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# Dynamics of long-lived foundation species: the history of *Quercus* in southern Scandinavia

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## Summary

**1.** The long-term history of *Quercus* in southern Scandinavia has received little attention despite its important role in modern conservation. In this study the 4000-year dynamics of *Quercus*, its habitat and other important taxa were analysed with pollen data from 25 small hollows and 6 regional sites across southern Scandinavia. The aim was to provide a context for understanding the species' current status and managing its future dynamics.

**2.** The results indicate that *Quercus* is much less abundant today than at any time during the previous 4000 years and corroborate the rapid decline reported in 18th- and 19th-century historical records. Modern pollen percentages are 45–60% of 17th-century values and only 20–35% of the maximum values reached in the 3rd century.

**3.** A strong positive correlation exists between the abundance of *Quercus* and the abundance of *Tilia, Corylus* and *Alnus*, which also experienced a steady decline across the region in the last two millennia. Climate change is the broad-scale driver of the observed dynamics, but human activity introduced considerable variation in the regional and temporal details of these changes. In the hemiboreal northern part of the study area the decline of *Quercus* appears to be controlled largely by competition with other tree species (especially *Pinus* and *Picea*), mediated by harvesting. In the temperate south part *Quercus* forests decreased through deforestation for agriculture.

**4.** Multivariate analyses indicate that although substantial phytogeographical variation has existed through past millennia the regional vegetation is more homogeneous today than in earlier periods.

**5.** *Synthesis*. The long-term decline and recent rapid reductions in *Quercus* populations throughout southern Scandinavia are striking and indisputable. From the perspective of both the populations of *Quercus* and its associated species of insects and epiphytes, the recent rate of decline is extremely rapid. Given the former abundance, longevity and capacity for persistence of *Quercus*, current populations of *Quercus* and its associated species appear to represent biological legacies in the midst of protracted decline. Based on these results, a reasonable conservation goal is to restore the abundance and distribution of *Quercus* to levels that preceded the drastic decline in the 18th and 19th centuries.

**Key-words:** Denmark, extinction debt, forest conservation, forest history, land-use history, oak, paleoecology, pollen analysis, *Quercus robur*, Sweden

## Introduction

Across southern Scandinavia only a few trees qualify as foundation species, i.e. species that exert an impact on community and ecosystem properties greatly disproportionate to their abundance (*sensu* Dayton 1972; Ellison *et al.* 2005). Two of these, *Fagus sylvatica* (European beech) and *Picea abies* (Norway spruce), are shade-tolerant species whose historical roles have been extensively investigated with regards to abundance and distribution (e.g. Iversen 1973; Huntley, Bartlein & Prentice 1989; Björkman 1996a; Giesecke 2004; Bradshaw & Lindbladh 2005; Seppä *et al.* 2009). In contrast, *Quercus* spp. (Oaks) include moderately shade-tolerant species (*Quercus robur* and *Quercus petraea*) that have received considerably less historical study despite their critical role in modern conservation. In spite of its scattered abundance in southern Scandinavia, the importance of the genus *Quercus* for Swedish and European biodiversity is difficult to overstate (Ranius *et al.* 2005). *Quercus* provides critical habitat for lichens and fungi (Ranius & Jansson 2000; Berg *et al.* 2002; Gärdenfors 2010)

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and represents the most important tree genus for red-listed invertebrates (Jonsell, Weslien & Ehnström 1998).

Many characteristics of *Quercus* in the Swedish landscape provide challenges for conservation management. These include its low abundance and vulnerability to further reductions, its scattered distribution and the extreme age of many individuals. In particular, there is uncertainty concerning the future status of *Quercus*, the resulting consequences for species that are dependent on *Quercus*, appropriate targets for the restoration of populations in the landscape, and the need for management to achieve these desired conditions (Ranius 2000; Hedin 2003; Nordén *et al.* 2007; Økland, Götmark & Nordén 2008; Tyler 2008). Some researchers have argued that conservation projections for the many rare insect and cryptogam species associated with *Quercus* are overly optimistic as they are based on persistence probabilities that do not appropriately account for long-term declines in *Quercus* and its associated habitats (Nilsson *et al.* 2005; Ranius, Eliasson & Johansson 2008). In their perspective, *Quercus* populations may be too scarce and fragmented to facilitate persistence and gene flow of rare species, which consequently exist under an 'extinction debt' (*sensu* Tilman *et al.* 1994; Hanski, Moilanen & Gyllenberg 1996).

To address these concerns and to examine the potential for future declines and extinction, studies have attempted to place the recent dynamics and status of *Quercus* in a historical context based on early 19th-century data (Hedin 2003; Ranius & Hedin 2004). However, effective evaluation of long-lived trees like *Quercus*, which produce biological legacies (*sensu* Lindenmayer & Franklin 2002) and habitats that may endure for many centuries, require an even longer time-perspective. *Quercus* frequently live 300 years in closed forests, 400–600 years in open woodlands and pastures and as much as *c.* 1000 years under optimal conditions (Niklasson & Nilsson 2005; Drobyshev *et al.* 2008). Furthermore, the coarse dead wood of *Quercus* may provide an important substrate for other taxa, especially insects, fungi and microbes, which endure over many hundreds of years. To provide insights into these critical ecological and conservation issues it is necessary to develop a regional reconstruction by employing an approach that combines the time-depth of paleoecology and the stand to landscape-scale spatial resolution of field sampling. The appropriate paleoecological approach for this effort combines the analysis of a network of small hollows, which yield local information, with the regional-scale record provided through the analysis of lake sediments (cf. Jacobson & Bradshaw 1981; Foster & Zebryk 1993) .

In our investigation of the ancient and recent history of *Quercus* we analysed the pollen data from 25 small hollow sites across southern Scandinavia (Fig. 1, Table 1). Small hollows act as local pollen collectors and yield stand to landscape-level information on vegetation composition and dynamics as well as natural and anthropogenic disturbances (Bradshaw 2007). In appropriate settings they may accumulate continuous sediment records spanning centuries to millennia and can, therefore, be regarded as analogous to extremely long-term permanent plots (*sensu* Jacobson & Bradshaw 1981). High-resolution records from a regional network of small hollows may then be analysed through Geographic Information System and multivariate statistics to provide a regional perspective that resolves the geographical detail and variation among vegetation zones, across major edaphic and environmental gradients or even among different land-uses in a single estate.

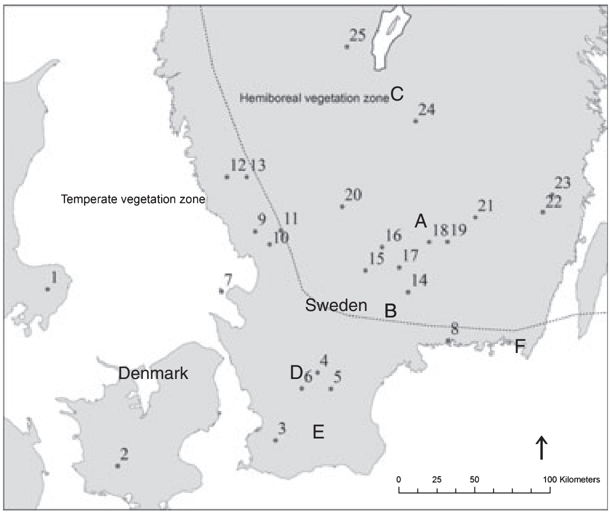

**Fig. 1.** Map of southern Scandinavia with the sites used in the study. See Table 1 for the names of the small hollow sites. The regional lake sites include: A, Lake Trummen and Lake Växjösjön; B, Lake Ranviken; C, Lake Kansjön; D, Ageröds Mosse; E, Lake Krageholmssjön; F, Lake Färskesjön.

To augment and contrast the local to regional understanding emerging from the network of hollows, we analysed the independent record of regional-scale vegetation dynamics provided by pollen analyses of sediment cores from six lakes distributed across the study region. In both sets of reconstructions we focused on interpreting the dynamics and drivers of changes in *Quercus* abundance during the last 4000 years. To enhance the conservation insights emerging from prior historical studies, we placed special emphasis on the 18th and 19th centuries, seeking to: evaluate the accuracy of the reconstructions of declines coming from historical records, provide additional insights into the dynamics of *Quercus* preceding this fairly well-documented period, and contrast these recent dynamics with those from previous millennia.

## Materials and methods

### REGIONAL HISTORY OF *QUERCUS* IN SOUTHERN SCANDINAVIA

Numerous pollen records and historical sources provide the history of regional forest dynamics that are useful for interpreting the spatially resolved patterns of change emerging from small hollows over the past few millennia. Records from lake sediments indicate that *Quercus* abundance peaked across southern Scandinavia through the thermal maximum 9000–6000 years ago (Iversen 1973; Berglund *et al.* 1996; Rasmussen 2005). However, from a maximum of > 20% of pollen in the mid Holocene *Quercus* declined substantially in most records (Figs 2 and 3; Björse, Bradshaw & Michelson 1996; Berglund

**Table 1.** Small hollow sites in Denmark and Sweden used in this study. $C^{14}$ and AMS refer to dating by conventional radiocarbon and accelerator mass spectrometry techniques

| ID | Site name | Reference | Location | Depositional environment | Historical land use | No. of radiocarbon dates and time span of profile |
|---|---|---|---|---|---|---|
| | **Temperate zone** | | | | | |
| 1 | Lövenholm | Unpubl. data | 56 44′ N 10 49′ E | Small wetland | Not defined | NA (9000 BC–present) |
| 2 | Suserup | Hannon, Bradshaw & Emborg (2000) | 55 22′ N 11 34′ E | Wetland 20 × 30 m | Not defined | 1 C14 & 5 AMS (4200 BC–present) |
| 3 | Torup | Hultberg *et al.* (2010) | 55 56′ N 13 21 E | Wetland 10 × 10 m | Not defined | 6 AMS (3700 BC–present) |
| 4 | Vasahus | Lindbladh *et al.* (2007) | 55 54′ N 13 38′ E | Peat bog 25 × 40 m | Outland | 4 C14 (1310 BC–present) |
| 5 | Kyllingahus | Lindbladh *et al.* (2007) | 55 53′ N 13 39′ E | Peat bog 15 × 50 m | Infield | 5 AMS (4100 BC–present) |
| 6 | Häggenäs | Lindbladh *et al.* (2007) | 55 53′ N 13 36′ E | Wetland 10 × 100 m | Infield | 5 AMS (350 AD–present) |
| 7 | Hälledammen | Molinari (2002) | 56 61′ N 13 01′ E | Pond 50 × 50 m | Outland | 4 AMS (850 BC–AD 1750) |
| 8 | Eriksberg | Hannon (Unpubl. data) | 56 11′ N 15 00′ E | Wetland 10 × 10 m | Not defined | 4 AMS (5200 BC–present) |
| 9 | Kalvaberget | Lindbladh *et al.* (2008) | 56 48′ N 12 54′ E | Wetland 150 × 25 m | Not defined | 8 AMS (600 BC–present) |
| 10 | Holkåsen | Lindbladh *et al.* (2008) | 56 48′ N 12 54′ E | Wetland in depression 50 × 10 m | Outland | 6 C14 (1500 BC–present) |
| 11 | Trälhultet | Lindbladh *et al.* (2008) | 56 48′ N 12 54′ E | Wetland 200 × 40 m | Outland | 4 AMS (1300 BC–present) |
| 12 | Bocksten a | Björkman (1997a) | 57 07′ N 12 34′ E | Fen *c.* 25 m in diameter | Outland | 4 C14 (700 BC–present) |
| 13 | Bocksten b | Björkman (1997a) | 57 07′ N 12 34′ E | Fen *c.* 30 × 40 m in diameter | Outland | 2 C14 (2500 BC–present) |
| | **Hemiboreal zone** | | | | | |
| 14 | Siggaboda | Björkman & Bradshaw (1996) | 56 28′ N 14 34′ E | Peat bog 5 × 5 m | Outland | 5 C14 (900 BC–present) |
| 15 | Råshult in-field | Lindbladh & Bradshaw (1998) | 56 37′ N 14 12′ E | Wetland 25 × 30 m | Infield | 7 C14 (2400 BC–present) |
| 16 | Djäknabygd | Lindbladh & Bradshaw (1998) | 56 37′ N 14 12′ E | Wetland 5 × 5 m | Outland | 5 C14 (3900 BC–present) |
| 17 | Nissatorp | Lindbladh & Bradshaw (1998) | 56 37′ N 14 12′ E | Wetland 15 × 100 m | Outland | 2 C14 (80 BC–present) |
| 18 | Osaby in-field | Lindbladh (1999) | 56 46′ N 14 47′ E | Lake fringe | Infield | 1 AMS & 4 C14 (1800 BC–present) |
| 19 | Osaby out-field | Lindbladh (1999) | 56 46′ N 14 47′ E | Wetland 20 m in diameter | Outland | 1 AMS & 4 C14 (5100 BC–present) |
| 20 | Flahult | Björkman (1997b) | 56 58′ N 13 50′ E | Small peatland 20 × 40 m | Not defined | 4 C14 (500 BC–present) |
| 21 | Storasjö | Eriksson (1996) | 56 55′ N 15 17′ E | Wetland 50 × 50 m | Outland | 5 C14 (700 BC–present) |
| 22 | Ekenäs | Valdemarsdotter (2001) | 56 57′ N 16 01′ E | Wetland 40 × 30 m | Infield | 2 AMS & 2 C14 (1500 BC–present) |
| 23 | Skärsgölarna | Lindbladh, Niklasson & Nilsson (2003) | 57 01′ N 16 07′ E | Wetland 50 × 30 m | Outland | 6 AMS (3900 BC–present) |
| 24 | Mattarp | Björkman (1996b) | 57 29′ N 14 37′ E | Peatland 25 m in diameter | Not defined | 5 C14 (5900 BC–present) |
| 25 | Ryfors | Abrahamsson (1996) | 57 55′ N 13 50′ E | Peatland 3 × 3 m | Not defined | 2 C14 (300 BC–present) |

*et al.* 2007). Written sources suggest a more recent decline over the past hundreds of years. An important timber for warships, *Quercus* was declared to be the property of the Swedish state by King Gustav Vasa in AD 1558. At the end of the 18th century the increasing population of more self-assured peasants successfully applied pressure on the state to allow access to *Quercus* trees, leading to an increase in harvesting (Eliasson 2002). According to subsequent state inventories from 1790 to 1825 the abundance of *Quercus* trees that met naval standards decreased by more than 80% across southern Sweden. Most of the decline appears to have occurred in meadows and arable

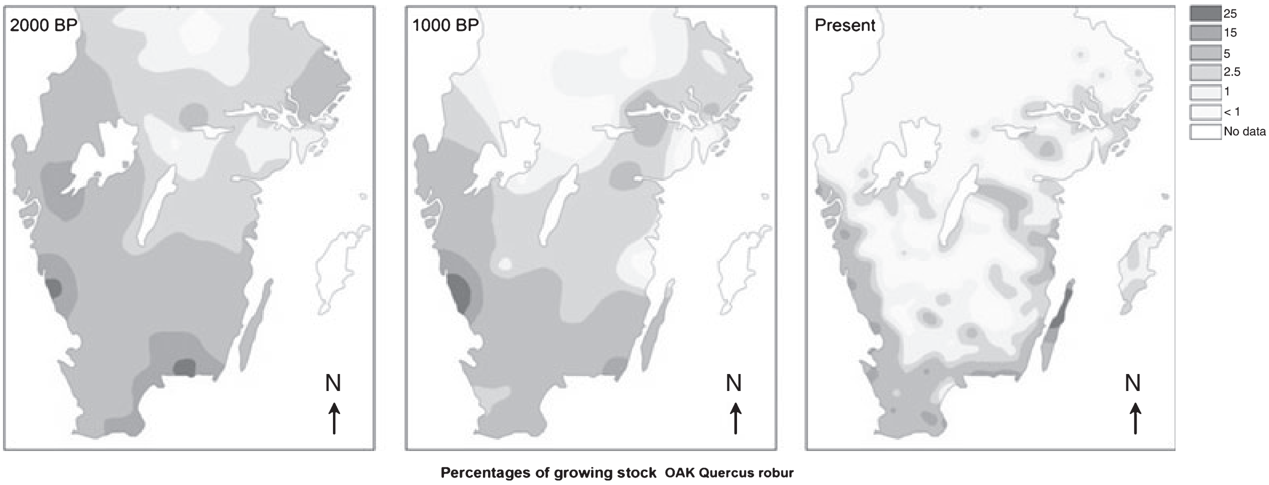

**Fig. 2.** Past and present distribution of *Quercus* in southern Sweden, modified from Björse, Bradshaw & Michelson (1996). The modern data are based on forest inventory data and represent percentages of the total growing stock. The data from 2000 and 1000 years BP represent estimated growing stock and are made from a network of 37 regional pollen sites. The maps are from the National Atlas of Sweden – Geography of Plants and Animals (Gustafsson & Ahlén 1996).

lands close to villages (Eliasson & Nilsson 2002). Royal ownership of *Quercus* officially ended in 1830, which resulted in a further increase in harvesting by peasants, and a corresponding decline in useful trees (Eliasson & Nilsson 2002; Hedin 2003). In Denmark, a general decline in forest cover also occurred from the 16th century onwards. In particular, during the period AD 1650–1750, and associated with an expansion of agricultural activities by an increasing human population, many forests of mature *Quercus* and *Fagus* were converted into dense brushwood (Fritzböger 1992). The landlords and the Crown foresters decried the loss of timber trees whereas peasants readily used the brushwood for coppice and grazing. In remaining forests *Fagus* gradually became dominant. The 18th century assessments contain little evidence of mature *Quercus* trees.

## STUDY OBJECT

Two species of *Quercus* occur in the region today: *Q. robur* (Pedunculate oak) and *Q. petraea* (Sessile oak). *Quercus robur* occurs throughout the temperate (nemoral) region and is one of the most widely distributed trees in Europe. It is a relatively light-demanding species that regenerates poorly under a closed canopy (Diekmann 1996; Vera 2000). It has a large site amplitude but is most competitive on dry and wet sites with low fertility where *F. sylvatica* grows less vigorously (Larsen, Raulund-Rasmussen & Callesen 2005). On fertile sites and in the absence of large-scale disturbance, *Q. robur is* also generally less competitive than *Ulmus* (Elm), *Tilia* (Linden), *Fraxinus* (Ash) and *Acer* (Maple) (Niklasson & Nilsson 2005). Historically it was probably rather tolerant to fires and also favoured by human activity (Bradshaw & Lindbladh 2005). *Quercus petraea* has a similar distribution and ecology as *Q. robur* but is much less common. Compared to *Q. robur* it has an even larger tolerance to sites with thin soils but is less tolerant of poorly drained conditions.

In Scandinavia *Quercus* has a southern distribution, centred along the coast in the temperate vegetation zone (Fig. 2). In this region a large proportion of the remaining forest is comprised of broadleaf trees but the total forest area is rather limited (< 30%) due to historical conversion to arable land and residential and commercial development. In the more northern hemiboreal zone *c.* 60% of the land is occupied by forests, but *Quercus* occurs as a minor component. Forests in this region are largely dominated by nearly pure stands of *P. abies* (*c.* 47% of total volume) and *Pinus sylvestris* (*c.* 29%) managed for timber production and characterized by low value for biodiversity. *Quercus* occurs both in natural stands and in forests intensively managed for timber production. Approximately one-third of the trees exceed 45 cm in diameter, with most of the larger trees occurring in natural stands (Nilsson *et al.* 2008). *Quercus* intended for timber production are usually cut by an age of *c.* 120 years, which is decades before they develop the 'old tree structures' of large stem diameter, coarse cracked bark and decay-infested hollows that provide important habitats for many insects and epiphytes species (Berg *et al.* 1994; Nilsson *et al.* 2005). A large proportion of the remaining older coarse trees grow in the former infields of estates (Eliasson & Nilsson 2002). Historically, estates were separated into infield (Swedish *inäga*) and outland (Swedish *utmark*), a division that persisted in large parts of southern Scandinavia for many hundred years until the early 20th century. Generally, infields lay closer to the village buildings and contained arable land and hay meadows, whereas outlands were largely forested and primarily used for grazing.

## SITE SELECTION AND REGIONAL VARIATION

With one exception all sites investigated for local records are small hollows or wetlands selected from previous studies (Table 1, Fig. 1). The additional site is Hälledammen, a *c.* 50-m diameter pond located on an island off the west coast of Sweden. The sites fall equally into the temperate (13 sites) and hemiboreal (12 sites) zones (cf. Ahti, Hämet-Ahti & Jalas 1968), which differ in vegetation, climate and physiography. The border between the zones corresponds largely to the historic border between Sweden and Denmark that persisted until AD 1658. Before extensive modern forestry the temperate zone was dominated by broad-leaved species (*Quercus*, *Tilia*, *Fagus*) whereas the hemiboreal zone was a transition zone comprised of both temperate and boreal trees (*Pinus*, *Picea*, *Betula*) and greater evergreen cover. The hemiboreal zone is slightly higher in elevation, has colder winters and is dominated by granite or gneiss bedrock in contrast to more fertile sedimentary bedrock in large parts of the temperate zone (Wastenson 1990). Across the study region 17 sites could be designated to a land-use practice: 12 in former outlands and 5 in former infields.

Regional pollen diagrams were obtained from the European Pollen Database, three from each vegetation zone (Fig. 1). These include Lake Trummen and Lake Växjösjön (Digerfeldt 1972, 1977), Ranviken (Digerfeldt 1973), Lake Kansjön (H. Jacobson, unpubl. data), Ageröds mosse (Nilsson 1964), Lake Krageholmssjön (Gaillard 1984) and Lake Färskesjön (Berglund 1966). Because the upper sediments of Lake Trummen are missing (Digerfeldt 1972), we used the pollen records from the adjacent Lake Växjösjön (Digerfeldt 1977) for the last 1200 years.

The records cover the last 4000 years and are geographically representative of the region. The pollen records from large sites are assumed to represent the regional vegetation at a scale of *c.* 100 × 100 km around each lake (Hellman *et al.* 2009b).

### DATA HANDLING, POLLEN SOURCE AREA AND STATISTICS

For all analyses of the pollen data, percentage values were employed rather than Pollen Accumulation Rates (PAR) as PARs were available for only 14 of the small hollow sites. Due to the large number of pollen analysts and varying taxonomic detail in the studies as well as the central focus on *Quercus*, we chose to focus on common taxa represented by at least 5% in one or more samples. Cyperaceae was excluded due to its frequent abundance in wetlands. Human land use was inferred from the relative abundance of Cerealia and the combined abundance of four easily identified and robust indicators of agricultural activities: *Rumex acetosa, R. acetosella*, *Artemisia*, *Plantago lanceolata* and *Polygnum aviculare* (Gaillard 2007). For comparison and statistical analysis, the pollen records were divided into 200-year and 100-year periods before and after AD 0, respectively. These period lengths represent a compromise between resolution and accuracy. For periods lacking samples (*c.* 20% in both zones), values were interpolated as the mean of the two adjacent periods. Maps of pollen values for each local site were developed for five periods: 200–399 BC and AD 200–299, 900–999, 1600–99 and 1900–99. Summary diagrams of the mean pollen percentages from the small sites for the major taxa were constructed for each of the vegetation zones as a mean to compare the development of the regional vegetation between the temperate and the hemiboreal zones. The percentages vary greatly among the small hollow sites, which corroborates the expectation that each site records pollen from a restricted source area within a given landscape (Sugita 1994). Based on simulated and empirical relation between pollen and vegetation in the south Swedish vegetation/landscape setting of the last 6000 years, the relevant source area of small sites (bogs and lakes) is estimated to be between *c.* 1000 and 2000 m in radius (Hellman, Bunting & Gaillard 2009a; Hellman *et al.* 2009b). However, we believe the mean value from each vegetation zone is a reasonable approximation for the regional development. The mean values for each zone remained consistent over time, exhibiting only small fluctuations between adjacent levels. The overall trends appear broadly representative and for most taxa the sites in a region display a similar pattern of change through time. Our assumption is, furthermore, supported by a quantitative modelling approach for vegetation reconstruction by Sugita (2007), which suggests that mean values from many small sites is a good estimator for the regional vegetation composition.

Spearman's partial correlation was used to examine the relationship between *Quercus,* other taxa and the agricultural indicators during the last 1800 years. To adjust for the effect of site, zero-one variables were used as partialized variables for the sites. Ordination by non-metric multidimensional scaling (NMS; McCune & Mefford 2006) employing Sorensen's relative distance was used to display the vegetation relationships among sites at four of the mapped time periods: AD 200–299, 900–999, 1600–99 and 1900–99. NMS was used because it performs well with non-normal data like pollen percentages (Clarke 1993; Quinn & Keough 2002) and Sorenson's relative distance is broadly effective with ecological data (Faith, Minchin & Belbin 1987). The calculations compared one- to six-dimensional solutions using the NMS autopilot in the 'slow and thorough' mode, where the program follows a pre-defined template (McCune & Mefford 2006).

The vegetation reconstructions were evaluated in relation to the northern hemisphere temperatures for the past 2000 years developed by combining low-resolution lake and ocean sediment proxies with tree-ring data (Moberg *et al.* 2005).

## Results

The regional dynamics of *Quercus* and comparison between the hemiboreal and temperate zones are displayed in the mean pollen values from the 25 small hollow sites and the percentage values from the regional sites (Fig. 3). Small hollow values for

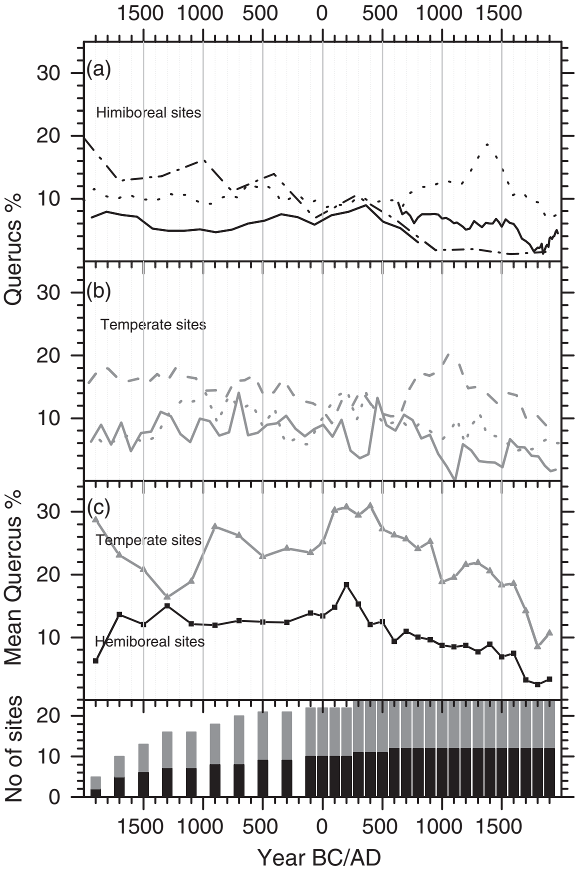

**Fig. 3.** *Quercus* pollen values from local and regional sites. (a) Hemiboreal regional sites: solid line is Lake Trummen (-AD 800) and Lake Växjösjön (AD 600-), dotted line is Lake Ranviken, dashed-dotted is Lake Kansjön. (b) Temperate regional sites: solid line is Ageröds mosse, dotted line is Lake Krageholmssjön, dashed-dotted line is Lake Färskesjön. (c) Mean pollen percentage of *Quercus* from the temperate and hemiboreal small hollow sites. The lower panel shows the number of small hollow sites included in their respective time periods. Each data point represents a 200-year or 100-year period. As an example: AD 1500 represents AD 1500–99, i.e. the 16th century.

*Quercus* from 1000–0 BC were 25–30% in the temperate zone and 12–14% in the hemiboreal zone. *Quercus* increased in both zones shortly after AD 0 and peaked around AD 100–400 in the temperate zone and AD 200 in the hemiboreal zone. Subsequently, *Quercus* decreased steadily in both zones, although exhibiting more stability from AD 1100 to 1600 in the temperate zone. *Quercus* showed a marked decrease in both zones in the 18th century and has had persistently low values through the last 300 years. A small increase occurred in the 20th century. The regional sites exhibit parallel records of declining percentages of *Quercus* over the last 2000 years. Overall, however, both the initial values and the magnitude of the declines were less in the lake than the small hollow sites. In the regional records pollen values for *Quercus* were *c.* 10% at AD 0 and decreased slowly to between 2% and 8% in the last century.

The vegetation exhibited strong regional patterns with *Tilia*, *Fagus*, Poaceae and agricultural indicators at higher values in the temperate zone than in the hemiboreal zone and *Pinus*, *Picea* and *Calluna* were more abundant in the hemiboreal zone (Fig. 4). Most taxa exhibited a significant relationship to *Quercus* through the period of *Quercus* decline over the last 1800 years (Table 2). *Quercus* was positively correlated with

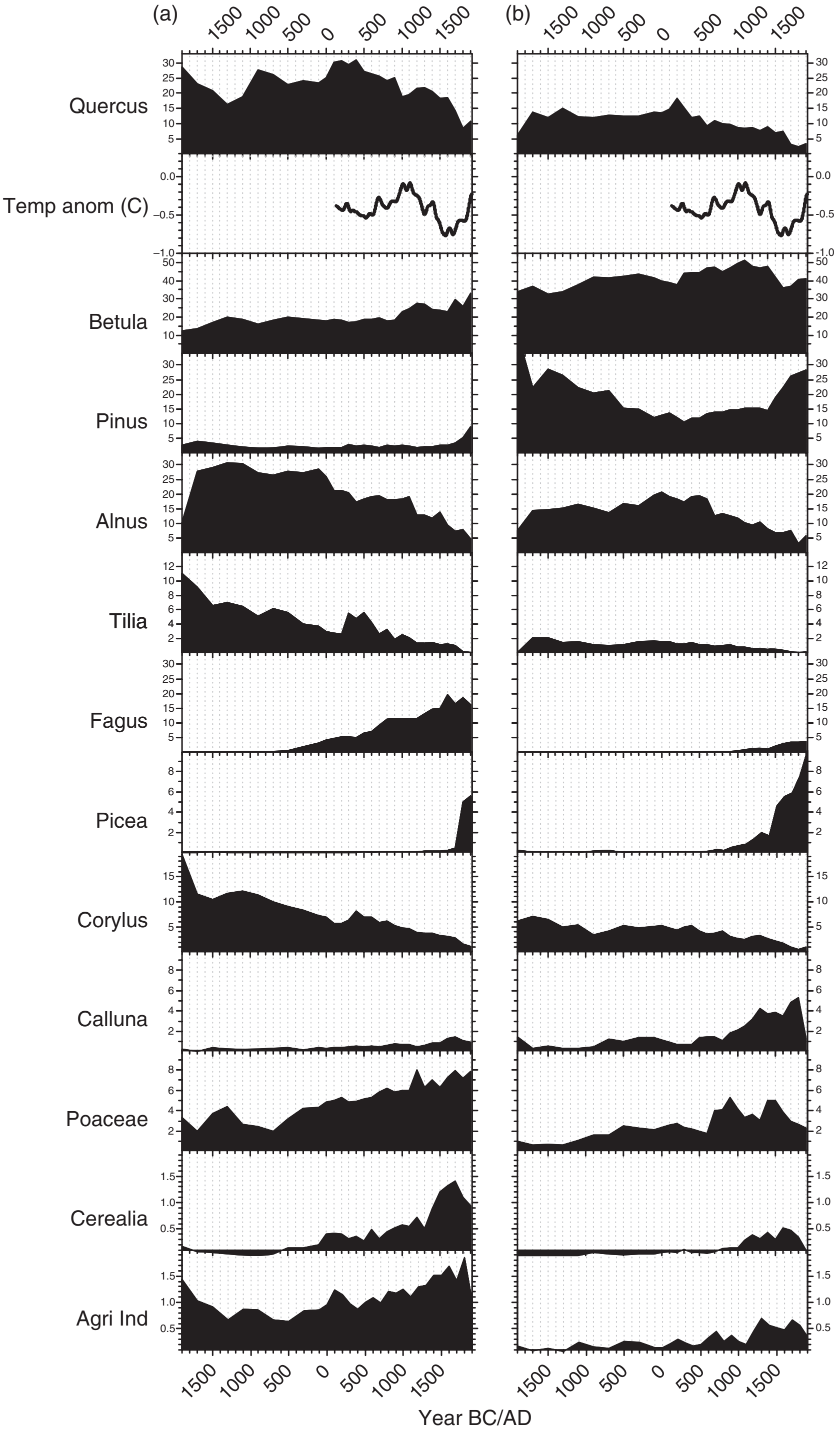

**Fig. 4.** Mean pollen percentage of all taxa and agricultural indicators included in the study from the (a) temperate and (b) hemiboreal sites. Note the different scales on the *y-axes*. Each data point represents a 200-year or 100-year period. As an example: AD 1500 represents AD 1500–99, i.e. the 16th century. The temperature data is from Moberg *et al.* (2005), temperature anomalies (low-frequency component AD 133–1925) from the northern hemisphere annual mean temperature 1961–90 average.

**Table 2.** Results from Spearman's partial correlation of the relationship during the last 1800 years between *Quercus,* other taxa and the agricultural indicators

| Temperate sites | $r^2$ | *P*-value | Hemiboreal sites | $r^2$ | *P*-value |
|---|---|---|---|---|---|
| Positive correlation | | | Positive correlation | | |
| *Tilia* | 0.44 | < 0.0001 | *Corylus* | 0.58 | < 0.0001 |
| *Corylus* | 0.32 | < 0.0001 | *Tilia* | 0.55 | < 0.0001 |
| *Alnus* | 0.22 | < 0.0001 | *Alnus* | 0.50 | < 0.0001 |
| Negative correlation | | | Negative correlation | | |
| Cerealia | −0.47 | < 0.0001 | *Pinus* | −0.54 | < 0.0001 |
| *Picea* | −0.41 | < 0.0001 | *Picea* | −0.52 | < 0.0001 |
| *Fagus* | −0.35 | < 0.0001 | Agricultural indicators | −0.26 | 0.0002 |
| *Pinus* | −0.28 | < 0.0001 | *Betula* | −0.20 | 0.004 |
| *Betula* | −0.26 | < 0.0001 | *Calluna* | −0.18 | 0.01 |
| Agricultural indicators | −0.24 | < 0.0001 | Cerealia | −0.17 | 0.015 |
| Poaceae | −0.17 | 0.0003 | Poaceae | −0.16 | 0.026 |
| *Calluna* | −0.13 | 0.0044 | | | |
| | | | No correlation | | |
| | | | *Fagus* | −0.13 | 0.052 |

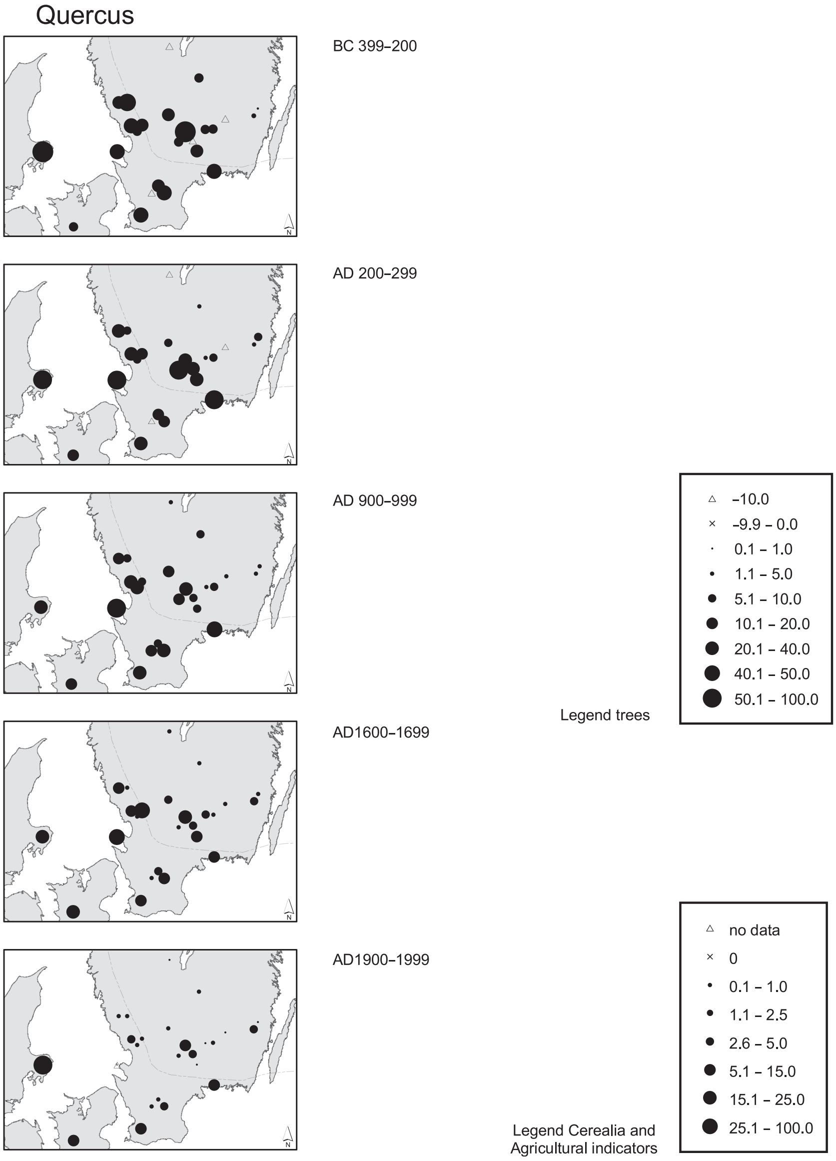

**Fig. 5.** Maps depicting the pollen percentages for selected taxa for five periods: 399–200 BC, AD 200–299, AD 900–999, AD 1600–99 and AD 1900–99. Note that NAP (Cerealia and agricultural indicators) have different classes than the tree taxa.

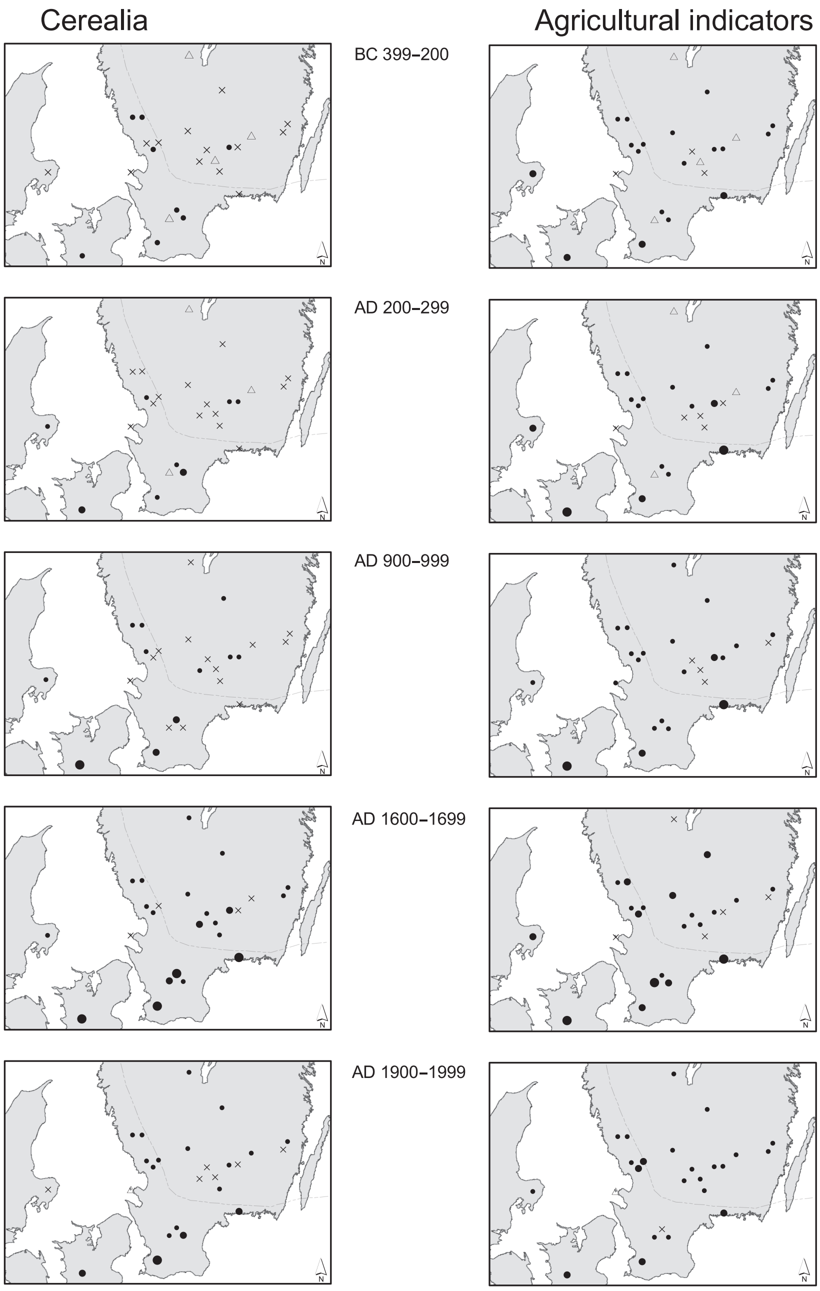

**Fig. 5b.** (*Continued*).

variations in *Tilia* and *Corylus* and less strongly to *Alnus* in the temperate zone and strongly with *Corylus, Tilia* and *Alnus* in the hemiboreal zone. Strong negative correlations occurred with Cerealia, *Picea* and *Fagus* in the temperate and *Pinus* and *Picea* in the hemiboreal zone. In the hemiboreal zone *Quercus* had no significant relationship to *Fagus*.

Pollen maps for the major taxa display the spatial patterns in vegetation over the last 2300 years (Fig. 5). *Quercus* was rather frequent and abundant (≥10% at most sites) until the 17th century, but somewhat less abundant in northern and north-eastern sites. It declined towards the 17th century but remained common around some sites in the south-central part of the hemiboreal zone where its abundance is low today (Figs 2 and 5). The development of the modern pattern, with *Quercus* common only at a few sites, became apparent only in the pollen map from the 20th century. *Pinus* was initially common only along the east coast, but increased dramatically at most northern sites from the 17th and 20th centuries. *Alnus* decreased regionally in the last centuries, especially in the south. *Corylus* and *Tilia* have consistently decreasing values across the region through time. Taking into account the low productivity and dispersal of its pollen, *Tilia* appears to have been abundant into the 10th century and to have remained relatively abundant around some northern sites longer than at southern sites. *Fagus* and *Picea* exhibited increasing values through time. *Fagus* expanded over the last 1000 years predominantly in the south. The expansion of *Picea* occurred over the last few hundreds of years in northern sites. Cerealia were recorded throughout the last two millennia but display maximum values in the 17th century when they are recorded

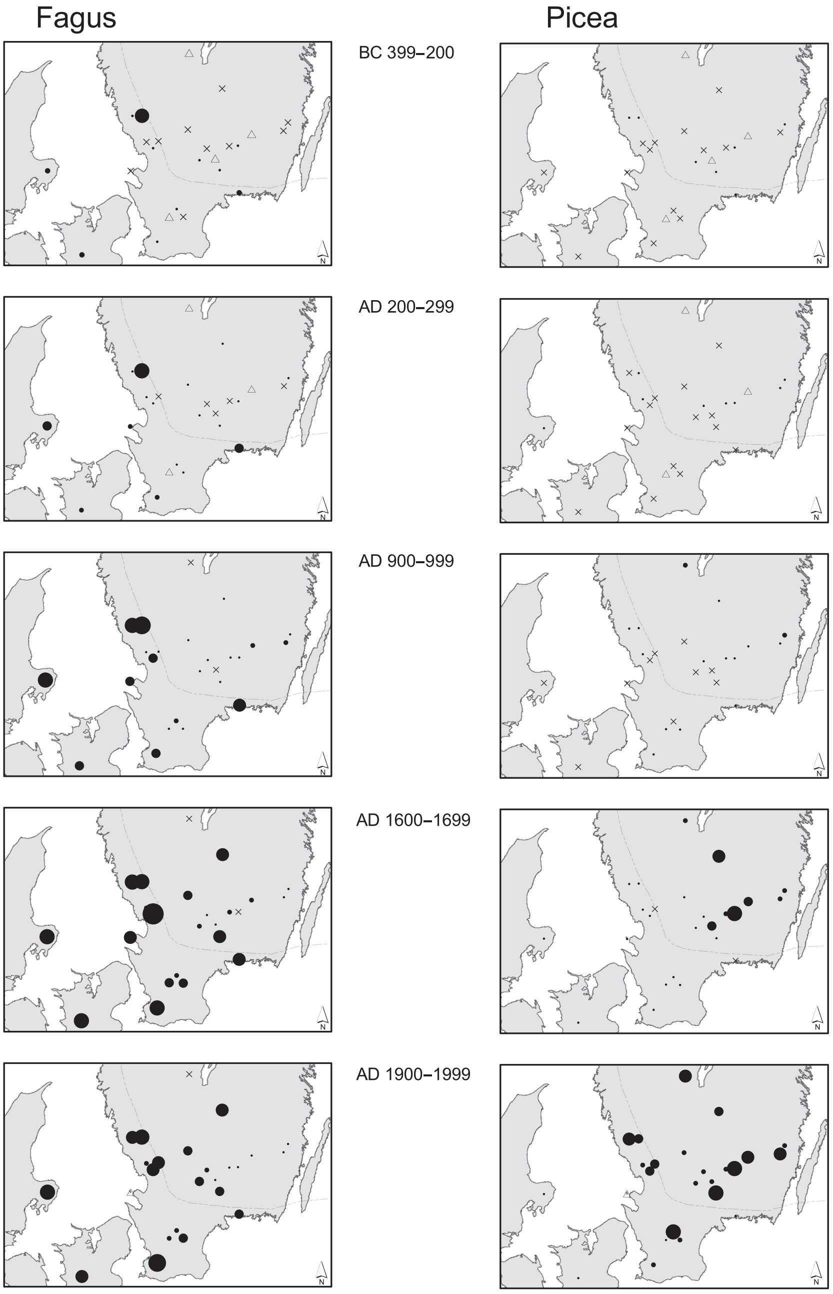

**Fig. 5c.** (*Continued*).

at most sites. A similar pattern is seen in the agricultural indicators, which were present in all periods, but became somewhat more frequent during the last 200 years.

The limited number of infield sites constrains the comparison with outfield sites to the period from AD 300 onward (Fig. 6). The mean *Quercus* value from outland sites decreased gradually from 25% to 15% between AD 300 and AD 1100. The percentage then dropped drastically over the past centuries to 2–3%. Mean values for infield sites were lower except at the very end of the record. Initially around 10%, they peaked at *c.* 13% around AD 800–1000 and then dropped steadily after that.

In the NMS analysis of the 14 taxa, 25 sites and 96 levels the final stress was 9.8%, which differs significantly ($P < 0.01$) from the randomized Monte Carlo tests. Axis scores were $r^2 = 0.38$, 0.33 and 0.22 for axes 1, 2, and 3, respectively. The boreal taxa *Picea*, *Pinus* and *Calluna* were grouped in the upper right in the diagram (Fig. 7). *Betula* was close to these taxa, but had lower scores on axis 1. The agricultural indicators, Cerealia and Poaceae were grouped together with weakly negative scores on both axes. The temperate taxa *Tilia* and *Corylus* were located together with *Alnus* in the lower part of the diagram. *Quercus* and *Fagus* were both in the lower left.

In the NMS diagram from AD 200–299 most temperate sites were located close to *Quercus*, *Tilia* and *Corylus,* whereas the hemiboreal sites were more evenly spread out in the diagram (Fig. 8). Overtime there was a tendency for more central clustering of all sites (less variation), a separation of hemiboreal and temperate sites, and a strong clustering of hemiboreal sites in the upper right, close to the boreal taxa. The distinction between the two regions emerged around

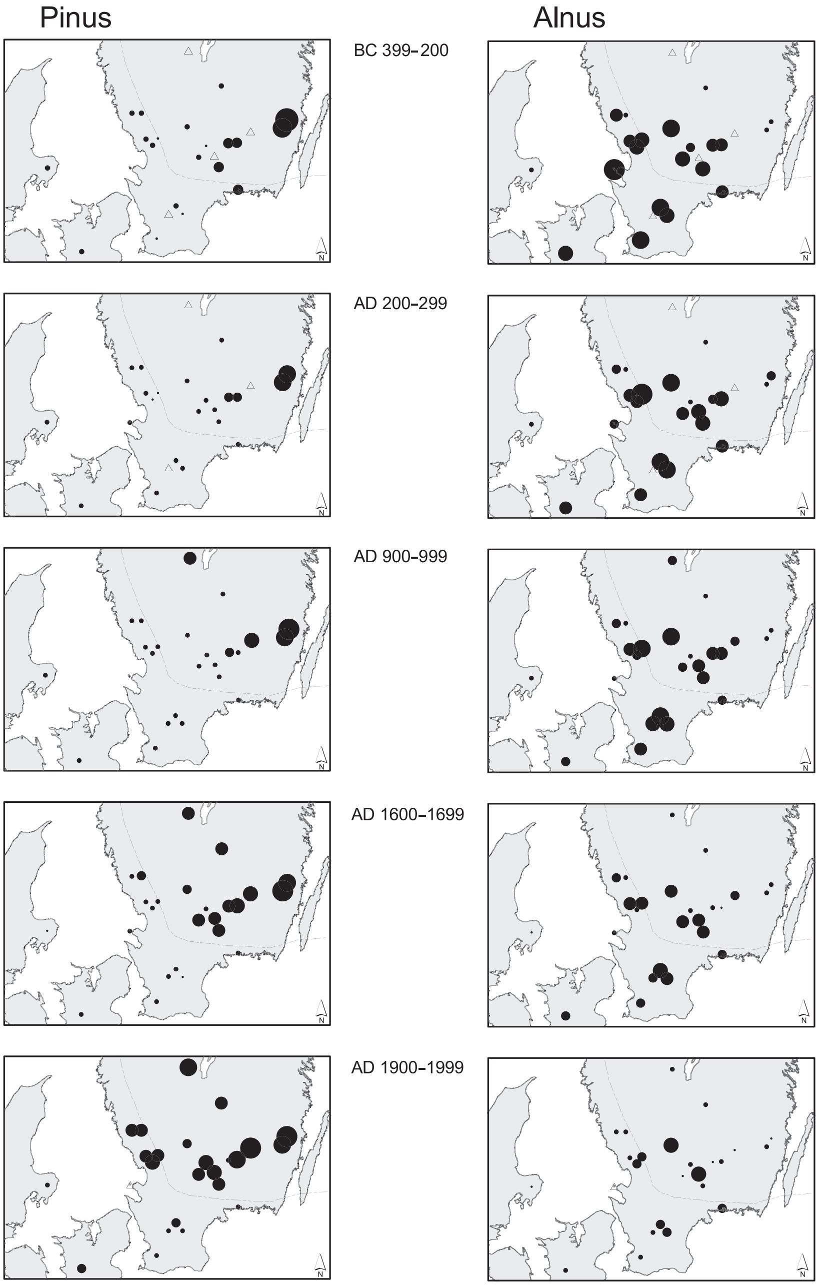

**Fig. 5d.** (*Continued*).

AD 900–999 and was greatest from AD 1600–99. At AD 1900–99, there was a clear break between the hemiboreal sites and many temperate sites. However, most temperate sites overlapped strongly with the hemiboreal sites due to the stronger influence of boreal taxa. Hence, during the last century there was a separation among temperate sites and a shift from the previous historical location and composition of temperate sites earlier in time.

## Discussion

### LONG-TERM DYNAMICS OF *QUERCUS* AND OTHER TREE TAXA

The relative decrease of *Quercus* pollen as recorded in the small hollows was greatest in both vegetation zones between the 17th and 19th century (Figs 3 and 5). These results confirm the reports of rapid decline of *Quercus* in 18th- and 19th-century historical records and place it into the context of much longer-term dynamics (Eliasson 2002; Eliasson & Nilsson 2002; Hedin 2003). Specifically, it is clear that the genus is much less abundant today than at any time during the previous 4000 years. In the hemiboreal zone modern pollen percentages are less than 45% of the values observed at AD 1600 and *c.* 20% of the maximum values reached in AD 200. The decline is somewhat less but nonetheless striking in the temperate zone, where the modern values are 60% and 35%, respectively, of the pre-historical values. The rapid and recent reductions of *Quercus* documented in historical records and the small hollows are more subtle in the regional pollen diagrams (Fig. 3; Regnell 1989; Thelaus 1989; Rasmussen 2005). The regional records often have low temporal

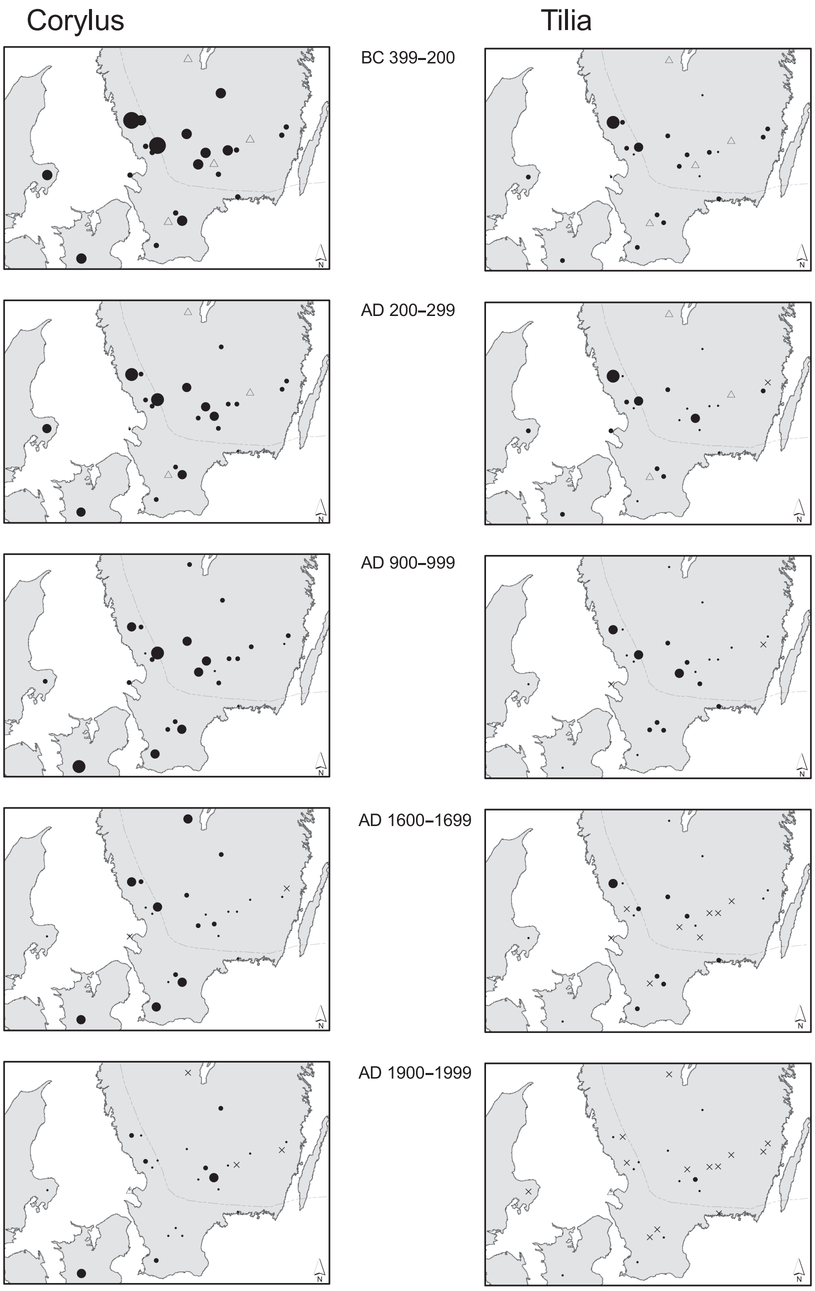

**Fig. 5e.** (*Continued*).

resolution in recent centuries where changes in arboreal pollen are abrupt and frequently obscured by major increases in non-arboreal taxa. The low absolute abundance of *Quercus* is also obscured on many forest maps as these frequently represent species in terms of percentages of forest growing stock and may consequently represent *Quercus* as a dominant species in largely deforested landscapes such as the coastal region (Fig. 2).

At the landscape scale there is a strong indication that the abundance and dynamics of *Quercus* populations varied across areas of different land-use (Fig. 6). Our data do not support the interpretation that *Quercus* was often more abundant in infields (arable land and hayfields) as a consequence of active management to protect this species (Eliasson & Nilsson 2002 and references therein). Although our sample of infield sites is small and should be interpreted with caution, the opposite trend is suggested at many sites. When our data allows for direct comparison (infields and outlands cored on the same estate), *Quercus* pollen percentages were comparable on infields and outlands (Råshult infield and outland – Lindbladh & Bradshaw 1998; Osaby infield and outland – Lindbladh 1999). One possible explanation for the discrepancy between the historical and pollen records is that historical inventories may have been biased towards the immediate vicinities of estates and villages and thereby overemphasized *Quercus* populations in those areas. A second possibility is that the historical sources accurately portray differences in large and valuable trees. Naval and other inventories were predominantly focused on large merchantable trees that were useful for construction of ships or buildings, whereas pollen records represent the

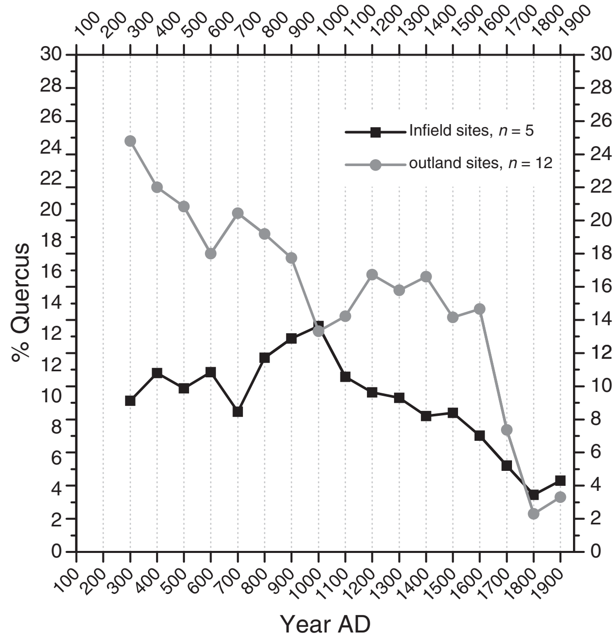

**Fig. 6.** Mean pollen percentage of *Quercus* from infield and outland sites. Each data point represents a 200-year or 100-year period. As an example: AD 1500 represents AD 1500–99, i.e. the 16th century.

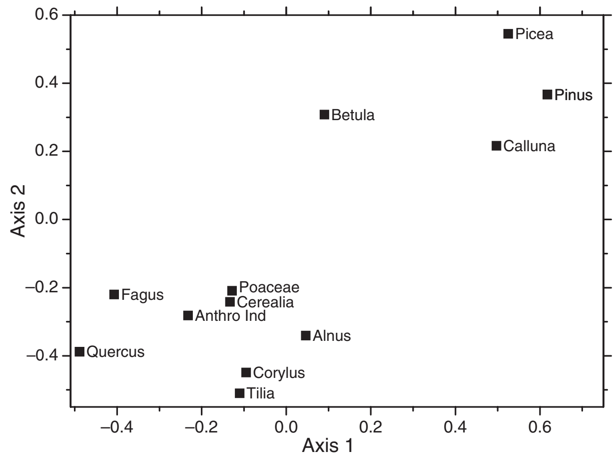

**Fig. 7.** Ordination axes 1 and 2 from the non-metric multidimensional scaling multivariate analysis with the values for the different taxa.

relative abundance and flowering of all sizes and qualities of trees. While larger trees may have been more abundant in the infields, the overall abundance of *Quercus* may have differed little across the landscape. Such variation in the distribution of larger and presumably older trees would be relevant from a conservation perspective, however, as the older trees were the carrier of many of today's rare species (Berg *et al.* 1994; Nilsson *et al.* 2002).

The strong positive correlation between *Quercus* and *Tilia*, *Corylus* and *Alnus* and the consistent steady decline of these taxa across southern Scandinavia during the last two millennia (Table 2; Fig. 4) suggests that climate change is the broad-scale driver of the observed dynamics (Huntley & Webb 1989; Pearson & Dawson 2003). However, the long-term decline of *Quercus* was consistent throughout the last 2000 years and no simple relationship occurs between this trajectory and changes in temperature, for instance through the warm early Middle Age or the comparatively cool Little Ice Age (Fig. 4). Our records do indicate that human activity induced complexities in both the regional variation and temporal details of these long-term dynamics. The initial decline of the thermophilous taxa, *Tilia* and *Corylus*, *c.* 4000 years ago in southern Scandinavia is most likely related to a decrease in temperature (Hammarlund *et al.* 2003; Seppä, Hammarlund & Antonsson 2005). *Quercus* and *Alnus* do not begin to decline until *c.* 2000 years ago, presumably in response to a further decrease in temperature (Seppä, Hammarlund & Antonsson 2005) and only after *Quercus* reaches a peak across the region (Fig. 4). *Quercus* is less shade-tolerant than *Tilia* and other temperate deciduous species (Diekmann 1996; Larsen, Raulund-Rasmussen & Callesen 2005), and may have been favoured by the increasingly open pastoral landscape initiated during the Bronze age (*c.* 1500–500 BC), particularly in the temperate zone (Berglund, Malmer & Persson 1991). Open conditions through this period are indicated by an increasing value of Poaceae and the low, but constant, record of agricultural indicators. The only *Alnus* species in the region today, *Alnus glutinosa*, occupies moist sites and is represented with high values in our local diagrams from wetland sites in contrast to many regional lake records (e.g. Digerfeldt 1972; Gaillard 1984). Although the dynamics of *Alnus* should reflect both the gradual decline in temperature and availability of suitable moist conditions generated by broad-scale climate change during the past 4000 years (Talantire 1974; Larsen, Raulund-Rasmussen & Callesen 2005; Seppä, Hammarlund & Antonsson 2005), it is likely that the long-term decline in this species also reflects the gradual clearing of the landscape of trees and conversion of wet forests into open meadows (Berglund, Malmer & Persson 1991).

## DRIVERS OF LONG-TERM VEGETATION DYNAMICS

The landscape-scale resolution of our pollen records provides insights into the details of the *Quercus* decline and the species and vegetation that replaced it. In the hemiboreal zone, the decline of *Quercus* appears to be controlled by competition with other forest species, mediated by human activity. *Picea* and *Pinus* are strongly negatively associated with *Quercus* and increase as it declines (Table 2). *Pinus* was common in the eastern hemiboreal zone in the beginning of our record (Fig. 5). On a landscape scale it is likely that *Pinus* replaced *Quercus* in the hemiboreal zone due to the strong similarities of the two species in terms of fire resistance and tolerance for both dry and wet sites (Table 2; Sykes, Prentice & Cramer 1996; Larsen, Raulund-Rasmussen & Callesen 2005; Bradshaw & Lindbladh 2005). Indeed, as *Pinus* became more common in the west after AD 900, there was a notable decline in *Quercus* (Fig. 5).

*Picea* entered the region from the north *c.* 1000 years ago. From there it spread south and east probably in response to

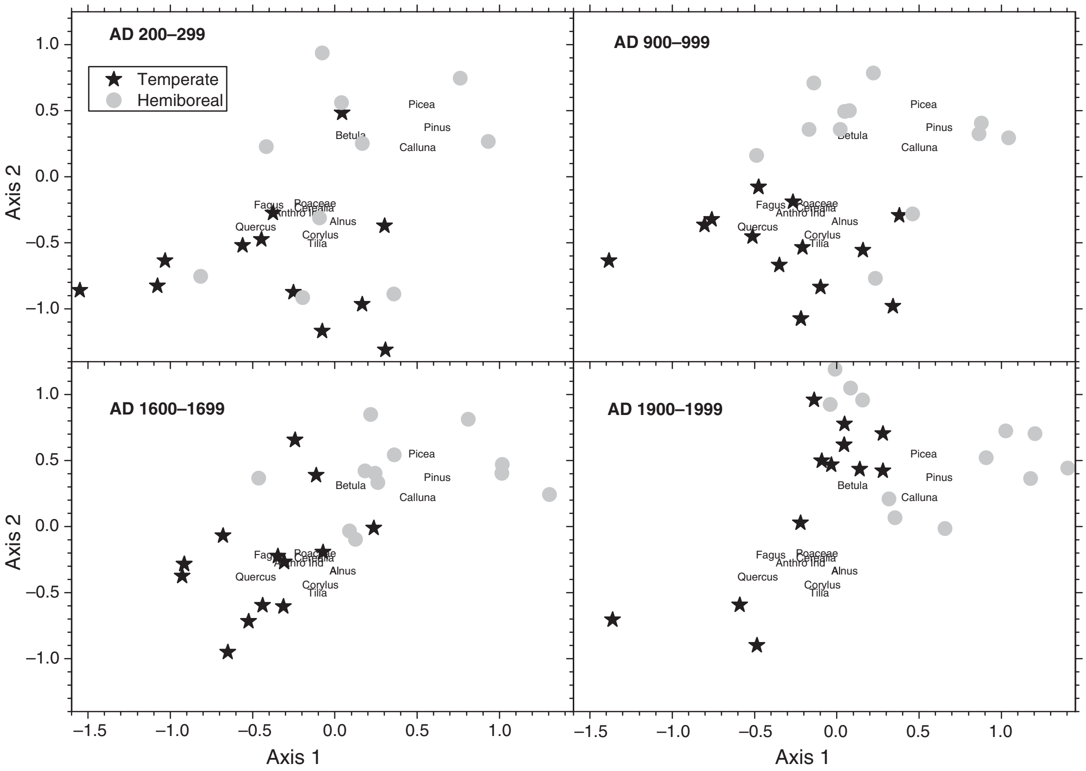

**Fig. 8.** Ordination axes 1 and 2 from the non-metric multidimensional scaling multivariate analysis with the values for the sites from the two vegetation zones and the taxa from four periods: AD 200–299, AD 900–999, AD 1600–99 and AD 1900–99.

colder and snowier conditions (Fig. 5; Bradshaw *et al.* 2000; Giesecke & Bennett 2004; Bradshaw & Lindbladh 2005), although the exact role of climate in this migration is not completely clear (Miller *et al.* 2008). *Picea* is a strong competitor with shade-tolerant temperate species (Seppä *et al.* 2009) and it is, therefore, likely that the decline of *Quercus* at many sites in the hemiboreal zone was due to competition with *Picea*. Although agricultural indicators are rather unimportant in the hemiboreal zone, it appears that selective cutting may have been a factor leading to a decline in *Quercus* and facilitating the initial entry of *Pinus* and *Picea* into forested sites. Such a development is described at the end of the 19th century when *Picea* entered into the area of its southernmost distribution in Sweden today (Hesselman & Schotte 1906). The increasing number of domestic animals and intense grazing when agriculture expanded during the mediaeval colonization (Lagerås 2007) likely promoted the decline of *Quercus* relative to the conifers and temperate deciduous trees that are more resistant to grazing (Götmark *et al.* 2005). The apparent persistence of *Quercus* at higher abundances on outlands until its decline *c.* 300 years ago may be due to its tolerance for unfertile, dry and moist sites (Fig. 6; Diekmann 1996).

In contrast to the hemiboreal zone, in the temperate zone *Quercus* forests were likely replaced by agriculture. Here, as in the hemiboreal zone, *Quercus* declined after its peak around AD 200–400, but coincident with a much greater increase of agricultural indicators (Table 2; Figs 4 and 5). While both Cerealia and agricultural indicators are low in abundance and show weak negative correlations with *Quercus* in the hemiboreal zone, in the temperate vegetation zone Cerealia are more prominent and more strongly negatively correlated to *Quercus*. It appears that in the south and west agricultural land began to replace *Quercus* in many places after the 5th century AD. In both zones modern forestry and regional planting produced the large regional increase of the two conifers during the last *c.* 150 years (Fig. 5; Hesselman & Schotte 1906).

Fire has been suggested as an important factor in controlling the historical abundance of *Quercus* (Niklasson, Lindbladh & Björkman 2002; Greisman & Gaillard 2009). Although not explicitly addressed in this study, forest fires were historically common in the hemiboreal zone until the mid 18th century (Niklasson & Drakenberg 2001; Bradshaw & Lindbladh 2005). Fire suppression in Sweden over the course of the last centuries is believed to have reduced *Quercus* regeneration (Niklasson, Lindbladh & Björkman 2002; Lindbladh, Niklasson & Nilsson 2003). However, a recent study examining charcoal and pollen in the same region as this study, found only a weak negative correlation between charcoal and *Quercus* pollen abundance (Bradshaw, Hannon & Lindbladh in press).

### REGIONAL PATTERN OF VEGETATION CHANGE

Ordination of the pollen data across the range of sites through time demonstrates major changes in the regional pattern of vegetation variation (Fig. 7). Although the sites exhibit regional variation today, at AD 200–299 temperate and hemiboreal sites were rather evenly mixed in the diagram. At that time many sites were strongly dominated by temperate taxa and

*Alnus,* and geographical variation was weakly expressed. The separation of sites into distinctive geographical groupings begins at AD 900–999 as sites from the two zones start to separate. This process continues through to AD 1900–99 when many of the temperate sites have higher scores on both axes, indicating a shift from temperate conditions at AD 200–299 to more hemiboreal conditions. However, since AD 200–299 the overall spread of site scores and the apparent variation in vegetation has declined across all sites and between the vegetation zones. Thus, while regional patterns emerged and persisted, the regional vegetation as a whole has become more homogenous, as reflected by the ordination, compared to previous periods. Much of this modern increase in similarity among the sites in the different zones is due to increased human impacts, in particular the widespread introduction of conifer forests in southern Sweden (Kardell 2004; Niklasson & Nilsson 2005). A similar homogenization of regional vegetation patterns can be seen in forests across the north-eastern United States as a consequence of similarities in broad-scale land use activities (Foster, Motzkin & Slater 1998; Oswald *et al.* 2008).

### IMPLICATIONS FOR CONSERVATION

This study provides a lengthy perspective for conservation management and insights into *Quercus* forests across the region. The long-term decline and recent rapid drop in *Quercus* populations throughout southern Scandinavia is striking and indisputable. While these results pertain to *Quercus* populations alone and not the many threatened species associated with *Quercus,* it is clear that this foundation taxon has undergone a major shift in abundance and distribution as a consequence of both broad-scale and local factors. Millennium-scale climatic change is a major factor driving the long-term decline of *Quercus* and changing abundance relative to other important tree taxa. However, the details of this decline, the late date (last 200–300 years) relative to other thermophilic tree species, and the close correlation between *Quercus* and numerous agricultural indicators underscores the important role of recent human activities.

From the perspective of both the populations of *Quercus* and its associated species of insects and epiphytes, the rate of decline is extremely rapid. For this long-lived tree, the last millennium represents no more than two to three generations. Meanwhile, studies of the rare Hermit beetle (*Osmoderma eremita)* demonstrate that individuals of this species have extremely restricted dispersal, perhaps only a couple of 100 m. As a consequence a *Quercus* stand can host a metapopulation of this beetle for several centuries (Hedin 2003; Ranius & Hedin 2004). Given the former abundance of *Quercus*, the tree species longevity, and the capability for persistence, it is likely that our current populations of *Quercus* and its associated species represent legacies of former conditions in a process of slow and spiralling decline that could lead to disappearance.

In order to reverse this trajectory it appears critical to re-establish *Quercus* population abundance and distribution to levels that existed in prior times and as documented in this study. To enhance population survival and facilitate dispersal among populations and in the face of future environmental changes, it is advisable to increase *Quercus* populations and establish increased connectivity among *Quercus* forests across the landscape and region. This activity should not only focus on infield sites (or on areas in their proximity) that represent conservation hotspots in the modern landscape (Nilsson 2001), but be applied also across the broader landscape and through the matrix of today's production forest. *Quercus* naturally regenerate in not too dense coniferous production forests, especially in dry and warm areas, and if the browsing pressure is not too strong (Götmark *et al.* 2005). The natural regeneration will probably increase under a warmer future climate (Sykes, Prentice & Cramer 1996). However, today's management regime overrides climate in controlling the abundance of the species. Current practices in coniferous production stands call for a total removal of all *Quercus* saplings during pre-commercial thinning (Götmark, Fridman & Kempe 2009).

As for future levels of *Quercus*, the taxon's abundance before the drastic decline in the 18th and 19th centuries would appear to provide a reasonable target. At that time many of the current rare or extinct *Quercus*-associated species did still occur (Osbeck 1996; H. Ljungberg, unpubl. data ). In order to reach this target which is biologically and historically modest, but logistically and economically ambitious, it will be necessary to (i) identify and implement the most cost-effective and efficient ways to regenerate and manage *Quercus* forests (Madsen & Löf 2005; Götmark 2007) and (ii) integrate the ongoing establishment and retention of biologically valuable *Quercus* into the management of conifer production forests (K. Widerberg, unpubl. data).

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