

## How long has the ‘hotspot’ been ‘hot’? Past stand-scale structures at Siggaboda nature reserve in southern Sweden

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Received: 25 September 2009 / Accepted: 5 March 2010 / Published online: 6 May 2010  
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**Abstract** Fossil pollen and plant macrofossils over the last 2000 years are documented from three small forest hollows in Southern Sweden. One of the sites is inside a 5 ha highly prized old growth mixed *Fagus sylvatica* and *Picea abies* forest of high biodiversity which has been protected since 1940. The other two hollows are located 400 and 700 m away in an outlying buffer zone established in 1995 which is mainly coniferous plantation forest. The results show that the area has been forested for at least 2000 years, but that forest composition has been under continuous change, most rapid over the last 200 years. The reduction of deciduous tree pollen particularly *Quercus*, *Tilia*, *Alnus* and *Corylus*, and the immigration of *Fagus* and *Picea* can be observed at all three sites. However, the temperate deciduous trees (*Quercus* or *Fagus*) have been much more common in the ‘hotspot’ than in the surrounding forests over the last c. 200 years, and significantly more common at least 2000 years before that. Even though the vegetation has been dynamic through time, the lower human intervention in the ‘hotspot’ area compared with the surrounding matrix forests has facilitated the longevity of deciduous trees and the many rare species which are associated with them. The palaeoecological record of key species and information on past

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use of the wider forest area revealed in this study, indicates how future management will require flexibility to maintain conservation ‘hotspots’.

**Keywords** Charcoal · Forest conservation · Historical records · Palaeoecology · Tree rings

## Introduction

In southern Swedish forests, conservation management policies are often guided by current ‘biodiversity hotspots’ where the presence of threatened wood-dependent species is used as a shortcut to indicate areas for protection (Nilsson et al. 1995, Roberge and Angelstam 2004). Biological hotspots do have a leading role to play in conservation, both in terms of preservation of their biological diversity and in their use as models (Myers et al. 2000), but how they have developed and their stability through time is often unknown. Past land-use history and disturbance frequency have an important effect on forest regeneration, structure and composition (Lindbladh et al. 2000; Vera 2000; Svenning 2002; Bradshaw et al. 2003; Birks 2005; Mitchell 2005). Factors which have an effect on both diversity and ecosystem function include fire, browsing and grazing, storms, in addition to the more recent planting programmes. Present day forest biodiversity research has demonstrated important relationships between openness of the forest canopy and the presence of insects and plants of high biodiversity value (Nilsson et al. 2002). Therefore, what the forests looked like before disturbance by people became intensive has become a major question for nature conservation. The length of time sites of less biological value have diverged from the old growth fragments provides interesting information on the long-term viability of isolated populations of threatened species, and can be an issue, when it comes to defining realistic restoration goals.

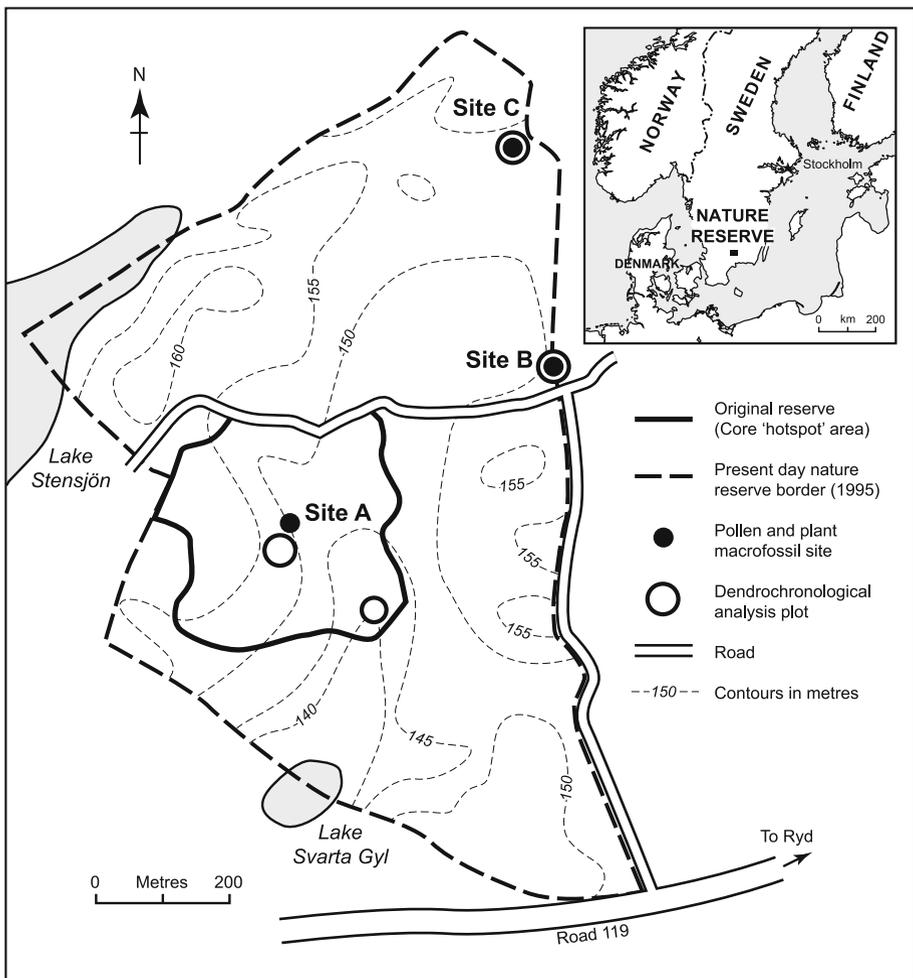
Long-term palaeoecological studies go some way to addressing these issues. They can reveal whether these biological hotspots are representative of the wider landscape in the past or whether they have always been different. They can be used to determine natural variability, to develop a strategy for coping with future climate scenarios, help to understand biological invasions and thresholds and to assess the length and extent of human influence in an area (Willis and Birks 2006; Willis et al. 2007; Feurdean and Willis 2008; Froyd and Willis 2008). Some areas of present day high biodiversity, and subsequent conservation interest, have been modified by human activity in the past (Segerström et al. 1996; Segerström 1997; Lindbladh et al. 2003; Willis et al. 2004). The information provided by a long term perspective can be used to form a scientific basis on which to assess which conservation strategy promoting biological values is the most appropriate for future planning (Honnay et al. 2004; Lindbladh et al. 2007, 2008).

Planning the appropriate forest structures for optimal biodiversity and natural value is the subject of intense debate throughout north-west Europe (Vera 2000; Svenning 2002; Mitchell 2005). Continuity and longevity of major host trees, even if scattered, can be important, as even though this is just a small part of the total biodiversity, woody species are often the keystone or foundation species with which many other dependent organisms are associated (Jonsell et al. 1998; Roberge and Angelstam 2004; Ellison et al. 2005; Gärdenfors 2005; Manning et al. 2006). They also provide a distinct microclimate, structural complexity, biological legacy, habitat for animals and cannot be replaced within a short period of time (100 s of years).

In southern Swedish forests, significant changes have taken place over the last 2000 years, driven by climatic change and former management (Björse and Bradshaw

1998; Lindbladh et al. 2000), which have consequences for current management. In addition, small isolated old growth fragments of temperate deciduous trees, notable for their associated lichen and beetle fauna can be found in amongst coniferous plantation forests (Nilsson et al. 1995; Nilsson 1997). Understanding the dynamics of these small remaining areas of high biological value within the wider landscape is becoming increasingly important in developing management strategies for protecting and maintaining them for the future.

What is the history of these ‘biodiversity hotspots’ and what management is most appropriate for their conservation? In this paper, we present a long-term palaeoecological study of a forest fragment in Southern Sweden with high biological value, with the surrounding forests which have been managed in the recent past, and which have low current ecological value (Fig. 1). This is the first time several closely located small hollows are



**Fig. 1** Map of the Siggaboda Nature Reserve in southern Sweden, showing the palaeoecological Sites A, B and C and the dendrochronological analyses plots

used to study the long-term development in a ‘hotspot’ in relation to the surrounding matrix. We use plant macrofossils, pollen, charcoal, dendrochronological techniques, historical data and Accelerator Mass Spectrometry (AMS)  $^{14}\text{C}$  dating to examine the dynamics of the woody species over the last 2000 years. We test the hypothesis that the ‘hotspot’ is ‘hot’ because it has been less disturbed by human activity than the surrounding forests of lower current biodiversity, and we examine the spatial and temporal variation of the vegetation within a small area.

## Study site

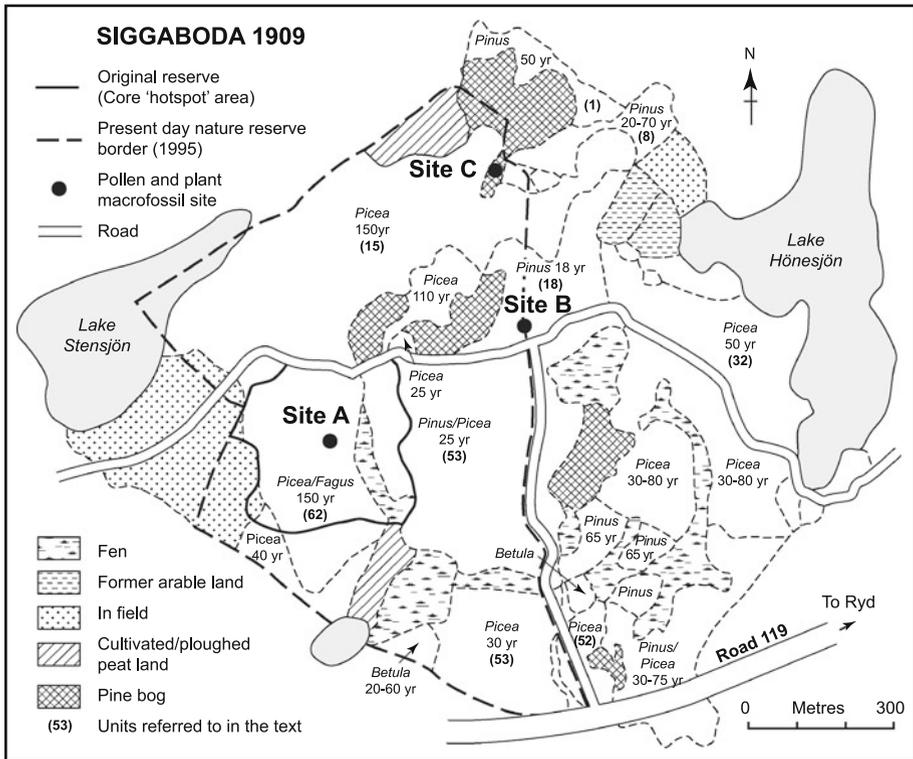
Siggaboda forest reserve (56°28' N, 14°34' E) lies on the border between the provinces of Småland and Blekinge, at the southern edge of the hemiboreal zone (Ahti et al. 1968) (Fig. 1). The original core ‘hotspot’ area of the reserve, which has been protected since the 1940s, is approximately 5 ha in size and consists of an old-growth, mixed age *Fagus sylvatica* (c. 60% of total basal area) and *Picea abies* (40%) stand. However, many of the old *Picea* trees have died in recent years due to bark beetle attacks and/or storms (Bolte et al. 2010). The oldest *Fagus* individuals are c. 250 years old, while *Picea* are generally younger, between 140 and 150 years old (Bolte et al. 2010), although there are a few which are over 200 years old. There is active regeneration. Only seedlings of *Picea* and *Fagus* are present around the palaeoecological site, but *Betula pendula* and *Alnus glutinosa* trees do occur within the 5 ha ‘hot spot’ area, along with a few individuals of *Betula pubescens*, *Sorbus aucuparia* and *Acer platanoides* (Bolte et al. 2010). *Pinus sylvestris* is extremely rare with only two mature living specimens present but several old, moss covered large diameter stumps have been found (Niklasson et al. 2002). There are many red listed, wood dependent species (Nilsson et al. 2002) of high conservation value, mainly as a result of old, living or dead beech trees (Nilsson et al. 1995). *Vaccinium myrtillus* is the dominant species in the understorey, while *Hylocomium splendens* and *Pleurozium schreberi* are dominant on dry ground, with *Polytrichum* species forming thick carpets without herbaceous vegetation on wetter areas (Niklasson et al. 2002). A buffer zone of almost pure *P. abies* forest of low biological value was added to the reserve in 1995 which are now between 80 and 115 years old (Niklasson et al. 2002). *B. pendula*, *B. pubescens*, *P. sylvestris* and *Salix caprea* are also present with occasional isolated *F. sylvatica* individuals of a similar age or older than the *P. abies* (Niklasson et al. 2002). Natural regeneration is now taking place with young dense seedlings of *Pinus*, *Picea* and *Betula*.

The bedrock in the reserve is granite gneiss, and there are occasional massive boulders scattered on the surface in the buffer zone which is otherwise undulating, but not rocky. Boulders are very abundant in the central ‘hotspot’ area. Mean annual rainfall is between 600 and 700 mm year<sup>-1</sup>, with mean July temperature between 15 and 16°C and mean January temperature between -2°C and -1°C (Ångström 1974).

## Methods

### Historical records

Historical records were obtained from the archives of the Legal, Financial and Administrative Services Agency (Kammarkollegium), the oldest public body in Sweden which dates back to the mid 1500s AD. Short general descriptions about the estate (c. 400 ha)



**Fig. 2** Map of the Siggaboda area drawn up in 1909 by the Demesne Board showing the main forest units present at that time

were available from 1685 and 1867, but lack detailed information about the conditions in the 5 ha core 'hotspot' area. The aim of these surveys is not clear but they may have been for taxation purposes. Records were also consulted from the National Archives (Riksarkivet) collected by the government organisation, the Swedish Forest Agency (Skogsstyrelsen) in 1879 (oak inventory) and from the Regional State Archives (the Demesne Board) in 1909 (forest management plan). A forestry plan drawn up by the Demesne Board in 1909 is presented on Fig. 2, representing the only written source with detailed information on forest age and composition at stand scale, including the reserve core area.

Field work

Three sites were analysed (Fig. 1). Site A, in the central 'biodiversity hotspot' part of the 5 ha forest protected since 1940, has been the subject of a previous pollen investigation (Björkman and Bradshaw 1996). The site is a wet *Sphagnum* covered small hollow, c. 10 m in diameter, set in one of the two small valleys that run through the reserve, and is surrounded by closed canopy *Picea* and *Fagus* forest with some *Betula*. The site was re-investigated for plant macrofossils and macrocharcoal >500 µm only. Pollen, plant macrofossils and macrocharcoal >500 µm were analysed from two small peat depressions of similar size in the surrounding buffer zone forest. Pollen Site B, located c. 400 m from the hotspot area, is a 100-year old, semi-open, managed conifer stand. Young, dense

seedlings of *Pinus*, *Picea* and *Betula* are now (2008) c. 0.5–1.5 m high due to a partial clearcut in the late 1990s. Pollen Site C, located c. 700 m from the ‘hotspot’ area, consists of a dense *P. sylvestris*/*P. abies* forest between 50 and 150 years old, with *B. pendula*, *B. pubescens* and some *Salix caprea*. Few seedlings or saplings are present. The buffer zone forests were actively managed until 1995, and in the case of Site C, regularly thinned.

Sediment cores were extracted from the centre of each depression, using a Wardenaar corer (Wardenaar 1987). The relevant pollen source area for these sorts of sites is interpreted as being 50–100 m in radius (Prentice 1985; Sugita 1994; Calcote 1995). Plant macrofossils are mostly deposited close to the parent vegetation and provide a local dimension to the vegetation reconstruction not easy to ascertain from pollen alone (Hannon 1999; Hannon et al. 2000). Macrocharcoal (>500  $\mu\text{m}$ ) can be considered to be of local origin (Ohlson et al. 2005).

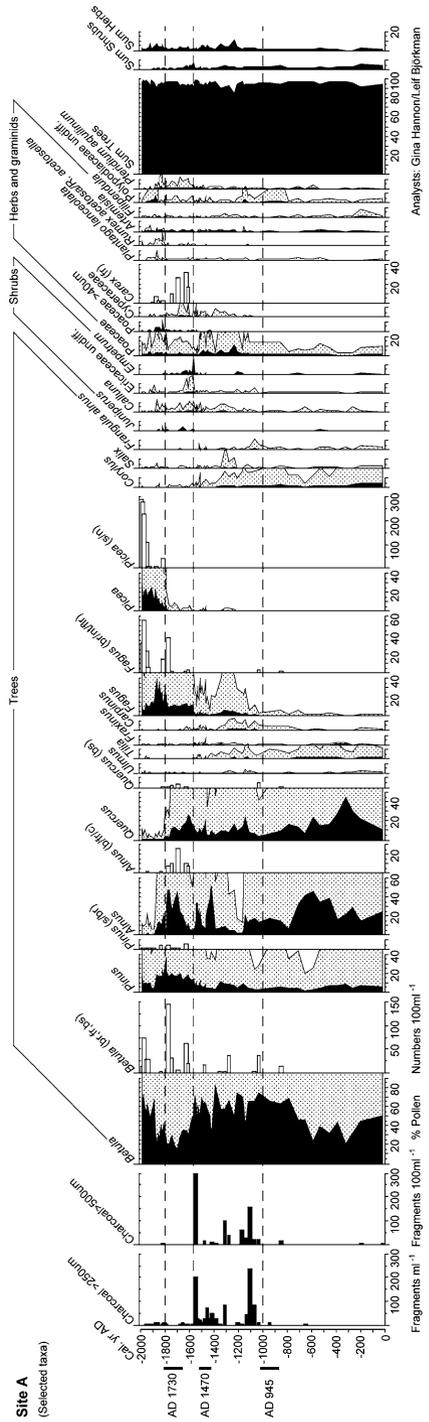
### Palaeoecological techniques

Pollen sub-samples were extracted from the monoliths taken at Site B and Site C from between 5 and 10 cm intervals and prepared using standard techniques (Berglund and Ralska-Jasiewiczowa 1986). The results are presented as percentage data where the pollen sum is made up of pollen from terrestrial plants excluding ferns, marsh and water plants (Figs. 3, 4). The pollen diagrams were drawn up using the computer programmes TILIA and TILIA GRAPH (Grimm 2004). After sub-sampling for pollen, continuous plant macrofossil samples of 100 ml in volume were extracted every 2 cm from all three sites. The samples were soaked overnight in 5% NaOH, after which they were washed through a sieve of 500  $\mu\text{m}$ . Macroremains were identified using plant keys (Bertsch 1941) and matched with specimens from a reference collection where possible. The results are presented together with macrocharcoal fragments >500  $\mu\text{m}$  as concentration per 100 ml of sediment or simply as presence (Figs. 4, 5). Macrocharcoal results (>250  $\mu\text{m}$ ) and selected pollen data from the earlier study by Björkman and Bradshaw (1996) have been correlated with the plant macrofossil data and macrocharcoal fragments >500  $\mu\text{m}$  from the new sediment sequence on Fig. 3, using radiocarbon dates to match the two profiles.

### Tree-ring analysis

A 157 m<sup>2</sup> (7.07 m radius) plot and a 314 m<sup>2</sup> (10 m radius) plot were used to analyse the age structure of the dominant oldest *Fagus* and *Picea* trees in the old growth part of the forest (Fig. 1). Selected trees from the canopy were cored in circular plots with a few individuals from the under storey. Most of the investigated trees were located within the central ‘hotspot’ area but a large number of *Pinus* trees, or stumps with fire scars, came from the extended reserve (Niklasson et al. 2002, Fig. 1). In the buffer zone Sites B and C, the sampling areas were 314 m<sup>2</sup> (10 m radius) circular plots around the pollen sites. Samples were taken from both the wetland area itself and the surrounding upland. Cores were extracted with a Swedish increment corer near the base of the trees while partial cross-sections were extracted with chain saw. The cores were glued to lists and cross-sections were glued to chip boards. Samples were then dried at room temperature and sanded with a belt sander down to grit 600. Ring counts, of very young trees, and cross datings were carried out under a dissecting microscope with up to 50 $\times$  magnification. Pointer years were identified and cross dating was carried out from the resulting list of pointer years according to methods presented by Yamaguchi (1991) and Stokes and Smiley (1968). Results are presented on Fig. 7.

**Fig. 3** Summary percentage pollen diagram and plant macrofossil and macrocharcoal concentrations from Site A in the ‘hotspot’ area of Siggaboda Nature Reserve. The shaded areas on the pollen profiles represent a 10× exaggeration of the scale. The pollen sum is made up of pollen from terrestrial plants excluding ferns, marsh and water plants. The *horizontal lines* represent the four phases where major compositional changes are considered to have taken place over the last two thousand years. The pollen values and macrocharcoal >250 um are after Björkman and Bradshaw (1996)







## Dating

Sediment slices of between 1 and 2 cm were used for AMS radiocarbon dating. Samples were evenly spread throughout the cores, dated in the Radiocarbon Dating Laboratory at the University of Uppsala and presented together with the radiocarbon dates from Björkman and Bradshaw (1996) on Table 1. All dates were converted from radiocarbon age to calibrated calendar years using OxCal software (v. 4.0: Bronk Ramsey 1995, 2001) and the calibration curve of Reimer et al. (2004). As most of the dates when calibrated showed two or more alternatives, the calibrated age used was the midpoint of the age range with the greatest probability. The ages for each pollen level were estimated by linear interpolation from these mid-points using the computer program TILIA2 (Grimm 2004), and assuming modern age at the top of the profiles.

## Results and discussion

### General vegetation history

The site in the central ‘hotspot’ area (Site A), set in rocky terrain, can be considered representative of both the forest on the sloping ground to the west of the site, and a wetter swamp forest area to the east of the site (Fig. 1). The sites in the buffer zone forests are located in flatter terrain with only occasional erratic boulders, representing both forests on

**Table 1** The AMS radiocarbon dates of sediment from Siggaboda Nature Reserve and bulk sediment dates from Björkman and Bradshaw (1996)

Site	Lab code	Depth (cm)	Technique & material	<sup>14</sup> C Date	Calibrated range (1 sigma)	Calibrated year
Site A	Ua-23911	26–27	AMS sediment	205 ± 35	AD 1650–1810	AD 1730
	Ua-22273	44–47	AMS sediment	425 ± 40	AD 1420–1520	AD 1470
	Ua-22274	66–67	AMS sediment	1095 ± 40	AD 870–1020	AD 945
	Ua-24104	97–98	AMS sediment	2970 ± 45	1320–1040 BC	1200 BC
Björkman and Bradshaw (1996)	Beta-53951	29.5	Bulk sediment	150 ± 60	AD1663–1896	AD 1779
	Beta-53952	42.0	Bulk sediment	330 ± 70	AD 1436–1669	AD 1552
	Beta-53953	56.7	Bulk sediment	460 ± 50	AD 1393–1522	AD 1457
	Beta-53954	72.0	Bulk sediment	940 ± 80	AD 971–1260	AD 1115
Site B	Ua-22673	40–41	AMS sediment	300 ± 40	AD 1480–1680	AD 1580
	Ua22674	55–56	AMS sediment	1740 ± 45	AD 200–400	AD 300
	Ua-22675	69–70	AMS sediment	2790 ± 45	AD 1050–830	940 BC
	Ua-22676	89–90	AMS sediment	5100 ± 50	3990–3770 BC	3880 BC
Site C	Ua-32702	16–18	AMS sediment	111 ± 0.4	AD 1810–1890	AD 1850
	Ua-22670	22–23	AMS sediment	445 ± 45 <sup>a</sup>	AD 1405–1522	
	Ua-22671	44–45	AMS sediment	900 ± 40	AD 1030–1230	AD 1130
	Ua-22672	79–80	AMS sediment	5845 ± 45	4800–4600 BC	4700 BC

The AMS measurements were made at the Radiocarbon Dating Laboratories at the University of Uppsala (Ua). All dates were calibrated using OxCal software (v. 4.0: Bronk Ramsey 1995, 2001) and the calibration curve of Reimer et al. (2004)

<sup>a</sup> This date was not used in drawing up the age/depth relationship as it deferred too much from the other dates and considered inaccurate

well drained ground and the wetter areas surrounding the hollows in which the cores were taken. The three pollen profiles show the same general development (Figs. 3, 4, 5) which might be expected from sites that are so close together, but they also show some site specific trends over the last 2000 years. The diagrams have been sub-divided into 4 time periods where major compositional changes are considered to have taken place.

#### 0–1000 AD

At Site A, in the central biodiversity ‘hotspot’ part of the reserve, the pollen diagram shows that *Quercus* and *Tilia* dominated the well drained soils with some *Ulmus* and *Fraxinus*, with *Corylus* in the shrub layer (Fig. 3). *Fagus* was originally thought not to be locally present in the forest until after a major fire 950 years ago (Björkman and Bradshaw 1996), but the plant macrofossil results reveal that isolated *Fagus* trees were already present 1100 years ago, probably on the drier slopes above the pollen site. *Quercus robur/petraea* bud scales were also recorded indicating local presence along with *B. pendula* fruits. *Betula* and *Alnus* were probably the major trees in the swamp forest close to the site with *Salix* spp. and *Frangula alnus*. Both dwarf shrub and herbaceous pollen representation were low suggesting closed canopy conditions. Low values of *Pinus* pollen are recorded, but without macrofossil support, *Pinus* is not considered locally present.

By contrast, Sites B and C, have proportionally far less of a contribution from *Quercus* and *Alnus*, and the pollen and the macrofossil record indicates that *Pinus* was probably the most important tree type on the better drained soils, with *Betula* on the wetter areas (Figs. 4, 5). This can be associated with the frequent fire disturbance as seen in the sedimentary charcoal record, most marked at Site C (Fig. 5). These fires may have been ground fires only, as arboreal pollen still constituted up to 90%, herbaceous pollen record was sparse and the forest is still interpreted as fairly closed. While theoretical studies have shown that even 90% arboreal pollen can mean up to 50% openness at lake sites (Sugita et al. 1999), such information has not been available for small hollows. A recent simulation run for small hollows, with a radius of 5 m using Pollscape, based on the simulation design used by Sugita et al. (1999), has shown that 90% arboreal pollen can mean 5–30% openness (Sugita pers. comm.). However, these simulations assume pollen is dispersed as single grains. Empirical data (Andersen 1970; Bradshaw 1981) have shown this not to be the case for small hollows. Consequently, 90% arboreal pollen is likely to be at the lower end of the range of openness proposed by Sugita (pers. comm.). The low pollen values for *Quercus* and *Alnus* suggest an insignificant role for these taxa in this part of the reserve whereas similar values to the central ‘hotspot’ area are recorded for *Tilia*, *Corylus* and *Ulmus* (Figs. 4, 5). *Fagus* pollen is recorded at both sites; most marked at Site B, but is unsupported by plant macrofossils. At Site C, where the highest frequency and numbers of sedimentary charcoal was recorded, there was a greater representation by dwarf shrub pollen types *Calluna vulgaris* and Ericaceae. Ericaceous taxa, particularly *Calluna* are known to have been burnt in order to improve land for grazing, and slash and burn techniques were used to promote agriculture in less rocky sites up to the end of the 1800s (Larsson 1989). Furthermore, regular values for *Juniperus communis* may be evidence of continual grazing, particularly domestic livestock (Gaillard et al. 1992) in the surrounds of this site.

#### 1000–1560 AD

The first major fire in the central biodiversity ‘hotspot’ area (Site A) (Fig. 3) was recorded c. 950 years ago, at the beginning of a period with frequent fires there until the mid 1500s

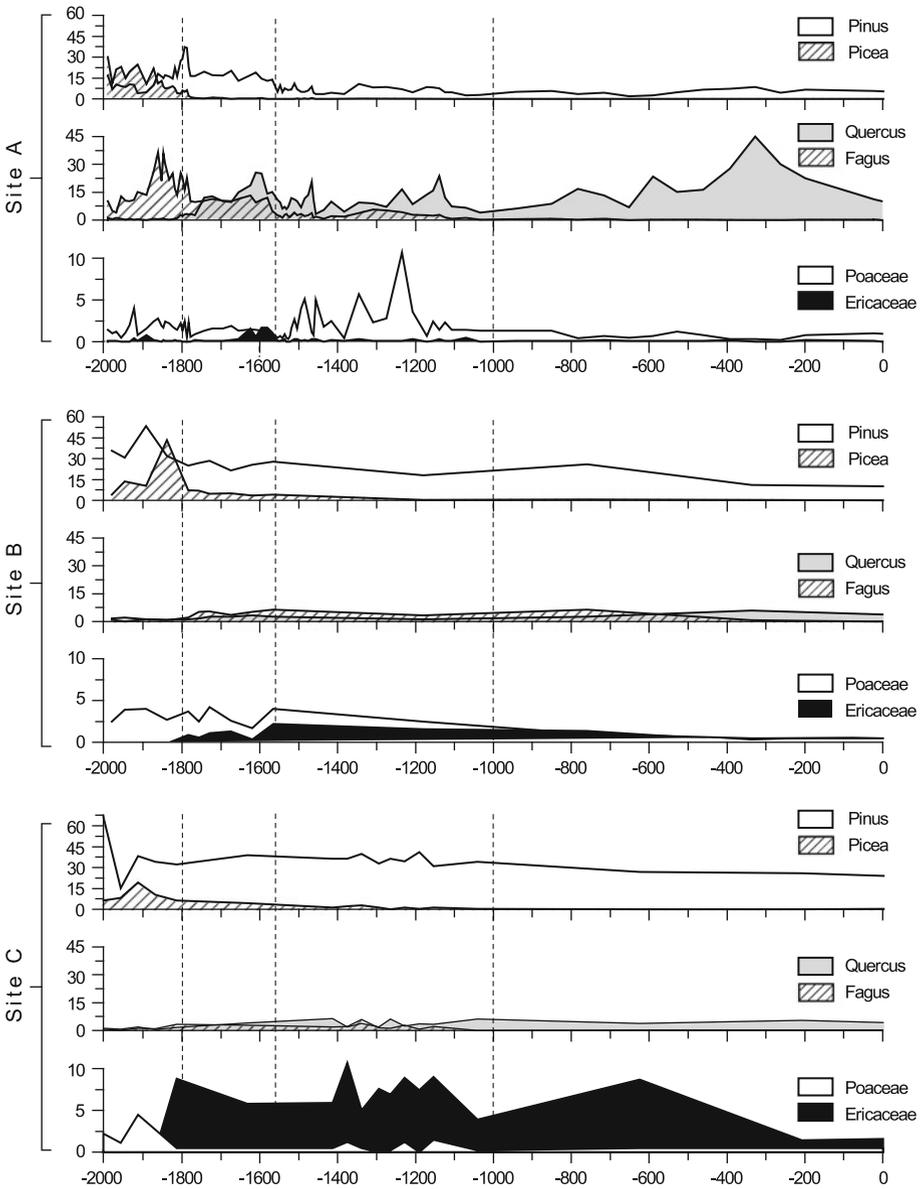
AD. This fire could be the same as that recorded at Site C (Fig. 4) but radiocarbon-based chronologies are not sufficiently precise to allow such exact correlations. Prior to the first fire, *Quercus* and *Fagus* macroremains are recorded at Site A (Fig. 3) but only *Betula* remains were recorded during the fire period itself, while *Betula* and *Pinus* needles, including charred needles, are constantly recorded at Sites B and C (Figs. 4, 5). Despite fire probably making the forest more open, arboreal pollen continued to reach values of up to 90% at all three sites. Low herb pollen percentages suggest continued dominance by trees. A notable change in forest dominants takes place during this period, with a decrease in *Quercus*, *Tilia*, *Ulmus* and *Corylus*, suggesting these taxa were becoming less important, particularly around Sites B and C. While both regional and local records show a general shift from temperate deciduous forest to coniferous forest one thousand years ago (Björse and Bradshaw 1998; Lindbladh et al. 2000), individual species show different abundance values when analysed in these stand-scale records, particularly when plant macrofossils are included in piecing together the vegetation history. *Quercus* was undoubtedly important in the central ‘hotspot’ forest stand, as evident from the macrofossils in this study, and the discovery of a *Quercus* stump, dated by tree ring analysis to have regenerated during the 15th century (Niklasson et al. 2002). Pollen from *Quercus* was never as common at Sites B and C (Fig. 6), and there was no macrofossil evidence for local presence suggesting that it may not have been that widespread in the area as a whole. The rough and rocky terrain in the central ‘hotspot’ area could have been an obstacle to both logging as well as grazing by domestic animals for thousands of years, which could explain the long-term prevalence of valuable *Quercus* trees there.

An increase in *Fagus* and *Carpinus* pollen, taxa which are often associated in southern Sweden with fire disturbance (Bradshaw and Lindbladh 2005), was observed at Sites A and C during this period (Figs. 3, 5). *Fagus* macrofossils were not recorded again until after the cessation of fire in the mid 1500s AD at Site A (Fig. 3) but were more varied and more plentiful in the central ‘hotspot’ area than at Site B (Fig. 4), where only sporadic leaf fragments were recorded. From both regional and local pollen data compilations, the southern hemi-boreal zone of Sweden appears to have been dominated by coniferous forests towards the end of this time period (Björse and Bradshaw 1998; Lindbladh et al. 2000), with *Picea* more prominent in the west and *Pinus* in the east. However, the stand scale pollen data from Site A reveals that there were some minor exceptions where deciduous trees were able to expand rapidly and regenerate freely due to the cessation of fire (Fig. 3).

Small increases in Poaceae, Cyperaceae and *Calluna* pollen percentages at Site A suggest some areas may have temporarily opened up in the central ‘hotspot’ area (Fig. 3). *Calluna* and *Juniperus* were still an important component of the forest at Site C (Fig. 5), where conditions were much more open there as a result of the continual fires seen in the sedimentary charcoal record, and probably more intensive use of the forests for livestock grazing. The fire scars in the tree ring record do not extend this far back in time, but two badly decayed *Pinus* stumps close to site C, with four to five scars from fires that had occurred between 20 and 40 year intervals, were located, that could be from some time in the 1400s–1600s AD (Niklasson et al. 2002).

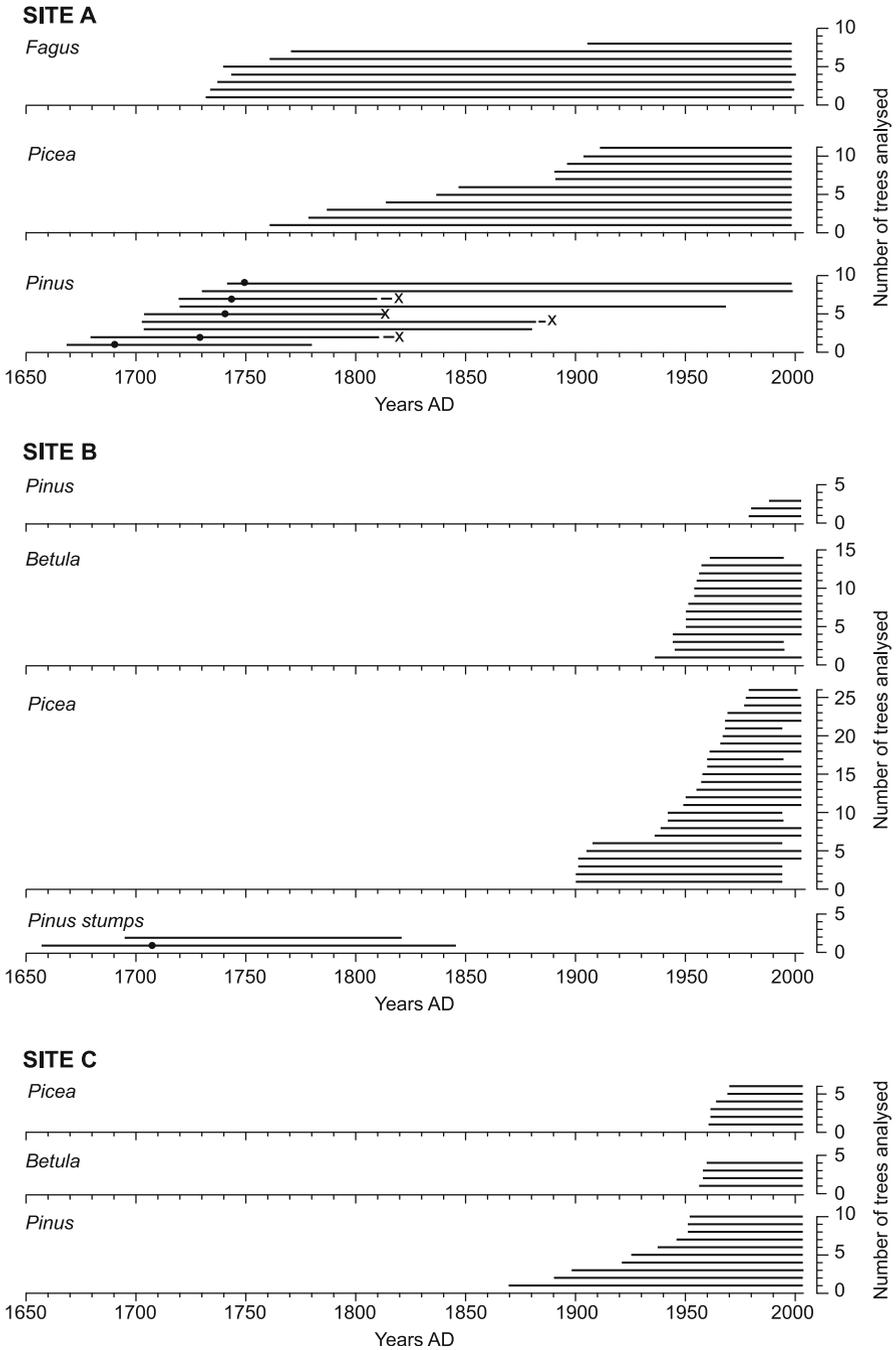
#### 1560–1800 AD

The plant macrofossil record shows that *Fagus* became securely established at Site A (Fig. 3) after the cessation of fire. *Fagus* is likely to have expanded from patches which had been protected from fire by the large boulders in the central area of the reserve,



**Fig. 6** Summary diagrams of selected taxa from all three sites scaled to the same age axis. Site A is after Björkman and Bradshaw (1996). The Y axis represents age and the X axis shows pollen percentages. The vertical lines represent the sub-division of the data into the four phases where major compositional changes are considered to have taken place over the last 2000 years

breaking up the ground layer and creating many small non-flammable areas. In the surrounding, more open forest, such protection was not afforded, as ground layer fuels were continuous and may have promoted the spread of fires. In the tree ring record, the oldest living *Fagus* individuals were established in the central ‘hotspot’ area c. 1730 AD



**Fig. 7** Germination of the major trees in the Siggaboda Nature Reserve from all three sites. Site A is after Niklasson et al. (2002). Each horizontal line represents one tree from each ‘age analysis area’ as illustrated on Fig. 1. The dots represent the fire scars on the *Pinus* stumps and X represents the date (or estimated date if on a dotted line), of cutting

(Fig. 7a). No living individuals were recorded at either of the buffer zone sites (Fig. 7b, c). While sparse macrofossil bracts were recorded at Site B, indicating some presence of this taxon until the 1700s AD (Fig. 4), fire disturbance continued to have an effect on vegetation composition at these sites and *Fagus* appears never to have established a stronghold there (Fig. 6b, c). The frequent fires and slash and burn activities may have prevented regeneration of this fire sensitive species.

Historical records from 1685 AD describe the Siggaboda estate as being mainly coniferous high forest, with some small *Quercus* stands (Legal, Financial and Administrative Services Agency (errand 99271834)). It seems that there were no large *Fagus* stands—just scattered beech trees in the area. *Fagus* was valuable and would have been mentioned in taxation records if it had been present in significant amounts. However, there were relatively large *Fagus* forests in the nearby Lönsboda area according to Weimarck (1953). A decline in *Quercus* pollen from the 1600s AD onwards was most marked at Site A, although it can be observed at the other two sites (Fig. 6). *Quercus* never appears to have been as prolific in the buffer zone forests as pollen values only hover around 5% throughout the pollen records there, whereas values of up to 30% are recorded in the central ‘hotspot’ Site A (Fig. 6). *Quercus* macroremains continued to be recorded at Site A until the 1800s AD but then disappear from the record (Fig. 3). This taxon is not present in the forest today. *Carpinus* pollen decreased at Site A (Fig. 3) as fire disturbance declined, but persisted in small numbers at the other two sites, where fire episodes continued to create open spaces (Figs. 4, 5). This taxon regenerates well after disturbance. Vast numbers of *Alnus*, *Betula* and *Fagus* macrofossils at Site A (Fig. 3), together with *P. sylvestris* seeds, suggests major post fire regeneration in what could have been temporarily partially open conditions, possibly after the fire in 1652, a summer with many tree-ring and historically documented extreme fires all over Sweden (Kohh 1975). This is supported by the tree ring results, which show that ten of the sampled *Pinus* stumps that had regenerated at several locations in the reserve, including the central ‘hotspot’ area, showed rapid initial growth, indicative of regeneration under open conditions (Fig. 7a).

Extensive logging of *Pinus* in the reserve took place towards the end of the 18th century as evidenced by the many *Pinus* stumps sampled (Fig. 7a). The fire scar record dated in some of these *Pinus* stumps in the core ‘hotspot’ area includes 11 fires between c. 1555 and 1748 AD (Niklasson et al. 2002), with a mix of small patchy burns and some larger fires. A fire scar from 1707 noted in the northern part of the reserve was recorded in a newly located *Pinus* stump at site B (Fig. 7b). Fires were set for primarily two reasons in the past: for improving grazing conditions and for slash-and-burn cultivation of turnips, grain or potatoes, including forest regeneration at a later stage. Five of the fire scars come from *Pinus* close to Site A between 1690 and 1750 AD, one of which records two fires at 1742 and 1747 AD. These are barely recorded in the sedimentary charcoal record from Site A (Fig. 3). Niklasson et al. (2002) have suggested that the possible disparity between the sedimentary charcoal record (>250  $\mu\text{m}$ ) (Fig. 3), and dated fire scars in the *Pinus* stumps (Fig. 6) could be because the sedimentary charcoal record has overlooked surface fires of low intensity or severity. The new macrocharcoal data (>500  $\mu\text{m}$ ) from Site A (Fig. 3), based on continuous and larger sample sizes (50  $\text{cm}^3$  of sediment per sample versus 0.2–0.4  $\text{cm}^3$ ), shows the same pattern as the earlier work (Fig. 3), so it is unlikely that undetected fires were a consequence of insufficient sampling or small sample size. The deposition of charcoal particles of this size is highly variable at these spatial scales (Ohlson and Tryterud 2000), and if a ground fire does not actually burn on the pollen site itself, sedimentary charcoal may not be deposited. Fire detection using sedimentary charcoal also depends on fire severity (Higuera et al. 2005). The sedimentary charcoal record from Sites

B and C, only 400 and 700 m away from Site A, indicates constant burning up until the 1800s AD, going some way to match the fire scar record. While slash-and-burn cultivation appears to have continued until the early 1900s in areas not far from Siggaboda, intentional burning for grazing is likely to have ended long before this (Larsson 1989; Niklasson and Nilsson 2005).

*Picea* macrofossil needles first recorded in the 1600s AD in the buffer zone forests (Figs. 4, 5) provide the first evidence that *Picea* was a natural, if minor, self-sown component there, which developed over many areas of south Sweden during this time period (Bradshaw and Lindbladh 2005). In the survey from 1867, the central part of the forest is recorded as containing old *Picea* and *Pinus* which were not cut due to difficulties of access, and that dead wood was common. We know from the pollen data that there must have been quite some *Fagus* in the core area in 1867, but the individual stand descriptions of the 1867 forest maps have been lost from the archives. If the ‘hotspot’ was the only area with *Fagus*, then it could have been too small to be mentioned in the written records available, which just give a short summary over the entire estate. However, on the 1867 map the ‘hotspot’ area is divided into stands no. 2-5 and separated from the rest of the forest, suggesting it was different. The pollen data is able to explain this, as higher incidence of deciduous trees.

In the tree ring record, the oldest *Picea* generation appears to have become established sometime after c. 1760s AD in the central area of the reserve (Fig. 7a), whereas in the buffer zone forests, the increase was seen towards the end of the 1800s AD (Fig. 7b, c). Expansion may have been locally held back by repeated slash-burn fires and once they ceased, this taxon expanded dramatically. The *Picea* macrofossil record from Site A dates from 1800 AD (Fig. 3), and is in agreement with the earlier pollen work suggested as representing rapid population expansion within a single generation (Björkman and Bradshaw 1996). The results from the buffer zone sites confirm that *Picea* was present in the surrounding forests from the 1500s, expanding into the central area in the 1800s AD. *Picea* was originally thought to expand into the central area without any obvious change in the disturbance regime (Björkman and Bradshaw 1996). The post fire expansion seen in the buffer zone sites with associated increased seed sources probably facilitated the spread of *Picea* into the old growth forest area at that particular time.

After the macrocharcoal peak in the mid 1550s AD, very little sedimentary charcoal was recorded at Site A (Fig. 3), but continued to be common in the extended reserve (Figs. 4, 5). A brief flush of ericaceous taxa and an almost continuous low representation by *Juniperus* and *Rumex* pollen at Site A has been suggested as evidence of some grazing and disturbance after the last major fire (Björkman and Bradshaw 1996). At Site C, the openness of the area increased around 1800 AD when shrub percentages fall and there is an increase in herbs together with the recovery of *Secale cereale* pollen (Fig. 5) when a farm may have become established in the area. The rocky nature of the central part of the reserve around Site A probably prevented cultivation.

#### 1800–2002 AD

The post fire increase in *Picea* pollen from c. 1800 AD together with a demise in deciduous taxa seen in all three pollen records (Figs. 3,4, 5) is consistent with the ending of fires in 1748 AD as seen in the dendrochronological record (Niklasson et al. 2002), and the sedimentary charcoal record from the pollen sites. A similar scenario has been recorded from sediments in Fiby forest in central Sweden (Hannon and Bradshaw 1992). The increase in *Picea* pollen resulted in a more uniform forest type in the buffer zone sites, with

a more marked presence of herbs (Figs. 4, 5) whereas in the central ‘hotspot’ area *Fagus* continued to be present although pollen percentages declined (Fig. 3). The recovery of so many *Pinus* and *Picea* macroremains in the upper reaches of the buffer zone sites (Figs. 4, 5) is the legacy of the large-scale planting/sowing programmes of the late 19th century. A low intensity logging period between 1880 and 1890 AD and cessation of grazing at marginal, low production sites were probably reasons for a new regeneration pulse of *Picea* observed in the tree ring record from Site A (Fig. 7a). At Site B, the forest was clearcut around 1880 AD, as seen in the interval between the two basal lines (*Pinus*) and a subsequent swift regeneration of *Picea* starting sometime just before 1900 AD (Fig. 7b). The expansion of *Picea* is roughly synchronous between diagrams, whereas the history of *Fagus* was not. This indicates local stand scale processes were more significant for this latter taxon. Macrofossils from *Fagus* were no longer recorded at Site B from c. 1700s AD onwards (Fig. 4).

In the historical records from 1879, foresters from the Swedish Forest Agency recorded in the National Archives that 568 misshapen and mostly rotten (ancient) *Quercus* were present at Siggaboda estate. However, the estate comprised ca 300 ha forest outside the present nature reserve, and we do not know the spatial distribution of these *Quercus*. Many of these *Quercus* may have been concentrated in the central, inaccessible part of the estate, not producing much pollen as they were probably dying. Eliasson and Nilsson (1999) claim that extensive felling and grazing of domestic animals is the reason why *Quercus* declined in southern Sweden in the 18th and 19th centuries. A forestry plan drawn up in 1909 by the Demesne Board (Fig. 2) sheds further light on the different forest units present at that time. The records close to Site A indicate that it was made up of c. 11 ha of 40% *Fagus* and 60% *Picea* (unit 62) (Fig. 2) whereas the forests surrounding pollen Sites B and C were made up of *Pinus* and *Picea* (Fig. 2). According to the management plan, a few 25 year old *Larix decidua* (Larch) were recorded just east of Site B (on the other side of the road) just a few metres from the sampling point, whereas 30 year old *Larix* were noted in units 52 and 53 close to Road 119. Some seeds of *Larix* were regularly mixed in with *Pinus* and *Picea* seeds during regeneration of the state owned forests during the 19th century (Mats Niklasson pers.comm) and a few *Larix* trees can still be found in the buffer zone forests. Interestingly, a *Larix* needle from around c. 1800 AD was found in the sediment from Site B.

The later continuous tree regeneration of *Picea*, *Betula* and *Pinus* in the buffer zone sites as seen in the dendrochronological record (Fig. 7b, c), could be as a result of the relaxation of grazing pressure, or the slight drying up of the wetland due to ditching or drainage, common in Siggaboda at the end of the 19th Century (Eliasson and Nilsson 1999), in addition to the planting programmes. At Site C, *Picea* are recorded in the tree ring record dating from the mid 1800s AD. On the wetland, there is a continuous slow regeneration of *Pinus* whereas *Picea* was more common on the mineral soil. Older *Pinus* stumps found at the site were too badly deteriorated to allow analysis. At Site B, *Picea* regenerates between 1900 and 1950 AD and the general pattern appears to be the same as in Site C with a transition from an open to rather dense forest without either *Fagus* or *Quercus*. By contrast, regeneration of *Fagus* and *Picea* are prominent at Site A (Fig. 7a) and *Pinus*, although present, has not regenerated successfully in the central ‘hotspot’ area of the reserve to date. The forest there has probably been too dark, with too few gaps large enough to allow *Pinus* regeneration. However, after the storm of 2005, some new gaps appeared in which some *Pinus* seedlings have become established, but competition is strong from *Betula* and *Picea*.

## Conclusion—conservation strategy

The long term perspective taken in this study has shown that the continuity of temperate deciduous trees in the central ‘hotspot’ area has been important biologically, because of their role as key substrates for many rare and endangered dependents (Jonsell et al. 1998). The central ‘hotspot’ area today is modified from a virgin state, but is closer to the original structure than the disturbed buffer zone forests and, more importantly, is source of biological diversity from both a floral and faunal point of view. *Fagus*, in the last 200 hundred years, has most likely taken over the biological role played by *Quercus* as a major host species for wood dependent organisms. Such a rather recent change of a foundation species has been recorded in other *Fagus* hotspots in southern Sweden, such as Torup (Hultberg et al. 2010) and Biskopstorp (Lindbladh et al. 2008). Relatively extensive forests of *Fagus* or *Fagus* mixed with *Pinus* existed in the 1700s AD, south of Siggaboda in the provinces of Skåne and Blekinge. Until that period, the populations at Siggaboda probably were a part of regional metapopulations. Most of these *Fagus* forests were cut in the late 1700s and early 1800s AD (Björnsson 1946, Weimarck 1953).

The multi-disciplinary approach taken in this work has allowed us to study long-term development of this ‘hotspot’ area in relation to the surrounding matrix forest, with a spatial and temporal resolution reaching far beyond the often scarce information from written historical sources. The temperate deciduous trees (either *Quercus* or *Fagus*) have been more common in the former for thousands of years, and much more so in the last c. 200 years. This is probably due to the broken terrain, which made fires rare, and logging difficult. The many rare species associated with temperate deciduous trees have been able to survive in the spatially limited ‘hotspot’ area when possibly the surrounding forests did not offer a suitable habitat. It is difficult to know if the low but continuous levels (2–6%) of pollen from *Quercus* and *Fagus* in the buffer zone sites, up to c. 1800 AD, mirror a large enough population of trees to harbour and facilitate spreading of the rare associated species between the ‘hotspot’ area and other *Quercus* and *Fagus* forests. If the levels have been high enough, the relatively short period of time of temperate deciduous trees in isolation (c. 200 years) could indicate that the rare dependent species in the ‘hotspot’ area run a high risk of becoming extinct when today’s oldest generation of *Fagus* trees die. If there are no replacement trees close enough for dispersal, there may be a so called “extinction debt” (cf. Hanski et al. 1996). However, if the deciduous tree populations in the buffer zone sites have not been high enough to harbour the rare associated species, the ‘hotspot’ may have been isolated for up to 2000 years.

Our data suggest that a rich biodiversity can persist in isolated areas as small as 5–10 ha for two centuries or longer. The vast majority of old-growth remnants (key habitats) in southern Sweden and elsewhere in temperate Europe are of a similar size and usually embedded in a matrix of plantation forests. Our data indicate that protection of these small remnants is worthwhile and that they may retain their biological values until restoration measures in the surrounding forests provide additional habitat for epiphytic and saproxylic specialist species. *Fagus* trees and structures connected to old *Fagus* trees which benefit biodiversity should therefore be promoted in both the reserve and the buffer zone forests. Structures and species from the ‘hotspot’ area should be encouraged to spread into buffer zone forests. Active encouragement of host deciduous trees for threatened dependent species is pertinent both to maintain the ‘hotspot’ and to increase the biodiversity of the extended reserve. The ‘hot spot’ represents perhaps the only example of an almost completely unmanaged forest stand in this region and as such, is a valuable reference area. This is of importance in understanding forest adaptation to climate change. The forest structure

and composition in the ‘hotspot’ area is an example of what ‘close-to-nature’ forestry might aspire to in southern Sweden.

**Acknowledgements** We thank Richard Bradshaw, Shinya Sugita and two reviewers for valuable comments and corrections. Thanks also go to the Swedish Environmental Protection Agency, for a research grant as part of the Conservation Chain research programme and to Sandra Mather (Geography Department, Liverpool University, UK) for drafting the figures.

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