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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.

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 *et al.* 1989; Björkman 1996a; Giesecke 2004; Bradshaw & Lindbladh 2005; Seppä *et al.* 2009). In contrast, *Quercus* spp. (Oaks) include moderately shade-tolerant species (*Q. robur* and *Q. 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 2005) and represents the most important tree genus for red-listed invertebrates (Jonsell *et al.* 1998).

74

75 Many characteristics of *Quercus* in the Swedish landscape provide challenges for
76 conservation management. These include its low abundance and vulnerability to further
77 reductions, its scattered distribution and the extreme age of many individuals. In particular,
78 there is uncertainty concerning the future status of *Quercus*, the resulting consequences for
79 species that are dependent on *Quercus*, appropriate targets for the restoration of populations in
80 the landscape, and the need for management to achieve these desired conditions (Ranius
81 2000; Hedin 2003; Nordén *et al.* 2007; Økland *et al.* 2008; Tyler 2008). Some researchers
82 have argued that conservation projections for the many rare insect and cryptogam species
83 associated with *Quercus* are overly optimistic as they are based on persistence probabilities
84 that do not appropriately account for long-term declines in *Quercus* and its associated habitats
85 (Nilsson *et al.* 2005; Ranius *et al.* 2008). In their perspective, *Quercus* populations may be too
86 scarce and fragmented to facilitate persistence and gene flow of rare species, which
87 consequently exist under an ‘extinction debt’ (*sensu* Tilman *et al.* 1994; Hanski *et al.* 1996).

88

89 To address these concerns and to examine the potential for future declines and extinction,
90 studies have attempted to place the recent dynamics and status of *Quercus* in a historical
91 context based on early 19th-century data (Hedin 2003; Ranius *et al.* 2004). However, effective
92 evaluation of long-lived trees like *Quercus*, which produce biological legacies (*sensu*
93 Lindenmayer & Franklin 2002) and habitats that may endure for many centuries, require an
94 even longer time-perspective. *Quercus* frequently live 300 years in closed forests, 400-600
95 years in open woodlands and pastures and as much as c. 1000 years under optimal conditions
96 (Niklasson & Nilsson 2005; Drobyshev *et al.* 2008). Furthermore, the coarse dead wood of
97 *Quercus* may provide an important substrate for other taxa, especially insects, fungi and
98 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 1990).

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 GIS 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.

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.

Material 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 to 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 (Fig. 2 and 3; Björse *et al.* 1996; Berglund *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 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 (Fritzbøger 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 *Fagus sylvatica* grows less vigorously (Larsen *et al.* 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 approximately 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 *Picea abies* (c. 47% of total volume) and *Pinus sylvestris* (ca 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 & Niklasson 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 *et al.* 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 seventeen sites could be designated to a land-use practice: twelve in former outlands and five 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 Väjösjön (Digerfeldt 1972; 1977), Ranviken (Digerfeldt 1973), Lake Kansjön (H. Jacobson unpublished), 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 Väjösjön (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 ca. 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 PAR (Pollen Accumulation Rates) 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 *Polygonum 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, 1600-1699 and 1900-1999. 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 (RSAP) of small sites (bogs and lakes) is estimated to be between c. 1000 and 2000 m in radius (Hellman *et al.* 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 anthropogenic indicators 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; PCord 5.10 software) 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, 1600-1699 and 1900-1999. Non-metric multidimensional scaling (NMS) was used because it performs well with non-normal data like pollen percentages (Clarke 1993; Quinn & Keough 2002) and Sorensen's relative distance is broadly effective with ecological data (Faith *et al.* 1987). The calculations compared one- to six-dimensional solutions using the NMS autopilot in the 'slow and thorough' mode, where the program follows a predefined template (McCune & Mefford 1999).

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 *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.

273 *Quercus* showed a marked decrease in both zones in the 18th century and has had persistently
274 low values through the last 300 years. A small increase occurred in the 20th century. The
275 regional sites exhibit parallel records of declining percentages of *Quercus* over the last 2000
276 years. Overall, however, both the initial values and the magnitude of the declines were less in
277 the lake than the small hollow sites. In the regional records pollen values for *Quercus* were c.
278 10% at AD 0 and decreased slowly to between 2 and 8% in the last century.

279

280 The vegetation exhibited strong regional patterns with *Tilia*, *Fagus*, Poaceae and
281 anthropogenic indicators at higher values in the temperate zone than in the hemiboreal zone
282 and *Pinus*, *Picea* and *Calluna* were more abundant in the hemiboreal zone (Fig. 4). Most taxa
283 exhibited a significant relationship to *Quercus* through the period of *Quercus* decline over the
284 last 1800 years (Table 2). *Quercus* was positively correlated with variations in *Tilia* and
285 *Corylus* and less strongly to *Alnus* in the temperate zone and strongly with *Corylus*, *Tilia* and
286 *Alnus* in the hemiboreal zone. Strong negative correlations occurred with Cerealina, *Picea* and
287 *Fagus* in the temperate and *Pinus* and *Picea* in the hemiboreal zone. In the hemiboreal zone
288 *Quercus* had no significant relationship to *Fagus*.

289

290 Pollen maps for the major taxa display the spatial patterns in vegetation over the last 2300
291 years (Fig. 5). *Quercus* was rather frequent and abundant ($\geq 10\%$ at most sites) until the 17th
292 century, but somewhat less abundant in northern and north-eastern sites. It declined towards
293 the 17th century but remained common around some sites in the south-central part of the
294 hemiboreal zone where its abundance is low today (Fig. 2 and 5). The development of the
295 modern pattern, with *Quercus* common only at a few sites, became apparent only in the pollen
296 map from the 20th century. *Pinus* was initially common only along the east coast, but
297 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 at most sites. A similar pattern is seen in the anthropogenic indicators, which were present in all periods, but became somewhat more frequent during the last two hundred 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 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 axis 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 anthropogenic 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 AD 900-999 and was greatest from AD 1600-1699. At AD 1900-1999 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 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 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 *et al.* 2005). *Quercus* and *Alnus* do not begin to decline until c. 2000 years ago, presumably in response to a further decrease in temperature (Seppä *et al.* 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 *et al.* 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 *et al.* 1991). Open conditions through this period are indicated by an increasing value of Poaceae and the low, but constant, record of anthropogenic 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. Gaillard 1984; Digerfeldt 1972). 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 (Tallantire 1974; Larsen *et al.* 2005; Seppä *et al.* 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 *et al.* 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 *et al.* 1996; Larsen *et al.* 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 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 anthropogenic 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 200-400 AD, but coincident with a much greater increase of anthropogenic indicators (Table 2; Fig. 4 and 5). While both *Cerealia* and anthropogenic 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 *et al.* 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 *et al.* 2002; Lindbladh *et al.* 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 *et al.* 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 1900-1999 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 *et al.* 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 anthropogenic 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 hundred meters. 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 *et al.* 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 *et al.* 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; Ljungberg *et al.* unpublished 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
(Koch Widerberg *et al.* unpublished data).

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Table 1. Small hollow sites in Denmark and Sweden used in this study. C¹⁴ 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	Unpublished	56 44'N 10 49'E	Small wetland	Not defined	Not available (9000 BC- present)
2	Suserup	Hannon <i>et al.</i> (2000)	55 22'N 11 34'E	Wetland 20x30m	Not defined	1 C14 & 5 AMS (4200 BC-present)
3	Torup	Hultberg <i>et al.</i> (2010)	55 56'N 13 21'E	Wetland 10x10m	Not defined	6 AMS (3700 BC-present)
4	Vasahus	Lindbladh <i>et al.</i> (2007)	55 54'N 13 38'E	Peat bog 25x40m	Outland	4 C14 (1310 BC-present)
5	Kyllingahus	Lindbladh <i>et al.</i> (2007)	55 53'N 13 39'E	Peat bog 15x50m	Infield	5 AMS (4100 BC-present)
6	Häggenäs	Lindbladh <i>et al.</i> (2007)	55 53'N 13 36'E	Wetland 10x100m	Infield	5 AMS (350 AD-present)
7	Hälledammen	Molinari (2002)	56 61'N 13 01'E	Pond 50x50m	Outland	4 AMS (850 BC-AD 1750)
8	Eriksberg	Hannon (unpublished)	56 11'N 15 00'E	Wetland 10x10m	Not defined	4 AMS (5200 BC-present)
9	Kalvaberget	Lindbladh <i>et al.</i> (2008)	56 48'N 12 54'E	Wetland 150x25m	Not defined	8 AMS (600 BC-present)
10	Holkåsen	Lindbladh <i>et al.</i> (2008)	56 48'N 12 54'E	Wetland in depression 50x10m	Outland	6 C14 (1500 BC-present)
11	Trälhultet	Lindbladh <i>et al.</i> (2008)	56 48'N 12 54'E	Wetland 200x40m	Outland	4 AMS (1300 BC-present)

12	Bocksten a	Björkman (1997a)	57 07'N 12 34'E	Fen c.25m in diameter	Outland	4 C14 (700 BC- present)
13	Bocksten b	Björkman (1997a)	57 07'N 12 34'E	Fen c.30x40m in diameter	Outland	2 C14 (2500 BC- present)
	Hemiboreal zone					
14	Siggaboda	Björkman and Bradshaw (1996)	56 28'N 14 34'E	Peat bog 5x5 m	Outland	5 C14 (900 BC- present)
15	Råshult in-field	Lindbladh and Bradshaw (1998)	56 37'N 14 12'E	Wetland 25x30m	Infield	7 C14 (2400 BC- present)
16	Djäknabygd	Lindbladh and Bradshaw (1998)	56 37'N 14 12'E	Wetland 5x5 m	Outland	5 C14 (3900 BC- present)
17	Nissatorp	Lindbladh and Bradshaw (1998)	56 37'N 14 12'E	Wetland 15x100m	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 20m in diameter	Outland	1 AMS & 4 C14 (5100 BC-present)
20	Flahult	Björkman (1997b)	56 58'N 13 50'E	Small peatland 20x40m	Not defined	4 C14 (500 BC- present)
21	Storasjö	Eriksson (1996)	56 55'N 15 17'E	Wetland 50x50m	Outland	5 C14 (700 BC- present)
22	Ekenäs	Valdemardotter (2001)	56 57'N 16 01'E	Wetland 40x30m	Infield	2 AMS & 2 C14 (1500 BC-present)
23	Skärsgölarna	Lindbladh <i>et al.</i> , (2003)	57 01'N 16 07'E	Wetland 50x30m	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 3x3m	Not defined	2 C14 (300 BC- present)

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

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Temperate sites			Hemiboreal sites		
	r^2	p-value		r^2	p-value
Positive correlation			Positive correlation		
Tilia	0.44	<.0001	Corylus	0.58	<.0001
Corylus	0.32	<.0001	Tilia	0.55	<.0001
Alnus	0.22	<.0001	Alnus	0.50	<.0001
Negative correlation			Negative correlation		
Cerealia	-0.47	<.0001	Pinus	-0.54	<.0001
Picea	-0.41	<.0001	Picea	-0.52	<.0001
Fagus	-0.35	<.0001	Anthropogenic indicators	-0.26	0.0002
Pinus	-0.28	<.0001	Betula	-0.20	0.004
Betula	-0.26	<.0001	Calluna	-0.18	0.01
Anthropogenic indicators	-0.24	<.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

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Figure captions

Figure 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 Våxjösjön, B. Lake Ranviken, C. Lake Kansjön, D. Ageröds Mosse, E. Lake Krageholmssjön, F. Lake Färskesjön.

Figure 2. Past and present distribution of *Quercus* in southern Sweden, modified from Björse *et al.* (1996). The modern data are based on forest inventory data and represent percentages of the total growing stock. The data from 2000 and 1000 BP (years Before Present) 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).

Figure 3. *Quercus* pollen values from local and regional sites. Panel A shows hemiboreal regional sites: solid line is Lake Trummen (-AD 800) and Lake Våxjösjön (AD 600-), dotted line is Lake Ranviken, dashed-dotted is Lake Kansjön. Panel B shows temperate regional sites: solid line is Ageröds mosse, dotted line is Lake Krageholmssjön, dashed-dotted line is Lake Färskesjön. Panel C is 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 1500-1599, i.e. the 16th century.

Figure 4. Mean pollen percentage of all taxa and anthropogenic indicators included in the study from the temperate and 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 1500-1599, 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.

Figure 5. Maps depicting the pollen percentages for selected taxa for five periods: 399-200 BC, AD 200-299, AD 900-999, AD 1600-1699 and AD 1900-1999. Note that Cerealia and anthropogenic indicators have different classes than the tree taxa.

Figure 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 1500-1599, i.e. the 16th century.

Figure 7. Ordination axes 1 and 2 from the NMS multivariate analysis (non-metric multidimensional scaling) with the values for the different taxa.

Figure 8. Ordination axes 1 and 2 from the NMS multivariate analysis (non-metric multidimensional scaling) with the values for the sites from the two vegetation zones and the taxa from four periods: AD 200-299, AD 900-999, AD 1600-1699 and AD 1900-1999.

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