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RESEARCH ARTICLE

From broadleaves to spruce – the borealization of southern Sweden

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Mixed or broadleaf forests were once common in many regions of Northern Europe, whereas today conifers often dominate. The aim of the study was to investigate the spatial and temporal patterns and processes which underlie this transition to *Picea abies* dominance in southern Sweden. We use recently developed paleoecological methods to determine long-term changes in the relative abundance of tree species, and digitalized National Forest Inventory (NFI) databases to assess more recent changes in the spatial coverage of *Picea* throughout the region. The novel combination of the two databases reveals that *Picea* became a widespread and abundant species in many parts of southern Sweden around 1000 years ago. After a brief decline in abundance starting around 500 years ago, NFI data indicate a rapid increase in the volume of *Picea* between 1920 and 1950, prior to the large-scale introduction of *Picea*-dominated plantation forests. The available evidence suggests that abandonment of forest grazing and slash-and-burn cultivation, as well as selection cutting benefited the natural establishment and growth of *Picea* during the first half of the twentieth century. Hence, prior to the impacts of industrialized forestry that began in the 1950s, other processes were already favouring increased *Picea* abundance.

Keywords: forest history; forestry; National Forest Inventory; paleoecology; *Picea abies*; pollen analysis; Norway spruce

Joel and Martin were in the forest cutting shingles for the roof. They hewed at pine and spruce and sawed the thin arms of the Småland forest which had pushed into northern Blekinge and there fumbled for a strangle-hold on hornbeam, lime, ash, hazels … hardened by their ten-thousand-year journey from Siberia, with now only a few patches of the Scandinavian peninsula left to conquer.
(From the novel *Flowering Nettle* by Nobel Prize winner Harry Martinson 1936)

Introduction

Mixed or broadleaf forests were once common in many regions of Northern Europe, but today conifers often dominate. This process of borealization has received significant attention in countries experiencing this transition, both with respect to the long-term underlying processes which span the majority of the Holocene (Berglund 1969; Tallantire 1977; Giesecke & Bennett 2004; Latalowa & van der Knaap 2006; Seppä et al. 2009; Tallavaara & Seppä 2012; Reitalu et al. 2013), as well as the shorter term anthropogenic drivers (Östlund et al. 1997; Emmer et al. 1998; Lagerås 2007; Niklasson et al. 2010; Lindbladh et al. 2011; Terauds et al. 2011; Cui et al. 2013).

Despite these assessments, the spatial and temporal patterns, and the processes which define this development, are still not fully known in many regions. In southern Sweden, a decline in thermophilous deciduous taxa, *Tilia* spp. and *Corylus avellana* (L.), began 4000 years ago, a development most likely related to a decrease in temperature (Hammarlund et al. 2003) and increased anthropogenic impacts (Iversen 1973). *Quercus* spp. and *Alnus* spp. began to decline about 2000 years ago, presumably in response to the same processes. Around the same time *Fagus sylvatica* (L.) immigrated to the region from the south, and *Picea abies* (L.) immigrated from the north (Gustafsson & Ahlén 1996; Bradshaw & Lindbladh 2005). It has been suggested that the resultant southern spread of *P. abies* was wave-like, fairly rapid and limited mostly by biological processes (Bradshaw & Lindbladh 2005; Bialozyt et al. 2012).

The current high volume and spatial extent of *P. abies* and *Pinus sylvestris* (L.) is primarily a result of production forest management during the twentieth century (Kardell 2004), resulting in coniferous stands comprising almost two thirds of total productive forest area with *Picea* comprising almost half of total forest volume (www.slu.se/skogsstatistik). For southern Sweden there remains uncertainty regarding those

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processes which preceded the large-scale influence of forestry, including developments related to climate change and/or historical shifts in land-use. It is important to disentangle the timing and contribution of these factors, as conifer dominance is thought to be a key driver behind the widespread population decline for many taxa dependent on broadleaved trees (Nilsson 1997; Jonsell et al. 1998; Gärdenfors 2010).

Uncertainty remains, in-part, due to previous limitations in the reliability of paleoecological techniques (Lindbladh et al. 2013). For example, whereas pollen data provide substantial temporal depth, it is often of limited spatial and temporal resolution, which creates significant challenges when interpreting the data (Davis 2000). Historical documents and inventories on the other hand, may provide spatial and temporal precision, but often lack the necessary temporal depth. Several recent advances have enabled us to overcome some of the previous limitations. First, advances in landscape-vegetation reconstruction algorithms now enable us to translate fossil pollen data into more realistic and robust estimations of past vegetation cover (Sugita 2007). Second, the digitization of the Swedish National Forest Inventory (NFI) historical data, from 1923 to the present, increases the possibility for assessing spatially explicit shifts in vegetation cover since the beginning of the twentieth century, and provides particularly high spatial resolution for southern Sweden.

Here we apply these recent advances in paleoecological methods and national forest cover databases to assess patterns associated with the changing abundance of *P. abies* in southern Sweden. The novel combination of these two datasets allows sufficient temporal and spatial precision and depth to provide clearer insights regarding the time scales and processes resulting in the dominance of southern Sweden's forest area by *P. abies*. Finally, on the basis of the result from this and other studies we discuss possible causal factors and the contribution of climate and agricultural influences which preceded forestry as the dominant force behind the recent versus long-term borealization of this region.

Materials and methods

Forest covers 63% of the land area in southern Sweden, defined as the nemoral (temperate) and hemiboreal vegetation zone (Sjörs 1965) (Figure 1). Commercial forestry dominates, and not more than approximately 3% of productive forest land is formally protected (www.slu.se/sv/webbtjanster-miljoanalys/statistik-om-skog/). *P. abies* (from here on *Picea*) is the most common tree species in the two vegetation zones (approximately 44% of total volume). *Picea* forests are planted as monocultures, and then pre-commercially and commercially thinned two to three times, with a rotation period of 50–70 years. *P. sylvestris* is the second most common tree

(33%). *Betula pendula* (Roth.)/*pubescens* (Ehrh.) (Birches) are the third most common (11%), followed by *Quercus robur* (L.)/*petraea* (Matt.) (Oaks) (3.3%), *Populus tremula* (L.) (Aspen) (2.6%), *Alnus glutinosa* (L.) (Alder) (2.4%) and *F. sylvatica* (Beech) (1.6%).

We used the Swedish NFI data to estimate total standing volume for *Pinus*, *Picea*, *Betula* and what are classified as "other deciduous trees" at county level from 1923 onwards (Anonymous 1932). Subsequent inventories are of higher taxonomic precision, but for comparison purposes we restricted ourselves to these four taxonomic categories. Today the NFI uses a systematic sampling grid with clustered plots, but until 1953 the inventory followed a belt-sampling design. The highest concentration of transects and plots was, and still is, located in southern Sweden (Axelsson et al. 2010). Data from the second NFI 1938–1952 are not yet available digitally; instead yearly estimates for the period 1927–1952 were calculated as interpolated values using the starting value from 1923 to 1929 (1925) and the five-year estimate for the period 1953–1957 (1955) as end value for the interpolation.

We used data from all counties in the hemiboreal and nemoral vegetation zones (Sjörs 1965) when presenting the data from southern Sweden (Figures 2 and 3). The borders between the zones are of course rough estimates and for the ease of simplicity we designated each of today's counties to a specific zone (Figure 1). We excluded northern counties that to a large degree are located in the boreal zone (i.e. Värmland, Närke, Gästrikland and Västmanland). We also excluded the island county of Gotland located in the Baltic Sea, except for the map of *Picea* volume (Figure 4) where it is included.

Some adjustments had to be done to make the inventories comparable for the whole time period; therefore the results will differ from official data from the Swedish NFI. As deciduous trees <50 mm dbh were excluded from inventories conducted in the 1920s the volume of deciduous trees presented in Figures 2, 3, 5 and 6 for 1925 is underestimated relative to later surveys. However as deciduous trees of <50 mm dbh represent only around 1% of the total forest volume during the 1940s, we expect the implications are minor. An additional difference in survey techniques that deserves consideration is that the volume of Picea per hectare of forest land in the 1925 survey is likely to be an overestimate compared to later survey periods. In the 1920s, trees on all land areas were included in the calculations, whereas from 1953 and onwards only trees on forest land were included. Considering the relatively few Picea trees found on other land-use classes we do not expect this difference in data collection to substantially impact on our results. Species that normally grow as shrubs were not included in the volume estimates (i.e. *Juniperus communis* (L.) (Juniper), *C. avellana* (Hazel) and *Salix* sp. (Willow)). *Larix* sp. (Larch) and species of
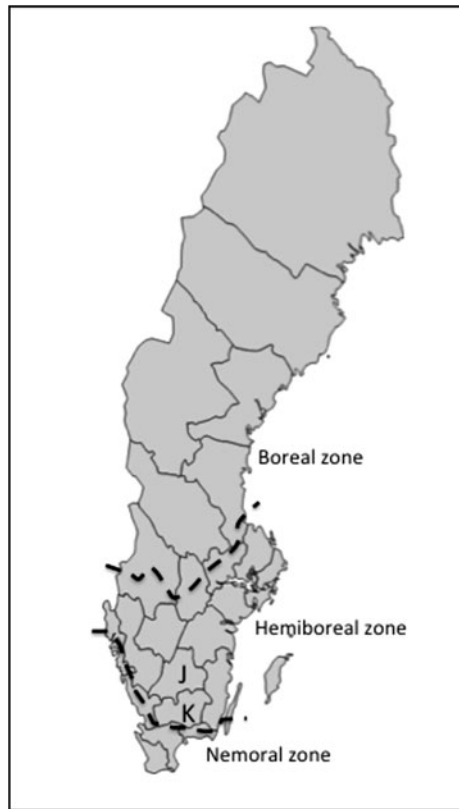
Figure 1. Map of Sweden with the vegetation zones indicated. J and K denote the counties of Jönköping and Kronoberg, respectively. The lakes used in the paleoecological studies, Lake Kansjön (Jönköping län) and Lake Trummen (Kronoberg län), are centrally located in respective county.
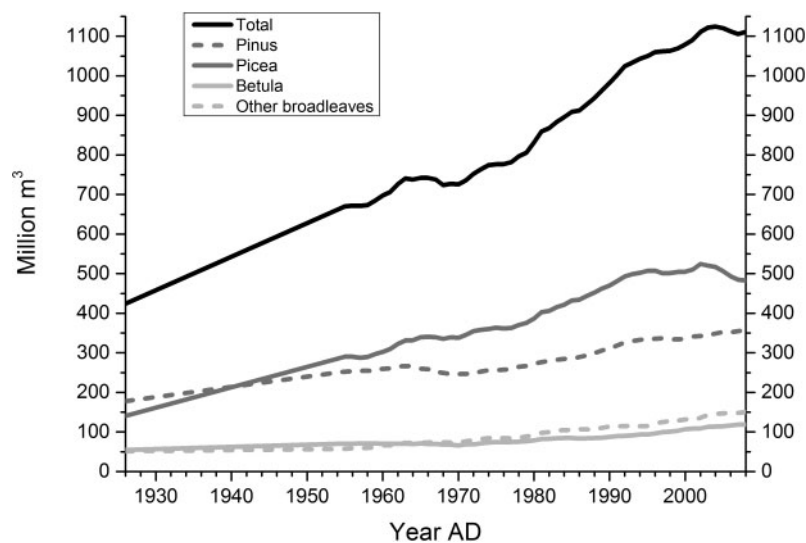
Figure 2. Volumes of different tree genera from 1925 to 2008 from the counties in southern Sweden in the hemiboreal and nemoral vegetation zones. Data from the Swedish National Forest Inventory (NFI). Note: All values between 1925 and 1955 are interpolated.

the *Pinus* genus other than *P. sylvestris* were included in "*Pinus*", except for the period 1923–1929 when *Larix* is included in "other deciduous". Other species of the *Picea* genus and *Abies* sp. were included in "*Picea*". None of these other species have been or currently are common enough to alter our results. For instance

today *Larix* represents <0.1% of total volume in the region.

We present maps of the volume per hectare of *Picea* from four time periods: 1925, 1955, 1985 and 2005. The 1925 map is based on county wise inventories either 1923 or 1927–1929, whereas for 1955, 1985 and 2005
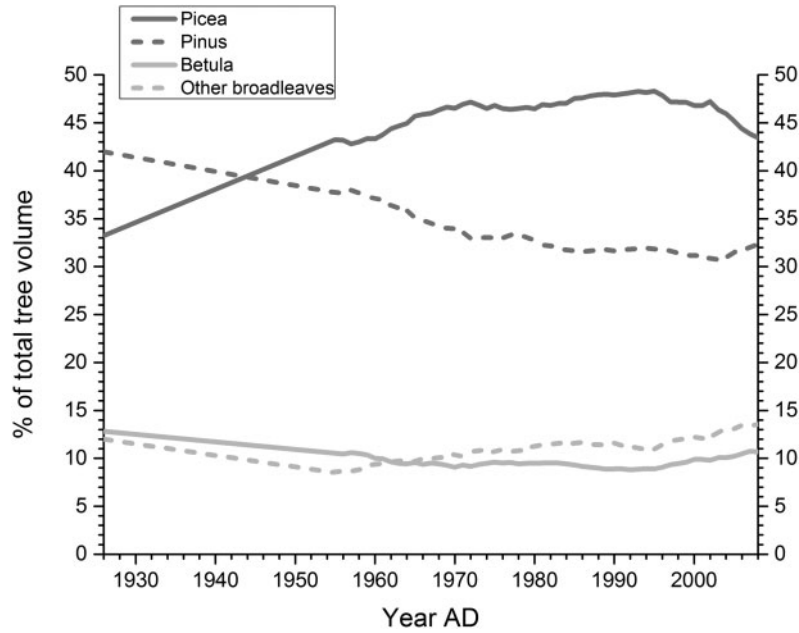
Figure 3. Percentage of total volume from 1925 to 2008 from the counties in southern Sweden in the hemiboreal and nemoral vegetation zones. Data from the Swedish National Forest Inventory (NFI). Note: All values between 1925 and 1955 are interpolated.
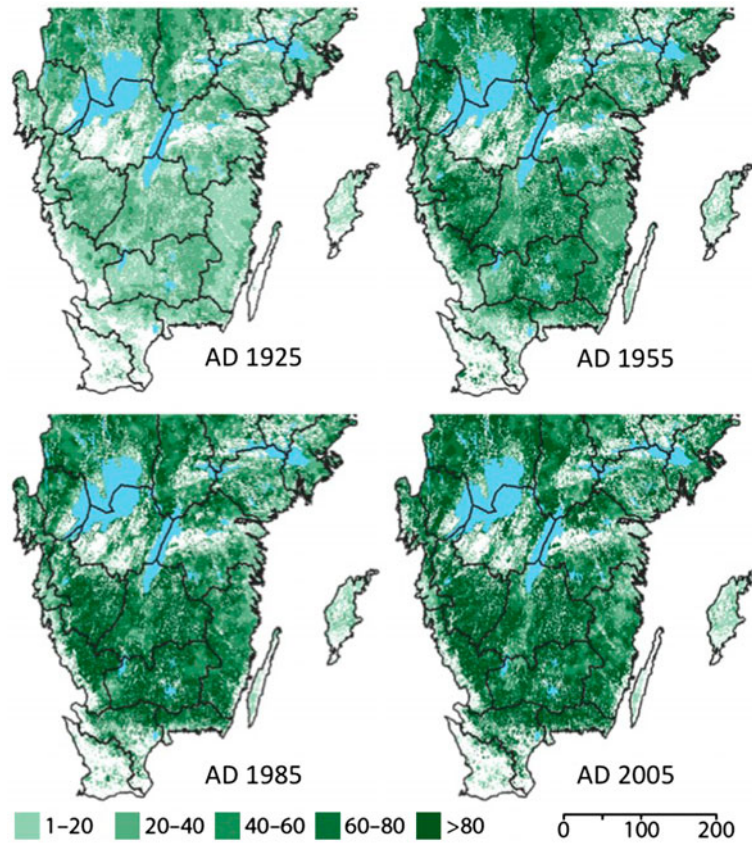

Figure 4. Map of southern Sweden showing volume per hectare of *Picea abies* at four different times. Data from the Swedish National Forest Inventory (NFI).

data are combined from five years (e.g. 1955 ± 2 years). This is because much larger areas were sampled during the first NFI compared to the other time periods. Data

consisting of coordinates and *Picea* volume were extracted for each time period. For the 1925 map the mid-points and average value for each 2 km segment

was used as in data; from 1955 and onwards the tract centre and tract average was used. The maps were produced in ArcMap 10.0 through interpolation of point data to continuous raster using the interpolation method of inverse distance weighting. The following settings were used: (1) power = 2; (2) maximum neighbours = 25; (3) minimum neighbours = 1; (4) major semiaxis = 25,000; (5) minor semiaxis = 25,000. These settings are used for all interpolated maps from the Swedish NFI. The resulting raster was then classified and spatial information about water bodies, arable land and mires was added to the map.

For the paleoecological part of the study we use the Holocene pollen records from Lake Trummen (Digerfeldt 1972) and Lake Kansjön (Jacobson, unpublished, data extracted from the European Pollen Database). New pollen percentage diagrams for these two sites can be found in Cui et al. (2013). Both lakes have a radius of ~400 m and are located relatively central in the two counties of Kronoberg and Jönköping, respectively, that is, in the central parts of southern Sweden (Figure 1). We used the REVEALS (Regional Estimates of VEgetation Abundance from Large Sites) model (Sugita 2007), which predicts regional vegetation abundance (in percentage cover or in proportions) from pollen assemblages in large lakes and bogs. According to validation studies in southern Sweden this approach effectively estimates the percentage cover of large vegetation units such as total trees, total herbs, total conifers and total broadleaved trees, and provides reasonable estimates for individual taxa such as *Pinus*, *Picea* and *Betula* (Hellman et al. 2008a). The REVEALS runs were performed using REVEALS.v4.2.2.forpublic.fast.exe (lake version). We present the model's output for the mean values for both lakes, and the maximum extent of the regional

vegetation (Zmax) was set to 100 km because vegetation beyond this distance was assumed to contribute <10% of the pollen to the studied lake basins (Sugita 2007; Hellman et al. 2008a, 2008b). The radius of 100 km fits well to the size of the two counties in question (Figure 1). In order to facilitate the comparison between the two records we also present the NFI data from these two counties (Figures 5 and 6). Time windows were created for best temporal resolution possible at respective sites, and are hence of different length over time. For more information regarding the REVEALS model, consult Sugita (2007).

Results

The NFI data for the hemiboreal and nemoral zones show an increase in total tree volume from 420 million m^3 in the 1920s to 1100 million m^3 today (Figure 2). *Picea* shows the largest increase, and became the most common tree species sometime between 1925 and 1955 both in terms of absolute and relative values (Figures 2 and 3). *Picea* increased from slightly less than 150 million m^3 to close to 500 million m^3, and its relative share increased from 33% to 43% during the time in question. The species has a slight drop at the end of the record as consequence of the Gudrun storm in 2005 (Valinger et al. 2014). Also *Pinus*, *Betula* and "other broadleaves" have increased their total volume since the first NFI (Figure 2), but they have approximately the same share today than during the first inventory (Figure 3).

The maps of *Picea* volume show *Picea* had roughly the same geographical distribution in the 1920s as during the later time windows (Figure 4). However, the volumes per hectare have greatly increased over the century. In
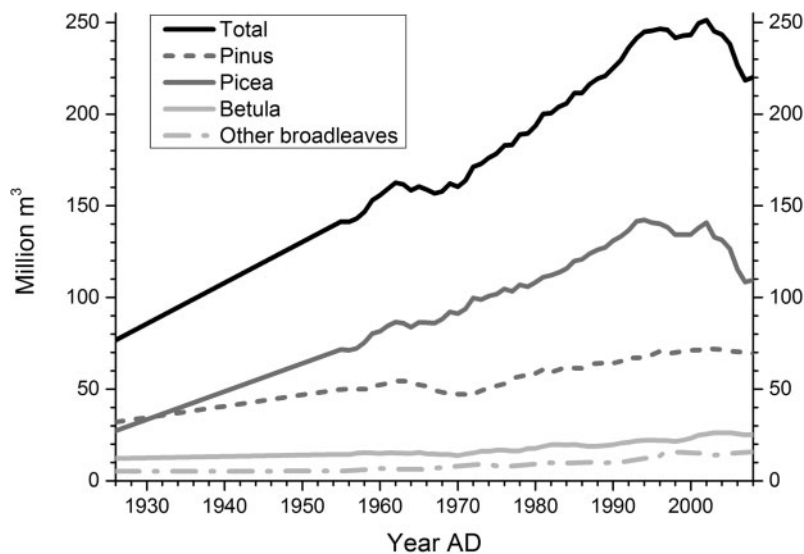

Figure 5. Volumes of different tree genera from 1925 to 2008 in the counties of Jönköping and Kronoberg. Data from the Swedish National Forest Inventory (NFI). Note: All values between 1925 and 1955 are interpolated.
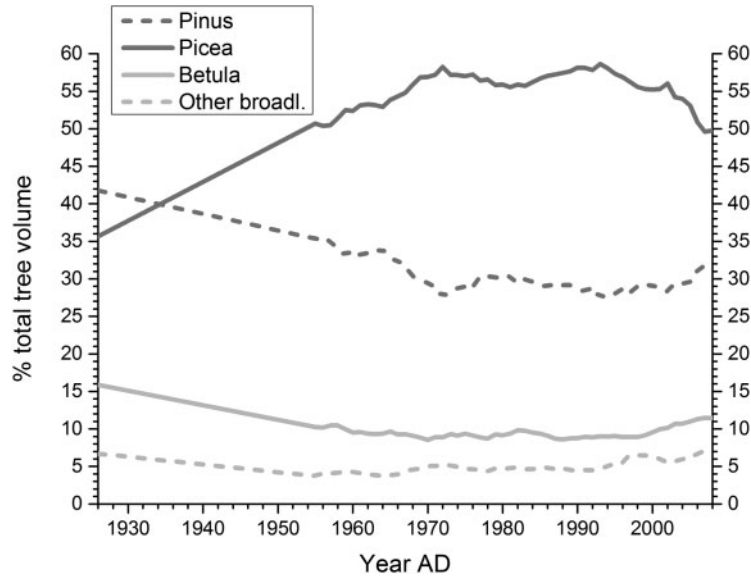
Figure 6. Percentage of total volume from 1925 to 2008 in the counties of Jönköping and Kronoberg. Data from the Swedish National Forest Inventory (NFI). Note: All values between 1925 and 1955 are interpolated.
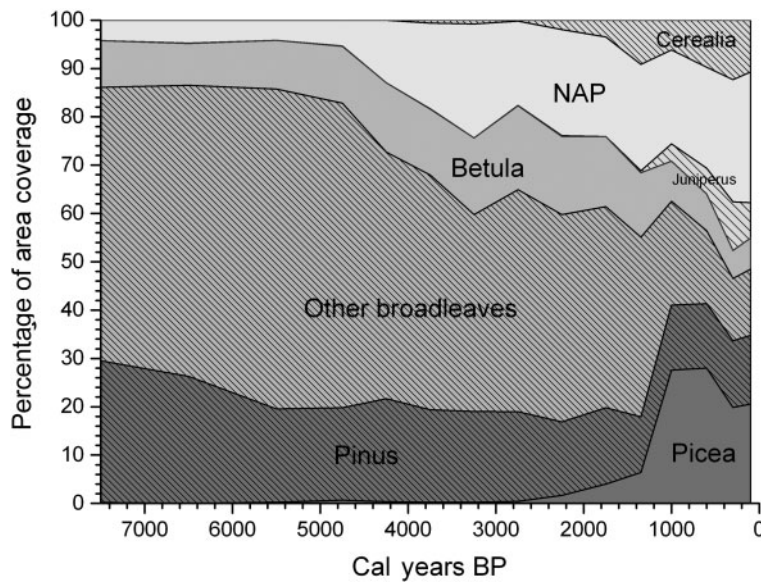

Figure 7.   Percentage area coverage from 7500 calibrated years BP (calendar years before present) to today. Data from two pollen analyses from Jönköping and Kronoberg counties. NAP is non-arboreal pollen, that is, pollen from other plants than trees. The group of "Other broadleaves" includes *Alnus, Betula, Populus, Salix, Sorbus Acer, Carpinus, Fagus, Fraxinus, Quercus, Tilia* and *Ulmus*.

the 1920s the volume per hectare for *Picea* was below 20 m^3/ha in the southern coastal counties, and between 20 and 40 in most other parts (Figure 4). The volumes increased up to the mid-1950s, to the extent that many areas possessed more than 60 m^3 sk/ha. These volumes increased further in the 1980s, with substantial amounts of area possessing volumes exceeding 80 m^3 sk/ha, with the only notable exception being a small margin in coastal areas and in the fertile plains both in the southwest and in the counties Västergötland and Östergötland further north. Similar or slightly reduced

volumes of *Picea* persist to the most recent time period considered.

For the counties of Jönköping and Kronoberg the NFI data indicate a similar pattern of development as for southern Sweden in general, but expressed at higher volumes of *Picea* (Figures 5 and 6). Correspondingly the percentage volume of "other broadleaves" is lower than that found for all counties (Figures 2 and 3).

When going further back in time, the area coverage for all vegetation based on the pollen data shows a large dominance of broadleaved forest in the counties of
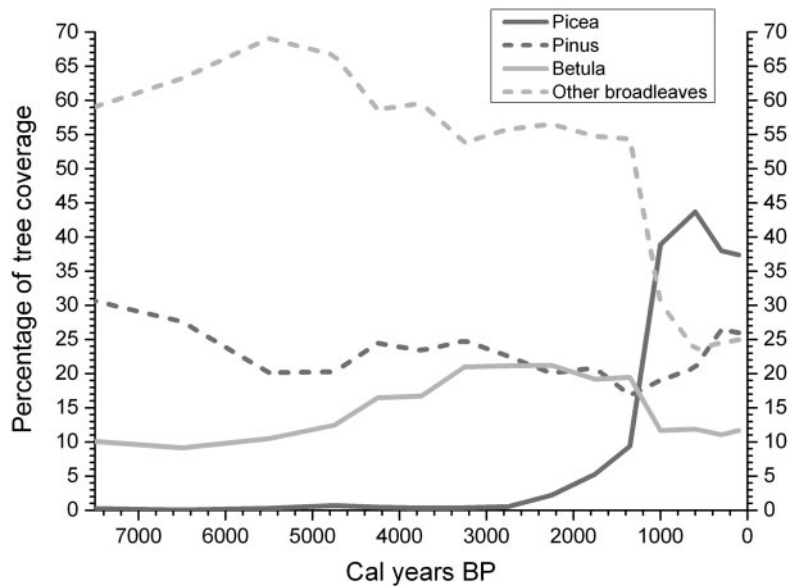
Figure 8.   Percentage area coverage for trees only from 7500 calibrated years BP (calendar years before present) to today. Data from two pollen analyses from Jönköping and Kronoberg counties.

Jönköping/Kronoberg during most of the record (Figures 7 and 8). About 4000–5000 years ago the shrub and field layer increased, and the first sign of Cerealia cultivation started to appear. Around 2500 years ago *Picea* entered the record, and between 1000 and 1500 years ago this species underwent a rapid increase, to approximately 20–25% of total coverage. During the same time period Cerealia and *Juniperus* increased. A corresponding decrease occurred among broadleaves whereas *Pinus* area cover was rather stable at the time. *Picea* became the most common tree species in terms of coverage around 1000 years ago, and reached a peak in this regard 500 years ago. After that, estimates of percentage cover indicate a decrease, while light demanding and anthropogenic taxa (*Juniperus*, Cerealia and other non-arboreal pollen, NAP) continue to increase. From 1800 to 2000, *Picea* corresponds to approximately 20% of total vegetation coverage (Figure 7), whereas this percentage reaches approximately 35% if only tree cover is included (Figure 8).

Discussion

Our results indicate that the process of borealization has a history of more than 2000 years in south-central Sweden (Berglund 1969; Giesecke & Bennett 2004; Bradshaw & Lindbladh 2005). However, the expansion of *Picea* came to a temporary halt around 500 years ago, and the NFI data indicate that it was not until the early twentieth century that a second phase of *Picea* expansion commenced with a rapid increase of standing volumes over a relatively short time period.

The available evidence thereby supports the conclusion that *Picea* has been one of the most common

trees in this region for at least 1000 years, with the dense stands of *Picea* arising in the early twentieth century.

Possible causal factors

Here we discuss the possible causal factors behind these developments which largely precede the introduction of modern forestry. *Picea*'s physiology likely benefited from the cold and damp climate that prevailed from 1500 to 2500 years ago (Moberg et al. 2005; Bialozyt et al. 2012); which overlaps with its westward and southern immigration into Scandinavia according to ours and others' results (Giesecke & Bennett 2004; Bradshaw & Lindbladh 2005). However, the largest coverage of *Picea* in the Jönköping/Kronoberg counties was during the relative warm Viking and early Medieval periods. This suggests that anthropogenic factors may have specifically contributed to the expansion of *Picea* during this time, as the period is characterized by increased human activity with the colonization of many new settlements in the region (Lindbladh & Bradshaw 1998; Lagerås 2007). One of the associated factors that could have favoured *Picea* relative to other tree species is the expansion of forest grazing by domestic animals. *Picea* is likely to benefit during this period as it is known to be less palatable to large grazing ungulates than either *Pinus* or the regionally occurring broadleaves species (Lindbladh & Bradshaw 1998; Kullberg & Bergström 2001). The pollen data from this study lends further support to this hypothesis (Figure 7). Several plant taxa, well known to be indicators of human activity, including Cerealia and *Juniperus*, increase their area of coverage concurrently with *Picea* (Behre 1981; Gaillard et al. 1992).

Agricultural revolution and grazing

With respect to observed changes in the occurrence of *Picea* since the twentieth century, we suggest that two primary drivers can account for the increase in *Picea's* volume: changes in agricultural practices and the introduction of silviculture. Agriculture became more intensive from nineteenth century onwards, and new methods for improving soil fertility were developed which eventually led to methods to enrich soils with artificial fertilizers (Myrdal 1997; Gadd 2000). There were in turn two consequences of this agricultural revolution that we suggest likely resulted in extensive impacts on the forests of southern Sweden: the cessation of both forest grazing and slash-and-burn cultivation. On the *utmark* (land of a village not used for permanent arable land or hay meadows) grazing was the primary land-use, but these lands were also used for slash-and-burn cultivation (Sjöbeck 1931; Weimarck 1953; Selander 1955; Larsson 1989a). High grazing pressure from domestic animals occurred on these lands for centuries or even millennia up until the end of the nineteenth century (Dahlström 2006; Lagerås 2007). During the eighteenth and nineteenth centuries even the least palatable trees were affected, resulting in many areas losing all or most tree cover (Malmström 1939). Because of the agricultural revolution in the beginning and mid-nineteenth century, better production outcomes could be achieved by using more efficiently produced fodder plants on arable land. The associated reduction in grazing pressure favoured the re-establishment of forests on these lands, as can be seen on cadastral maps at the time (Lagerås 2007; Cui 2013). Another pollen study from south-central Sweden using REVEALS supports the hypothesis that changes in agricultural practices were important drivers of the *Picea* increase prior to mid-last century (Fredh et al. 2012). The temporally precise study shows an increase in *Picea* coverage by between 20% and 50% during the transition from traditional to modern land-use from AD 1880 to 1940. At the same time *Juniperus* and grasses increased significantly, probably as corresponding responses to changing grazing pressure and reduced mowing.

Agricultural revolution and slash-and-burn cultivation

The cessation of slash-and-burn cultivation is an additional likely driver of *Picea's* increased abundance during the nineteenth and twentieth centuries. Historical documents from a parish in southern Sweden report that slash-and-burn fields occurred at four times the frequency of permanent fields in the beginning of the nineteenth century (Weimarck 1953). Accounts describe the capacity of slash-and-burn practices to act as a restraint on *Picea* expansion. Slash-and-burn agriculture operated by burning forest, and then often rotating between crops of turnips and rye, before allowing some period of mowing and grazing, before shifting to a new

location and allowing the land some period of natural forest regeneration. This generally resulted in a tree succession composed of pioneer species of broadleaved trees and *Pinus*, prior to being burnt once again as the slash-and-burn cycle repeats. However, these slash-and-burn agriculture practices decreased in the mid-nineteenth century, and stopped completely in the early twentieth century (Larsson 1989b). Once they ceased, there were no obstacles to allow *Picea* to establish and subsequently outgrow their broadleaf and *Pinus* competitors (Weimarck 1953). Farmers were not always happy with this development. An old farmer in the 1940s tells about the situation in his youth, ending with the important point that such active efforts to stop the regeneration of *Picea* no longer occurred: "There were tens of thousands, if not hundreds of thousands of spruce seedlings that have been pulled from the slash-and-burnt land here" (Weimarck 1953). This citation is indicative of just how strong the capacity was for *Picea* to take advantage of such circumstances without the need for active silvicultural intervention. It is notable that the same type of human land-use may have had a different effect depending on timing and/or intensity. Such a complex relationship may apply to slash-and-burn cultivation. It was basically negative for *Picea* when intensively and repeatedly used, but promoting once it ended, as described above. Examples of naturally regenerated dense *Picea* cohorts under a shelter of older *Pinus* or broadleaved trees can still be found in several southern Swedish forest reserves (Karlsson 2000; Niklasson & Drakenberg 2001).

Silviculture

In addition to favourable changes in agricultural practices, *Picea's* increase in volume, and the consolidation of its southern migration was aided in some cases by earlier forms of silviculture. In the beginning of the twentieth century the value of timber increased, which resulted in a corresponding increase in the interest in organized silviculture (Kardell 2004; Brunet et al. 2012). This drove the afforestation of the *Calluna* heaths with *Picea* and *Pinus* in southernmost and coastal southern Sweden at this time (Malmström 1939; Blennow & Hammarlund 1993). During 1907–1924 an area of 572,000 ha was reforested by different organizations (Kardell 2004). Hence, in many open coastal areas planting played a major role in the expansion of *Picea*.

However, these highly organized regeneration activities were probably not conducted to the same extent throughout southern Sweden. The interior part of southern Sweden was restocked at essentially the same time as the coastal areas according to the NFI data, but despite that the evidence for organized planting activities is rather rare. The few statistics and estimates available

indicate that only limited planting occurred in these regions (Enander 2007). Natural regeneration without active intervention was still a commonly employed "method" of establishing forest stands up until the end of the 1940s, and may have been a primary driver of *Picea*'s increase in southern Sweden's interior. On privately owned estates (50% of all forest land) from 1926 to 1945 planting was limited to 10,000–30,000 ha per year in southern Sweden (Enander 2007). This indicates that during this period (1926–1945) a maximum of approximately 5% of privately owned land may have been planted. Whereas low harvesting rates for older forests, and management attempts to increase stocking density at this time would both lead to increased volumes (Enander 2007), the sum total of factors associated with silviculture appears insufficient to account for the majority of the increase in forest volume in the region from the 1920s to the 1950s.

In addition to natural regeneration methods, *Picea* also is likely to have benefited from selective cutting approaches, which were still widespread in the early twentieth century. Hesselman and Schotte (1906) noted, during extensive field inventories to determine the southwest limit of *Picea*'s distribution at the beginning of the twentieth century, that *Picea* was still migrating south. This was reportedly facilitated by the "the aimless, disorderly dimension cuttings which greatly benefit the spruce advance. In the small gaps, created by the axe in the stand, the more shade tolerant spruce is more easily established compared to the more light demanding pine".

It is possible that the changes in agricultural land-use followed by selective cuttings made the forests increasingly too dark for its main competitors, *Pinus* and *Betula*, and thereby acted as primary contributors to *Picea*'s increases during the first half of last century in central southern Sweden. From boreal/temperate transition zones outside of Europe, there is similar evidence that artificial regenerations and intense forestry is not always necessary for comprehensive increases in forest density and altered tree species composition. The North-eastern United States had a similar development as southern Sweden with respect to historical forest cover. Agriculture and deforestation by European colonists during the eighteenth and nineteenth centuries was followed by an extensive recovery of the forest from AD 1875 and onward (Foster et al. 1998). In central Massachusetts the forest area increased from a low point of less than 40% to more than 85% today, and the composition changed to more shade tolerant and valuable timber species. These changes occurred almost solely as a result of natural reforestation, with even less influence of silviculture than occurred in southern Sweden during the first half of the twentieth century.

Conclusions

The picture that emerges is that prior to the recent consequences of modern forestry, *Picea*'s occurrence was already widespread in many regions of southern Sweden and resulted from a mix of climatic, biotic and anthropogenic factors that have taken place over several thousand years, similar as has been described in a case study from the Swiss Alps (Rey et al. 2013). It was not until the twentieth century that *Picea* became a dominant tree species in southern Sweden in terms of standing volume. Our results also show that its rate of increase during the entire twentieth century was rather constant, suggesting that changing agricultural practices and earlier selective cuttings were already favouring *Picea* prior to the highly organized plantation forestry practices that began in the 1950s. Hence, our results modify a perception sometimes encountered in Sweden, that the dominance of *Picea* today was primarily driven by modern forestry since the 1950s (Nilsson 1990).

None of this negates the view that the introduction of modern forestry and the clear-cut system in the 1950s, combining artificial regeneration and even-aged monocultures, created structures, ages and conditions with few similarities to natural forests, and has thereby threated the survival of many forest species in the region (Gärdenfors 2010). Moreover, although landscapes in southern Sweden were already highly modified by the beginning of the twentieth century, the forests in the 1920s were probably relatively heterogeneous in terms of structures and tree species composition. These conditions were likely to be far more conducive to the retention of forest biodiversity than is provided by production forests today, a pattern of development consistent with the forests of northern Sweden and Norway at the time (Linder & Östlund 1998; Lie et al. 2012).

In summary, the history of *Picea* in southern Sweden forms an important background to today's biodiversity issues, and helps us to estimate the degree of naturalness sought during reserve selection, as well as in identifying the potential for forest restoration. Our results indicate that the first half of the twentieth century is a key period in these respects. Research is now needed to further investigate the role of silviculture and organized forestry in southern Sweden during that period – a period, as we have shown here, of rapid landscape transformation eloquently described by Harry Martinson recalling memories from his youth (see opening quotation).

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