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Boreal tree species selection enhances forest carbon stocks through above- rather than below-ground changes

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ABSTRACT

Forest management has the potential to impact the net forest carbon (C) balance, and a better understanding of how tree species influence soil C provides a potential tool to promote higher C uptake and storage in forests. In this study, we utilized two common garden experiments located in northern and central Sweden to compare soil organic C stocks associated with six different boreal tree species (*Betula pendula*, *Larix sp.*, *Picea abies*, *Picea glauca*, *Pinus contorta* and *Pinus sylvestris*), approximately 30 years after planting. We measured both above- and below-ground C inputs and C outputs via decomposition and analyzed how these factors influenced soil C stocks. Our results showed that the vertical distribution of SOC differed between the species, and furthermore, many of the SOC input and output processes measured were species-dependent. Despite this, we found no differences in total belowground soil C stock between the species. The aboveground biomass C stocks, in contrast, were highly species-specific, with the rank order of species differing between the two sites. As such, our study indicates that tree species choice may serve as a tool to promote ecosystem C stocks, and in turn enhance the climate change mitigation potential of forests.

1. Introduction

Boreal forests store about one third of the global forest carbon (C) pool, and the majority of this C stock can be found in the soil (Pan et al., 2011; Skogsdata, 2017). Forest management has the potential to impact the net forest C balance (the sum of all C inputs and outputs), and a better understanding of how tree species selection influences soil organic carbon (SOC) dynamics could provide yet another tool for enhancing boreal forests' climate change mitigation potential. However, despite decades of research (Mayer et al., 2020; Prescott and Vesterdal, 2013), the mechanism by which different tree species accumulate soil organic carbon (SOC) remains difficult to disentangle from site-specific factors (Mayer et al., 2020). Interactions between tree species and other factors such as soil properties, soil biota, and local climate can all serve as influential controls on SOC (Augusto and Boča, 2022; Prescott and Vesterdal, 2013; Verstraeten et al., 2018).

It is recognized that the variability in the quality and quantity of above-ground litter inputs of different species can alter soil processes, which in turn can increase or decrease soil C (Xu et al., 2013). However, many studies have found little or no difference in aboveground litterfall C between different tree species when compared in common garden or paired stand studies (Vesterdal et al., 2013). Some evidence suggests that conifers and deciduous species can have different effects on the vertical distribution of soil C and organic horizon C stocks, which may be due to differences in litterfall C inputs and rooting activity (Hansson et al., 2013a; Vesterdal et al., 2013). Deciduous trees, have been found to promote SOC in the mineral soil; however, in boreal forests effects are often found to be small and inconsistent (Gundale et al., 2024; Prescott and Vesterdal, 2013). Interactions with environmental factors further complicate these relationships, and the quantities of above ground litter inputs are also shown to be dependent on site fertility and associated tree biomass production (Hansen et al., 2009; Matala et al., 2008). In contrast, much less is known about belowground litter C inputs, in large part due to the difficulty of quantifying these fluxes. Fine root turnover rates are likely affected by local climate and site factors, and appear to increase with increasing mean annual temperature and precipitation (Yuan and Chen, 2010), and differs among tree species (Hansson et al., 2013b). Evidence also suggests that fine root turnover may be a similar or larger C input to soil than aboveground litter (Gundale et al., 2024), with this input being concentrated mainly in the mineral soil (Kleja

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et al., 2008). Other studies have found higher root production by broadleaf species than by conifers (Oostra et al., 2006; Withington et al., 2006), which may also contribute to differences in the vertical distribution of soil C between species.

Different tree species also have different resource acquisition strategies, associated with their functional traits, referred to as the "plant economics spectrum" (Reich et al., 1997). Plant traits can be defined on a spectrum from "acquisitive" to "conservative," indicating high resource capture that supports rapid growth (e.g. high specific leaf area and/or high leaf nutrient content) or resource conservation strategies that correspond with slow growth rates (e.g. high levels of structural defence, low specific leaf area and/or high lignin content), respectively (Díaz et al., 2016). The former traits are typically found in early-successional tree species such as *Betula pendula* or *Pinus sylvestris,* whereas the latter are generally found in late-successional species, such as *Picea abies*. Trait coordination is also speculated to be analogous across the whole plant, indicating that both above and belowground litter inputs would exhibit similar "qualities" (Spitzer et al., 2025; Weigelt et al., 2021). These trade-offs in "acquisitive" or "conservative" plant function should translate into different rates of decomposition, where increasing rates often are associated with higher litter nitrogen (N) content, and decreasing rates instead generally occur under higher litter lignin content (Gundale et al., 2024; Liski et al., 2003; Prescott, 2010; Zhang et al., 2008). However the "early" stages of quality-dependent decay may not necessarily predict soil organic C accumulation, and a "maximum decomposition limit" has been suggested (Berg and Ekbohm, 1993), which corresponds to the point when the litter "becomes" humus and enters its second phase of decomposition (Berg et al., 1996; Prescott et al., 2000). Long term results indicate that the decay rate of different types of litter (and litter from different species) may converge at this point (Prescott et al., 2004), meaning trait differences between species might not matter as much as quantity of litter input, or local environmental conditions.

In this study, we utilized two common garden experiments located in northern and central Sweden to compare soil organic C stocks associated with six different boreal tree species, approximately 30 years after planting. We further explored the role of above and belowground C inputs, and C outputs via decomposition, and how these factors influenced soil C stocks. We tested the following hypotheses:

1. Tree species will differ in their soil C stocks and soil C vertical distribution (organic versus mineral horizons).
2. The species differences in soil C stocks will be linked to their differences in litter production and decomposition rates.
3. Species-specific growth responses to local and regional climate variability will serve as an important control on soil C stocks.

2. Materials and methods

2.1. Site description and sampling design

Two common garden experiments were utilized in this study, one located in northern Sweden and one located in central Sweden. The northern site, Svartberget (64°15′N 19°47′E), was established in 1992 and consisted of 10 tree species, divided over 30 plots and 3 blocks. The central site, Garpenberg (60°18′N 16°17′E), was established in 1995 and consisted of 8 tree species, divided over 20 plots and 3 blocks. All species present on both sites are common in the boreal region, including four species native to Sweden, *Betula pendula*, *Pinus sylvestris, Larix sukaczewii* and *Picea abies.* The remaining species are considered exotic species in Sweden, (*Abies lasiocarpa, Abies sibirica, Picea glauca, Picea mariana, Pinus banksiana, Pinus contorta* and *Pseudotsuga menziesii*). There were three replicate plots for each species at Svartberget, (i.e., a complete block design), whereas at Garpenberg *Betula pendula* and *Larix sp.* were only present in two blocks (i.e., an incomplete block design; Fig. 1). At Garpenberg there were also two species of *Larix* present, one plot of *Larix sibirica* (*sukaczewii)* and two plots of *Larix marschlinsii*. Due to the low replication of each of these species at this site, we treat *Larix* at the genus level, i.e., *Larix* sp. to enable statistical analysis. In total 6 species (*Betula pendula, Larix* sp.*, Picea abies, Picea glauca, Pinus contorta and Pinus sylvestris*) were common between the two common garden experiments. At establishment all plots were scarified and planted using a

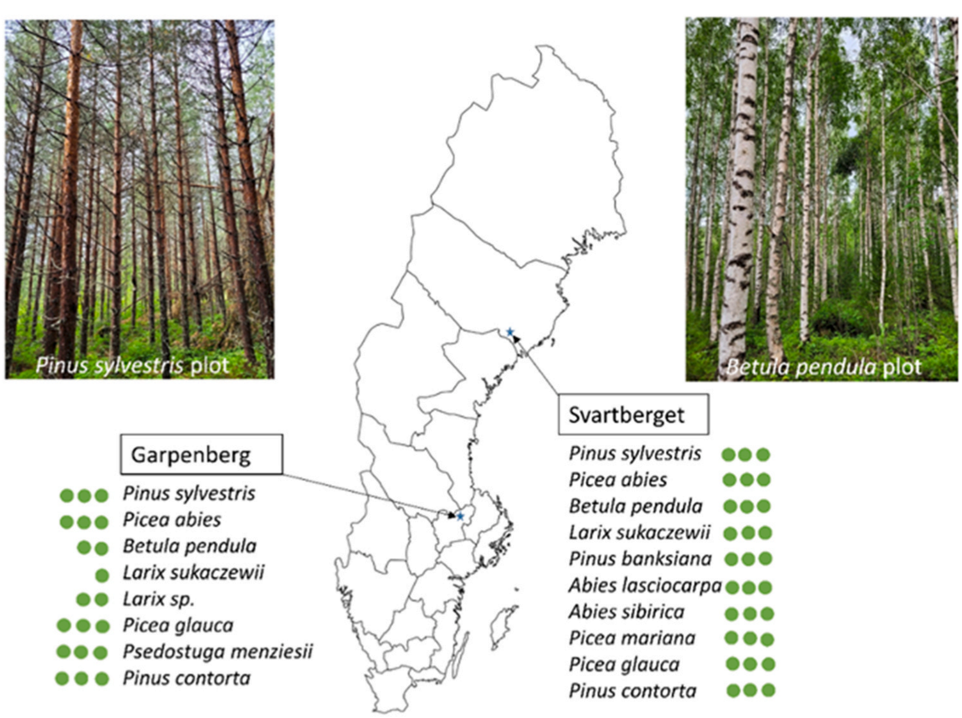

Fig. 1. Map showing the locations of the two field sites in Sweden. Tree species monocultures present at each site are listed and the number of green dots indicate the number of replicate plots of each species found at the site. Photos are of one replicate plot of two species, source: (Spitzer et al., 2025).

seedling spacing of 2 m, resulting in 289 seedlings per plot.

Both sites had a similar site index (SI), defined as the average height that the dominant trees of a particular species will attain at a specific reference age. Svartberget had an SI value of 22 (H100) and Garpenberg had an SI value of 23 (H100). The average growing season temperature during 2018–2022 was 13.3°C at Svartberget and 15.9°C at Garpenberg (Swedish Meteorological and Hydrological Institute, "SMHI", 2025). Both sites at the time of establishment were classified as spruce forest of bilberry type (Påhlsson, 1995), however with mixed occurrences of *Pinus sylvestris*. The soil is a relatively shallow podzol developed on glacial till (moraine). For more information about the site properties, see Table 1.

2.2. Tree growth and above ground biomass

Forest inventory at both sites was performed during 2022 by randomly selecting 20 trees in each plot and measuring tree height and diameter. Stems per hectare were calculated by total count of trees in each plot and scaling this value to the hectare level. The aboveground biomass was then calculated using the data from the forest inventory and the appropriate biomass equation. For tree species native to Sweden, except *Larix sp.*, we used Marklund's biomass functions to convert stem volume to biomass (Marklund, 1988). For *Larix sp.*, equation 136 in Zianis et al., (2005) was utilized. For all other tree species, the biomass equation from Jenkins et al., (2003) was utilized, with different constants used for each species (supplemental 2). Only functions constructed for total aboveground biomass were considered and selected for the calculations. Any ground vegetation present in the measured plots was not inventoried due to its very minor contribution to the aboveground C stock, and therefore was not included in our calculations.

2.3. Litter fall

Between August 2021 and August 2022 aboveground litter was collected using circular (48 cm in diameter) litter traps with a mesh bottom. Three traps per plot were installed and emptied twice: once after snowmelt and again in late summer. The traps were placed $\geq$ 1 m from the nearest tree, at a maximum distance of 10 m from the plot center, and at least 10 m from the nearest adjacent trap. This approach was used to effectively sample the center of each plot, while avoiding edge effects and litter inputs from adjacent plots. The collected litter was pooled at the plot level, transported to the lab, and dried at 70° C for at least 48 h. The litter was then sorted into leaves or other detritus (e.g. twigs), saving only leaves or needles from the tree species native to the plot. The samples were then weighed, and a subsample was milled and analyzed for total N and C concentrations (g/g dry mass) using an isotope ratio mass spectrometer (DeltaV,Thermo Fisher Scientific, Bremen, Germany) and an elemental analyzer (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany). After analysis, the C and N concentrations were multiplied with the combined dry weight of the pooled samples from each plot, and then upscaled to Mg ha^{-1} using the combined area of the litter traps used in each plot. Coarse and woody debris (sticks, branches, bark cones etc.,) from each species was collected between 2022 and 2023. A 2 × 2 m square in the center of each plot was cleared of any debris, then marked and left for one year. After this period, any new material entering the plot was collected, dried at 70 °C for 48 h, and then weighed. The weight of the samples was then upscaled to Mg ha^{-1} using the plot area. For upscaling, the C content of the coarse and woody debris biomass was assumed to be 50 %.

Table 1
Site description of the two common garden experiments utilized in this study. The soil properties are mean values calculated across all plots.

Site properties	Svartberget	Garpenberg
Site index (H100)	22	23
Elevation a.s.l.	300	195
Slope (%)	> 15	< 5
GDD, (base +5°C) *	792	950
Moisture regime	Mesic	Mesic
number of plots	30	20
Size of plots (m^2)	1156	1156
Seedling spacing (m) *	2 × 2	2 × 2
Trees * plot^{-1}*	289	289
Soil type	Podzol	Podzol
Parent material	Moraine	Moraine
Soil texture	Sandy silt	Coarse silt
pH (Humus)	4.25	3.98
pH (Mineral soil 0–20 cm)	5.30	4.78
C/N (Humus)	33.8	25.6
C/N (Mineral soil 0–20 cm)	30.5	26.7

Note: *Growing degree days (GDD), seedling spacing and number of trees per plot are given at the time of site establishment.

2.4. Fine root production

To measure fine root production, we used ingrowth cores, a method extensively used in ecosystem studies (Brunner et al., 2013), which we adapted from (Forsmark et al., 2021). The cores were made from nylon mesh (Sintab Product, AB Sweden) with 2 mm mesh openings and in early summer 2021, fine-root ingrowth cores (5 cm wide and 20 cm long) were installed vertically at the centre of each of the four sides in every plot, at a minimum distance of 3 m from the plot edge and at least 70 cm away from the closest tree. Each core was filled with sieved (2 mm) mineral soil from a pit at the center of the same plot where it was installed (which was packed in the cylinder to approximately the same bulk density as the surrounding soil), and then buried within the mineral soil to a depth of 20 cm. The removed organic layer was placed back on top of the cylinder which was then left to incubate. Two years after installation (with an incubation time of 24 months), the root-ingrowth cores were collected. The incubation time of 24 months was chosen to allow for two full growing seasons, which both minimized the initial disturbance effect and root biomass turnover during the measurement period (Brunner et al., 2013; Finér et al., 2011). After collection, the root-ingrowth cores were transported to the lab, the soil was removed, and the root biomass from individual ingrowth cores was pooled at the plot level. The pooled root biomass was then dried at 70°C for at least 48 h and sorted, removing everything except fine roots from the tree species native to each individual plot. The remaining biomass was weighed and then upscaled to Mg ha^{-1} y^{-1} using the combined volume of the root ingrowth cores installed in each plot. The C content of the fine root biomass was assumed to be 50 % (Nilsson et al., 2008; Spitzer et al., 2025), and the values were adjusted for stoniness of each plot (described below).

2.5. Decomposition rate

To measure decomposition rate for each tree species, we used litter bags made from a nylon mesh with 100 μm openings (Sintab Product, AB Sweden). The mesh size was chosen to allow for microbial processes and fungal ingrowth, but to exclude soil macrofauna. In total 600 bags were used in the experiment, with half of them filled with tree species litter gathered from litter traps the year before, and half filled with material from the organic layer (i.e. "humus-layer"). At the beginning of autumn 2022 all bags were filled with 3 g of dry mass and were then gently put back in the field just beneath the organic layer, at the intersection with the mineral soil, and in the same plot as their respective litter origin. Consequently, we placed 6 litter bags and 6 humus bags in each plot. A year later all bags were collected and brought back to the lab, dried in 70° C for at least 48 h, and weighed to allow calculation of mass loss. Values from individual bags were pooled at the plot level before statistical analysis.

2.6. Soil sampling

In the summer of 2021, the organic horizon and mineral soil were systematically sampled in a grid pattern at 10 locations in each plot (i.e. sub-samples). For the organic horizon we used a PVC tube (Ø10 cm) fitted with a serrated blade and the top 0–10 and 10–20 cm layers of the mineral soil were collected with a metal core sampler (diameter 1.59 cm). Sampling was limited to 20 cm depth to avoid inconsistency caused by reaching the parent material in some locations across both sites. The collected material was pooled at the plot level, sieved (2 mm mesh) and then dried at 70 C° for at least 48 h, and later stored at room temperature until analysis. The samples were later milled, and total C and N concentrations were analyzed using an isotope ratio mass spectrometer (DeltaV,Thermo Fisher Scientific, Bremen, Germany) and an elemental analyzer (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany). Soil pH was measured in all plots using dried samples from all soil layers by mixing 10 ml of soil and 10 ml of deionized water.

Stone and boulder content (SB) at both sites was estimated using the rod penetration method, where an iron rod with a diameter of 10 mm was driven through the soil until it reached a stone or boulder (Viro, P.J., 1952). This was done at 60 points in a grid pattern at each site. The mean penetration depth was calculated as volumetric content of stones and boulders in percent using Viro (1952) modified by Stendahl et al., (2009), using the regression equation SB = 82.5 – 2.75*Si, where Si is the mean penetration depth of the 60 sample points.

Carbon stocks in the organic layer were calculated by multiplying the C concentration with the combined dry weight of the pooled samples from each plot, and then upscaled to Mg ha^{-1} using the combined cross-sectional area of the subsamples in each plot. The C stocks in mineral soil were calculated using bulk density functions, equation 31 from Nilsson and Lundin, (2006). The C concentrations obtained in the previous analysis were thus multiplied with the value of the calculated bulk density and the total volume of each mineral soil layer, yielding an upscaled value of Mg ha^{-1} for all plots.

2.7. Calculations and statistical analyses

All statistical analyses were carried out using R 4.2.1 (R Core Team, 2024) and we considered individual plots as the unit of replication. While we gathered data from all 50 plots present in our experiment, our analysis only focused on the six tree species present on both sites (*Betula pendula, Larix sp., Picea abies, Picea glauca, Pinus contorta and Pinus sylvestris*). This resulted in 35 plots in total divided over 2 sites and 6 blocks (3 blocks per site, except for *Betula pendula* and *Larix sp.* which were only present in 2 blocks at Garpenberg, *Larix sp.* was however instead present two times within one block due to different planted species, Fig. 1). Information including all species present at both sites can be found in appendix Fig. 1. For all analyses, except when testing tree species and site interaction, we used a mixed model (Bates et al., 2003) ANOVA type III with fixed effect of tree species, and a random effect of site. Our somewhat limited dataset prohibited more complex mixed models where the blocking factor was nested under site, however, model testing based on the AIC criterion showed that models with random effects of site generally outperformed models with a random effect of block. When testing tree species and site interaction block was instead included as a random factor.

We first analysed only the tree species effect on ecosystem C, tree biomass and soil C (in all soil layers), after which we tested each of our measured variables (above ground biomass, root growth, litterfall, coarse and woody debris, decomposition rate in litter and humus and soil pH) against tree species to ascertain which of these were species dependent. Finally, all variables were tested together (without interactions) against each soil layer and total soil C. If any variable shown to be species dependent in the preceding statistical test also showed evidence of effecting soil C, this was taken as confirmation that tree species were able to affect soil C stock in our experiment. To avoid problems with multicollinearity, tree species was excluded from our statistical model in the final step due to being used in the previous model, along with tree biomass, since the variable was highly correlated with other model variables (variance inflation factor ~ 3 or higher). Lastly, we used a linear model to test tree species and site interaction against ecosystem C, tree biomass and soil C to ascertain if different tree species were affecting C stock differently depending on environmental factors. Post hoc analysis, when performed, was based on estimated marginal means and Tukey's adjustment (Lenth et al., 2025). Model responses were checked for normality and homoscedasticity with the aid of residual plots, which resulted in a log transformation (natural logarithm) of all variables, except soil pH.

For all statistical tests, we used the terminology suggested in Muff et al., (2022), where different ranges of p-values are reported on a continuum from "little or no evidence" to "very strong evidence". A p-value of 0.0001–0.001 subsequently was interpreted as very strong evidence, a value of 0.001–0.01 as strong evidence, 0.01–0.05 as moderate evidence, 0.05–0.1 as weak evidence, and p-values > 0.1 as no evidence.

3. Results

Our results show that the largest average SOC stock across the two sites was found for *Pinus contorta,* and while *Pinus contorta* also ranked among the top species in measured above ground tree biomass, the highest above ground C stock was found in *Larix* sp., which also consequently ranked the highest in total ecosystem C stock (Fig. 2). When testing total ecosystem C and above ground biomass C between the tree species, we found very strong evidence for differences ($p < 0.001$). However, we found no evidence of a total SOC stock difference between the species (Fig. 2). The analysis of tree species effects on soil C distribution however showed strong evidence ($p = 0.005$) of a difference in SOC between species within the deepest mineral soil layer (10–20 cm; Table 2a). The species with the highest SOC stock in this mineral soil layer, *Pinus contorta*, had c. 40 % more C than the species with the lowest C stock in this soil layer, *Larix* sp. (Fig. 2). For the organic layer or the upper mineral soil layer (0 – 10 cm) there was no significant effect of tree species on the C stock (Fig. 2, Table 2).

Our analysis showed very strong evidence ($p < 0.001$) for an effect of tree species on tree biomass, amount of coarse woody debris, amount of litterfall, rate of litter mass loss and rate of root growth (Table 2b). We found no significant tree species effect on humus mass loss and soil pH (Table 2b). The tree species differences between these variables did not in general translate into differences in soil C, except for the amount of litterfall, for which we found moderate evidence for an effect on C in the deepest layer of the mineral soil (Table 2c). For soil pH we found strong evidence for an effect on the overall soil C stock ($p < 0.001$), moderate evidence of an effect in the 0–10 cm mineral soil layer ($p = 0.028$) and strong evidence ($p = 0.003$) of an effect on the deepest 10–20 cm mineral soil layer (Table 2c).

We also tested the effect of site on forest ecosystem C stock, tree biomass and total soil C stock (Table 3). We found that the interaction between species and site showed very strong evidence ($p < 0.001$) for affecting tree biomass C. Furthermore, ecosystem C stock also displayed an interaction effect between species and site, the evidence was however weak ($p = 0.064$), indicating that the strong influence of the tree species on the ecosystem C stock is only weakly related to the site. In contrast, total soil C stock showed very strong evidence ($p < 0.001$) of being affected only by site.

The results also show that despite the fact that the two experimental sites were established at the same time, tree biomass for most species tended to be higher at the northern compared to the site in central Sweden. This was particularly noticeable for the broadleaved species, *Betula pendula*, and for *Picea abies* (Fig. 3). In contrast, SOC was generally lower in the northern site than in the central, which was also displayed by the strong evidence (< 0.001) for an effect of site on total soil C stock

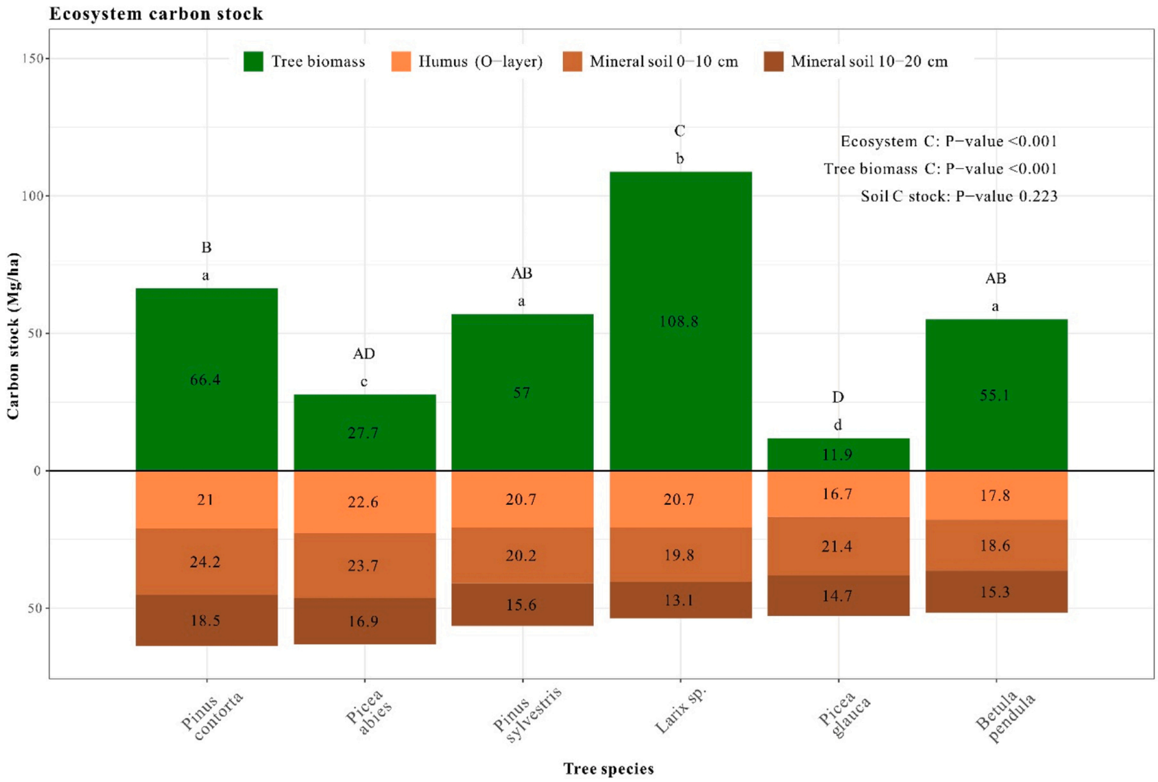

Fig. 2. The average amount of C stock in different ecosystem compartments for different tree species at both sites (n = 6 species^{-1}, except *Betula pendula* where n = 5). The species are organized in descending order, starting with the highest belowground C stock. Letters above or below bars indicate significant differences between species. Top capital letters = post hoc test of ecosystem C and bottom letters = post hoc test of tree biomass C. Additional information can be found in supplemental table 3.

with no significant interaction effect of species (Table 3).

4. Discussion

The purpose of this study was to assess whether tree species selection could serve as a management tool to increase below-ground SOC stocks. Further, we aimed to determine if some key variables related to soil C input and output could be used to explain eventual differences between the tree species in our experiment after approximately 30 years. Some previous studies have shown that while different tree species can affect SOC accumulation within different soil layers, the total C stock are not always affected (Mayer et al., 2020); and there is some evidence of differences in SOC distribution between conifer and broadleaves species (Mayer et al., 2020). Our results largely agree with these results and indicate that tree species can at least partially affect soil C distribution, as the SOC in the deepest mineral soil layer showed strong evidence ($p = 0.005$) of a species response (Table 2a). However, the differences in our study were not shown to be between conifers and broadleaves, but between *Pinus contorta* and *Larix* sp., which showed the highest and lowest C stock of all species within the deepest soil layer, respectively. Our analysis also indicated that belowground soil C stock is more dependent on site factors than tree species, as the total soil C stock showed very strong evidence ($p < 0.001$) of being site dependent (Table 3). In contrast, tree biomass, and in turn ecosystem C stocks, showed weak evidence ($p = 0.064$) for an interaction between tree species and site (Table 3).

For our first and second hypotheses, we predicted that total soil C stocks and soil C vertical distribution would differ between tree species, and that these differences would be due to species-specific differences in litter production and decomposition rate. We found little evidence to support these predictions, which could be due to strong legacy effects of the relatively large soil C stocks that had accumulated prior to the establishment of the experiment. Nonetheless, we did find some evidence that tree species affected soil C in the deepest (10–20 cm) mineral soil layer over the duration of our experiment, where *Larix* sp. and *Pinus contorta* differed both from each other, and all other tree species (*Pinus contorta* showed the highest C stock of all species and *Larix sp.* the lowest). Further, we found that litterfall showed a significant positive relationship with soil C stock in the deepest mineral soil layer. While not explicitly measured in this study, these results may reflect differences in dissolved organic carbon (DOC) dynamics. Other studies have shown that DOC degradability and fluxes can vary due to tree species (Kiikkilä et al., 2006; Merilä et al., 2024), potentially leading to differences in vertical stratification of soil C within different mineral layers over time. We also found that many of our other measured C input and output variables showed evidence of differences among tree species, although we did not find evidence that these differences translated into differences in soil C stocks. For instance we found that aboveground litter production varied significantly between species, whereas similar experiments report little variation between species, linking differences instead to local site fertility (Augusto et al., 2015; Hansen et al., 2009). In comparison to aboveground litter production, data on fine root production are much more scarce (Mayer et al., 2020) and there is no clear pattern of how fine root production rates differ between boreal tree species, or contribute to soil C stocks (Augusto et al., 2015). Our data showed that fine root production differed strongly among species ($p < 0.001$), but these differences did not translate into differences in soil C stocks.

Focusing on our decomposition measurements, the analyses revealed that litter mass loss, which represents the early stages of decomposition, showed very strong evidence ($p < 0.001$) to differ between species, where *Picea glauca* and *Pinus sylvestris* exhibited the lowest (18 %) and highest (26 %) rate of mass loss, respectively (table S1). Humus mass loss on the other hand did not differ between the species ($p = 0.205$).

Table 2
Visible at the top (a) are the results of testing SOC in different ecosystem compartments and soil layers (distribution) against tree species. The middle part (b) of the table shows the respective p-values of our measured variables when tested against tree species. The bottom part (c) of the table displays measured variables that show weak evidence or higher when tested against SOC in different soil layers. Each result is presented with their respective Chisq (X^2) and p-values.

(a) SOC stocks & distribution			
Ecosystem compartment	Model variables	X^2-value	p-value
Ecosystem C stock	Species	117.57	**< 0.001**
Tree biomass	Species	425.19	**< 0.001**
Total soil C stock	Species	6.960	0.223
Humus C stock	Species	7.905	0.161
Mineral soil 0–10 cm	Species	5.627	0.344
Mineral soil 10–20 cm	Species	16.879	**0.005**
(b) Soil properties and C fluxes			
Measured variables	Model variables	X^2-value	p-value
pH Humus	Species	4.972	0.419
pH mineral soil 0–10 cm	Species	4.912	0.426
pH mineral soil 10–20 cm	Species	1.360	0.928
Average pH (all soil layers)	Species	4.930	0.424
Tree Biomass	Species	425.19	**< 0.001**
Woody coarse debris	Species	139.473	**< 0.001**
Litterfall	Species	29.757	**< 0.001**
Root growth	Species	29.465	**< 0.001**
Litter mass loss	Species	23.109	**< 0.001**
Humus mass loss	Species	7.204	0.205
(c) Variables affecting SOC			
Soil layer	Model variables	X^2-value	p-value
Total soil horizon	pH	13.889	**< 0.001**
O-Layer (Humus)	-	-	-
Mineral soil 0–10 cm	pH	4.869	**0.028**
Mineral soil 10–20 cm	pH	7.210	**0.003**
	Litterfall	3.589	**0.045**

Note: To avoid problems with multicollinearity, tree species was excluded from our statistical model in the final step when comparing all variables together against soil C (bottom part of table, c) due to being used in the previous test, along with tree biomass since the variable being highly correlated with other model variables (variance inflation factor ~ 3 or higher).

Table 3
Results of testing SOC in different ecosystem compartments against tree species and site interaction. Each result is presented with their respective Chisq (X^2) and p-values.

Species & Site interaction			
Ecosystem compartment	Model variables	X^2-value	p-value
Ecosystem C stock	Species	26.182	**< 0.001**
	Site	0.990	0.423
	Species:Site	1.668	**0.064**
Tree biomass	Species	172.440	**< 0.001**
	Site	87.161	**< 0.001**
	Species:Site	6.786	**< 0.001**
Total soil C stock	Species	1.382	0.227
	Site	19.024	**< 0.001**
	Species:Site	1.450	0.202

This result supports the idea that decay rate differences across species may converge at a “maximum decomposition limit” (Berg and Ekbohm, 1993; Prescott et al., 2004), corresponding to the point when litter “becomes” humus (Berg et al., 1996; Prescott et al., 2000). At this later stage of decomposition, local environmental site factors (temperature, moisture etc.) might play a larger role in controlling decomposition processes than the initial litter quality differences between the species (Prescott et al., 2000).

Soil pH was the only variable we measured that served as a strong significant predictor for soil C (Table 2c). This effect was independent of tree species identity in our dataset, i.e. soil pH did not significantly differ between the tree species. Plant growth can indeed acidify the rhizosphere through the uptake of cations in biomass, which over time can lead to a buildup of hydrogen ion concentration in the soil solution. Many studies do show that differences in tree species characteristics can affect this process so that e.g. conifer species acidify the soil more than broadleaved species (Augusto et al., 2015; Kjønaas et al., 2021; Mareschal et al., 2010; Oostra et al., 2006). The differences in soil acidity between conifer and broadleaved species has however been shown to be minor, i.e. a few tenths of a pH unit (Augusto et al., 2015). The relatively young age of our experiment and/or the fact that all but one species *(Betula pendula)* in our experiment were conifers may also have affected our results. Further, legacy effects may have been stronger than the effect of the current stand, and could have obscured any species effects on soil pH, which instead may manifest over longer time scales.

For our third hypothesis we expected that tree species-specific growth responses to local and regional climate variability (represented by our different sites, Table 1) would serve as an important control on SOC stocks. In contrast to our prediction, we found no evidence for an interaction effect between tree species and site ($p = 0.202$) on SOC stocks (Table 3). We did however find weak evidence ($p = 0.064$) that total ecosystem C stocks were influenced by an interaction between tree species and site, which was mainly driven by strong evidence ($p < 0.001$) for species-specific differences in aboveground tree biomass C (Table 3). On both experimental sites, tree species with “acquisitive” traits (*Betula pendula, Larix* sp.*, Pinus contorta* and *Pinus sylvestris*) that usually dominate early in forest succession were shown to exhibit higher levels of tree biomass C than “conservative” trait species (*Picea abies* and *Picea glauca*) that usually dominate later in forest succession (Gundale et al., 2024). This is expected as the experiments are still quite young in relation to the length of a normal forest rotation of 60–100 years in boreal managed forests, and the much longer successional dynamics in unmanaged forest (Nilsson et al., 2022). In addition, the rank order between species in relation to their above ground tree biomass C stock differed between sites, mainly in that *Betula pendula* and *Pinus sylvestris* had a similar aboveground biomass when present on the northern site; while, in the central site *Betula pendula* biomass and annual growth was smaller than those of *Pinus sylvestris*, and more equaled *Picea abies* (Fig. 3). This suggests that there is a potential for managers to optimally match species with site characteristics to maximize ecosystem C stocks (Augusto et al., 2025). For instance, in our northern site, a hypothetical mixture of *Larix sp.* with *Pinus contorta* and/or *Betula pendula* could potentially enhance above- as well as belowground C stock, whereas in the central site a hypothetical mixture of *Larix sp.* and *Picea abies* could potentially achieve the best effect.

The explanation for the rank order differences in ecosystem C observed in our study requires more data than what we have available, but an important difference between our sites, except their geographical distance, is the slope (Table1). Svartberget is located at the lower part of a hillside, creating a natural drainage, while Garpenberg is situated on flat terrain. This means that the Garpenberg site generally has longer periods when the soil is fully saturated with water i.e. after heavy rains or snowmelt, which likely slows down decomposition (Prescott, 2010) and promotes accumulation of soil organic matter, irrespective of the tree species present (Fig. 3). Further research should explore a mechanistic basis underpinning these species by site interactions, and additional pathways through which they influence soil C stocks.

5. Conclusion

This study presented data on tree species effects on soil C stocks based on measurements from two common garden experiments. Our results show that while many soil C inputs and outputs are species dependent, these differences did not translate into differences in total belowground soil C stocks over a 30 year-long time period. However, we found a species effect on C in the deepest mineral soil layer. Our results also point toward the idea that abiotic site factors such as climate and

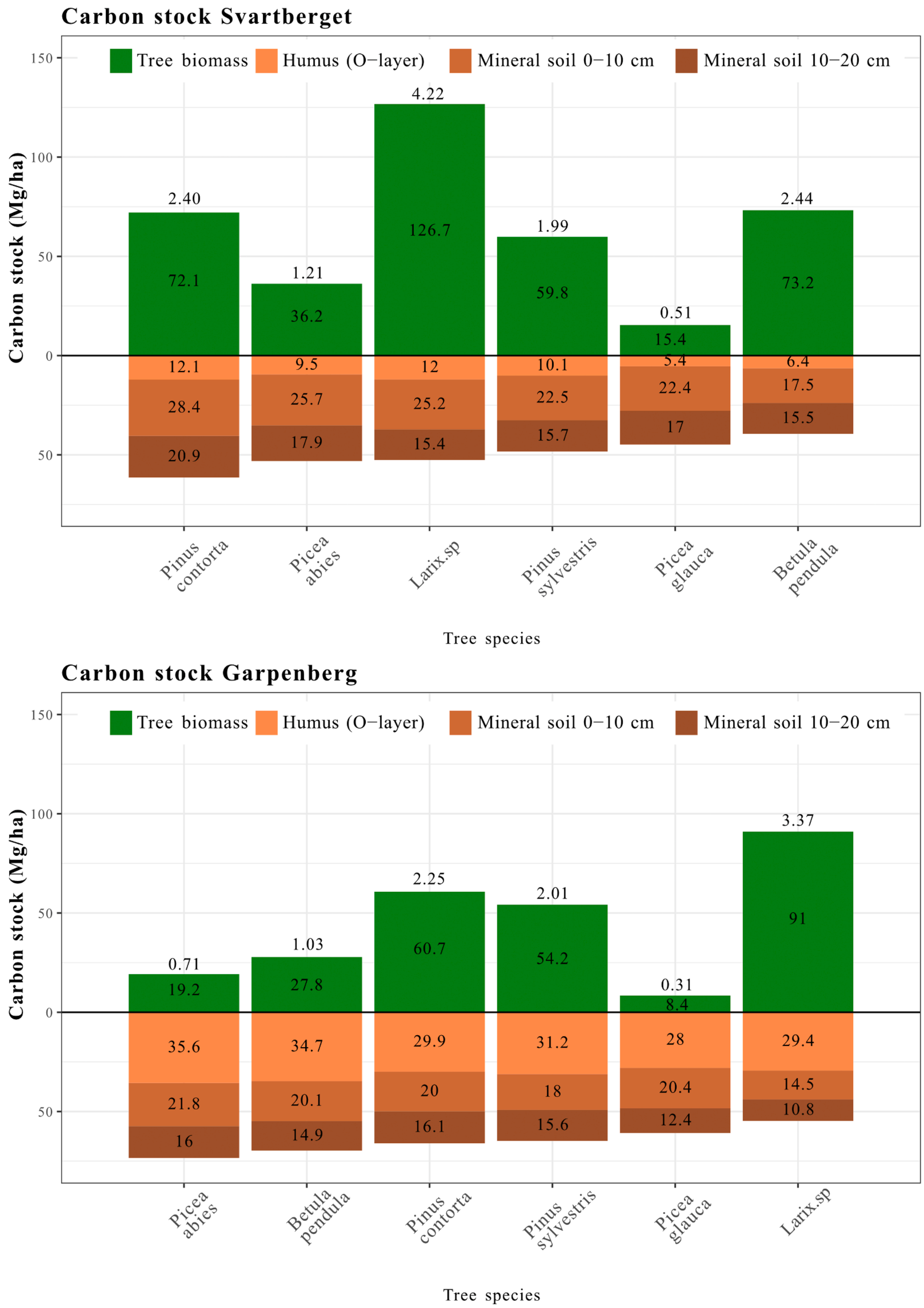

Fig. 3. The average amount of C stock in different ecosystem compartments for different tree species at Svartberget (n = 3 species^{-1}) and Garpenberg (n = 3 species^{-1}, except *Betula pendula* where n = 2). The species are organized in descending order, starting with the highest belowground C stock, numbers above bars show the average annual growth in above ground biomass C (Mg C ha^{-1} y^{-1}) since establishment, Svartberget is the most productive site for all tree species except *Pinus sylvestris*.

slope may be more important than tree species for the accumulation of total soil C. Despite these results, there is still an argument to be made that tree species choice can be beneficial as a tool to mitigate climate change. The aboveground biomass C stocks we observed were highly species specific and translated into significant differences in total ecosystem C stocks, which may in the long term also translate into more pronounced tree species effects on soil C. Our results are also in line with larger meta-analysis studies indicating that tree species could be chosen based on their site-specific growth potential, which can serve to maximize ecosystem carbon stocks, and in turn the climate mitigation potential of boreal forests.

CRediT authorship contribution statement

Marcus Larsson: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Clydecia M. Spitzer:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Michael J. Gundale:** Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization. **Annika Nordin:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Data curation, Conceptualization.

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Declaration of Competing Interest

Marcus Larsson reports financial support was provided by Stora Enso AB. Annika Nordin reports a relationship with Stora Enso AB that includes: employment. Co-author reports a previous relationship (2016–2020) with Sveaskog AB that included: board membership (A. N.). Co-author declare no conflicts of interest, and do not have any commercial affiliations (M.J.G. and C.M.S).

Appendix

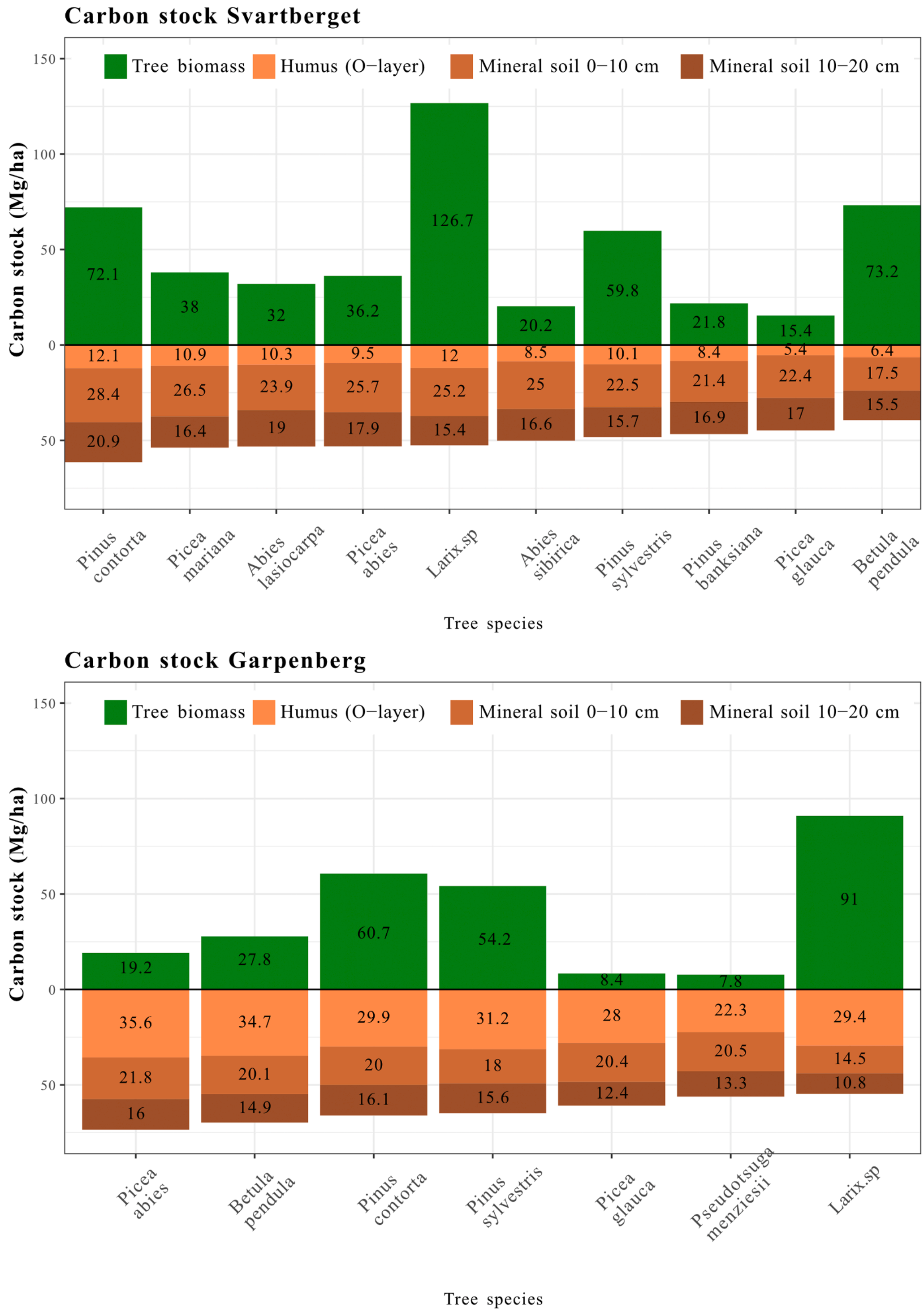

Fig. appendix 1. The average amount of C stock (Mg C ha) in different ecosystem compartments for all different tree species at Svartberget (n = 3 species^{-1}) and Garpenberg (n = 3 species^{-1}, except *Betula pendula* where n = 2). The species are organized in descending order, starting with the highest belowground C stock

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123060.

Data availability

Data will be made available on request.

References

Augusto, L., Boča, A., 2022. Tree functional traits, forest biomass, and tree species diversity interact with site properties to drive forest soil carbon. Nat. Commun. 13, 1097. https://doi.org/10.1038/s41467-022-28748-0.

Augusto, L., De Schrijver, A., Vesterdal, L., Smolander, A., Prescott, C., Ranger, J., 2015. Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests. Biol. Rev. 90, 444–466. https://doi.org/10.1111/brv.12119.

Augusto, L., Borelle, R., Boča, A., Bon, L., Orazio, C., Arias-González, A., Bakker, M.R., Gartzia-Bengoetxea, N., Auge, H., Bernier, F., Cantero, A., Cavender-Bares, J., Correia, A.H., De Schrijver, A., Diez-Casero, J.J., Eisenhauer, N., Fotelli, M.N., Gâteblé, G., Godbold, D.L., Gomes-Caetano-Ferreira, M., Gundale, M.J., Jactel, H., Koricheva, J., Larsson, M., Laudicina, V.A., Legout, A., Martín-García, J., Mason, W. L., Meredieu, C., Mereu, S., Montgomery, R.A., Musch, B., Muys, B., Paillassa, E., Paquette, A., Parker, J.D., Parker, W.C., Ponette, Q., Reynolds, C., Rozados-Lorenzo, M.J., Ruiz-Peinado, R., Santesteban-Insausti, X., Scherer-Lorenzen, M., Silva-Pando, F.J., Smolander, A., Spyroglou, G., Teixeira-Barcelos, E.B., Vanguelova, E.I., Verheyen, K., Vesterdal, L., Charru, M., 2025. Widespread slow growth of acquisitive tree species. Nature. https://doi.org/10.1038/s41586-025-08692-x.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2003. lme4: Linear Mixed-Effects Models using "Eigen" and S4. https://doi.org/10.32614/CRAN.package.lme4.

Berg, B., Ekbohm, G., 1993. Decomposing needle litter in Pinus-Contorta (lodgepole Pine) and Pinus-Sylvestris (Scots Pine) monocultural systems - is there a maximum Mass-Loss. Scand. J. For. Res. 8, 457–465. https://doi.org/10.1080/02827589309382792.

Berg, B., Johansson, M.-B., Ekbohm, G., McClaugherty, C., Rutigliano, F., Santo, A.V.D., 1996. Maximum decomposition limits of forest litter types: a synthesis. Can. J. Bot. 74, 659–672. https://doi.org/10.1139/b96-084.

Brunner, I., Bakker, M.R., Björk, R.G., Hirano, Y., Lukac, M., Aranda, X., Børja, I., Eldhuset, T.D., Helmisaari, H.S., Jourdan, C., Konôpka, B., López, B.C., Miguel Pérez, C., Persson, H., Ostonen, I., 2013. Fine-root turnover rates of european forests revisited: an analysis of data from sequential coring and ingrowth cores. Plant Soil 362, 357–372. https://doi.org/10.1007/s11104-012-1313-5.

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gorné, L.D., 2016. The global spectrum of plant form and function. Nature 529, 167–171. https://doi.org/10.1038/nature16489.

Finér, L., Ohashi, M., Noguchi, K., Hirano, Y., 2011. Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. For. Ecol. Manag. 262, 2008–2023. https://doi.org/10.1016/j.foreco.2011.08.042.

Forsmark, B., Nordin, A., Rosenstock, N.P., Wallander, H., Gundale, M.J., 2021. Anthropogenic nitrogen enrichment increased the efficiency of belowground biomass production in a boreal forest. Soil Biol. Biochem. 155, 108154. https://doi.org/10.1016/j.soilbio.2021.108154.

Gundale, M.J., Axelsson, E.P., Buness, V., Callebaut, T., DeLuca, T.H., Hupperts, S.F., Ibáñez, T.S., Metcalfe, D.B., Nilsson, M.-C., Peichl, M., Spitzer, C.M., Stangl, Z.R., Strengbom, J., Sundqvist, M.K., Wardle, D.A., Lindahl, B.D., 2024. The biological controls of soil carbon accumulation following wildfire and harvest in boreal forests: a review. Glob. Change Biol. 30, e17276. https://doi.org/10.1111/gcb.17276.

Hansen, K., Vesterdal, L., Schmidt, I.K., Gundersen, P., Sevel, L., Bastrup-Birk, A., Pedersen, L.B., Bille-Hansen, J., 2009. Litterfall and nutrient return in five tree species in a common garden experiment. For. Ecol. Manag. Tradit. For. Relat. Knowl. Asia 257, 2133–2144. https://doi.org/10.1016/j.foreco.2009.02.021.

Hansson, K., Fröberg, M., Helmisaari, H.-S., Kleja, D.B., Olsson, B.A., Olsson, M., Persson, T., 2013a. Carbon and nitrogen pools and fluxes above and below ground in spruce, pine and birch stands in Southern Sweden. For. Ecol. Manag. 309, 28–35. https://doi.org/10.1016/j.foreco.2013.05.029.

Hansson, K., Helmisaari, H.-S., Sah, S., Lange, H., 2013b. Fine root production and turnover of tree and understorey vegetation in Scots pine, silver birch and Norway spruce stands in SW Sweden. For. Ecol. Manag. 309, 58–65. https://doi.org/10.1016/j.foreco.2013.01.022.

Jenkins, J., Chojnacky, D., Heath, L., Birdsey, R., 2003. National scale biomass estimators for United States tree species. For. Sci. 49, 12–35. https://doi.org/10.1093/forestscience/49.1.12.

Kiikkilä, O., Kitunen, V., Smolander, A., 2006. Dissolved soil organic matter from surface organic horizons under birch and conifers: degradation in relation to chemical characteristics. Soil Biol. Biochem. 38, 737–746. https://doi.org/10.1016/j.soilbio.2005.06.024.

Kjønaas, O.J., Bárcena, T.G., Hylen, G., Nordbakken, J.-F., Økland, T., 2021. Boreal tree species change as a climate mitigation strategy: impact on ecosystem c and n stocks and soil nutrient levels. Ecosphere 12, e03826. https://doi.org/10.1002/ecs2.3826.

Kleja, D.B., Svensson, M., Majdi, H., Jansson, P.-E., Langvall, O., Bergkvist, B., Johansson, M.-B., Weslien, P., Truusb, L., Lindroth, A., 2008. Pools and fluxes of carbon in three Norway spruce ecosystems along a climatic gradient in Sweden.

Lenth, R.V., Banfai, B., Bolker, B., Buerkner, P., Giné-Vázquez, I., Herve, M., Jung, M., Love, J., Miguez, F., Piaskowski, J., Riebl, H., Singmann, H., 2025. emmeans: Estimated Marginal Means, aka Least-Squares Means.

Liski, J., Nissinen, A., Erhard, M., Taskinen, O., 2003. Climatic effects on litter decomposition from Arctic tundra to tropical rainforest. Glob. Change Biol. 9, 575–584. https://doi.org/10.1046/j.1365-2486.2003.00605.x.

Mareschal, L., Bonnaud, P., Turpault, M.P., Ranger, J., 2010. Impact of common european tree species on the chemical and physicochemical properties of fine earth: an unusual pattern. Eur. J. Soil Sci. 61, 14–23. https://doi.org/10.1111/j.1365-2389.2009.01206.x.

Marklund, L.G., 1988. Biomassafunktioner för tall, gran och björk i Sverige: Biomass functions for pine, spruce and birch in Sweden. Umeå.

Matala, J., Kellomäki, S., Nuutinen, T., 2008. Litterfall in relation to volume growth of trees: analysis based on literature. Scand. J. For. Res. 23, 194–202. https://doi.org/10.1080/02827580802036176.

Mayer, M., Prescott, C.E., Abaker, W.E.A., Augusto, L., Cécillon, L., Ferreira, G.W.D., James, J., Jandl, R., Katzensteiner, K., Laclau, J.-P., Laganière, J., Nouvellon, Y., Paré, D., Stanturf, J.A., Vanguelova, E.I., Vesterdal, L., 2020. Tamm review: influence of forest management activities on soil organic carbon stocks: a knowledge synthesis. For. Ecol. Manag. 466, 118127. https://doi.org/10.1016/j.foreco.2020.118127.

Merilä, P., Lindroos, A.-J., Helmisaari, H.-S., Hilli, S., Nieminen, T.M., Nöjd, P., Rautio, P., Salemaa, M., Ťupek, B., Ukonmaanaho, L., 2024. Carbon stocks and transfers in coniferous boreal forests along a latitudinal gradient. Ecosystems 27, 151–167. https://doi.org/10.1007/s10021-023-00879-5.

Muff, S., Nilsen, E.B., O'Hara, R.B., Nater, C.R., 2022. Rewriting results sections in the language of evidence. Trends Ecol. Evol. 37, 203–210. https://doi.org/10.1016/j.tree.2021.10.009.

Nilsson, P., Kempe, G., Toet, H., Petterson, H., 2008. Skogsdata 2008: aktuella uppgifter om de svenska skogarna från riksskogstaxeringen: tema: skogens roll för klimatet. Skogsdata.

Nilsson, P., Roberge, C., Dahlgren, J., Fridman, J., 2022. Skogsdata 2022. Tema: den formellt skyddade skogen. Skogsdata.

Nilsson, T., Lundin, L., 2006. Uppskattning av volymvikten i svenska skogsjordar från halten organiskt kol och markdjup.

Oostra, S., Majdi, H., Olsson, M., 2006. Impact of tree species on soil carbon stocks and soil acidity in Southern Sweden. Scand. J. For. Res. 21, 364–371. https://doi.org/10.1080/02827580600950172.

Påhlsson, L., 1995. Vegetationstyper i Norden. Nordiska Ministerrådet, Köpenhamn.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the World's forests. Science 333, 988–993. https://doi.org/10.1126/science.1201609.

Prescott, C., 2010. Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? Biogeochemistry 101, 133–149. https://doi.org/10.1007/s10533-010-9439-0.

Prescott, C., Vesterdal, L., Preston, C., Simard, S., 2004. Influence of initial chemistry on decomposition of foliar litter in contrasting forest types in British Columbia. Can. J. For. Res. 34, 1714–1729. https://doi.org/10.1139/X04-040.

Prescott, C.E., Vesterdal, L., 2013. Tree species effects on soils in temperate and boreal forests: emerging themes and research needs. For. Ecol. Manag. 309, 1–3. https://doi.org/10.1016/j.foreco.2013.06.042.

Prescott, Cindy E., Maynard, D.G., Laiho, R., 2000. Humus in Northern forests: friend or foe? For. Ecol. Manag. 133, 23–36. https://doi.org/10.1016/S0378-1127(99)00295-9.

R Core Team, 2024. R: The R Project for Statistical Computing [WWW Document]. URL ⟨https://www.r-project.org/⟩ (accessed 6.14.22).

Reich, P.B., Walters, M.B., Ellsworth, D.S., 1997. From tropics to tundra: global convergence in plant functioning. Proc. Natl. Acad. Sci. 94, 13730–13734. https://doi.org/10.1073/pnas.94.25.13730.

Skogsdata, 2017. Skogsdata 2017. Aktuella uppgifter om de svenska skogarna från riksskogstaxeringen. Institutionen för skogslig resurshushållning, Sveriges lantbruksuniversitet, Umeå.

SMHI [WWW Document], 2025. SMHI. URL ⟨https://www.smhi.se/⟩ (accessed 4.11.25).

Spitzer, C.M., Jämtgård, S., Larsson, M.J., Gundale, M.J., 2025. Aboveground and belowground trait coordination across twelve boreal forest tree species. Sci. Rep. 15, 680. https://doi.org/10.1038/s41598-024-84162-0.

Stendahl, J., Lundin, L., Nilsson, T., 2009. The stone and boulder content of Swedish forest soils. CATENA 77, 285–291. https://doi.org/10.1016/j.catena.2009.02.011.

Verstraeten, G., Vancampenhout, K., Desie, E., De Schrijver, A., Hlava, J., Schelfhout, S., Verheyen, K., Muys, B., 2018. Tree species effects are amplified by clay content in acidic soils. Soil Biol. Biochem. 121, 43–49. https://doi.org/10.1016/j.soilbio.2018.02.021.

Vesterdal, L., Clarke, N., Sigurdsson, B.D., Gundersen, P., 2013. Do tree species influence soil carbon stocks in temperate and boreal forests? (Influence of tree species on forest soils: New evidence from field studies). For. Ecol. Manag. 309, 4–18. https://doi.org/10.1016/j.foreco.2013.01.017.

Viro, P.J., 1952. Kivisyyden Määrittämisestä (On determination on stoniness), 40. Communicationes Instituti Forestalis Fenniae, pp. 1–19 (1952).

Weigelt, A., Mommer, L., Andraczek, K., Iversen, C.M., Bergmann, J., Bruelheide, H., Fan, Y., Freschet, G.T., Guerrero-Ramírez, N.R., Kattge, J., Kuyper, T.W., Laughlin, D.C., Meier, I.C., Van Der Plas, F., Poorter, H., Roumet, C., Van Ruijven, J., Sabatini, F.M., Semchenko, M., Sweeney, C.J., Valverde-Barrantes, O.J., York, L.M., McCormack, M.L., 2021. An integrated framework of plant form and function: the belowground perspective. N. Phytol. 232, 42–59. https://doi.org/10.1111/nph.17590.

Withington, J.M., Reich, P.B., Oleksyn, J., Eissenstat, D.M., 2006. Comparisons of structure and life span in roots and leaves among temperate trees. Ecol. Monogr. 76, 381–397. https://doi.org/10.1890/0012-9615(2006)076[0381:COSALS]2.0.CO;2.

Xu, S., Liu, L.L., Sayer, E.J., 2013. Variability of above-ground litter inputs alters soil physicochemical and biological processes: a meta-analysis of litterfall-manipulation experiments. Biogeosciences 10, 7423–7433. https://doi.org/10.5194/bg-10-7423-2013.

Yuan, Z.Y., Chen, H.Y.H., 2010. Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: literature review and Meta-Analyses. Crit. Rev. Plant Sci. 29, 204–221. https://doi.org/10.1080/07352689.2010.483579.

Zhang, D., Hui, D., Luo, Y., Zhou, G., 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. J. Plant Ecol. 1, 85–93. https://doi.org/10.1093/jpe/rtn002.

Zianis, D., Muukkonen, P., Mäkipää, R., Mencuccini, M., 2005. Biomass and stem volume equations for tree species in Europe. Silva Fenn. Monogr. 2005, 1–63. https://doi.org/10.14214/sf.sfm4.