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

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25

26 **Summary**

27

- 28 1. The long-term history of *Quercus* in southern Scandinavia has received little attention
29 despite its important role in modern conservation. In this study the 4000-year
30 dynamics of *Quercus*, its habitat and other important taxa were analysed with pollen
31 data from 25 small hollows and 6 regional sites across southern Scandinavia. The aim
32 was to provide a context for understanding the species' current status and managing its
33 future dynamics.
- 34 2. The results indicate that *Quercus* is much less abundant today than at any time during
35 the previous 4000 years and corroborate the rapid decline reported in 18th - and 19th-
36 century historical records. Modern pollen percentages are 45-60% of 17th-century
37 values and only 20-35% of the maximum values reached in the 3rd century.
- 38 3. A strong positive correlation exists between the abundance of *Quercus* and the
39 abundance of *Tilia*, *Corylus* and *Alnus*, which also experienced a steady decline across
40 the region in the last two millennia. Climate change is the broad-scale driver of the
41 observed dynamics, but human activity introduced considerable variation in the
42 regional and temporal details of these changes. In the hemiboreal northern part of the
43 study area the decline of *Quercus* appears to be controlled largely by competition with
44 other tree species (especially *Pinus* and *Picea*), mediated by harvesting. In the
45 temperate south part *Quercus* forests decreased through deforestation for agriculture.
- 46 4. Multivariate analyses indicate that although substantial phytogeographical variation
47 has existed through past millennia the regional vegetation is more homogeneous today
48 than in earlier periods.

49 5. *Synthesis*. The long-term decline and recent rapid reductions in *Quercus* populations
50 throughout southern Scandinavia are striking and indisputable. From the perspective
51 of both the populations of *Quercus* and its associated species of insects and epiphytes,
52 the recent rate of decline is extremely rapid. Given the former abundance, longevity
53 and capacity for persistence of *Quercus*, current populations of *Quercus* and its
54 associated species appear to represent biological legacies in the midst of protracted
55 decline. Based on these results, a reasonable conservation goal is to restore the
56 abundance and distribution of *Quercus* to levels that preceded the drastic decline in
57 the 18th and 19th centuries.
58

59 **Introduction**

60
61 Across southern Scandinavia only a few trees qualify as foundation species, i.e. species that
62 exert an impact on community and ecosystem properties greatly disproportionate to their
63 abundance (*sensu* Dayton 1972; Ellison *et al.* 2005). Two of these, *Fagus sylvatica* (European
64 beech) and *Picea abies* (Norway spruce), are shade-tolerant species whose historical roles
65 have been extensively investigated with regards to abundance and distribution (e.g. Iversen
66 1973; Huntley *et al.* 1989; Björkman 1996a; Giesecke 2004; Bradshaw & Lindbladh 2005;
67 Seppä *et al.* 2009). In contrast, *Quercus* spp. (Oaks) include moderately shade-tolerant species
68 (*Q. robur* and *Q. petraea*) that have received considerably less historical study despite their
69 critical role in modern conservation. In spite of its scattered abundance in southern
70 Scandinavia, the importance of the genus *Quercus* for Swedish and European biodiversity is
71 difficult to overstate (Ranius *et al.* 2005). *Quercus* provides critical habitat for lichens and
72 fungi (Ranius & Jansson 2000; Berg *et al.* 2002; Gärdenfors 2005) and represents the most
73 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; Drobyshév *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

99 ecological and conservation issues it is necessary to develop a regional reconstruction by
100 employing an approach that combines the time-depth of paleoecology and the stand to
101 landscape-scale spatial resolution of field sampling. The appropriate paleoecological approach
102 for this effort combines the analysis of a network of small hollows, which yield local
103 information, with the regional-scale record provided through the analysis of lake sediments
104 (cf. Jacobson & Bradshaw 1981; Foster & Zebryk 1990).

105

106 In our investigation of the ancient and recent history of *Quercus* we analysed the pollen data
107 from 25 small hollow sites across southern Scandinavia (Fig. 1, Table 1). Small hollows act as
108 local pollen collectors and yield stand to landscape-level information on vegetation
109 composition and dynamics as well as natural and anthropogenic disturbances (Bradshaw
110 2007). In appropriate settings they may accumulate continuous sediment records spanning
111 centuries to millennia and can therefore be regarded as analogous to extremely long-term
112 permanent plots (*sensu* Jacobson & Bradshaw 1981). High-resolution records from a regional
113 network of small hollows may then be analysed through GIS and multivariate statistics to
114 provide a regional perspective that resolves the geographical detail and variation among
115 vegetation zones, across major edaphic and environmental gradients or even among different
116 land-uses in a single estate.

117

118 To augment and contrast the local to regional understanding emerging from the network of
119 hollows we analysed the independent record of regional-scale vegetation dynamics provided
120 by pollen analyses of sediment cores from six lakes distributed across the study region. In
121 both sets of reconstructions we focused on interpreting the dynamics and drivers of changes in
122 *Quercus* abundance during the last 4000 years. To enhance the conservation insights
123 emerging from prior historical studies, we placed special emphasis on the 18th and 19th

124 centuries, seeking to: evaluate the accuracy of the reconstructions of declines coming from
125 historical records, provide additional insights into the dynamics of *Quercus* preceding this
126 fairly well documented period, and contrast these recent dynamics with those from previous
127 millennia.

128

129 **Material and methods**

130

131 **Regional history of *Quercus* in southern Scandinavia**

132 Numerous pollen records and historical sources provide the history of regional forest
133 dynamics that are useful for interpreting the spatially resolved patterns of change emerging
134 from small hollows over the past few millennia. Records from lake sediments indicate that
135 *Quercus* abundance peaked across southern Scandinavia through the thermal maximum 9000
136 to 6000 years ago (Iversen 1973; Berglund *et al.* 1996; Rasmussen 2005). However, from a
137 maximum of >20% of pollen in the mid Holocene *Quercus* declined substantially in most
138 records (Fig. 2 and 3; Björse *et al.* 1996; Berglund *et al.* 2007). Written sources suggest a
139 more recent decline over the past hundreds of years. An important timber for warships,
140 *Quercus* was declared to be the property of the Swedish state by King Gustav Vasa in AD
141 1558. At the end of the 18th century the increasing population of more self-assured peasants
142 successfully applied pressure on the state to allow access to *Quercus* trees, leading to an
143 increase in harvesting (Eliasson 2002). According to subsequent state inventories from 1790
144 to 1825 the abundance of *Quercus* trees that met naval standards decreased by more than 80%
145 across southern Sweden. Most of the decline appears to have occurred in meadows and arable
146 lands close to villages (Eliasson & Nilsson 2002). Royal ownership of *Quercus* officially
147 ended in 1830, which resulted in a further increase in harvesting by peasants, and a
148 corresponding decline in useful trees (Eliasson & Nilsson 2002; Hedin 2003). In Denmark a

149 general decline in forest cover also occurred from the 16th century onwards. In particular,
150 during the period AD 1650-1750, and associated with an expansion of agricultural activities
151 by an increasing human population, many forests of mature *Quercus* and *Fagus* were
152 converted into dense brushwood (Fritzbøger 1992). The landlords and the Crown foresters
153 decried the loss of timber trees whereas peasants readily used the brushwood for coppice and
154 grazing. In remaining forests *Fagus* gradually became dominant. The 18th century
155 assessments contain little evidence of mature *Quercus* trees.

156

157 **Study object**

158 Two species of *Quercus* occur in the region today: *Q. robur* (Pedunculate oak) and *Q. petraea*
159 (Sessile oak). *Quercus robur* occurs throughout the temperate (nemoral) region and is one of
160 the most widely distributed trees in Europe. It is a relatively light-demanding species that
161 regenerates poorly under a closed canopy (Diekmann 1996; Vera 2000). It has a large site
162 amplitude but is most competitive on dry and wet sites with low fertility where *Fagus*
163 *sylvatica* grows less vigorously (Larsen *et al.* 2005). On fertile sites and in the absence of
164 large-scale disturbance, *Q. robur* is also generally less competitive than *Ulmus* (Elm), *Tilia*
165 (Linden), *Fraxinus* (Ash) and *Acer* (Maple) (Niklasson & Nilsson 2005). Historically it was
166 probably rather tolerant to fires and also favoured by human activity (Bradshaw & Lindbladh
167 2005). *Quercus petraea* has a similar distribution and ecology as *Q. robur* but is much less
168 common. Compared to *Q. robur* it has an even larger tolerance to sites with thin soils but is
169 less tolerant of poorly drained conditions.

170

171 In Scandinavia *Quercus* has a southern distribution, centred along the coast in the temperate
172 vegetation zone (Fig. 2). In this region a large proportion of the remaining forest is comprised
173 of broadleaf trees but the total forest area is rather limited (<30%) due to historical conversion

174 to arable land and residential and commercial development. In the more northern hemiboreal
175 zone approximately 60% of the land is occupied by forests, but *Quercus* occurs as a minor
176 component. Forests in this region are largely dominated by nearly pure stands of *Picea abies*
177 (c. 47% of total volume) and *Pinus sylvestris* (ca 29%) managed for timber production and
178 characterized by low value for biodiversity. *Quercus* occurs both in natural stands and in
179 forests intensively managed for timber production. Approximately one-third of the trees
180 exceed 45 cm in diameter, with most of the larger trees occurring in natural stands (Nilsson *et*
181 *al.* 2008). *Quercus* intended for timber production are usually cut by an age of c. 120 years,
182 which is decades before they develop the ‘old tree structures’ of large stem diameter, coarse
183 cracked bark and decay-infested hollows that provide important habitats for many insects and
184 epiphytes species (Berg *et al.* 1994; Nilsson & Niklasson 2005). A large proportion of the
185 remaining older coarse trees grow in the former infields of estates (Eliasson & Nilsson 2002).
186 Historically, estates were separated into infield (Swedish *inäga*) and outland (Swedish
187 *utmark*), a division that persisted in large parts of southern Scandinavia for many hundred
188 years until the early 20th century. Generally, infields lay closer to the village buildings and
189 contained arable land and hay meadows, whereas outlands were largely forested and primarily
190 used for grazing.

191

192 **Site selection and regional variation**

193 With one exception all sites investigated for local records are small hollows or wetlands
194 selected from previous studies (Table 1, Fig. 1). The additional site is Hälledammen, a c. 50-
195 m diameter pond located on an island off the west coast of Sweden. The sites fall equally into
196 the temperate (13 sites) and hemiboreal (12 sites) zones (cf. Ahti *et al.* 1968), which differ in
197 vegetation, climate and physiography. The border between the zones corresponds largely to
198 the historic border between Sweden and Denmark that persisted until AD 1658. Before

199 extensive modern forestry the temperate zone was dominated by broad-leaved species
200 (*Quercus*, *Tilia*, *Fagus*) whereas the hemiboreal zone was a transition zone comprised of both
201 temperate and boreal trees (*Pinus*, *Picea*, *Betula*) and greater evergreen cover. The hemiboreal
202 zone is slightly higher in elevation, has colder winters and is dominated by granite or gneiss
203 bedrock in contrast to more fertile sedimentary bedrock in large parts of the temperate zone
204 (Wastenson 1990). Across the study region seventeen sites could be designated to a land-use
205 practice: twelve in former outlands and five in former infields.

206

207 Regional pollen diagrams were obtained from the European Pollen Database, three from each
208 vegetation zone (Fig. 1). These include Lake Trummen and Lake Väjösjön (Digerfeldt 1972;
209 1977), Ranviken (Digerfeldt 1973), Lake Kansjön (H. Jacobson unpublished), Ageröds mosse
210 (Nilsson 1964), Lake Krageholmssjön (Gaillard 1984) and Lake Färskesjön (Berglund 1966).
211 Because the upper sediments of Lake Trummen are missing (Digerfeldt, 1972), we used the
212 pollen records from the adjacent Lake Väjösjön (Digerfeldt, 1977) for the last 1200 years.
213 The records cover the last 4000 years and are geographically representative of the region. The
214 pollen records from large sites are assumed to represent the regional vegetation at a scale of
215 ca. 100 × 100 km around each lake (Hellman *et al.* 2009b).

216

217 **Data handling, pollen source area and statistics**

218 For all analyses of the pollen data, percentage values were employed rather than PAR (Pollen
219 Accumulation Rates) as PARs were available for only 14 of the small hollow sites. Due to the
220 large number of pollen analysts and varying taxonomic detail in the studies as well as the
221 central focus on *Quercus*, we chose to focus on common taxa represented by at least 5% in
222 one or more samples. Cyperaceae was excluded due to its frequent abundance in wetlands.
223 Human land use was inferred from the relative abundance of Cerealia and the combined

224 abundance of four easily identified and robust indicators of agricultural activities: *Rumex*
225 *acetosa*, *R. acetosella*, *Artemisia*, *Plantago lanceolata* and *Polygonum aviculare* (Gaillard
226 2007). For comparison and statistical analysis, the pollen records were divided into 200-year
227 and 100-year periods before and after AD 0, respectively. These period lengths represent a
228 compromise between resolution and accuracy. For periods lacking samples (c. 20% in both
229 zones) values were interpolated as the mean of the two adjacent periods. Maps of pollen
230 values for each local site were developed for five periods: 200-399 BC and AD 200-299, 900-
231 999, 1600-1699 and 1900-1999. Summary diagrams of the mean pollen percentages from the
232 small sites for the major taxa were constructed for each of the vegetation zones as a mean to
233 compare the development of the regional vegetation between the temperate and the
234 hemiboreal zones. The percentages vary greatly among the small-hollow sites, which
235 corroborates the expectation that each site records pollen from a restricted source area within
236 a given landscape (Sugita 1994). Based on simulated and empirical relation between pollen
237 and vegetation in the south Swedish vegetation/landscape setting of the last 6000 years, the
238 relevant source area (RSAP) of small sites (bogs and lakes) is estimated to be between c. 1000
239 and 2000 m in radius (Hellman *et al.* 2009a; Hellman *et al.* 2009b). However, we believe the
240 mean value from each vegetation zone is a reasonable approximation for the regional
241 development. The mean values for each zone remained consistent over time, exhibiting only
242 small fluctuations between adjacent levels. The overall trends appear broadly representative
243 and for most taxa the sites in a region display a similar pattern of change through time. Our
244 assumption is furthermore supported by a quantitative modelling approach for vegetation
245 reconstruction by Sugita (2007), which suggests that mean values from many small sites is a
246 good estimator for the regional vegetation composition.

247

248 Spearman's partial correlation was used to examine the relationship between *Quercus*, other
249 taxa and the anthropogenic indicators the last 1800 years. To adjust for the effect of site, zero-
250 one variables were used as partialized variables for the sites. Ordination by non-metric
251 multidimensional scaling (NMS; PCord 5.10 software) employing Sorensen's relative
252 distance was used to display the vegetation relationships among sites at four of the mapped
253 time periods: AD 200-299, 900-999, 1600-1699 and 1900-1999. Non-metric
254 multidimensional scaling (NMS) was used because it performs well with non-normal data like
255 pollen percentages (Clarke 1993; Quinn & Keough 2002) and Sorenson's relative distance is
256 broadly effective with ecological data (Faith *et al.* 1987). The calculations compared one- to
257 six-dimensional solutions using the NMS autopilot in the 'slow and thorough' mode, where
258 the program follows a predefined template (McCune & Mefford 1999).

259

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

263

264 **Results**

265

266 The regional dynamics of *Quercus* and comparison between the hemiboreal and temperate
267 zones are displayed in the mean pollen values from the 25 small hollow sites and the
268 percentage values from the regional sites (Fig. 3). Small hollow values for *Quercus* from
269 1000-0 BC were 25-30% in the temperate zone and 12-14% in the hemiboreal zone. *Quercus*
270 increased in both zones shortly after AD 0 and peaked around AD 100-400 in the temperate
271 zone and AD 200 in the hemiboreal zone. Subsequently, *Quercus* decreased steadily in both
272 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 Cerealia, *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

298 regionally in the last centuries, especially in the south. *Corylus* and *Tilia* have consistently
299 decreasing values across the region through time. Taking into account the low productivity
300 and dispersal of its pollen, *Tilia* appears to have been abundant into the 10th century and to
301 have remained relatively abundant around some northern sites longer than at southern sites.
302 *Fagus* and *Picea* exhibited increasing values through time. *Fagus* expanded over the last 1000
303 years predominantly in the south. The expansion of *Picea* occurred over the last few hundreds
304 of years in northern sites. Cerealia were recorded throughout the last two millennia but
305 display maximum values in the 17th century when they are recorded at most sites. A similar
306 pattern is seen in the anthropogenic indicators, which were present in all periods, but became
307 somewhat more frequent during the last two hundred years.

308

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

315

316 In the NMS analysis of the 14 taxa, 25 sites and 96 levels the final stress was 9.8%, which
317 differs significantly ($p < 0.01$) from the randomized Monte Carlo tests. Axis scores were $r^2 =$
318 0.38, 0.33 and 0.22 for axis 1, 2, and 3, respectively. The boreal taxa *Picea*, *Pinus* and
319 *Calluna* were grouped in the upper right in the diagram (Fig. 7). *Betula* was close to these
320 taxa, but had lower scores on axis 1. The anthropogenic indicators, Cerealia and Poaceae were
321 grouped together with weakly negative scores on both axes. The temperate taxa *Tilia* and

322 *Corylus* were located together with *Alnus* in the lower part of the diagram. *Quercus* and
323 *Fagus* were both in the lower left.

324

325 In the NMS diagram from AD 200-299 most temperate sites were located close to *Quercus*,
326 *Tilia* and *Corylus*, whereas the hemiboreal sites were more evenly spread out in the diagram
327 (Fig. 8). Overtime there was a tendency for more central clustering of all sites (less variation),
328 a separation of hemiboreal and temperate sites, and a strong clustering of hemiboreal sites in
329 the upper right, close to the boreal taxa. The distinction between the two regions emerged
330 around AD 900-999 and was greatest from AD 1600-1699. At AD 1900-1999 there was a
331 clear break between the hemiboreal sites and many temperate sites. However, most temperate
332 sites overlapped strongly with the hemiboreal sites due to the stronger influence of boreal
333 taxa. Hence, during the last century there was a separation among temperate sites and a shift
334 from the previous historical location and composition of temperate sites earlier in time.

335

336 **Discussion**

337

338 **Long-term dynamics of *Quercus* and other tree taxa**

339 The relative decrease of *Quercus* pollen as recorded in the small hollows was greatest in both
340 vegetation zones between the 17th and 19th century (Figs. 3 and 5). These results confirm the
341 reports of rapid decline of *Quercus* in 18th- and 19th-century historical records and place it into
342 the context of much longer-term dynamics (Eliasson 2002; Eliasson & Nilsson 2002; Hedin
343 2003). Specifically, it is clear that the genus is much less abundant today than at any time
344 during the previous 4000 years. In the hemiboreal zone modern pollen percentages are less
345 than 45% of the values observed at AD 1600 and c. 20% of the maximum values reached in
346 AD 200. The decline is somewhat less but nonetheless striking in the temperate zone, where

347 the modern values are 60% and 35%, respectively, of the pre-historical values. The rapid and
348 recent reductions of *Quercus* documented in historical records and the small hollows are more
349 subtle in the regional pollen diagrams (Fig. 3; Regnell 1989; Thelaus 1989; Rasmussen 2005).
350 The regional records often have low temporal resolution in recent centuries where changes in
351 arboreal pollen are abrupt and frequently obscured by major increases in non-arboreal taxa.
352 The low absolute abundance of *Quercus* is also obscured on many forest maps as these
353 frequently represent species in terms of percentages of forest growing stock and may
354 consequently represent *Quercus* as a dominant species in largely deforested landscapes such
355 as the coastal region (Fig. 2).

356

357 At the landscape scale there is a strong indication that the abundance and dynamics of
358 *Quercus* populations varied across areas of different land-use (Fig. 6). Our data do not support
359 the interpretation that *Quercus* was often more abundant in infields (arable land and
360 hayfields) as a consequence of active management to protect this species (Eliasson & Nilsson
361 2002 and references therein). Although our sample of infield sites is small and should be
362 interpreted with caution, the opposite trend is suggested at many sites. When our data allows
363 for direct comparison (infields and outlands cored on the same estate), *Quercus* pollen
364 percentages were comparable on infields and outlands (Råshult infield and outland –
365 Lindbladh & Bradshaw 1998; Osaby infield and outland – Lindbladh 1999). One possible
366 explanation for the discrepancy between the historical and pollen records is that historical
367 inventories may have been biased towards the immediate vicinities of estates and villages and
368 thereby overemphasized *Quercus* populations in those areas. A second possibility is that the
369 historical sources accurately portray differences in large and valuable trees. Naval and other
370 inventories were predominantly focused on large merchantable trees that were useful for
371 construction of ships or buildings, whereas pollen records represent the relative abundance

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

377

378 The strong positive correlation between *Quercus* and *Tilia*, *Corylus* and *Alnus* and the
379 consistent steady decline of these taxa across southern Scandinavia during the last two
380 millennia (Table 2; Fig. 4) suggests that climate change is the broad-scale driver of the
381 observed dynamics (Huntley & Webb 1989; Pearson & Dawson 2003). However, the long-
382 term decline of *Quercus* was consistent throughout the last 2000 years and no simple
383 relationship occurs between this trajectory and changes in temperature, for instance through
384 the warm early Middle Age or the comparatively cool Little Ice Age (Fig. 4). Our records do
385 indicate that human activity induced complexities in both the regional variation and temporal
386 details of these long-term dynamics. The initial decline of the thermophilous taxa, *Tilia* and
387 *Corylus*, c. 4000 years ago in Southern Scandinavia is most likely related to a decrease in
388 temperature (Hammarlund *et al.* 2003; Seppä *et al.* 2005). *Quercus* and *Alnus* do not begin to
389 decline until c. 2000 years ago, presumably in response to a further decrease in temperature
390 (Seppä *et al.* 2005) and only after *Quercus* reaches a peak across the region (Fig. 4). *Quercus*
391 is less shade-tolerant than *Tilia* and other temperate deciduous species (Diekmann 1996;
392 Larsen *et al.* 2005), and may have been favoured by the increasingly open pastoral landscape
393 initiated during the Bronze age (c. 1500-500 BC), particularly in the temperate zone
394 (Berglund *et al.* 1991). Open conditions through this period are indicated by an increasing
395 value of Poaceae and the low, but constant, record of anthropogenic indicators. The only
396 *Alnus* species in the region today, *Alnus glutinosa*, occupies moist sites and is represented

397 with high values in our local diagrams from wetland sites in contrast to many regional lake
398 records (e.g. Gaillard 1984; Digerfeldt 1972). Although the dynamics of *Alnus* should reflect
399 both the gradual decline in temperature and availability of suitable moist conditions generated
400 by broad-scale climate change during the past 4000 years (Tallantire 1974; Larsen *et al.* 2005;
401 Seppä *et al.* 2005), it is likely that the long-term decline in this species also reflects the
402 gradual clearing of the landscape of trees and conversion of wet forests into open meadows
403 (Berglund *et al.* 1991).

404

405 **Drivers of long-term vegetation dynamics**

406 The landscape-scale resolution of our pollen records provides insights into the details of the
407 *Quercus* decline and the species and vegetation that replaced it. In the hemiboreal zone the
408 decline of *Quercus* appears to be controlled by competition with other forest species,
409 mediated by human activity. *Picea* and *Pinus* are strongly negatively associated with *Quercus*
410 and increase as it declines (Table 2). *Pinus* was common in the eastern hemiboreal zone in the
411 beginning of our record (Fig. 5). On a landscape scale it is likely that *Pinus* replaced *Quercus*
412 in the hemiboreal zone due to the strong similarities of the two species in terms of fire
413 resistance and tolerance for both dry and wet sites (Table 2; Sykes *et al.* 1996; Larsen *et al.*
414 2005; Bradshaw & Lindbladh 2005). Indeed, as *Pinus* became more common in the west after
415 AD 900, there was a notable decline in *Quercus* (Fig. 5).

416

417 *Picea* entered the region from the north c. 1000 years ago. From there it spread south and east
418 probably in response to colder and snowier conditions (Fig. 5; Bradshaw *et al.* 2000; Giesecke
419 & Bennett 2004; Bradshaw & Lindbladh 2005), although the exact role of climate in this
420 migration is not completely clear (Miller *et al.* 2008). *Picea* is a strong competitor with shade-
421 tolerant temperate species (Seppä *et al.* 2009) and it is therefore likely that the decline of

422 *Quercus* at many sites in the hemiboreal zone was due to competition with *Picea*. Although
423 anthropogenic indicators are rather unimportant in the hemiboreal zone, it appears that
424 selective cutting may have been a factor leading to a decline in *Quercus* and facilitating the
425 initial entry of *Pinus* and *Picea* into forested sites. Such a development is described at the end
426 of the 19th century when *Picea* entered into the area of its southernmost distribution in
427 Sweden today (Hesselman & Schotte 1906). The increasing number of domestic animals and
428 intense grazing when agriculture expanded during the mediaeval colonization (Lagerås 2007)
429 likely promoted the decline of *Quercus* relative to the conifers and temperate deciduous trees
430 that are more resistant to grazing (Götmark *et al.* 2005). The apparent persistence of *Quercus*
431 at higher abundances on outlands until its decline c. 300 years ago may be due to its tolerance
432 for unfertile, dry and moist sites (Fig. 6; Diekmann 1996).

433

434 In contrast to the hemiboreal zone, in the temperate zone *Quercus* forests were likely replaced
435 by agriculture. Here, as in the hemiboreal zone, *Quercus* declined after its peak around 200-
436 400 AD, but coincident with a much greater increase of anthropogenic indicators (Table 2;
437 Fig. 4 and 5). While both Cerealia and anthropogenic indicators are low in abundance and
438 show weak negative correlations with *Quercus* in the hemiboreal zone, in the temperate
439 vegetation zone Cerealia are more prominent and more strongly negatively correlated to
440 *Quercus*. It appears that in the south and west agricultural land began to replace *Quercus* in
441 many places after the 5th century AD. In both zones modern forestry and regional planting
442 produced the large regional increase of the two conifers during the last c. 150 years (Fig. 5;
443 Hesselman & Schotte 1906).

444

445 Fire has been suggested as an important factor in controlling the historical abundance of
446 *Quercus* (Niklasson *et al.* 2002; Greisman & Gaillard 2009). Although not explicitly

447 addressed in this study, forest fires were historically common in the hemiboreal zone until the
448 mid 18th century (Niklasson & Drakenberg 2001; Bradshaw & Lindbladh 2005). Fire
449 suppression in Sweden over the course of the last centuries is believed to have reduced
450 *Quercus* regeneration (Niklasson *et al.* 2002; Lindbladh *et al.* 2003). However, a recent study
451 examining charcoal and pollen in the same region as this study found only a weak negative
452 correlation between charcoal and *Quercus* pollen abundance (Bradshaw *et al.* in press).

453

454 **Regional pattern of vegetation change**

455 Ordination of the pollen data across the range of sites through time demonstrates major
456 changes in the regional pattern of vegetation variation (Fig. 7). Although the sites exhibit
457 regional variation today, at AD 200-299 temperate and hemiboreal sites were rather evenly
458 mixed in the diagram. At that time many sites were strongly dominated by temperate taxa and
459 *Alnus*, and geographical variation was weakly expressed. The separation of sites into
460 distinctive geographical groupings begins at AD 900-999 as sites from the two zones start to
461 separate. This process continues through to AD 1900-1999 when many of the temperate sites
462 have higher scores on both axes, indicating a shift from temperate conditions at AD 200-299
463 to more hemiboreal conditions. However, since AD 200-299 the overall spread of site scores
464 and the apparent variation in vegetation has declined across all sites and between the
465 vegetation zones. Thus, while regional patterns emerged and persisted, the regional vegetation
466 as a whole has become more homogenous, as reflected by the ordination, compared to
467 previous periods. Much of this modern increase in similarity among the sites in the different
468 zones is due to increased human impacts, in particular the widespread introduction of conifer
469 forests in southern Sweden (Kardell 2004; Niklasson & Nilsson 2005). A similar
470 homogenization of regional vegetation patterns can be seen in forests across the north-eastern

471 United States as a consequence of similarities in broad-scale land use activities (Foster *et al.*
472 1998; Oswald *et al.* 2008).

473

474 **Implications for conservation**

475 This study provides a lengthy perspective for conservation management and insights into
476 *Quercus* forests across the region. The long-term decline and recent rapid drop in *Quercus*
477 populations throughout southern Scandinavia is striking and indisputable. While these results
478 pertain to *Quercus* populations alone and not the many threatened species associated with
479 *Quercus*, it is clear that this foundation taxon has undergone a major shift in abundance and
480 distribution as a consequence of both broad-scale and local factors. Millennium-scale climatic
481 change is a major factor driving the long-term decline of *Quercus* and changing abundance
482 relative to other important tree taxa. However, the details of this decline, the late date (last
483 200-300 years) relative to other thermophilic tree species, and the close correlation between
484 *Quercus* and numerous anthropogenic indicators underscores the important role of recent
485 human activities.

486

487 From the perspective of both the populations of *Quercus* and its associated species of insects
488 and epiphytes, the rate of decline is extremely rapid. For this long-lived tree the last
489 millennium represents no more than two to three generations. Meanwhile, studies of the rare
490 Hermit beetle (*Osmoderma eremita*) demonstrate that individuals of this species have
491 extremely restricted dispersal, perhaps only a couple of hundred meters. As a consequence a
492 *Quercus* stand can host a metapopulation of this beetle for several centuries (Hedin 2003;
493 Ranius & Hedin 2004). Given the former abundance of *Quercus*, the tree species longevity,
494 and the capability for persistence, it is likely that our current populations of *Quercus* and its

495 associated species represent legacies of former conditions in a process of slow and spiralling
496 decline that could lead to disappearance.

497

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

512

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

520 retention of biologically valuable *Quercus* into the management of conifer production forests
521 (Koch Widerberg *et al.* unpublished data).

522

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530

531 **References**

- 532 Abrahamsson, Å. (1996) Pollenanalytisk studie i Ryfors Gammelskog, Vastergötland. MSc
533 thesis. Lund University, Lund, Sweden.
- 534 Ahti, T., Hämet-Ahti, L. & Jalas, J. (1968) Vegetation zones and their sections in
535 northwestern Europe. *Annales Botanica Fennica*, **5**, 169-211.
- 536 Berg Å., Ehnström B., Gustafsson L., Hallingbäck T., Jonsell M. & Weslien J. (1994)
537 Threatened plant, animal, and fungus species in Swedish forests: Distribution and
538 habitat associations. *Conservation Biology*, **8**, 718-731.
- 539 Berg, A., Gärdenfors, U., Hallingbäck, T. & Norén, M. (2002) Habitat preferences of red-
540 listed fungi and bryophytes in woodland key habitats in southern Sweden - Analyses of
541 data from a national survey. *Biodiversity and Conservation*, **11**, 1479-1503.
- 542 Berglund, B.E. (1966). Late-Quaternary vegetation in eastern Blekinge, south-eastern
543 Sweden. *Opera Botanica*, **12**, 3-180.

- 544 Berglund, B.E., Malmer, N., Persson, T. (1991) Landscape-ecological aspects of long-term
545 changes in the Ystad area. The Cultural Landscape During 6000 years in Southern
546 Sweden — the Ystad Project. (ed Berglund, B.E.), *Ecological Bulletins*, **41**, 405–424.
- 547 Berglund, B.E., Björkman, L., Holmqvist, B.H. & Persson, T. (2007) Skånes
548 vegetationshistoria – förändringar under 17 000 år. *Floran i Skåne: arterna och dess*
549 *utbredning* (ed T. Tyler), pp. 27-38. Lunds botaniska förening.
- 550 Berglund, B.E., Digerfeldt, G., Gaillard, M.-J., Engelmark, R., Karlsson, S., Risberg, J. and
551 Miller, U. (1996). Palaeoecological Events During the last 15 000 years (eds Berglund,
552 B.E., Birks, H.J.B., Ralska-Jasiewiczowa, M., and Wright, H.E.). pp. 233-280. , Wiley
553 and Sons, New York. Björkman, L. (1996a) The Late Holocene history of beech *Fagus*
554 *sylvatica* and Norway spruce *Picea abies* at stand scale in southern Sweden. Lundqua
555 thesis Volume 39. Lund University, Lund
- 556 Björkman, L. (1996b) Long-term population dynamics of *Fagus sylvatica* at the northern
557 limits of its distribution in southern Sweden: a palaeoecological study. *The Holocene*, **6**,
558 225–234.
- 559 Björkman, L. (1997a) The history of *Fagus* forest in southwestern Sweden during the last
560 1500 years. *The Holocene*, **7**, 419–32.
- 561 Björkman, L. (1997b) The role of human disturbance in the local Late Holocene
562 establishment of *Fagus* and *Picea* forests at Flahult, western Småland, southern Sweden.
563 *Vegetation History and Archaeobotany*, **6**, 79-90.
- 564 Björkman, L. & Bradshaw, R.H.W. (1996) The immigration of *Fagus sylvatica* L. and *Picea*
565 *abies* (L.) Karst. into a natural forest stand in southern Sweden during the last two
566 thousand years. *Journal of Biogeography*, **23**, 235-244.

567 Björse, G., Bradshaw, R.H.W. & Michelson, D.B. (1996) Calibration of regional pollen data
568 to construct maps of former forest types in southern Sweden. *Journal of*
569 *Paleolimnology*, **16**, 67-78.

570 Bradshaw, R.H.W (2007) Pollen methods and studies - Stand-Scale Palynology.
571 “Encyclopedia of Quaternary Science” (ed S.A. Elias), pp. 2535-2543. Elsevier,
572 Amsterdam.

573 Bradshaw, R.H.W., Hannon, G. & Lindbladh, M. (In press) The role of fire in southern
574 Scandinavian forests during the late Holocene. *International Journal of Wildland Fire*.

575 Bradshaw, R.H.W., Holmqvist, B.H., Cowling, S.A. & Sykes, M.T. (2000) The effect of
576 climate change on the distribution and management of *Picea abies* in southern
577 Scandinavia. *Canadian Journal of Forest Research*, **30**, 1992-1998.

578 Bradshaw, R.H.W. & Lindbladh, M. (2005) Regional spread and stand-scale establishment of
579 trees in North-West Europe. *Ecology*, **86**, 1679–1686.

580 Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community
581 structure. *Australian Journal of Ecology*, **18**, 117–143.

582 Dayton, P.K. (1972) Toward and understanding of community resilience and the potential
583 effects of enrichments to benthos at McMurdo Sound, Antarctica. *Proceedings of the*
584 *colloquium on conservation problems in Antarctica* (ed B.C. Parker). Allen Press
585 Lawrence, KS.

586 Diekmann, M. (1996) Ecological behaviour of deciduous hardwood trees in Boreo-nemoral
587 Sweden in relation to light and soil conditions. *Forest Ecology and Management*, **86**, 1-14.

588 Digerfeldt, G. (1972) The post-glacial development of Lake Trummen. *Folia Limnologica*
589 *Scandinavica*, No. **16**, 1-104 CWK Gleerup, Lund.

590 Digerfeldt, G. (1973). The post-glacial development of the bay Ranviken, Lake Immeln, I
591 Regional vegetation history, II Water level changes. University of Lund Department of
592 Quaternary Geology Report 1,1-59.

593 Digerfeldt, G. (1977) Palaeoecological Studies of the Recent Development of Lake
594 Väckjösjön. *Archiv für Hydrobiologie*, **79**, 465-477.

595 Drobyshev, I., Niklasson, M., Linderson, H., Sonesson, K., Karlsson, M., Nilsson, S.G. &
596 Lanner, J. (2008) Lifespan and mortality of old oaks – combining empirical and
597 modeling approaches to support their management in Southern Sweden. *Annals of*
598 *Forest Science*, **65**, 401.

599 Eliasson, P. (2002) Skog, makt och människor. *Kungliga Skogs och lantbruksakademien.*
600 *Skogs- och lantbrukshistoriska meddelande nr 25*. Stockholm (in Swedish with English
601 summary).

602 Eliasson P. & Nilsson S.G. (2002) You should hate young oaks and young Noblemen - The
603 environmental history of oak in eighteenth- and nineteenth-century Sweden.
604 *Environmental History*, **7**, 659-677.

605 Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R.,
606 Kloeppe, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse,
607 N.L. Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle,
608 B. & Webster, J.R. (2005) Loss of foundation species: Consequences for the structure
609 and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*, **3**,
610 479-486.

611 Eriksson, G. (1996) *Skogshistoria, kulturpåverkan och urskogsvärden i fem skogsreservat i*
612 *Kronobergs län*. Examensarbete 20 p, Ekologisk botanik, Umeå Universitet.

613 Faith, D.P., Minchin, P.R. & Belbin, L. (1987) Compositional dissimilarity as a robust
614 measure of ecological distance. *Vegetatio*, **69**, 57–68.

615 Foster, D.R., Motzkin, G. & Slater, B. (1998) Land-use history as long-term broad-scale
616 disturbance: regional forest dynamics in central New England. *Ecosystems*, **1**, 96-119.

617 Foster, D.R. & Zebryk T.M. (1993) Long-term vegetation dynamics and disturbance history
618 of a *Tsuga*-dominated forest in New England. *Ecology* **74**, 982-998.

619 Fritzböger, B. (1992) *Danske skove 1500-1800*. PhD thesis, Odense University, Denmark.

620 Gaillard. M.-J. (1984) A palaeohydrological study of Krageholmssjön (Scania, South
621 Sweden). Regional vegetation history and water-level changes. *LUNDQUA Report 25*.

622 Gaillard, M.-J. (2007) Archaeological Applications – past human impact inferred from pollen
623 data. “Encyclopedia of Quaternary Science” (ed S.A. Elias), pp. 2570-2595. Elsevier,
624 Amsterdam.

625 Gärdenfors, U. (2005) *Red-listed species in Sweden 2005*. ArtDatabanken, SLU, Uppsala.

626 Giesecke, T. (2004) The Holocene Spread of Spruce in Scandinavia. PhD thesis, Acta
627 Universitatis Upsaliensis, Uppsala.

628 Giesecke, T. & Bennett, K.D. (2004) The Holocene spread of *Picea abies* (L.) Karst. in
629 Fennoscandia and adjacent areas. *Journal of Biogeography*, **31**, 1523-1548.

630 Götmark, F. (2007) Careful partial harvesting in conservation stands and retention of large
631 oaks favor oak regeneration. *Biological Conservation*, **140**, 349-358.

632 Götmark, F., Berglund, Å. & Wiklander, K. (2005) Browsing damage on broadleaved trees in
633 seminatural temperate forest in Sweden, with a focus on oak regeneration. *Scandinavian*
634 *Journal of Forest Research*, **20**, 223-234.

635 Götmark, F., Fridman, J. & Kempe, G. (2009) Education and advice contribute to increased
636 density of broadleaved conservation trees, but not saplings, in young forest in Sweden.
637 *Journal of Environmental Management*, **90**, 1081-1088.

638 Götmark, F., Fridman, J., Kempe, G. & Norden, B. (2005) Broadleaved tree species in
639 conifer-dominated forestry: Regeneration and limitation of saplings in southern Sweden.
640 *Forest Ecology and Management*, **214**, 142-157.

641 Greisman, A. and Gaillard M.-J. (2009). The role of climate variability and fire in early and
642 mid Holocene forest dynamics of southern Sweden. *Journal of Quaternary Science*, **24**,
643 593-611.

644 Gustafsson, L. & Ahlén, I. (eds) (1996) National Atlas of Sweden - Geography of Plants and
645 Animals. SNA Publishing, Stockholm.

646 Hammarlund, D., Björck, S., Buchardt, B., Israelson, C. & Thomsen, C.T. (2003) Rapid
647 hydrological changes during the Holocene revealed by stable isotope records of lacustrine
648 carbonates from Lake Igelsjön, southern Sweden. *Quaternary Science Review*, **22**, 353–
649 370.

650 Hannon, G., Bradshaw, R.H.W. & Emborg, J. (2000) 6000 years of forest dynamics in
651 Suserup Skov, a semi-natural Danish woodland. *Global Ecology and Biogeography*,
652 **9**,101-114.

653 Hanski I., Moilanen, A. & Gyllenberg, M. (1996) Minimum viable metapopulation size.
654 *American Naturalist*, **147**, 527–541.

655 Hedin, J. (2003) Metapopulation ecology of *Osmoderma eremita* - dispersal, habitat quality
656 and habitat history. PhD thesis, Lund University, Sweden.

657 Hellman, S., Bunting, M.J. & Gaillard, M.J. (2009a) Relevant Source Area of Pollen in
658 patchy cultural landscapes and signals of anthropogenic landscape disturbance in the
659 pollen record: A simulation approach. *Review of Palaeobotany and Palynology*, **153**,
660 245-258.

- 661 Hellman, S., Gaillard, M.-J., Bunting, J. & Mazier, F. (2009b) Relevant source area of pollen
662 in past cultural landscapes - a simulation approach. *Review of Palaeobotany and*
663 *Palynology* **153**, 259-271.
- 664 Hesselman, H. & Schotte, G. (1906) Granen vid sin sydvästgräns i Sverige. *Meddelanden från*
665 *Statens skogsförsöksanstalt*, **H. 3**, 1-52. Stockholm.
- 666 Hultberg, T., Brunet, J., Broström, A. & Lindblad, M. (2010) Forest in a cultural landscape –
667 the vegetation history of Torup in southernmost Sweden. *Ecological Bulletins*, **53**, 000–
668 000.
- 669 Huntley, B., Bartlein, P.J. & Prentice, I.C. (1989) Climatic control of the distribution and
670 abundance of beech (*Fagus L.*) in Europe and North America. *Journal of Biogeography*,
671 **16**, 551–560.
- 672 Huntley, B. & Webb III., T. (1989) Migration: species' response to climatic variations caused
673 by changes in the earth's orbit. *Journal of Biogeography*, **16**, 5-19.
- 674 Iversen, J. (1973) The development of Denmark's Nature since the Last Glacial. Danmarks
675 *Geologiske Undersøgelse*, **7C**, 1–126.
- 676 Jacobson, G.L. & Bradshaw, R.H.W. (1981) The selection of sites for paleovegetational
677 studies. *Quaternary Research*, **1**, 80-96.
- 678 Jonsell M., Weslien J. & Ehnström B. (1998) Substrate requirements of red-listed saproxylic
679 invertebrates in Sweden. *Biodiversity and Conservation*, **7**, 749-764.
- 680 Kardell, L. (2004) *Svenskarna och skogen: del 2 : från baggböleri till naturvård*.
681 Skogsstyrelsens förlag, Jönköping, Sweden.
- 682 Lagerås, P. (2007). *The Ecology of Expansion and Abandonment*. National Heritage Board,
683 Sweden.
- 684 Larsen, J. B., Raulund-Rasmussen, K. & Callesen, I. (2005) Træartsvalet – de enkelte
685 træarters økologi. *DST - Dansk Skovbrugs Tidsskrift*, **90**, 139-169.

686 Lindbladh, M., Niklasson, M. & Nilsson, S.G. (2003) Long-time record of fire and open
687 canopy in a high biodiversity forest in southeast Sweden. *Biological Conservation*, **114**,
688 231-243.

689 Lindbladh, M. & Bradshaw, R.H.W. (1998) The origin of present forest composition and
690 pattern in southern Sweden. *Journal of Biogeography*, **25**, 463-477.

691 Lindbladh, M. (1999) The influence of former land-use on vegetation and biodiversity in the
692 boreo-nemoral zone of Sweden. *Ecography*, **22**, 485-498.

693 Lindbladh, M., Brunet, J., Hannon, G., Niklasson, M., Eliasson, P., Eriksson, G. & Ekstrand,
694 A. (2007) Forest history as a basis for ecosystem restoration – a multi-disciplinary case-
695 study in a south Swedish temperate landscape. *Restoration Ecology*, **15**, 284-295.

696 Lindbladh, M., Niklasson, M., Karlsson, M., Björkman, L. & Churski, M. (2008) Close
697 anthropogenic control of *Fagus* establishment and expansion in a Swedish protected
698 landscape – implications for forest history and conservation. *Journal of Biogeography*, **35**,
699 682-697.

700 Lindenmayer, D. B. & Franklin, J. F. (2002) Conserving forest biodiversity: a comprehensive
701 multiscaled approach. Island Press ,Washington, D.C..

702 Madsen, P. & Löf, M. (2005) Reforestation in southern Scandinavia using direct seeding of
703 oak (*Quercus robur* L.). *Forestry*, **78**, 55-64.

704 McCune, B. & Mefford, M.J. (1999) Multivariate Analysis of Ecological data, Version 4.
705 MjM Software Design. Gleneden Beach, Oregon, USA.

706 Miller, P.A., Giesecke, T., Hickler, T., Bradshaw, R.H.W, Smith, B., Seppä, H., Valdes, P.J.
707 & Sykes, M.T. (2008) Exploring climatic and biotic controls on Holocene vegetation
708 change in Fennoscandia. *Journal of Ecology* **96**, 247–259.

- 709 Moberg, A., Sonechkin, D.M., Holmgren, K., Datsenko, N.M. & Karlén, W. (2005) Highly
710 variable Northern Hemisphere temperatures reconstructed from low- and high-
711 resolution proxy data. *Nature* 433, 613-617.
- 712 Molinari, C. (2002) 2500 years of Forest Dynamics at Söndre Skog, a semi-natural Forest on
713 Hallands Väderö island, Southern Sweden. Ms thesis, Turin University, Italy.
- 714 Niklasson, M. & Nilsson S.G. (2005) *Skogsdynamik och arters bevarande*. Studentlitteratur,
715 Sverige.
- 716 Niklasson, M. & Drakenberg, B. (2001) A 600-year tree-ring fire history from Norra Kvill
717 National Park, southern Sweden: implication for conservation strategies in the
718 hemiboreal zone. *Biological Conservation*, **101**, 63-71.
- 719 Niklasson, M., Lindbladh, M. & Björkman, L. (2002) A long-term record of *Quercus* decline,
720 logging and fire history in a southern Swedish *Fagus-Picea* forest. *Journal of*
721 *Vegetation Science*, **13**, 765-774.
- 722 Nilsson P., Kempe G., Toet, H. & Petersson, H. (2008) *Skogsdata 2008: aktuella uppgifter*
723 *om de svenska skogarna från Riksskogstaxeringen : Tema: Skogens roll för klimatet*
724 *Skogsdata vol 2008*.
- 725 Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg,
726 H., Mikusinski, G. & Ranius, T. (2002) Densities of large living and dead trees in old-
727 growth temperate and boreal forests. *Forest Ecology and Management*, **161**, 189–204.
- 728 Nilsson, S.G., Niklasson, M., Hedin, J., Eliasson, P. & Ljungberg, H. (2005) Biodiversity and
729 sustainable forestry in changing landscapes - principles and Southern Sweden as an
730 example. *Journal of Sustainable Forestry*, **21**, 11-43.
- 731 Nilsson S.G. (2001) Sydsveriges viktigaste områden för bevarandet av hotade arter—
732 vedskalbaggar som vägvisare till kärnområdena. *Fauna och Flora*, **96**, 59–70.

- 733 Nilsson, T. (1964) Standard pollen diagramme und C14 datierungen aus dem Ageröds mosse in
734 mittleren schonen. *Lund Universitets Årsskrift* N.F. 2, 59 (7), 52 p.
- 735 Nordén, B., Paltto, H. Götmark, F. & Wallin, K. (2007) Indicators of biodiversity, what do
736 they indicate? - Lessons for conservation of cryptogams in oak-rich forest. *Biological*
737 *Conservation*, **135**, 369-379.
- 738 Økland, B., Götmark, F. & Nordén, B. (2008) Oak woodland restoration: testing the effects
739 on biodiversity of mycetophilids in southern Sweden. *Biodiversity and Conservation*,
740 **17**, 2599-2616.
- 741 Osbeck, P. (1996) *Djur och natur i södra Halland under 1700-talet*. Bokförlaget Spektra,
742 Halmstad.
- 743 Oswald, W.W., Faison, E.K., Foster, D.R., Doughty, E.D., Hall, B.H. & Hansen, B.C. (2008).
744 Post-glacial changes in spatial patterns of vegetation across southern New England.
745 *Journal of Biogeography*, **34**, 900–913.
- 746 Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the
747 distribution of species: are bioclimate envelope models useful? *Global Ecology and*
748 *Biogeography*, **12**, 361-371.
- 749 Quinn, G.P. & Keough, M.J. (2002) *Experimental Design and Data Analysis for Biologists*.
750 Cambridge University Press, Cambridge.
- 751 Ranius, T. (2000) Population biology and conservation of beetles and pseudoscorpions
752 associated with hollow oaks. PhD thesis, Lund University, Sweden.
- 753 Ranius, T., Aguado, L.O., Antonsson, K., Audisio, P., Ballerio, A., Carpaneto, G.M., Chobot,
754 K., Gjurašin, B., Hanssen, O., Huijbregts, H., Lakatos, F., Martin, O., Neculiseanu, Z.,
755 Nikitsky, N.B., Paill, W., Pirnat, A., Rizun, V., Ruicănescu, A., Stegner, J., Süda, I.,
756 Szwałko, P., Tamutis, V., Telnov, D., Tsinkevich, V., Versteirt, V., Vignon, V., Vögeli,

757 M. & Zach, P. (2005) *Osmoderma eremita* (Coleoptera, Scarabaeidae, Cetoniinae) in
758 Europe. *Animal Biodiversity and Conservation*, **28**, 1–44.

759 Ranius, T., Eliasson, P. & Johansson, P. (2008) Large-scale occurrence patterns of red-listed
760 lichens and fungi on old oaks are influenced both by current and historical habitat
761 density. *Biodiversity and Conservation*, **17**, 2371–2381.

762 Ranius, T. & Hedin, J. (2004) Hermit beetle (*Osmoderma eremita*) in a fragmented landscape:
763 predicting occupancy patterns. *Species conservation and management: case studies* (eds
764 H.R. Akçakaya, M.A. Burgman, O. Kindvall, C.C. Wood, P. Sjögren–Gulve, J.S.
765 Hatfield & M.A. McCarthy), pp. 162–170. Oxford Univ. Press, New York.

766 Ranius, T. & Jansson, N. (2000) The influence of forest regrowth, original canopy cover and
767 tree size on saproxylic beetles associated with old oaks. *Biological Conservation*, **95**,
768 85–94.

769 Regnell, J. (1989) Vegetation and land-use history during 6000 years. Palaeoecology of the
770 cultural landscape at two lake sites in southern Skåne, Sweden. Lundqua thesis, Volume
771 27. Lund University.

772 Rasmussen, P. (2005) Mid- to late-Holocene land-use change and lake development at
773 Dallund Sø, vegetation and landuse history inferred from pollen data. *The Holocene*, **15**,
774 1116–1129.

775 Seppä, H., Alenius, T., Bradshaw, R.H.W., Giesecke, T., Heikkilä, M. & Muukkonen, P.
776 (2009) Invasion of Norway spruce (*Picea abies*) and the rise of the boreal ecosystem in
777 Fennoscandia. *Journal of Ecology*, **97**, 629–640.

778 Seppä, H., Hammarlund, D. & Antonsson, K. (2005) Low-frequency and high-frequency
779 changes in temperature and effective humidity during the Holocene in south-central
780 Sweden: implications for atmospheric and oceanic forcings of climate. *Climate*
781 *Dynamics*, **25**, 285–297.

- 782 Sugita, S. (1994) Pollen representation of vegetation in quaternary sediments: Theory and
783 method in patchy vegetation. *Journal of Ecology*, **82**, 881-897.
- 784 Sugita, S. (2007) Theory of quantitative reconstruction of vegetation. I. Pollen from large
785 sites REVEALS regional vegetation. *Holocene* **17**, 229–241.
- 786 Sykes, M.T., Prentice, I.C. & Cramer, W. (1996) A bioclimatic model for the potential
787 distributions of north European tree species under present and future climates. *Journal*
788 *of Biogeography*, **23**, 203-233.
- 789 Talantire, P.A. (1974) The paleohistory of the Grey Alder (*Alnus incana* (L.) Moench.) and
790 the Black Alder (*Alnus glutinosa* (L.) Gaertn.) in Fennoscandia. *New Phytologist*, **73**,
791 529-546.
- 792 Thelaus, M. (1989) Late Quaternary vegetation history and palaeohydrology of the Sandsjön-
793 Årshult area, southwestern Sweden. Lundqua thesis, Volume 26, Lund University.
- 794 Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. (1994) Habitat destruction and the
795 extinction debt. *Nature*, **371**, 65-66.
- 796 Tyler, M. (2008) British oaks: a concise guide. Crowood Press, Marlborough, UK.
- 797 Valdemarsdotter, Å. (2001) En skogshistorisk undersökning från östra Småland
798 Vegetationsutveckling och brandhistorik från Ekenäs i Hornsö-området de senaste 3000
799 åren. Ms thesis 64. Southern Swedish Forest Research Centre, SLU Alnarp.
- 800 Vera, F.W.M. 2000. Grazing Ecology and Forest History. CABI Publishing, Oxon, UK.
- 801 Wastenson, L. (ed) (1990) National Atlas of Sweden – The Forests. SNA Publishing,
802 Stockholm.
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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 20×30m	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	Djåknabygd	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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822 **Figure captions**

823

824 Figure 1. Map of southern Scandinavia with the sites used in the study. See Table 1 for the
825 names of the small hollow sites. The regional lake sites include: A. Lake Trummen and Lake
826 Väjösjön, B. Lake Ranviken, C. Lake Kansjön, D. Ageröds Mosse, E. Lake Krageholmssjön,
827 F. Lake Färskesjön.

828

829 Figure 2. Past and present distribution of *Quercus* in southern Sweden, modified from Björse
830 *et al.* (1996). The modern data are based on forest inventory data and represent percentages of
831 the total growing stock. The data from 2000 and 1000 BP (years Before Present) represent
832 estimated growing stock and are made from a network of 37 regional pollen sites. The maps
833 are from the National Atlas of Sweden – Geography of Plants and Animals (Gustafsson &
834 Ahlén 1996).

835

836 Figure 3. *Quercus* pollen values from local and regional sites. Panel A shows hemiboreal
837 regional sites: solid line is Lake Trummen (-AD 800) and Lake Väjösjön (AD 600-), dotted
838 line is Lake Ranviken, dashed-dotted is Lake Kansjön. Panel B shows temperate regional
839 sites: solid line is Ageröds mosse, dotted line is Lake Krageholmssjön, dashed-dotted line is
840 Lake Färskesjön. Panel C is mean pollen percentage of *Quercus* from the temperate and
841 hemiboreal small hollow sites. The lower panel shows the number of small hollow sites
842 included in their respective time periods. Each data point represents a 200-year or 100-year
843 period. As an example: AD 1500 represents AD 1500-1599, i.e. the 16th century.

844

845 Figure 4. Mean pollen percentage of all taxa and anthropogenic indicators included in the
846 study from the temperate and hemiboreal sites. Note the different scales on the y-axes. Each
847 data point represents a 200-year or 100-year period. As an example: AD 1500 represents AD
848 1500-1599, i.e. the 16th century. The temperature data is from Moberg *et al.* (2005),
849 temperature anomalies (low-frequency component AD 133-1925) from the northern
850 hemisphere annual mean temperature 1961-90 average.

851

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

855

856 Figure 6. Mean pollen percentage of *Quercus* from infield and outland sites. Each data point
857 represents a 200-year or 100-year period. As an example: AD 1500 represents AD 1500-1599,
858 i.e. the 16th century.

859

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

862

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

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