

Invasion of Norway spruce (*Picea abies*) and the rise of the boreal ecosystem in Fennoscandia

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Summary

1. Norway spruce (*Picea abies*), one of the dominant tree species in Eurasia, has spread slowly westward in northern Europe, invading eastern Finland about 6500 calibrated years ago (cal. years BP), eastern central Sweden about 2700 cal. years BP and southern Norway about 1000 cal. years BP. Its spread is the most recent and best constrained invasion of a main tree species in northern Europe and allows an assessment of colonization patterns and associated competitive replacement processes.

2. We analysed five selected high-resolution pollen accumulation rate (PAR) -records along a 700-km long transect in the direction of *P. abies* invasion from eastern Finland to central Sweden across the present *P. abies*- and *Pinus sylvestris*-dominated southern boreal zone.

3. Our results show that the *P. abies* population increased in size from the time of the initial expansion to levels comparable with the modern in 100–550 years. At each site *P. abies* invaded a dense, intact *Pinus–Betula–Alnus* forest, mixed with temperate deciduous taxa, particularly *Tilia cordata* and *Corylus avellana*. The resident mixed forest provided no or weak resistance to the colonization of *P. abies*, and the variable population growth rate was therefore not caused by compositional differences in the resident forest but by other, possibly local edaphic factors.

4. Of the taxa that formed the resident forest, *T. cordata* responded most strongly to the invasion of *P. abies*. This suggests that the mid-Holocene *T. cordata* population decline was not directly climate-induced but resulted from competitive replacement due to overlapping ecological niches with *P. abies*, a stronger competitor.

5. *Synthesis.* The rise to dominance of *P. abies* was caused not only by its rapid population growth but by associated competitive suppression of other taxa, leading to a major ecosystem change from a mixed conifer-deciduous forest to the modern *P. abies*- and *P. sylvestris*-dominated boreal conifer forest in central Fennoscandia. This competitive suppression by *P. abies* is still reflected in the scattered occurrence and generally weak performance of *T. cordata* in the boreal zone of Europe and may influence its distribution and abundance patterns under predicted future climate scenarios.

Key-words: boreal ecosystem, competitive interactions, Holocene, invasion, palaeoecology, *Picea abies*, pollen accumulation rates, *Tilia cordata*

Introduction

The prospect of global warming has generated a major interest in climate-induced plant range shifts and associated invasion processes (Pitelka *et al.* 1997; Ronce 2001; Walther *et al.* 2002; Gillson *et al.* 2008; Thuiller *et al.* 2008). Retrospective

and experimental investigations show that an invasion of a competitive plant species can change not only ecosystem composition and structure but also environmental processes and factors such as soil and light properties, hydrological conditions, nutrient cycles and disturbance regimes (Gómez-Aparacio *et al.* 2008). Many of the ecological and environmental consequences of invasions become apparent only slowly, over decades or centuries (Pearson 2005; Strayer *et al.* 2006), and

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cannot be comprehensively documented by observational investigations alone (Pitelka *et al.* 1997; Davis *et al.* 1998; Bradshaw & Lindbladh 2005; Strayer *et al.* 2006). A more complete understanding requires long-term retrospective records that cover the whole ecosystem alternation process from the initial colonization to the new stage where the invasive species has attained its maximum population level. Such records can be provided by analyses of palaeoecological records preserved in sediment layers (Pitelka *et al.* 1997; von Holle *et al.* 2003; Willis & Birks 2006; Gillson *et al.* 2008).

Some attempts have been made to use pollen records to investigate post-glacial competitive interactions by assessing species replacement patterns during the immigration of a new species (Ritchie 1984; Bennett & Lamb 1988; MacDonald 1993; Bennett 1994; Bradshaw & Lindbladh 2005). Yet, the full potential of the palaeoecological records has not been used for increasing our understanding of critically important processes of colonization, population growth and competitive species interactions associated with species range shifts. The main reason for this may be a technical one. Palaeoecologists have traditionally investigated past range shifts by analysing fossil pollen from sediments and by depicting the results as percentage pollen diagrams. But, as the pioneers of pollen analysis understood (von Post 1916; Davis 2000), a major weakness of the percentage pollen data is that the values of individual taxa are always dependent on the abundance of other plant taxa. Thus, an immigration of a new species will always lead to a decrease of other pollen types, even if there is no real decrease in the populations of these other species.

The use of pollen accumulation rate (PAR) data potentially overcomes the inherent weaknesses of percentage data. PAR is an estimate of the accumulation of pollen at the sediment surface (per cm² or other space unit) per year. PAR data consists of individual values for each pollen and spore type that are independent from each other, and are therefore free of the problems arising from the interdependent nature of the percentage pollen records. PAR values are usually calculated for the most important tree species, with the aim to provide precise records of past tree population sizes, measured either as canopy coverage or biomass. Recent work in northern Europe has shown that despite potential sources of error due to pollen and sediment redeposition (Bonny & Allen 1984; Davis *et al.* 1984), PAR values can often reflect relatively reliably the vegetation around the sampling sites. Modern PAR values obtained from the Fennoscandian lake-sediment cores are in general consistent with the long-term PAR values obtained from pollen traps (Hicks 2001; Seppä & Hicks 2006; Giesecke & Fontana 2008). Moreover, post-glacial PAR records from multiple sites within the same region often show consistent long-term trends for individual species, which indicates that within-basin sedimentological processes in the different lakes are of minor importance (Seppä & Hicks 2006; Giesecke & Fontana 2008).

Here we investigate the colonization and population growth patterns and subsequent ecological changes associated with the invasion of Norway spruce (*Picea abies* (L.) Karsten) in the modern boreal zone of Europe. Pollen and plant

macrofossil evidence from lake and peat sediments in northern Europe show that from its late-glacial and early Holocene range in northern Russia *P. abies* spread westwards to eastern Finland about 6500 cal. years BP, to western Sweden about 2500–2000 cal. years BP and to southwestern Norway during the last 1000 years. It is conceivable that *P. abies* is still expanding its southern and western distribution limits, although this is difficult to test as it has been planted beyond these natural limits (Huntley & Birks 1983; Giesecke & Bennett 2004; Eide *et al.* 2006). We use PAR values obtained from five lakes located along an east-to-west transect in the direction of the spread of *Picea* in central Fennoscandia. At present *P. abies* is one of the dominant tree species in this region, forming dense and shady stands as stable, end-successional climax communities. Its colonization and subsequent rise to dominance provide therefore a valuable opportunity to investigate the role of the abiotic and biotic factors associated with the colonization process and to test the influence of an invasion of a new, competitive tree species on forest structure, composition and ecosystem functions on centennial to millennial time-scales.

Methods

PAR records were obtained from five lakes, Lakes Kirkkolampi, Orijärvi, Laihalampi, Nautajärvi in Finland and Lake Klotjärnen in Sweden, along an east-to-west transect in the boreal forest zone in northern Europe (Fig. 1; Table 1). The boreal forest in the region is a structurally relatively simple mixed forest, dominated by *P. abies*, Scots pine (*Pinus sylvestris* L.), downy birch (*Betula pendula* Roth) and silver birch (*B. pubescens* Ehrh.). Grey alder (*Alnus incana* L.) and black alder (*Alnus glutinosa* L.) are common. The temperate deciduous tree species, mainly pendunculate oak (*Quercus robur* L.), small-leaved lime (*Tilia cordata* Mill.) and hazel (*Corylus avellana* L.) occur scattered in the southern part of the region.

The five pollen records were selected for the present study because they were obtained from relatively similar lakes in terms of their size, morphometry, hydrography, climatology and surrounding vegetation. Moreover, the sediment cores obtained from these lakes have a high temporal resolution with the number of pollen samples for the last 10 000 years ranging from 111 from Lake Klotjärnen to 269 from Lake Nautajärvi. All lakes are well-dated, with the age–depth models suggesting stable sedimentary conditions during the study period. Lake Nautajärvi has an exceptionally accurate chronology as it is an annually laminated lake (Ojala & Tiljander 2003). Lake Orijärvi was dated by producing a magnetic palaeosecular curve and correlating it with the corresponding curve from Lake Nautajärvi (Alenius *et al.* 2007). The sediment cores from Lakes Kirkkolampi, Laihalampi and Klotjärnen were radiocarbon-dated. More detailed information on the radiocarbon dates, calibration and age–depth curves are given in Alenius & Laakso (2006), Heikkilä & Seppä (2003) and Giesecke (2005). The pollen percentage diagrams from all five sites are shown in Appendix S1.

Pollen analysis at each site followed the standard procedures including hydrofluoric acid and acetolysis treatments (Moore *et al.* 1991). A minimum of 500 terrestrial pollen and spores were identified from each sample. For estimation of pollen concentration values, volumetric (1 cm³ or 0.5 cm³) sediment subsamples were obtained from the sediment cores and spiked with *Lycopodium* tablets (Stockmarr 1971). Concentrations were calculated by multiplying the sum of

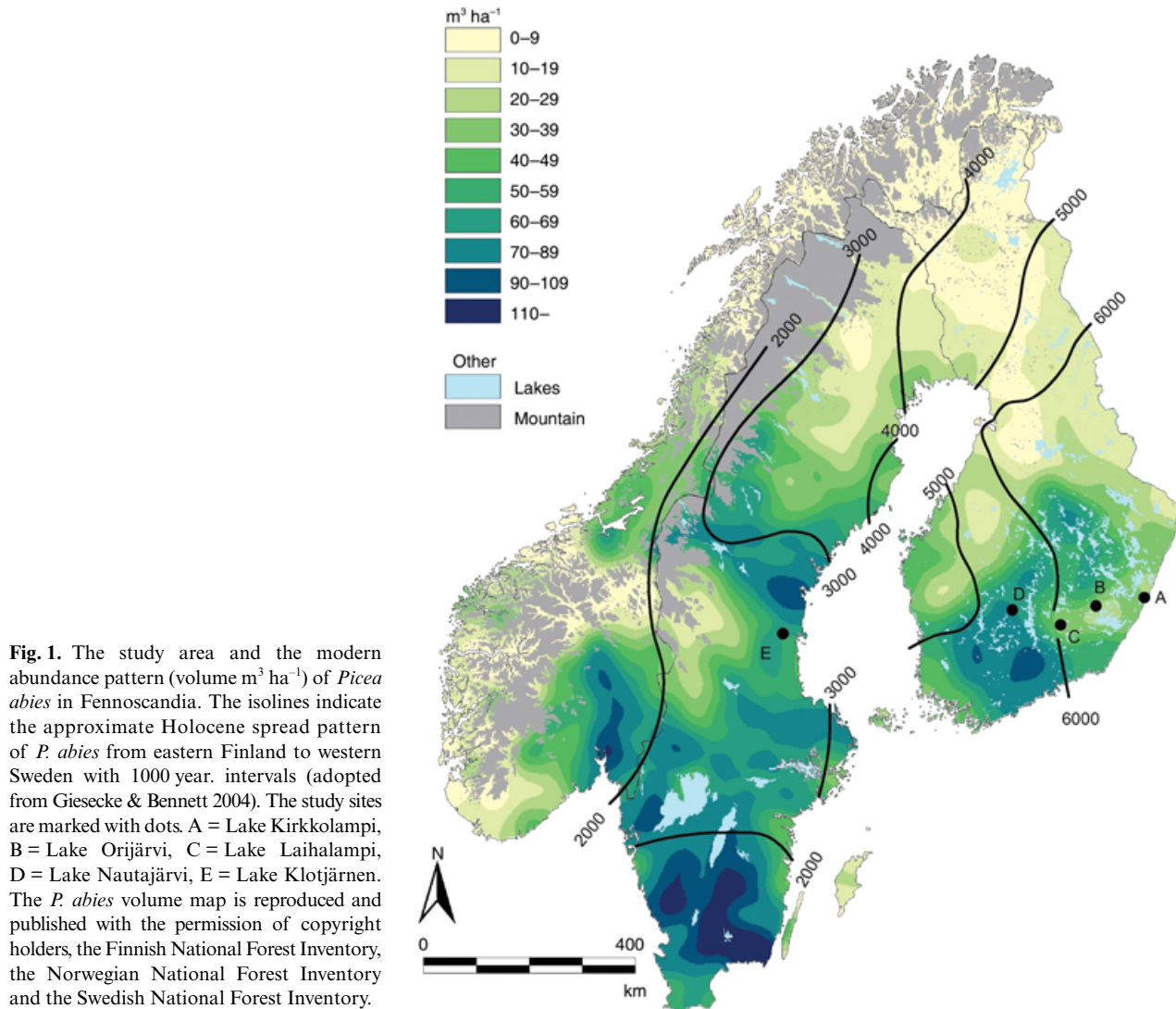


Fig. 1. The study area and the modern abundance pattern (volume $\text{m}^3 \text{ha}^{-1}$) of *Picea abies* in Fennoscandia. The isolines indicate the approximate Holocene spread pattern of *P. abies* from eastern Finland to western Sweden with 1000 year intervals (adopted from Giesecke & Bennett 2004). The study sites are marked with dots. A = Lake Kirkkolampi, B = Lake Orijärvi, C = Lake Laihalampi, D = Lake Nautajärvi, E = Lake Klotjärnen. The *P. abies* volume map is reproduced and published with the permission of copyright holders, the Finnish National Forest Inventory, the Norwegian National Forest Inventory and the Swedish National Forest Inventory.

Table 1. The modern PAR (grains $\text{cm}^{-2} \text{year}^{-1}$) and biomass values of *Picea abies* in Finland and Sweden, at sites ranging from *P. abies*-dominated southern boreal forest to beyond the northern distribution limit of *P. abies* in northern Fennoscandia. The modern *P. abies* above-ground biomass values (t ha^{-1}) were obtained from the National Forestry Inventory Statistics and are shown for zones ranging from 500 to 4500 m measured from the shores of the lakes (Seppä *et al.* 2009). The modern PAR value is defined as the average of the last 150 years

Site	Latitude (North)	Longitude (East)	Size (ha)	Modern PAR	Modern biomass 500 m range	Modern biomass 1000 m range	Modern biomass 4500 m range
Laihalampi	61°29'18"	26°05'	25.5	732	30,02	30,10	43,50
Nautajärvi	61°48'	24°41'	18.9	791	29,54	33,36	32,02
Kirkkolampi	61°47'	30°00'	72	675	No data	No data	No data
Orijärvi	61°40'	27°14'	25.9	690	10,89	21,25	21,75
Klotjärnen	61°49'	16°32'	2	612	No data	No data	No data
Akuvaara	67°07'	27°41'	4	29	0	0	0
Tsuolbmajavri	68°41'	22°05'	14	8	0	0	0
Toskaljavri	69°12'	21°28'	100	5	0	0	0

each pollen type by the ratio of the added and counted marker grains and the PAR values were calculated from the pollen concentration values by multiplying the concentration of each subsample by the sedimentation rate (Davis & Deevey 1964).

The modern PAR values were defined for eight sites in Fennoscandia to explore the correlation of the PAR values and the three population

sizes (Table 1). The value for Lake Orijärvi was defined by calculating the average PAR of the 14 pollen samples dating from the 20th century. The rest of the sites have a lower number of pollen samples analysed from the top sediment section and their modern PAR values were defined as the average of the last 150 years. This time period was chosen due to the fact that the age–depth model used for

calculating the PAR values may not apply well to the few top centimetres of unconsolidated sediment. In addition, calculating the modern value as a long-term average instead of using only the topmost sample is reasonable, given the high variance of the PAR values. Modern population sizes of the key tree taxa were defined as above-ground biomass values (t ha^{-1}), using the stand volume ($\text{m}^3 \text{ha}^{-1}$) data of the multi-source National Forest Inventory provided by the Finnish Forest Research Institute (for methodology, see Tomppo 1993). The stand volume was converted to the total above-ground biomass of each class using the biomass expansion-factors developed by Lehtonen *et al.* (2004) and P. Muukkonen, A. Lehtonen and M. Starr (unpublished data). The populations near the shoreline (0–100 m from the shoreline) were evaluated by using our own field measurements. In this approach the d.b.h. measured for each tree was converted to above-ground biomass by using biomass equations developed by Muukkonen (2007) (*Picea* and *Pinus*) and Johansson (1999) (deciduous trees).

Cross-correlations were calculated between the *P. abies* PAR and PAR of other important tree taxa to explore the influence of the colonization and population growth of *P. abies* on the population dynamics of the key tree taxa of the resident forest. In cross-correlation analysis two time-series are moved stepwise against each other in the time domain and the correlation is computed at each step. The aim of this analysis is to detect correlations between two time-series records, such as two PAR records, over a particular time period, and to account for the fact that the effect may not be immediate because there can be a time lag before the dependent variable responds to a change of the independent variable (*P. abies* PAR in our records) (Green 1995; Tinner *et al.* 1999). Here the analyses were carried out over a time-window of 2000 years with the increase of *P. abies* near the centre of the window. All data series were re-sampled to even time steps of 50 years using a linear interpolation between the original samples that had time intervals near 50 years during the rise of *P. abies* PAR in all datasets. Calculations and manipulations were carried out using the software package MATLAB.

Results

PAR VALUES AND THEIR EVALUATION

The basis for the use of the PAR as a proxy for past population size is the assumption that the PAR of a given pollen type is positively correlated with the size of the population of the plant taxa around the study site. In the case of *P. abies*, this assumption can be tested by comparing modern PAR and modern biomass values from eight sites in northern Europe (Table 1). At sites located outside the current range of *P. abies* the modern *P. abies* PAR is about 5–30 grains $\text{cm}^{-2} \text{year}^{-1}$. This agrees with the find of 50 *P. abies* grains $\text{cm}^{-2} \text{year}^{-1}$ coinciding with the first firm evidence for the presence of *P. abies* near (within few km) a site (Giesecke 2005). In the study sites located within the range of *P. abies* in the southern boreal zone, the modern PAR value ranges from about 610 to 790 $\text{cm}^{-2} \text{year}^{-1}$ (Table 1). Although the number of observations is too low to estimate statistically the correlation between the modern volume and PAR values, it appears that the presence of sparse or dense *P. abies* forest can be reliably identified from the PAR data and that the modern *P. abies* PAR values are generally larger with larger modern *P. abies* biomass. Values above 50 grains $\text{cm}^{-2} \text{year}^{-1}$ reflect the local presence of a sparse

P. abies population and values above 500 grains $\text{cm}^{-2} \text{year}^{-1}$ are typical in the *P. abies*- and *P. sylvestris*-dominated forest, where the *P. abies* above-ground biomass usually varies between 20 and 50 t ha^{-1} .

The Holocene *P. abies* PAR records are shown in Fig. 2. The results reflect the east-to-west spread of *P. abies*, indicating an approximate time difference of 4000 years between the local establishment at Lake Kirkkolampi in eastern Finland and at Lake Klotjärnen in Sweden and an average spreading rate of 0.2 km year^{-1} from eastern to western Finland. The rise of PAR values was abrupt at Lakes Orijärvi, Nautajärvi and Klotjärnen and more gradual at Lakes Kirkkolampi and Laihalampi. At all Finnish sites the period of highest PAR values, and thus the period of highest biomass, dates roughly to 4000–1500 cal. years BP, when *P. abies* PAR at Lakes Kirkkolampi, Orijärvi and Nautajärvi is consistently 1400–1600 grains $\text{cm}^{-2} \text{year}^{-1}$. Lake Laihalampi has PAR values of over 2000 grains $\text{cm}^{-2} \text{year}^{-1}$, probably because local edaphic conditions are more favourable for *P. abies* and because the proportion of lakes and bogs in the vicinity of the lake is smaller than at other sites. At Lake Klotjärnen the average PAR value at 2500–1500 cal. years BP is about 1500 grains $\text{cm}^{-2} \text{year}^{-1}$, which is consistent with the majority of the Finnish sites.

All PAR records show a marked declining trend during the late Holocene, starting at Lake Kirkkolampi 1700 cal. years BP and at the other sites about 1000 cal. years BP. This decline coincides with the beginning of intense agriculture and forest clearance, especially in the form of slash-and-burn cultivation in the boreal zone of Scandinavia (Nilsson 1997; Lindbladh *et al.* 2000; Pitkänen *et al.* 2002; Seppä *et al.* 2009). The records suggest that these new land-use practices particularly impacted the fire-intolerant *P. abies* (Pitkänen *et al.* 2002; Vanha-Majamaa *et al.* 2007; Seppä *et al.* 2009). The *P. abies* PAR values fell below 600 $\text{cm}^{-2} \text{year}^{-1}$ at each site 600 cal. years BP, suggesting the smallest regional *P. abies* population. A slight recovery has taken place at most sites during the last 100–150 years, apparently due to reforestation, cessation of slash-and-burn cultivation and decreased fire frequency.

PICEA COLONIZATION AND POPULATION GROWTH

Once the relationship between the *P. abies* PAR and biomass values has been approximately established, it can be used to reconstruct past population and forest community dynamics during the colonization and subsequent population growth of *P. abies* in Europe (Fig. 3). Detailed PAR records from the lakes unambiguously reflect the site-specific patterns of the colonization. *Picea abies* colonized the easternmost site, Lake Kirkkolampi, 6600 cal. years BP. The modern PAR level, about 700 grains $\text{cm}^{-1} \text{year}^{-1}$, was reached 6050 cal. years BP, but was followed by a transient decline starting 5800–5500 cal. years BP. The maximum PAR level, about 1300–2000 grains $\text{cm}^{-2} \text{year}^{-1}$, was attained 4800 cal. years BP, 1800 years after the initial colonization (Fig. 2). At the second easternmost site, Lake Orijärvi, colonization started 6100 cal. years

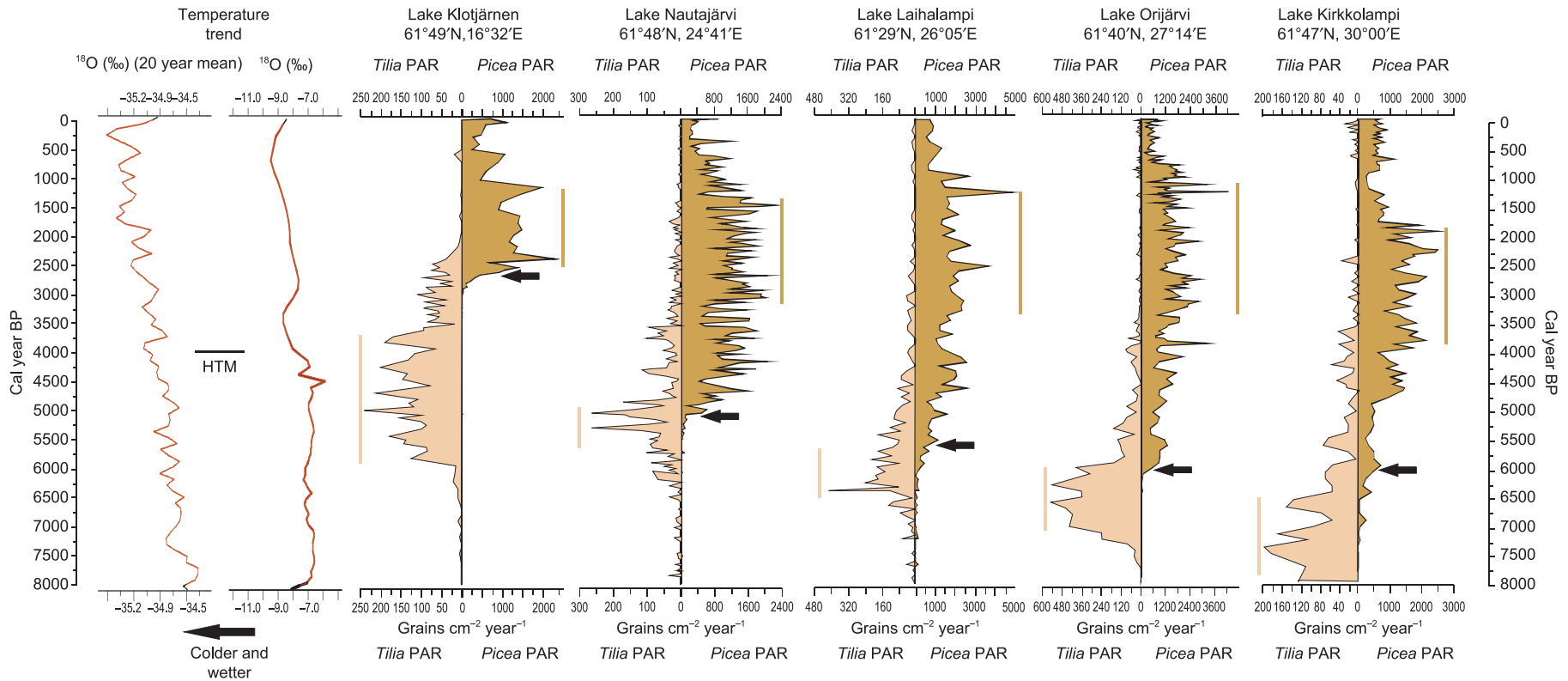


Fig. 2. The general PAR values of *Picea abies* at the five study sites, indicated on the right-hand side of the y-axis. The sites are arranged along the direction of the spread from the right (east) to the left (west). The PAR values of *Tilia cordata* are shown on the left-hand side of the y-axis to reflect its population dynamics during and after the colonization process of *P. abies* in Fennoscandia. The arrows indicate when the *P. abies* PAR reached the value comparable with the modern at each site and the light and dark vertical lines point to the periods of maximum *P. abies* and *T. cordata* populations. Two curves indicating the Holocene climate trends are shown on the left. The NGRIP $\delta^{18}\text{O}$ record is derived from an ice core in central Greenland and indicates a general temperature pattern in the North Atlantic region (Johnsen *et al.* 2001). Other temperature records confirm that this curve in general is valid for northern Europe as well. The southern Swedish $\delta^{18}\text{O}$ record is obtained from isotopic composition of a calcareous lake sediment core and reflects main trends both in temperature and hydrological conditions (Hammarlund *et al.* 2003; Seppä *et al.* 2005). HTM denotes the approximate end of the warm, dry and relatively stable mid-Holocene period in northern Europe.

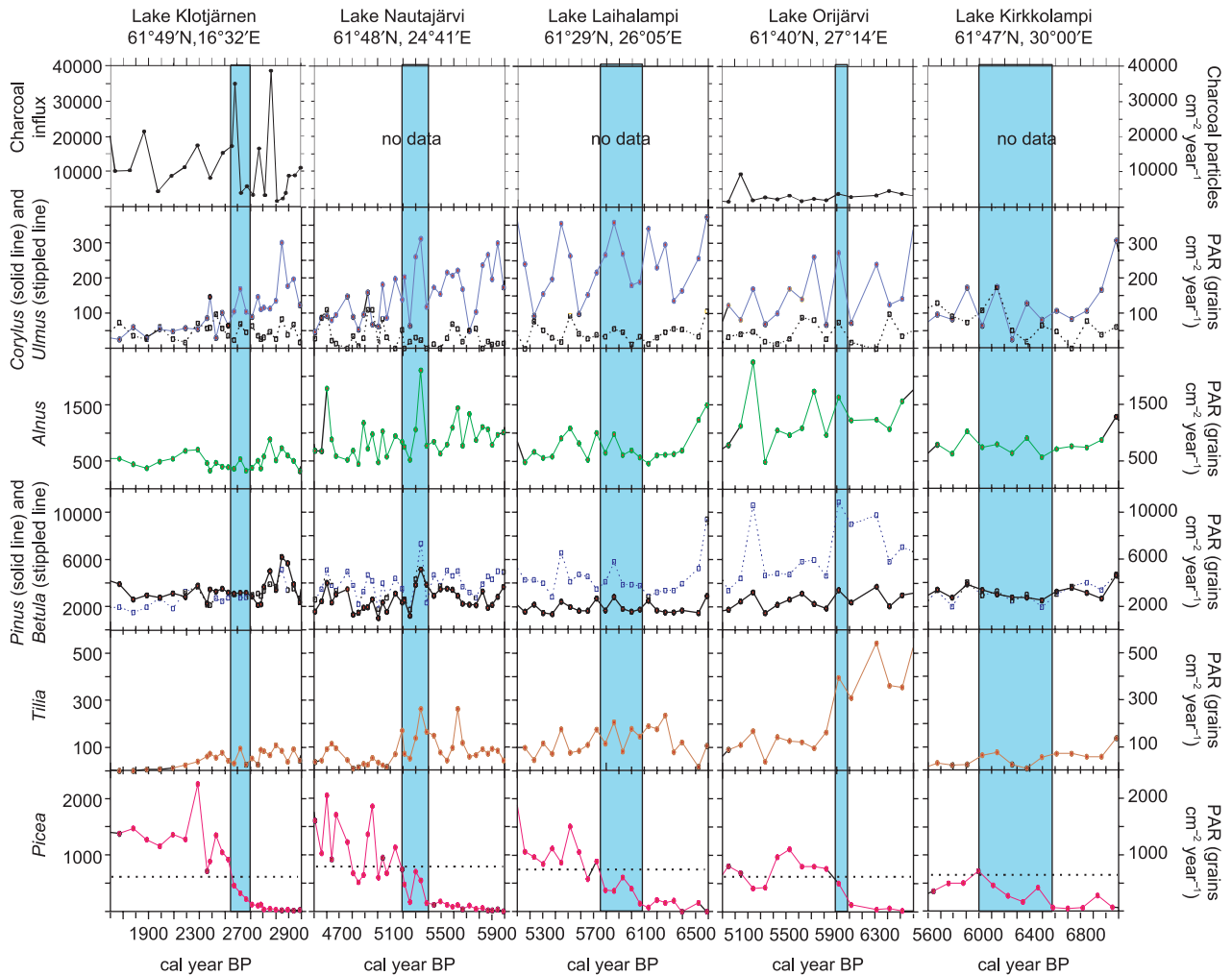


Fig. 3. The PAR records as indicators of forest population dynamics during and after the *Picea abies* colonization at the five study sites. The stippled line indicates the modern *P. abies* PAR value at each site and the light-blue columns reflect the period from the colonization (the onset of the rise of the PAR curve) to the modern level.

BP and was followed by rapid population growth. By 6000 cal. years BP, within 100 years, the *P. abies* PAR values had grown to about 600 grains $\text{cm}^{-2} \text{year}^{-1}$, corresponding to the modern *P. abies* PAR in the vicinity of the lake (Fig. 3). The third site, Lake Laihalampi, 57 km west of Lake Orijärvi, was colonized by *P. abies* 6050 cal. years BP, but the modern PAR level of about 800 grains $\text{cm}^{-2} \text{year}^{-1}$ was attained 450 years later, thus suggesting slower population growth here. At the fourth site in Finland, Lake Nautajärvi, 67 km west of Lake Laihalampi, *P. abies* immigrated 5400 cal. years BP, and attained a PAR value comparable to the modern (700 $\text{cm}^{-2} \text{year}^{-1}$) in 200 years, followed by a slower population growth and a PAR level of about 1000 grains $\text{cm}^{-2} \text{year}^{-1}$ about 4800 cal. years BP. At Lake Klotjärnen in Sweden, *P. abies* colonized 2700 cal. years BP, followed by rapid population growth. The modern population size was reached within 300 years, thus corresponding roughly with the growth rate recorded at Lake Nautajärvi in Finland.

PAR records also provide evidence of the resident forest composition and structure before and during *P. abies*

colonization. All sites show relatively comparable patterns of species composition and their PAR values. The dominant tree taxa at all sites during the colonization were *Pinus*, *Betula* and *Alnus*, while *Tilia* and *Corylus* were much more common than at present (Fig. 3). The PAR values of all these taxa are stable and high before the onset of the colonization. Along with the lack of peaks in the charcoal records (Fig. 3) and pollen from species that would indicate opening of the vegetation, such as Poaceae (see Heikkilä & Seppä 2003; Alenius *et al.* 2007), this suggests that *P. abies* invaded a dense, closed-canopy *Pinus–Betula–Alnus–Tilia–Corylus* forest without any large-scale disturbance-related openings during the colonization. Once established, *P. abies* populations at some sites grew rapidly, apparently without constraints on population growth, whereas at other sites population growth was a slower process constrained either by internal or external factors. We can only speculate about the reasons for the slower and more fluctuating population growth at some sites. The composition of the resident forest cannot be the key factor because it was remarkably similar at all sites. The reason may be related to biological

factors, such as variable intensity and frequency of release events or small disturbances that may be necessary for the seedlings of the invasive species to recruit into the canopy (Martin & Marks 2006), but it may also be related to changes in the physical environment such as changing soil moisture, paludification and peatland expansion in the vicinity of the lakes which can cause episodic decreases and expansions of the local *P. abies* populations.

When a new tree species invades an intact closed-canopy forest, competition for space and resources will inevitably lead to changes in the resident plant community (Davis *et al.* 1998; Bradshaw & Lindbladh 2005). The impact the invasion of *P. abies* had on the structure and composition of the mid-Holocene mixed forest can be assessed by examining the PAR values of the resident tree taxa during and after the invasion. All five detailed records unambiguously demonstrate that the tree species that most clearly declined was *T. cordata* (Figs 2–4). In Finland the *T. cordata* populations started to decline abruptly or more gradually about 200 years after the onset of the population growth of *P. abies*, when the size of the *P. abies* population around the lakes was comparable to the modern. This decline was particularly dramatic at Lake Orijärvi, where *T. cordata* attained a PAR value of about 400 grains cm⁻² year⁻¹, suggesting that it was an abundant, possibly dominant tree species around the lake before the *P. abies* invasion. At all four sites *T. cordata* PAR values remained at about 50–100 grains cm⁻² year⁻¹ after the rise of *P. abies*, until a gradual decrease towards the present trace values during the last 3000–4000 years (Fig. 2).

The westernmost record from Lake Klotjärnen in Sweden is remarkable because there the *T. cordata* population started to decline 4000 cal. years BP, about 1300 years before the immigration of *P. abies* (Fig. 2). Hence, this decline was not caused by interspecific competition with *P. abies* but by other internal or external factors. The *T. cordata* population around the lake was near to the northern distribution limit of the species during the mid-Holocene (Giesecke 2005) and the likely reason for the decline was a climatic cooling that started about 4000 cal. years BP in northern Europe (Hammarlund *et al.* 2003; Seppä *et al.* 2005) (Fig. 2). However, after the decrease the *T. cordata* PAR value remained at 70–100 grains cm⁻² year⁻¹, corresponding to the modern PAR value of *T. cordata* recorded at the northern part of the temperate zone where it is present (Eide *et al.* 2006). Thus, the cooling that started about 4000 cal. years BP reduced the local *T. cordata* population but the species remained present as scattered stands at favourable sites in the region, in a way comparable to the present northernmost scattered *T. cordata* stands, until a total disappearance when *P. abies* invaded the region 2700 cal. years BP.

The results of the cross-correlation analysis show that the other main tree taxa show a less clear population decline during the *P. abies* colonization (Fig. 4). *Pinus sylvestris* shows no or little change during the *P. abies* colonization and population growth, probably because *P. sylvestris* predominantly grows in drier and more nutrient-poor soils than *P. abies*, thus avoiding major competitive exclusion by the more

shade-tolerant *P. abies*. *Betula* has been observed to have declined in central Sweden as a result of *P. abies* invasion (Giesecke 2005). This is supported by the results of the cross-correlation analysis, showing that the reduction of *Betula* PAR with the rise of *P. abies* was significant at Lakes Kirkkolampi, Orijärvi and Klotjärnen. *Corylus avellana* and *Ulmus* also indicate significant negative correlations with *P. abies* at most sites, although with a varying time offset before and after the rise of *P. abies*. In contrast, the population of *Alnus* was least affected by the *P. abies* invasion. This feature, also observed in central Sweden (Giesecke, 2005), is unexpected because both *Alnus* species, *A. incana* and *A. glutinosa*, are relatively light-demanding and have overlapping soil requirements with *P. abies* (Dahl 1998).

The positive and negative time lags in the cross-correlation analysis can be interpreted in different ways. A positive lag will be seen if the *P. abies* population starts to expand in a particular habitat and slowly moves into locations with different soil and light conditions, thereby affecting some species later than others. A negative lag indicates that a species declined before the expansion of *P. abies* had started. Thus environmental conditions such as climate or disturbance regime may have led to the decline of one species and possibly facilitated the expansion of *P. abies*. Another interpretation is that the expansion of a *P. abies* population at some distance from the site led to competitive replacement by a species with a pollen type that is more easily airborne (e.g. *Betula*) than the heavy *P. abies* pollen. The site would therefore receive less pollen from long-distance sources before *P. abies* was established at the site and had started flowering.

Discussion

Ecosystems are transient, changing when new species attain dominance and replace one or several key components of the previous ecosystem (Jackson & Overpeck 2000; Jackson 2006). The records shown here reflect the invasion of *P. abies* and the resulting striking Holocene ecosystem change in Fennoscandia. They show how the former species-rich mixed ecosystem was invaded by *P. abies* and gradually changed to a modern boreal forest, dominated by *P. abies* and *P. sylvestris*. This ecosystem change happened gradually from east to west, as the spread of *P. abies* forest caused a decrease in the distribution of the mixed conifer-deciduous forest. During the mid-Holocene, about 5500 cal. years BP, the eastern half of southern Finland was thus part of the boreal ecosystem and the western half was still dominated by the mixed conifer-deciduous forest, while by about 3000 cal. years BP southern Finland was a part of the boreal forest but areas at the comparable latitude in central Sweden were still predominantly characterized by mixed conifer-deciduous forest.

Locally, the ecosystem change takes place as a result of population growth of the invasive taxon and subsequent suppression of the resident taxa. The PAR data and associated population reconstructions shown here provoke questions about the ecological processes leading to the change in forest composition. An important feature of these records is the

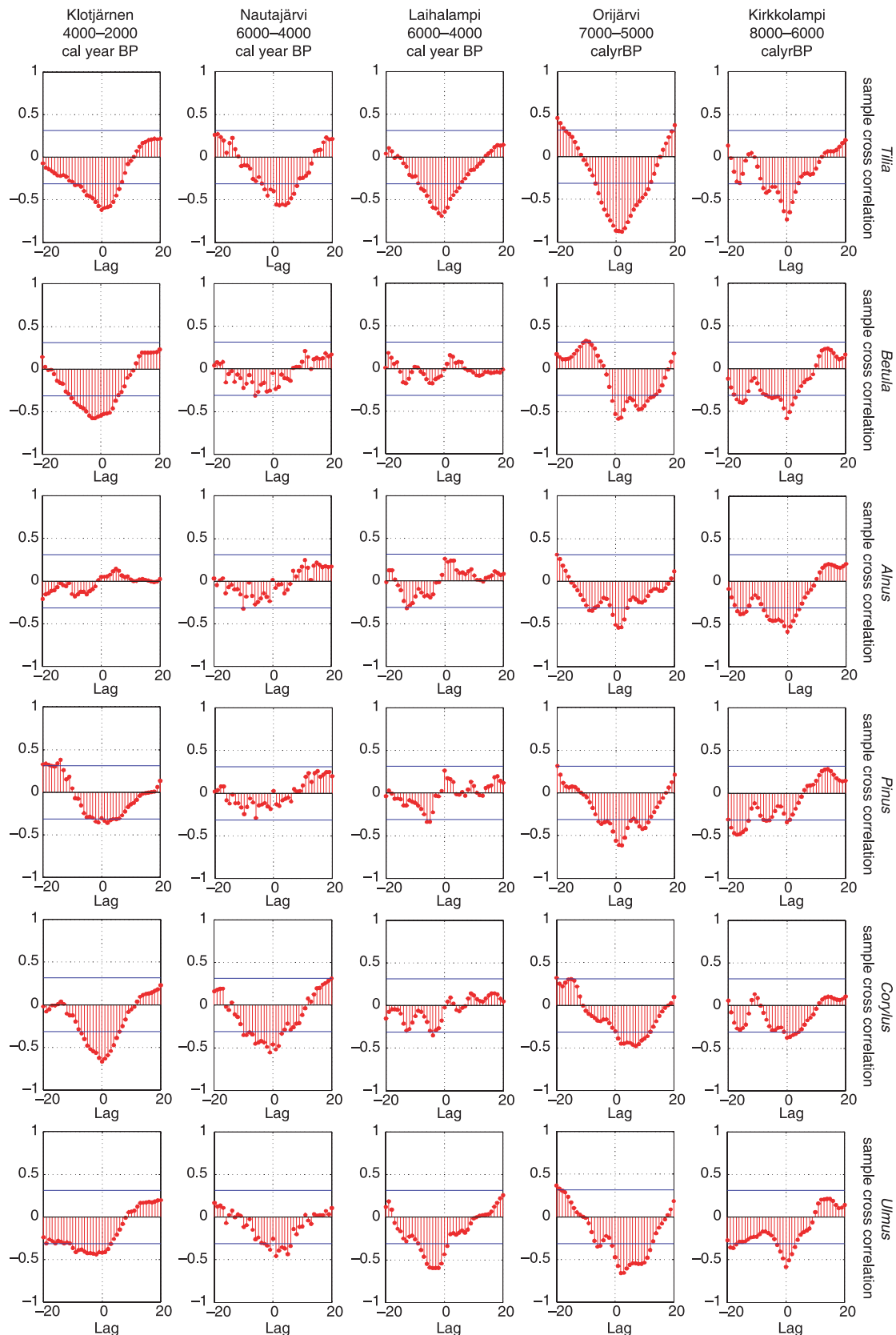


Fig. 4. The cross-correlations showing the influence of the colonization and population growth of *Picea abies* on the population dynamics of the most important tree taxa of the resident forest. The analyses were carried out with 50-year time lags before and after the *P. abies* colonization at each site. The y-axis indicates the correlation coefficient between the *P. abies* PAR and the each species. The solid horizontal lines show the limits of statistically significant values.

species-specific response of the resident taxa to the invasion of a new competitive tree species. The different response patterns reflect differences in the fundamental niches the resident tree taxa occupy and provide insights to the ecological processes during *P. abies* colonization. The key aspect of interspecific competition is the role of overlapping ecological niches (Bennett & Lamb 1988; Lawesson & Oksanen 2002). Although the boreal *P. abies* and temperate *T. cordata* are markedly different in terms of their modern 'climatic envelopes' (Dahl 1998), they share the same substrate requirements, preferring relatively nutrient-rich and moist soils (Diekmann 1996). *Tilia cordata* is more drought-tolerant and can be found on well-drained soils but is absent on very wet soils where *P. abies* can be present. Most importantly, *T. cordata* is a relatively shade-intolerant species in its main distribution area in the temperate zone (Pigott 1991; Prentice & Helmsaari 1991; Diekmann 1996; Lawesson & Oksanen 2002), while *P. abies* is a shade-tolerant species. Particularly on moist substrates *P. abies* can out-compete shade-intolerant species and create dense stands that represent the end-successional, climax stages in the boreal forest of northern Europe. The fact that the decline of *T. cordata* took place a few hundreds of years after the immigration of *P. abies* and at the same time when *P. abies* had reached its modern population density suggests that the sexual regeneration of *T. cordata* was suppressed because of shading by the *P. abies* population. Other, indirect influences that can result from the development of a *P. abies*-dominated forest, such as gradual soil acidification, development of a thick litter layer and associated raw humus layer, or altered mineralization rates (Havas & Kubin 1983; Levula *et al.* 2003) are not supported by the data because such processes are gradual and should be reflected in slower decreases of the *T. cordata* populations.

Overall, the PAR data suggest that the invasion of *P. abies* caused a major reduction of the *T. cordata* population in the northern part of *T. cordata*'s distribution range in northern Europe (Fig. 2). This suppression is still reflected in the rare and scattered occurrence of *T. cordata* in its northernmost range in the *P. sylvestris*- and *P. abies*-dominated forest. For example, in Finnish national parks forest management practices – mainly removal of tall *P. abies* trees – are necessary to promote the survival of the northernmost *T. cordata* stands. However, further south in the temperate-boreal zone no similarly abrupt decline of *T. cordata* pollen percentages was observed, suggesting that there *T. cordata* was better able to resist the immigration of *P. abies* (Digerfeldt 1977; Giesecke 2005), possibly because the shade-tolerance and competitive ability of *T. cordata* can vary spatially in Europe (Diekmann, 1996). This is consistent with the present relatively weak competitive performance of *P. abies* in the natural forest stands in eastern central Europe. For example, in Bialowieza National Park in Poland, the largest old-growth forest in central Europe, *P. abies* only occurs as scattered stands, and its regeneration is confined to disturbed, semi-open sites, whereas *T. cordata* is one of the dominant components of the forest (Falinski 1986; Peterken 1996; Mitchell & Cole 1998). Thus, the competitive interaction between these two species is spatially

constrained, with the niche of *T. cordata* becoming narrower towards the northern part of its distribution range.

The clear, gradual population decline of *T. cordata* all over the central and southern parts of the boreal zone raises questions about the role of the non-biotic, mainly climatic factors as drivers of past changes in the boreal forest – was the mid-Holocene *T. cordata* population decline a prime example of a major range reduction caused by purely competitive species interactions without any role of climatic change? A positive answer would suggest a significantly smaller, competition-limited realized environmental niche than the potential niche (Pearman *et al.* 2007) for *T. cordata* during the mid-Holocene and would invalidate an important assumption of species distribution models that relate species distributions to climate and use this information for predicting distribution changes under past and future climate conditions (Thuiller 2004; Hijmans & Graham 2006; Pearman *et al.* 2007). However, the answer may be negative for a number of reasons. The *T. cordata* PAR values of 50–100 grains cm⁻² year⁻¹ after the *P. abies* invasion suggest that *T. cordata* remained present around the study sites after the *P. abies* invasion, so that the major population reduction may not imply a reduction of the northern range of *T. cordata*. In addition the Lake Klotjärnen record from Sweden shows that *T. cordata* started to retreat there 4000 cal. years BP, during the onset of cooling but before the immigration of *P. abies*, reflecting the importance of climate in controlling the retreat of the northern distribution limit of *T. cordata*.

Furthermore, it is possible that the decline of the *T. cordata* population during the immigration of *P. abies* was an indirectly climate-driven process, as the underlying factor that promoted the westward spread of *P. abies* may have been a gradual climatic change (Tallantire 1977; Bradshaw *et al.* 2000; Seppä *et al.* 2005), although this hypothesis remains equivocal (Giesecke & Bennett 2004; Miller *et al.* 2008). The palaeoclimatic records do not suggest a gradual climatic change that would correspond with the pattern of spread of *P. abies* (Fig. 2), but it is important to note that the existing records mostly reflect climatic conditions during the summer or the growing season, whereas the gradually colder winters with increasing snowfall have been suggested as the predominant climatic factors that influenced the *P. abies* spread (Huntley 1998; Bradshaw *et al.* 2000; Seppä *et al.* 2005). Thus, while the approach presented here permits a more detailed investigation of the past competitive interactions and their ecological consequences, unravelling the underlying roles of the internal and external drivers requires the use of independent climatic proxy methods.

Conclusions

Picea abies, one of the major components of the boreal forest, has spread westward in northern Europe during the last 7000 years, becoming the dominant species especially on mesic and nutrient-rich sites. Its invasion had a major impact on the resident flora and altered the structure and function of the forest communities in the region, eventually causing the

development of the modern boreal ecosystem. The new high-resolution PAR records from five sites in Fennoscandia show that *P. abies* invaded a species-rich mixed forest at all five sites, consisting mostly of *Betula*, *P. sylvestris* and *Alnus*, but including significant proportions of *T. cordata*, *C. avellana*, and other temperate deciduous species. The time it took for the *P. abies* population to grow from the point of colonization to the modern population level varied from 100 years at Lake Orijärvi to 450–550 years at Lakes Kirkkolampi and Laihalampi. The variance in growth rate was not caused by differences in the composition of the resident forest or in the inherent invasibility of the ecosystem (Lonsdale 1999), but probably by other factors, such as local disturbance dynamics or local edaphic factors. *Picea abies* was an invasive species with competitive advantage and the speed of its spread was limited by inherent dispersal properties, not by the competitive interaction with the resident forest or by forest fires or other large-scale disturbances. Similar invasions of shade-tolerant tree taxa have been observed in recent experimental investigations (e.g. of the invasion of *Acer platanoides*), suggesting that shade-tolerant tree species can colonize dense, intact resident forest (Martin & Marks 2006). Thus, there are palaeoecological and neo-ecological data to indicate that the idea of robust invasion resistance of intact forests may have been exaggerated and the theory suggesting that invasive trees do not spread into a closed-canopy forest without disturbance (Elton 1958; Pearsall 1959; von Holle *et al.* 2003) may need to be modified to account for the life-history traits of the invasive tree species.

The most distinct change in the resident forest after colonization was the decline of *T. cordata*, one of the major components of the forest before the *P. abies* invasion. At all sites *T. cordata* became rare during the *P. abies* colonization and has remained so during the late Holocene. This suggests strongly overlapping ecological niches for the two species, with a competitive edge for *P. abies*, probably because *T. cordata* is particularly shade-intolerant towards the northern part of its range. Thus, the fragmented occurrence and the generally weak present performance of *T. cordata* within its climatic space in central and southern Scandinavia, often assigned to human interference (Berglund 1969; Behre 1988; Björse & Bradshaw 1998; Cowling *et al.* 2002), have a longer antiquity than human influence, dating back to the time of invasion of *P. abies*, and are probably primarily a result of competitive exclusion by *P. abies*. This palaeoecological dimension of modern tree distribution patterns, observed also in the temperate forests in Europe (Peterken & Game 1984; Wulf 1997; Dupré & Ehrlén 2002), must be incorporated into analyses of species composition and distribution patterns in the present boreal forest (Dupré & Ehrlén 2002).

The suppression of *T. cordata* by *P. abies* can be relevant for predictions of future ecosystem processes (Neilson *et al.* 2005). In Sweden, dynamic vegetation and gap models predict that future warming will promote a major northward spread of temperate deciduous tree species including *T. cordata* (Sykes & Prentice 1996; Koca *et al.* 2006). By the year 2100 *T. cordata* will be a major component of the forest in central Sweden, its range reaching along the Swedish east coast up to

68°N (Koca *et al.* 2006). This scenario is unlikely, however, if the current dense *P. abies* forest continues to dominate on the mesic soils in central and northern Sweden and elsewhere in northern Europe. *Tilia cordata* may be able to expand its range but in *P. abies*-dominated regions its population size will be reduced by the resident *P. abies* populations. However, it is possible that the predicted warming and especially the predicted increasing summer dryness will cause a decrease of the abundance of *P. abies* in the boreal zone. Thus, a possible large-scale decline of the *P. abies* population in the boreal zone would enhance the possibility of *T. cordata* spreading northwards.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Pollen percentage diagrams from all five sites.

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