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Boreal tree species change as a climate mitigation strategy: impact on ecosystem C and N stocks and soil nutrient levels

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Abstract. To increase the annual uptake of CO_2 as well as the long-term storage of carbon (C) in forests, the Norwegian government consider large-scale replacements of native, deciduous forests with faster-growing species like Norway spruce. To assess the effects of tree species change on ecosystem C and nitrogen (N) stocks and soil chemistry, we used a paired plot approach including stands of native downy birch and planted 45- to 60-yr-old Norway spruce. The birch stands were used as reference for the assessment of differences following the tree species change. We found significantly higher C and N stocks in living tree biomass in the spruce stands, whereas no significant differences were found for dead wood. The cover of understory species groups, and the C and N stocks of the aboveground understory vegetation were significantly higher in the birch stands. The tree species change did not affect the soil organic carbon (SOC) stock down to 1 m soil depth; however, the significantly higher stock in the forest floor of the spruce stands suggested a re-distribution of SOC within the profile. There was a significant positive correlation between the SOC stock down to 30 cm soil depth and the total ecosystem C stock for the birch stands, and a negative correlation for the spruce stands. Significant effects of tree species change were found for C and N concentrations, C/N, exchangeable acidity, base saturation, and exchangeable Ca, K, Mg, Na, S, and Fe in the organic horizon or the upper mineral soil layer. The total ecosystem C stock ranged between 197 and 277 Mg/ha for the birch stands, and 297 and 387 Mg/ha for the spruce stands. The ecosystem C accumulation varied between 32 and 142 Mg/ha over the past 45–60 yr, whereas the net ecosystem C capture was considerably lower and potentially negative. Our results suggest that the potential to meet the governments' targets to increase C sequestration depend on the C debt incurred from the removed birch stands, the rotation length, and potentially also the susceptibility of the different stand types to future risk factors related to climate change.

Key words: *Betula pubescens;* boreal forest; carbon; dead wood; downy birch; ecosystem stocks; nitrogen; Norway spruce; *Picea abies;* soil organic carbon; soil chemistry; understory vegetation.

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Introduction

Boreal forests make up about one third of all forests on our planet and represent a crucial global reservoir of carbon (C) (Bradshaw and Warkentin 2015). Estimates of C fluxes indicate that approximately 30% of the Earth's terrestrial C sequestration takes place in this biome (Warkentin and Bradshaw 2012). Thus, the stability of the reservoir, as well as a continuous sequestration, is vital to the atmospheric C budget (Bradshaw and Warkentin 2015). In Norway, where forests cover 37% of the land base (FAO 2015), the C stocks in the forest biomass have steadily increased since the 1920s due to a national investment in forest tree planting. In western Norway, the predominant form of these historical afforestation and reforestation activities typically involved a change in tree species from native pine or birch-dominated forests to spruce forests, mostly Norway spruce (*Picea abies* (L.) H. Karst.) planted outside its natural habitat.

Globally, increased C sequestration in forests, including afforestation and tree planting, is proposed to be among the most effective measures to mitigate the escalating climate change (Eggermont et al. 2015, IPCC 2018, Bastin et al. 2019, Sippel et al. 2020). Large-scale tree species change is considered to be part of the Norwegian government climate change mitigation policies, as a means to increase both the annual uptake of CO_2 and the long-term storage of C in forests (Norwegian Ministry of Environment 2012). Model results suggested a substantial increase in the C accumulation in standing tree biomass over a rotation period when birch stands were replaced with planted Norway spruce in intermediate to high productive areas (The Norwegian Environmental Agency 2013). Although tree species change is expected to increase the carbon density of the forests, the harvesting or removal of less productive forests will incur a carbon debt, which is frequently ignored (Law and Waring 2015, Malcolm et al. 2020). This carbon debt needs to be considered in order to determine the net effect of a given forestry mitigation strategy.

In addition to changes in biomass production, a change from native birch to planted Norway spruce generally alters the structure and microclimate of the forest, reflected by a shift from light and open stands to darker, denser stands (Aarrestad et al. 2013). Such changes will affect the species composition, species abundances, and plant diversity of the understory vegetation, as well as its biomass. The three bioclimatic sections represented in Western Norway (Moen 1999) reflect variation in topography, precipitation, and other environmental factors. This variation contributes to a higher plant diversity and a higher understory vegetation cover in the western native forest systems compared to boreal forests in other parts of Norway (cf. Økland 1996). Although the understory vegetation biomass in boreal forests is generally low compared to the standing tree biomass (Hansson et al. 2013), its annual input of litter, especially from vascular plants, may be comparable to that of the trees (Nilsson and Wardle 2005). Thus, tree species effects on the understory vegetation may in the long term affect belowground C and N processes and stocks, as well as concentrations of soil nutrients (ibid.).

Whereas the CO_2 uptake by trees dominates C accumulation in boreal forest ecosystems, the soil constitutes the major C pool. Soil may store two to five times more C than the trees (Bradshaw and Warkentin 2015), and estimates from Norwegian forests indicate that about 77% of the C stock is allocated to the soil and 23% to the vegetation (Grønlund et al. 2010). Tree species have been found to affect SOC stocks in European and North American temperate and boreal forests (Vesterdal et al. 2013). Effects were most pronounced for forest floors, but inconclusive as to whether tree species affect the size of the SOC stock or merely the distribution of C within the soil profile (ibid.). Whereas broadleaved tree species have been suggested to give higher SOC accumulation than coniferous species following afforestation (Laganiere et al. 2010), common garden experiments in SW Sweden, Poland, and Finland have shown significantly more SOC under Norway spruce than under silver birch (Hansson et al. 2011, Mueller et al. 2012, Olsson et al. 2012).

Tree species may influence not only the SOC stocks, but also the nitrogen (N) stocks. Fennoscandian studies report that soil N stocks are significantly higher in Norway spruce stands compared to birch stands (Hansson et al. 2011, Olsson et al. 2012). N is tightly linked to the C cycle and C sequestration in forests, as availability of inorganic and organic N affects the production of plant biomass, and the C/N ratio affects the dynamics of decomposition and accumulation as well as the loss of N from forest systems (Berg and Tamm 1994, De Vries et al. 2006, Mueller et al. 2012, Högberg et al. 2017). C/N ratio and C concentration were the most important soil properties explaining variation in stand productivity across Sweden (Van Sundert et al. 2018). On the other hand, C/N and soil chemical characteristics such as available and total pools of soil nutrients and soil pH were found to be poor predictors of productivity across a wide range of acidic forest soils (Hansson et al. 2020). Tree species may potentially affect the chemical characteristics and the biogeochemical processes of the soil, directly or indirectly, and thus the long-term soil fertility (Bergkvist and Folkeson 1995, Fischer et al. 2007, Mueller et al. 2012). While nutrients affect the functioning of the forest ecosystem as well as responses to environmental changes, they are frequently overlooked in C cycle studies (Van Sundert et al. 2018).

In the current paper, we assess the effects of tree species change from native birch to planted Norway spruce on the ecosystem C and N stocks, as well as on understory vegetation cover and soil chemical characteristics. The tree species change comprised a combined effect of tree species and management in the form of tree planting. We use a paired plot approach, where potential differences are expected to represent the effect of the tree species change. We hypothesize that replacing birch forests with planted Norway spruce will: (1) increase the C and N stocks in both tree biomass and soil, (2) decrease the C and N stock and cover of the understory vegetation, (3) promote an allocation of C and N from the mineral soil to the forest floor, and (4) acidify the soil and reduce the concentrations of exchangeable nutrients. The current results are part of a larger study on effects of tree species change on the total C balance, including the fate of the harvested wood and its substitution effects, effects on albedo, soil organic matter stability, and soil microbial functional diversity.

Materials and Methods

Site description

Four study locations were selected in the counties Vestland and Møre and Romsdal in Western Norway (Table 1). The site selection was based on suggestions from the local forest service, high-resolution aerial photographs, and site visitation including a brief soil survey to confirm comparable soil between stands. The criteria for the site selection were paired stands of mature native birch and planted Norway spruce that were delineated by a property boundary, thus having similar slope, exposition, altitude, and edaphic factors. Originally, five locations were chosen (Appendix S1: Fig. S1); however, soil data from the northernmost location Molde indicated differences in edaphic factors, which impeded tree species comparisons. As data on ecosystem C and N stocks are generally scarce, selected data from Molde are included in the online supplementary material (Appendix S1: Table S3).

All locations were positioned within a markedly oceanic bioclimatic section in the middle boreal vegetation zone (Moen 1999). The stands were located on hillsides with varying slopes, altitudes, and aspects as given in Table 1. This contributed to some variation in the local climate. For each location, the meteorological data (Table 1) were based on 1×1 km resolution gridded climate data provided by the Norwegian Meteorological Institute (Lussana et al. 2018*a*, *b*). The temperature values were corrected according to the difference in elevation between a given location and the nearest meteorological grid point, assuming a temperature lapse rate of 0.65°C per 100 m (Skaugen et al. 2003). For calculations of the temperature sum during the growing season (growing degree-day sum; GDD sum) and growing season precipitation sum (GS Prec. sum), the start and end of the growing season were defined as the day when daily mean temperature exceeded 5°C for at least 5 d, and when 10-d mean temperature fell below 5°C, respectively (Skaugen and Tveito 2004). Soil temperature was measured with TMS-4 soil probes sensors (TOMST, Praha, Czech Republic) at six points in each macro-plot at 6 cm soil depth over one year with a measurement frequency of 15 min and an accuracy of $\pm$0.5°C.

The bedrock is Precambrian dioritic to granitic gneiss at all locations except at Jølster II, where it consists of Precambrian gneiss with granodioritic to granitic composition and augen. At all locations, the bedrock is covered by thick moraine deposits (NGU 2020). The soil texture and the soil types are relatively similar across sites, and the stone volume is generally high (≥20%) (Table 1).

Typical native species in Western Norway are Scots pine (*Pinus sylvestris*) and broadleaves. The current deciduous stands were dominated by native, naturally occurring, downy birch (*Betula pubescens* Ehrh.) and scattered common juniper (*Juniperus communis* L.) at all locations. Stranda also contained some regrowth of Norway spruce as well as gray alder (*Alnus incana* (L.) Moench), all with a stem diameter predominantly <5 cm. The stands were subjected to occasional selective cutting for firewood through time, whereas the

Table 1. Location, climatic factors, and soil characteristics for paired stands of native birch and planted Norway spruce at four locations in Western Norway.

Type	Parameter	Jølster I	Jølster II	Ørsta	Stranda
Location	Latitude	61°30′39″N	61°30′22″N	62°9′2″N	62°16′23″N
	Longitude	6°17′54″E	6°12′46″E	6°12′2″E	6°51′5″E
	Aspect	N	N	E-NE	S-SE
	Slope (%)†	41 (3)	31 (1)	21 (4)	28 (5)
	Stand elevation (m asl)	225-250	335-345	210	430
	MET elevation (m asl)‡	267	451	171	556
Climate	MAT (°C)	4.99	3.95	6.17	3.41
	GDD sum	953	784	1040	672
	Soil temp. birch (°C)	5.2	4.9	5.3	5.2
	Soil temp. spruce (°C)	5.2	4.7	4.8	5.2
	MAP (mm)	2394	2614	1951	1584
	GS Prec. sum	912	932	842	545
Soil	Stone volume (%)	20.0 (2.2)	24.9 (1.6)	32.3 (2.6)	31.4 (3.2)
	Soil type	Podzol	Regosol/Podzol	Regosol	Podzol
	Soil texture	Loamy sand/ sandy loam.	Sandy loam	Sandy loam/loam.	Sandy loam/ silt loam, loam.

Notes: Climate is based on data from the Norwegian Meteorological Institute (Lussana et al. 2018*a*, *b*). Mean annual temperature (MAT), mean annual precipitation (MAP), growing degree-days sum (GDD sum), and sum of precipitation during growing season (GS Prec. sum) are average values for the period 1986–2015, whereas soil temperature (Soil T) is based on average daily values for the years 2016–2017 for the given stands. Soil type is based on WRB (2015) and stone volume on the rod penetration method (Stendahl et al. 2009). Dominant soil texture of the soil pits is given, with additional texture classes found in one or two of the horizons.

† 100% slope equals 45°.

‡ Altitude at the meteorological grid point.

understory vegetation was subjected to some rough grazing mainly by sheep and wild deer.

Prior to the planting of Norway spruce, the birch trees were felled or killed by girdling/pesticides (spraying or poisonous axe) and left on site to rot. The number of stumps in a late stage of decomposition (decay class 4–5) suggests that felling was the dominant method of removing the original birch stand at Jølster I and Ørsta (Table 2). Generally, the Norway spruce stands received no management after planting and were subjected to self-thinning. Grazing is assumed to be virtually absent following canopy closure due to the change in understory vegetation. Basic stand characteristics are summarized in Table 2.

Experimental design

Each location consisted of paired stands of adjacent mature planted Norway spruce and native birch, where the birch stand represents the reference for the assessment of differences in C and N stocks and soil chemistry following the tree species change. Three paired macro-plots, each 144 m^2, were established at each location, giving a total of 24 macro-plots (four locations, three macro-plots per tree species and location). These were placed within 225 m^2 plots (approx. NFI size of plots in the National Forest Inventory, Viken 2017) used for tree measurements.

Methods

*Trees.—*The number of years since planting give the stand age of Norway spruce, while the age of the birch stands is based on counts of annual rings in increment cores sampled at breast height from the dominant trees in the stands. For the latter age estimates, we included 7 yr for the trees to get to breast height (Viken 2017). Tree height (H) and diameter at breast height (dbh) were measured on all standing living and dead trees with a minimum dbh of at least 5 cm and H of at least 1.3 m (Viken 2017). For downed dead wood, the length and the diameter of the top and end were measured for logs with a minimum length of 1.3 m and a diameter of at least 6.3 cm at the end. Likewise, the cross-sectional diameter of stumps from earlier cuttings was measured when average diameter was at least 6.3 cm. This excluded smaller pieces and fine downed wood, which will

Table 2. Stand characteristics for paired stands of native birch and planted Norway spruce at four locations in Western Norway.

Stand characteristics	Jølster I		Jølster II		Ørsta		Stranda	
	Birch	Spruce	Birch	Spruce	Birch	Spruce	Birch	Spruce
Total stand age (years)	103	60	101	45	104	60	87	45
Stand age at dbh (years)	96	43	95	35	97	44	80	38
Site index H_{40}	B11	G23	B11	G23	B11	G23	B11	G23
No. trees (ha^{-1})	1052	1585	978	1363	1037	2119	1881	1719
Mean dbh (cm)	15.4	19.9	15.3	19.6	13.5	17.3	14.1	16.6
Minimum dbh (cm)	5.9	6.7	5.0	5.3	5.2	6.1	5.2	5.2
Maximum dbh (cm)	33.6	36.5	36.2	45.4	32.3	38.1	33.1	35.3
Mean height (m)	13.6	19.4	12.2	15.8	10.1	17.0	11.4	15.0
Minimum height (m)	5.2	7.2	2.6	3.0	3.2	4.4	3.0	4.0
Maximum height (m)	20.0	29.9	18.4	27.0	18.6	27.0	18.7	24.4
Volume (m^3/ha)	148	595	134	485	103	558	215	374
Basal area (m^2/ha)	22.3	54.8	21.8	52.3	18.3	56.6	35.4	42.9
Above and belowground living tree biomass (Mg/ha)	138	402	133	355	105	388	208	272
Total dead biomass (Mg/ha)	7.8	22.4	9.9	9.5	5.5	30.6	14.2	16.4

Notes: Total stand age (reference year 2016) refers to the year of planting for Norway spruce and stand age at breast height of dominant trees +7 yr for birch according to Viken (2017). Site index is based on the H_{40} system, where B11 and G23 represent the mean tree height in meters at 40 yr breast height age in birch and spruce stands, respectively. The volume is including bark.

underestimate the total C stock of dead wood. The decay status of each standing dead tree, downed dead wood, and stump was determined according to five classes (Viken 2017). The relative proportion of remaining dry biomass for the decay stages 1–5 used for both spruce and birch were based on data from Næsset (1999) as adopted in Stokland et al. (2016). The relative proportion amounted to 0.975, 0.875, 0.625, 0.375, and 0.125, for decay class 1–5, respectively. Due to the lack of empirical data, we assumed the same proportion of remaining dry biomass for birch as for Norway spruce.

C and N stocks in living aboveground (stem, live branches, needles/leaves, dead branches) and belowground (stumps, roots [diameter ≥2 mm]) tree biomass were estimated. To calculate living and dead tree biomass, we used single tree biometric functions with dbh and H as predictor variables for aboveground birch (Smith et al. 2014) and Norway spruce (Marklund 1988), and dbh for belowground birch (Smith et al. 2016) and Norway spruce (Petersson and Ståhl 2006). To estimate C stocks in living and dead biomass, a C fraction of dry matter equal to 0.5 was applied (Mäkinen et al. 2006, Bright et al. 2020). The estimated C stocks in dead wood were adjusted for the proportion of remaining dry biomass for the five decay stages (Næsset 1999).

N stock in aboveground living biomass was estimated using N concentrations for different biomass fractions in paired stands of birch and spruce given in Alriksson and Eriksson (1998). N stock estimates in belowground biomass were based on the average N concentrations in spruce and birch stump and root systems in paired stands located in Jädraås and Svartberget, Sweden (Hellsten et al. 2013). N concentrations in biomass vary with N availability in the ecosystem (Boxman et al. 1998, Kjønaas and Stuanes 2008). The concentration in needles given by Alriksson and Eriksson (1998) from northeastern Sweden was within the range found in stands subjected to ambient and chronically elevated N input in southwestern Sweden (Kjønaas and Stuanes 2008). For N stocks in dead wood, a varying degree of N retention and N fixation is expected at different decay stages (Herrmann and Bauhus 2018, Rinne-Garmston et al. 2019). Thus, N stocks in dead wood were not included in the ecosystem N stock estimates.

Following the felling of, and subsequent CO_2 release from, the original birch stand, the net C budget of spruce stands started out with a negative C balance, a C debt (Law and Waring 2015). The calculation of the C debt incurred by the removal of the original birch stands was based on the assumption that the C stocks of the current and original birch stands were similar. Due to continuous cover of birch forest through time, birch stands were assumed to be in a near-steady state, which included the occasional selective cutting. The assumption of a near-steady state was evaluated based on measured birch stumps in the spruce stands at the locations Jølster I and Ørsta (Appendix S1: Section 1). Assuming the relationship between above- and belowground biomass being similar for the current and the original birch stands, the results support the assumption of a near-steady state over the past 60 yr. The birch stands which existed where the spruce stands are today (the original birch [OB] of the current spruce [CS] stands) had a similar C stock relative to the birch stands studied here, or slightly higher when including the selection cutting (Appendix S1: Section 1). Based on a potentially conservative assumption of similar C stocks in the living tree biomass of the current birch (CB) stands and the original birch of the spruce stands, the net C capture in living biomass (LB) following the tree species change was estimated in two steps according to the following two equations:

$$\Delta \mathrm{C\ stock_{LB}} = \mathrm{C\ stock_{(CS\_LB)}} - \mathrm{C\ stock_{(CB\_LB)}} \quad (1)$$

$$\mathrm{Net\ C\ capture_{LB}} = \Delta \mathrm{C\ stock_{LB}} - \mathrm{C\ stock_{(OB\_LB)}} \quad (2)$$

where ΔC stock (Mg/ha) expresses the C accumulation in the above- and belowground living tree biomass of the spruce stands relative to the C stock in the current birch stands. The net C capture in living tree biomass (Mg/ha) takes into account the C debt incurred by the felling of the original birch stands and is based on $\mathrm{C\ stock_{(OB\_LB)}} = \mathrm{C\ stock_{(CB\_LB)}}$.

Understory vegetation.—Within each macroplot, the biomass of the understory vegetation was harvested from six randomly positioned 0.5 m × 0.5 m subplots, giving a total of 72 spruce and 72 birch understory vegetation subplots. Before harvesting the understory vegetation, the cover for each of four species groups ([1] small trees; [2] dwarf shrubs; [3] herbs, ferns, and graminoids; and [4] bryophytes) within the subplots was recorded, and inclination and aspect were measured using a compass clinometer. All aboveground plant parts giving cover within the subplot boundaries were included in the harvested biomass, even for plants rooted outside the subplot. Due to the low number of small trees, their biomass was grouped together with dwarf shrubs into the species group ligneous plants. Thus, the harvested material was grouped as: (1) ligneous plants, (2) herbs, ferns, and graminoids, and (3) bryophytes. The harvested material was pre-sorted in the field, brought to the laboratory, and stored frozen until the sorting was completed. The sorted material was dried at 70°C to constant weight before weighing. Like other studies (cf. (Sigurdsson et al. 2005, Hansson et al. 2013, Smith et al. 2017), we applied an indirect method to estimate C and N stocks, based on C and N concentrations previously measured in plant groups with similar species composition in a study in Western Norway (T. Økland et al., *unpublished data*; Appendix S1: Table S4).

Soil.—1. Soil sampling with auger.—The forest floor and the upper 30 cm of the mineral soil were collected by use of cylindrical augers (diameter = 6.6 cm for the forest floor, diameter = 2.6 cm for the mineral soil) in a grid consisting of 20 sampling points per macro-plot (named grid samples hereafter). At Stranda, the grid lines were slightly moved to avoid sampling in close proximity to the occasional Norway spruce and gray alder trees in the birch plots. The soil was divided into the forest floor layer (LFH) based on diagnostic horizons, and three mineral soil layers based on soil depth (M1 = 0–5 cm, M2 = 5–15 cm, and M3 = 15–30 cm). Fine earth bulk density (BD) of each layer was determined for each bulked grid sample based on the diameter of the soil core, the sum of the thickness of each sample of a given layer, and the total weight of the fine earth fraction (<2 mm) in each bulked sample. For more details, see Appendix S1: Section 2.

2. Sampling of soil profiles.—Due to the high stone content which limited the sampling depth of the grid sample to 30 cm, additional soil samples from 30 cm down to approx. 1 m soil depth, or the presence of the C-horizon, were collected from one 1x1m soil pit in each of the birch and spruce stands at each location. The BD in the profiles was determined from four samples (steel corer) in each diagnostic horizon at similar soil depths as the grid samples, and calculated based on the weight of the fine earth fraction (<2 mm) and the volume of the steel corer (100 cm^3). In cases where the deeper BC- and C-horizons were too compact to be sampled, a proxy BD based on the highest BD in the given profile was used. This may underestimate the SOC stock of these layers. The soil profiles were classified according to the World Reference Base for soil resources (IUSS Working Group 2015).

3. Sample processing and chemical analyses.—In the laboratory, the soil samples were stored frozen until pretreatment, then weighed, dried in cabinets with forced air circulation (25°C), and sieved through a 2-mm sieve. The sieved fine earth fraction (<2 mm) and the different coarse fractions (roots and gravel + stones > 2 mm, green plant debris) were weighed separately. The fine earth fraction was finely ground (planet mill) prior to C and N analysis. All soil samples were analyzed for total C and N (Elementar Vario EL equipped with a TCD detector), pH (H_2O) (PHM 220), and dry matter (105°C) (Ogner et al. 1999). Due to the acidity of the soil (pH range 4.20 ± 0.07–4.97 ± 0.02), the total C was interpreted as total organic C. Additionally, the grid samples were analyzed for exchangeable elements (1 mol/L NH_4NO_3, Thermo Jarell Ash ICP-IRIS HR Duo). Base saturation (BS (%); Na^+, K^+, Ca^{2+}, Mg^{2+}) was determined relative to effective cation exchange capacity (CEC; $mmol_c$/kg). The soil profile samples were analyzed for oxalate extractable Fe and Al and ODOE (optical density in oxalate extract) (van Reeuwijk 2002). Particle size distribution of the fine earth fraction (<2 mm) of soil profile mineral horizons was quantified based on the method of sedimentation (pipette; clay and silt fractions) and wet sieving (sand fractions) (Krogstad et al. 1991). For details, see Appendix S1: Section 2.

4. Stock calculations.—The SOC and N stocks down to 30 cm mineral soil were estimated based on BD (g/cm^3), C and N concentrations (%), and the thickness (cm) of each bulked layer (LFH, M1, M2, and M3) in the grid sample dataset. The average SOC and N stocks in the deeper 30–100 cm mineral soil were based on BD, C, and N concentrations and thickness of the diagnostic horizons in each of the two profiles at each location. The SOC and N stocks down to 1 m soil depth were calculated as the sum of the grid samples (LFH-30 cm mineral soil) at each macro-plot and the mean SOC and N stocks in the deeper soil profiles (30–100 cm soil depth) at each location, as no significant differences between tree species were found for the M2 and M3 stocks of the grid samples ($P = 0.99$ and 0.93 for the C stocks in the M2 and M3 layers, respectively).

Stone volume (coarse fraction [CF]) was assessed based on (1) the weight of stones and small rock fractions (SRF) from each of the two soil profiles per location, and (2) the rod penetration method (Eriksson and Holmgren 1996) in the macro-plots as part of the grid sampling. The latter was based on an assessment of stone and boulders down to 30 cm soil depth and the assumption of an even distribution of the CF through the entire mineral soil profile. The average volume of CF across all locations in the mineral soil down to 1 m soil depth was similar for the two methods, amounting to $25.9\% \pm 9.9$ and $22.5\% \pm 1.6$, respectively ($\pm$SE). As the rod penetration method reflected the volume of CF in, and variation between, each macro-plot, the stocks in the mineral soil down to 1 m was corrected for the CF based on this approach. The volume of CF was calculated according to model A in Stendahl et al. (2009). The total SOC and N stocks were calculated as follows:

$$\text{CF }(\%) = 1 - ((\text{stone volume})/100) \quad (3)$$

$$\begin{aligned} \text{Total stock (Mg/ha)} = {} & \text{stock}_{\text{LFH}} \\ & + ((\text{stock}_{(\sum \text{M1, M2, M3})} \\ & + \text{stock}_{(\sum 30-100 \text{ cm min soil})}) \\ & \times \text{CF}) \quad (4) \end{aligned}$$

Statistical analyses

Statistical analyses of the effect of tree species change on C and N stocks in trees, understory vegetation and soil were performed using a mixed effects model, where tree species was set as fixed variable and location and plot within location were set as random variables. Tree stocks were tested based on single tree data in each of the six macro-plots per location, with tree species and biomass component as fixed effects. Differences in C and N stocks between the different plant species groups of the understory vegetation were tested based on data from the six microplots in each of the six macro-plots, and with tree species and plant group as fixed effects. Additionally, the three understory vegetation plant species groups, as well as the tree biomass components, were tested separately using a mixed effects model where location and plot within location were set as random variables and tree species as fixed effect. Differences in SOC and soil N stocks as well as chemical characteristics between birch and spruce stands were tested based on one bulked soil sample per layer for each of the six macro-plots per location, with tree species and soil layer as fixed effects. For statistical analysis on ecosystem C and N stocks, all stocks in soil, understory vegetation, and trees were included, except stumps in decay classes 4–5, which were assumed to originate from the stands prior to the tree species change, and N stocks in dead wood. Data on SOC and N stocks, density, thickness, and exchangeable elements except sulfur (S) were log transformed prior to the statistical analysis, whereas the data on C and N concentrations, C/N, exchangeable acidity, pH, BS, CEC, and S did not require a log transformation. The analysis on the understory vegetation as well as the total ecosystem C and N stocks was based on zero-skewness transformed data standardized to a 0-1 scale. The statistical analysis was conducted using the GLIMMIX procedure of the SAS/STAT software, version 9.4 for Windows (SAS Institute Inc. 2017). Details on the mixed effect models are given in Appendix S1: Section 3.

Spearman's rank correlation based on the 24 plots (12 spruce and 12 birch) was used to test for significant correlations between C and N stocks in vegetation and soil as well as between C and N stocks, soil chemical parameters, aspect, and slope (SAS 2017), using a confidence level of 95%. The Spearman's rank correlation coefficient is in the following denoted by r_s.

Results

Stand characteristics

The majority of both the spruce and birch stands had a single layered canopy, although there were some suppressed or understory trees in both forest types. Compared to the birch trees, the spruce trees showed higher growth at all locations, as expressed by mean dbh and mean height per stand (Table 2). The number of trees per ha was, expectedly, also higher for the planted spruce stands, which all together gave higher volume and total living biomass compared to the birch stands (Table 2).

C and N stocks in standing living tree biomass

The C and N stocks varied between different biomass components and fractions of living and dead biomass (Table 3). The C stock in total living biomass, as well as in above- and belowground living biomass, was significantly higher in the spruce stands relative to the birch stands (Table 3; $P < 0.0001$, 0.004, <0.0001, respectively, Appendix S1: Table S5). There was no significant effect of location (Appendix S1: Table S5), yet the mean C stock in total living biomass varied between 136 and 201 Mg/ha for the spruce stands, being lowest in the south facing location Stranda and highest in the north facing Jølster I. For birch, the range was 52–104 Mg/ha, being lowest in the northeast facing Ørsta and highest in Stranda (Table 3). The N stock in total living biomass and aboveground living biomass was also significantly higher in spruce relative to birch (Table 3; $P < 0.0001$, Appendix S1: Table S5).

The ratio aboveground: belowground C stocks in living tree biomass were 2.6 ($\pm$0.03) and 3.1 ($\pm$0.07) for birch and spruce stands, respectively. The ratio belowground: total living tree C stock was suggested to be larger in birch compared to spruce stands, whereas the ratio stem: total living tree C stocks were slightly smaller in birch relative to spruce, amounting to 54% ($\pm$0.8) in birch and 57% ($\pm$1.4) in spruce stands.

The estimated net C capture in living tree biomass following the tree species change varied between a net accumulation of 89 ($\pm$29) Mg/ha at Ørsta and a net loss of 73 ($\pm$30) Mg/ha at Stranda (Table 3). The results suggest a higher total C capture in the two 60-yr-old stands at Jølster I and Ørsta compared to the two 45-yr-old stands Jølster II and Stranda, whereas the mean annual rates at Ørsta, Jølster I, and Jølster II were relatively similar, amounting to 1.5 ($\pm$0.5), 1.0 ($\pm$0.1), and 1.0 ($\pm$0.6) $Mg \cdot ha^{-1} \cdot yr^{-1}$, respectively. At Stranda, an annual net loss of C amounted to 1.6 ($\pm$0.7) $Mg \cdot ha^{-1} \cdot yr^{-1}$ over the current lifespan.

Dead wood

All stands contained both standing and downed dead wood (Table 2). Especially in the

Table 3. Carbon (C) and nitrogen (N) stocks (mean, with SE in parentheses) in different fractions of above- and belowground living tree biomass and C stocks in dead wood in stands of native birch and planted Norway spruce in Western Norway.

Biomass components	Biomass fraction	Tree species	Jølster I	Jølster II	Ørsta	Stranda	Average
C stock (Mg/ha)							
Living aboveground	Stem	Birch	38.9 (0.06)	35.6 (0.07)	27.3 (0.06)	56.3 (0.04)	**39.5**† (6.09)
		Spruce	121 (0.09)	97.6 (0.12)	114 (0.06)	74.2 (0.05)	**102** (10.46)
	Crown‡	Birch	11.5 (0.02)	12.4 (0.03)	10.2 (0.02)	18.9 (0.02)	**13.3** (1.95)
		Spruce	33.4 (0.02)	34.0 (0.04)	34.1 (0.02)	27.5 (0.02)	**32.2** (1.59)
	Total	Birch	50.4 (0.08)	47.9 (0.10)	37.5 (0.07)	75.2 (0.06)	**52.8** (7.98)
		Spruce	155 (0.11)	131.7 (0.16)	149 (0.08)	102 (0.07)	**134** (11.84)
Living belowground	Stump + root	Birch	18.6 (0.03)	18.5 (0.04)	14.9 (0.03)	29.0 (0.02)	**20.2** (3.05)
		Spruce	46.2 (0.03)	45.9 (0.06)	45.6 (0.02)	34.1 (0.02)	**43.0** (2.94)
Total C stock	Living biomass	Birch	69.0 (0.11)	66.5 (0.14)	52.4 (0.10)	104 (0.07)	**73.0** (11.02)
		Spruce	201 (0.14)	178 (0.22)	194 (0.10)	136 (0.09)	**177** (14.57)
Net C capture	Living biomass	Spruce	62.8 (7.17)	44.7 (25.09)	89.3 (28.87)	−72.5 (30.06)	31.1 (35.73)
Dead wood above- and belowground	Standing	Birch	2.06 (0.02)	3.75 (0.08)	2.63 (0.22)	5.04 (0.070)	3.37 (0.66)
		Spruce	4.53 (0.11)	2.97 (0.01)	3.96 (0.01)	5.43 (0.04)	4.23 (0.52)
	Downed	Birch	0.60 (0.01)	1.19 (0.03)	0.03 (0.00)	1.57 (0.00)	0.85 (0.34)
		Spruce	1.02 (0.02)	1.59 (0.02)	2.63 (0.00)	2.11 (0.01)	1.84 (0.35)
	Stump+root	Birch	1.26 (0.03)	0.00 (0.00)	0.10 (0.01)	0.48 (0.01)	0.46 (0.29)
		Spruce	5.65 (0.03)	0.19 (0.05)	8.70 (0.03)	0.66 (0.02)	3.80 (2.05)
	Total	Birch	3.92 (0.06)	4.94 (0.11)	2.76 (0.23)	7.09 (0.09)	4.68 (0.92)
		Spruce	11.2 (0.16)	4.75 (0.08)	15.3 (0.05)	8.20 (0.06)	9.86 (2.24)
N stock (kg/ha)							
Living aboveground	Stem	Birch	132 (0.21)	121 (0.23)	93 (0.19)	191 (0.14)	**134** (20.72)
		Spruce	436 (0.31)	351 (0.44)	412 (0.22)	267 (0.18)	**367** (37.65)
	Crown	Birch	190 (0.32)	199 (0.42)	171 (0.29)	316 (0.22)	**219** (32.96)
		Spruce	471 (0.29)	487 (0.56)	488 (0.22)	400 (0.25)	**462** (20.89)
	Total	Birch	322 (0.53)	320 (0.66)	263 (0.48)	508 (0.36)	**353** (35.17)
		Spruce	907 (0.59)	838 (1.01)	900 (0.45)	667 (0.43)	**828** (55.83)
Living belowground	Stump + root	Birch	326 (0.50)	325 (0.67)	258 (0.50)	507 (0.36)	354 (53.39)
		Spruce	527 (0.36)	529 (0.67)	526 (0.28)	391 (0.27)	493 (34.18)
Total N stock	Living biomass	Birch	649 (1.01)	645 (1.31)	521 (0.98)	1014 (0.71)	**707** (106.53)
		Spruce	1435 (0.95)	1367 (1.67)	1426 (0.73)	1058 (0.70)	**1322** (89.09)

† Significant differences ($P < 0.05$) between tree species in bold.
‡ Crown = needles/leaf + twigs + branches.

60-yr stands at the locations Jølster I and Ørsta, a natural thinning of suppressed spruce trees was accounted for as downed trees. The stands contained a varying number of old stumps in different decay classes. The number of stumps was higher and the average remaining biomass in the decaying stumps lower in spruce stands compared to birch (Appendix S1: Table S1). Decaying stumps were also more prevalent in the spruce stands at Jølster I and Ørsta compared to the other birch and spruce stands. The estimated total original stump and root biomass before decay varied between 1.0 and 37.2 Mg/ha in the spruce stands and 0.0 to 7.3 Mg/ha in the birch stands (Appendix S1: Table S1).

There were no significant differences between tree species for total C stocks in dead wood, nor for the different dead wood components (Table 3).

Understory vegetation

Cover of understory vegetation species groups.— The mean cover of ligneous plants as well as herbs, ferns, and graminoids were higher in the birch stands relative to the spruce stands at all locations (Fig. 1), while the mean cover of the two groups varied between birch stand locations. In the spruce stands, small trees as well as herbs, ferns, and graminoids had generally very low cover at all locations, while dwarf shrubs were

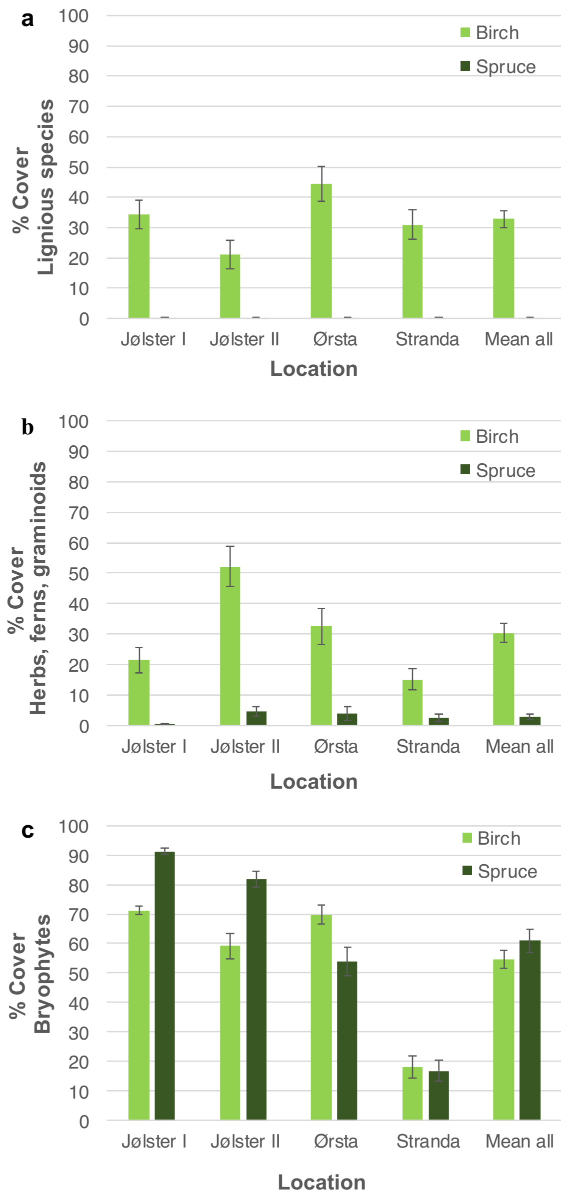

Fig. 1. Mean cover (%) of the species groups ligneous plants (dwarf shrubs + small trees) (a), herbs + ferns + graminoids (b), and bryophytes (c) in paired stands of native birch and planted Norway spruce at four locations in Western Norway. $n = 18$ subplots in each stand type at each location.

basically absent. The cover of bryophytes in the north facing spruce stands at Jølster I and Jølster II was considerably higher than in the birch stands at these locations, and it was higher than in the south-facing spruce stand at Stranda (Fig. 1).

C and N stocks in understory vegetation biomass.—The total C and N stocks of the aboveground biomass of understory vegetation were significantly higher in the birch than in the spruce stands (Table 4, $P < 0.0001$, Appendix S1: Table S5). In line with this, the C and N stocks of the two groups ligneous plants and herbs, ferns, and graminoids were significantly higher in birch relative to spruce stands (Table 4, $P = 0.0001$ and 0.0008, respectively, Appendix S1: Table S5). The C and N stocks of bryophytes varied between locations by a factor of 6 in the birch stands and a factor of 16 in the spruce stands, being highest in the spruce stand at Jølster I (Table 4). Altogether, the mean C stock of the understory vegetation in the birch stands was more than twice that of the spruce stands.

Soil

Soil C and N stocks.—The SOC stock in the LFH horizon was significantly higher in the spruce stands relative to the birch stands (Fig. 2a; $P = 0.005$), which corresponded to a significantly higher thickness and C concentration (Table 5; $P < 0.0001$). The BD in the LFH horizon was on the other hand significantly higher in the birch stands (Table 5; $P < 0.0001$). In the mineral soil, there was no significant difference in C concentration, BD or stone content between the two stand types (Table 5). No significant effect of the tree species change was found in the total SOC and N stocks down to 1 m soil depth (Table 6, Appendix S1: Table S6). Both the SOC and N stocks decreased significantly with increasing soil depth down to 30 cm in both stand types (Fig. 2a, b). A significant interaction between tree species and soil layer was found in the SOC stocks ($P = 0.006$, Appendix S1: Table S6), based on the significantly higher SOC accumulation in the LFH horizon in spruce relative to birch stands. A suggested loss of SOC in the mineral soil following the tree species change at all locations except Jølster II was not significant (Appendix S1: Fig. S3a), nor was the mean overall loss in the N stocks in spruce relative to birch significant (Appendix S1: Fig. S3b). However, the relative difference in accumulation and loss between the stand types was more pronounced in the older stands at Jølster I and Ørsta (60 yr) compared to Jølster II and Stranda (45 yr) (Appendix S1: Fig. S3b).

Table 4. Carbon (C) and nitrogen (N) stocks (mean, with SE in parentheses) in aboveground living biomass of plant species groups and total aboveground understory vegetation in stands of native birch and planted Norway spruce at four locations in Western Norway.

Plant species group	Tree species	Jølster I	Jølster II	Ørsta	Stranda	Average
C stock (Mg/ha)						
Ligneous plants	Birch	0.57 (0.13)	0.36 (0.09)	1.58 (0.37)	0.57 (0.13)	**0.77**† (0.09)
	Spruce	<0.01 (<0.01)	<0.01 (<0.01)	<0.01 (<0.01)	<0.01 (<0.01)	**<0.01** (<0.01)
Herbs, ferns, graminoids	Birch	0.17 (0.04)	0.44 (0.10)	0.29 (0.07)	0.13 (0.03)	**0.26** (0.03)
	Spruce	<0.01 (<0.01)	0.04 (0.01)	0.02 (<0.01)	<0.01 (<0.01)	**0.02** (<0.01)
Bryophytes	Birch	1.15 (0.27)	0.64 (0.15)	0.68 (0.16)	0.19 (0.04)	0.67 (0.08)
	Spruce	1.62 (0.38)	0.91 (0.21)	0.50 (0.12)	0.10 (0.02)	0.78 (0.09)
Total	Birch	1.89 (0.45)	1.44 (0.34)	2.55 (0.60)	0.89 (0.21)	**1.69** (0.20)
	Spruce	1.62 (0.38)	0.94 (0.22)	0.52 (0.12)	0.11 (0.02)	**0.80** (0.09)
N stock (kg/ha)						
Ligneous plants	Birch	12.7 (3.0)	8.10 (1.91)	35.4 (8.3)	12.8 (3.0)	**17.2** (2.0)
	Spruce	<0.01 (<0.01)	0.02 (<0.01)	0.01 (<0.01)	0.01 (<0.01)	**0.01** (<0.01)
Herbs, ferns, graminoids	Birch	5.94 (1.40)	14.6 (3.4)	9.84 (2.32)	4.27 (1.01)	**8.67** (1.02)
	Spruce	0.05 (0.01)	1.24 (0.29)	0.56 (0.13)	0.16 (0.04)	**0.50** (0.06)
Bryophytes	Birch	17.9 (4.2)	9.93 (2.34)	10.1 (2.4)	2.94 (0.69)	10.2 (1.2)
	Spruce	25.1 (5.9)	14.1 (3.3)	7.32 (1.73)	1.56 (0.37)	12.0 (1.4)
Total	Birch	36.5 (8.6)	32.7 (7.7)	55.4 (13.0)	20.0 (4.7)	**36.1** (4.3)
	Spruce	25.2 (5.9)	15.3 (3.6)	7.89 (1.86)	1.73 (0.41)	**12.52** (1.48)

† Significant differences ($P < 0.05$) between tree species in bold.

*Soil chemistry.—*There was a significant effect of tree species change, as well as a significant interaction between tree species and soil layer for C and N concentrations, C/N, exchangeable acidity, BS, and the exchangeable elements Ca, Mg, and S (Table 5, Appendix S1: Table S6). Further, a significant interaction between tree species and layer was found for CEC, K, Mn, Na, and P, whereas exchangeable Fe showed only a significant tree species effect (Table 5, Appendix S1: Table S6). In birch, significantly higher concentrations of N were found in the LFH horizon, and of Ca and Mg in the M1 layer. In spruce, the LFH horizon showed significantly higher C/N and concentrations of C, Na, K, and exchangeable acidity, whereas significantly lowers BS was found in the M1 layer relative to birch (Fig. 3, Table 5). As observed for SOC and N stocks, a distinct depth distribution was found, showing decreasing concentrations with increasing soil depth, as illustrated by BS, exchangeable Ca, and exchangeable acidity (Fig. 3a–c). C/N differed from this trend, with no significant difference between layers and soil depths down to 30 cm in the birch stand, while the C/N in the LFH horizon of the spruce stands was significantly higher relative to the mineral soil layers (Fig. 3d). Effects of tree species change on microelements are given in the Appendix S1: Tables S7, S8.

Ecosystem C and N stocks, accumulation, and net C capture

There was a significant increase in the total ecosystem C stock following the tree species change ($P = 0.003$; Appendix S1: Table S6). The total C stock varied between 208 (±7) and 357 (±22) Mg/ha with the smallest stock in birch and the largest in spruce, both found at the location Ørsta (Fig. 4a). The ecosystem N stock did not differ significantly between birch and spruce stands and varied between 6703 (±99) and 9211 (±439) kg/ha where both maximum and minimum values were found in the birch stands (Fig. 4b).

The estimated ecosystem C accumulation after the spruce planting (ΔC) varied between 36 (±9) and 149 (±16) Mg/ha (Fig. 5a). However, when including the C debt from the original birch in the spruce stand, the net ecosystem C capture varied from a net loss of 69 (±25) to a net accumulation of 97 (±18) Mg/ha (Fig. 5b). The annual net ecosystem C capture at Ørsta, Jølster I, and Jølster II amounted to 1.6 (±0.3), 1.1 (±0.3), and 1.1 (±0.4) $Mg \cdot ha^{-1} \cdot yr^{-1}$, respectively, whereas at

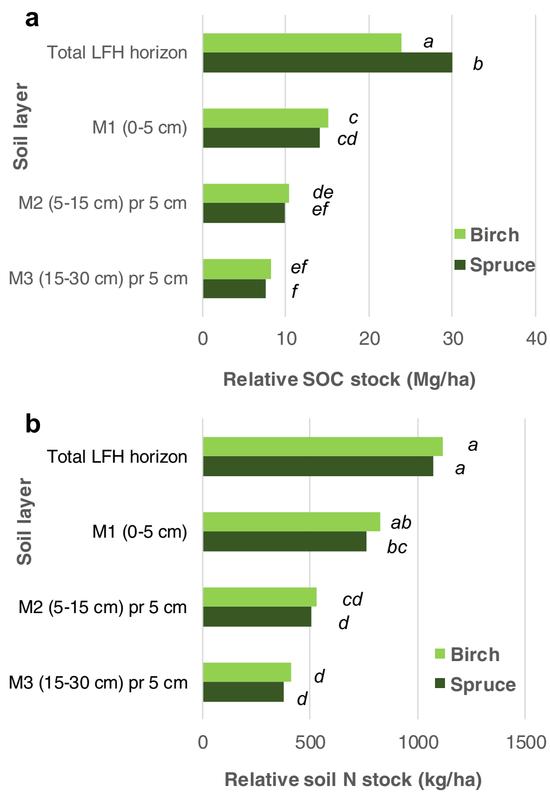

Fig. 2. Relative stocks of soil organic carbon (SOC) (a) and nitrogen (N) (b) in the LFH layer and three mineral soil layers (M1 [0–5 cm], M2 [5–15 cm], and M3 [15–30 cm]) in paired stands of native birch and planted Norway spruce at four locations in Western Norway. The relative stocks are based on the same thickness (5 cm) in the mineral soil. Letters in italics indicate significant differences between tree species and soil layers ($P < 0.05$).

Stranda the annual net loss amounted to 1.5 (±0.7) Mg·ha^{-1}·yr^{-1} over the current lifespan. For ecosystem N stocks, the difference between the tree species (ΔN) varied from a loss of 271 (±185) kg/ha (Stranda) to an accumulation of 612 (±297) kg/ha (Jølster II) (Fig. 5c), which equals an annual loss or accumulation of 6 and 14 kg·ha^{-1}·yr^{-1}, respectively.

Ecosystem correlations and ratios

Relationships between C and N stocks in different ecosystem compartments.—The C stock in living vegetation amounted to 31% (±1.9) and 52% (±1.7) of the total ecosystem C stock in the birch and spruce stands, respectively, whereas the SOC stock was 66% (±1.9) and 45% (±1.8) of the total ecosystem C stock, respectively. For both tree species, the major part of the ecosystem N stock was found in the soil, amounting to 90% (±0.7) and 83% (±1.2) in the birch and spruce stands, respectively.

The ratio SOC: C stock in living tree biomass was generally lower in the spruce stands compared to the birch stands, varying from 0.9 to 2.1 in spruce and from 1.1 to 4.9 in birch stands, with a mean of 1.4 (±0.1) and 3.3 (±0.4), respectively. The mean ratio dead wood: total ecosystem C stock for both stand types combined was 2.0 (±0.3).

The total ecosystem C stock showed a strong positive correlation with the C stock in living tree biomass for both tree species (Fig. 6a). A significant positive correlation was also found between the total ecosystem C stock and the SOC stock down to 30 cm soil depth for the birch stands, whereas a significant negative correlation was found for the spruce stands (Fig. 6b). For spruce, there was also a significant negative correlation between the C stocks in living tree biomass and the mineral SOC stock (Fig. 6c). For birch stands, a significant negative correlation was found between the C stocks in living tree biomass and the understory vegetation (Fig. 6d).

The significant correlations between the total ecosystem C stock and the ecosystem N stock were positive in birch and negative in spruce (Fig. 7a). As expected, the ecosystem N stock showed a strong positive correlation with the total soil N stock (1 m soil depth; Fig. 7b). In the spruce stands, the N stock in the mineral soil (0–30 cm) was negatively correlated with the N stock in living trees (Fig. 7c) as well as with the understory vegetation C and N stocks ($P < 0.05$, Appendix S1: Table S9). In the birch stand, the LFH SOC stock was significantly and negatively correlated with understory vegetation N stocks, and for spruce, this relationship was close to significant (Fig. 7d). Additionally, significant negative correlations were found between the understory C and N stocks of the spruce stands and the SOC and N stocks in the combined LFH + mineral soil layer (LFH-30 cm) ($P < 0.05$, Appendix S1: Table S9).

For dead wood, there was a significant negative correlation between the C stocks in downed

Table 5. Soil characteristics (mean, with SE in parentheses) in the forest floor (LFH) and three mineral soil layers in paired stands of native birch and planted Norway spruce in Western Norway.

	LFH		M1 (0–5 cm)		M2 (5–15 cm)		M3 (15–30 cm)	
Soil characteristics	Birch	Spruce	Birch	Spruce	Birch	Spruce	Birch	Spruce
BD (g/cm^3)	**0.15** (0.01)	**0.11** (0.01)	0.37 (0.03)	0.40 (0.03)	0.52 (0.03)	0.50 (0.03)	0.48 (0.02)	0.46 (0.03)
Stone volume (%)	0.00 (0.00)	0.00 (0.00)	25.9 (1.8)	28.4 (2.6)	25.9 (1.8)	28.4 (2.6)	25.9 (1.8)	28.4 (2.6)
Thickness (cm)	**3.96**† (0.28)	**5.73** (0.38)	5.0	5.0	10.0	10.0	15.0	15.0
C (%)	**40.9** (0.8)	**47.9** (0.7)	12.4 (1.6)	10.9 (1.3)	5.85 (0.66)	5.93 (0.66)	4.79 (0.43)	4.96 (0.48)
N (%)	**1.88** (0.07)	**1.69** (0.05)	0.69 (0.11)	0.60 (0.09)	0.30 (0.04)	0.30 (0.04)	0.24 (0.02)	0.25 (0.03)
pH	4.41 (0.06)	4.20 (0.07)	4.56 (0.07)	4.45 (0.08)	4.95 (0.04)	4.78 (0.05)	4.97 (0.02)	4.85 (0.05)
Fe (mmol/kg)	0.63 (0.08)	0.82 (0.10)	0.67 (0.09)	1.07 (0.16)	0.60 (0.10)	0.71 (0.14)	0.33 (0.04)	0.34 (0.06)
Al (mmol/kg)	18.6 (84.7)	24.8 (4.9)	14.6 (2.6)	19.2 (2.6)	12.9 (1.0)	14.4 (0.8)	12.3 (0.7)	12.5 (0.9)
CEC	342 (7)	361 (8)	93.8 (10.0)	84.0 (8.9)	48.8 (3.2)	50.6 (3.2)	43.4 (2.8)	43.2 (3.4)
K (mmol/kg)	**20.6** (0.9)	**24.8** (1.2)	4.50 (0.42)	3.40 (0.35)	1.21 (0.14)	1.11 (0.14)	0.83 (0.12)	0.74 (0.14)
Mg (mmol/kg)	38.9 (1.8)	36.5 (1.3)	**6.68** (0.69)	**3.51** (0.41)	1.16 (0.09)	0.88 (0.11)	0.61 (0.07)	0.56 (0.10)
Mn (mmol/kg)	3.24 (0,48)	3.24 (0.97)	0.43 (0.17)	0.22 (0.13)	0.10 (0.05)	0.14 (0.08)	0.08 (0.03)	0.16 (0.06)
Na (mmol/kg)	**7.00** (0.52)	**10.6** (0.6)	2.18 (0.17)	2.04 (0.16)	1.04 (0.09)	1.07 (0.11)	0.94 (0.11)	0.98 (0.12)
P (mmol/kg)	3.80 (0.84)	4.22 (0.91)	0.30 (0.06)	0.15 (0.03)	0.04 (0.00)	0.04 (0.00)	0.02 (0.00)	0.03 (0.00)
S (mmol/kg)	**3.14** (0.09)	**3.76** (0.14)	1.21 (0.17)	1.18 (0.16)	0.47 (0.06)	0.61 (0.08)	0.40 (0.04)	0.49 (0.06)

Note: Mean values across four locations.
† Significant differences ($P < 0.05$) between tree species within layers in bold.

Table 6. Soil organic carbon (SOC) and nitrogen (N) stocks (mean, with SE in parentheses) in the LFH layer, and two mineral soil depths as well as the total stocks down to 1 m in paired stands of native birch and planted Norway spruce at four locations in Western Norway.

Soil layer	Tree species	Jølster I	Jølster II	Ørsta	Stranda	Average
C stock (Mg/ha)						
LFH	Birch	23.1 (4.7)	17.6 (0.8)	19.8 (2.4)	35.3 (1.0)	**23.9**† (3.9)
	Spruce	30.2 (0.8)	20.7 (1.0)	28.8 (3.6)	40.3 (4.1)	**30.0** (4.0)
Mineral 0–30 cm	Birch	54.6 (2.5)	53.9 (2.8)	64.0 (6.3)	68.6 (4.3)	60.3 (3.6)
	Spruce	49.0 (6.4)	56.1 (3.5)	54.8 (9.6)	66.9 (3.4)	56.7 (3.7)
Mineral 30–100 cm	Birch	63.5 (9.1)	81.5 (6.7)	70.4 (12.1)	47.4 (11.6)	65.7 (7.1)
	Spruce	63.5 (9.1)	81.5 (6.7)	70.4 (12.1)	47.4 (11.6)	65.7 (7.1)
Total LFH-100 cm	Birch	141	153	154	151	149 (3)
	Spruce	143	158	154	155	151 (3)
N stock (kg/ha)						
LFH	Birch	977 (190)	801 (13)	892 (145)	1809 (163)	1120 (232)
	Spruce	1027 (87)	749 (57)	933 (160)	1575 (117)	1071 (178)
Mineral 0–30 cm	Birch	2474 (104)	2803 (208)	3160 (346)	4039 (434)	3119 (337)
	Spruce	2211 (372)	2783 (316)	2629 (401)	3977 (249)	2900 (379)
Mineral 30–100 cm	Birch	2523 (248)	3611 (61)	3242 (1042)	2266 (601)	2935 (312)
	Spruce	2523 (248)	3611 (61)	3242 (1042)	2266 (601)	2935 (312)
Total LFH-100 cm	Birch	5973	7215	7294	8114	7096 (286)
	Spruce	5760	7142	6804	7819	6828 (269)

† Significant differences ($P < 0.05$) between tree species in bold.

dead wood and stumps decay classes 1–3 and understory vegetation for both the spruce and birch (Fig. 8a). A significant positive correlation was, on the other hand, found between the C stocks in the standing dead wood and the LFH horizon of spruce stands (Fig. 8b).

Relationships between C and N stocks and soil chemistry.—The C stock in living tree biomass of the birch stands was significantly negatively correlated with pH in both the LFH and the mineral soil layers (0–30 cm) (Fig. 9a, b), whereas a significant positive correlation was found between the

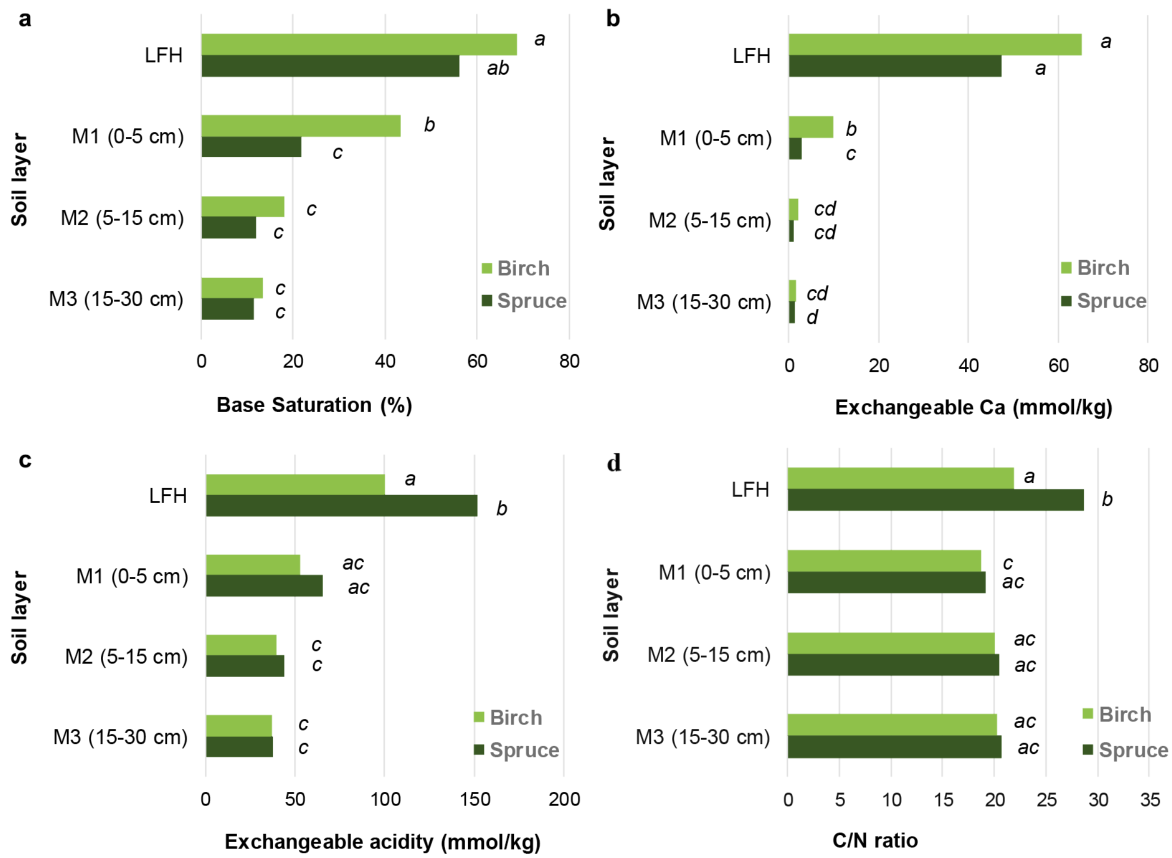

Fig. 3. Depth and species related differences in base saturation (a), exchangeable Ca (b), exchangeable acidity (c) and C/N ratio (d) in the LFH layer and three mineral soil layers (M1, M2 and M3) in paired stands of native birch and planted Norway spruce at four locations in Western Norway. Letters in italics show significant differences ($P < 0.05$) between tree species and layers.

C stock in living tree biomass and the BS and exchangeable Ca concentrations of the LFH horizon (Fig. 9c, d). In the spruce stands, a significant negative correlation was found between the C and N stocks in living tree biomass and the mineral soil exchangeable Ca and Mg concentration, and BS (Fig. 10a–c).

The understory vegetation C and N stocks in the spruce stands were positively correlated with aspect (Appendix S1: Table S7), and predominantly significantly negatively correlated to most of the element concentrations, especially those in the mineral soil (Appendix S1: Tables S10–S13).

The SOC stock in the LFH horizon of the spruce stands was negatively correlated with exchangeable P concentrations in the mineral soil (Fig. 10d) and with the mineral soil exchangeable Fe concentrations (Appendix S1: Table S11). On the other hand, in the spruce stands the SOC stock in the LFH horizon was positively correlated with BD, CEC, and the exchangeable Si concentration in the LFH horizon, as well as with the pH in the mineral soil (Appendix S1: Tables S10, S11).

In both stand types, a positive correlation was found between the mineral soil SOC stock and exchangeable acidity, and between the mineral soil SOC stocks and most of the mineral soil exchangeable element concentrations (Appendix S1: Table S11). In the birch stands, this positive correlation was also found for the mineral soil N stocks (Appendix S1: Table S13). Predominantly negative correlations were, on the other hand, found between most of the exchangeable element concentrations in the mineral soil and aspect for both stand types (Appendix S1: Table S11).

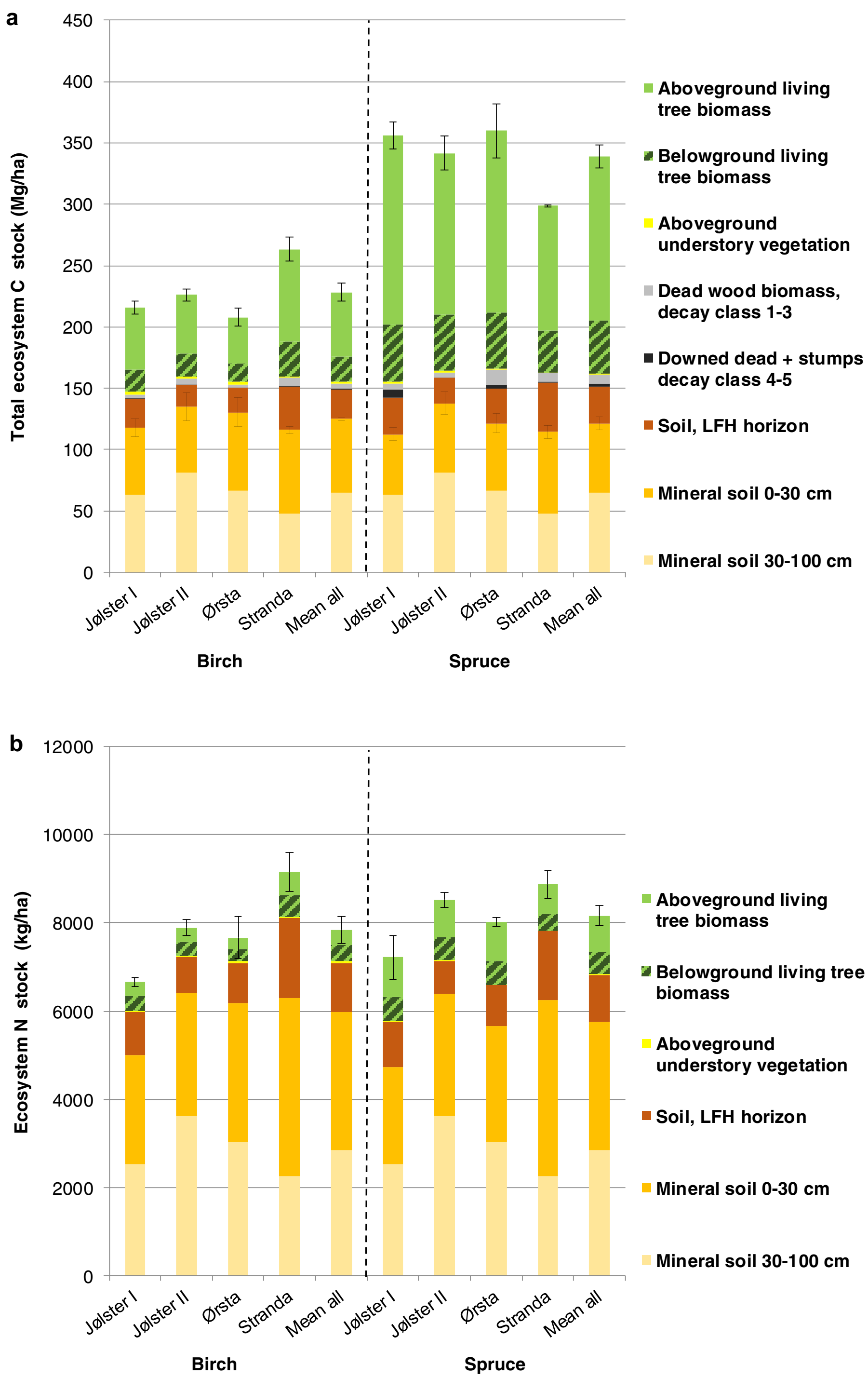

Fig. 4. Total ecosystem C stocks (a), and ecosystem N stocks excluding dead wood (b), for paired stands of native birch and planted Norway spruce at four locations in Western Norway, as well as mean values across locations. (Error bars = SE for total stocks).

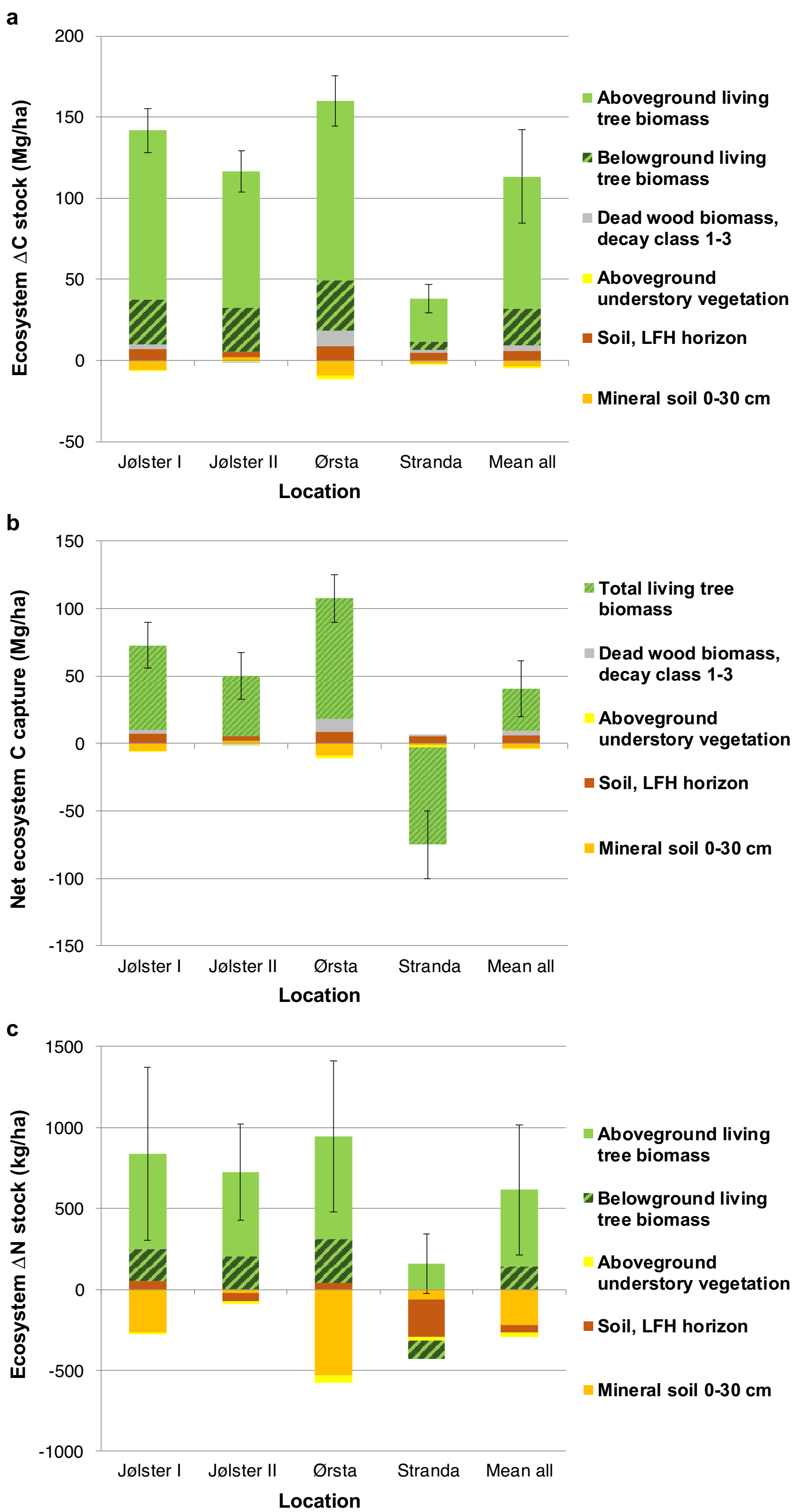

Fig. 5. Relative differences (Δ) in ecosystem C stocks in birch and spruce (a), net ecosystem C capture,

(Fig. 5. *Continued*)
including estimated C debt from the original birch in the spruce stand (b), and relative differences (Δ) in ecosystem N stocks excluding dead wood (c) based on paired stands of native birch and planted Norway spruce (Error bars = SE for total stocks). The period for accumulation/loss was 45 (Jølster II, Stranda) and 60 yr (Jølster I, Ørsta).

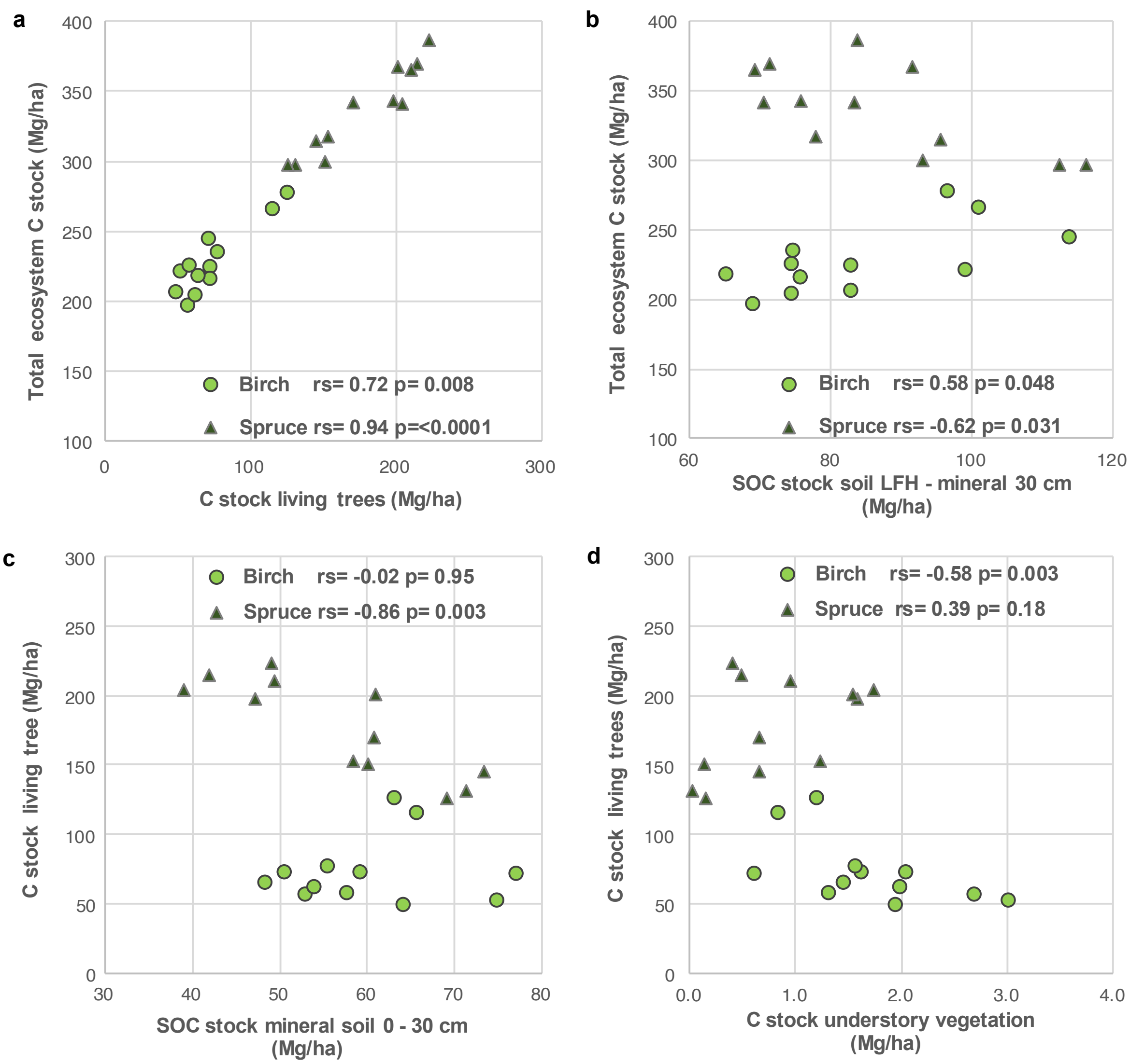

Fig. 6. Correlations between ecosystem C stocks, and the C stocks in living tree biomass, the LFH horizon, the mineral soil, and the understory vegetation. Spearman's rank correlation coefficient (rs) and *P*-values from paired stands of native birch and planted Norway spruce in Western Norway.

Discussion

Ecosystem C and N stocks and interactions

*Trees.—*C accumulation in living trees was the predominant factor that affected the total ecosystem C stocks of the two forest systems. As hypothesized, the change from native birch to planted Norway spruce led to an increase in the C stock of the living tree biomass. The increase is potentially a combination of a species effect and a management effect related to tree planting. Results from national and international studies

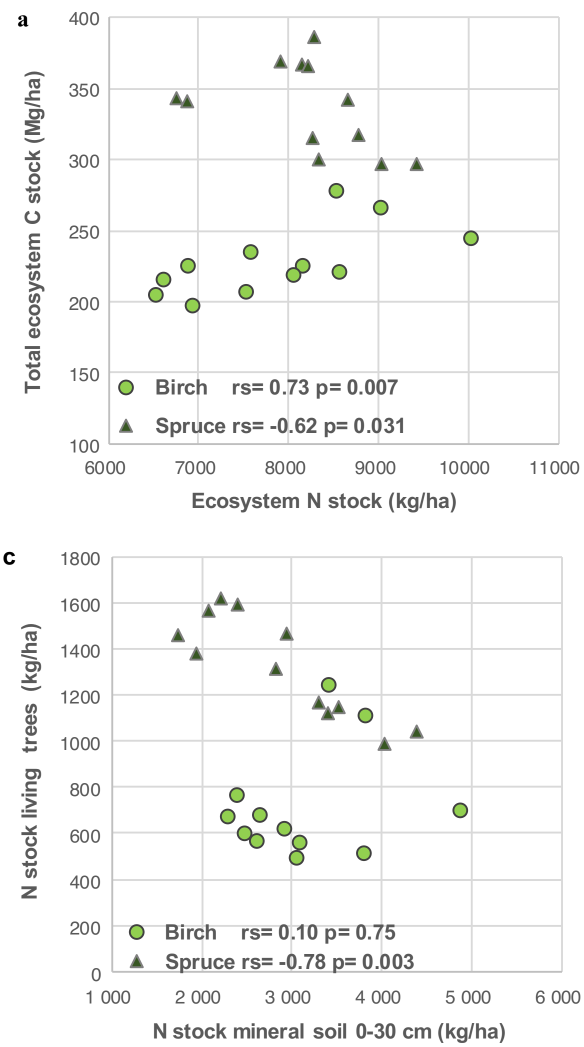

Fig. 7. Correlations between ecosystem C and N stocks, N stocks in living tree biomass, LFH horizon and mineral soil, and understory vegetation. Spearman's rank correlation coefficient (rs) and p-values from paired stands of native birch and planted Norway spruce in Western Norway.

comparing C stocks in planted stands of birch and Norway spruce are contrasting. The total tree biomass was found to be lower in Norway spruce relative to downy birch (*Betula pubescens*) in 40-yr-old stands in SE Norway (Andreassen et al. 2017), and relative to silver birch (*Betula pendula* Roth) in 27-yr-old stands in NE Sweden (Alriksson and Eriksson 1998). On the other hand, significantly higher biomass and C stock was found in 50-yr-old Norway spruce relative to birch in a common garden experiment in southern Sweden (Hansson et al. 2013). The basal area (BA) of the spruce stands in the latter study was almost twice that of the birch stands (Hansson et al. 2011). Higher BA was also found in 30-yr-old Norway spruce relative to birch in central Finland (Smolander et al. 2005), related to the higher stand density in spruce. In the current study, the average BA in birch relative to spruce was 49% across all locations, with a range from 32% at Ørsta to 83% at Stranda. The difference in stand density between the birch and spruce stands was the highest and lowest among the locations.

Stranda had the smallest C stock in living tree biomass among the spruce stands but the largest

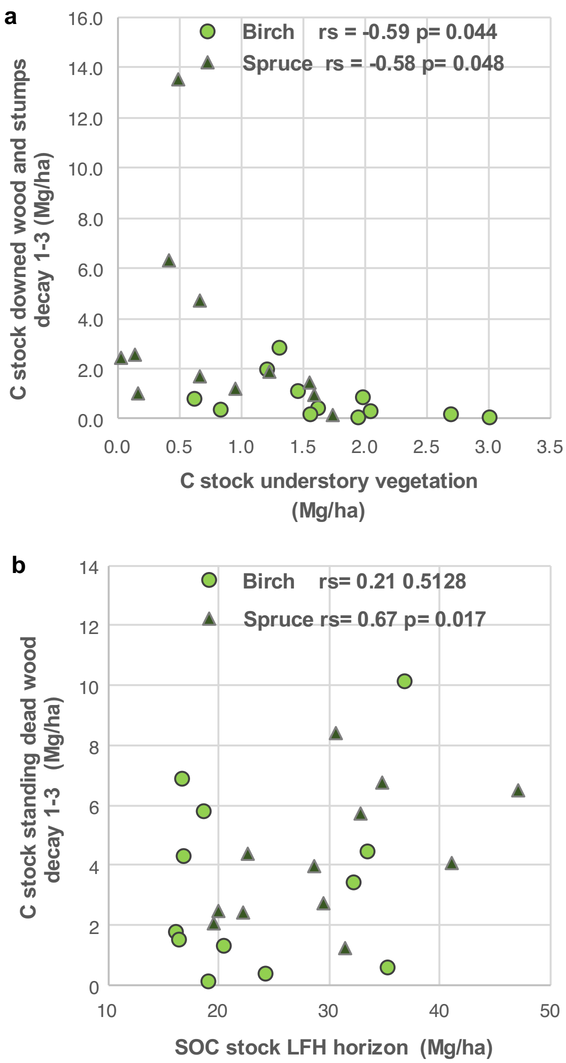

Fig. 8. Correlations between C stocks in downed dead wood and stumps, and understory vegetation (a) and in standing dead wood and the LFH horizon (b). Decay refers to decay classes, where 1 is the category of the least decomposed wood of a total of five classes. Spearman's rank correlation coefficient (rs) and *P*-values from paired stands of native birch and planted Norway spruce in Western Norway.

C stock among the birch stands, whereas Ørsta had the second largest C stock among the spruce stands and the smallest C stocks among the birch stands. Increasing stand age generally increase the average carbon stock in stands (Raymer et al. 2011, Lundmark et al. 2018). Thus, stand age may partly explain the differences in the living biomass C stock between the locations, as a higher C stock was observed in the two 60-yr spruce stands (Ørsta, Jølster I) relative to the two 45-yr stands (Stranda, Jølster II). Additionally, site specific factors may affect the tree growth and thus the C accumulation potential of the planted Norway spruce, as well as the birch stands. The general climatic data suggest that Stranda had the lowest mean annual temperature (MAT) and temperature sum during the growing season (GDD sum) among all locations. The mean annual soil temperatures at the locations were, on the other hand, relatively similar, which may potentially be due to a combination of the higher elevation and the south-facing aspect at Stranda. Still, the higher elevation may potentially present more harsh climatic conditions during periods when the incoming radiation is low. In Norway spruce, effects of temperature on C accumulation have been closely connected to nutrient availability, especially N (Sigurdsson et al. 2013). Soils at Stranda had the highest N stocks of all locations, and thus, N availability does not seem to explain the low relative C accumulation in spruce. Differences in provenances and their adaptation to local climate conditions may be decisive for the C accumulation (Milesi et al. 2019, Zeltins et al. 2019), and although differences in provenance were observed, only Ørsta had this information recorded (Schwarzwald). Thus, a combination of differences consisting of BA/stand density, stand age and climate may then explain at least parts of the absolute and relative differences in the C and N stocks in living tree biomass following the tree species change.

The relative difference in living biomass C stocks following the tree species change was in the lower end of the estimates given by The Norwegian Environmental Agency (2013), which amounted to 137–183 Mg/ha in 90-yr-old stands, as opposed to the 32–142 Mg/ha in the current study. Differences in stand age partly explain this divergence. Additionally, the biomass models for both birch and spruce differ between the current study and that of The Norwegian Environmental Agency (2013). Uncertainties related to biomass models may also affect the relative C accumulation estimates between birch and spruce. Whereas the biomass model for birch have been developed and validated for Norwegian birch

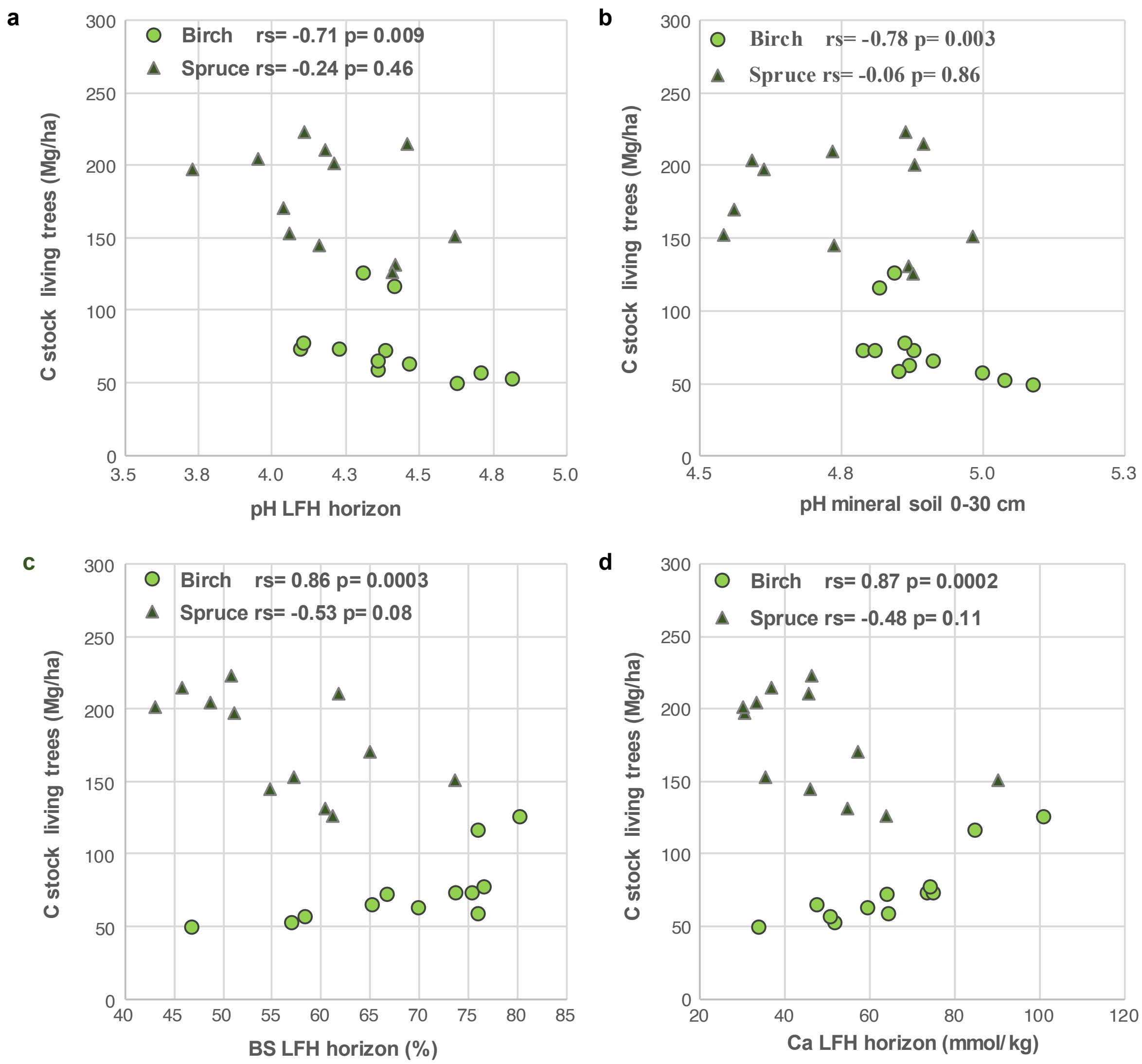

Fig. 9. Correlations between C stock in living tree biomass and soil pH in the LFH horizon and mineral soil (0–30 cm), as well as with base saturation (BS) and exchangeable Ca in the LFH horizon. Spearman rank correlation coefficients (rs) and *P*-values from paired stands of native birch and planted Norway spruce in Western Norway.

forests (Smith et al. 2014, 2016), the Swedish models for Norway spruce (Marklund 1988, Petersson and Ståhl 2006) are commonly used (e.g., Bright et al. 2020) in spite of limited validation for Western Norway.

The estimated climate mitigation potential of The Norwegian Environmental Agency (2013) did not take into account a potential C debt related to a CO_2 loss from the original birch stand following a tree species change. According to the local forest service, previous stand replacements in Western Norway mainly involved leaving the original birch stands on site to rot. When including this C debt, the mean annual net C capture was 24–32% of the estimated annual accumulation suggested by The Norwegian Environmental Agency (2013). At present, harvesting of spruce stands in Western Norway commonly occurs between stand age 45 and 60 yr. An increase in the rotation length, that is, the time period between two final fellings, is expected to increase the net C capture, as a

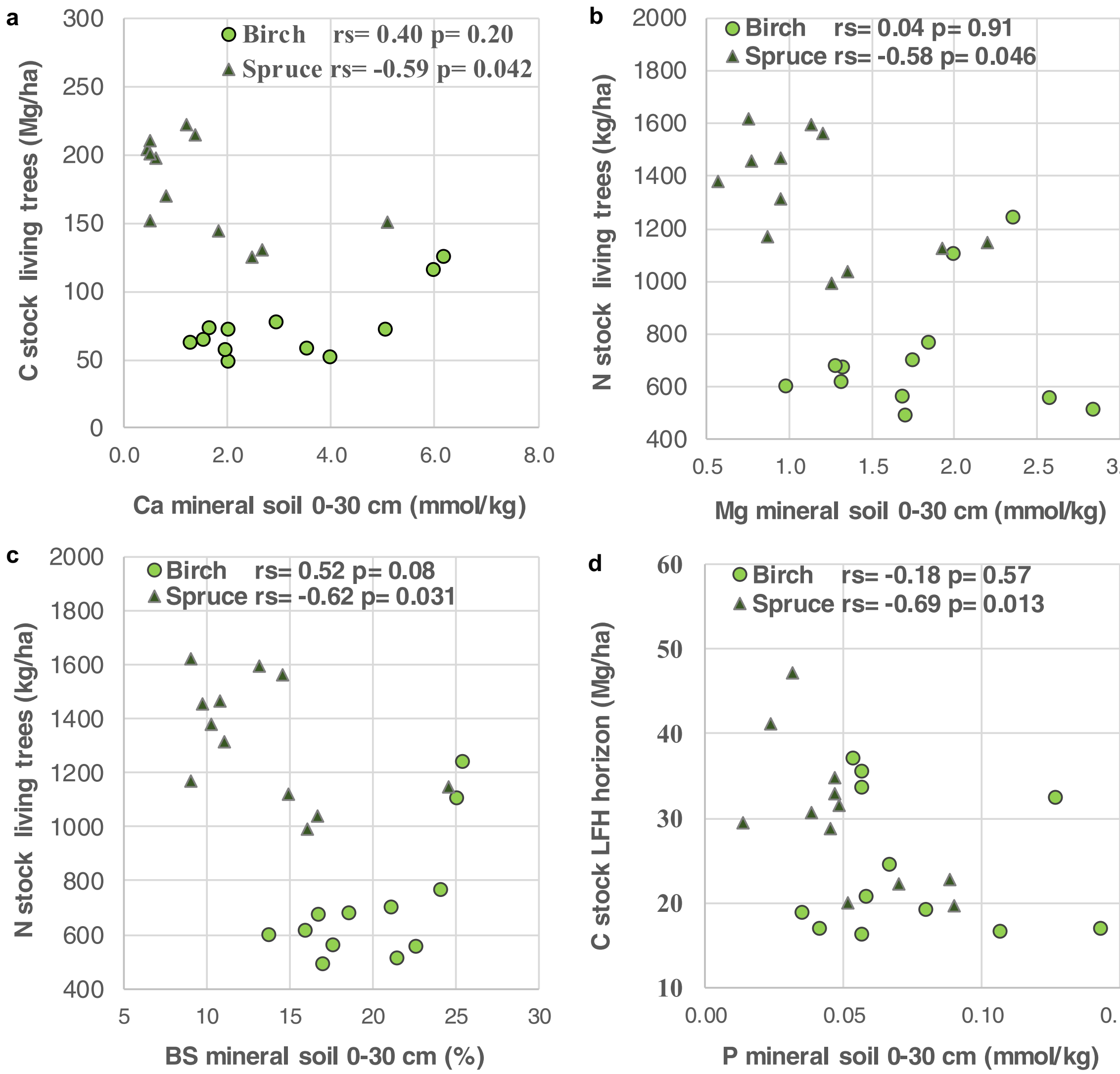

Fig. 10. Correlations between C and N stock in living tree biomass and base saturation (BS) and exchangeable Ca and Mg in the mineral soil (0–30 cm), as well as between the C stock in the LFH horizon and exchangeable P in the mineral soil (0–30 cm). Spearman rank correlation coefficients (rs) and *P*-values from paired stands of native birch and planted Norway spruce in Western Norway.

moderate increase of the rotation length from 75 to 85 yr for spruce stands on similar high site index has been suggested to increase the C stock as well as the overall climate benefit of the forest (Lundmark et al. 2018). The total effect of the mitigation strategy related to a net C capture will, however, also depend on the use of the harvested wood and the substitution effects of wood products, including firewood (ibid). A larger fraction of the accumulated C in the spruce stands may contribute to higher substitution effects due to the suggested larger C stock in the stem component relative to in birch. Despite these uncertainties, the results suggest that given the current rotation length of 45–60 yr, the net C capture in tree biomass related to tree species change may be small, and potentially negative, when the tree species change involves C debt from birch stands beyond the stand initiation stage.

Dead wood.—Dead wood has been found to play an important role for long-term storage of C in forests (Pukkala 2018), including carbon sequestration in forest soils (Blonska et al. 2019). The mean dead wood to total forest ecosystem C stock in the current study was approximately double the estimate for European boreal forests (0.9%), and one third of the average for boreal forests (6%) (Pan et al. 2011). Despite the lack of a significant difference in dead wood between the birch and spruce stands, the data suggest a considerably higher C stock in dead wood in the two 60-yr spruce stands, both compared to the two 45-yr stands and to their paired birch stands. The different decay classes of the stumps in the two 60-yr-old stand suggest thinning in the Ørsta spruce stand. Thus, a potential effect of tree species change on C stocks in the dead wood compartments may depend on stand age, management history, and potentially also on stand density.

Understory vegetation.—As hypothesized, replacing birch forest with planted Norway spruce decreased the total C and N stock as well as the coverage of the understory vegetation. The decrease was related to the species group ligneous plants and the group herbs, ferns, and graminoids, and was most likely caused by changes in the environmental conditions following the tree species change. A reduced transmission of light to the ground due to the higher tree density and canopy cover in mature planted spruce stands (Augusto et al. 2002) results in more shady conditions than the more open birch forests, which strongly affected the abundance of dwarf shrubs, herbs, ferns, and graminoids. The significantly lower abundances of species belonging to these plant groups in the spruce relative to the birch stands concur with results reported in previous studies (Smolander and Kitunen 2002, Sigurdsson et al. 2005, Hansson et al. 2013), as well as studies comparing Norway spruce and deciduous forests (Augusto et al. 2002). Also in the birch stands, effects of tree density were reflected in the negative correlations between the C and N stocks in living tree biomass and understory vegetation. The significant negative correlation between the understory vegetation and the C stocks in downed dead wood and stumps decay classes 1–3 in both stand types may reflect a higher input of dead branches and tops to the ground in the denser stands relative to the more open stands with abundant understory vegetation.

The low contribution of understory vegetation to the total ecosystem C and N stocks was as expected (Nilsson and Wardle 2005, Muukkonen et al. 2006). However, despite the low stocks, the high annual turnover rate of understory vegetation may create a substantial litter flux rich in C, N, and other nutrients (Nilsson and Wardle 2005). The relative difference in the understory vegetation C stock between the birch and spruce stands was considerably larger in the current study than what was observed by Hansson et al. (2011). Their results, which showed a similar overall C input from aboveground tree and understory litter in the birch and spruce stands, was mainly related to differences in the understory vegetation species groups (ibid.).

Bryophytes contributed to 37% and 85% of the total understory vegetation C stock in the birch and spruce stands, respectively. The significant correlation between understory vegetation C stock and aspect in the spruce stands reflects the influence of topography on the establishment and long-term survival of bryophytes, where northern aspects allow more extensive bryophyte growth even in dark and dense spruce stands due to the more humid conditions (Økland 1996, Smith et al. 2017). The presence of only a few large dominant bryophyte species in the dense north faced spruce stands differed from the generally higher number of bryophyte species found in native old unmanaged Norwegian spruce forests (Økland 1996). The most dominant bryophyte species in the current study was the pleurocarpous moss *Hylocomium splendens,* which made up a thick and extensive mat in the north faced spruce stands. The fixation of atmospheric N_2 by cyanobacteria associated with this and other feather mosses (DeLuca et al. 2002, Lindo et al. 2013) may have contributed to the positive correlation between the understory N stock and aspect in the spruce stands. On the other hand, the negative correlation between the C and N stocks in the understory vegetation and the mineral soil as well as the combined LFH + mineral soil N stocks in the spruce stands, indicate that the underlying factors and processes are complex.

While the suggested relationship between the understory vegetation C stock and the LFH SOC stock was similar in the two forest types, they may reflect different processes. In the spruce stands this may be related to the density of the bryophyte mat, where a dense cover prevents needle litter from penetrating into the decomposition zone of the LFH layer, and thus affect the litter mass as well as the nutrient fluxes to the soil (Bonnevie-Svendsen and Gjems 1956). Additionally, bryophyte mats increase moisture retention and affect the insulation against temperature fluctuations in the upper soil layers (Nilsson and Wardle 2005). Moist bryophyte mats may in turn affect the rates of decomposition negatively. Further, decomposition of bryophyte litter is slow compared to that of the understory vascular plants (Bonnevie-Svendsen and Gjems 1956, Lang et al. 2009). Thus, the combined litter from bryophytes and spruce needles is expected to contribute to the significant buildup of SOC stock in the LFH horizon in the spruce relative to the birch stands. In the birch stands, the significant negative correlation between the N stock of the understory vegetation and the LFH SOC and N stocks may be related to the litter quantity and quality of the different understory vegetation species groups. Altogether, this is reflected in the higher decomposition rates in the birch stands (103 ± 30) relative to the spruce stands (57.1 ± 13) of the current study (M. Hansen, T. G. Bárcena, and O. J. Kjønaas, *unpublished data*), as was also observed in the study of Hansson et al. (2013).

Soil.—Contrary to our hypothesis, the planting of Norway spruce did not increase the total SOC stock down to 1 m soil depth. The results are in alignment with previous findings of no clear trend in tree species effects on total SOC stocks (Augusto et al. 2015). However, as hypothesized, the tree species change indicates a re-distribution of SOC within the soil profile following spruce planting, reflected by the significant accumulation of SOC in the LFH horizon. This concurs with the Swedish study on Norway spruce and birch of Hansson et al. (2011), as well as studies comparing coniferous and deciduous stands (Gardenas 1998, Gurmesa et al. 2013, Vesterdal et al. 2013, Dawud et al. 2017, Laganiere et al. 2017), although no difference in the LFH horizon has also been observed (Ransedokken et al. 2019). For the mineral soil, the current results differed from the study of Hansson et al. (2011), which showed significantly larger SOC stocks in mineral soils under spruce compared to birch. In other studies, the effects on mineral soils have generally been found to be minor (Vesterdal et al. 2013), or being limited to the uppermost mineral soil (Gurmesa et al. 2013, Cremer et al. 2016).

While the C sequestration rate in soil is low compared to that in living biomass, its importance in a climate change perspective lies in its large C stock (Grønlund et al. 2010, Bradshaw and Warkentin 2015), as well as its potential for long-term C storage especially in undisturbed or unmanaged systems (Clemmensen et al. 2013). Generally, SOC stocks in Norwegian forests have been found to be high compared to those of Sweden and Finland (Olsson et al. 2009, Rantakari et al. 2012, Strand et al. 2016). A positive correlation between SOC stocks and precipitation and/or temperature has been found in coarse sandy Nordic forest soils (Callesen et al. 2003) as well as in the Norwegian ICP Forests Level I sites (Strand et al. 2016) where soils in western Norway harbor the largest SOC stock (de Wit and Kvindesland 1999). Thus, potentially, climatic conditions may partly explain the relatively high SOC stocks as compared to Nordic and European studies (Callesen et al. 2003, Hansson et al. 2011, De Vos et al. 2015).

In the native birch stands, a major part of the ecosystem C stock was found in the soil. The ratio SOC: living biomass C in the birch stands was similar to the ratios given by Pan et al. (2011) and Bradshaw and Warkentin (2015), but considerably lower for the spruce stands. In both the spruce and the birch stands, however, the relative SOC to total ecosystem C stock was lower than reported by Grønlund et al. (2010). The similar SOC stocks in the birch and spruce stands within the current rotation length of 45–60 yr are potentially a combined effect of a loss and a subsequent accumulation of SOC following the removal of the original birch in the spruce stands (Nave et al. 2010, Blonska et al. 2019, Mayer et al. 2020). A prolonged rotation period may increase the soil C stocks of the spruce stands, as the suggested recovery period of the forest floor SOC stock following clear-cut in forests growing on Podzols may be up to 70 yr (Nave et al. 2010).

However, the net long-term tree species effect is uncertain (Vesterdal et al. 2013, Mayer et al. 2020).

In addition to the suggested reallocation of SOC from the mineral soil to the LFH horizon in the spruce stands, the negative correlation between the SOC stock of the mineral soil and the C stock in living tree biomass suggests a preferential allocation of ecosystem C from the mineral SOC pool to the tree biomass. The distribution of SOC within the soil profile is expected to reflect the shallower rooting depth of spruce (Hansson et al. 2011, Dawud et al. 2016), as well as a limited input of above- and belowground litter from the understory vascular plants compared with the birch stands. The positive correlation between the LFH horizon of the spruce stand and standing dead wood may suggest increased input of litter to the LFH horizon from the dying crown compartment, which support the SOC accumulation in the LFH layer. Altogether, this may affect the stocks as well as the stability of the SOC (Vesterdal et al. 2013, Lukina et al. 2020), and thus the long-term storage of SOC in the forest ecosystem.

N is the major limiting factor for tree growth in boreal forests, and N limitation typically constrains the buildup of C (Tamm 1991, Högberg et al. 2017). Contrary to our hypothesis, the tree species change did not significantly increase the total N stocks in the soil down to 1 m soil depth, nor did the planting of Norway spruce promote an allocation of N from the mineral soil to the forest floor. The significant negative correlation between the N stocks of the mineral soil and the N stock in living trees in the spruce stands suggests a mining from the mineral soil with an increasing tree biomass. At all locations except Stranda, the ecosystem accumulation of N in spruce relative to birch stands suggests an input of N which may be related to N deposition and canopy interactions. The complex topography of the coastal region of western Norway renders accurate estimates of anthropogenic N input at the different locations challenging. However, MAP and annual total ecosystem N accumulation rates were both highest at the southwestern Jølster II and lowest in the northeastern Stranda, which may support the presence of an N deposition gradient as indicated by Fischer et al. (2007). Inorganic N in throughfall + stemflow has been found to be 1.5–3 times higher in spruce canopies relative to birch (Bergkvist and Folkeson 1995), which may partly be related to the larger canopy surface area in spruce (Zaltauskaite and Juknys 2011). Additionally, the lower tree density in birch stands will play a role, as will the canopy filtering of N, which is strongly seasonal in the birch stands (Bergkvist and Folkeson 1995). A higher filtration in spruce stands was reflected in the significantly larger concentration of exchangeable Na from sea salts in the soil of the spruce relative to the birch stands. The negative correlation between the ecosystem C and N stocks in spruce stands, despite inputs of N from filtering in the crown, may potentially be related to N leaching following the tree species change. At Stranda, the high ecosystem N stock is most probably related to the presence of N_2 fixing alder (Merila et al. 2002, Mitchell and Ruess 2009), resulting in input of N rich litter as well as a lateral flow of N originating from stands upslope. This N input did, however, not result in higher SOC stocks compared to the other locations.

Tree species change and soil chemical characteristics

Managing multiple ecosystem services, and addressing trade-offs between C sequestration, nutrient availability, and long-term ecosystem resilience are currently among the most pressing areas for sustainability research (Renard et al. 2015). Our results suggest that the current tree species change may potentially affect future soil fertility through increased nutrient depletion. As hypothesized, planting of Norway spruce reduced the exchangeable concentrations of elements, specifically key base cations. However, increases in certain element concentrations were also found. The significantly higher exchangeable K, Na, and S in the LFH horizon of the spruce stands concur partly with higher K and Na in the Swedish study of Hansson et al. (2011). Results in the two studies were contrasting for other nutrient concentrations: Hansson et al. (2011) found a significantly higher exchangeable base cation pool, including higher Ca and Mg, in the LFH layer of the spruce relative to the birch stands along with no significant difference in the exchangeable elements of the mineral soil, as opposed to the significantly lower exchangeable

Ca, Mg, and BS in the M1 layer in the spruce of the current study. The negative correlations between the C and N stocks in living trees and exchangeable Ca and BS in the mineral soil in spruce suggest, as with N, an increasing translocation of nutrients within the ecosystem with an increasing tree biomass.

The significant positive correlation between SOC and exchangeable Ca in the mineral soil of the birch stand may potentially reflect a combination of intrinsic differences in tissue chemistry between the tree species (Augusto et al. 2002), input of Ca in belowground litter related to the deeper rooting pattern of birch (Hansson et al. 2011, Dawud et al. 2016), as well as litter input from the understory vegetation. For spruce stands, the significant positive correlation between the exchangeable Si concentration and SOC stocks in the LFH horizon, along with the significantly higher exchangeable Si concentration in the LFH layer relative to birch stands, may reflect a possible influence of Si on Norway spruce needle decomposition and the formation of raw humus, which historically has been given some attention (e.g., Bonnevie-Svendsen and Gjems 1956).

Differences in element concentrations in the soils of the two stand types may also be related to differences in input and output patterns related to the above-mentioned filtering processed in the crown, processes affecting weathering rates, as well as fungal transport of elements from the mineral soil (Bergkvist and Folkeson 1995, Binkley and Giardina 1998, Augusto et al. 2002, Clarholm and Skyllberg 2013). Leaching losses from both stand types may be amplified by the relatively high precipitation levels in the region, and affected by aspect and slope, as suggested by their negative correlation with most of the exchangeable elements, especially in the mineral soil. A similar correlation pattern was also found between the understory vegetation and exchangeable element concentrations and between the understory vegetation and aspect in the spruce stands, where the more humid conditions of the northern aspects may be the common factor.

As hypothesized, the tree species change affected the soil acidity as indicated by the significant increase in exchangeable acidity in the LFH horizons of the spruce stands. Higher acidity under spruce concurs with previous studies comparing Norway spruce and birch (Bergkvist and Folkeson 1995, Hansson et al. 2011), Norway spruce and European beech (Cremer and Prietzel 2017), and conifer and deciduous species (Augusto et al. 2015). The positive correlation between exchangeable acidity and SOC stocks in the mineral soil of both stand types also concurs with Mueller et al. (2012), who interpreted this as an organic matter stabilization process. Tree species have been found to strongly influence soil pedogenic processes, including acidification and podzolization, even in a short-term perspective (Bonnevie-Svendsen and Gjems 1956, Legout et al. 2016). The negative correlation between Fe in the mineral soil and the SOC stock of the forest floor of the spruce stand may reflect more tightly bound Fe related to podzolization; however, the results for SOC, Fe + Al, and pH combined did not suggest increased podsolization processes that can be attributed to the tree species change within the current time frame.

Tree species change in a climate perspective

Potential future mitigation effects from forests will depend on how the tree species will be affected by climate change-driven threats to ecosystem functioning and resilience. Typical disturbance regimes associated with climate change include increased disturbance from wind and pathogens with wetter conditions, and more frequent droughts, insect infestations, and wildfires under drier conditions (Seidl et al. 2017). The projected regional climate change includes increasing temperature and precipitation; however, increasing climate change related periodic drought stress during dry summer spells cannot be excluded (Norwegian Centre for Climate Services 2020).

The re-distribution of SOC from the mineral soil to the LFH layer increases the vulnerability of the system to SOC losses related to temperature increases (Bond-Lamberty et al. 2018). Further, the preference of Norway spruce roots for humus-rich soil horizons (Puhe 2003), and the potentially shallower rooting depth of spruce relative to birch (Hansson et al. 2011, Dawud et al. 2016) will increase the stand susceptibility to drought stress, which is considered a large threat to the health of boreal conifer forests (Rosner et al. 2018). Drought stress may also render spruce stands more risk prone to biotic damage such as bark beetle outbreaks (Ryan 2002, Jonsson and Lagergren 2018, Timmermann et al. 2018, Kosunen et al. 2019).

On the other hand, the potentially larger allocation of biomass belowground, a deeper root system, as well as defoliation in the fall when extreme storm events are more frequent, make birch stands less susceptible to windthrows and a subsequent temporarily reduction in the forest C sink strength (Ryan 2002, Koster et al. 2011, Subramanian et al. 2019). Windthrows increase the amount of available fuel (Rogers et al. 2015). Additionally, the moisture content of what is the typical LFH layer in spruce stands: loosely compacted with a depth >4–6 cm, is found to be the most significant seasonal factor which influences fire intensity and severity, including the depth of burn and belowground effects (Rogers et al. 2015). Whereas results from studies on recent fire history and model simulations have suggested a reduced response of wildfire to climatic change in several boreal forest systems (Flannigan et al. 1998), historic data on Norwegian forest fires show increased late-season fire frequency with increasing summer temperatures (Rolstad et al. 2017). In addition to a potential loss of SOC accumulated in the LFH layer during wildfire events, shallow-rooted species rarely survive ground fires (Rogers et al. 2015).

Recent assessments of future risk levels in boreal and temperate forest systems have suggested tree species change from monoculture Norway spruce to birch or deciduous forests, Scots pine and mixed forests (Cremer and Prietzel 2017, Astrup et al. 2018, Subramanian et al. 2019). Our results support the need for short- and long-term strategies that include risk assessments and risk management implementations to ensure resilient future C storage and capture in forest biomass and preservation of SOC and nutrient stocks.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3826/full