentral Norway in the late summer and autumn of 2021. We localized nine sites from *Gjøvik* in the north to *Halden* in the south, spanning an area of 200 km north to south and 150 km east to west and reaching from approximately 180 to 550 m.a.s.l. Mean annual temperature varied between 1.6 °C in *Gravberget* to 5.9 °C in *Aremark*, and mean annual precipitation spanned from 747 mm in *Søndre Land* to 958 mm in *Skotjernfjellet*. The area was selected because it represents forests in Norway with an early onset of clearcutting practices.

Figure 1: Theoretical study set-up of pairs of near-natural and clear-cut stands

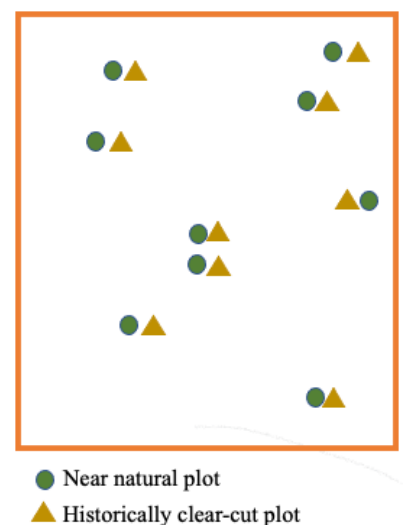


Table 1: Mean annual temperature and precipitation in study sites (WorldClim, 2020)

Pair nr.	Location	Temp °C	Precipitation mm
1	Skotjernfjellet	2.96	958
2	Gullenhaugen	2.32	924
3	Gravberget	1.62	811
4	Våler	2.64	772
5	Varaldskogen	3.35	882
6	Øytjernet	2.30	755
7	Søndre Land	3.11	747
8	Aremark	5.89	860
9	Blåfjell	4.89	870

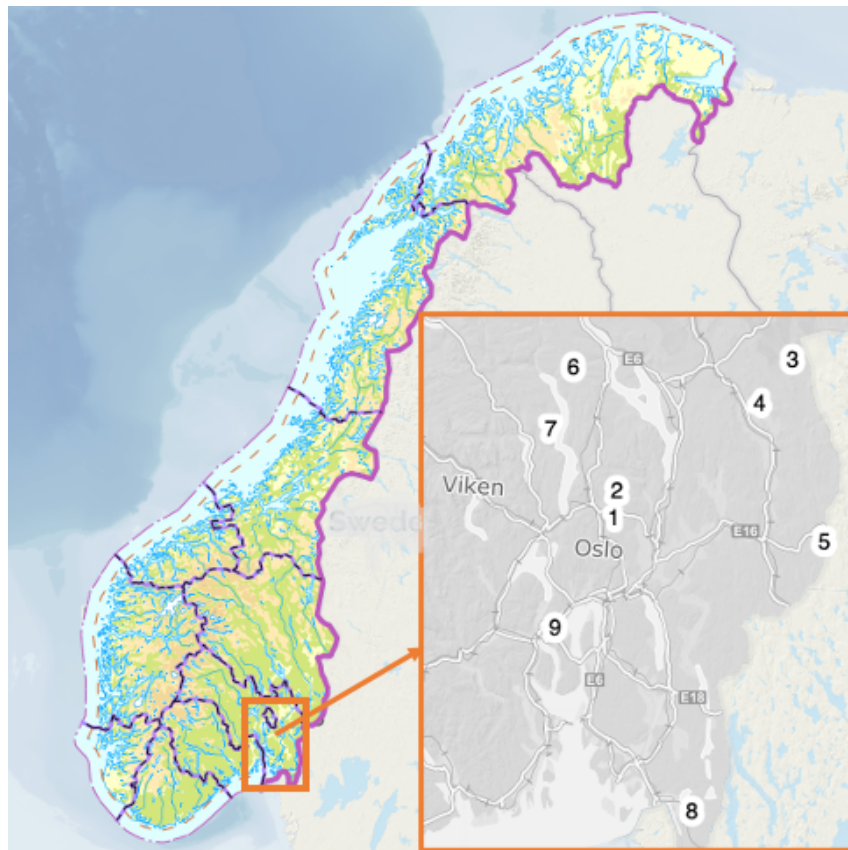


Figure 2: Overview map of study sites in south-central Norway (Norgeskart).

We localized two stands at each site with contrasting management history, but similar abiotic conditions. Data was sampled in nine pairs, consisting of a clear-cut plot and a near-natural plot. We measured and established plots of 225 m², most of which are 15 × 15 m. All stands have a minimum size of 0.5 ha to avoid edge-effects.

Picea abies was the dominating tree species, additionally there were some sparse occurrences of *Pinus sylvestris*, *Betula* spp. and *Sorbus aucuparia*. The understory community was dominated by bilberry or graminoid/herb species and the bottom layer was covered with feathermosses or spruce needle litter. Common species were dwarf shrubs *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and *Linnaea borealis*, graminoids *Avenella flexuosa* and *Luzula pilosa*, and some forbs like *Melampyrum* spp., *Maianthemum bifolium* and *Oxalis acetosella*.

Matching sites and site qualifications

When seeking for plot locations we tried to find comparable clear-cuts and near-natural stands. To investigate forestry effects, we needed the potential differences between plots to relate only to the forestry history, we therefore tried to minimize other physical differences (table 2). The site qualifications are a guidance describing the ideal pair, however, forest ecosystems are dynamic and will have some variation, so our ideal matching plots with forestry history as the only difference are likely impossible to find.

Table 2: List of site qualifications and guidelines when searching for matching plots.

Site qualifications and guidelines

1. Homogenous/similar topography, slope direction and inclination
 2. Matching site index and soil-profiles, including soil stoniness
 3. Avoid steep terrain of practical reasons
 4. Avoid bottom of hills due to altered effects on water-regime
 5. Avoid *Sphagnum*, or make sure it matches across the pair
 6. Matching vegetation types (indicates similar water regimes)
 7. Sufficient buffer to open areas like marsh, fields, roads, lakes etc.
 8. Avoid signs of thinning and ditches
 9. Avoid signs of bark beetle attacks
 10. If signs of forest fire make sure it matches across the pair
 11. Avoid signs of dead wood-removal in NN-plots
-

Field study design

Placement of sub-plots

We randomized six subplot positions in a grid of the plot, avoiding the outer 1 m of the 15×15 m, and used the same coordinates in all plots. After locating all subplots, litter traps were assembled 2.5 m north of the subplot and we harvested biomass in frames of 0.5×0.5 m (0.25 m²) 1 m south of the litter trap (fig. 3). At each plot basal area was measured using a relascope.

Subplots with individual numbers and marking sticks were located while ensuring that they were representative for the topography and vegetation in the plot. Some subplots had to be relocated due to stones, trees, or other obstacles. For most relocations, we tried to move the subplot 1 m up on the y-axis, then 1 m to the right on the x-axis and so on following clockwise order. New alternative coordinates were made if none of the alternative locations were fitting.

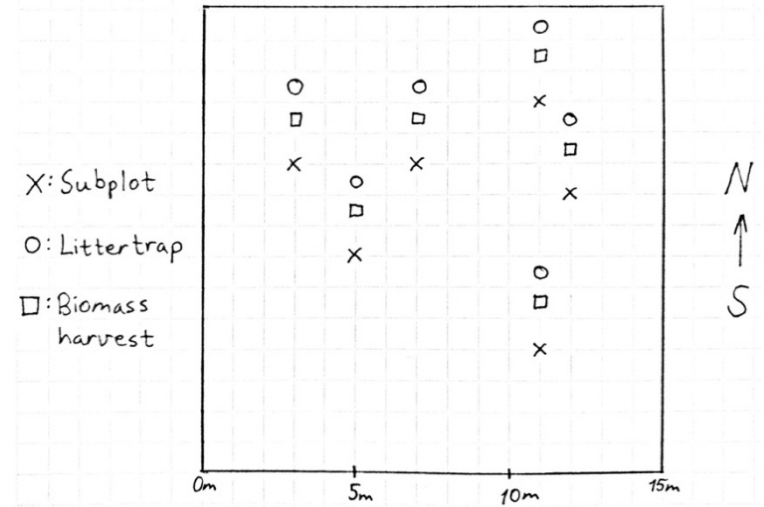


Figure 3: Overview of the field study design with actual coordinates for subplots, littertraps and biomass harvesting.

Collecting and sorting understory samples

We harvested understory vegetation during the three last weeks of August 2021. To harvest vegetation, we used kitchen scissors and tried to leave the upper soil-layer intact. Some green plant-parts, mainly bryophytes and dwarf shrub stems, were left behind due to time restrictions resulting in lack of a small proportion of the standing understory biomass in our data (fig. 4). Samples were roughly sorted into functional groups in field (bryophytes, lichens, forbs, graminoids, pteridophytes, bilberry, other dwarf shrubs, tree saplings), and kept in the freezer at -20°C before fine sorting in the lab. To minimize variation in the results due to subjective differences when sorting, all samples from subplot number one were sorted by the same person(s), then all samples from subplot number two etc.

In one subplot per plot, we separated bilberry stems and leaves to enable a more precise estimate of bilberry litter input, given that leaves are shed each year and thus contribute to yearly litter input, while stems are perennial and only occasionally turned into litter. Separation of leaves and stems additionally allowed for comparisons of C and N concentrations.

Functional group cover estimates and species-lists

Percentage cover of functional groups (bryophytes, lichens, forbs, graminoids, pteridophytes, dwarf shrubs, trees) were visually estimated in intervals of 5 % for all 0.25 m² frames and photographed for later reference. We made lists of vascular plant species in the subplots and did a brief search in the whole plot to look for species that were not present in the subplots.



Figure 4: Subplot number 6-31 in Gravberget near-natural plot 6 before and after harvesting (left) and assembled litter-trap in near-natural plot 17 Blåfjell (right).

Collecting and sorting tree litter

To collect aboveground tree litter, we constructed and assembled litter-traps in field during the three last weeks of August 2021. Traps were systematically placed in each plot (fig. 3). Within the pair all traps were installed the same day or the following to minimize potential differences in litter input. The litter-traps were made of a 0.15 m² metal ring fixed to three wooden poles, and a mesh fabric bag that was open in the top and closed by a thread in the bottom without contact to the forest floor to avoid soil-microorganisms from starting decomposition processes in the collected litter material (fig. 4). A proportion of the litterfall from surrounding trees were caught by the six traps in each plot. Litter-traps were emptied, by opening the thread and collecting the material in paper bags, during the two first weeks of November 2021. The samples were stored in the freezer at -20°C before sorting. Collected litter was sorted into five fractions (spruce needles, pine needles, deciduous leaves, cones, and rest) in December 2021. The rest fraction mainly consisted of twigs, bark, and lichens (see picture in appendix).

Laboratory design and chemical analysis

After thawing and sorting understory biomass to plant functional group and aboveground tree litter to fraction, all samples were dried at 30 °C in drying cabinets for a minimum of five days. Samples were dried following the sorting procedure from mid-September to mid-December 2021. Once all samples were dry, we started weighing the harvested biomass per functional group or fraction, per subplot. After weighing, samples were pooled per functional group per plot.

Carbon and nitrogen analysis

As a preparation for carbon and nitrogen analysis all the pooled samples were homogenized and ground to assure a representative subsample for the whole plot. Samples with bigger volumes of biomass like bryophytes, or more resistant material like lignified stems and cones, were first processed in a big soil grinder. Then, a sub-sample was pulverized in a ball mill (RETSCH

Mixer Mill MM400). Smaller samples, like lichens and forbs, were directly homogenized and pulverized in the ball mill, without pre-homogenizing in the soil grinder. Equipment was cleaned with ethanol in-between different functional groups and fractions.

Dry matter data were calculated based on approximately 0.5-2.5 grams of ground samples dried at 105°C until constant weight. In plots with functional groups that had too small sample sizes to determine dry matter, average values for the given fraction from other locations were used.

Carbon and nitrogen concentrations of 5 mg sample were measured with a Micro cube elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany) by gas chromatography using a thermal conductivity detector after digesting the samples at 1200 °C. Some samples had to be re-run due to machine errors. Data output gave C and N concentrations (%) in functional group or fraction per plot that was later used to calculate C and N stocks (g/m²) in each functional group or fraction in each subplot corrected for dry matter.

Data analysis

To test the effect of forest type on aboveground tree litter, understory biomass, carbon- and nitrogen stocks, I fitted linear mixed effects models (Bates et al., 2015) using forest type and fraction as fixed effects. Subplot nested in plot and pair were used as random factors to reduce variation due to geographical differences across the pairs. Model assumptions were checked visually, and because the residuals were not normally distributed, I calculated F and p -values using permutation tests with 1000 iterations using the `perm.lmer` function of the `permutest` R package. Pairwise comparisons between fractions across forest type were performed as a post-hoc test with the function `emmeans`, estimated marginal means, using model estimates from the function `bootstrap_parameters` of the `parameters` package with at least 1000 permutations. I ran separate models for each response variable in understory data and tree litter data.

For bilberry leaves/stems ratio I used a non-parametric paired Wilcoxon signed rank test, and to test bilberry cover in relation to basal area and forest type I partly followed the same procedure as with the other linear mixed effects models.

Figures in R were made with `ggplot2` (Wickham, 2016). *Norgeskart* (2022) and Microsoft PowerPoint was used for making maps. Mean annual temperature and precipitation (1970-2000) was retrieved in QGIS from WorldClim (Fick & Hijmans, 2017). All statistical tests and figures were performed in RStudio, R version 4.1.1.

Results

Understory biomass

Bryophytes and bilberry were the main contributors to the understory biomass in both forest types, followed by minor contributions from other dwarf shrubs and graminoids (fig. 6). The remaining functional groups represented a very small fraction of the overall standing understory biomass. Near-natural forests had on average 35 % higher understory biomass (fig. 5). This relation further translates into higher stocks of carbon and nitrogen. The difference was entirely driven by bilberry being much more abundant in near-natural plots, while the other functional groups were unresponsive to forest type, causing a significant interaction effect.

Bilberry stems represented a bigger proportion of the total bilberry biomass (~85 %) than leaves. Estimated proportion of leaves was approximately 14.1 % in near-natural stands and 14.5 % in clear-cuts. When comparing means with a Wilcoxon signed-rank test there were no differences in proportion of bilberry leaves in clear-cuts and near-natural stands ($p=0.844$).

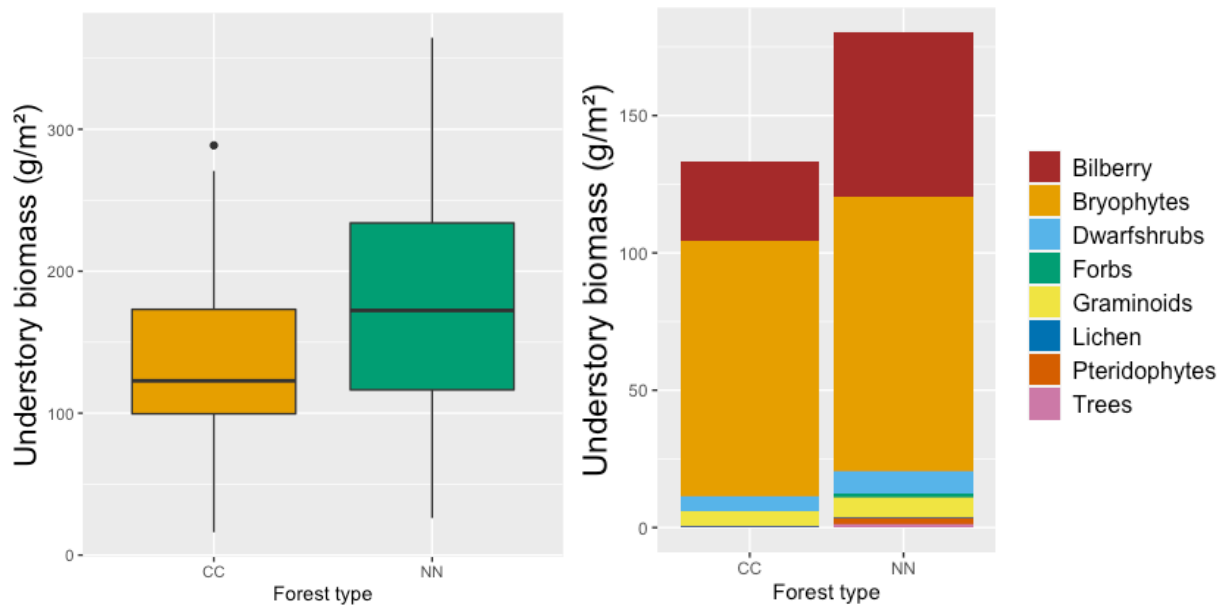


Figure 5: Standing understory biomass stock in grams per square meter in clear-cut CC and near-natural NN forest (left).

Figure 6: Stacked bar-plot distribution of understory functional groups (bilberry, bryophytes, other dwarf shrubs, forbs, graminoids, lichens, pteridophytes, small trees) (right).

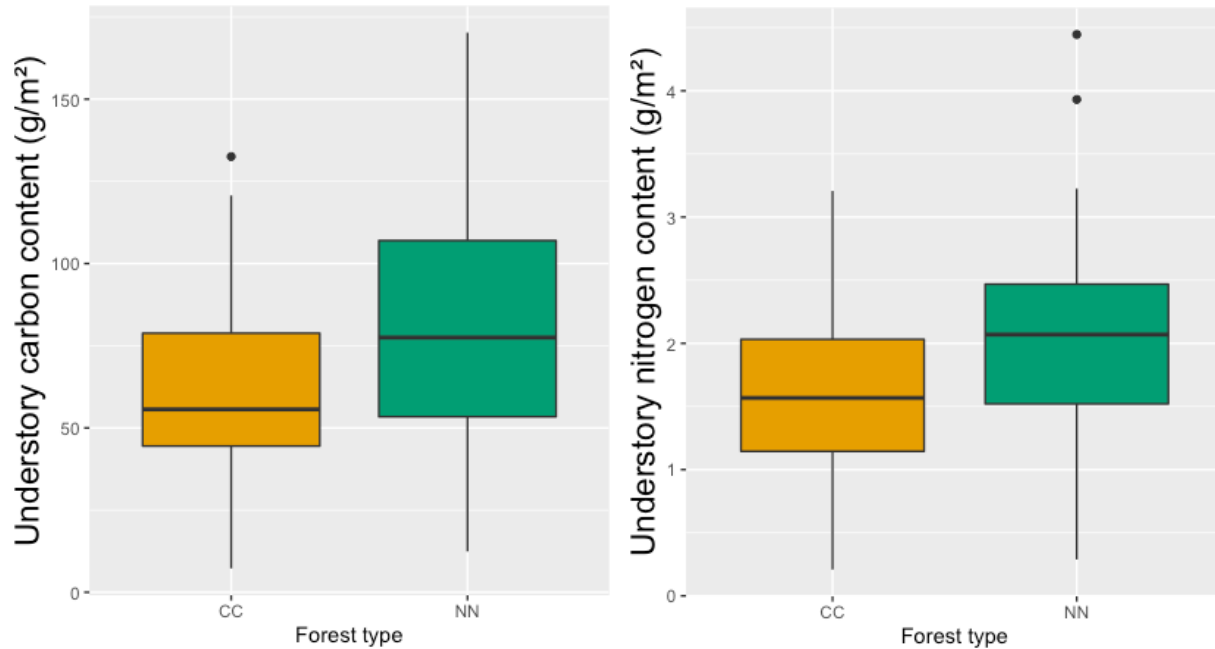


Figure 7: Carbon (left) and nitrogen (right) stocks in aboveground understory biomass, measured in grams per square meter in clear-cuts CC and near-natural NN forest.

Table 3: Effect of forest type (clear-cut or near-natural), fraction (cones, leaves, rest, spruce- and pine needles) and forest type*fraction interaction on the response variables biomass, carbon, and nitrogen in aboveground tree litter flux. *F* and *p*-values.

Response variable	Forest type	Fraction	Interaction
Biomass	38.38 (p<0.001)	85.88 (p<0.001)	4.47 (p<0.001)
Carbon	41.25 (p<0.001)	78.32 (p<0.001)	4.90 (p<0.001)
Nitrogen	31.32 (p<0.001)	107.32 (p<0.001)	3.60 (p<0.001)

Concentrations of C and N in understory biomass

Analysis of carbon and nitrogen concentrations of aboveground understory biomass indicated no differences between near-natural stands and clear-cuts based on average concentrations. Total averages across both forest types suggest that there is 45.6 % carbon and 1.17 % nitrogen in understory plant-communities, not taking relative contribution per functional group into account. Bilberry stems, followed by trees (small tree saplings) had the highest C-concentrations among all functional groups, while forbs had the lowest (~42 %), followed by bryophytes and lichens. Bilberry leaves and forbs had higher concentrations of nitrogen (~2 %) than other functional

groups (~1 %) across both forest types. Whereas bilberry stems had approximately 1 % of N, indicating that C:N-ratio was higher in bilberry stems than in bilberry leaves. However, bilberry leaves and stem results should be treated with caution as they are based on fewer samples, only one subplot per plot given that there was presence of bilberry, while *bilberry (total)* is based on five subplots per plot. All other functional groups are based on six subplots per plot.

Table 4: Carbon concentration, standard error, and min-max range in understory functional groups across near-natural and clear-cut forest types. Lichens in CC only had one sample, hence no min-max and SE.

Average concentration of carbon (%) \pm SE and min-max range		
Functional group	Near-natural	Clear-cut
Bilberry (total)	48.3 \pm 0.1 (47.8–48.7)	48.2 \pm 0.2 (47.5–49.0)
Bilberry leaves	47.3 \pm 0.2 (46.6–47.9)	46.9 \pm 0.2 (46.0–47.4)
Bilberry stems	48.6 \pm 0.1 (48.3–49.0)	48.7 \pm 0.2 (48.3–49.6)
Bryophytes	44.3 \pm 0.1 (43.7–44.7)	44.4 \pm 0.1 (43.6–45.1)
Dwarf shrubs	47.9 \pm 0.5 (45.6–49.0)	47.7 \pm 1.0 (42.2–49.6)
Forbs	42.3 \pm 0.7 (40.5–44.4)	42.1 \pm 0.5 (41.4–43.2)
Graminoids	44.3 \pm 0.1 (43.8–44.5)	45.0 \pm 0.8 (44.0–50.6)
Lichen	43.4 \pm 0.3 (42.0–43.9)	44.0
Pteridophytes	46.3 \pm 1.2 (43.9–47.6)	45.6 \pm 1.2 (43.1–47.1)
Trees	48.3 \pm 0.9 (46.2–53.3)	47.2 \pm 0.6 (46.0–48.7)

Table 5: Nitrogen concentration, standard error, and min-max range in understory functional groups across near-natural and clear-cut forest types. Lichens in CC only had one sample, hence no min-max and SE.

Average concentration of nitrogen (%) \pm SE and min-max range		
Functional group	Near-natural	Clear-cut
Bilberry (total)	0.99 \pm 0.04 (0.83–1.13)	0.99 \pm 0.03 (0.83–1.11)
Bilberry leaves	1.86 \pm 0.10 (1.34–2.26)	1.98 \pm 0.09 (1.62–2.32)
Bilberry stems	0.86 \pm 0.03 (0.75–1.00)	0.93 \pm 0.04 (0.81–1.14)
Bryophytes	1.34 \pm 0.10 (0.84–1.99)	1.29 \pm 0.06 (0.95–1.56)
Dwarf shrubs	0.98 \pm 0.05 (0.79–1.23)	0.97 \pm 0.06 (0.63–1.10)
Forbs	1.82 \pm 0.22 (1.19–2.33)	1.59 \pm 0.07 (1.38–1.66)
Graminoids	1.34 \pm 0.03 (1.22–1.45)	1.16 \pm 0.07 (0.83–1.38)
Lichen	1.10 \pm 0.15 (0.78–1.60)	0.88
Pteridophytes	0.97 \pm 0.05 (0.89–1.06)	1.28 \pm 0.14 (1.00–1.45)
Trees	0.91 \pm 0.07 (0.63–1.13)	1.20 \pm 0.17 (0.89–1.67)

Bilberry biomass and basal area

Bilberry biomass decreased with increasing basal area, an inverted proxy for light availability, in clear-cut stands (fig. 8). Meanwhile, in near natural stands, bilberry was unresponsive to basal area, causing a significant forest type * basal area interaction (table 6).

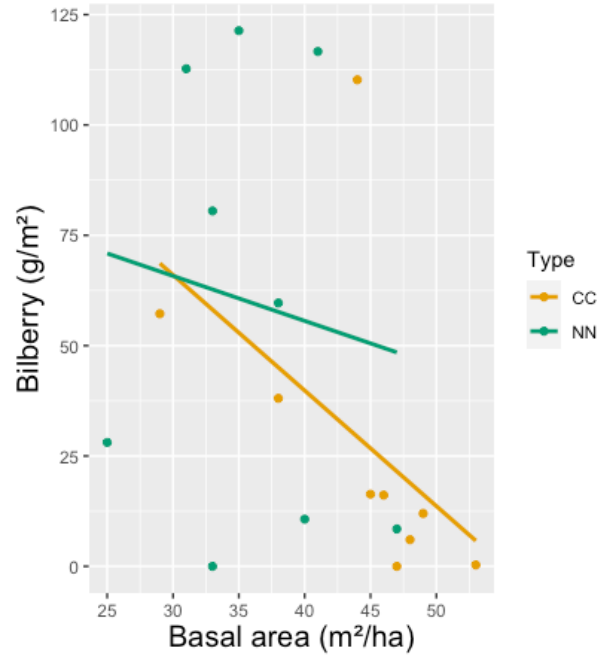


Figure 8: Basal area (decreasing light-availability in the forest floor) and bilberry biomass stock in grams per square meter in clear-cut CC and near-natural NN forest types.

Table 6: Bilberry biomass response to forest type and basal area.

Response variable	Forest type	Basal area	Interaction
Bilberry	0.07 (p=0.006)	1.04 (p=0.013)	0.19 (p=0.002)

Species richness

Based on cover estimations we found that five out of seven functional groups had higher presence in near-natural stands than in clear-cuts, meaning that the group were present in a higher number of subplots (appendix table 8). The biggest difference of occurrence was among trees, forbs, and dwarf shrubs including bilberry that were present in more near-natural subplots. Bryophytes were the only functional group present in all subplots, and graminoids were present in more clear-cut subplots. Average number of understory species was, however, 10.4 in both clear-cuts and near-natural stands. Meaning that near-natural plots had higher variation in number of species, but there were no major differences in species richness among forest types.

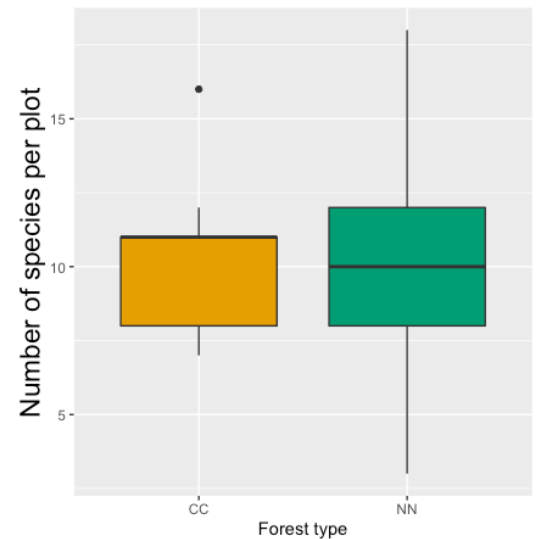


Figure 9: Number of counted species per plot across clear-cuts and near-natural stands.

Aboveground tree litter flux

Aboveground tree litter fluxes did not differ between forest types (table 7). On average there was approximately between 25 g and 35 g of litterfall per square meter per month. There were however large differences between fractions, and the rest-fraction was three times larger in near-natural forest than in clear-cuts. This resulted in a significant interaction term because the other fractions did not respond to forest type, or non-significantly in the opposite direction (deciduous leaves). Nonetheless, this finding should be treated with caution, considering that the tendency of high aboveground tree litterfall in near-natural stands mainly is driven by a large rest-input in the littertraps in one single site (Våler). Carbon and nitrogen fluxes are related to the total aboveground tree litter flux and similarly did not differ between forest types.

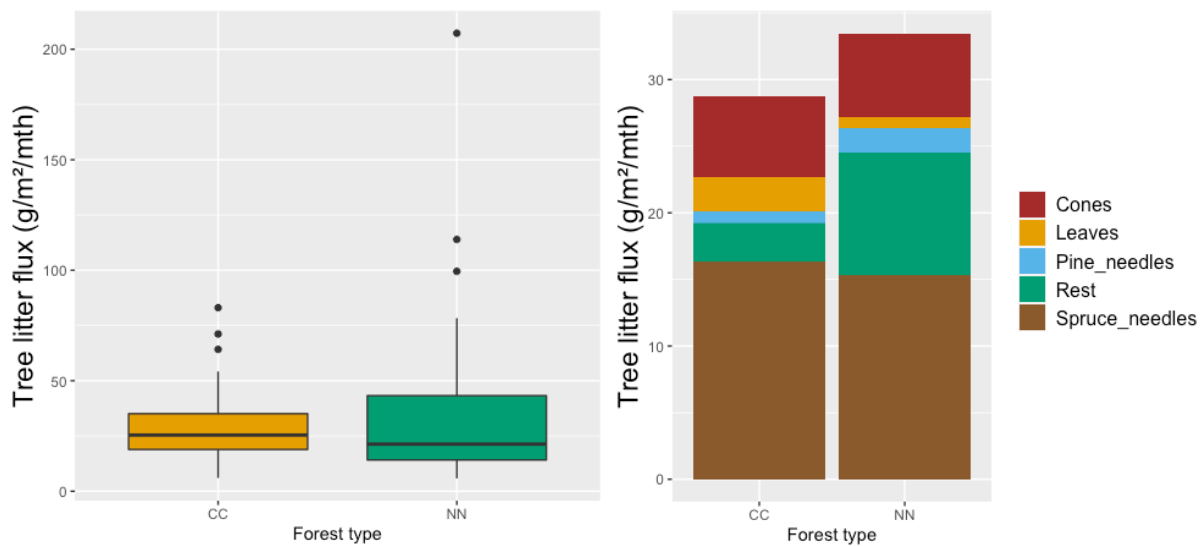


Figure 10: Flux of aboveground tree litter in grams per square meter per month in clear-cut CC and near-natural NN forest (left). Stacked bar-plot distribution of aboveground tree litter-fraction fluxes (cones, leaves, rest, spruce- and pine needles) (right).

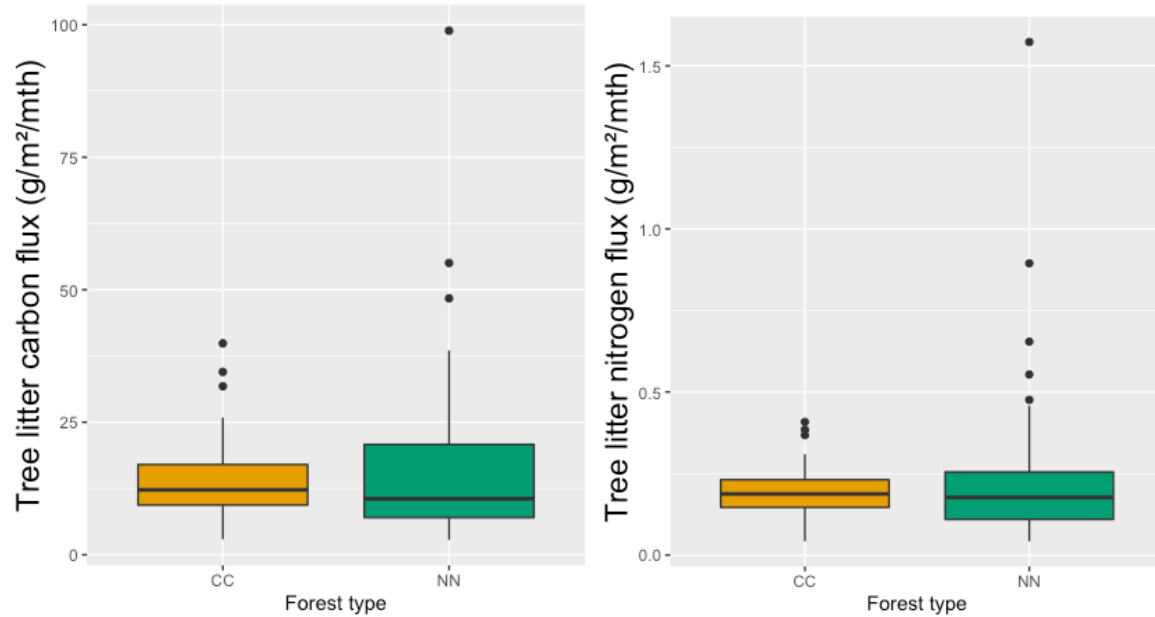


Figure 11: Flux of carbon (left) and nitrogen (right) in aboveground tree litter in grams per square meter per month in clear-cut CC and near-natural NN forest.

Table 7: Effect of forest type (clear-cut or near-natural), fraction (cones, leaves, rest, spruce- and pine needles) and forest type*fraction interaction on the response variables biomass, carbon, and nitrogen in aboveground tree litter flux. *F* and *p*-values.

<i>Response variable</i>	<i>Forest type</i>	<i>Fraction</i>	<i>Interaction</i>
Biomass	0.02 (<i>p</i> =0.593)	16.30 (<i>p</i><0.001)	2.24 (<i>p</i><0.001)
Carbon	0.02 (<i>p</i> =0.614)	16.06 (<i>p</i><0.001)	2.26 (<i>p</i>=0.002)
Nitrogen	0.08 (<i>p</i> =0.310)	16.01 (<i>p</i><0.001)	2.38 (<i>p</i><0.001)

Concentrations of C and N in aboveground tree litter

All fractions of aboveground tree litter consisted of approximately 50 % carbon with standard errors between 1 – 0.2 % for both forest types. The biggest difference in C-concentration among tree litter fractions was between pine needles and spruce needles. Nitrogen concentrations were lower in cones and pine needles than in deciduous leaves, rest, and spruce needles for both forest types. Average N-concentration for all fractions of aboveground tree litter was 0.75%.

Table 8: Carbon concentration, standard error, and min-max range in aboveground tree litter fractions across near-natural and clear-cut forest types.

Average concentration of carbon (%) \pm SE and min-max range		
Fraction	Near-natural	Clear-cut
Cones	49.1 \pm 0.2 (48.4–50.2)	49.2 \pm 0.4 (48.0–51.1)
Deciduous leaves	49.6 \pm 0.5 (48.3–50.8)	50.2 \pm 0.4 (49.2–51.9)
Pine needles	51.7 \pm 0.2 (51.5–51.8)	51.3 \pm 0.4 (50.4–51.8)
Spruce needles	48.5 \pm 0.2 (47.8–49.3)	48.2 \pm 0.3 (46.4–49.1)
Rest	50.5 \pm 1.0 (47.7–58.3)	50.1 \pm 0.2 (48.8–50.9)

Table 9: Nitrogen concentration, standard error, and min-max range in aboveground tree litter fractions across near-natural and clear-cut forest types.

Average concentration of nitrogen (%) \pm SE and min-max range		
Fraction	Near-natural	Clear-cut
Cones	0.42 \pm 0.07 (0.19–0.88)	0.37 \pm 0.06 (0.19–0.57)
Deciduous leaves	1.18 \pm 0.18 (0.93–1.73)	1.12 \pm 0.13 (0.87–1.87)
Pine needles	0.42 \pm 0.00 (0.41–0.42)	0.43 \pm 0.03 (0.38–0.46)
Spruce needles	0.77 \pm 0.03 (0.67–0.92)	0.70 \pm 0.02 (0.60–0.82)
Rest	0.99 \pm 0.06 (0.67–1.19)	1.08 \pm 0.05 (0.79–1.34)

Discussion

In this study we investigated long-term effects of clearcutting within one rotation period on aboveground tree litter flux and understory biomass in south central Norwegian bilberry-spruce forests. Interestingly, we found support for the first hypothesis that (1) *clearcutting results in less understory vegetation biomass*, but our data did not indicate that (2) *clear-cuts had higher aboveground litter input from trees*.

Near-natural stands had higher understory biomass than clear-cuts, driven by differences in bilberry abundance. Bryophytes and dwarf shrubs, mainly bilberry, represented the largest proportion of biomass in both forest types, while all other functional groups had only minor contributions to the total aboveground understory biomass stock. Standing understory biomass reflect annual litter input for some functional groups. This is especially true for deciduous plants like bilberry and annual plants like many forbs and graminoids. Our results imply that litter input was higher in near-natural stands as bilberry was the main driver of higher biomass stocks. Meanwhile, bryophyte biomass is less directly linked to litter input depending on litter

production rate, and one would need to make annual litter inputs estimates. Despite differences in understory biomass stocks, the average number of species per plot was similar across the two forest types indicating that biomass differences were not driven by species richness but rather by the domination of bilberry in near-natural stands. A possible explanation for this lack of response to forest type might be that potential differences in species composition after clearcutting equalizes if clear-cuts develop for longer than 20 years (Tonteri et al., 2016).

Total bilberry biomass included a big proportion of perennial stems, even so, it is likely that high bilberry biomass in near-natural stands will be reflected in higher annual understory litter input due to annual shedding of leaves. Bilberry is an important keystone species in boreal forests, prefers partial shading, and typically represent a substantially high proportion of soil nutrient inputs (Hensgens et al., 2020). Our finding that bilberry decreased with higher basal areas, which is a proxy for decreasing light availability, in clear-cut sites, and its higher abundance in near-natural forests is congruent with other studies looking at stand density effects on bilberry cover. For example, Eldegard et al. (2019) found that bilberry cover in Norway increased with stand age, peaking at intermediate stand densities. Other studies suggest that the introduction of intensive industrial forestry has resulted in a decrease in bilberry cover across Fennoscandian forests (Hedwall et al., 2013; Miina et al., 2009). Our results indicate that growing conditions were more favorable in near-natural stands than in clear-cuts, though, near-natural stands had higher variations in bilberry biomass across different plots, implying that it is not exclusively an ideal habitat, supported by Eldegard et al. (2019).

Bryophytes represented the largest proportion of understory biomass but did not respond to forest type. This lack of response to forest type could be because bryophytes are less regulated by tree canopy density than understory vascular plants. This is supported by Majasalmi & Rautiainen (2020) that studied relations between understory vegetation and tree canopy properties in a southern boreal forest in Finland and ultimately found no connection between cover of forest floor species and tree density. While the vascular plants of the understory often is limited by light-availability (Landuyt et al., 2020), bryophytes dominating in the bottom layer is often more limited by water-availability (Hart & Chen, 2006). This local abiotic factor is altered

by increasing tree density, but data suggest that our plots had sufficient throughfall for bryophytes to thrive and that presumably water-availability was not a limiting factor.

Even though bryophytes showed no response to forest type it probably influences soil C-input and sequestration considering its big contribution to understory standing biomass and its low decomposition rates. Moss decompose extremely slow compared to bilberry, and fairly slow compared to needles (Hilli et al., 2010). Congruent with this, Turetsky et al. (2010) showed that moss litter decomposition resembled that of recalcitrant woody-tissues like stems and branches. Consequently, if there is a higher proportion of litter-inputs from moss and woody tissues there will be slower decomposition, likely resulting in higher organic matter accumulation in the forest floor. Though, this effect may be partly counteracted by the positive impact of the moss-layer on decomposition rates of other vascular litter (Jackson et al., 2013). The complicated interaction of long-term forestry effects, stand density, and understory litter production remains an important field of research.

Our data did not support the second hypothesis of higher aboveground tree-litter input in clear-cuts, even though clear-cuts had a tendency of higher basal areas than near-natural stands. Not surprisingly, spruce needles contributed with most of the monthly aboveground tree litter flux in both forest types, and more than half of the total monthly litter flux in the clear-cut stands. Cones from spruce and pine contributed substantially to the monthly flux in both forest types, and might be more important in a C-storage context than indicated through to its relative contribution to the total flux (Hågvar, 2016).

Our results might be influenced by the short duration of the litter-trap experiment. Covering minimum one year cycle, but ideally several years, with continuous emptying of the litter traps throughout all seasons would provide more reliable results with minimized effects of between-year variation in litter production (Berg & Laskowski, 2005; Zhang et al., 2014). Another explanation for the lack of response to forest history on aboveground tree litter fluxes could be that the difference of tree densities in our plots are not adequate to lead to actual changes in litter production, given that our near natural plots might be denser than old natural forests that truly have not been affected by management. Old natural forests are typically more heterogenous than

dense production forests, and often driven by gap dynamics (Kuuluvainen & Aakala, 2011; McCarthy, 2001) therefore they might require larger sampling areas to cover local variation. Moreover, our plots were selected on the criteria of finding matching sites, and an alternative approach with randomly selected plots might have modified our results. However, it remains unsure whether longer time series or other study-sites of aboveground tree litter flux would reveal a response to the forest management history.

Concentrations of carbon and nitrogen in understory biomass and aboveground tree litter were similar between clear-cuts and near-natural stands, in contrast to C and N stocks that were higher in understory biomass in near-natural stands. As expected, there were higher C-concentrations in lignified tissue like bilberry stems and tree saplings among understory functional groups. Interestingly, bryophytes consisted of 44 % C in both forest types. This relatively low C-concentration should be recognized as bryophytes constitute the largest proportion of the understory standing biomass in both forest types. Our results suggest that average concentrations of C were 46 % in aboveground understory biomass, and 50 % in aboveground tree litter. There are some differences in C and N concentrations between litter from different sources that preferably should be accounted for when doing large scale estimates of C and N stocks, especially because functional groups contribute with varying amounts of annual litter production depending on their relative abundance in the plant-community. However, there is a current lack of accessible empirical data describing understory C and N concentrations in Norwegian forests and more research is needed.

There are no generalized estimates of plant tissue nitrogen concentration due to big variances between species. We found N concentrations spanning between 0.37 % in cones to 1.98 % in bilberry leaves across both forest types in all studied litter fractions. N concentrations did not seem to differ drastically between overstory litter (0.7 % average) and understory biomass (1.2 % average). These results partly concurs with Landuyt et al. (2020), that found significantly higher N concentrations in the understory in all European forest ecosystems studied, including boreal forests in Finland. However, Landuyt et al. (2020) only analyzed non-lignified tissue and is therefore not fully comparable with our results that included lignified tissue from dwarf shrubs and small trees. Furthermore, understory functional group specific data on N concentrations from

Kjønaas et al. (2021; see appendix) sampled in western Norway spruce forests compares with our results with only some minor deviations. Ligneous plant N concentrations were particularly similar, whereas there were slightly higher N concentrations in herbs/ferns/graminoids and bryophytes in the study by Kjønaas et al (2021).

Cones and pine needles had the lowest N-concentrations among tree litter fractions and reduced the total average concentration of N, but these fractions are not expected to contribute greatly to the total annual litter flux when studying Norway spruce dominated forests. Whereas spruce needles had higher monthly litter inputs and N concentrations. Some studies suggests that needle-litter with high nitrogen concentrations can leave more organic material to accumulate in the forest floor in a long-term perspective (Berg, 2014, 2018; Berg et al., 2001; Hågvar, 2016). Higher rates of humus accumulation in relation to higher N concentrations applied for coniferous needle-litter in the study by Berg et al. (2001), but it remains unknown whether the same mechanism applies for other types of litter. Our results indicate differences in N concentrations across different litter-sources that might be affected by this mechanism to varying extents. Ranging from 0.37 % in cones to 1.18 % in deciduous leaves in aboveground tree litter, and from 0.86 % in bilberry stems to 1.98 % in bilberry leaves in the understory biomass. There were nevertheless no major differences between N concentrations in the two forest types.

Comparing annual litter input from overstory versus understory would give important insights on how plant functional groups regulate carbon-fluxes, but this would require prolonged tree litter collection and calculations of understory litter flux based on understory vegetation biomass. Furthermore, the relation of litter production from different plant functional groups strongly depends on local ecosystem properties and therefore studies differ in their results considering relative litter-contributions from overstory vs. understory (Hansson et al., 2013; Hensgens et al., 2020; Hilli et al., 2010; Landuyt et al., 2020). For example, Landuyt et al. (2020) found higher annual leaf litter production from trees than from non-lignified aboveground understory biomass in boreal forests in Finland, and this litter production pattern applied for all included types of European forest ecosystems. Independent of its origin, higher total input of litter like we indirectly found in near-natural forests through a higher understory biomass, will potentially have positive effects on soil C-storage due to higher C-inputs.

Importantly, boreal forests are facing greater pressure due to population growth and thereby an increased demand of timber-products. Timber is used as a more sustainable alternative replacing other materials, and intensive forestry is seen as a measure to capture more CO₂ from the atmosphere. However, we do not fully understand how ecosystems are affected by clearcutting in the long run. Furthermore, boreal forests will be increasingly affected by climate change in the proximate future and the whole boreal forest biome might switch from being a C-sink to becoming a C-source (Jandl et al., 2015). Altered species compositions existing of more fast growing species with high decomposability litter, in combination with changes in the microbial community might lead to higher litterfall and increased soil respiration, and ultimately a decrease in the soil C-reservoirs (Kausrud et al., 2022). Assessing how forest ecosystem carbon-fluxes are affected by clearcutting therefor remains a highly important research topic in a global change ecology approach.

Conclusion

In conclusion, our results indicated that total understory biomass, and thus potentially the carbon input through litter, was higher in near-natural forest than in clear-cuts. Aboveground tree litter flux measurements did not indicate major differences between clear-cuts and near-natural sites, though this should be studied further. More importantly, this study provided actual measurements of carbon- and nitrogen concentrations in the main understory functional groups and aboveground tree litter fractions in Norwegian bilberry-spruce dominated forests, whereas most studies are based on estimates of carbon and comparable nitrogen concentrations provided in other datasets. Data provided in this thesis may be used to upscale C and N stocks on a landscape level while acknowledging relative concentrations and contributions of C and N from different aboveground tree litter fractions and understory functional groups, and further enhance our knowledge of the complex C and N fluxes in boreal forests. Further, more research is needed to strengthen our understanding of how modern forestry is affecting aboveground litter fluxes in boreal forest ecosystems in a longer time perspective.

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Appendix

1. Confidence intervals of aboveground tree litter biomass (with 2000 iterations)

Type	Fraction	Lower HPD	Upper HPD
CC	Cones	1.0399	3.58
NN	Cones	1.2734	3.79
CC	Leaves	-0.2721	2.26
NN	Leaves	-0.9034	1.61
CC	Pine needles	-1.0311	1.48
NN	Pine needles	-0.4676	2.05
CC	Rest	-0.0215	2.43
NN	Rest	2.4329	4.95
CC	Spruce needles	5.2287	7.82
NN	Spruce needles	4.7350	7.28

2. Confidence intervals of aboveground tree litter carbon (1000 iterations)

Type	Fraction	Lower HPD	Upper HPD
CC	Cones	0.5735	1.805
NN	Cones	0.5890	1.792
CC	Leaves	-0.0819	1.110
NN	Leaves	-0.4202	0.774
CC	Pine needles	-0.5026	0.725
NN	Pine needles	-0.2435	0.964
CC	Rest	0.0207	1.214
NN	Rest	1.2662	2.480
CC	Spruce needles	2.5425	3.766
NN	Spruce needles	2.2513	3.420

3. Confidence intervals of aboveground tree litter nitrogen

Type	Fraction	Lower HPD	Upper HPD
CC	Cones	0.0000489	0.0182
NN	Cones	0.000621	0.0185
CC	Leaves	0.00130	0.0190
NN	Leaves	-0.00566	0.0122
CC	Pine needles	-0.00709	0.0111
NN	Pine needles	-0.00522	0.0130
CC	Rest	0.00343	0.0210
NN	Rest	0.0225	0.0406
CC	Spruce needles	0.0368	0.0544
NN	Spruce needles	0.0391	0.0570

4. Confidence intervals of understory biomass

Type	Fraction	Lower HPD	Upper HPD
CC	Bilberry	0.05031	0.0884
NN	Bilberry	0.12699	0.1655
CC	Dwarf shrubs	-0.00609	0.0321
NN	Dwarf shrubs	0.00130	0.0384
CC	Forbs	-0.01906	0.0196
NN	Forbs	-0.01176	0.0288
CC	Graminoids	-0.00143	0.0372
NN	Graminoids	0.00564	0.0447
CC	Lichen	-0.01861	0.0182
NN	Lichen	-0.02046	0.0198
CC	Bryophytes	0.27372	0.3105
NN	Bryophytes	0.29933	0.3363
CC	Pteridophytes	-0.01843	0.0199
NN	Pteridophytes	-0.01488	0.0235
CC	Trees	-0.01671	0.0219
NN	Trees	-0.01490	0.0232

5. Confidence intervals of understory carbon

Type	Fraction	Lower HPD	Upper HPD
CC	Bilberry	2.5438	4.372
NN	Bilberry	6.2926	8.140
CC	Dwarf shrubs	-0.2306	1.591
NN	Dwarf shrubs	0.1438	1.866
CC	Forbs	-0.9027	0.869
NN	Forbs	-0.07041	1.103
CC	Graminoids	-0.1029	1.650
NN	Graminoids	-0.0342	1.626
CC	Lichen	-0.8181	0.874
NN	Lichen	-0.8238	0.922
CC	Bryophytes	9.5031	11.289
NN	Bryophytes	10.1644	11.958
CC	Pteridophytes	-0.8331	0.879
NN	Pteridophytes	-0.6222	1.117
CC	Trees	-0.9180	0.902
NN	Trees	-0.7195	1.007

6. Confidence intervals of understory nitrogen

Type	Fraction	Lower HPD	Upper HPD
CC	Bilberry	0.04952	0.0897
NN	Bilberry	0.12647	0.1637
CC	Dwarf shrubs	-0.00645	0.0326
NN	Dwarf shrubs	-0.00107	0.0374
CC	Forbs	-0.01948	0.0172
NN	Forbs	-0.01149	0.0268
CC	Graminoids	-0.00201	0.0386
NN	Graminoids	0.00647	0.0445
CC	Lichen	-0.01914	0.0202
NN	Lichen	-0.01784	0.0192
CC	Bryophytes	0.26992	0.3098
NN	Bryophytes	0.29894	0.3365
CC	Pteridophytes	-0.01849	0.0202
NN	Pteridophytes	-0.01363	0.0249
CC	Trees	-0.01912	0.0193
NN	Trees	-0.01679	0.0237

7. Establishment and emptying of littertraps

Pair	Plot	Established	Emptied	Nr. of days
1	1	09.08.2021	11.11.2021	94
1	2	10.08.2021	11.11.2021	93
2	3	11.08.2021	10.11.2021	91
2	4	11.08.2021	10.11.2021	91
3	5	13.08.2021	04.11.2021	83
3	6	14.08.2021	04.11.2021	82
4	7	14.08.2021	03.11.2021	81
4	8	14.08.2021	03.11.2021	81
5	9	18.08.2021	02.11.2021	76
5	10	17.08.2021	02.11.2021	77
6	11	20.08.2021	05.11.2021	77
6	12	19.08.2021	05.11.2021	78
7	13	25.08.2021	06.11.2021	73
7	14	24.08.2021	06.11.2021	74
8	15	26.08.2021	13.11.2021	79
8	16	26.08.2021	13.11.2021	79
9	17	31.08.2021	07.11.2021	68
9	18	31.08.2021	07.11.2021	68

8. Counted presence of functional groups based on percentage cover estimates. Total of 54 subplots in clear-cuts, and 54 subplots in near-natural stands.

	CC	NN	Difference
Bryophytes	54	54	0
Lichens	2	6	4
Forbs	12	18	6
Graminoids	38	34	4
Pteridophytes	7	8	1
Dwarf shrubs	39	44	5
Trees	9	15	6

9. Picture of rest fraction from littertraps in plot 11 to exemplify contents of the rest fraction.





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