# The Long-Term History of Temperate Broadleaves in Southern Sweden

Tove Hultberg
*Faculty of Forest Sciences*
*Southern Swedish Forest Research Centre*
*Alnarp*

Doctoral Thesis
Swedish University of Agricultural Sciences
Alnarp 2015

Acta Universitatis agriculturae Sueciae
2015:12

Cover: Autumn in Dalby Söderskog, southernmost Sweden (photo: T. Hultberg).

ISSN 1652-6880
ISBN (print version) 978-91-576-8222-2
ISBN (electronic version) 978-91-576-8223-9

Print: SLU Repro, Alnarp 2015

# The Long-Term History of Temperate Broadleaves in Southern Sweden

## Abstract

Temperate broadleaves used to be abundant in the primeval forests in southern Sweden, yet today they cover only fractions of the forest land. Considering the present small area of the forest type, the habitat is of considerable interest for biodiversity, and knowledge about the history of temperate broadleaves is crucial for forest conservation and management. The main method used for studying past forest composition is pollen analysis, yet differences in pollen production and dispersal among taxa have hampered the estimation of historical cover of temperate broadleaves. By applying the Landscape Reconstruction Algorithm (LRA), a new model for translating pollen data into quantitative cover estimates, significantly improved understanding of the vegetation cover can be gained.

The applications of the LRA to local and regional pollen data from southern Sweden carried out in this thesis show that in many areas, large cover of temperate broadleaves prevailed locally until rather recently, which is likely to be an important cause for the survival of the many threatened species associated with these tree taxa today, although in small and vulnerable populations. Many of our study sites showed no tendencies of local decline of temperate broadleaves until during the most recent 500 years, which is considerably later than in the region as a whole, as well as what has often been emphasized in other studies. For *Tilia*, the cover of which has confounded researchers since the introduction of pollen analysis, the decline in the southernmost parts of the country was not as early as commonly thought, but in general almost as recent as for many other temperate broadleaves.

In this thesis it is also shown that in many presently protected biodiversity hotspots the forest composition changed radically during the last 500 years, and hence not even these hotspots can be claimed to have unbroken continuity back to ancient forests, or to be a reflection of “natural” forest in southern Sweden. Land use changes, such as forest clearance for agricultural purposes, as well as grazing and browsing by domestic animals are likely to have been important causes for this vegetation change.

*Keywords:* Temperate broadleaves, southern Sweden, pollen analysis, the Landscape Reconstruction Algorithm, human impact, the Holocene, forest grazing, threatened forest species.

*Author’s address:* Tove Hultberg, SLU, Southern Swedish Forest Research Centre,
P.O. Box 49, 230 53Alnarp, Sweden
*E-mail:* Tove.Hultberg@ slu.se

For Pehr, who taught me that flowers have names.

> There remains the incredibly tedious task of examining tens of thousands of pollen grains in the column under a microscope, counting them, and then identifying the plant species producing each grain by comparison with modern pollen from known plant species.
>
> (Diamond 2005)

# Contents

# List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Hultberg T., Brunet J. Broström A. and Lindbladh M. (2010). Forest in a cultural landscape – the vegetation history of Torup in southernmost Sweden. *Ecological Bulletins* 53:141-153.

II Hultberg T., Gaillard M.-J., Grundmann B. and Lindbladh M. (in press) Reconstruction of past landscape openness using the Landscape Reconstruction Algorithm (LRA) applied on three local pollen sites in a southern Swedish biodiversity hotspot. Accepted for *Vegetation History and Archaeobotany*; http://link.springer.com/article/10.1007/s00334-014-0469-8

III Hultberg T., Sallnäs O., Hannon, G. E. and Lindbladh M. Different for how long? A study of long-term forest continuity and tree species composition in four protected forests in southern Sweden (manuscript).

IV Hultberg T., Lagerås P., Björkman L., Sköld E. and Lindbladh M. Past dynamics of *Tilia* in southern Sweden: Driving forces underlying population declines during late Holocene (manuscript).

Papers I-II are reproduced with the permission of the publishers.

The contribution of Tove Hultberg (TH) to the papers included in this thesis was as follows:

I TH did 40% of the planning, 70% of the sampling, 60% of the analysis and 50% of the article writing.

II TH did 50% of the planning, 60% of the sampling, 60% of the analysis and 60% of the article writing.

III TH did 30% of the planning, 90% of the sampling, 70% of the analysis and 60% of the writing.

IV TH did 40% of the planning, 100% of the sampling, 70% of the analysis and 70% of the article writing.

# Abbreviations

| | |
|---|---|
| BP | Before Present |
| ERV | Extended R (ratio) Value |
| HTM | Holocene Thermal Maximum |
| KNN | k Nearest Neighbour |
| LOVE | LOcal Vegetation Estimates |
| LRA | Landscape Reconstruction Algorithm |
| NFI | National Forest Inventory |
| PPE | Pollen Productivity Estimates |
| REVEALS | Regional Estimates of VEgetation Abundance from Large Sites |
| RSAP | Relevant Source Area of Pollen |

# 1 Introduction

## 1.1 Temperate broadleaves in southern Sweden

Temperate broadleaved forest is considered to have dominated large parts of Europe during most of the Holocene (Iversen 1964, 1973, Birks et al. 1975). In southern Sweden today, temperate broadleaves in contrast constitute only around 7% of the tree volume on productive forest land (Official Statistics Sweden 2014). Temperate broadleaves comprise more than half of the tree species considered indigenous in Sweden, most of which are however extremely rare in natural habitats today. The by far most common genera of temperate broadleaves today are *Fagus* and *Quercus*, both most abundant in the temperate zone in the southernmost parts of the country (Swedish Forest Agency 2005).

### 1.1.1 Biodiversity of temperate broadleaves

Considering the small area covered by temperate broadleaves today, the habitat type is of considerable value for biodiversity, but it also has cultural - as well as amenity values (Bengtsson 2005, Sjöman et al. 2012). Among red-listed forest organisms in Sweden, more than half are associated with temperate broadleaved forests (Berg et al. 1994, 1995, Gärdenfors 2010). The two tree taxa with the most associated saproxylic invertebrates (which is one of the largest groups of threatened forest organisms) are both temperate broadleaves; *Quercus* sp. and *Fagus sylvatica* (Jonsell et al. 1998, Larsson et al. 2011).

Also *Tilia*, which is considered to have been abundant in the primeval forest, yet is rarely found in the wild today, has more specialized species associated with it than many other tree taxa (Jonsell et al. 1998, Jonsell and Andersson 2011). This mismatch between habitat occurrence and number of associated species has been suggested to be due to a larger historical distribution of temperate broadleaves (Berg et al. 1995).

Today there is a general acceptance of the importance of areas' long-term ecological history for the understanding of present biodiversity (Foster 2002, Willis and Birks 2006, Willis et al. 2007, Lindbladh et al. 2013), as contemporary forests provide very limited indications concerning long-term tree species composition in northern Europe (Lindbladh et al. 2013). Temperate broadleaved forests are among the most disturbed natural ecosystems globally (Hannah et al. 1995) and using longer time perspectives could therefore be illuminating in order to understand more natural conditions of these forests (Froyd and Willis 2008, Dietl and Flessa 2011).

## 1.2 Paleoecology in the study of temperate broadleaves

The study of past landscapes and ecosystems is known as paleoecology, which is closely related to geology, biology and botany, as well as to history and archaeology (Birks and Birks 1980, Gaillard 2000). A unique benefit of paleoecology as compared to neo-ecology is the time perspective, as it enables identification of phenomena beyond timescales of direct human experience, which might only correspond to one or two tree generations (Mitchell 1998).

The palaeoecological method most commonly used to identify changes in tree species composition is pollen analysis. This method makes use of the fact that pollen, which is released in large amounts from most flowering plants, can be preserved in natural anaerobic environments such as peat mosses or lakes (Seppä 2007). The deposit studied by a paleoecologist has been described as a type of permanent plot, or an automatic sampling device, which has been collecting data for thousands of years (Jacobson 1988), and such natural archives have been used to study vegetation developments since the early 20th century (Hesselman 1916, von Post 1916).

### 1.2.1 From pollen proportions to forest cover

Modern pollen studies have largely confirmed the earlier notion that temperate broadleaves, apart from the late arrival *Fagus*, used to be considerably more abundant in the past in southern Sweden (Berglund 1991, Björkman 1996a, b, Björkman and Bradshaw 1996, Björse and Bradshaw 1998, Lindbladh et al. 2000, Lindbladh et al. 2008, Lindbladh and Foster 2010).

However, the study of the past cover of temperate broadleaved forest, which includes a broad spectrum of taxa, has been severely hampered by the very different properties of the plant taxa concerning pollen production and dispersal. These differences have been known since the introduction of pollen analysis (Hesselman 1916) and have affected our understanding of the land area covered by a certain taxa or vegetation type, as the pollen proportions in the deposit do not equal the vegetation producing it.

Whereas studies from the mid-20th century often focused on the impact of climate fluctuations (von Post 1946, Fries 1965, Iversen 1973), more recent publications emphasized also the importance of land use changes, such as clearance for cultivation and/or grazing (Rackham 1980, Thelaus 1989, Bradshaw et al. 1994, Lagerås et al. 1995, Lagerås 1996, 2000, Lindbladh et al. 2000, Björkman 2002). Early detailed demonstrations of the impact of prehistoric people on vegetation in Scandinavia were carried out in the 1940’s, by Johannes Iversen (1941), but the interaction of humans and their environment is still among the priority research questions in paleoecology (Seddon et al. 2014). However, because many of the open land plant species, including grasses and cereals, produce comparatively little pollen and therefore are underrepresented in the pollen spectra, grazing by domestic animals and other agricultural activities are difficult to interpret using pollen percentages only (Vera 2000, Bunting et al. 2004, Sugita 2007a, b, Smith et al. 2010, Trondman et al. 2014).

### 1.2.2 Modern land cover reconstructions

A recently introduced method to quantify pollen data into more robust vegetation reconstructions is the Landscape Reconstruction Algorithm (LRA) (Sugita 2007a, b). The LRA has been validated in different parts of the world and in different landscapes, and has proven to facilitate reliable vegetation cover estimates for southern Sweden, both on a regional and local scale (Hellman et al. 2008, Fredh et al. 2012, Cui et al. 2013).

By using pollen data from multiple small sites in southern Sweden and by applying the LRA, it is possible to gain a considerably better picture of the cover of temperate broadleaves at different points in time, as well as the general landscape development including agricultural practices. Furthermore, the more reliable estimates of vegetation cover provide better precision when studying the establishment and/or extinction of plant taxa; especially in the case of taxa with low pollen production, such as *Tilia*, as the probability of finding pollen from small populations of these taxa is low. The same is true for cereals and several other open land taxa and taxa indicative of anthropogenic activities. Hence, small populations might be overlooked in conventional pollen diagrams and therefore earlier conclusions of the timing of establishment or extinction may be faulty. Using the vegetation cover estimates provided by the LRA, also small populations can be studied with a considerably better precision.

## 1.3 Objectives

The main objective of this thesis was to increase the knowledge about the development of temperate broadleaved forest in southern Sweden in a perspective of 5000 years. Specifically, my research aimed to assess the following issues:

- What can be learned about the cover of temperate broadleaves in southern Sweden during the last 5000 years, by using multiple sites and the vegetation cover estimates provided by the Landscape Reconstruction Algorithm?
- Today many protected forests in southern Sweden harbour large amounts of temperate broadleaves compared to the region as whole. Is this a pattern which has distinguished the presently protected areas also in a time perspective of thousand years or longer?
- Climate is the most important driver of vegetation distribution on a continental scale, but what impact did land-use changes have on temperate broadleaves in different parts of the studied region and during different time periods?
- During the studied 5000 years, climate deteriorated and human impact on vegetation increased. How did *Tilia*, which has been suggested to be sensitive to both, as well as indicative of original forest, develop during this period?

# 2 Methods

## 2.1 Temperate broadleaves

In Sweden, temperate broadleaves include the indigenous species *Acer campestre* (field maple), *Acer platanoides* (Norway maple), *Carpinus betulus* (hornbeam), *Fagus sylvatica* (beech), *Fraxinus excelsior* (ash), *Prunus avium* (wild cherry), *Quercus robur* (pedunculate oak), *Quercus petraea* (sessile oak), *Tilia cordata* (small-leaved lime), *Tilia platyphyllos* (large-leaved lime), *Ulmus glabra* (wych elm), *Ulmus minor* (small-leaved elm) and *Ulmus laevis* (European white elm), several of which are extremely rare in natural habitats today (Almgren et al. 2003). Temperate broadleaves are distinguished from boreal broadleaves such as *Betula* sp. (birch), *Populus tremula* (aspen) and *Salix* sp. (sallow) mainly by their more southern geographical distribution (Diekmann 1994). Although it is not traditionally considered a temperate broadleaved tree in Sweden due to its shrub-like stature (Almgren et al. 2003), also *Corylus avellana* (hazel) is included here based on its distribution in Sweden, which is very similar to that of *Quercus* (Hultén 1971).

Temperate broadleaved forest is defined by Swedish law as forest covering ≥ 0.5 ha forest land, where ≥ 70% of the basal area consists of broadleaves, > 50% of which are temperate broadleaves, or ≥ 1 ha of forest land using the same composition but occurring on grazed land (Swedish Foresty Act 1979).

## 2.2 Study area

All study sites used in this thesis are located in southernmost Sweden (fig 1). Three sites per area (the areas being the protected areas Biskopstorp, Råshult, Siggaboda and Hornsö-Allgunnen) were used in order to study local differences in vegetation development using LRA reconstructions. The use of several sites provides better spatial resolution of vegetation cover (Hjelle et al. 2012), and is also an important feature of the LRA. The large lakes used for the

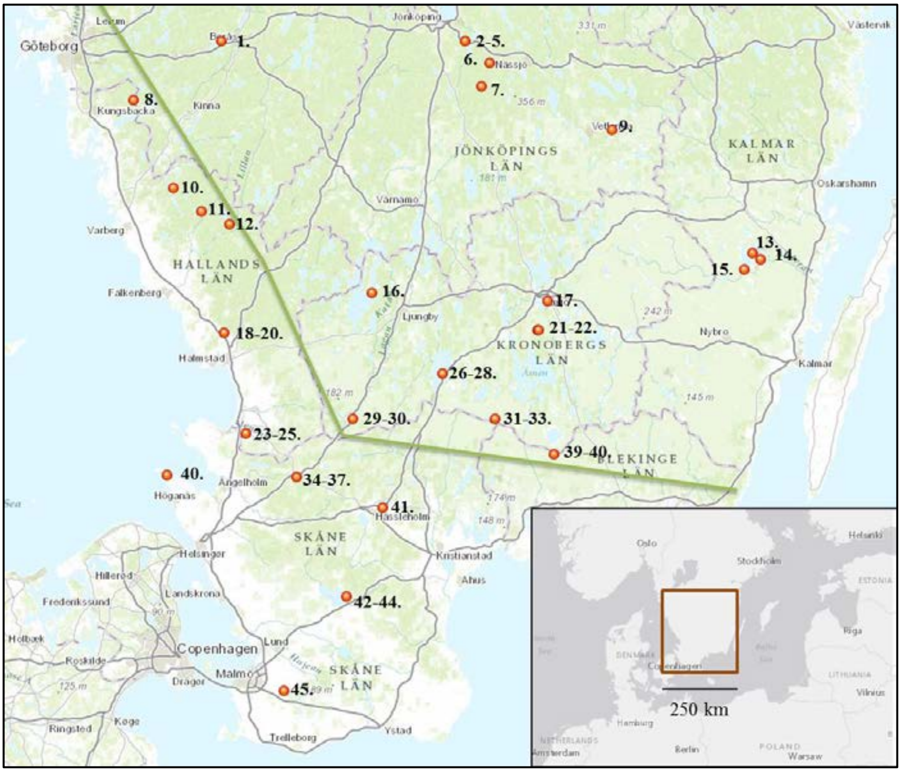

*Figure 1.* Location of the studied sites in southern Sweden, and the studied region in a northern European perspective. The numbers correspond to the sites in table 1, and the green line roughly to the border between the temperate (southwest) and the hemi-boreal (northeast) vegetation zones.

reconstruction of regional vegetation by the LRA are Lake Sämbosjön, Lake Trummen and Lake Kansjön (fig. 1, table 1).

Although each pollen study has a specific and unique focus, the compilation of data from multiple formerly used sites provides an opportunity to explore also other vegetation patterns than the study was originally designed for (Mitchell 2010). In Paper II and III, data from several formerly published sites was included in the LRA reconstruction of vegetation on both local and regional scales (table 1). For Paper IV, pollen data from even more sites were compiled, and altogether 42 small sites in southern Sweden were analysed in order to gain better understanding of the development of *Tilia* (table 1).

Table 1. Pollen sites used in the thesis, and their respective original reference, site type, vegetation zone and paper.

| Nr. | Site name | Original publication | Site type | Vegetation zone | Paper |
|---|---|---|---|---|---|
| 1. | Hestra | Björkman and Regnell (2001) | Small peatbog | Hemi-boreal | IV |
| 2. | Öggestorpsdalen | Björkman (2003a) | Small peatbog | Hemi-boreal | IV |
| 3. | Avegöl | Lagerås (1996) | Small lake | Hemi-boreal | IV |
| 4. | Bråtamossen | Lagerås et al. (1995) | Peatbog | Hemi-boreal | IV |
| 5. | Rogberga | Björkman (2003a) | Fen | Hemi-boreal | IV |
| 6. | Lake Kansjön | Cui et al. (2013) | Large lake | Hemi-boreal | II |
| 7. | Mattarp | Björkman (1996a) | Small peatland | Hemi-boreal | IV |
| 8. | Store mosse | Björkman (2003a) | Peatbog | Temperate | IV |
| 9. | Alseda | Björkman (2001a) | Small peatbog | Hemi-boreal | IV |
| 10. | Lake Sämbosjön | Digerfeldt (1982) | Large lake | Temperate | III |
| 11. | Bocksten A | Björkman (1996a) | Very small fen | Temperate | IV |
| 12. | Yttra Berg | Sköld et al. (2010) | Peatbog | Temperate | IV |
| 13. | Lillegölen | Paper II | Peat bog | Hemi-boreal | II,III,IV |
| 14. | Skärsgölarna | Lindbladh et al. (2003) | Small peatland | Hemi-boreal | II,III,IV |
| 15. | Ekenäs | Valdemardotter (2001) | Peat land | Hemi-boreal | II,III,IV |
| 16. | Flahult | Björkman (1996a) | Small peatland | Hemi-boreal | IV |
| 17. | Lake Trummen | Digerfeldt (1971) | Large lake | Hemi-boreal | II,III,IV |
| 18. | Trälhultet | Björkman (2000b) | Small peatland | Temperate | III,IV |
| 19. | Holkåsen | Lindbladh et al. (2008) | Peatland | Temperate | III,IV |
| 20. | Kalvaberget | Lindbladh et al. (2008) | Peatland | Temperate | III,IV |
| 21. | Osaby in-field | Lindbladh (1999) | Small peatland | Hemi-boreal | IV |
| 22. | Osaby out-field | Lindbladh (1999) | Small peatland | Hemi-boreal | IV |
| 23. | Baggabygget | Björkman (2005) | Very small fen | Temperate | IV |
| 24. | Dömestorp | Björkman (2002) | Peatland | Temperate | IV |
| 25. | Uddared | Björkman (2000a) | Small bog | Temperate | IV |
| 26. | Råshult | Lindbladh and Bradshaw (1995) | Small peatland | Hemi-boreal | III,IV |
| 27. | Nissatorpet | Lindbladh and Bradshaw (1998) | Peatland | Hemi-boreal | III,IV |
| 28. | Djäknabygd | Lindbladh and Bradshaw (1998) | Small peatland | Hemi-boreal | III,IV |
| 29. | Skogshyddan | Björkman (2003b) | Peatbog | Hemi-boreal | IV |
| 30. | Exhult | Björkman and Ekström (2003) | Large peatbog | Hemi-boreal | IV |
| 31. | Ellabrohult | Hannon et al. (2010) | Small peatland | Hemi-boreal | III,IV |

| | | | | | |
|---|---|---|---|---|---|
| 32. | Siggaboda/<br>Siggaboda core | Björkman and Bradshaw (1996) | Small peatland | Hemi-boreal | III,IV |
| 33. | Crossroads/<br>Siggaboda crossroads | Hannon et al. (2010) | Small peatland | Hemi-boreal | III,IV |
| 34. | Flinkasjön | Björkman (2004) | Lake | Temperate | IV |
| 35. | Grisavad | Lagerås (2007) | Peatbog | Temperate | IV |
| 36. | Östra Ringarp | Lagerås (2007) | Recently overgrown small lake | Temperate | IV |
| 37. | Bjärabygget | Lagerås (2007) | Large peatbog | Temperate | IV |
| 38. | Västragylet | Björkman and Sjögren (2003) | Small lake | Hemi-boreal | IV |
| 39. | Ire | Björkman and Sjögren (2003) | Small peatland | Hemi-boreal | IV |
| 40. | Kullaberg | Björkman (2001b) | Small peatland | Temperate | IV |
| 41. | Skeakärret | Lagerås (2002) | Small peatland | Temperate | IV |
| 42. | Häggenäs | Lindbladh et al. (2007) | Small peatland | Temperate | IV |
| 43. | Vasahus | Lindbladh et al. (2007) | Small peatland | Temperate | IV |
| 44. | Kyllingahus | Lindbladh et al. (2007) | Small peatland | Temperate | IV |
| 45. | Torup | Paper I | Very small peatland | Temperate | I,IV |

### 2.2.1 Vegetation zones

Two main vegetation zones dominate southern Sweden (fig. 1); the temperate zone (also known as the nemoral zone or the southern deciduous forest region) in southernmost and south-western Sweden, and the hemi-boreal (or boreo-nemoral) zone in the north-eastern parts, as defined by Sjörs (1965). The two zones are not physically delimited, but their classification is based on a combination of factors, such as the regional climate, physiogeography, and the flora and fauna (Sjörs 1965, Ahti et al. 1968, Aldentun 1997).

## 2.3 Pollen analysis

Angiosperms (flowering plants) dominate the vegetation of most terrestrial ecosystems and consist of roughly 250,000 – 300,000 extant species worldwide, more than all other land plants combined (Crane et al. 1995). Pollen is the male sexual reproduction organ of angiosperms, and the individual pollen grains are very small (0.015-0.100 mm), but have relatively distinct shapes and surface structures (fig. 2) (Seppä 2007).

The cell walls of living pollen grains are made of two layers; an outer layer (exine) consisting of sporopollenin and an inner layer (intine), made of cellulose and very similar in construction to an ordinary cell wall. Whereas the intine decomposes soon after the pollen grain dies, the very resistant exine with its characteristic form and sculpture can remain for significant amounts of time (Moore et al. 1991). The resistant nature of the exine is taken advantage of in the laboratory treatment in order to remove as much other material as possible from the samples; organic material is removed using sodium hydroxide (NaOH) and acetolysis (acetic anhydride $(CH_3CO)_2O$ + sulphuric acid $H_2SO_4$), and mineral material is removed using hydrofluoric acid (HF) (Berglund and Ralska-Jasiewiczowa 1986).

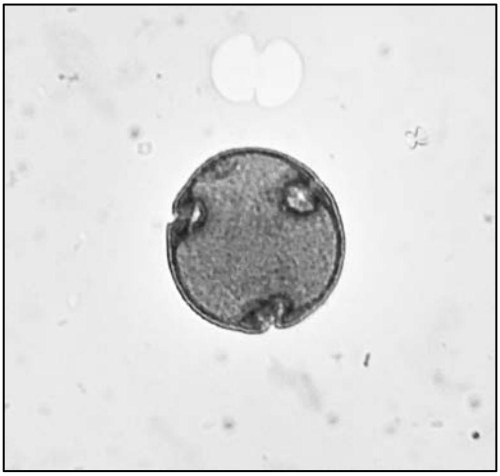

*Figure 2. Tilia* pollen grain. Photo: Fredrik Olsson, photo editing: Lina Hultberg

In the late 19th century, bogs became a focus of interest in Scandinavia in order to study changes in climate over time, using pollen (micro fossils) and other parts of plants, such as leaves, flowers or buds (macro fossils) (Blytt 1886). This interest was soon widened to comprise also the study of vegetation development (Sernander 1908, von Post 1916). In the early 20th century, pollen analysis was revolutionized by the Swedish geologist Lennart von Post (fig. 3) by introducing pollen diagrams, and his dissertation in 1916 is usually seen as the start of pollen analysis, or palynology, as a method for reconstructing past landscapes (Traverse 1988). Pollen analysis provides a proxy for vegetation communities on spatial scales from continental biomes to forest stands (Mitchell 2010), and temporal spectra from the extinction of dinosaurs 65 million years ago (Vajda et al. 2001) to studies of the last few centuries with a temporal resolution of decades (Fredh et al. 2012).

*Figure 3.* Lennart von Post during the recovery of Bulverket, a wooden fortification at the bottom of Lake Tingstäde träsk, Gotland, Sweden. Photo: Ture J. Arne 1927, from the National Heritage Board archive. Expired copyright.

## 2.4 Quantitative vegetation reconstructions

Despite the benefits of conventional pollen analysis, the results of it do not simply equal the vegetation that once produced the pollen. The most fundamental reason for the mismatch between pollen proportion and vegetation cover is connected to the fact that all plant taxa do not produce equal amounts of pollen. The pollen production is greatly dependent on the dispersal strategy of the plant, and plants relying on pollen dispersal by animals typically produce considerably less pollen than plants adapted to wind-pollination (Faegri and Iversen 1989).

The problem of overcoming these differences and translating pollen data into quantitative vegetation reconstructions is as old as palynology itself (Hesselman 1916, von Post 1916). However, the effort on identification of pollen taxa during the 1930s and 1940s gave rise to intense analytical work (Kristiansen 2002), and in the mid-20th century several researchers started renewed work on the matter of translating pollen percentages into vegetation shares (Erdtman 1946, Anonymous 1947, Fagerlind 1952). Davis (1963), suggested R-values (R for ratio) by comparing the pollen percentage in modern lake sediment to the percentages of different tree taxa in the surrounding forest in Vermont, US. Several refinements of the approach was presented (Andersen 1970, 1973) and with time the model was transformed into the Extended R-values (ERV) model (Parsons and Prentice 1981, Prentice and Parsons 1983) also known as the Prentice-model. The Prentice-model was from the early 1990s onwards extended into the Prentice-Sugita model.

### 2.4.1 The Landscape Reconstruction Algorithm

A more recent tool is the Landscape Reconstruction Algorithm (LRA), developed by Sugita (1993, 2007a, b). This is an approach which uses the various ERV models, as well as an adaptation of the R-value model and other concepts. The LRA is a multistep framework for quantitative reconstruction of vegetation. It consists of two models; REVEALS (Regional Estimates of VEgetation Abundance from Large Sites) and LOVE (LOcal Vegetation Estimates). REVEALS estimates regional vegetation composition within $10^4$-$10^5$ $km^2$ using pollen from large lakes, i.e. lakes ≥ 100-500 ha in size (Sugita 2007a). In the regional vegetation reconstructions presented in this thesis (Paper II-IV), 1-2 large lakes were used. This is sufficient for the application of the LRA, yet even more robust estimates would have been obtainable if more lake records had been available.

These reconstructions in turn are used in the application of the LOVE model (Sugita 2007b) together with pollen data from small sites to calculate the background pollen, the RSAP (Relevant Source Area of Pollen) of these small sites and estimate local vegetation cover within this RSAP.

A benefit of using formerly published pollen records is that considerably more sites can be used than would otherwise be possible. A downside is that studies are rarely carried out in exactly the same way. Common variations are the number of pollen levels (subsamples extracted from the sampled sediment core), the number of radiocarbon dated subsamples used for age determination, and differences in pollen counts (i.e. how many pollen grains were counted at each level). The LRA can be applied to samples of low pollen counts, but the result will be less reliable and often have large standard errors. The same is true for individual taxa with low pollen counts (such as Cerealia in many studies, e.g. Paper III).

The LRA is still experimental, but REVEALS and/or LOVE have been validated in Michigan and Wisconsin, US (Sugita et al. 2010), Denmark (Nielsen and Odgaard 2010), Switzerland (Soepboer et al. 2010) and southern Sweden (Hellman et al. 2008, Cui et al. 2013, Cui et al. 2014a). In order to estimate the vegetation cover, several important parameters are required, such as pollen production estimates (PPE) and fall speed. Both are assumed to be constant through time (Sugita 2007a, b, Sugita et al. 2007), yet PPEs can differ between geographical regions (Mazier et al. 2012). Other factors influencing the PPE is the age at which trees start to flower, as well as the structure and light conditions in the forest (Matthias et al. 2012). Examples of taxa known to produce little or no pollen in shaded forest conditions are *Corylus*, *Quercus* and *Tilia* (Pigott 1991, Vera 2000).

In the following text, proportions of taxa based on pollen percentages will be referred to as such, whereas vegetation proportions as estimated by the LRA will be referred to as vegetation cover.

## 2.5 Site selection

When selecting a study site, a rule of thumb is that the larger the wetland, the larger the terrestrial surroundings reflected (Jacobson and Bradshaw 1981). The majority of the studied sites in this thesis (fig. 1, table 1) were chosen in order to reflect local forest conditions in southern Sweden (fig. 4), and are hence small sites, mainly so called small forest hollows. Small forest hollows is not an exact definition, but usually refers to wetlands of ≤ 1 ha (Overballe-Petersen and Bradshaw 2011), in opposite to e.g. larger wetlands, or lakes such as the ones used to reflect the regional vegetation in Paper II, III and IV.

*Figure 4.* Sampling of the wetland Lillegölen using a Wardenaar sampler, 2009. Photo: Matts Lindbladh.

The surrounding reflected by a certain wetland is commonly known as the "pollen source area" (Jacobson and Bradshaw 1981) or the "Relevant Source Area of Pollen" (RSAP) (Sugita 1994, Sugita et al. 2007), which is the area beyond which the pollen-vegetation correlation does not improve. The pollen proportion is inversely proportional to the distance from the source (Janssen 1972) and despite that fairly large shares ($\geq 50\%$) of the pollen can come from outside the RSAP in a small forest hollow, the pollen proportion within the RSAP is sufficient to record the stand scale vegetation heterogeneity (Sugita 1994, Calcote 1995).

## 2.6 Charcoal analysis

Fire is an important ecological function able to affect vegetation in a wide range of ecosystems (Finsinger et al. 2014). One direct method of estimating fire frequencies in the past is by charcoal analysis. The charcoal fragments can be extracted by soaking the sampled sediment in sodium hydroxide (NaOH) overnight and sieving the remains. The findings are usually separated into macrocharcoal (>0.5 mm) and microcharcoal (0.15-0.5 mm). Most techniques quantify charcoal as either the total number of pieces or the surface area ($mm^2$) of charcoal in a particular age class (Higuera et al. 2010). Charcoal analysis using the total number of macrocharcoal pieces was used in Paper I.

## 2.7 kNN

kNN Sweden are spatially explicit countrywide estimates of forest attributes derived from satellite images and National Field Inventory (NFI) data (Reese et al. 2002, Reese et al. 2003). The datasets owe their names to the estimation algorithm used – *k Nearest Neighbour* (kNN). In average, some 1250 NFI plots (6-years' time span) are used in the estimation of one satellite scene (Reese et al. 2003). The size of pixels is 25*25 meters, and the estimated attributes are standing wood volume by tree species, mean stand age, height and total biomass.

The method is rather new, but has already been used in ecological research (Lindbladh et al. 2011a) as well as for the Swedish National Forest Inventory (2014). In Paper III, kNN is used to estimate the present vegetation of the studied protected areas, as well as the regional vegetation of southern Sweden.

## 2.8 Radiocarbon dating

The most common method for absolute dating of organic material younger than 50,000 years is radiocarbon dating. The method was developed in the 1940's and is based on the fact that all living organisms absorb carbon dioxide from the atmosphere (Bowman 1990). The carbon in the carbon dioxide occurs in three isotopes, one of which ($^{14}C$) occur in extremely low proportions compared to the other two, yet deviates from them by being weakly radioactive and decays to $^{14}N$ with a half-life of 5570±30 years (Walker 2005).

In principle, the $^{14}C$ formation and decay is in equilibrium in all living organisms, yet when an organism dies and ceases to take up carbon dioxide, $^{14}C$ decays, and no new $^{14}C$ is absorbed (Bowman 1990). How much $^{14}C$ is left in relation to $^{12}C$ at a certain point in time is hence a measure of the time elapsed since the organic matter died (Andréasson 2006). Today the Accelerator Mass Spectrometry (AMS) technique, which detects the specific elements and hence requires considerably smaller samples, is readily used (Bowman 1990). All ages in Paper I-IV are based on radiocarbon datings, and in the pollen studies original to this work (in Paper I and III), AMS dating technique is used.

Since the $^{14}C/^{12}C$ ratio has not been stable through time, radiocarbon years need to be calibrated into calendar years (Olsson 1986, Walker 2005, Andréasson 2006). Different methods of calibration can be used. The ones used here is Oxcal (Ramsey 1995, Ramsey and Lee 2013) (Paper I) and Clam (Blaauw 2010) (Paper II-IV). The total uncertainty of the dating is dependent not only on the uncertainty in the age determination and possible contamination, but to a large extent also on the precision of other measurements, such as the distance between samples in a core. The resultant radiocarbon years are given with $\pm\sigma$ statistical certainty (Olsson 1986) and presented in years before present (BP). This "present" is however not moving forwards as time passes, but is set to 1950 (Walker 2005).

## 2.9 Other possible methods for studying past vegetation changes

In this thesis, mainly forest composition and cover of different species in a time perspective of 5000 years were studied, using pollen data and LRA vegetation reconstructions. However, also plant macro fossils such as leaves, flowers or buds, as well as stomata from coniferous needles could have been used for the study of long-term forest composition (Hannon 1999, Ammann et al. 2014). The area reflected by these methods is however considerably more local than using pollen, and there are presently no methods for converting such data into vegetation cover.

Fossil beetle remains is another possible proxy for past tree species distribution (Whitehouse and Smith 2010), and the technique can also be used for studying qualitative aspects of forests, such as tree size, tree age and stages of decay, as many beetle taxa have very specific habitat requirements (Jonsell et al. 1998, Dahlberg and Stokland 2004). Analysis of fossil beetle remains was tested within the frame of this doctoral project, yet proved to require substantial amounts of sediment, as well as very specific skills in beetle species identification, and was therefore not possible to fit into the present work.

For shorter time sequences, maps and land surveys of different kinds can be used for tracing vegetation changes over a couple of centuries, both concerning forest cover and composition on a landscape scale (Paper I) (Lindbladh et al. 2011b) and disturbances such as wind and fire (Schulte and Mladenoff 2005).

# 3 Results

## 3.1 Paper I

The aim of the study was to gain a better understanding of the forest continuity, in a presently forested area surrounded by an agricultural landscape, but also of the local history of *Fagus sylvatica*. Torup Forest is located in southernmost Sweden, and is the very last forest outpost in a densely populated area heavily characterized by agriculture and developments, but the forest is also a regional core area for biodiversity associated with temperate broadleaves. Torup is mainly used for recreational purposes, yet not formally protected. The 360 ha forest is presently dominated by *Fagus sylvatica*. Pollen and charcoal analysis were carried out on sediment from a small forest hollow and chronological control was obtained by six $^{14}$C dates.

The pollen analysis revealed that mainly *Alnus*, in combination with small amounts of pollen from other deciduous trees, dominated the site from ~6000 BP to 2300 BP, whereas open land taxa such as grasses and herbs, as well as anthropogenic pollen indicators, were rare. *Fagus* became detectable in the pollen record around 3000 BP, around the same time as continuous curves of cereals and other anthropogenic indicators appeared. By 2300 BP, the proportion of tree pollen started to decrease, and open land pollen proportions indicated considerable areas of open land. From around 700 BP onwards, several non-arboreal pollen taxa decreased somewhat, while Cerealia and *Fagus* continued to increase almost uninterrupted up to present. During the same period, all other temperate broadleaves decreased. The only findings of conifers in the pollen record were from the last couple of centuries, most likely as a result of planting for timber production.

The results suggest that the present dominance of *Fagus* in Torup is relatively new, and a conclusion based on the study is that present high biodiversity depends more on the continuity of temperate broadleaved forest in general than on the continuity of particular tree species. The long-term development of the studied site is very similar to those of other sites in the region, mainly concerning the development of *Fagus*, but to some extent also *Quercus*. The dissimilarities of these sites, which were emerging around 2000 BP, are interpreted as differences mainly in the intensity of human impact.

## 3.2 Paper II

The Hornsö-Allgunnen area in south-eastern Sweden has for a century been acknowledged as an insect hotspot. It is considered to host the most species-rich insect fauna in northern Europe; in particular many rare, wood-associated insects have been found here. Several hypotheses for this high biodiversity has been put forward, but never tested for more than small parts of the area. At present the 9000 ha semi-protected "eco-park" is dominated by *Picea abies* (Norway spruce), *Pinus sylvestris* (Scots pine) and *Betula* sp. In this study three small wetlands were used, which together comprise a considerably larger area than previously studied, and the vegetation cover was estimated using the LRA.

The results showed important similarities between the studied sites during the last 3000 years, mainly concerning the large estimated cover of *Pinus* and other light-demanding taxa such as *Calluna* (heather), *Betula* and Poaceae. The relatively light-demanding *Quercus* seems to have a different history in Hornsö-Allgunnen than in the surrounding region, as well as in southern Sweden in general. In large parts of the Hornsö-Allgunnen area *Quercus* sustained during the 19th and 20th centuries, while it decreased in the rest of southern Scandinavia. This could be important for the present biodiversity, as *Quercus* has more other taxa associated with it than any other tree genus in Sweden. Also, the comparably large share of *Pinus* and the late establishment of *Fagus* and *Picea* indicate that the forests of the study area differed from the general tree species composition in the region during most of the studied period.

The study suggests that the Hornsö-Allgunnen area has been covered by continuously open forest, dominated by light-demanding and fire-favoured species such as *Pinus*, *Calluna* and *Betula* for at least three thousand years, whereas temperate broadleaves other than *Quercus* have been rare. The very few findings of anthropogenic indicators show that agriculture most likely was not the main disturbance behind the openness, although small scale agriculture might have contributed to some extent. Rather than agriculture, the data from this and other studies of the area point to fire as an important factor contributing to long-term openness and hence to the biodiversity of the forest in Hornsö-Allgunnen in the past.

## 3.3 Paper III

Formally protected areas are important in the effort to preserve biodiversity. For forest biodiversity in particular, tree species composition, and the continuity of that tree species composition, have been suggested as some of the most important aspects. In southern Sweden, the high contemporary biodiversity of many protected areas has been partly explained by the high proportions of temperate broadleaves relative to their surroundings. In order to test whether the proportion of broadleaves in these protected areas have been distinct from the region in general also in a time perspective of thousand years or longer, the LRA was applied to pollen data from four protected areas dispersed over southern Sweden.

Despite differences among the sampled protected areas, the results show a common pattern of continuity in vegetation cover up to the most recent 500 years, in which a) proportions of open land taxa increased; b) *Picea* and *Fagus* established; and c) temperate broadleaves declined to all time low proportions. Up to 500 BP, both temperate and boreal broadleaves were considerably more abundant than at present in all studied protected areas, although mixed with *Pinus* in the eastern areas. Only very low proportions of anthropogenic indicators were found in any of the areas and in some cases none at all. Today, the *Picea* cover is even larger than estimated by LRA for the last 500 years, and constitutes 20-69% of the vegetation in the studied protected areas.

The results suggest that the studied protected areas maintained forest cover and considerably larger proportions of temperate broadleaves up to rather recently as compared to the surrounding region; at most sites in the protected areas, open land taxa did not increase until during the most recent 500 years. Apparently, the biodiversity value of these areas remain despite that the proportions of temperate broadleaves are lower during the latest time window than ever before. The study hence emphasises the value of the considerably longer time perspective provided by paleoecology, which could be crucial to understand vegetation changes further back in time than one or two tree generations.

## 3.4 Paper IV

Although a rare element in Swedish forests today, *Tilia* (lime tree) was once a dominating tree genus both in southern Sweden and in other parts of northern Europe. The *Tilia* decline has traditionally been attributed to climate change towards colder and wetter conditions during the Bronze Age. Despite its often radical decline, the timing and causes behind it is not completely unravelled, probably partly as a result of the difficulty to quantify the past occurrence of *Tilia* due to its low pollen production. In this study, pollen data from 42 sites in southern Sweden were compiled in order to trace regional patterns concerning the development of *Tilia* as reflected by pollen percentages. Furthermore the Landscape Reconstruction Algorithm was applied to pollen data from 12 of these sites in order to assess vegetation cover, of *Tilia* as well as other taxa, regionally and locally through time.

The study shows that *Tilia* was most abundant in southern Sweden around 6000 BP, during the warm period known as the Holocene Thermal Maximum (HTM). After 4000 BP the genus decreased in the hemi-boreal zone, most likely connected to the climate deterioration at that time. In the temperate zone however, it persisted at similar levels as during the HTM up to at least 1300 BP, and at some sites even longer. The decline in the temperate zone occurred in close temporal connection with an increase in cereal pollen and decreasing tree cover, and it can be concluded that the development of *Tilia* in the temperate zone most likely was highly affected by human disturbance, such agricultural management.

A similar pattern, with local persistence of *Tilia* up till 1000-500 BP, or even longer, can be seen among the LRA sites. Furthermore, the vegetation cover as estimated by the LRA confirms the underestimation of *Tilia* using pollen percentages, and suggests that it might have been up to five times more abundant than reflected in the pollen data.

# 4 Discussion

## 4.1 Quantitative vegetation reconstructions of past forests

The research presented in this thesis has contributed to considerably improved understanding of the cover of temperate broadleaves in southern Sweden. Although the study of temperate broadleaves in the area using paleoecological techniques is not new, the cover of temperate broadleaves has been difficult to interpret due to the different pollen properties of the many taxa involved. In Paper II, III and IV, the LRA was applied to pollen data from sites dispersed over southern Sweden in order to facilitate better understanding of the development of temperate broadleaves in the area. The results of these studies confirm the underestimation of tree taxa such as *Tilia* and *Picea* and the overestimation of *Betula*, *Fagus* and *Quercus*, but also the underestimation of several common open land taxa such as *Calluna* and Poaceae, as well as cereals (Paper II-IV) (fig. 5). In addition to the better understanding of the abundance of individual taxa which our analyses provide, a benefit of the use of vegetation cover as estimated by the LRA relative to pollen percentages is the possibility to cluster the cover of different taxa into vegetation types, such as temperate broadleaves. Furthermore, the historical development of taxa uncommon in pollen analysis due to its low pollen production, such as *Tilia* and cereals, can be studied with a considerably better precision using the LRA.

However, pollen from some tree taxa, including the temperate broadleaves *Acer* (maple), *Fraxinus* (ash) and *Carpinus* (hornbeam) are rarely found in Holocene sediments from southern Sweden regardless of time period. Even using the LRA, the estimates of vegetation cover of these taxa are therefore very low and scattered, and difficult to discuss with any certainty.

## 4.2 The primeval forest and decline of temperate broadleaves

At the start of the studied period, by 5000 BP, temperate broadleaves dominated large parts of southern Sweden, although with variation both on a regional and local spatial scale (Paper I, II, III). All temperate broadleaves presently considered indigenous in Sweden had by then migrated into the region, except the late arrivals *Fagus sylvatica* and *Carpinus betulus* (Almgren et al. 2003). The regional abundance of temperate broadleaves followed a west-eastern gradient with considerably higher cover in the western areas (close to 90% locally in both Biskopstorp and Råshult during the oldest time windows) (Paper III) and lower in the eastern (maximum 27% of the vegetation cover at any time window at Hornsö-Allgunnen) (Paper II, III). Temperate broadleaves declined in the western temperate region from the start of the studied period, but was not replaced by another forest type, but mainly by open land. During these 5000 years, the estimated tree cover decreased from 84% to 18%, and in the last couple of centuries the region was dominated by open land (Paper III). The early and marked decline of temperate broadleaves in the western temperate zone is very similar to the development in Denmark, where the forest was largely replaced by arable land and *Calluna* (Odgaard and Rasmussen 2000, Nielsen et al. 2012).

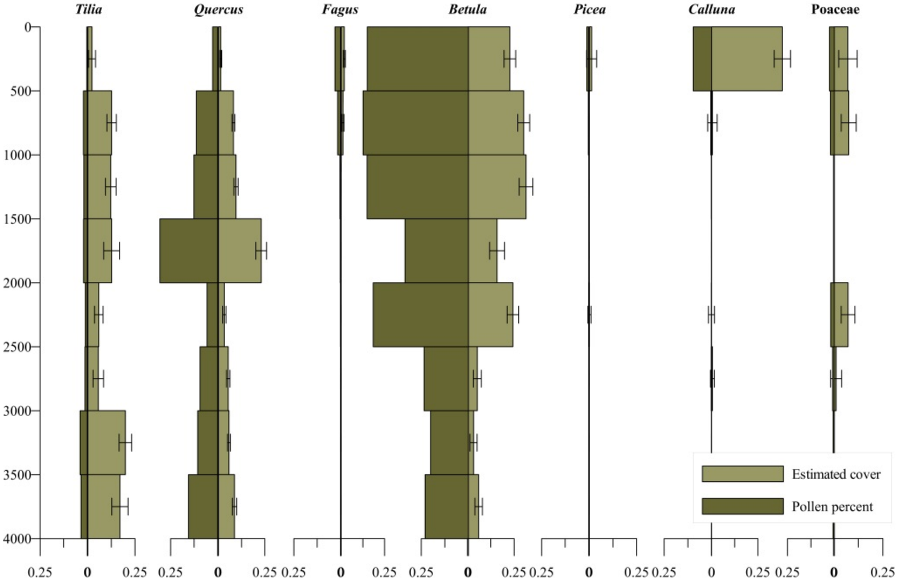

*Figure 5.* An example of the differences between vegetation cover and pollen percentages. Pollen percentages (left) and vegetation cover, with standard errors, as estimated by LOVE (right) of selected taxa, Råshult.

The pattern in the hemi-boreal zone was similar, although it occurred later and was less obvious. While the cover of temperate broadleaves decreased somewhat from 2500 BP simultaneous to a decreasing forest cover, the cover of *Pinus* and boreal broadleaves remained more or less unchanged up to 1500 BP. During the most recent time window, temperate broadleaves covered 12%, relative to >50% at the start of the period (Paper III). The low tree cover (20%) along the west coast and the somewhat higher in the inland region (55%) during the last 500 years (Paper III) is consistent with Kaplan et al. (2009), suggesting that deforestation mainly occurred along the coasts of southern Sweden, whereas the inland remained >50% forest covered as late as 150 BP.

Around 2000 BP, *Fagus* established in the temperate zone and *Picea* in the hemi-boreal (Paper II, III), consistent with *Fagus* immigrating from southwest (Björkman 1996a, Bradshaw and Lindbladh 2005, Berglund et al. 2007) and *Picea* from northeast (Bradshaw and Lindbladh 2005). The establishment of *Fagus* and/or *Picea* has been suggested to be of crucial importance for the development of the other temperate broadleaves in Scandinavia, as they often coincide with decline of these taxa in pollen studies (Bradshaw and Lindbladh 2005, Seppä et al. 2009a). This close temporal connection was found also in Paper III, where *Picea*, and locally also *Fagus* became important at stand scale during the most recent 500 years, a period of large changes in forest composition at the local scale.

## 4.3 Climate change or human impact?

Climate is the ultimate driver of the distribution and abundance of trees on a continental and long-term temporal scale (Huntley and Webb 1989, Svenning et al. 2009). As climate changed towards colder and wetter conditions during the studied period (Moberg et al. 2006, Seppä et al. 2009b), borealization of the vegetation, i.e. the selective decline in thermophilous temperate broadleaves relative the more boreal taxa (broadleaves as well as conifers) could be expected. Such a shift in the long-term development can be seen in Paper III and IV, yet the pattern is complex as the temperate broadleaves were probably not directly replaced by this new forest type, but mainly by open land.

There are also clear connections between the temperate broadleaves' decline and climate. For *Tilia*, climate was probably the most important determinant in the hemi-boreal zone, whereas in the more southern temperate zone, the persistence of *Tilia* until considerably later indicates that local factors, such as land use changes, might have been more important (Paper IV). For temperate broadleaves in general, as well as estimated forest cover, the decline started earlier and was considerably more marked in the temperate zone than in the hemi-boreal (Paper III), contrary to what would have been expected if a harsher climate in the hemi-boreal zone would have been the sole cause for the decline. Furthermore, the local sites remained covered by temperate broadleaved forest considerably longer than the region in general, a difference in timing emphasising the importance of local disturbance factors (Paper III).

A reasonable conclusion is that climate fluctuations have been crucial for the persistence of temperate broadleaved species close to their distribution limit, such as *Tilia* (Pigott and Huntley 1981). However, the difference in timing of temperate broadleaves' decline between the zones as well as the temporal connection to a decreasing tree cover, both as estimated by the LRA (Paper III, IV) and pollen percentages (Paper I), suggests that although climate has most likely been an important determinant, the role of human land use for the development of temperate broadleaves should not be underestimated.

## 4.4 Land-use changes

The negative impact of human activities on the historical development of temperate broadleaves in southern Sweden has been emphasised also by earlier studies (Berglund 1969, 1991, Bradshaw et al. 1994, Lindbladh 1999, Lindbladh et al. 2000, Berglund and Börjesson 2002, Lindbladh et al. 2007, Sköld et al. 2010). But what kind of land-use changes were they?

### 4.4.1 Arable land

A human disturbance which can be inferred with certainty from pollen analysis is the cultivation of cereals, as these do not grow in natural environments (Behre 1981, 1988, Gaillard 2013). In the western temperate zone, cultivation of cereals occurred in increasing proportions from 5000 BP according to the studied regional sites (Paper III). During the most recent time windows, almost half the vegetation cover of the region consisted of cereals, in combination with the anthropogenic indicators *Plantago lanceolata* (ribwort plantain) and *Rumex* sp. (sorrel) (Paper III). This development is comparable to the cover of these taxa in Denmark and northern Germany during the same period (Nielsen et al. 2012), yet considerably higher than in the hemi-boreal zone (Paper III), where cereals and anthropogenic indicators constituted maximum 16% of the estimated cover during the most recent 500 years.

Among the local sites for which vegetation cover was reconstructed (Paper II, III) the cover of cereals and anthropogenic indicators was considerably lower, and almost exclusively occurred in the temperate zone. This apparent difference of agricultural indicators on a local scale compared to regional might be an effect of the sites biased to presently forested areas, partly due to the general lack of wetlands in the modern agricultural landscape due to drainage.

Although small scale cultivation of cereals in a forested landscape can be difficult to detect, as the small proportion of cereal pollen becomes “invisible” in the tree pollen matrix (Hicks 1998), the compilation of 42 small pollen sites in southern Sweden show that cultivation of cereals can be detected also on a local spatial scale (Paper IV). In both zones the mean cereal pollen for these sites increased around 1200 BP, and the highest mean pollen proportions (around 2%) were found 300 BP, and correspond to approximately twice as much as both present time and the time before 500 BP (Paper IV).

### 4.4.2 Meadows and grazing

Whereas cereals were abundant on a regional scale, the local decline in temperate broadleaves mainly occurred in temporal connection to increased cover of open land (Paper III) (fig. 6). Although grasslands cannot be used as indicators of human impact per se, as they are also natural habitats (Gaillard 2013), abrupt changes are often associated with human activities.

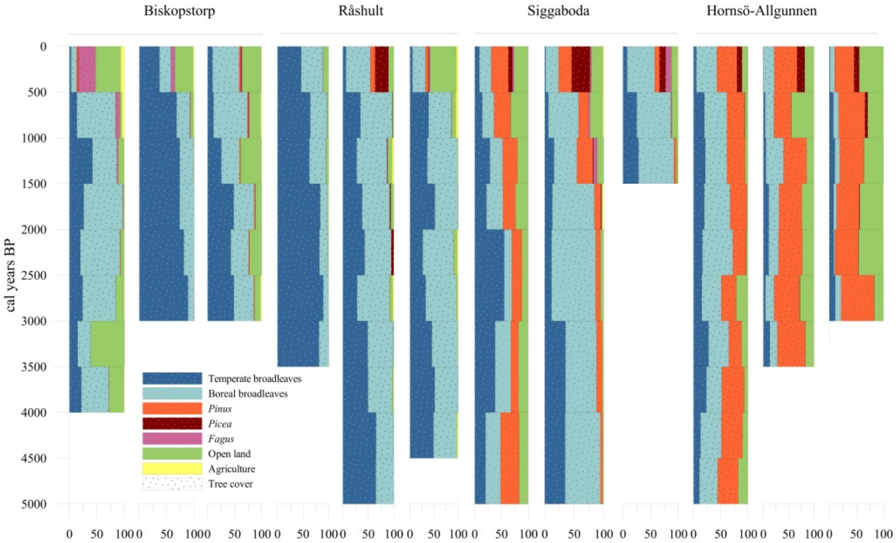

*Figure 6*. Estimated cover of all studied hotspot sites in Paper III. Temperate broadleaves: *Acer*, *Carpinus*, *Corylus*, *Fraxinus*, *Quercus*, *Tilia* and *Ulmus*. Boreal broadleaves: *Alnus*, *Betula* and *Salix*. Open land: *Calluna*, Cyperaceae, *Filipendula*, *Juniperus*, Poaceae and *Ranunculus*. Agriculture: Cerealia, *Secale*, *Rumex* and *Plantago lanceolata*.

Up to the late 19th century, grasslands were of considerable areal extent according to historical sources, usually at a ratio of at least 2:1 compared to arable land (Cousins 2001) based on the importance of nutrient circulation using animal manure as fertilizer (Berglund et al. 2014). Traditional Swedish agriculture divided land into infields and outland. The infields were located close to the settlements and consisted of fenced arable land and hay meadows on fertile soils (Myrdal 1998, Dahlström 2006, Berglund et al. 2014). The meadows were often partly wooded with deciduous trees and shrubs which were pollarded or coppiced for winter fodder (Sjöbeck 1932, Häggström 1998, Slotte 2000). The outlands on the other hand were located outside the village itself, on poorer soil and often shared among several villages, and usually grazed by domestic animals (Sjöbeck 1932, Dahlström 2006, Berglund et al. 2014). This forest grazing became increasingly important during the last millennium, and was area-wise a dominating land-use during the 19th century (Dahlström 2006). The combined effect of these; creation of arable land and wooded meadows together with forest grazing, which were all abundant during the last 500 years, are reasonable causes for the reduction in tree cover during this period as seen in Paper III.

In some areas, both in southern Sweden and other parts of Scandinavia, intense grazing in combination with slash-and-burn cultivation, or deforestation in combination with overgrazing, resulted in heathlands (Overland and Hjelle 2009, Hjelle et al. 2010, Berglund et al. 2014). The very low estimated forest cover (≤ 20%) during the last 1000 years in the western temperate zone could be a reflection of this (Paper III). There, *Calluna* may have replaced temperate broadleaves around 200 BP, at least partly due to overgrazing on sensitive sand areas, and burning of heather for improved grazing (Lindbladh et al. 2011b). Although most likely less abundant on a regional scale (Paper III), *Calluna* heaths did occur also in parts of the hemi-boreal zone (Cui et al. 2013, Cui et al. 2014a). The comparably large cover of *Calluna* and low tree cover in Hornsö-Allgunnen (Paper III) is however not likely to be a result of overgrazing, but rather of dry soils in combination with recurring fires, as the large proportion of open land cover as well as the abundance of *Calluna* is consistent throughout the studied period (Paper II).

### *The disappearance of meadows*

Neither *Picea* nor *Fagus* were generally tolerated in wooded meadows or other grasslands, due to the negative effect on grazing caused by the shading *Fagus* (Sjöbeck 1932) and the inappropriateness of *Picea* for pollarding for animal fodder (Björkman 1996a, Nilsson 1997, Lindbladh and Bradshaw 1998, Kullberg and Bergström 2001).

Meadows and grazed land were most extensive in the late 19th century (Morell 2001, Dahlström 2006), and still in the beginning of the 20th century meadows comprised 3.8 million hectares, corresponding to almost 10% of the land area in Sweden (Bernes 2014). During the latest century, meadows were converted into arable land or planted with forest, and as forest grazing were abandoned, at some places as late as in the 1930s, also the outlands developed into forest (Dahlström et al. 2006). To a large extent, these formerly open areas were colonized by *Fagus* and *Picea*, probably as an effect of the cessation of the traditional agricultural management (Fredh et al. 2012).

*Figure 7.* The present *Fagus* forest at Torup. Photo: Tove Hultberg.

*Fagus* is known to benefit from human disturbance (Björkman 1996a, Lindbladh et al. 2008), and in some areas its colonization was appreciated and even favored on the land owned by the nobility, as it was beneficial for pigs feeding and hunting (Lindqvist 1931, Sjöbeck 1932, Fritzboger 1994). For Torup (Paper I) this could be an important reason underlying the present dominance of *Fagus* (fig. 7) as the establishment of a noble estate in the area around the 14th century coincides with the main *Fagus* expansion at the site.

However, also *Picea*, which has been suggested to be less dependent on human impact for its establishment before the industrial forestry started in the mid-20th century (Giesecke 2005, Seppä et al. 2009a, Bialozyt et al. 2012) might have benefited from the disturbance as its immigration took place into a landscape opened up by forest grazing by domestic animals, which most likely favoured its rapid dispersal (Björkman 1996a, Lindbladh et al. 2014).

### 4.4.3 Fire

All cultivation, as well as to some extent grazing, requires open land, and some forest clearance has therefore been as prerequisite for agriculture in most areas (Kalis et al. 2003). One way of clearing forest is by fire, and many areas in southern Sweden have frequently experienced both natural fires and human caused fires (Niklasson and Drakenberg 2001, Olsson et al. 2010, Cui et al. 2014b).

At Torup (Paper I), traces of fire mainly occur 2000-600 BP, which is also a period where we see other clear indications of human impact; sudden decrease in the original forest indicators *Tilia* and *Alnus* simultaneous to increases in cereals, grasses and herbs. The cessation of fire at Torup at 600 BP corresponds rather well with the suggested cessation of fires around 500 BP in the temperate zone in general (Bradshaw et al. 2010).

*Figure 8.* Controlled burning for conservation purposes in a nature reserve in south-eastern Sweden. Photo: Tove Hultberg

In the hemi-boreal zone (fig. 8), fires were generally more abundant and ceased later (Niklasson and Drakenberg 2001, Bradshaw et al. 2010). At Hornsö-Allgunnen (Paper II), recurring fires are suggested to have shaped the landscape up to the 20th century (Niklasson and Drakenberg 2001, Lindbladh et al. 2003, Niklasson et al. 2010), probably partly as a result of dry soils due to the very low annual precipitation (Alexandersson et al. 1991) in combination with the highest density of lightning ignitions in Sweden (Granström 1993). Throughout the studied 5000 years, the area was dominated by fire-favoured or fire-resistant taxa such as *Pinus* in combination with *Calluna* (Zackrisson 1977, Nilsson 1997). The cover of temperate broadleaves are considerably lower than at the other studied areas (Paper III), probably due to the negative impact of fire on these taxa (Bradshaw et al. 2010).

Despite the low cover of temperate broadleaves (Paper II, III), Hornsö-Allgunnen is considered to host the most species-rich insect fauna in northern Europe; in particular many rare, wood-associated insects are found in the area (Nilsson and Huggert 2001, Ehnström and Axelsson 2002). Among the areas used for vegetation reconstructions, Hornsö-Allgunnen was by far the most open during the entire studied period (Paper III). The recurring fires probably created important sun-exposed habitats, which are preferred by 24% of the wood associated red-listed insects in Sweden (Jonsell et al. 1998, Dahlberg and Stokland 2004). Moreover, around 5% of the wood associated insects in southern Sweden are specifically dependent on burned wood (Jonsell et al. 1998), and the late cessation of forest fires in the area as compared to many other parts of southern Sweden is likely to have been crucial also for them.

## 4.5 *Tilia* as a case study

An interesting element of the decline in temperate broadleaves during the last 5000 years is the genus *Tilia*. *Tilia* is considered to be indicative of original forest, i.e. forest more or less unaffected by human activities (Rackham 1980, Lindbladh et al. 2000, Bradshaw et al. 2005). It has been pointed out as a dominating tree taxa in primeval forests in northern Europe (Iversen 1973, Birks et al. 1975, Berglund 1991), in some areas present in extreme abundances in the past (Grieg 1982). Furthermore, the genus has been pointed out as sensitive to changes towards colder climate (Pigott and Huntley 1981) as well as to human exploitation of woodland (Pigott 1991), both of which occurred during the 5000 years included in this study. Today, *Tilia* is a mere curiosity in southern Sweden, constituting around 0.1% of the total volume on productive forest land (Official Statistics Sweden 2014).

Our compilation of data from 42 pollen sites in southern Sweden shows that *Tilia* was most abundant in southern Sweden around 6000 BP, during the Holocene Thermal Maximum (HTM) (Paper IV), which fits well with the notion of *Tilia* as a thermophilous taxa (Pigott and Huntley 1981, Pigott 1991).

However, the dynamics of *Tilia* as reflected in Paper IV is not just a general increase and decline connected to a changing climate. In the temperate zone, in spite of the climate deterioration, *Tilia* pollen continued to remain rather abundant up 1300 BP or longer (Paper IV). This sustenance of *Tilia* until long after the end of the HTM is confirmed by the vegetation cover of *Tilia* as estimated by the LRA, which suggests that *Tilia* was a common forest component at many sites up to 500 BP or longer (Paper IV). These results, in combination with the close temporal connection between the *Tilia* decline in the temperate zone and both the decrease in tree cover and increase in cereals (the latter from approximately 1200 BP onwards), indicate that the loss of *Tilia* as a common forest tree in the temperate zone in Sweden might be considerably more recent than the Bronze Age decline suggested by pollen studies from the mid-20th century (von Post 1946, Fries 1965, Iversen 1973). But it also suggests that climate deterioration was most likely not the only agent causing it. Rather, the ultimate cause for the loss of *Tilia* as an abundant forest tree in Scandinavia was probably a combination of climate change and changes in land use.

A very similar pattern has been shown in Britain (Turner 1962, Grant et al. 2011), where human impact was suggested to be the main, although not the only, cause for the *Tilia* decline. There, however, the *Tilia* decline occurred considerably earlier, probably due to earlier land-use changes in Britain as compared to southern Sweden. These results, using *Tilia* as a case study of the primeval forest, shows that although its distribution was most likely fragmented, *Tilia* and probably also other components of the primeval forest are likely to have been abundant up to relatively recently in southernmost Sweden. Furthermore, they show that the final destruction of the primeval forest was largely caused by human activities.

## 4.6 Effects on biodiversity

Irrespective of both vegetation zone and initial proportions, the cover of temperate broadleaves (except *Fagus*) is today lower than ever during the studied 5000 years (Papers II, III, IV). This substantial decline could explain the disproportionally large amount of threatened species associated with the forest type. The mere persistence of temperate broadleaves up to during the last

500 years at stand level (Paper III, IV) has ensured the survival of these associated taxa, although in small, fragmented and vulnerable populations.

It is however important to point out that although the decline of temperate broadleaved forest can largely be explained by clearance for agricultural purposes, the decline has not been stopped by the abandonment of that land-use. Rather, as the traditional management of agricultural land was abandoned, the open areas were replaced by forests of mainly *Picea*, but in some areas also *Fagus*.

A similar development has been seen in New England, where a predominantly wooded region were opened up by European settlers who cleared the forest for agricultural purposes around 400 BP (Motzkin and Foster 2002, Foster and Motzkin 2003). Similar to southern Sweden, the region is today largely forested again, yet the forest composition has changed. While the change in Sweden mainly was towards *Picea*, in New England the change was towards a more homogenous forest dominated by short-lived, early successional tree species (Thompson et al. 2013). Likewise, in Japan the establishment of an agricultural landscape caused a decline of many indigenous tree species, followed by a further decrease in species diversity, and afforestation by mainly light-demanding tree taxa, after the recent abandonment of these traditional techniques (Berglund et al. 2014).

In Sweden, *Picea* alone presently constitute about half of all productive forest land (Official Statistics Sweden 2014), as an effect of both modern forestry with large-scale plantations of *Picea* monocultures and changed agricultural practices during the 20th century (Larsson et al. 2011, Lindbladh et al. 2014). In addition to this dramatic change in species composition, many forests are now considerably denser and darker than in the early 20th century (Lindbladh et al. 2014), causing a threat not only to taxa associated with temperate broadleaves, but also to the many species which benefited from the areal increase of agriculture (Berglund et al. 2008).

### 4.6.1 Biodiversity hotspots in a production forest matrix

In both the temperate and hemi-boreal zone, the forest composition and the forest cover changed considerably later among the studied local sites than in the surrounding region (Paper III). When comparing these two spatial scales, it is however important to keep in mind that the vegetation cover at the regional scale is estimated for large areas ($10^4$-$10^5$ $km^2$) (Sugita 2007a) over which vegetation is not homogenously distributed, but an average of many different smaller land units. The local sites studied here are hence not likely to have been unique in their maintenance of forest cover, and should not be thought of as isolated islands of forest in a region largely characterized by agriculture.

However, the large cover of open areas and cultivated land in the region relative the local studied sites (Paper III) do indicate that the local sites, which are all presently forested biodiversity hotspots, have indeed been different from the regional mean.

At present, the studied local sites are considered to be biodiversity hotspot areas. Despite this later decline of temperate broadleaves at the local hotspots (Paper III), more or less extensive vegetation changes took place also there during the last 500 years, as has been shown also for other areas in southern Sweden (Fredh et al. 2012, Cui et al. 2014a). At present, *Picea* or *Pinus* dominate the vegetation both in the region as whole and the studied hotspot sites in Paper III, which are all protected today (fig. 9).

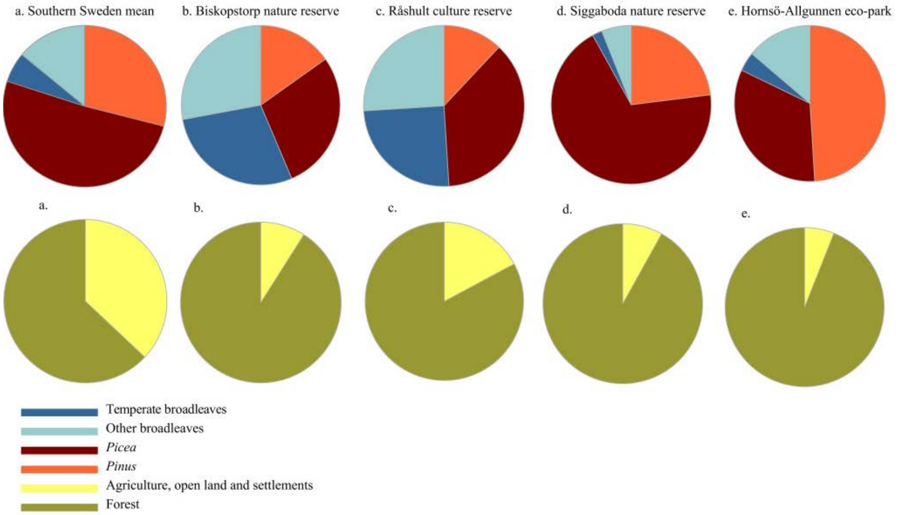

*Figure 9.* Present forest composition as estimated by the kNN, in the hotspot sites and in southern Sweden. Temperate broadleaves: *Fagus sylvatica* and *Quercus robur*.

Similar results were found in central Sweden, where Woodland Key Habitats (which are by definition areas which host or could be expected to host red-listed species) experienced dramatic changes in structure due to the cessation of forest fires and increased forestry management during the last 150 years (Ericsson et al. 2005). It could therefore be argued that the difference between the present biodiversity hotspots and their surrounding is rather small, both in southern and central Sweden. However, both for the local sites in Paper III, and in the Woodland Key Habitats studied by Ericsson et al. (2005), these hotspots have considerably higher conservation values than the *Picea* dominated managed forest landscape surrounding them, despite the present similarity in tree species composition. Although the proportions of temperate broadleaves in the protected areas studied in this thesis are lower than they used to be, it is obviously enough to maintain many of these rare taxa, at least in a shorter perspective. Areas such as these can be used as reservoirs from which temperate broadleaves and species associated with them can proliferate and spread, if given the opportunity. If not, the worst-case scenario is that many threatened species will go extinct also in these hotpots.

These findings suggests that the time perspective of a few centuries or even shorter which is commonly used in studies concerning forest continuity (Kirby et al. 1998, Graae 2000, Goldberg et al. 2007, Fritz et al. 2008, Eriksson et al. 2010, Matuszkiewicz et al. 2013, Palo et al. 2013) might be too short to understand the distribution of species associated with presently fragmented habitat types. Here the collaboration between paleoecologists and ecologists could be crucial, as paleoecology can provide a time perspective rarely used but very important for conservation (Reitalu et al. 2014).

## 4.7 Values of temperate broadleaves for human wellbeing

Even if not studied in this thesis, the long-term connection between people and broadleaved forest in southern Sweden is an important aspect as expressed by human health and people’s perception of forest and urban areas. Temperate broadleaves are abundantly planted in urban areas throughout Scandinavia (Sjöman et al. 2012) and temperate broadleaved forests reportedly increases people’s perceived value of a forest visit as compared to other types of forests (Norman et al. 2011) although also mixed forests, containing both conifers and broadleaves, are preferred to even-aged coniferous stands, i.e. modern production forest (Nielsen et al. 2007).

Broadleaved forests have even proven to be beneficial for public health, even more so than nature in general (Annerstedt et al. 2010). Furthermore, historical continuity or historical richness, i.e. the perception of different time layers or the amount and diversity of cultural elements, is among the most important aspects concerning people’s perception of the forest (Tveit et al. 2007). These benefits of temperate broadleaves for human wellbeing furthermore emphasize the importance of temperate broadleaved taxa for the future.

# 5 Conclusions

Temperate broadleaves are rare in natural habitats in Sweden today, and despite their importance for present biodiversity, little is known about their past cover. Using pollen data and the newly developed Landscape Reconstruction Algorithm, we were able to draw unique conclusions concerning the historical cover of temperate broadleaves.

- Temperate broadleaves prevailed locally until rather recently in southern Sweden, which is likely to be an important cause for the survival of the many presently threatened species associated with temperate broadleaves, although in small and vulnerable populations.
- Despite the long continuity of temperate broadleaves in present biodiversity hotspots, the forest composition often changed radically also in these areas during the most recent 500 years. Hence, not even the vegetation of present protected areas could be claimed to have unbroken continuity back to ancient forests, or to be a reflection of “natural” forest in southern Sweden.
- For *Tilia*, the cover of which has confounded researchers since the introduction of pollen analysis, the decline in the southernmost parts of the country was not as early as commonly thought, but in general almost as recent as for many other temperate broadleaves.
- Differences in the development of *Tilia* in the temperate and the hemi-boreal zone illustrate that these zones really are very different concerning physiogeography and climate, and our data indicate that climate played a crucial role in the *Tilia* decline in the hemi-boreal zone.
- Despite the temporal correlation between *Picea* dominance and the relatively low proportions of temperate broadleaves today, a natural immigration of the strong competitor *Picea* is not likely to be the main cause for the decline of temperate broadleaves in southern Sweden. Rather,

this shift is likely to be an effect of changing land-use and modern forestry benefiting *Picea*.

- Long-term studies such as pollen analyses are crucial for the understanding of the present distribution of threatened species as the legacies of past changes in forest composition and disturbances can prevail for centuries or even longer. Such studies therefore provide an important basis for how to preserve these threatened species for the future.

The studies included in this thesis show that although a wealth of pollen studies has been carried out in the region, there is still much to discover using multiple sites and new techniques. However, the data and methods used here only provide information about tree species composition and vegetation cover. By combining them with other paleoecological proxies, such as analysis of fossil insect remains or dendrochronology, more can be learned about aspects such as the quality and historical management of the forest. Paleoecology therefore has a great potential for providing detailed insights into historical habitats and better understanding of present biodiversity, and for influencing conservation strategies. However, in order to fulfil that potential, the knowledge gained from paleoecology needs to be communicated and incorporated with neo-ecology, or it will simply be the study of what once was.

# Acknowledgements

My most sincere thanks to my supervisor Matts Lindbladh, for taking me on-board, standing behind me through six years and despite two maternity leaves - and taking the time to read and improve endless (!) manuscript drafts. To Marie-José Gaillard for stepping in as my co-supervisor and trying to teach me all there is to it about quantitative vegetation reconstructions. My warmest thanks to you both!

To the always friendly and hospitable staff at the Alnarp library and their counterparts at other libraries, for inexhaustibly helping me find things no one ever looks for, and to Violeta, Margareta and Kent – you do know that there would be no research at all without you, right? A warm thank you also to all the people I clung to as a barnacle to imbibe your knowledge on certain matters, or simply turned to for aid of different sorts: to Gina Hannon for introducing me to macrofossils and inviting me to Liverpool, Anna-Kari Trondman, Qiao-Yu Cui, and Shinya Sugita for LRA support (yes, I do realise how you must have sighed for every new email…). To Britt Kniesel (then Grundmann) for trusting me with teaching you pollen analysis and to my bug guys; Fredrik Olsson and Magnus Hellqvist for beetle analysis (we still have to get those results into publishable shape, right?) and nice talks. To David Ventorp for taking another job and leaving the position vacant! Finally to the best set of colleagues I ever had, to Annika Felton to correcting the English of this thesis, and to Emma Holmström, Anna Monrad Jensen, Claes Regander and Marta Santander for sharing ups and downs of both life and thesis. Thank you.

Finally to my dearest and sweetest ones; Nora, Hanne and Robin. Mina älsklingar.

# References

Ahti, T., L. Hämet-Ahti, and J. Jalas. 1968. Vegetation zones and their sections in northwestern Europe. Annales Botanici Fennici **5**:169-211.

Aldentun, Y. 1997. Gränsen mellan nemorala och boreo-nemorala zonen. Skogforsk, Uppsala.

Alexandersson, H., C. Karlström, and S. Larsson-McCann. 1991. Temperaturen och nederbörden i Sverige 1961-90. Referensnormaler., SMHI, Norrköping.

Almgren, G., L. Jarnemo, and D. Rydberg. 2003. Våra ädla lövträd. Skogsstyrelsen, Jönköping.

Ammann, B., W. O. van der Knaap, G. Lang, M.-J. Gaillard, P. Kaltenrieder, M. Rösch, W. Finsinger, H. E. Wright, and W. Tinner. 2014. The potential of stomata analysis in conifers to estimate presence of conifer trees: examples from the Alps. Vegetation History and Archaeobotany **23**:249-264.

Andersen, S. T. 1970. The relative pollen productivity and pollen representation of north european trees, and correction factors for tree pollen spectra. Geological Survey of Denmark, Copenhagen.

Andersen, S. T. 1973. The differential pollen productivity of trees and its significance for the interpretation of a pollen diagram from a forested region.*in* H. J. B. Birks and R. G. West, editors. Quaternary Plant Ecology. Blackwell Scientific Publications, Oxford.

Andréasson, P.-G., editor. 2006. Geobiosfären, en introduktion. Studentlitteratur, Lund.

Annerstedt, M., J. Norman, M. Boman, L. Mattsson, P. Grahn, and P. Währborg. 2010. Finding stress relief in a forest. Ecological Bulletins **53**:33-42.

Anonymous. 1947. Diskussionsinleg i nordisk kvartärgeologiskt möte den 5.9 november 1945. Geologiska föreningens i Stockholm förhandlingar **69**:240-252.

Behre, K.-E. 1981. The interpretation of anthropogenic indicators in pollen diagrams. Pollen et spores **23**:225-245.

Behre, K.-E. 1988. The role of man in European vegetation history.*in* B. Huntley and T. I. Webb, editors. Vegetation history. Kluwer Academic Publishers, Dordrecht.

Bengtsson, R. 2005. Variation in common lime (*Tilia* x *europaea* L.) in Swedish gardens of the 17th and 18th centuries. Swedish University of Agricultural Sciencies, Alnarp.

Berg, A., B. Ehnström, L. Gustafsson, T. Hallingbäck, M. Jonsell, and J. Weslien. 1994. Threatened plant, animal, and fungus species in Swedish forests - distribution and habitat associations. Conservation Biology **8**:718-731.

Berg, A., B. Ehnström, L. Gustafsson, T. Hallingbäck, M. Jonsell, and J. Weslien. 1995. Threat levels and threats to red-listed species in Swedish forests. Conservation Biology **9**:1629-1633.

Berglund, B. E. 1969. Vegetation and human influence in south Scandinavia during prehistoric time. Oikos suppl. **12**:9-28.

Berglund, B. E., editor. 1991. The cultural landscape during 6000 years in southern Sweden - The Ystad project. Ecological Bulletins, Copenhagen.

Berglund, B. E., L. Björkman, B. H. Holmqvist, and T. Persson. 2007. Skånes vegetationshistoria - förändringar under 17 000 år. Pages 27-38 *in* T. Tyler, K.-A. Olsson, H. Johansson, and M. Sonesson, editors. Floran i Skåne. Arterna och deras utbredning. Lunds botaniska förening, Lund.

Berglund, B. E. and K. Börjesson. 2002. Markens minnen. Landskap och odlingshistoria på småländska höglandet under 6000 år. National Heritage Board, Stockholm.

Berglund, B. E., J. Kitigawa, P. Lagerås, K. Nakamura, N. Sasaki, and Y. Yasuda. 2014. Traditional farming landscapes for sustainable living in Scandinavia and Japan: Global revival through the Satoyama initative. Ambio **43**:559-578.

Berglund, B. E., T. Persson, and L. Björkman. 2008. Late quaternary landscape and vegetation diversity in a North European perspective. Quaternary International **184**:187-194.

Berglund, B. E. and M. Ralska-Jasiewiczowa. 1986. Pollen analysis and pollen diagrams.*in* B. E. Berglund, editor. Handbook of Holocene Palaeoecology and Palaeohydrology. The Blackburn Press, Caldwell, New Jersey.

Bernes, C. 2014. Biologisk mångfald i Sverige. Naturvårdsverket, Stockholm.

Bialozyt, R., L. R. Bradley, and R. H. W. Bradshaw. 2012. Modelling the spread of *Fagus sylvatica* and *Picea abies* in southern Scandinavia during the late Holocene. Journal of Biogeography **39**:665-675.

Birks, H. J. B. and H. H. Birks. 1980. Quaternary palaeoecology. Edward Arnold Ltd., London.

Birks, H. J. B., J. Deacon, and S. Peglar. 1975. Pollen maps for british-isles 5000 years ago. Proceedings of the Royal Society Series B-Biological Sciences **189**:87-105.

Björkman, L. 1996a. The late Holocene history of beech *Fagus sylvatica* and Norway spruce *Picea abies* at stand-scale in southern Sweden. Lund University, Lund.

Björkman, L. 1996b. Long-term population dynamics of *Fagus sylvatica* at the northern limits of its distribution in southern Sweden: a palaeoecological study. The Holocene **6**:225-234.

Björkman, L. 2000a. Pollenanalys av en lagerföljd från Uddared, Laholms kommun. LUNDQUA Uppdrag, Lund.

Björkman, L. 2000b. Pollenanalytisk undersökning av en torvmarkslagerföljd från Trälhultet i Biskopstorps naturreservat, Halmstads kommun. LUNDQUA Uppdrag, Lund.

Björkman, L. 2001a. Pollenanalytisk undersökning av en mosselagerföljd från Alseda, Vetlanda kommun. LUNDQUA Uppdrag, Lund.

Björkman, L. 2001b. The role of human disturbance in Late Holocene vegetation changes on Kullaberg, southern Sweden. Vegetation History and Archaeobotany **10**:201-210.

Björkman, L. 2002. Paleoekologisk undersökning av torvmarker i Dömestorpsområdet på Hallandsås nordsluttning, Hasslövs socken, Laholms kommun., LUNDQUA Uppdrag, Lund.

Björkman, L. 2003a. Pollenanalytisk slutundersökning av tre torvmarkslokaler från Öggestorps och Rogberga socknar inför ombyggnaden av Riksväg 31, delen Öggestorp-Åkarp, Jönköpings län. LUNDQUA Uppdrag, Lund.

Björkman, L. 2003b. Pollenanalytisk undersökning av en torvmarkslagerföljd från den arkeologiska undersökningslokalen "Område 2" nordost om Köphult inför ombyggnaden av E4:an, delen länsgränsen till Strömsnäsbruk, Markaryds kommun. LUNDQUA Uppdrag, Lund.

Björkman, L. 2004. Detaljerad pollenanalytisk undersökning av tre lagerföljder (Flinkasjön, E4:13, E4:16) från Örkelljungatrakten i nordvästra Skåne. LUNDQUA Uppdrag, Lund.

Björkman, L. 2005. Pollenanalytisk undersökning av en torvmarkslagerföljd från Baggabygget i Rönnö naturreservat, Laholms kommun. LUNDQUA Uppdrag, Lund.

Björkman, L. and R. Bradshaw. 1996. The immigration of *Fagus sylvatica* L. and *Picea abies* (L.) Karst. into a natural forest stand in southern Sweden during the last 2000 years. Journal of Biogeography **23**:235-244.

Björkman, L. and J. Ekström. 2003. Pollenanalytisk undersökning av en torvmarkslagerföljd från den arkeologiska undersökningslokalen "Område 12/13" nordväst om Exhult inför ombyggnaden av E4.an, delen länsgränsen till Strömsnäsbruk, Markaryds kommun. LUNDQUA Uppdrag, Lund.

Björkman, L. and J. Regnell. 2001. Markanvändning och vegetationshistoria i Hestraområdet, Borås kommun. LUNDQUA Uppdrag Lund.

Björkman, L. and P. Sjögren. 2003. Long-term history of land-use and vegetation at Ire, an agriculturally marginal area in Blekinge, south Sweden. Vegetation History and Archaeobotany **12**:61-74.

Björse, G. and R. Bradshaw. 1998. 2000 years of forest dynamics in southern Sweden: suggestions for forest management. Forest Ecology and Management **104**:15-26.

Blaauw, M. 2010. Methods and code for 'classical' age-modelling of radiocarbon sequences. Quaternary Geochronology **5**:512-518.

Blytt, A. 1886. On variations of the climate in the course of time II. Nature **34**:239-242.

Bowman, S. 1990. Radiocarbon dating. British Museum Publications Ltd, London.

Bradshaw, R., P. Gemmel, and L. Björkman. 1994. Development of nature-based silvicultural models in southern Sweden: The scientific background. Forest and Landscape Research **1**:95-110.

Bradshaw, R. H. W. and M. Lindbladh. 2005. Regional spread and stand-scale establishment of *Fagus sylvatica* and *Picea abies* in Scandinavia. Ecology **86**:1679-1686.

Bradshaw, R. H. W., M. Lindbladh, and G. E. Hannon. 2010. The role of fire in southern Scandinavian forests during the late Holocene. International Journal of Wildland Fire **9**:1040-1049.

Bradshaw, R. H. W., A. Wolf, and P. F. Moller. 2005. Long-term succession in a Danish temperate deciduous forest. Ecography **28**:157-164.

Bunting, M. J., M.-J. Gaillard, S. Sugita, R. Middleton, and A. Broström. 2004. Vegetation structure and pollen source area. The Holocene **14**:651-660.

Calcote, R. R. 1995. Pollen source area and pollen productivity: Evidence from forest hollows. Journal of Ecology **83**:591-601.

Cousins, S. A. O. 2001. Analysis of land-cover transitions based on 17th and 18th century cadastral maps and aerial photographs. Landscape Ecology **16**:41-51.

Crane, P. R., E. M. Friis, and K. R. Pedersen. 1995. The origin and early diversification of angiosperms. Nature **374**:27-33.

Cui, Q.-Y., M.-J. Gaillard, G. Lemdahl, L. Stenberg, S. Sugita, and G. Zernova. 2014a. Historical land-use and landscape change in southern Sweden and implications for present and future biodiversity. Ecology and Evolution **4**:3555-3570.

Cui, Q.-Y., M.-J. Gaillard, G. Lemdahl, S. Sugita, A. Greisman, G. L. Jacobson, and F. Olsson. 2013. The role of tree composition in Holocene fire history of the hemiboreal and southern boreal zones of southern Sweden, as revealed by the application of the Landscape Reconstruction Algorithm: Implications for biodiversity and climate-change issues. The Holocene **23**:1747-1763.

Cui, Q.-Y., M.-J. Gaillard, F. Olsson, A. Greisman, G. Lemdahl, and G. Zernova. 2014b. A case study of the role of climate, humans, and ecological stting in Holocene fire history of northwestern Europe. Science China Earth Sciences.

Dahlberg, A. and J. N. Stokland. 2004. Vedlevande arters krav på substrat. Swedish Forest Agency, Jönköping.

Dahlström, A. 2006. Betesmarker, djurantal och betestryck 1620-1850. Centrum för biologisk mångfald, Uppsala.

Dahlström, A., S. A. O. Cousins, and O. Eriksson. 2006. The history (1620-2003) of land use, people and livestock, and the relationship to present plant species diversity in a rural landscape in Sweden. Environment and History **12**:191-212.

Davis, M. B. 1963. On the theory of pollen analysis. American Journal of Science **261**:897-912.

Diamond, J. 2005. The vanished forest. Collapse: How societies choose to fail or succeed. Penguin, London.

Diekmann, M. 1994. Deciduous forest vegetation in Boreo-nemoral Scandinavia. Uppsala University, Uppsala.

Dietl, G. P. and K. W. Flessa. 2011. Conservation paleobiology: putting the dead to work. Trends in Ecology & Evolution **26**:30-37.

Digerfeldt, G. 1971. The post-glacial development of Lake Trummen, Småland, central south Sweden. Regional development, water level development and palaeolimnologic development. Lund University, Lund.

Digerfeldt, G. 1982. The holocene development of Lake Sämbosjön. Department of Quaternary Geology, Lund University, Lund.

Ehnström, B. and R. Axelsson. 2002. Insektsgnag i bark och ved. Artdatabanken, SLU, Uppsala.

Erdtman, G. 1946. An introduction to pollen analysis. Chronica Botanica Company, Waltham.

Ericsson, T. S., H. Berglund, and L. Östlund. 2005. History and forest biodiversity of woodland key habitats in south boreal Sweden. Biological Conservation **122**:289-303.

Eriksson, S., H. Skånes, M. Hammer, and M. Lönn. 2010. Current distribution of older and deciduous forests as legacies from historical use patterns in a Swedish boreal landscape (1725-2007). Forest Ecology and Management **260**:1095-1103.

Faegri, K. and J. Iversen. 1989. Textbook of pollen analysis. Fourth edition. The Blackburn Press, Caldwell.

Fagerlind, F. 1952. The real signification of pollen diagrams. Botaniska notiser **2**:185-224.

Finsinger, W., K. Ryan, J. Fevre, and E. K. Magyari. 2014. A guide to screening charcoal peaks in macrocharcoal-area records for fire-episode reconstructions. Holocene **24**:1002-1008.

Foster, D. 2002. Insights from historical geography to ecology and conservation: lessons from the New England landscape. Journal of Biogeography **29**:1269-1275.

Foster, D. R. and G. Motzkin. 2003. Interpreting and conserving the openland habitats of coastal New England: insights from landscape history. Forest Ecology and Management **185**:127-150.

Fredh, D., A. Broström, L. Zillén, F. Mazier, M. Rundgren, and P. Lagerås. 2012. Floristic diversity in the transition from traditional to modern land-use in southern Sweden A.D. 1800-2008. Vegetation History and Archaeobotany **21**:439-452.

Fries, M. 1965. The late-quaternary vegetation of Sweden. Acta Phytogeographica Suecica **50**:269-284.

Fritz, Ö., L. Gustafsson, and K. Larsson. 2008. Does forest continuity matter in conservation? - A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. Biological Conservation **141**:655-668.

Fritzboger. 1994. Kulturskoven. Dansk skovbrug fra oldtid til nutid. Gyldendal, Copenhagen.

Froyd, C. A. and K. J. Willis. 2008. Emerging issues in biodiversity & conservation management: The need for a palaeoecological perspective. Quaternary Science Reviews **27**:1723-1732.

Gaillard, M.-J. 2000. Vegetations - och landskapshistoria i ett långt tidsperspektiv - till vilken nytta? Pages 135-162  Installation Växjö Universitet 2000. University of Växjö, Växjö.

Gaillard, M.-J. 2013. Archaeological applications. Pages 880-904 *in* S. A. Elias, editor. Encyclopedia of Quaternary Science Elsevier, Amsterdam.

Giesecke, T. 2005. Moving front or population expansion: How did *Picea abies* (L.) Karst. become frequent in central Sweden? Quaternary Science Reviews **24**:2495-2509.

Goldberg, E., K. Kirby, J. Hall, and J. Latham. 2007. The ancient woodland concept as a practical conservation tool in Great Britain. Journal for Nature Conservation **15**:109-119.

Graae, B. J. 2000. The effect of landscape fragmentation and forest continuity on forest floor species in two regions of Denmark. Journal of Vegetation Science **11**:881-892.

Granström, A. 1993. Spatial and temporal variation in lightning ignitions in Sweden. Journal of Vegetation Science **4**:737-744.

Grant, M. J., M. P. Waller, and J. A. Groves. 2011. The *Tilia* decline: vegetation change in lowland Britain during the mid and late Holocene. Quaternary Science Reviews **30**:394-408.

Grieg, J. 1982. Past and present lime woods of Europe.*in* M. Bell and S. Limbrey, editors. Archaeological aspects of woodland ecology. Symposia of the Association for Environmental Archaeology No. 2, BAR International Series.

Gärdenfors, U. 2010. Rödlistade arter i Sverige. Artdatabanken, Uppsala.

Hannah, L., J. L. Carr, and A. Lankerani. 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. Biodiversity and Conservation **4**:128-155.

Hannon, G. E. 1999. The use of plant macrofossils and pollen in the palaeoecological reconstruction of vegetation. Swedish University of Agricultural Science, Alnarp.

Hannon, G. E., M. Niklasson, J. Brunet, P. Eliasson, and M. Lindbladh. 2010. How long has the 'hotspot' been 'hot'? Past stand-scale structures at Siggaboda nature reserve in southern Sweden. Biodiversity and Conservation **19**:2167-2187.

Hellman, S., M.-J. Gaillard, A. Broström, and S. Sugita. 2008. The REVEALS model, a new tool to estimate past regional plant abundance from pollen data in large lakes: validation in southern Sweden. Journal of Quaternary Science **23**:21-42.

Hesselman, H. 1916. Yttrande med anledning av L. von Post's föredrag om skogsträdpollen i sydsvenska torfmosselagerföljder. Geologiska Föreningen i Stockholm Förhandlingar **38**:390-392.

Hicks, S. 1998. Fields, boreal forests and forest clearings as recorded by modern pollen deposition. Pages 53-66 *in* M.-J. Gaillard and B. E. Berglund, editors. Quantification of land surfaces cleared of forests during the Holocene - Modern pollen/vegetation/landscape relationships as an aid to the interpretation of fossil data. Gustav Fischer, Stuttgart.

Higuera, P. E., D. G. Gavin, P. J. Bartlein, and D. J. Hallett. 2010. Peak detection in sediment-charcoal records: impacts of alternative data analysis methods on fire-history interpretations. International Journal of Wildland Fire **19**:996-1014.

Hjelle, K. L., L. S. Halvorsen, and A. Overland. 2010. Heathland development and relationship between humans and environment along the coast of western Norway through time. Quaternary International **220**:133-146.

Hjelle, K. L., T. Solem, L. S. Halvorsen, and L. I. Åstveit. 2012. Human impact and landscape utilization from the Mesolithic to medieval time traced by high spatial resolution pollen analysis and numerical methods. Journal of Archaeological Science **39**:1368-1379.

Hultén, E. 1971. Atlas över växternas utbredning i Norden. Generalstabens litografiska anstalts förlag, Stockholm.

Huntley, B. and T. Webb. 1989. Migration - Species Response to Climatic Variations Caused by Changes in the Earths Orbit. Journal of Biogeography **16**:5-19.

Häggström, C.-A. 1998. Pollard meadows: multiple use of human-made nature. Pages 33-41 *in* K. J. Kirby and C. Watkins, editors. The ecological history of European forests. CAB International, Oxon.

Iversen, J. 1941. Landnam i Danmarks stenalder. Danmarks Geologiske Undersogelse., Copenhagen.

Iversen, J. 1964. Vegetational Succession in the Post-Glacial. Journal of Animal Ecology **33**:59-70.

Iversen, J. 1973. The development of Denmark's nature since the last glacial. Geological Survey of Denmark.

Jacobson, G. L. 1988. Ancient permanent plots: sampling in paleovegetational studies. Quaternary Research **16**:80-96.

Jacobson, G. L. and R. H. W. Bradshaw. 1981. The selection of sites for paleovegetational studies. Quaternary Research **16**:80-96.

Janssen, C. R. 1972. Local and regional pollen deposition. Quaternary plant ecology. The 14th symposium of the British Ecological Society, University of Cambridge 28-30 March 1972.

Jonsell, M. and K. Andersson. 2011. Vedlevande skalbaggar på lind. Entomologisk tidskrift **132**:167-186.

Jonsell, M., J. Weslien, and B. Ehnström. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation **7**:749-764.

Kalis, A. J., J. Merkt, and J. Wunderlich. 2003. Environmental changes during the Holocene climatic optimum in central Europe - human impact and natural causes. Quaternary Science Reviews **22**:33-79.

Kaplan, J., K. M. Krumhardt, and N. Zimmermann. 2009. The prehistoric and preindustrial deforestation of Europe. Quaternary Science Reviews **28**:3016-3034.

Kirby, K. J., C. M. Reid, D. Isaac, and R. C. Thomas. 1998. The ancient woodland inventory in England and its uses. Pages 323-336 *in* K. J. Kirby and C. Watkins, editors. The ecological history of European forests. CAB International, Oxon.

Kristiansen, K. 2002. The birth of ecological archaeology in Denmark: history and research environment 1850-2000.*in* F. Anders and K. Kristian, editors. The neolithisation of Denmark, 150 years of debate.

Kullberg, Y. and R. Bergström. 2001. Winter browsing by large herbivores on planted deciduous seedlings in southern Sweden. Scandinavian Journal of Forest Research **16**:371-378.

Lagerås, P. 1996. Farming and forest dynamics in an agriculturally marginal area of southern Sweden, 5000 BC to present: a palynological study of Lake Avegöl in the Småland Uplands. The Holocene **6**:301-314.

Lagerås, P. 2000. Järnålderns odlingssystem och landskapets långsiktiga förändring. Hamnedas röjningsröseområden i ett paleoekologiskt perspektiv. Pages 167-229 *in* P. Lagerås, editor. Arkeologi och paleoekologi i sydvästra Småland. National Heritage Board, Lund.

Lagerås, P. 2002. Skog, slåtter och stenröjning: paleoekologiska undersökningar i trakten av Stoby i norra Skåne. Pages 363-411 *in* A. Carlie, editor. Skånska regioner – tusen år av kultur och samhälle i förändring. . Arkeologiska undersökningar. Riksantikvarieämbetet, Stockholm.

Lagerås, P. 2007. The ecology of expansion and abandonment. Medieval and post-medieval land-use and settlement dynamics in a landscape perspective. National Heritage Board, Lund.

Lagerås, P., K. Jansson, and A. Vestbö. 1995. Land-use history of the Axlarp area in the Småland uplands, southern Sweden: palaeoecological and archaeological investigations. Vegetation History and Archaeobotany **4**:223-234.

Larsson, A., U. Bjelke, A. Dahlberg, and J. Sandström. 2011. Tillståndet i skogen - rödlistade arter i ett nordiskt perspektiv. Uppsala.

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

Lindbladh, M., A.-L. Axelsson, T. Hultberg, J. Brunet, and A. Felton. 2014. From broadleaves to spruce - the boralization of southern Sweden. Scandinavian Journal of Forest Research **29**:686-696.

Lindbladh, M. and R. Bradshaw. 1998. The origin of present forest composition and pattern in southern Sweden. Journal of Biogeography **25**:463-477.

Lindbladh, M., R. Bradshaw, and B. H. Holmqvist. 2000. Pattern and process in southern Swedish forests during the last 3000 years, sensed at stand and regional scales. Journal of Ecology **88**:113-128.

Lindbladh, M. and R. H. W. Bradshaw. 1995. The development and demise of a Medieval forest-meadow system at Linnaeus' birthplace in southern Sweden: implications for conservation and forest history. Vegetation History and Archaeobotany **4**:153-160.

Lindbladh, M., J. Brunet, G. E. Hannon, M. Niklasson, P. Eliasson, G. Eriksson, and A. Ekstrand. 2007. Forest history as a basis for ecosystem restoration - a multidisciplinary case study in a south Swedish temperate landscape. Restoration Ecology **15**:284-295.

Lindbladh, M., A. Felton, R. Trubins, and O. Sallnäs. 2011a. A landscape and policy perspective on forest conversion: Long-tailed tit (*Aegithalos* *caudatus*) and the allocation of deciduous forests in southern Sweden. European Journal of Forest Research **130**:861-869.

Lindbladh, M. and D. Foster. 2010. Dynamics of long-lived foundation species: the history of *Quercus* in southern Sweden. Journal of Ecology **98**:1330-1345.

Lindbladh, M., S. Fraver, J. Edvardsson, and A. Felton. 2013. Past forest composition, structures and processes - How paleoecology can contribute to forest conservation. Biological Conservation **168**:116-127.

Lindbladh, M., T. Hultberg, M. K. Widerberg, and A. Felton. 2011b. Halland's forests during the last 300 years: a review of Malmström (1939). Scandinavian Journal of Forest Research **26 (suppl. 10)**:81-90.

Lindbladh, M., M. Niklasson, M. Karlsson, L. Björkman, and M. Churski. 2008. Close anthropogenic control of *Fagus sylvatica* establishment and expansion in a Swedish protected landscape - implications for forest history and conservation. Journal of Biogeography **35**:682-697.

Lindbladh, M., M. Niklasson, and S. G. Nilsson. 2003. Long-term record of fire and open canopy in a high biodiversity forest in southeast Sweden. Biological Conservation **114**:231-243.

Lindqvist. 1931. Den skandinaviska bokskogens biologi. Svensk skogsvårdsförbunds tidskrift **3**.

Matthias, I., A. B. Nielsen, and T. Giesecke. 2012. Evaluating the effect of flowering age and forest structure on pollen productivity estimates. Vegetation History and Archaeobotany **21**:471-484.

Matuszkiewicz, J. M., A. Kowalska, A. Kozlowska, E. Roo-Zielinska, and J. Solon. 2013. Differences in plant-species composition, richness and community structure in ancient and post-agricultural pine forests in central Poland. Forest Ecology and Management **310**:567-576.

Mazier, F., M.-J. Gaillard, P. Kunes, S. Sugita, A.-K. Trondman, and A. Broström. 2012. Testing the effect of site selection and parameter setting on REVEALS-model estimates of plant abundance using the Czech Quaternary Palynological Database. Review of palaeobotany and palynology **187**:38-49.

Mitchell, F. J. G. 1998. The investigation of long-term successions in temperate woodland using fine spatial resolution pollen analysis. Pages 213-223 *in* K. J. Kirby and C. Watkins, editors. The ecological history of European forests. CAB International, Oxon.

Mitchell, F. J. G. 2010. Exploring vegetation in the fourth dimension. Trends in Ecology and Evolution **26**:45-52.

Moberg, A., D. M. Sonechkin, K. Holmgren, N. M. Datsenko, and W. Karlén. 2006. Highly variable Northern Hemisphere temperatures reconstructed from low- and high-resolution proxy data. Nature **433**:613-617.

Moore, P. D., J. A. Webb, and M. E. Collinson. 1991. Pollen analysis. Second edition. Blackwell Scientific Publications, Oxford.

Morell, M. 2001. Jordbruket i industrisamhället 1870-1945. Natur och Kultur/LTs förlag, Stockholm.

Motzkin, G. and D. R. Foster. 2002. Grasslands, heathlands and shrublands in coastal New England: historical interpretations and approaches to conservation. Journal of Biogeography **29**:1569-1590.

Myrdal, J. 1998. Jordbrukets första femtusen år. Natur och Kultur/LTs förlag, Stockholm.

Nielsen, A. B., T. Giesecke, M. Thauerlauf, I. Feeser, K.-E. Behre, H.-J. Beug, S.-H. Chen, J. Christiansen, W. Dörfler, E. Endtmann, S. Jahns, P. de Klerk, N. Kühl, M. Latalowa, B. Odgaard, P. Rasmussen, J. R. Stockholm, R. Voigt, J. Wiethold, and S. Wolters. 2012. Quantitative reconstructions of changes in regional openness in north-central Europe reveal new insights into old questions. Quaternary Science Reviews **47**:131-149.

Nielsen, A. B. and B. Odgaard. 2010. Quantitative landscape dynamics in Denmark through the last three millenia based on the Landscape Reconstruction Algorithm. Vegetation History and Archaeobotany **19**:375-387.

Nielsen, A. B., S. B. Olsen, and A. Lundhede. 2007. An economic valuation of the recreational benefits associated with nature-based forest management practices. Landscape and Urban Planning **80**:63-71.

Niklasson, M. and B. Drakenberg. 2001. A 600-year tree-ring fire history from Norra Kvills National Park, southern Sweden: implications for conservation strategies in the hemiboreal zone. Biological Conservation **101**:63-71.

Niklasson, M., I. Drobyshev, and T. Zielonka. 2010. A 400-year history of fires on lake islands in south-eastern Sweden. International Journal of Wildland Fire **19**:1050-1058.

Nilsson, S. G. 1997. Forests in the temperate-boreal transition: natural and man-made forests. Ecological Bulletins **46**:61-71.

Nilsson, S. G. and L. Huggert. 2001. Vedinsektsfaunan i Hornsö-Allgunnenområdet i östra Småland. Länsstyrelsen Kalmar län, Kalmar.

Norman, J., L. Mattsson, and M. Boman. 2011. Rekreationsvärden i Skånes och Blekinges skogar - hur viktig är ädellövskogen? , Swedish University of Agricultural Sciences, Faculty of Forest Sciences, Umeå.

Odgaard, B. V. and P. Rasmussen. 2000. Origin and temporal development of macro-scale vegetation patterns in the cultural landscape of Denmark. Journal of Ecology **88**:733-748.

Official Statistics Sweden. 2014. Skogsdata. Institutionen för skoglig resurshushållning, Uppsala.

Olsson, F., M.-J. Gaillard, G. Lemdahl, A. Greisman, P. Lanos, D. Marguerie, N. Marcaux, P. Skoglund, and J. Wäglind. 2010. A continuous record of fire covering the last 10,500 calendar years from southern Sweden - The role of climate and human activities. Palaeogeography Palaeoclimatology Palaeoecology **291**:128-141.

Olsson, I. U. 1986. Radiometric dating.*in* B. E. Berglund, editor. Handbook of Holocene Palaeoecology and Palaeohydrology. The Blackburn Press, New Jersey.

Overballe-Petersen, M. V. and R. H. W. Bradshaw. 2011. The selection of small forest hollows for pollen analysis in boreal and temperate forest regions. Palynology **35**:146-153.

Overland, A. and K. L. Hjelle. 2009. From forest to open pastures and fields: cultural landscape development in western Norway inferred from two pollen records representing different spatial scales of vegetation. Vegetation History and Archaeobotany **18**:459-476.

Palo, A., M. Ivask, and J. Liira. 2013. Biodiversity composition reflects the history of ancient semi-natural woodland and forest habitats. Compilation of an indicator complex for restoration practice. Ecological Indicators **34**:336-344.

Parsons, R. W. and I. C. Prentice. 1981. Statistical approaches to R-values and the pollen-vegetation relationship. Review of palaeobotany and palynology **32**:127-152.

Pigott, C. D. 1991. *Tilia cordata* Miller. Journal of Ecology **79**:1147-1207.

Pigott, C. D. and J. P. Huntley. 1981. Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range. 3. Nature and cause of seed sterility. New phytologist **87**:817-839.

Prentice, I. C. and R. W. Parsons. 1983. Maximum likelyhood linear calibration of pollen spectra in terms of forest composition. Biometrics **39**:1051-1057.

Rackham, O. 1980. Ancient woodlands; its history, vegetation and uses in England. Arnold, London.

Ramsey, C. B. 1995. Radiocarbon calibration and analysis of stratigraphy: the OxCal program. Radiocarbon **37**:425-430.

Ramsey, C. B. and S. Lee. 2013. Recent and planned developments of the program OxCal. Radiocarbon **55**:720-730.

Reese, H., M. Nilsson, T. G. Pahlen, O. Hagner, S. Joyce, U. Tingelöf, M. Egberth, and H. Olsson. 2003. Countrywide estimates of forest variables using satellite data and field data from the national forest inventory. Ambio **32**:542-548.

Reese, H., M. Nilsson, P. Sandström, and H. Olsson. 2002. Applications using estimates of forest parameters derived from satellite and forest inventory data. Computers and Electronics in Agriculture **37**:37-55.

Reitalu, T., P. Kunes, and T. Giesecke. 2014. Closing the gap between plant ecology and Quaternary palaeoecology. Journal of Vegetation Science **25**:1188-1194.

Schulte, L. A. and D. J. Mladenoff. 2005. Severe wind and fire regimes in northern forests: historical variability at the regional scale. Ecology **86**:431-445.

Seddon, A. W. R., A. W. Mackay, A. G. Baker, H. J. B. Birks, E. Breman, C. E. Buck, E. C. Ellis, C. A. Froyd, J. L. Gill, L. Gillson, E. A. Johnson, V. J. Jones, S. Juggins, M. Macias-Fauria, K. Mills, J. L. Morris, D. Nogues-Bravo, S. W. Punyasena, T. P. Roland, A. J. Tanentzap, K. J. Willis, M. Aberhan, E. N. van Asperen, W. E. N. Austin, R. W. Battarbee, S. Bhagwat, C. L. Belanger, K. D. Bennett, H. H. Birks, C. B. Ramsey, S. J. Brooks, M. de Bruyn, P. G. Butler, F. M. Chambers, S. J. Clarke, A. L. Davies, J. A. Dearing, T. H. G. Ezard, A. Feurdean, R. J. Flower, P. Gell, S. Hausmann, E. J. Hogan, M. J. Hopkins, E. S. Jeffers, A. A. Korhola, R.

Marchant, T. Kiefer, M. Lamentowicz, I. Larocque-Tobler, L. Lopez-Merino, L. H. Liow, S. McGowan, J. H. Miller, E. Montoya, O. Morton, S. Nogue, C. Onoufriou, L. P. Boush, F. Rodriguez-Sanchez, N. L. Rose, C. D. Sayer, H. E. Shaw, R. Payne, G. Simpson, K. Sohar, N. J. Whitehouse, J. W. Williams, and A. Witkowski. 2014. Looking forward through the past: identification of 50 priority research questions in palaeoecology. Journal of Ecology **102**:256-267.

Seppä, H. 2007. Pollen analysis, principles.*in* S. A. Elias, editor. Encyclopedia of Quaternary Science. Elsevier, Amsterdam.

Seppä, H., T. Alenius, R. H. W. Bradshaw, T. Giesecke, M. Heikkila, and P. Muukkonen. 2009a. Invasion of Norway spruce (*Picea abies*) and the rise of the boreal ecosystem in Fennoscandia. Journal of Ecology **97**:629-640.

Seppä, H., A. E. Bjune, T. R.J., H. J. B. Birks, and S. Veski. 2009b. Last nine-thousand years of temperature variability in Northern Europe. Climate of the Past **5**:523-525.

Sernander, R. 1908. On the evidence of postglacial changes of climate furnished by the peat-mosses. Geologiska föreningens i Stockholm förhandlingar **30**:465-473.

Sjöbeck, M. 1932. Lövängen och dess betydelse för det sydsvenska bylandskapets uppkomst och utveckling. Svenska skogsvårdsföreningens tidskrift **29**:132-160.

Sjöman, H., J. Östberg, and O. Bühler. 2012. Diversity and distribution of the urban tree population in ten major Nordic cities. Urban Forestry & Urban Greening **11**:31-39.

Sjörs, H. 1965. Forest regions. The plant cover of Sweden. Acta Phytogeographica Suecica, Uppsala.

Sköld, E., P. Lagerås, and B. E. Berglund. 2010. Temporal cultural landscape dynamics in a marginal upland area: agricultural expansions and contractions inferred from palynological evidence at Yttra Berg, southern Sweden. Vegetation History and Archaeobotany **19**:121-136.

Slotte, H. 2000. Lövtäkt i Sverige och på Åland: metoder och påverkan på landskapet. Swedish University of Agricultural Sciences, Uppsala.

Smith, D., N. J. Whitehouse, M. J. Bunting, and H. Chapman. 2010. Can we characterise "openness" in the Holocene palaeoenvironmental record? Modern analogue studies of insect faunas and pollen spectra from Dunham Massey deer park and Epping Forest, England. The Holocene **20**:1-22.

Soepboer, W., S. Sugita, and A. F. Lotter. 2010. Regional vegetation-cover changes on the Swiss Plateau during the past two millennia: A pollen-based reconstruction using the REVEALS model. Quaternary Science Reviews **29**:472-483.

Sugita, S. 1993. A model of pollen source area for an entire lake surface. Quaternary Research **39**:239-244.

Sugita, S. 1994. Pollen representation of vegetation in quaternary sediments: Theory and method in patchy vegetation. Journal of Ecology **82**:881-897.

Sugita, S. 2007a. Theory of quantitative reconstruction of vegetation I: pollen from large sites REVEALS regional vegetation composition. The Holocene **17**:229.

Sugita, S. 2007b. Theory of quantitative reconstruction of vegetation II: all you need is LOVE. The Holocene **17**:243-257.

Sugita, S., M.-J. Gaillard, S. Hellman, and A. Broström. 2007. Model-based reconstruction of vegetation and landscape using fossil pollen.*in* The 35th International Conference on Computer Applications and Quanttative Methods in Archaeology (CAA), Berlin.

Sugita, S., T. Parshall, R. R. Calcote, and K. Walker. 2010. Testing the Landscape Reconstruction Algorithm for spatially explicit reconstruction of vegetation in northern Michigan and Wisconsin. Quaternary Research **74**:289-300.

Swedish Forest Agency. 2005. Ädellövskogens roll i samhället. Skogsvårdsstyrelsen Södra Götaland.

Swedish Foresty Act. 1979. Skogsvårdslag. 1979:429. Notisum.

Swedish National Forest Inventory. 2014. http://skogskarta.slu.se/.

Svenning, J.-C., C. Flojgaard, N. Morueta-Holme, J. Lenoir, S. Normand, and F. Skov. 2009. Big moving day for biodiversity? A macroecological assessment of the scope for assisted colonization as a conservation strategy under global warming Earth and Environmental Science **8**:1-12.

Thelaus, M. 1989. Late Quaternary vegetation history and palaeohydrology of the Sandsjön-Årshult area, southwestern Sweden. Lund University, Lund.

Thompson, J. R., D. Carpenter, N., C. V. Cogbill, and D. R. Foster. 2013. Four centuries of change in northeastern United States forests. PLOS ONE **8**:1-15.

Traverse, A. 1988. Paleopalynology, Boston.

Trondman, A.-K., M.-J. Gaillard, F. Mazier, S. Sugita, R. M. Fyfe, A. B. Nielsen, C. L. Twiddle, P. Barratt, H. J. B. Birks, A. E. Bjune, L. Björkman, A. Broström, C. J. Caseldine, R. David, J. Dodson, W. Dörfler, E. Fischer, B. van Geel, T. Giesecke, T. Hultberg, L. Kalnina, M. Kangur, W. O. van der Knaap, T. Koff, P. Kunes, P. Lagerås, M. Latalowa, J. Lechterbeck, C. Leroyer, M. Leydet, M. Lindbladh, L. Marquer, F. J. G. Mitchell, B. Odgaard, S. Peglar, T. Persson, A. Poska, M. Rösch, H. Seppä, S. Veski, and L. Wick. 2014. Pollen-based quantitative reconstructions of Holocene regional vegetation cover (plant-functional types and land-cover types) in Europe suitable for climate modelling. Global Change Biology.

Turner, J. 1962. The *Tilia* decline: an anthropogenic interpretation. New phytologist **61**:328-341.

Tveit, M., Å. Ode, and G. Fry. 2007. Key concepts in a framework for analysing visual landscape character. Landscape Research **31**:229-255.

Vajda, V., J. I. Raine, and C. J. Hollis. 2001. Indication of global deforestation at the cretaceous-tertiary boundary by New Zealand fern spike. Science **294**:1700-1702

Valdemardotter, Å. 2001. En skogshistorisk undersökning i östra Småland. Vegetationsutveckling och brandhistorik de senaste 3000 åren vid Ekenäs i Hornsöområdet. Swedish University of Agricultural Sciences, Alnarp.

Walker, M. 2005. Quaternary dating methods. Chichester, John Wiley & sons, Ltd.

Vera, F. W. M. 2000. Grazing ecology and forest history. CABI Publishing, Cambridge.

Whitehouse, N. J. and D. Smith. 2010. How fragmented was the British Holocene wildwood? Perspectives of the "Vera" grazing debate from the fossil beetle record. Quaternary Science Reviews **29**:539-553.

Willis, K. and H. Birks. 2006. What is natural? The need for a long-term perspective in biodiversity conservation. Science **314**:1261-1265.

Willis, K. J., M. B. Araujo, K. D. Bennett, B. Figueroa-Rangel, C. A. Froyd, and N. Myers. 2007. How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. Philosophical Transactions of the Royal Society B-Biological Sciences **362**:175-186.

von Post, L. 1916. Skogsträdpollen i sydsvenska torfmosselagerföljder. Geologiska föreningens i Stockholm förhandlingar **38**:384-394.

von Post, L. 1946. The prospect for pollen analysis in the study of the earth's climatic history New phytologist **45**:193-217.

Zackrisson, O. 1977. Influence of forest fires on north Swedish boreal forest. . Oikos **29**.