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Birch distribution and changes in stand structure in Sweden's young forests

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ABSTRACT

Silver birch (*Betula pendula* Roth) and downy birch (*Betula pubescens* Ehrh.) are the two most common broadleaf species in Sweden, together making up approximately 12% of the standing timber volume. The two birch species are usually not distinguished in practice, although they tend to differ in terms of volume production, timber quality, and site preferences. To map the proportion of the two birch species in Sweden's young forests, we used survey data from 123 stands 6–7 years after clearfelling, and data from Sweden's meteorological and hydrological institute. We also examined Sweden's young forests in terms of area, volume, and stem density between 1983 and 2021, using national forest inventory data. Proportions of the two birch species varied significantly across Sweden, and the average temperature sum over the first five years after clearfelling explained 72% of the variation. There was no significant change in area of forest classified as young forest in Sweden, over the last four decades, although there was a significant increase in volume and stem density in Sweden's young forests, with birch making up most of the increase in stem numbers.

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Introduction

Silver birch (*Betula pendula* Roth) and downy birch (*Betula pubescens* Ehrh.) are the most common deciduous tree species in Sweden and together account for approximately 12% of total standing timber volume (SLU 2023). Naturally regenerated birch is commonly found in mixtures with coniferous tree species (Holmström *et al.* 2019; Holmström *et al.* 2021; Huuskonen *et al.* 2021; Lee *et al.* 2023), but it is also common in stand edges, riparian zones, and green tree retention forestry (Vanha-Majamaa and Jalonen 2001; Felton *et al.* 2016; Holmström *et al.* 2016b). The two birch species are not usually distinguished in forestry operations and surveys (SLU 2023), even though silver birch is known to exhibit higher stem growth and quality (Heräjärvi 2001). One explanation for this is that the phenology of the two birch species can be similar and identification is time-consuming and imprecise when the tree is over 20 years of age (Lundgren *et al.* 1995; Eriksson *et al.* 1996). Unless otherwise specified, the term birch hereafter refers to both species.

The Swedish National Forest Inventory (NFI) differentiates between the two species in their registration of sample trees and shows that downy birch is the most common birch species in Sweden (Riksskogstaxeringen 2022). It has been suggested that downy birch is more efficient at seed production than silver birch, and more so in the northern areas of Fennoscandia (Rousi *et al.* 2019). Silver birch is known to prefer more sandy and silty soils than downy birch, as it is more sensitive to flooding. Downy birch is more often found on sites with less favourable conditions, on more compact, poorly aerated soils and peatlands (Sutinen *et al.* 2002).

Rotational forestry in Fennoscandia relies mainly on soil scarification followed by planting, of either Norway spruce (*Picea abies* H. Karst.) or Scots pine (*Pinus sylvestris* L.) (Luke 2020; Skogsstyrelsen 2024). The planted forests are diversified through natural regeneration during a stand's development, mainly by broadleaves such as birch (Holmström *et al.* 2016a; Ara *et al.* 2021). The most common method for birch regeneration in Fennoscandia is natural regeneration, although planting and seeding of silver birch does occur (Cameron 1996; SLU 2023; Skogsstyrelsen 2024). Birch can easily establish spontaneously on clear felled areas due to seed dispersal from surrounding forests (Karlsson 2001; Holmström *et al.* 2016a). This occurs even without soil scarification (Perala and Alm 1990; Holgén and Hånell 2000; Götmark *et al.* 2005) but becomes more abundant with increasing soil disturbance e.g. after soil scarification which creates patches of bare mineral soil (Fries 1984; Karlsson and Nilsson 2005; Lidman *et al.* 2023). Soil scarification decreases the competition with surrounding vegetation for water (Örlander *et al.* 1990; Karlsson 2003; Johansson *et al.* 2013), and increases the establishment and survival rate of seedlings (Karlsson 2002; Karlsson and Nilsson 2005). The interaction between soil moisture and choice of soil scarification method also has an impact on germination success (Nilsson *et al.* 2002; Lidman *et al.* 2023).

Until recently, birch and other broadleaf species lacked economic value within Swedish forestry and were removed to promote the growth of conifers. Higher demand and prices for coniferous timber was a driving factor in the active removal of broadleaved species, particularly birch

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and aspen (*Populus tremula* L.) (Östlund *et al.* 2022). More recently, the value and use of birch wood in the Swedish forest industry has increased considerably (Woxblom and Nylinder 2010; Skogsstyrelsen 2014; Skogsstyrelsen 2024).

The objectives of this study were to map the area and composition of Sweden's young forests over the past 40 years, and the proportion of birch saplings today. We used long term data from the Swedish NFI and conducted a birch survey which focused on mapping the proportions of birch species on clearcuts across the country.

Material and methods

National forest inventory data

Data about Sweden's young forests was provided by the Swedish National Forest Inventory (NFI) (Riksskogstaxeringen 2022). In this study, young forest was defined as the NFI classifications B2 (plots with an average tree height between 1.3 and 3 m) and B3 (plots with an average tree height over 3 m, with several dominating and co-dominant trees of less than 10 cm diameter). Sample plot data was provided for all plots in the NFI classes B2 and B3 between the years 1983 and 2021. For a thorough explanation of the procedures and methods used to compile the Swedish National Forest inventory, see Fridman *et al.* (2014).

Layout of the birch survey

A grid with a side of 130 km was placed over a map of Sweden (Figure 1), and 13 sample nodes selected, ranging from the northern region "Jokkmokk" (66.61° N, 19.82° E) to "Växjö" (56.87° N, 14.80° E), in the south. In each region, 10 clear felled sites within 30 km of the sample node were randomly selected. The sites were found using the Swedish Forest Agency's open-source database of clearfellings (Skogsstyrelsen 2022), which is based on detection of forest canopy changes using satellite imagery. All clearfellings selected as sites were at least two hectares in size, classified as forest clearfellings with intentional artificial regeneration, and harvested in 2014. All sites were inventoried between the autumn of 2019 and the spring of 2020. Before the field inventory, all sites were examined, using the most current orthophoto in ArcMap, to identify anomalies such as non-traditional harvesting measures. If a clearfelled site turned out to be a shelterwood or some other type of partially harvested site, it was replaced with a new randomly selected site.

A second smaller grid with a side of 30 m was placed over each site, each node in the grid representing a potential centre point for a sample plot with a radius of 1.5 m. The first 20 sample plots that were at least 10 m from the clearcut edge were inventoried, starting from the south and heading north. The southernmost part of the clearcut was ignored and the starting point moved further north if that part of the clearcut was some sort of mire or peatland, or a set aside for nature conservation purposes. Only plots on mineral soil were included.

With this random selection method, both the ownership and accessibility of the sites identified were unknown. Some sites were subsequently excluded because private forest roads were gated, meaning that the final number of sites varied between regions from 7 to 10.

Variables measured in the field survey

All seedlings of all tree species on the sample plots taller than 0.2 m were recorded by species. Silver birch and Downy birch were differentiated by inspecting the bark of year-old shoots and leaves. Silver birch generally has yearly shoots with a warty and uneven texture, while downy birch usually has smooth bark with a hairy texture (Raulo 1987; Ashburner and McAllister 2016). The mean heights of the two highest seedlings of each species were measured per sample plot. Where only one seedling of a species was present, this was measured and used for the mean value estimate. Soil moisture class (dry, dry-mesic, mesic, moist, or wet) (Hägglund and Lundmark 1981) and the percentage of bedrock covering the area of the sample plot were recorded at plot level. Auxiliary data at stand level were also recorded, including the species of planted seedlings, occurrence of soil scarification, signs of notable browsing pressure, and whether or not harvest residues (tops, branches etc.) had been removed prior to planting. If a stand had been pre-commercially thinned, it would have been excluded from the inventory.

Regional climate features of the field survey

The weather data used were produced by the Swedish Meteorological and Hydrological Institute (SMHI), and were based on the re-analysis of meteorological observations conducted by the European FP7 project (https://www.uerra.eu). Temperature sum was defined as the daily sum of temperature in degrees Celsius, exceeding 5°C, and thereafter summarised by month and year. The weather attributes were calculated for the centre of each sample node, and used as regional climate features, with monthly data summarised as annual values for selected years or five-year averages (Table 1. and Table A, in Appendix).

Data analysis

Proportions in Sweden's young forests

Data from the Swedish national forest inventory was used to test the significance of changes in area, volume and stem density in Sweden's young forests between the sampling periods 1983–1987 and 2017–2021. A Wilcoxon matched-pairs test was performed to compare five-year means of area (hectares) of young forest, using Sweden's 21 counties as sampling units. A Wilcoxon rank sum (also known as Mann–Whitney) test was conducted to test the difference in stem density (stems) and standing volume (m^3) per tract (a standard NFI sampling unit) weighted by area, for each year. These two forms of tests were used since the data was not normally distributed. The package *stats* (R Core Team 2022) was used to carry out the tests, with a significance level of $p < 0.05$.

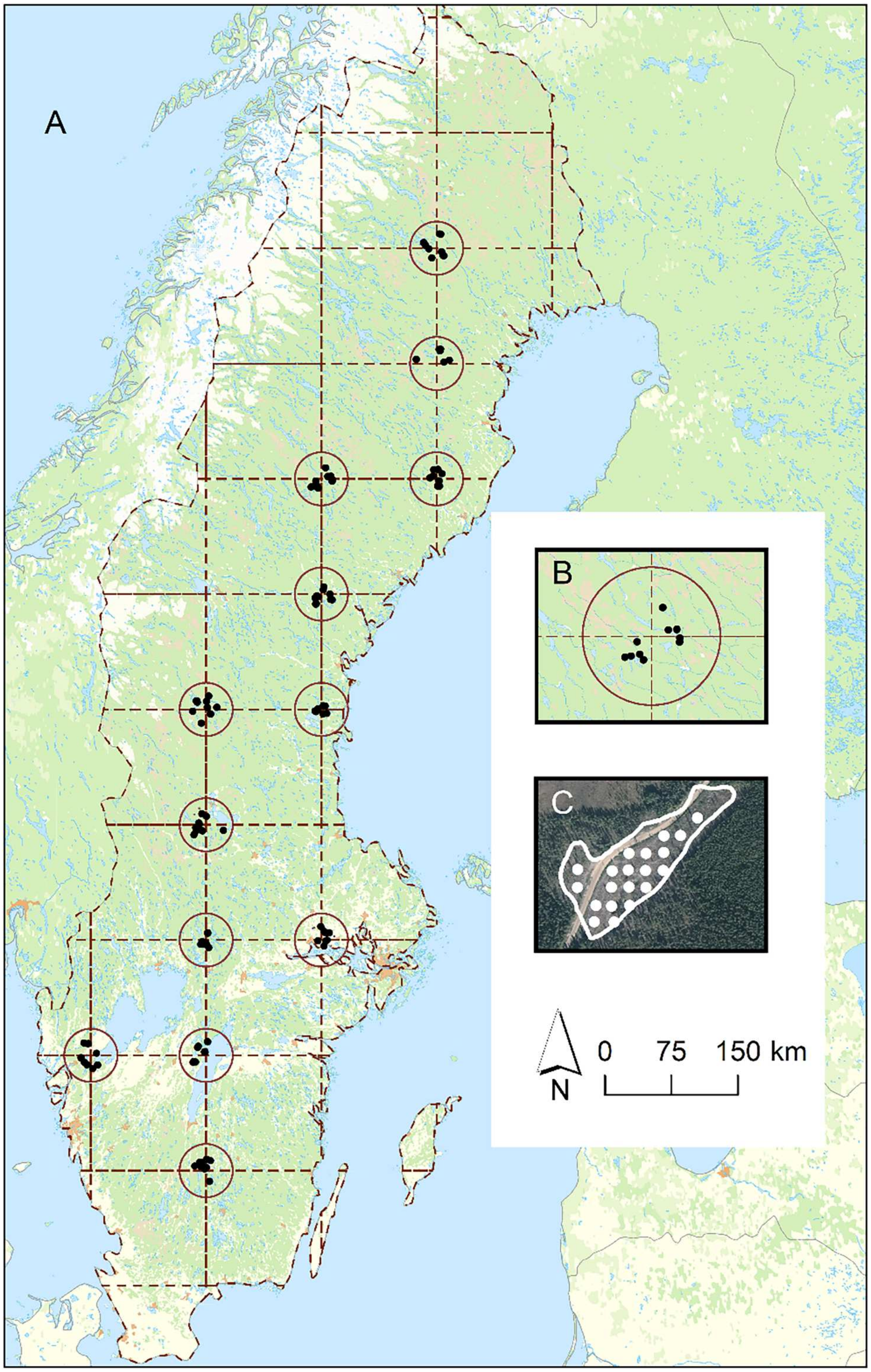

Figure 1. The distribution of (A) the survey sample nodes over Sweden, illustrated by (B) sites within the sample node, and (C) sample plots on one of the sites.

Abundance of birch and proportion of birch species

Seedling density, tree species proportion (%), and the dominant birch species were retrieved from the inventory data per sample plot. Then, the mean values for each clearcut were calculated using the plot values. The regional average was calculated as the arithmetic mean of the sites in each sampling node. The relative distribution of the two birch species was calculated, both in terms of abundance (the proportion of seedling numbers) and in terms of growth advantage (the proportion of the highest seedling on each plot).

Regression models were used to evaluate whether features of the regional climate could explain the variation in the proportion of silver birch and differences between regions Equation (1).

$$Y = f(\textit{regional climate features}_i) + \varepsilon \quad (1)$$

Table 1. List of regional climate features that were tested in the linear model Equation (1).

Abbreviations	*Regional climate features*	Unit
$Tsum_m$	Average temperature sum for the first five years after clearfelling	°C
$Tsum_0$	Temperature sum for the year of clearfelling	°C
$Tsum_1$	Temperature sum for the year after clearfelling	°C
$PVsum_0$	Sum of precipitation during the vegetation period the year of clearfelling	mm
$Psum_1$	Sum of precipitation for the year after clearfelling	mm
$PVsum_m$	Average sum of precipitation during the vegetation period in the first five years after clearfelling	mm
$Psum_m$	Average sum of precipitation for the first five years after clearfelling	mm
Lat	Latitude of each sample node	Decimal degrees

where the response variable *Y* was the average proportion of silver birch seedlings in all birch seedlings calculated for each site and then region, and thereafter arcsine transformed to fulfil the assumption of normality. The various *regional climate features* (Table 1) were tested in the model after finding correlations with the response variable using the visual analysis function *ggpairs* from the *GGally* package (Schloerke *et al.* 2021). No interactions between the *regional climate features* were tested in Equation (1) since there was no way to rule out correlations. The package *car* (Fox and Weisberg 2019) was used to carry out analysis of variance, with a significance level of $p < 0.05$. All statistical tests were carried out using R 4.2.2 (R Core Team 2022).

Results

National forest inventory data

The stem density in Sweden's young forest changed significantly between the periods 1983–1987 and 2017–2021 (Table 2), with the five-year mean increasing from 3800 to 6500 st ha^{-1}. Birch represented the largest increase in stem density, the five-year mean increasing from 1800 to 3600 st ha^{-1} (Figure 2). However, the stem density of birch in young forests moved in two directions during this period: the area with zero birch increased from 26% to 32% while the area with high stem density more than doubled. The area with more than 5000 birch st ha^{-1} increased from 10% to 24% and the area with more than 10.000 birch st ha^{-1}, increased from 4% to 11%. Standing volume per hectare in the young forest changed significantly between the periods 1983–1987 and 2017–2021 for all tree species combined (Table 2), with the five-year mean increasing from 21 to 37 m^3 ha^{-1} (Figure 3). The species displaying the greatest increase in volume were Norway spruce, birch, and Scots pine, the five-year means increasing from 6 to 11, 5 to 9, and 9 to 12 m^3 ha^{-1} respectively (Figure 3). However, there was no significant change in total area of young forest in Sweden between the two periods (Figure 4, Table 2).

Table 2. Summary output from a Wilcoxon matched-pairs test comparing five-year means of area of young forest between 1983–1987 and 2017–2021, using Sweden's 21 counties as sampling units, and summary outputs of Wilcoxon rank sum (Mann-Whitney) tests comparing the yearly area weighted stem density and volume of Sweden's young forests between the periods 1983–1987 and 2017–2021, for all species combined.

Variable (unit)		V/W	*p*-value
Area (hectares)	*All tree species*	160	0.128
Volume (m^3/tract)	*All tree species*	3153360	<0.001
Stem density (st/tract)	*All tree species*	3162541	<0.001

Note: Using the national forest inventory's "tracts" as sampling units.

Abundance of birch and proportion of birch species across Sweden

In total, our survey included 123 clearfelled sites. Most sites were planted with either Scots pine (68 sites), Norway spruce (32 sites), or the two in combination (6 sites), lodgepole pine (*Pinus contorta* Bol.) (5 sites), or no signs of planting (12 sites), 6 or 7 years after harvest. We found indications of soil scarification on 85% of the sites (Table 3). Naturally regenerated birch was found on all but two sites, at densities varying between 127 and 6422 saplings ha^{-1} for silver birch, and 643–10,143 saplings ha^{-1} for downy birch (Table 4). Birch was the most abundant naturally regenerated tree species followed by aspen (*Populus tremula* L.), rowan (*Sorbus aucuparia* L.) and willow (*Salix caprea* L.). The two birch species varied significantly in their distribution across the country, with an increasing proportion of silver birch with increasing temperature sum (Figure 5, Table 5). Out of the tested climate features, the model Equation (1) using mean temperature sum for the first five years after clearfelling ($Tsum_m$) produced the highest degree of explanation for the variation in birch species proportions with $R^2 = 0.72$ (Table 5).

Discussion

Young forest in Sweden has become denser, and the NFI data shows that this mainly is due to an increase in birch stems (Figure 2, Table 2). Similarly, the standing volume in the young forest has increased significantly. However, the main increase in volume comes from Norway spruce, Birch and Scots pine combined (Figure 3, Table 2). Young forest contains 70% more volume today than in 1993 and the volume of birch has almost doubled over the past 30 years (Figure 3). The combination of increased volume and stem density reflects a change in how young forests are managed.

One possible explanation for the increase in birch is that, in this century, pre-commercial thinning (PCT) in Sweden is done at greater mean height than in earlier times (Skogsstyrelsen 2014; SLU 2023). Before changes to the Swedish Forestry Act in 1993, stem density in young forests was regulated (SFS 1979, 1993). The ban on using phenoxy acids (*Hormoslyr* in Swedish or *Agent Orange* in English) on a large scale in Swedish forests during the 1970s (Bärring 1978; Lisberg Jensen 2006), is another potential explanation to the increase in stem density of deciduous species such as birch. A further explanation is the recent intensification and increasingly common use of soil scarification compared with regeneration practices in the 1980s. The most common method of soil scarification in Sweden today is disc trenching (Bergqvist *et al.* 2011; Hansson *et al.* 2017). Disc trenching creates continuous rows or harrows, with

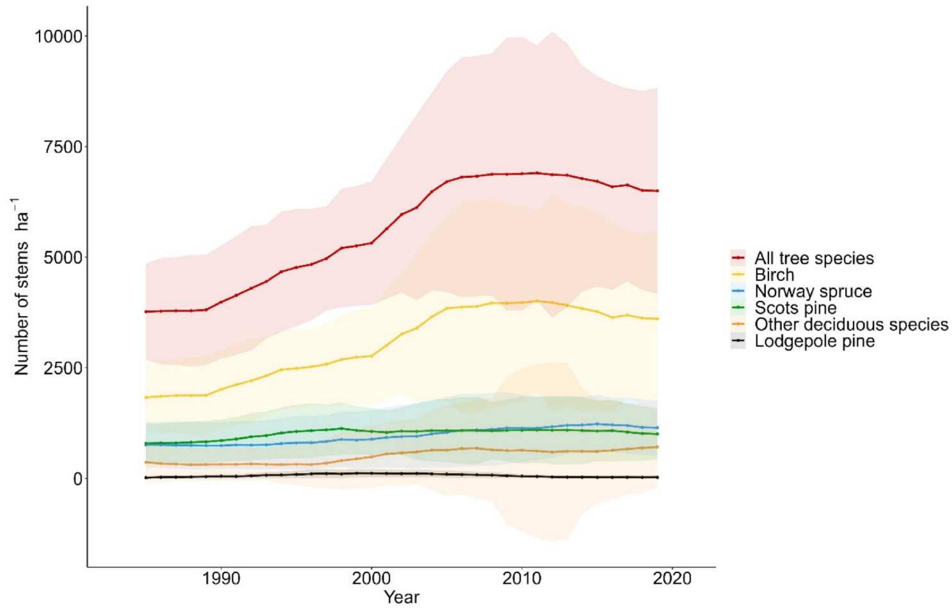

Figure 2. Five-year mean stem density in Sweden's young forests between 1985 and 2019 for each tree species and all species combined: the shaded area shows standard deviation.

larger areas of bare mineral soil or disturbed soil than from the intermittent methods used in the past (Örlander *et al.* 1990). Greater soil disturbance, as produced by current forest regeneration methods, favours natural regeneration of birch (Fries 1984; Karlsson and Nilsson 2005; Lidman *et al.* 2023). Although there was no significant change in young forest area between the periods 1983–1987 and 2017–2019, there were large fluctuations interim (Figure 4, Table 2). The increase and decrease in area of young forest in northern and middle Sweden between 1983 and 2021 follows the increase and decrease in clearfelled area that occurred between 1960 and 1980 with a time lag (Figure 4). The lag effect arises from the different lengths of time for which stands are classified as young forest (several years) or as clear felled (just a couple of years). It is not uncommon for stands older than 35 years to fit the NFI's definition of a young forest in northern Sweden, due to harsh growing conditions and low productivity (SLU 2023).

There was a significant difference in the numbers of naturally regenerated silver and downy birch seedlings in different parts of Sweden (Figure 5, Table 5). The mean temperature sum for the first five years after clearfelling ($Tsum_m$) explained 72% of the variation in the proportion of the two birch species across the country (Table 5). The effects of several

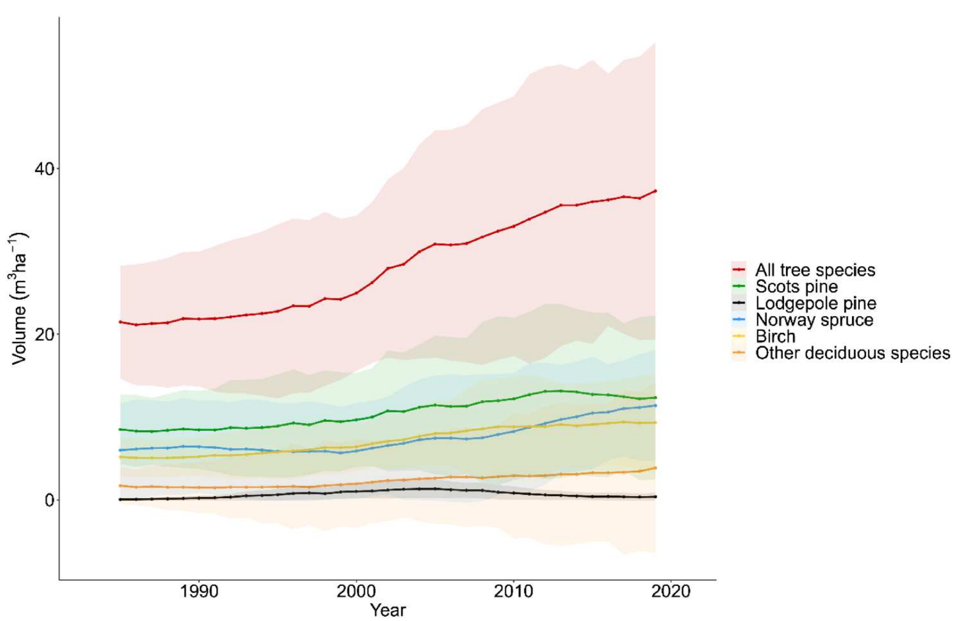

Figure 3. Five-year mean of standing volume in Sweden's young forests between 1985 and 2019 for each tree species and all species combined: the shaded area shows standard deviation.

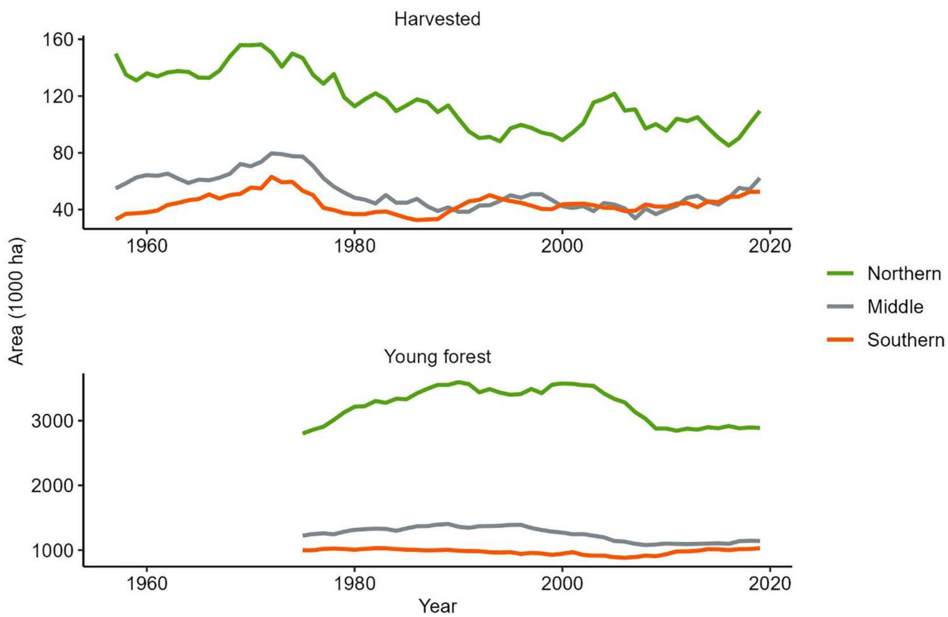

Figure 4. Clearfelled area between 1957 and 2019, and area of young forest between 1975 and 2019, for Sweden´s northern, middle and southern parts, in five-year means from the Swedish NFI. Y-axis with differing scales. Young forest is defined as the NFI classifications B2 (plots with an average height between 1.3 and 3 m) and B3 (plots with an average height over 3 m, with several dominating and co-dominant trees of less than 10 cm in diameter). Northern Sweden includes the counties: Norrbotten, Västerbotten, Jämtland, Västernorrland and Gävleborg. Middle Sweden includes: Dalarna, Värmland, Örebro, Västmanland, Uppsala, Södermanland, Stockholm. Southern Sweden includes: Västergötland, Östergötland, Gotland, Jönköping, Kalmar, Halland, Kronoberg, Blekinge, Skåne.

other climate features (Table 1), i.e. annual precipitation and precipitation sum during the vegetation period, were also tested in the model, but $Tsum_m$ produced the highest degree of explanation for the variation in seedling numbers between species across the country (Table 5). The NFI data for proportion by volume shows a similar pattern at the regional scale (far north, north, central, and southern regions of Sweden) with the proportion of downy birch increasing as one moves further north (Riksskogstaxeringen 2022). The temperature sum generally decreases with increasing latitude in Sweden, provided that all other conditions are equal. However, in this study, latitude alone only explained 47% of the variation in the proportion between the two birch species across the country (Table 5). A possible explanation for this is that the temperature sum, which explains most of the variation in proportion of the two birch species, also correlates with latitude in a more complex way, since it also depends on other factors such as distance to the coast and altitude. The most common birch species across the entire country was downy birch: this aligns with data from the NFI (Riksskogstaxeringen 2022) which also shows downy birch as dominant. However, when considering the tallest birch seedling per plot rather than the total number of birch seedlings on each sample plot, the difference between the two species seems to decrease (Figure 5). The species of the tallest seedling is likely to be a better predictor of the proportions of the two birch species in the future stand. Birch has a tendency to self-thin if a stand is to become too dense (Hynynen 1993; Lidman *et al.* 2021) as it is a shade-intolerant pioneer species (Nygren and Kellomäki 1983; Fischer *et al.* 2002; Hynynen *et al.* 2009). The sample plots was only 1.5 m in radius, so it is likely that the tallest seedling in each plot has the best chance of surviving and outcompeting other seedlings.

Table 3. Latitude, number of sites planted with each species, number of sites with signs of soil scarification, and soil moisture class per plot by region.

Sample node Region name	Latitude Decimal degrees	No. sites planted with *Picea abies*	*Pinus sylvestris*	*Pinus Contorta*	*Pinus sylvestris* & *Picea abies*	No. of sites Without planting	with soil scarification	No. of sample plots With soil moisture class Dry/Mesic/moist-Wet
Jokkmokk	66.55	0	10	0	0	0	10/10	0/187/13
Piteå	65.39	0	7	0	0	0	7/7	0/136/4
Åsele	64.29	0	10	0	0	0	10/10	3/147/50
Vindeln	64.23	3	2	5	0	0	7/10	0/142/58
Sollefteå	63.13	0	7	0	2	1	9/10	6/181/13
Sveg	61.97	0	8	0	0	2	5/10	0/199/1
Hudiksvall	61.95	2	6	0	0	0	7/8	0/157/3
Mora	60.80	2	6	0	2	0	10/10	1/194/4
Storfors	59.64	4	4	0	2	0	9/10	0/177/23
Västerås	59.63	3	3	0	0	2	6/8	0/152/5
Skövde	58.47	3	4	0	0	3	9/10	0/165/15
Trollhättan	58.44	6	0	0	0	4	6/10	10/124/66
Växjö	57.30	9	1	0	0	0	10/10	0/181/19

Table 4. Recorded species composition in the form of average number of stems per species, hectare and region, and average height (dm) of the two tallest seedlings in each plot for each region within brackets.

Region name	*Betula pendula*	*Betula pubescens*	*Picea abies*	*Pinus sylvestris*	*Sorbus aucuparia*	*Populus tremula*	*Salix caprea*	Other species	All species
Jokkmokk	127 (8)	955 (9)	56 (7)	1896 (4)	14 (4)	205 (7)	311 (6)	0	3565
Piteå	141 (5)	1101 (5)	60 (2)	1890 (5)	70 (4)	101 (6)	283 (4)	0	3648
Åsele	226 (5)	2978 (6)	85 (16)	1676 (5)	340 (5)	269 (6)	290 (5)	7 (10)	5871
Vindeln	3359 (9)	10143 (8)	1188 (6)	1259 (7)	764 (4)	332 (6)	856 (5)	56 (19)	17960
Sollefteå	2058 (10)	4336 (9)	1103 (7)	1450 (8)	1995 (7)	1344 (9)	629 (6)	290 (17)	13206
Sveg	1011 (8)	643 (6)	35 (5)	4032 (5)	0	127 (6)	85 (3)	14 (11)	5949
Hudiksvall	3227 (14)	2838 (12)	734 (9)	1203 (8)	2661 (14)	716 (24)	530 (13)	35 (24)	11945
Mora	868 (8)	4125 (8)	747 (8)	4102 (8)	446 (5)	1135 (10)	2632 (5)	14 (60)	13666
Storfors	1676 (15)	2936 (15)	1902 (9)	1719 (6)	248 (7)	99 (10)	340 (9)	49 (13)	8969
Västerås	3916 (15)	2398 (11)	1638 (11)	1880 (9)	1227 (9)	3434 (10)	782 (11)	849 (9)	15615
Skövde	6423 (15)	5036 (13)	1860 (9)	5461 (7)	870 (8)	594 (11)	962 (9)	176 (9)	21383
Trollhättan	3919 (15)	5298 (11)	1860 (11)	1655 (9)	3374 (9)	1924 (10)	1118 (11)	112 (9)	20655
Växjö	1613 (14)	5390 (14)	2242 (11)	1323 (6)	622 (7)	219 (8)	332 (7)	7 (3)	11749

Note: Other species = Alnus incana, Alnus glutinosa, Fagus sylvatica & Sorbus intermedia.

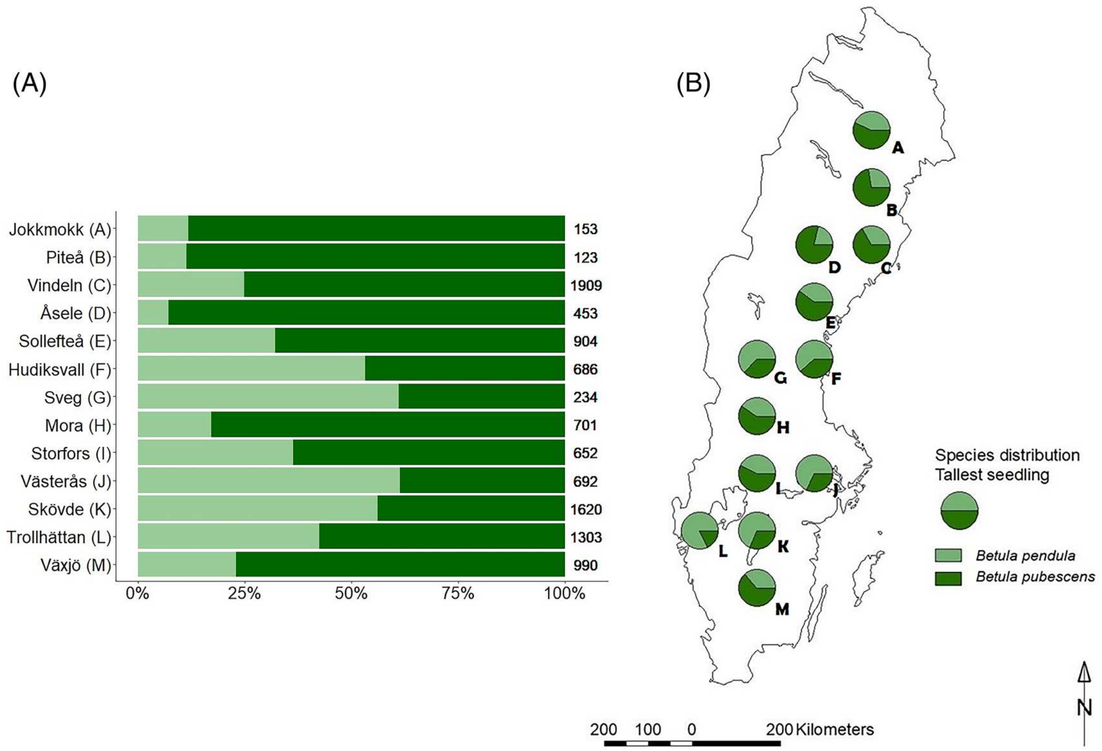

Figure 5. Panel A. The proportion of silver birch (*Betula pendula*) and downy birch (*Betula pubescens*) seedlings in stem numbers per region, moving north to south. Total number of birches found in each region is given to the right of each bar. Panel B. The proportion of silver birch (*Betula pendula* Roth) and downy birch (*Betula pubescens* Ehrh.) for the tallest seedling on each plot, for each region: A, Jokkmokk; B, Piteå; C, Vindeln; D, Åsele; E, Sollefteå; F, Hudiksvall; G, Sveg; H, Mora; I, Storfors; J, Västerås; K, Skövde; L, Trollhättan; M, Växjö.

Naturally regenerated broadleaf species within a planted conifer stand can be used by forest owners to create a mixed species stand without additional costs (Holgén and Hånell 2000; Götmark *et al.* 2005). To fulfil the FSC standard requirements in Sweden, at least 10% broadleaves should be mixed into stands dominated by conifers (FSC 2020).

Table 5. Equation (1) summary output of analysis of variance (type II Wald χ^2 test), model estimate and adjusted R^2.

Regional climate features	Estimate	Sum of squares	Degrees of freedom	*F*-value	*p*-value	Adjusted R^2
$Tsum_m$	0.0007	0.55	1	32.45	<0.001	0.724
$Tsum_0$	0.0008	0.54	1	30.63	<0.001	0.712
$Tsum_1$	0.0008	0.55	1	31.48	<0.001	0.718
$PVsum_0$	0.0009	0.26	1	5.80	0.04	0.286
$Psum_1$	<0.0001	<0.01	1	<0.01	0.98	−0.091
$PVsum_m$	0.0009	0.18	1	3.50	0.09	0.173
$Psum_m$	0.0002	<0.01	1	0.06	0.80	−0.085
Lat	−0.0607	0.38	1	11.42	0.01	0.464

Note: Regional climate features shown in Table 1.

Where a large number of planted seedlings are damaged, e.g. by pine weevil or ungulate browsing, spontaneous regeneration could also offer an alternative way of fulfilling the Swedish Forestry Act requirements for a specified number of seedlings per hectare depending on site conditions (Skogsvårdslagstiftningen 2019). Mixing naturally regenerated birch into a Norway spruce monoculture is also an efficient way of increasing biodiversity and species richness for example of birds (Felton *et al.* 2011, 2021; Lindbladh *et al.* 2017) or vascular plants in the understory (Hedwall *et al.* 2019; Salemaa *et al.* 2023). However, a positive effect on vascular plant species richness also depends on stem density, not just the proportions of birch and Norway spruce (Hedwall *et al.* 2019; Salemaa *et al.* 2023), so the positive effect on vascular plants of mixing birch into a Norway spruce stand might be lost if stem density is not considered at the same time. This creates a conflict of interest between sparser forests for biodiversity, and denser forests for biomass production, since dense stands generally produce more volume (Niemistö 2013; Pretzsch 2020; Lidman *et al.* 2021). Stand density also tends to have a detrimental impact on birch growth, given that birch is a shade-intolerant primary species (Nygren and Kellomäki 1983; Fischer *et al.* 2002; Hynynen *et al.* 2009). This could potentially explain why the presence of birch often decreases in conifer stands as they age (Holmström *et al.* 2021).

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Data availability statement

The datasets generated during the current study, apart from the data provided by the Swedish National Forest Inventory, are available from the corresponding author on reasonable request. The data provided by the Swedish National Forest Inventory is available through Riksskogstaxeringen, SLU, Umeå, https://www.slu.se/riksskogstaxeringen.

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Appendix

List of regional climate features for each region. For definitions of abbreviations, see Table 1.

Region name	$Tsum_m$	$Tsum_0$	$Tsum_1$	$PVsum_0$	$Psum_1$	$Psum_m$	$PVsum_m$
Jokkmokk	898	1004	817	425	964	803	522
Piteå	941	1086	812	426	844	698	440
Åsele	890	1020	747	509	825	746	465
Vindeln	1083	1230	983	530	783	721	471
Sollefteå	1081	1149	880	590	771	709	482
Sveg	1013	1106	767	817	979	871	646
Hudiksvall	1255	1346	1083	591	704	651	453
Mora	1203	1235	979	740	961	857	616
Storfors	1435	1488	1209	656	1037	871	653
Västerås	1672	1677	1542	622	746	636	533
Skövde	1606	1635	1376	753	845	752	649
Trollhättan	1620	1718	1408	992	1152	986	917
Växjö	1549	1650	1320	748	823	804	690