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How spruce and pine fare in a wooded meadow without management for a century

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Abstract

Spruce (*Picea abies*) and pine (*Pinus sylvestris*) dominate much of Scandinavia, but it is unclear how these species fare in places not subjected to forestry. Currently, evidence suggests that in the absence of disturbance, spruce will increase while pine will decrease. The term "sprucification" has been coined to describe the landscape-wise change. We tested this prediction in a 3.4 ha wooded meadow in southern Sweden set aside for free development in 1923. Comparing with older data, we assessed how tree density, basal area and size distribution has changed since 1937 when trees were mapped. We also estimated annual mortality and recruitment of new trees. The number of trees had declined since 1937, while the basal area had increased somewhat. Spruce but not pine had shifted its geographic distribution within the reserve. Mortality was three times higher among spruce than pine. Recruitment of new trees was modest, with most being spruce. Size distribution of spruce changed substantially over time with a loss of small trees and addition of large trees. Size distribution of pine, however, remained unaffected, except for the decline in the number of small trees. On balance, despite a century of free development, there was no clear evidence for sprucification in this former wooded meadow, now a dense mixed forest.

Keywords: Sweden; *Pinus sylvestris*; *Picea abies*; agricultural land; over-growth

Introduction

A century ago, a significant research issue in Sweden was the importance of human influence on vegetation dominated by deciduous trees in southern Sweden (Romell 1966, Söderqvist 1986, Backeus and Hytteborn 2019, Milberg 2020). Such land had traditionally been used for hay production or grazing (Emanuelsson 2009). Agricultural utilization of the landscape in southern Sweden was probably at its maximum a century ago. Hence, there were no reference areas with a history of being untouched by humans or domestic animals. Consequently, it was unclear what would happen if agricultural land like a meadow was left to its own device without human interference, which is why a meadow was set aside for free development in in southern Sweden in 1923. Although we have learnt a lot about the development of abandoned agricultural land since 1923 (e.g Huhta 1996, Losvik 1999, Milberg et al. 2017, Abadie et al. 2021, Milberg and Tälle 2023, Prangel et al. 2023), it is worth revisiting "natural experiments" like these for at least three reasons. First, trees are long-lived, and a long-term follow-up is needed (e.g. Kardell and Fiskesjö 1999, von Oheimb and Brunet 2007, Hytteborn et al. 2017). Second, agricultural usage of the landscape has declined over the last century and today large tracts of forest in southern Sweden grow on former hay meadows that were abandoned and allowed to become overgrown (Milberg et al. 2019). Third, it is likely that management of species-rich grasslands will cease in many areas currently grazed, due to increasing shortage of animals for such purposes, and the cost for maintenance of protected land requiring management (grazing or mowing) will increase. Hence, especially in areas with protection, or receiving support for traditional management, we need to understand the processes involved during their overgrowth to be able to make cost-effective management decisions.

Two key attributes of species are believed to be at play during overgrowth: the ability of tree species to regenerate in shade, and their ability to grow in shade. Initially, several species would be able to regenerate from seed or suckers, as well as grow well, because of initial openness of the tree canopy in wooded meadows. As shade at ground level increase, however, only species able to regenerate in shade get established while self-thinning in the stand eliminates individuals of the more shade-intolerant species. More long-term, canopy trees will die, potentially opening up for both regeneration and growth of tree species (e.g. Margalef-Marrase et al. 2022). This simple model predicts that a shade-tolerant species would generally do well during over-growth while a shade-sensitive one would not. Tree species typically can differ greatly in shade-tolerance (Kobe et al. 1995, Walters and Reich 1996, Mason et al. 2004, Löf et al. 2007, Käber et al. 2021), and often regeneration and growth in shade correlate (e.g. Lin et al. 2001). Swedish tree species are often ranked from those tolerant to shade (e.g. spruce) to those sensitive to shade (e.g. pine). This autecological difference of the two most important

forest trees in Sweden has led to a prediction that spruce will do well during overgrowth (e.g. Lindbladh et al. 2014) while pine will not, leading to a shift in tree species composition in forested reserves (Fassl et al. 2024). Data from a 50-year period, however, show no apparent shift in tree species composition in favour of spruce in boreal coniferous reserves (Hedwall and Mikusiński 2016). Similarly, sprucification has been suggested as an inevitable consequence of abandonment of wooded meadows (Oldén et al. 2017), but long-term follow-ups are missing.

In the current study, we addressed the following questions regarding spruce and pine in a south-Swedish wooded meadow that had been left undisturbed for a century. Overall, we expected pine to decline and spruce to increase over time (cf. Oldén et al. 2017). More specifically we considered the following data: and the expected outcome:

(i) Density of trees: we expected spruce to increase and pine to decrease;
(ii) Basal area of trees: we expected basal area to increase in both species (as it is mainly driven by growth of the larger trees, and such trees might be more resilient to shade), and especially so for spruce that recruit in shade;
(iii) Size distribution of tree populations: we expected the population of pine to have fewer smaller trees over time, while size distribution of spruce would change less over time as smaller-sized trees are added to the population;
(iv) Mortality: we expected higher mortality among the shade-sensitive pine than the shade-tolerant spruce;
(v) Recruitment of new trees: we expected the shade-tolerant spruce to add more trees over time than the shade-sensitive pine.

Material and method

Study site

Vessers Udde is situated in the hemiboreal zone. Most of the area had been intensively used by humans for hay for many centuries, and the tree cover of the wooded meadow was dominated by oak, with some hazel (Kardell and Fiskesjö 1999). Rutger Sernander (1866–1944), a towering figure in early ecology and nature conservation in Sweden, and a professor at Uppsala University, was instrumental in the protection of Vessers Udde in Östergötland 1923 (Sernander 1922).

Management at Vessers Udde continued up until protection (Julin 1948), when the area consisted of a combination of open, sun-exposed grass-dominated areas and areas with shrubs and trees (Sernander 1925). This spatial pattern was apparent also in the 1930s (Julin 1948). Hence, our two study species were not uniformly distributed in the reserve. In fact, the pines were mainly around rock outcrops in the centre and SW while spruce was mainly in the northern half of the reserve. The latter partly involved land that had been exposed when the adjacent lake was lowered 1.8 m in the late 1850s (Svahn 2001).

The clay soil in the reserve has a glacial origin and carries many stones and boulders (Sernander 1925). Our study area was 3.42 ha (excluding water and a small island from the current reserve boundaries).

When protected in 1923, the expressed purpose was to set aside a former meadow and allow it to develop without human interference (Finndin and Milberg 2024). The intention was to allow research into the "original state" of the southern Swedish "löväng". A parallel reserve was protected with the same purpose near Uppsala ("Uppsala Universitets Naturpark"; Sernander 1912), but that contained very few coniferous trees (both at the onset and today; Hytteborn et al. 2017).

Vessers Udde was fenced on the landside in 1922, but deer and wild boar can access either over the fence or via the unfenced shoreline (especially during the months the lake is ice-covered). The abundance of ungulates (roedeer, fallow deer, moose) remained low in the region but has increased substantially since 1980 (Bergstedt et al. 2017). Feral wild boar started to appear in Östergötland in the 1990s (Jägareförbundet 2022) and has visited the reserve since at least 2014 (personal observation) but probably earlier.

Previous and current tree data collections

Between 1935 and 1941, Erik Julin conducted a comprehensive study, eventually resulting in his PhD thesis (Julin 1948). In 1937, he mapped all trees and shrubs and their crown projection. For trees, only those > 10 cm at breast height (dbh) were noted, and on the maps different size classes were illustrated as symbols of different size (size classes used were 10–19 cm, 20–29 cm, etc., Julin 1948). The published 1937 maps of pine and spruce were digitalized, and georeferenced using borders and prominent features. By zooming and measuring the symbols on a digital version of the maps, we could count the number of trees, and assigned each tree to a size class, with accuracy.

In 1979 and again in 1991–1992, all trees were counted and dbh measured, but they were not mapped (Kardell and Fiskesjö 1999). The raw data from that study are archived at SLU, that generously provided us copies. From these raw data, we extracted (i) number of trees, (ii) basal area, and (iii) size distribution of pine and spruce at these two points in time.

In April 2022, we mapped all pine and spruce using printouts of the 1937 maps. Hence, we specifically searched for trees present in 1937, as well noting all new trees. For each tree, we recorded dbh by two perpendicular measurements that were averaged (in case of trees > 50 cm, circumference was recorded instead, and from this dbh was calculated).

In the current study, dbh data from 1979, 1991/2 and 2022 were assigned to the size classes as used in 1937, to facilitate easy comparisons. The basal area and number of trees were then calculated by size class for all four time points.

Furthermore, mortality of trees between 1937 and 2022 was calculated, as well as the addition of new trees (> 10 cm dbh) over the same time period. Mortality was calculated as the annual % loss, hence assuming an exponential decay (i.e. mortality is constant, but the number of trees lost per year decrease as the population of living trees decrease). Apart from mortality among all trees, we also calculated annual mortality for three size classes of trees: 10–20 cm, 20–30 cm, and > 30 cm dbh since 1937, to assess whether mortality was size-dependent.

Results

Overview

What was a recently abandoned wooded meadow a century years ago, with open areas with species-rich ground vegetation (Sernander 1925), is today a dense, mixed forest, dominated by deciduous trees and shrubs in the centre (mainly oak and hazel), and coniferous trees towards the margins. Today, navigation is compromised by the large amounts of deadwood, which is particularly abundant in the north (deadwood was near-absent in 1937; Julin 1948). Small spruce, < 10 cm dbh, that were not considered in the present study, were present along the shores in the northern half of the reserve, while no pine of corresponding size was found.

Change in number of trees and basal area

The number of trees had decreased for both pine and spruce (Figure 1a). The largest decrease was among spruce (51%) and least among pine (15%).

In contrast, basal area had increased over the study period for pine (24%), while spruce had decreased somewhat (7%; Figure 1b). For both spruce and pine, however, basal area initially increased, but saw a drop after 1991/2 (Figure 1b).

Mortality among trees and recruitment of new trees

Of the trees present in 1937, 71% and 34% of the spruce and pine had died by 2022, which corresponded to annual mortality rates of 1.41%$^{-year}$ and 0.50%$^{-year}$ (Table 1). Furthermore, in 2022 newly, recruited trees (> 10 cm dbh) made up 39% and 5% of spruce and pine, respectively (Table 1). Hence, spruce exhibited extensive dynamics while pine was stable.

To evaluate whether mortality was size-dependent, we calculated annual mortality rate for three size classes, albeit numbers were small in some cases. Among spruce, mortality was highest among the smallest trees (10–20 cm dbh) while highest mortality for pine was in the largest

Table 1. Tree dynamics (number of trees per ha) from 1937 to 2022 in the nature reserve Vessers Udde (3.5 ha) protected in 1922 and surveyed in 1937 and 2022. Only trees > 10 cm dbh were mapped

	Pinus sylvestris	*Picea abies*
Mortality among 1937 trees (%)	34.3	71.3
Annual tree mortality (%) among trees in 1937		
> 10 cm	0.50	1.41
10–20 cm	0.40	1.56
20–30 cm	0.32	0.71
> 30 cm	0.69	1.18
New recruits among trees in 2022 (%)	5.1	39.2

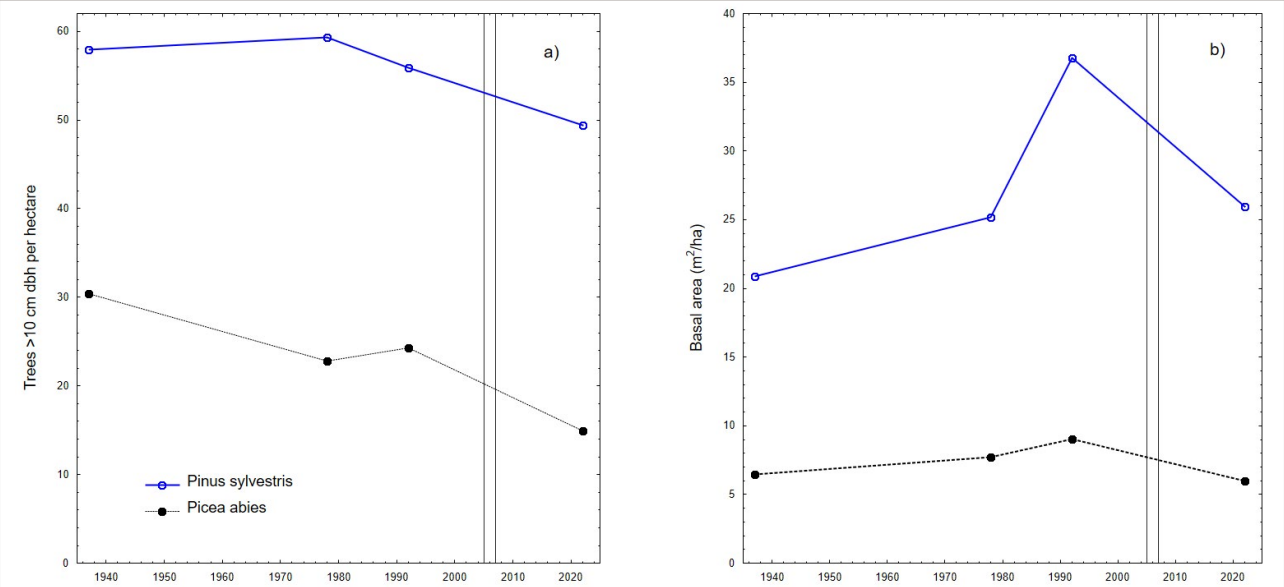

Figure 1. Change over time in 1a) Number of trees and 1b) basal area per hectare in a former meadow left to be overgrown in 1922

Vertical lines represent two significant storm events.

size class (> 30 cm dbh) (Table 1). In both species there was also a tendency towards an expected u-shape, i.e. with lowest mortality among intermediate-sized trees (Table 1).

In 1937, many spruce were in the NE of the reserve. In 2022, however, no spruce remained there, only windthrown trees (all logs had fallen towards east and were downed already during a visit in 2014, personal observation). There was no corresponding geographic shift of distribution over time for pine.

Size distribution of tree populations

The most apparent changes in size distribution were partly similar between the two tree species: a reduction among smaller trees, as well as a small increase among the larger trees (Figure 2). The largest trees in 2022 had 20–30 cm larger dbh than in 1937 (Figure 2).

Pine in the reserve had decreased over time (Figure 1a) and this was mainly a consequence of losses among the smaller size classes (Figure 2a). In contrast, spruce showed a more consistent size distribution, suggesting that mortality had struck not only small trees but also large ones, and recruitment had to some extent kept up the number of small trees (Figure 2b).

Discussion

We expected five conclusions to emerge from data, and here we briefly review how these assumptions turned out.

Did the density of spruce increase and pine decrease? No, there was no support for this in data. Instead, the density of both species decreased over time, suggesting the slow decline of both species in the mixed forest that has developed since 1923. Hence, there was no evidence for sprucification when considering the density of trees. Did basal area of both species increase? This was true up until the 1991-2 follow-up, when there had been a small (spruce) and large (pine) increase in basal area. After that, both species declined – presumably through the loss of several large trees during the storms of 2005 and 2007. Considering only the 86-year follow-up (i.e. 1937 vs 2022), basal area of spruce was unchanged, while pine had increased somewhat. So, the general premise, that basal area is mainly driven by the growth of the larger trees, stands but this can then be modulated by catastrophic events like storms. No evidence for sprucification was apparent in data on basal area.

Did the size distribution of pine change more than that of spruce? The size distribution of both species changed, and in similar ways. First, there had been a substantial loss of small tress (through growth, mortality and poor recruitment). Second, the growth of large trees had added to the larger size classes. On balance, however, spruce was the species with the most dramatic overall changes. There was no apparent effect of sprucification seen in the size distribution data.

Was mortality higher in pine than spruce? This was not true, and mortality was instead three times higher among the 1937 spruces compared with pines. Again, there was no support for sprucification in data. There are few estimates of mortality comparable to ours from protected forests. In premontane north Swedish boreal forests, spruce mortality was much lower than the 1.41%$^{-year}$ recorded in our study (0.63%$^{-year}$, Hofgaard 1993b and 0.60%$^{-year}$, Fraver et al. 2008). It is to be expected that the much higher productivity of forest in southern Sweden compared

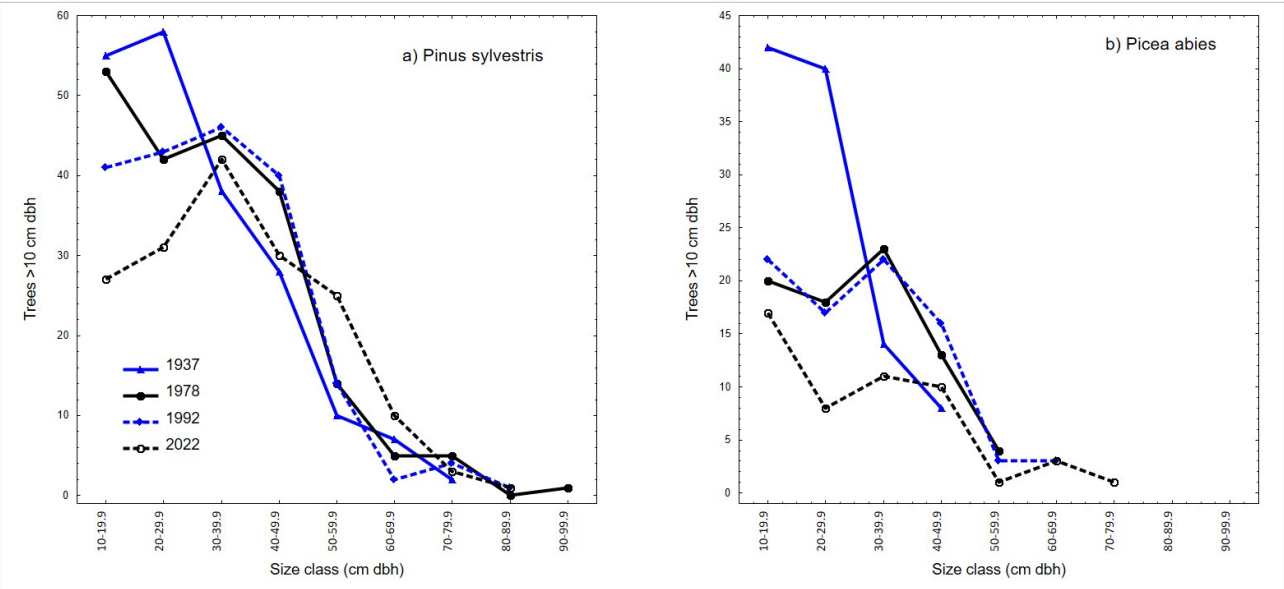

Figure 2. Change over time in 1a) Number of trees and 1b) basal area per hectare in a former meadow left to be overgrown in 1922

Vertical lines represent two significant storm events.

with pre-mountain northern forests would be reflected also in tree mortality rates. Besides, our study involved a period of canopy closure in a mixed forest, while Hofgaard (1993b) and Fraver et al. (2008) studied old-growth spruce forests with gap dynamics. In Norwegian production forests, on the other hand, mortality in the absence of cutting (and ignoring the smallest size class to make data more comparable to ours) was higher than in our study: 1.8%$^{-year}$ for spruce and 1.3%$^{-year}$ for pine (Eid and Tuhus 2001), compared with our 1.4 and 0.5%$^{-year}$. There is no apparent explanation for this difference. That mortality in spruce and pine was size dependent is expected (e.g. Monserud and Sterba 1999, Eid and Tuhus 2001, Rouvinen et al. 2002, Coomes and Allen 2007, Ahnlund Ulvcrona et al. 2011). Often, mortality is highest among smaller stems, but mortality can also so be high among the larger stems (in the absence of management). A similar trend was seen in our small data set: lowest mortality was among intermediate-sized trees of both spruce and pine.

Has spruce recruited better than pine since 1937? Yes, new recruits made up a much larger part of the tree population in 2022 for spruce (39%) than pine (5%). Hence, this variable confirmed previous studies concluding that spruce recruit better in shade than pine (e.g. Lexerød and Eid 2005, Käber et al. 2021). This variable suggested potential sprucification through differential recruitment.

Tree dynamics

It is apparent that after abandonment, the 1920s was a period of recruitment presumably mainly in the open areas, leading to the tree populations in 1937 being biased toward small/young trees. The smallest size-class registered then made up 40% of the spruce and 28% of the pine. Spruce was also the tree species with the most recruitment after 1937 (39% of the trees in 2022), while very few pines (5%) had been recruited to the smallest size class recorded (10– 19 cm dbh). Hence, pine seems to have exploited the open areas after abandonment, while the recruitment of spruce has continued under a dense tree canopy.

Due to poor temporal resolution in data, we cannot pin-point when self-thinning started, but the fact that mortality in both species were relatively high among the trees belonging to the smallest size class in 1937 suggests it has been a significant factor (cf. Eid and Tuhus 2001, Bravo-Oviedo et al. 2006). For spruce, the storms of 2005 and 2007 felled many large stems, adding to the high mortality in the large size class; spruce is more sensitive to wind than pine under Swedish conditions (Liu and Hytteborn 1991, Valinger 1996, Valinger and Fridman 2011, Hedwall and Mikusinski 2016). Causes of death of pine is often attributed to crowding/self-thinning (e.g. Das et al. 2011, Ahnlund Ulvcrona et al. 2014), while biotic factors seem to play a less prominent role compared with spruce (Hedwall and Mikusinski 2016).

Spruce was the species with highest dynamic: high mortality and considerable recruitment. The loss of spruce from the NE of the reserve due to windfall is noteworthy: despite several large spruce present for a century, these had left no offspring in this part of the reserve, suggesting that there are limits to recruitment in shade for this species.

Looking ahead

What to expect in the future in the reserve? Pines with a high canopy is destined to remain an important tree species in the reserve as they are unlikely to be "overtopped" by other trees. Whether there might be opportunity for recruitment, however, is unclear. Large windthrows, disease outbreaks, or extreme ungulate browsing are unlikely to create sufficiently large and long-lasting opening for pine recruitment (Nilsson and Gemmel 1993, Karlsson and Örlander 2000). In contrast, spruce is likely to be more responsive to even smaller openings, as there is a sparse population of saplings (of varying age) surviving in the shade and ready to grow (Sernander 1936, Hofgaard 1993a, Hytteborn and Verwijst 2014).

What about the broader implications of our case study? First, we confirmed the long-term importance of the difference in regeneration niche between spruce and pine (Luguza et al. 2020). Second, we showed that this is not just a phenomenon in forests (Fassl et al. 2024), but also on former agricultural land (Oldén et al. 2017). Third, we were unable to find clear evidence for "sprucification" (Lindbladh et al. 2014, Fassl et al. 2024) over the century studied, suggesting that the high regeneration of spruce is counteracted by a high mortality (cf. Hedwall and Mikusiński 2016). Fourth, our results contradict a previous space-for-time successional study of wooded meadows in Finland that concluded sprucification to be inevitable (Oldén et al. 2017). We are not, however, inclined to dismiss sprucification of protected areas on longer time scales, due to the long lifespan of pines (Andersson and Nicklasson 2004, Sandström et al. 2020). Instead, the cue to longer-term sprucification might be the poor regeneration of pine in protected habitats as well as in production forest.

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