The impact of past land-use change on floristic diversity in southern Sweden : a quantitative approach based on high-resolution pollen data

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Abstract

This thesis explores the relationship between land-use and floristic diversity over the last three millennia in the uplands of southern Sweden. A quantitative approach based on high-resolution pollen data was applied, using the Landscape Reconstruction Algorithm (LRA), historical maps/aerial photographs, palynological richness and new ways to estimate past evenness at regional and local spatial scales, which enable estimates of the rate and degree of change in land-use and floristic diversity. The results show that agricultural land-use was most widespread AD 350-1850 at a regional scale, and a period of land-use expansion followed by regression AD 350-750 was identified. The land-use patterns were similar around the local study sites, with agricultural expansion during the 13^{th} century, partly abandoned landscape around AD 1400, re-establishment during the $15\text{-}16^{th}$ century and a transition from traditional to modern land-use during the 20^{th} century. Palynological richness responds within 20 to 80 years during agricultural expansion and regression both at regional and local scales, which provides quantitative estimates of the ecosystem resilience to land-use changes. During succession from open land to more tree covered habitats, floristic richness may increase temporarily during c. 40 years. The REVEALS and LOVE-based evenness introduced in this thesis reflects changes in landscape composition and the extent of available habitats. The more widespread agriculture from the 13^{th} to 19^{th} century was of substantial importance for achieving the high floristic diversity that characterizes the traditional landscape, which can allow species favoured by traditional management, succession and woodlands to coexist. The modern landscape is unusual in a centennial to millennial perspective with more habitats related to coniferous woods and fewer habitats related to deciduous trees and open land taxa, which may not be sustainable to preserve floristic diversity in the future. This thesis provides some examples of long-term (decadal to millennial scale) impacts of land-use changes on floristic diversity at regional and local scales, and the adopted approach is potentially a useful tool for conservation strategies when planning management within specific areas.

Key words: Pollen analysis, Floristic diversity, Quantitavite vegetation reconstructions, Ecosystem management

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This thesis is based on four papers listed below as Appendices I-IV. Paper I has been publised in Vegetation History and Archaeobotany. Paper II is submitted to Biogeosciences Discussions. Paper III and IV are unpublished manuscripts.

Appendix I: Fredh, D., Broström, A., Zillén, L., Mazier, F., Rundgren, M. and Lagerås, P. 2012. Floristic diversity in the transition from traditional to modern land-use in southern Sweden A.D. 1800–2008. Vegetation History and Archaeobotany 21, 6, 439-452.

Appendix II: Fredh, D., Broström, A., Rundgren, M., Lagerås, P., Mazier, F. and Zillén, L. The impact of land-use change on floristic diversity at regional scale in southern Sweden 600 B.C.-A.D. 2008. Submitted to Biogeosciences Discussions.

Appendix III: Mazier, F., Broström, A., Bragée, P., Fredh, D., Stenberg, L., Thiere, G., Sugita, S. and Hammarlund, D. Two hundred years of changing land-use in the South Swedish Uplands: pollen-based reconstructions using the Landscape Reconstruction Algorithm compared with historical maps. Manuscript.

Appendix IV: Fredh, D., Mazier, F., Bragée, P., Lagerås, P., Rundgren, M., Hammarlund, D. and Broström, A. The effect of local land-use change on floristic diversity around two lakes in southern Sweden A.D. 1000-2008. Manuscript.

Contents

1. Introduction

The rapid increase in human population and the development in technology during the last century have altered many ecosystems and the conditions for numerous species (Millennium Ecosystem Assessment, 2005). Anthropogenic activities are now recognised as the main driver of global environmental change, which has resulted in a general decline of biodiversity (Rockström et al., 2009; Barnosky et al., 2011). The ongoing extinction rate is several times higher than can be considered natural, and land-use is one of the most important drivers for this biodiversity loss (Sala 2000; Vitousek, 1997).

To preserve our biodiversity we need to develop a land-use system capable of combining production targets with preservation and promotion of biodiversity (Emanuelsson, 2009; Harrison et al. 2010). A global agreement, The Convention on Biological Diversity (CBD) was ratified in 1992 by 168 nations to address these problems, and includes aims for conservation and sustainable use of all aspects of biodiversity, such as genetic resources, species, and ecosystems (CBD, 1992). In 2010, CBD developed a new strategy that includes 20 biodiversity targets to be implemented internationally, which may help countries to establish and develop effective management of ecosystems (CBD, 2010).

The concept of ecosystem services is a useful tool to implement biodiversity targets (Harrison et al., 2010). This framework identifies services provided by natural ecosystems, for example cultural resources such as recreation and aesthetic values and production services such as food and timber. Using this approach it is easier to compare different ecosystems and make adequate priorities (Millennium Ecosystem Assessment, 2005).

Because land-use and ecosystem properties differ between regions, the conditions for implementation of such a framework vary (Millennium Ecosystem Assessment, 2005). In northwest Europe, areas with high biodiversity are often related to traditional agriculture, which has favoured many species over thousands of years (Berglund et al., 2008; Emanuelsson, 2009). One of the main problems in this region is the rapid transition from small-scale traditional agriculture to modern land-use with more focus on industrial agriculture and commercial forestry (Poschlod et al., 2005). The remaining areas with high biodiversity are few and fragmented, and nature conservancy management of these areas is not optimised to preserve species in a longer time perspective (Cousins, 2011; Emanuelsson, 2009).

In Sweden, most of the biodiversity strategies and action plans are integrated into several of the 16 environmental quality objectives that have been approved by the Parliament (National report, 2009). The authorities responsible for the objectives specifically relevant for terrestrial plant biodiversity are the Swedish Environmental Protection Agency (responsible for A Rich Diversity of Plant and Animal Life and Thriving Wetlands), the Swedish Board of Agriculture (responsible for A Varied Agricultural Landscape) and the Swedish Forestry Agency (responsible for Sustainable Forests).

To better manage the impact of future land-use changes on biodiversity we need a range of methods and tools to understand different ecological processes related to past and present land-use, such as direct observations, palaeoecological records, experiments, climate models, ecophysiological models and population models (Dawson et al., 2011). Because ecosystem responses may occur over decades or centuries, it is essential to increase our knowledge about the impact of historical land-use on biodiversity (Jackson and Hobbs, 2009; Willis and Bhagwat, 2010). Only palaeoecological methods provide continuous records of changes in vegetation composition over time, but such reconstructions are clearly strengthened by comparisons with historical maps and historical data (Willis et al., 2010; Haslett et al., 2010). To make the knowledge about long-term processes acquired through palaeoecological studies accessible and useful for ecosystem management requires an active strategy to merge reconstructions with observations made by ecologists and other scientists interested in the biodiversity of the modern landscape (Emanuelsson, 2009).

Ecosystem management may be defined as: 'Ecosystem management integrates scientific knowledge of ecological relationships within a complex socio-political and values framework toward the general goal of protecting native ecosystem integrity over the long term' (Grumbine, 1994). This definition includes the general goal to mitigate the loss of biodiversity by including human activities and occupancy as one important component within these ecosystems.

Palaeoecological methodologies have advanced in recent years, especially with regard to the quantification of past vegetation change (Davis, 2000; Sugita, 2007a; 2007b; Hellman et al., 2009). Based on pollen extracted from sediments, the Landscape Reconstruction Algorithm (LRA) has enabled new ways to study past land-use and biodiversity changes (Sugita, 2007a; 2007b). LRA compensates for biases related to how vegetation is represented in the pollen record, which makes it possible to quantify past vegetation composition within regional and local scales. This method also makes it possible to describe past floristic diversity using the two parameters richness and evenness. Previously, estimates of past floristic diversity have been restricted to the number of different pollen taxa found within a time interval as a proxy for floristic richness (Birks and Line, 1992). High evenness describes situations when all taxa within an area are represented by similar spatial coverage, whereas low evenness characterizes landscapes where a few species dominate the coverage (Van Dyke, 2008).

Previous studies based on fossil pollen assemblages commonly focused on long-term changes in a perspective of hundreds to thousands of years (Berglund, 1991; Berglund et al., 2008). However, to relate past vegetation changes to historical land-use development and modern ecology we need a research design allowing reconstructions at a higher temporal resolution. This involves the use of additional dating techniques not applied in traditional pollen studies.

Combining high-resolution pollen analysis with detailed absolute chronologies and quantitative estimates of vegetation and floristic diversity, we can estimate the rate and degree of change in land-use intensity and coverage in relation to floristic diversity. This approach allows for a better understanding of how current ecosystems will respond to present and future land-use changes and provides information useful for ecosystem management.

The aims of the study were to:

- Develop a study design to quantify changes in past land-use and floristic diversity based on pollen records of decadal resolution, using LRA, palynological richness and new ways to estimate past evenness.
- Analyse how agricultural land-use changes over the last three millennia in southern Sweden impacted on floristic diversity on regional and local spatial scales.
- Provide quantitative estimates of the rate of change in land-use coverage characterizing past periods of high floristic diversity, which may guide present and future ecosystem management.

2. Study area

2.1 Present day conditions

The study area is situated in the upland area of southern Sweden, here defined as the area above 200 m a.s.l., in the central part of the province of Småland (Fig. 1). Presently, the land-use is dominated by forestry, but grass and crop cultivation occur on the most suitable soils. The bedrock consists of crystalline bedrock of granitic and gneiss composition and is covered by sandy till and occasional glacifluvial deposits (Fredén, 1994). Mean annual temperatures are 5-7°C, and mean annual precipitation varies from 600 to 1,200 mm on an east-west gradient (Raab and Vedin, 1995). The study area is part of the boreo-nemoral zone characterized by woodland with a mixture of coniferous and deciduous trees, with *Picea* and *Pinus* as the dominant trees (Sjörs, 1963). The tree cover is 72%, shrubs 1%, herbs 21% and Cerealia (including Secale) 6% (Hellman et al., 2008b).

2.2 Regional land-use development

The general land-use history of the upland area of southern Sweden is known from palaeoecological studies, archaeological evidence and historical data. These data reveal a dynamic agricultural land-use pattern with expansion and regression phases during the last 6000 years (Hyenstrand, 1979, Lagerås, 1996; Berglund et al., 2002). The human impact has been relatively low as compared to lowlands and agricultural land-use was dominated by grazing (Berglund et al., 2002). Single farms dominated throughout agricultural history, but some settlements became organized in hamlets and villages during the Iron Age, 500 BC to AD 1050 (Myrdal and Morell, 2011). One important step in the land-use development was the transition from shifting cultivation to farming based on permanent fields, which became widespread in the uplands of southern Sweden around the 11th century (Emanuelsson, 2009). The shifting cultivation involved regular clearing of vegetation, which released nutrients sufficient for crop cultivation during a few years. In-between clearings the land was grazed for some time and lay fallow for long periods. Farming based on permanent cultivation was centred on fields close to the settlements. These fields received regular nutrient supply from meadows and pastures via livestock. This landscape had a clear separation between cultivated fields, meadows and common land around the farms (Berglund et al., 2002). During medieval times (c. AD 900-1200) there was a general land-use expansion in the uplands of southern Sweden. This expansion was interrupted by the late-medieval agrarian crisis, which resulted in an estimated abandonment of up to 50 percent of all farms (Myrdal, 2012). During the 16th century the population started to increase again, and farms were re-established (Lagerås, 2007). During the agricultural revolution (c. AD 1700-1900) arable fields were combined to form larger units, and the common land was split up and divided between farmers (Gadd, 2000). In addition, better management of manure, crop rotation, irrigation and marling led to a much higher production yield (Myrdal and Morell, 2011; Emanuelsson, 2009). As a complement to the permanent surfaces used for agriculture, temporary fields were cleared (slash-and-burn agriculture) and used for a couple of years, before they were allowed to overgrow by bushes and trees (Larsson, 1974). The maximum extent of agricultural land-use occurred in the late 19th century. During the last century small-scale agriculture changed towards modern land-use dominated by crop cultivation and commercial forestry (Antonsson and Jansson, 2011).

2.3 Local population history and site descriptions

The study sites, Lake Fiolen, Åbodasjön and Lindhultsgöl, are situated in the parishes Slätthög and Moheda (Fig. 1). These parishes were established around AD 1000, but the first population data is from AD 1571. By this time at least a few settlements were located within a few kilometres distance of the study lakes (Andersson Palm, 2000; Larsson, 1980). During the 18th century the population started to increase rapidly and a population peak was reached in the end of the 19th century, followed by a distinct decrease in rural population due to industrialization.

Lake Fiolen was selected to reconstruct the regional vegetation and Åbodasjön and Lindhultsgöl were considered suitable for local scale vegetation reconstruction. The latter two were also selected in relation to a research project investigating the causes of recent increases in lake-water dissolved organic carbon (DOC) concentrations observed in Scandinavia (Bragée et al., in prep).

Fiolen, situated at 226 m a.s.l., is an oligotrophic lake with an area of 1.60 km^2 and an estimated catchment of 5.1 km^2. The lake is situated within a nature reserve, consisting of arable fields and woodlands, and has been subjected to limnological research since the early 20th century. The lake is fed by two inlets, situated in the south and east, and the outlet is in the north. Several ditches drain into the lake from nearby woodlands.

Åbodasjön, situated at 221 m a.s.l., is an oligotrophic lake with an area of 0.53 km^2 and an estimated catchment of 12 km^2. The village of Åboda (40 residents in 2004) is situated west of the lake, and the area around the lake is open to semi-open with mainly broadleaved trees and cultivated fields. The remaining part of the catchment is dominated by managed coniferous woodland, peat deposits, grasslands and cultivated fields. The lake is fed by two inlets, situated in the south and north-east, and the outlet is in the south-west.

Lindhultsgöl, situated 212 m a.s.l., is a mesotrophic lake covering 0.07 km^2, and its catchment is estimated to 0.50 km^2. There are no natural inlets, and the outlet consists of an artificial ditch in the south. The catchment is dominated by

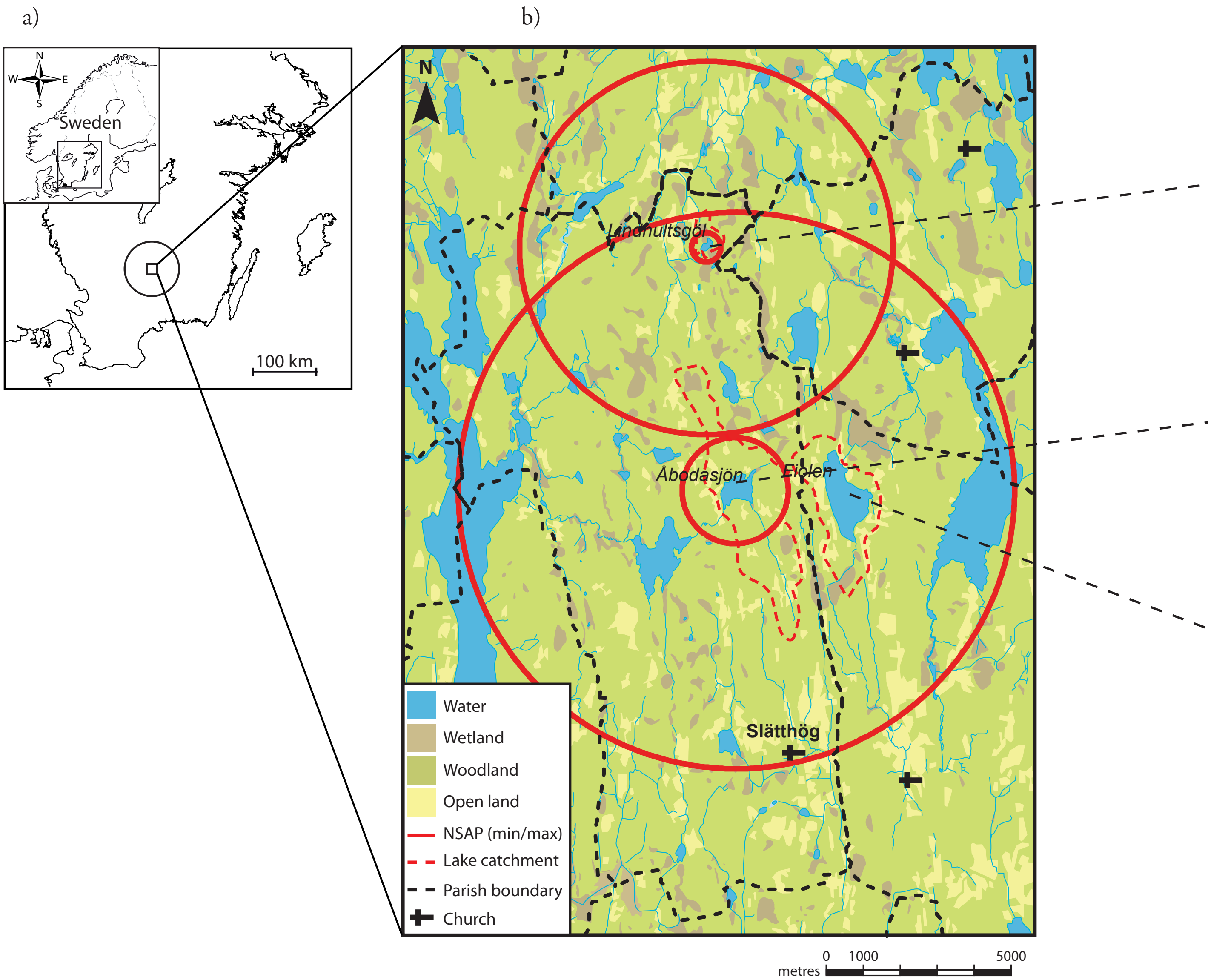


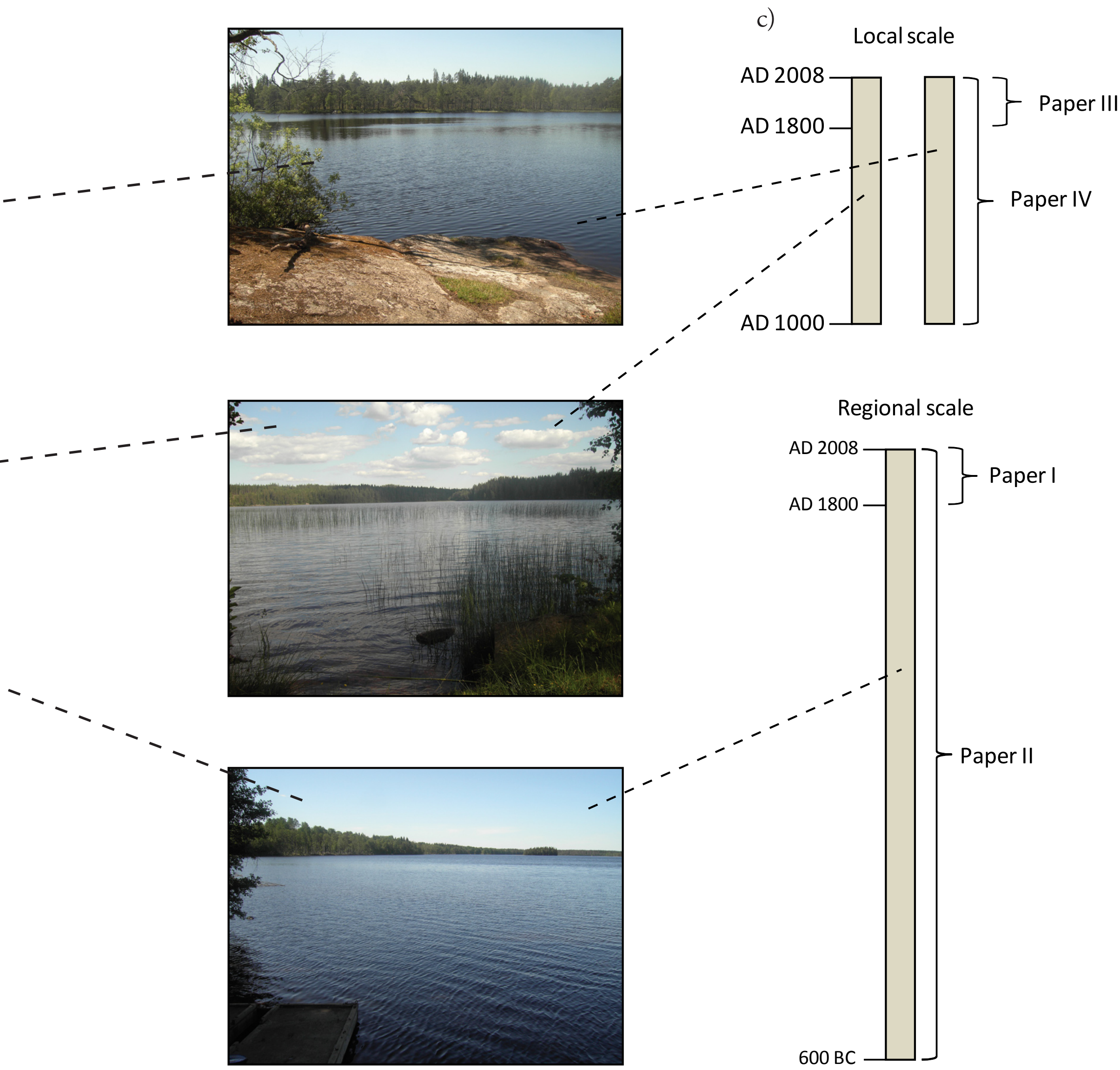
Figure 1. a) The study area in southen Sweden. The black circle (50 km radius) represents the regional area reconstructed. b) The investigated sites Lindhultsgöl, Åbodasjön and Fiolen, and the local areas reconstructed within the necessary source area of pollen (NSAP). c) Principal sketch of sediment cores and time periods used in Appendix I-IV.

managed coniferous woodland and peat deposits with shrubs and scattered pine trees. At least two ditches drain into the lake from nearby bogs and woodland.

3. Methods

3.1 Fieldwork, subsampling and core correlation

Sediment cores were retrieved from Lake Fiolen, Lake Åbodasjön and Lake Lindhultsgöl in spring 2008 (Fig. 2). The upper part of the sediment sequences were collected using a gravity corer (HTH-Kajak corer; Renberg and Hansson, 2008) and subsampled in the field into plastic boxes at contiguous 5 mm intervals. The lower parts of the sediment sequences were collected with piston and Russian corers (Jowsey, 1966) and sealed before transport to the laboratory in Lund. Subsamples from the sediment cores were taken out at varying intervals for analysis of pollen composition, charcoal analysis, spheroidal carbonaceous particle (SCP) content, mineral magnetic parameters, X-ray fluorescence spectroscopy (XRF), total organic carbon (TOC), stable Pb isotopes, radiocarbon (^{14}C) and ^{210}Pb dating. Correlations between the cores were carried out using mineral magnetic properties (Thompson et al., 1980) and element compositions based on the XRF measurements (Boyle, 2000).



3.2 Dating

3.2.1 Radiocarbon (^{14}C)

^{14}C dating was used to date organic remains in the sediment sequence. Macrofossil samples and bulk gyttja samples were dated using accelerator mass spectroscopy (AMS) at the Radiocarbon Dating Laboratory at Lund University. The macrofossils were extracted from the sediments using a 250 µm sieve. Only very small amounts were found, and terrestrial material was identified in most samples. Because of very small sample sizes, pre-treatment (HCl and NaOH) could only be carried out for three of the macrofossil samples. The OxCal program (v. 4.1.7) and the CaliBomb program were used for calibration of ^{14}C dates based on calibration curves constructed from terrestrial and atmospheric samples (Levin and Kromer, 2004; Levin et al., 2008; Reimer et al., 2009).

3.2.2 ^{210}Pb and ^{137}Cs

^{210}Pb dating was used to date the uppermost part of the sediment sequences spanning the last c. 150 years. Samples were analysed for the activity of ^{210}Pb, ^{137}Cs and ^{226}Ra via gammaspectrometry at the Gamma Dating Centre, Institute of Geography at the University of Copenhagen, Denmark. The fraction of total ^{210}Pb that is deposited on the lake surface from the atmosphere, i.e. the unsupported ^{210}Pb, was calculated based on the ^{226}Ra data

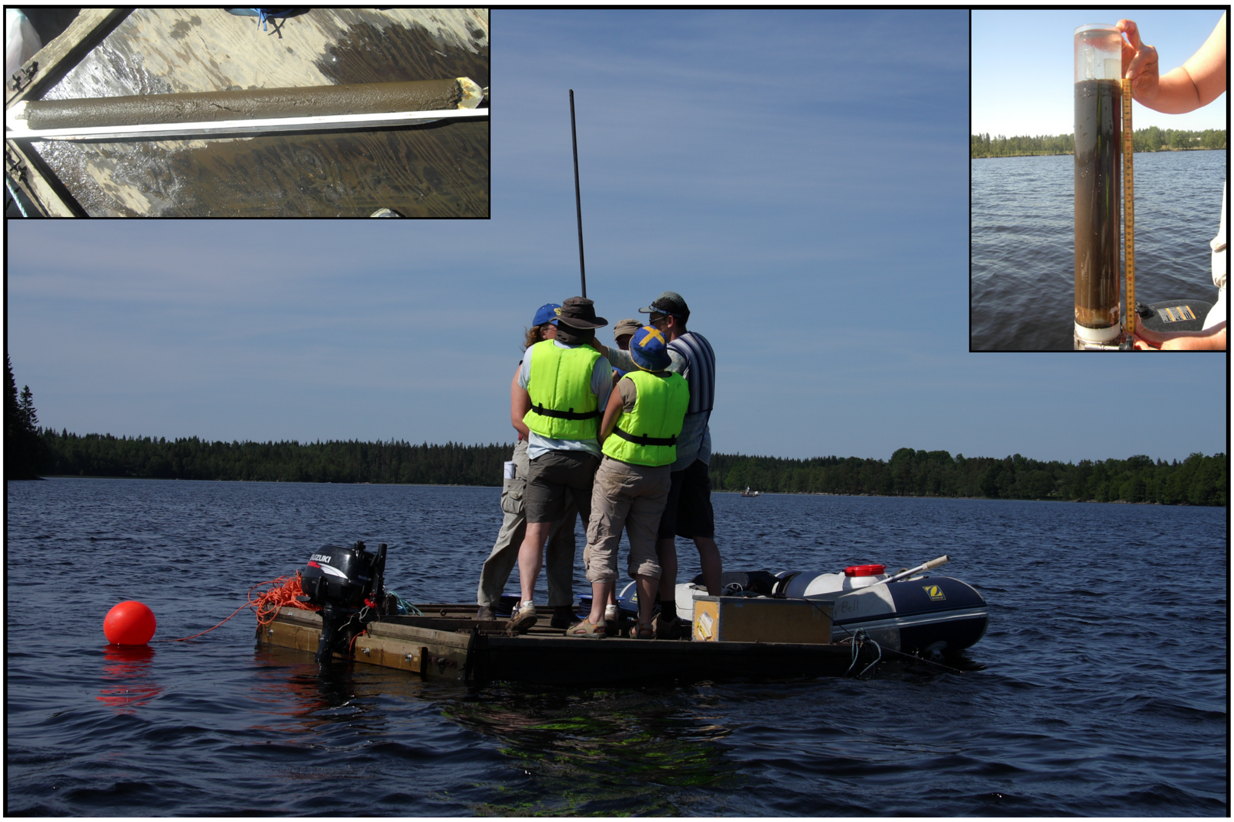


Figure 2. Sediment sampling in Lake Fiolen and examples of retrieved Russian and gravity cores.

obtained. Selected samples were included in the Constant Rate of Supply (CRS) model to calculate ages for each level (Appelby, 2001). Below the level for the lowermost sample the activity of ^{210}Pb was calculated by assuming a constant sedimentation rate. Variations in ^{137}Cs activity can be used as time markers and this isotope was therefore measured with the aim to validate the CRS-model (Appleby, 2001).

3.2.3 Lead pollution

Atmospheric lead deposition recorded in lake sediments originates from historical mining activities and emissions from combustion of leaded petrol. The pollution history, measured in sediments using total lead concentrations and lead isotope ratios ($^{206}Pb/^{207}Pb$), is similar between lakes in Sweden and may be used as a chronological framework (Brännvall et al., 2001; Renberg et al., 2001). Time markers may be identified at AD 0 (Roman peak), AD 900-1000 (Medieval expansion), AD 1200 (Medieval peak), AD 1975 (Modern maximum) and sometimes a few more. The highest amount of lead emissions occurred between the 1950s and the 1970s, and the highest lead concentrations in sediments are found in the interval corresponding to this age. Total lead concentrations in lake sediments show a gradient with higher values in the south compared to the north, which reflects the pattern of dispersal from south and central Europe. Sulphide ores used in medieval times had a typical lead isotope ratio of about 1.17 and emissions from petrol a typical ratio of 1.15. Both of these are lower than the natural isotope ratio of bedrocks in Sweden.

Lead was measured in selected samples using XRF to determine total lead concentration (Boyle, 2000), and using acid dissolution (EPA 3052) and Quadrapole ICP-MS to determine both total lead concentration and lead isotope composition. The XRF measurements were carried out at the Environmental Magnetism Laboratory at the Department of Geography, Liverpool University, UK, and the Acid Dissolution (EPA 3052) and Quadrapole ICP-MS measurements at the

Department of Geography, Durham University, UK. In the absence of a standard method to infer uncertainty estimates for the pollution markers, we used an approximation of 50 years uncertainty for all markers except the modern maximum at AD 1975, which was assigned an uncertainty of 5 years.

3.2.4 Spheroidal carbonaceous particles (SCP)

Several known events during recent centuries have had an impact on the environment and have left markers in the lake sediments. Here, we used spheroidal carbonaceous particles (SCP) as chronological markers to validate the chronology (Wik and Renberg, 1996). These markers are related to the burning of fossil fuels in transport and industry. SCP (<50 µm) were counted simultaneously with pollen on each slide (contiguous 0.5 cm) and due to low counts added together for each 5 cm interval.

3.3 Pollen and charcoal analysis

The samples for pollen analysis were prepared using standard methods and mounted on slides for further identification using a light microscope (Berglund and Ralska-Jasiewiczowa, 1986). Pollen grains were identified to species, genus or family level, facilitated by keys (Beug, 1961; Beug, 2004; Punt, 1976-2003; Moore et al., 1991) and the reference collection at the Department of Geology, Lund University. Phase contrast microscopy was used for detailed examination, for example for separation between different genera of Cerealia-type based on exine ornamentation (Beug, 2004).

Using the constructed chronologies, ages for each sample were estimated. Based on these age estimates, pollen counts from several levels were pooled together to attain at least 1000 grains for each time window. Time-window years were used to attain similar sample resolution throughout the sequences and to reduce the year-to-year variation in pollen proportions. These proportions may vary due to differences in weather conditions during the season of pollen production (Hicks, 1999; Autio and Hicks, 2004), but such influence is only relevant in the uppermost part of the sediment sequences where sedimentation rate and sample resolution are higher. For Fiolen 20-year time windows were used between AD 1800 and 2000 and 20-150 years between 600 BC and AD 1800. For Åbodasjön and Lindhultsgöl 20-year time windows were used between AD 1200 and 2000 and 50 years between AD 1000 and 1200. Charcoal fragments (10-200 µm) were counted simultaneously with pollen in samples from Lindhultsgöl. Charcoal concentrations were estimated based on counting of Lycopodium clavatum spores added to each sample in a known quantity (Stockmar, 1971).

3.4 Landscape reconstruction algorithm (LRA)

3.4.1 REVEALS and LOVE models

The LRA approach is an objective method to estimate vegetation composition by compensating for known biases in how vegetation are represented in the pollen record (Sugita, 2007a; 2007b). LRA integrates correction for pollen productivity, fall speed, wind speed and the distance from the plants. Previously, estimates of actual vegetation have been difficult to obtain due to differences in pollen productivity and dispersal characteristics between taxa (Sugita, 1994; Broström et al., 1998; 2004 Sugita et al., 1999; Davis, 2000; Sugita, 2007a; 2007b). Tree taxa are in general overrepresented, and many herb taxa often underrepresented, in pollen assemblages compared to their abundance in the surrounding vegetation (Bradshaw and Webb, 1985; Broström et al., 1998; 2004; Sugita et al., 1999; Davis 2000).

These new tools for modelling vegetation composition of past landscapes rely on a theoretical framework (Davis, 1963; Andersen, 1970; Parsons and Prentice, 1981; Prentice, 1985; Sugita, 1993), simulations (Sugita, 1994; Sugita et al., 1999), and on studies of the relationship between surface pollen assemblages and modern vegetation (Broström et al. 1998; 2004; 2005). The LRA approach comprises two steps (Sugita, 2007a; 2007b).

In the first step the submodel Regional Estimates of Vegetation Abundance from Large Sites (REVEALS), which uses pollen counts from large lakes (>100 ha), is used to quantify the regional

(10^4-10^5 km^2) vegetation composition (Sugita, 2007a). Simulations and empirical studies have shown that site-to-site variation in pollen loading between large lakes within a region is small and that the pollen composition in the sediments from such lakes correspond to the regional vegetation cover (Sugita, 1994; Hellman et al., 2008b). The REVEALS model has been empirically validated in Sweden, Switzerland and the USA (Hellman et al., 2008b; Soepboer et al., 2010; Sugita et al., 2010).

In the second step the LOVE model is used to reconstruct local vegetation (2-20 km^2) based on pollen counts from small lakes (1-100 ha), by compensation for the regional pollen loading obtained with REVEALS (Sugita, 2007b). The local scale is defined by the relevant source area of pollen (RSAP), which is the distance beyond which correlations between pollen loading and vegetation abundance do not continue to improve (Sugita, 1994). The background pollen loading that comes from beyond this distance can be considered as a constant for similar-sized lakes within a region at a specific time. Within the RSAP the pollen loading may vary between sites depending on local vegetation composition.

The size of the RSAP depends mainly on lake size and spatial patterns and patchiness of plant communities in the region (Sugita, 1994; Bunting et al., 2004; Broström et al., 2005; Sugita et al., 2010). The LOVE model includes an estimation of the necessary source of pollen (NSAP) at each site; this site-specific area is defined as the smallest radius at which all taxa included in the LOVE reconstruction reach positive values between 0.0 and 1.0 (Sugita, 2007b; Sugita et al., 2010). The 'LRA-based RSAP' satisfies this premise at all sites for all taxa and corresponds to the largest NSAP. In theory, the larger the number of sites studied, the more robust the estimate of the 'LRA-based RSAP'.

The LOVE model output is the sum of distance-weighted plant abundance (DWPA) within the RSAP which means that the LOVE model takes into consideration that plants closer to the sample point contribute more grains to the pollen assemblage that plants further away (Sugita, 2007b).

In this study, based on pollen counts from Lake Fiolen, the REVEALS program (v. 4.2.2, Sugita,

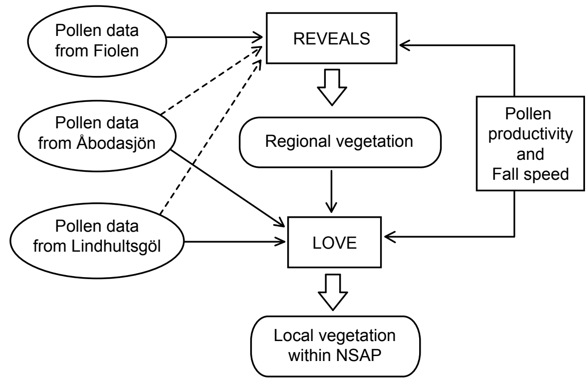


Figure 3. Flow chart illustrating how the Landscape Reconstruction Algorithm was used in this study to quantify past regional and local land-cover. In Appendix I and II, the REAVALS model was applied to pollen counts from Fiolen. In Appendix III and IV the REVEALS model was applied to pollen counts from Fiolen and Åbodasjön prior to LOVE modelling based on pollen counts from Lindhultsgöl. Similarly, the REVEALS model was applied to pollen counts from Fiolen and Lindhultsgöl prior to LOVE modelling based on pollen counts from Åbodasjön.

unpublished) was used to provide quantitative estimates of vegetation composition at a regional scale (within a 50 km radius). The REVEALS model was also used to estimate the regional background pollen for input to the LOVE model (Fig. 3). In addition, the LOVE model was used to quantify vegetation proportions within the RSAP at Åbodasjön and Lindhultsgöl, respectively. In these cases the regional pollen loading was estimated based on data from two sites, i.e., pollen counts from Lake Fiolen and Åbodasjön as background when the LOVE model was applied to Lindhultsgöl, and pollen counts from Lake Fiolen and Lindhultsgöl as background when the LOVE model was applied to Åbodasjön. Preliminary tests on our data have shown that REVEALS should be run on two sites in order to get reliable regional vegetation composition estimates (Appendix III).

3.4.2 Input parameters and assumptions

The REVEALS and LOVE models require raw pollen counts, various parameter inputs and assumptions. PPEs and standard errors for 26 taxa from southern Sweden and Denmark were used, and fall speeds of pollen from the literature (Eisenhut, 1961; Sugita et al., 1999; Broström et al., 2004; Nielsen, 2004; Broström et al., 2008). The LRA assumes constant PPE through time (Sugita, 2007a; 2007b). The REVEALS and LOVE versions used in this study (v. 4.2.2 and v. 3.2.0) assume neutral atmospheric conditions and that pollen is transported above the canopy and that wind is uniform in all directions with a speed of 3 m s^{-1} (Prentice, 1985; 1988; Sugita, 1993; 1994; 2007a; 2007b). The LOVE model assumes that the lake basin is circular. The site radius (m) is calculated from the total area (ha) assuming that the site shape is circular. The maximum spatial extent of the regional vegetation (Z_{max}) was set to 50 km, as most of the pollen grains found originate from within this area (Hellman et al., 2008a; 2008b) and different values (i.e. 50, 100 and 200 km) of this parameter have been shown not to affect the REVEALS output (Mazier et al., 2012). For each time window, the LOVE model calculates vegetation proportions within a circular area at an increasing distance away from the lake shore until the NSAP is reached. The pollen dispersal-deposition function specifically designed for lakes was used, Sugita's model, which assumes that pollen grains deposited on a lake surface are totally mixed and evenly deposited on the basin floor (Sugita, 1993). Standard errors for the estimates of regional and local vegetation abundance, respectively, were calculated in the REVEALS and LOVE programs using a hybrid of the delta method (Stuart and Ord, 1994) and Monte Carlo simulations (Sugita, 2007a).

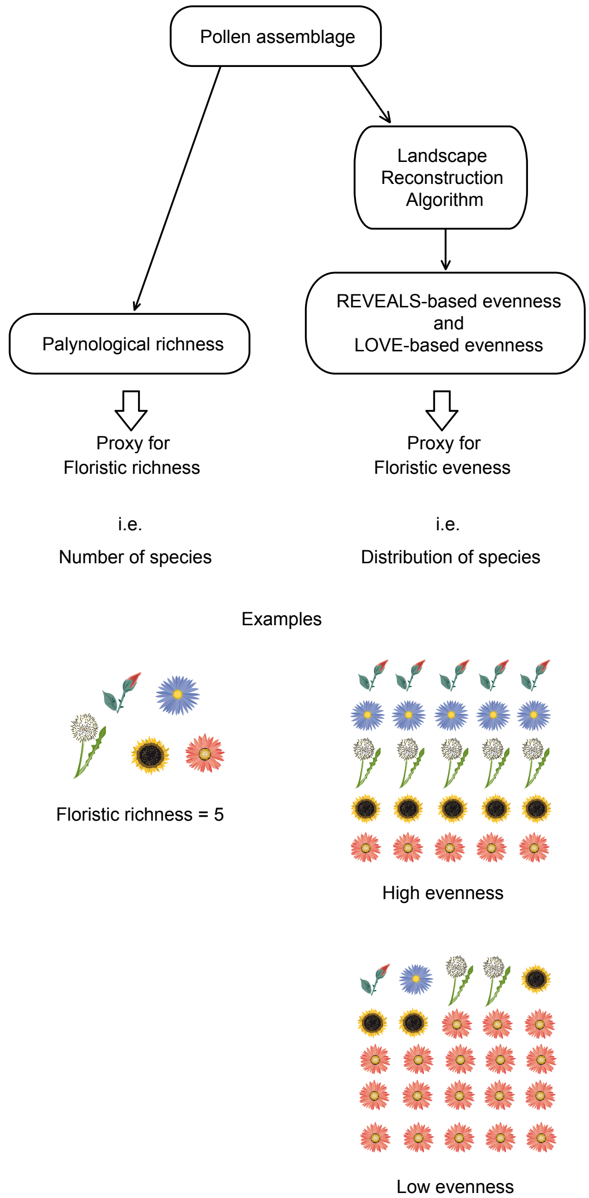


Figure 4. Principal sketch of how floristic diversity was reconstructed using palynological richness and REVEALS/LOVE-based evenness.

3.5 Qualitative Assessment of Difference (QAD)

The QAD method objectively assesses differences (> or = or <) in plant abundance of individual taxa between sites using pollen assemblages from two sites of similar size (Sugita et al., 2006). The QAD assumes similar RSAP and background pollen loading between sites, and in contrast to the LRA, the QAD output is not quantitative and the source area cannot be estimated. The QAD was applied to pollen counts from Åbodasjön and Lindhultsgöl and compared with the LOVE output. In this way the robustness of the LRA could be tested, and because the QAD result is independent of regional pollen loading the influence of this parameter in the LOVE model could be evaluated.

3.6 Reconstruction of floristic diversity

Floristic diversity is usually measured in the modern landscape using the two components richness and evenness (Van Dyke, 2008). Richness is the number of taxa and evenness is the relative abundance of taxa. High evenness describes situations when all taxa within an area are represented by similar spatial coverage, whereas low evenness characterizes landscapes where a few species dominate the coverage.

When studying past landscapes, palynological richness, the number of different pollen and spore taxa identified in a sample, is commonly used as a proxy for floristic richness (Odgaard, 1999). This measure can also be recalculated using rarefaction to compensate for differences in total pollen counts between samples so that different samples can be compared (Birks and Line, 1992). The palynological richness is therefore expressed as the expected number of pollen taxa for a constant pollen sum which is defined as the lowest pollen sum for a set of samples. The calculations in this study were based on all terrestrial taxa.

Estimates of past floristic evenness have rarely been attempted because it has not been possible to estimate vegetation proportions in the landscape. Moreover, a clear relationship between pollen sample evenness and surrounding vegetation has not been found (Odgaard, 1994; Meltsov et al., 2011). However, the quantitative estimates of vegetation cover provided by the REVEALS and LOVE models have now enabled estimates of past evenness. This study introduces REVEALS- and LOVE-based evenness as a proxy for floristic evenness on a regional and local scale, respectively. Based on the proportional abundances estimated by the REVEALS and LOVE models the Shannon index was calculated, which combines the number of taxa and the relative abundance of taxa to estimate floristic diversity (Magurran, 2004; Odgaard, 2007; van Dyke, 2008). Subsequently, floristic evenness was calculated for each sample using the ratio between Shannon index and maximum evenness, when all taxa are equally frequent, also known as the Pielou's evenness index (Pielou, 1966; Magurran, 2004; Odgaard, 2007). Pielou's evenness index may vary between 0 and 1. The index is 1 when all taxa cover equal proportions of the reconstructed area. Lower values are attained when a few taxa cover large proportions and other taxa cover small proportions within an area. LOVE-based evenness was estimated for all 26 taxa used in the REVEALS and LOVE calculations, but also for trees and herbs separately. In this way REVEALS- and LOVE-based evenness may be used in addition to palynological richness to provide a more complete reconstruction of past floristic diversity (Fig. 4).

3.7 Historical maps and aerial photographs

Historical maps and aerial photographs were used to estimate land-use changes and for comparison with the LOVE-output over the last 200 years. These maps and photographs are available in digital format at the Swedish Land Survey (www.lantmateriet.se), and were compiled within a two kilometre radius around Åbodasjön and Lindhultsgöl. Within these areas maps and photographs were available for four time periods, 22 maps from the early 19th century (the storskifte reform), 22 maps from the late 19th century (the laga skifte reform), six maps from AD 1946-1947 (Economic map) and one Orthophoto from AD 2005. The storskifte reform and laga skifte reform maps were produced to enable land-division between farmers and therefore mainly show the economic value of the lands (Gadd, 2000). From these maps it was possible to separate cultivated fields, meadows, common land, wetlands and lakes. The Economic map and the Orthophoto are based on aerial photographs, which provide more information about vegetation cover. From these aerial photographs it was possible to separate cultivated fields, grasslands, coniferous woodlands, deciduous woodlands, wetlands and lakes. After maps and photographs had been rectified, i.e. adjusted to the same scale and projection, and digitized using the ArcGIS 9.2 program, land-use categories were classified and their total areas calculated for each time period and lake. Land use categories were distance weighted using the same taxon specific function as in the LOVE model, to enable comparison with local vegetation estimates from the LOVE output.

3.8 Population data

A record of population changes within the 92 parishes located within a 50 km radius from Fiolen covering the last c. 200 years was compiled from a database hosted by Umeå University (http://www.ddb.umu.se/). The rural population within the region was estimated by subtracting the five largest parishes containing towns and/or large villages.

From the parish Slätthög, where Åbodasjön and Lindhultsgöl are situated, local population data were compiled for the period AD 1571-2000 based on church books and official population data (Andersson Palm, 2000).

4. Summary of papers

4.1 Appendix I

Fredh, D., Broström, A., Zillén, L., Mazier, F., Rundgren, M. and Lagerås, P. 2012. Floristic diversity in the transition from traditional to modern land-use in southern Sweden A.D. 1800–2008. Vegetation History and Archaeobotany 21, 6, 439-452.

Rapid land-use changes during recent decades have resulted in a global decline of biodiversity (Millennium Ecosystem Assessment, 2005). In southern Sweden, land-use types associated with high floristic diversity have generally decreased in favour of cultivated fields and forest plantations (Morell, 2001). This paper analyses the relationship between land-use and floristic diversity in the transition from traditional to modern land-use management during the period AD 1800-2008, which can be useful for current ecosystem management.

Based on pollen extracted from lake sediments, we used the Regional Estimates of Vegetation Abundance from Large Sites (REVEALS) model to quantify land-cover changes on a regional scale (50 km radius) at 20-year intervals. The REVEALS model corrects for biases related to how vegetation is represented in the pollen record, such as differences in pollen productivity and fall speed between taxa (Sugita, 2007a). This method also makes it possible to describe past floristic diversity using the two components richness and evenness. Previously, estimates of past floristic diversity have been restricted to the number of different pollen taxa found within a time interval as a proxy for floristic richness (Birks and Line, 1992). We introduce REVEALS-based evenness, which is a measure of the relative abundance of common taxa that are present within an area, by applying evenness indices to the REVEALS output.

We identified a transition period of 60 years between AD 1880 and 1940 when the total tree cover increased and the tree composition changed from deciduous to coniferous dominance. Within the shrinking area of open land, arable land taxa expanded, while the number and coverage of herbs in the remaining grasslands decreased. The succession from open grasslands to more tree-covered habitats initially favoured palynological richness, which reached its highest values during the first 40 years of the transition period. The highest REVEALS-based evenness was recorded in the time of traditional land-use and at the beginning of the transition period, reflecting higher habitat diversity at these time intervals. Our results support a more dynamic ecosystem management that changes between traditional land-use and phases of succession (<40 years) to promote floristic diversity. The palaeoecological methodology developed and applied in this study provides estimates of rate and degree of land-use and floristic diversity that may guide present and future ecosystem management.

4.2 Appendix II

Fredh, D., Broström, A., Rundgren, M., Lagerås, P., Mazier, F. and Zillén, L. The impact of land-use change on floristic diversity at regional scale in southern Sweden 600 B.C.-A.D. 2008. Submitted to Biogeosciences Discussions.

One of the main ecological challenges during this century is to mitigate the expected loss of species due to rapid land-use changes (Barnosky et al., 2011). In many regions, such as northwest Europe, agricultural land-use has influenced vegetation and biodiversity for thousands of years (Berglund et al., 2008). A better understanding of these historical responses is essential to make adequate priorities and implement realistic nature conservancy efforts, highlighting the importance of palaeobotanical records (Jackson and Hobbs, 2009).

This study explores the relationship between land-use and floristic diversity between 600 BC and AD 2008 in the uplands of southern Sweden. We focus on the period AD 350 to 750 to investigate the impact of an inferred, short-lived (<200 years) period of land-use expansion and subsequent land abandonment on vegetation composition and floristic diversity.

We use fossil pollen assemblages and the

Regional Estimates of Vegetation Abundance from Large Sites (REVEALS) model to quantitatively reconstruct land-cover at a regional scale (Sugita, 2007a). Floristic richness and evenness are estimated using palynological richness and REVEALS-based evenness, respectively. The observed vegetation response is compared to that recorded during the transition from traditional to modern land-use management at the end of the 19th century.

Our results suggest that agricultural land-use was most widespread between AD 350 and 1850, which correlates broadly with high values of palynological richness. REVEALS-based evenness was highest between AD 500 and 1600 which indicates a more equal distribution among taxa during this time interval. Palynological richness increased during the inferred land-use expansion after AD 350 and decreased during the subsequent

Table 1. Author contributions to Appendices I-IV.

	Appendix I	Appendix II	Appendix III	Appendix IV
Fieldwork	D. Fredh A. Broström L. Zillén F. Mazier M. Rundgren P. Lagerås	D. Fredh A. Broström L. Zillén F. Mazier M. Rundgren P. Lagerås	P. Bragée F. Mazier A. Broström D. Hammarlund	P. Bragée F. Mazier A. Broström D. Hammarlund
Core correlation and sample preparation	D. Fredh	D. Fredh	P. Bragée	P. Bragée
Mineral magnetic measurments	D. Fredh	-	-	-
X-ray fluorescence measurements	D. Fredh	D. Fredh	P. Bragée	P. Bragée
Age-depth model construction	D. Fredh M. Rundgren L. Zillén A. Broström P. Lagerås	D. Fredh M. Rundgren L. Zillén A. Broström P. Lagerås	P. Bragée D. Fredh D. Hammarlund	P. Bragée D. Fredh D. Hammarlund
Pollen analysis	D. Fredh	D. Fredh	F. Mazier D. Fredh	F. Mazier D. Fredh
Charcoal analysis	-	-	-	D. Fredh
Spheroidal carbonaceous particle analysis	D. Fredh	-	-	-
'Landscape Reconstruction Algorithm' modelling	D. Fredh	D. Fredh	F. Mazier	D. Fredh
Palynological richness and REVEALS/ LOVE-based evenness calculations	D. Fredh	D. Fredh	-	D. Fredh
'Qualitative Assessment of Difference' modelling	-	-	F. Mazier	-
Historical maps and aerial photographs treatment	-	-	A. Broström L. Stenberg D. Fredh G.Thiere	-
Data interpretation	D. Fredh A. Broström L. Zillén F. Mazier M. Rundgren P. Lagerås	D. Fredh A. Broström L. Zillén F. Mazier M. Rundgren P. Lagerås	F. Mazier A. Broström P. Bragée D. Fredh S. Sugita D. Hammarlund	D. Fredh A. Broström F. Mazier P. Lagerås M. Rundgren P. Bragée D. Hammarlund

regression AD 550-750, while REVEALS-based increased throughout this period. The values of palynological richness during the last few decades are within the range observed during the last 1650 years. However, REVEALS-based evenness shows much lower values during the last century compared to the previous c. 2600 years, which indicates that the distribution of present day vegetation is unusual in a millennial perspective. Our results show that regional-scale changes in land-use have had clear impacts on floristic diversity in southern Sweden, with a vegetation response time of less than 20 to 50 years. Moreover, they show the importance of traditional land-use to attain high biodiversity and suggest that ecosystem management should include a regional landscape perspective.

4.3 Appendix III

Mazier, F., Broström, A., Bragée, P., Fredh, D., Stenberg, L., Thiere, G., Sugita, S. and Hammarlund, D. Two hundred years of changing land-use in the South Swedish Uplands: comparison of pollen-based reconstruction using the Landscape Reconstruction Algorithm with historical maps. Manuscript.

Understanding the effects of human land-use changes on terrestrial and aquatic ecosystem is fundamental for development of environmental management strategies. Long-term records on decadal to millennial time scales based on natural archives enable assessment of ecosystem variability and responses to past human-induced disturbances and may be linked to modern monitoring data. Lake sediments offer a multitude of ecological, physical and chemical proxies for reconstruction of past environmental changes in lakes and their surrounding landscapes in response to human impact (Willis and Birks, 2006; Renberg et al., 2009).

This study explores the spatial and temporal land-use variability in southern Sweden during the last 200 years at 20-year intervals based on pollen analysis of lake sediments. Local quantitative estimates of plant abundance based on 14 taxa around two lakes, Åbodasjön and Lindhultsgöl, in the uplands of southern Sweden were obtained using the recently developed Landscape Reconstruction Algorithm (LRA).

The direction of difference between the LRA-based estimates from the two lake sites was compared using the Qualitative Assessment of Difference (QAD) method (Sugita et al., 2006). This method is designed to enable objective comparison of the local vegetation composition for individual taxa between two nearby sites. The two methods yielded generally consistent results with the exception of rare taxa at a few levels, which demonstrates that differences in LRA-based vegetation estimates can be confidently ascribed to ecological differences between the two lakes.

The performance of the LRA approach was evaluated by comparing LRA-based estimated for four land-use categories (cropland, grassland/meadows, wetland, outland/woodland) to land-use abundance derived from historical maps (storskifte reform, laga skifte reform and Economic map) and Orthophoto. The reconstructed vegetation is broadly similar to the observed one, although the model tended to overestimate grassland cover by 10–30% for the last two maps.

The results show that landscape around Åbodasjön is mainly dominated by mixed-forest and meadows while wetlands are more common around Lindhultsgöl, and the land use has been more variable around Lindhultsgöl than around Åbodasjön over the last 200 years. Around Åbodasjön the coverage of deciduous trees increased significantly in the late 19th century followed by an expansion of coniferous woodlands until today, which mainly reflect reduced grazing pressure allowing succession from open grasslands to woodlands, while around Lake Lindhultsgöl the woodland becomes dominated by *Picea* from 1960.

Although it is not possible to distinguish the differences in spatial structure of vegetation within the reconstructed local area, the LOVE model can give information of land-use dynamics over shorter time intervals and with larger coverage for a specific time window than a series of cadastral maps. Such reconstructions can be strengthened by comparisons with historical maps and historical data in order to better assess the spatial pattern of vegetation within the RSAP.

The results on land-use dynamics will be useful for a better understanding of the effect of land-use change on terrestrial and aquatic system and for conservation strategies by demonstrating and quantifying variability in spatial and temporal diversity of vegetation composition in the past.

4.4 Appendix IV

Fredh, D., Mazier, F., Bragée, P., Lagerås, P., Rundgren, M., Hammarlund, D. and Broström, A. The effect of local land-use change on floristic diversity around two lakes in southern Sweden A.D. 1000-2008. Manuscript.

Anthropogenic influence during recent decades has resulted in a decline of biodiversity mainly due to rapid land-use changes (MacDonald et al., 2008). To mitigate further loss of species the development of a land-use system capable of combining production targets with preservation of biodiversity is needed (Harrison et al., 2010). In many regions, the modern land-use is unusual in a longer time perspective (Sala, 2000). In northwest Europe, species-rich areas related to traditional agriculture have become fragmented and remain as islands in the modern production landscape, which are clearly divided between cultivated fields and commercial forestry (Poschlod et al., 2005).

In this study the relationship between land-use and floristic diversity is analysed around two lakes in southern Sweden, Åbodasjön and Lindhultsgöl, over the last thousand years. Pollen analysis and the Local Vegetation Estimates (LOVE) model are used to quantify land-cover at local scales with high resolution (20 to 50 years). Floristic richness is estimated using palynological richness, and we introduce LOVE-based evenness as a proxy for floristic evenness on a local scale based on the LOVE output. The results reveal a dynamic land-use pattern, with agricultural expansion during the 13th century, partly abandoned landscape around AD 1400, re-establishment during the 15-16th century and a transition from traditional to modern land-use during the 20th century. The inferred response time of c. 20 years of palynological richness during rapid agricultural expansion indicates how fast plants can spread across areas that have been cleared. Succession from open land to more tree-covered landscape may favour floristic richness during a period of about 40 years.

The results indicate that more widespread agriculture during the 13th to 19th centuries was of substantial importance for attaining the high floristic diversity that characterizes the traditional landscape. The modern land-use, with more habitats related to coniferous woodland and fewer habitats related to deciduous trees and open land taxa, may not be sustainable to preserve floristic diversity in the future. The variability of the past agricultural landscape provides information about land-use types that promote floristic diversity, which is useful for nature conservancy when planning the management within a specific area.

5. Challenges/approaches to study past land-use and biodiversity

This study has developed and applied a methodology to analyse past land-use and floristic diversity dynamics. The adopted approach includes high-resolution pollen analysis, a combination of detailed chronological methods, quantitative vegetation reconstruction, historical maps and quantitative estimation of floristic richness and evenness. With this approach it is possible to estimate the rate and degree of change in land-use and floristic diversity.

5.1 Quantitative land-cover reconstructions

Quantification of past vegetation composition was made using the LRA, which includes the REVEALS and LOVE models and converts raw pollen data into vegetation coverage at regional and local scales (Sugita, 2007a; 2007b). These sub-models make it possible to quantify the degree of vegetation change through time, and therefore objectively interpret pollen diagrams and compare different sites. This is one of the first times these models have been used in southern Sweden (Sugita et al., 2008). Because error estimates are included in the REVEALS and LOVE estimates, it is also possible to identify significant changes of vegetation cover.

The REVEALS model was run with input of fossil pollen data from one large lake (Fiolen, 160 ha, Appendix I-II), which should be sufficient to describe the regional vegetation cover (Sugita, 1994;

2007a; Hellman et al., 2008b). However, pollen assemblages may vary through time between and within lakes as an effect of sediment focusing or inaccurate chronologies. Therefore, to estimate the regional vegetation composition based on the REVEALS model it is preferable to use several lakes (Sugita, 2007a; Hellman et al., 2008b). For the subsequent LOVE-modelling, we used two lakes to estimate the regional pollen loading, which should provide more reliable estimates (Appendix III-IV).

The LOVE model output is distance weighted, which means that LOVE compensates for the fact that taxa growing closer to the lakes contribute more to the pollen recorded than plants growing at a greater distance. However, because we do not know the distribution of the plants that contributed to the pollen assemblages, the interpretations above assume that that the changes in vegetation, reflected by the DWPA records occurred at similar distances from the lakes (Sugita, 2007b). Theoretically, an increase in DWPA could reflect either an expansion in coverage or that plants moved closer to the lake shore. However, it is reasonable to assume that most of the changes in DWPA represent actual changes in vegetation cover.

The LOVE model quantifies vegetation composition within the RSAP, i.e. the smallest area for which it is possible to quantitatively reconstruct vegetation based on pollen counts (Sugita, 1994; Sugita, 2007b). If several sites are used in the LOVE model, the largest NSAP is used to calculate vegetation composition for each specific site (Sugita 2007b). In this study, the LOVE model was run based on pollen data from two relatively small lakes, Åbodasjön (50 ha) and Lindhultsgöl (7 ha), separately. The NSAP provided is therefore different for these lakes; the generally smaller NSAP for Lindhultsgöl is reasonable considering the smaller lake size. The NSAPs are rather variable through time for both lakes. This indicates that spatial patterns and patchiness of plant communities in the region have changed, which has a strong influence of the RSAP size (Bunting et al., 2004; Broström et al., 2005). However, more local variations in pollen assemblages possibly have the same effect.

Based on the REVEALS and LOVE outputs we have interpreted land-use changes throughout the studied periods. Agricultural land-use were mainly identified using the coverage of Cerealia, Poaceae and herbs, which can be related to different land-use types common in the traditional agricultural landscape. We also used other taxa that are favoured by open land, such as *Juniperus* and *Corylus*. These interpretations were strengthened by changes in woodland species, such as *Carpinus*, *Fraxinus* and *Quercus*. The openness, which includes all open land taxa, gives an estimate of the extent of agricultural land-use. In this way, periods of agricultural expansion and regression could be identified. Periods of succession from open land to more tree-covered vegetation were also identified. These successions could be related to abandonment of open land for example after the late medieval crises AD 1350 or during the transitions from traditional to modern land-use management around AD 1900.

For some pollen taxa, the interpretation of land-use types is not straightforward. This is especially true for Poaceae, which includes a large group of species that may react differently to land-use changes (Broström et al., 2008). A change in Poaceae coverage and other herbs could be interpreted both as an expansion and a regression. For example, during decreased grazing pressure, the pollen production could increase initially due to increased possibility to flower, which could be interpreted as an expansion of grasslands. During the transition from traditional to modern land-use, the areas used for agriculture was reduced, but the coverage of Poaceae, reflected by the REVEALS and LOVE model, increased or remained at a similar level in our records. This can be explained by the introduction of grass cultivation on the fields, which compensated for the decreased extent of meadows and pastures. Grasses are also present in both meadows and pastures, which are two separate land-use categories in the traditional agriculture, and are therefore not possible to separate by the coverage of Poaceae alone.

The QAD method was used to provide objective comparison of the difference in local vegetation composition between Åbodasjön and Lindhultsgöl over the last 200 years, which can be compared with the LOVE output. The results show a good agreement between the two approaches, except for some cases when the rare taxa are considered.

Therefore for the concerned taxa and time intervals, interpretation of the LRA-based estimates needs caution, while for the other cases where we have a good agreement between the two approaches. In this way, the QAD method can be used to test the reliability of the LRA output.

5.2 Comparison with historical maps and aerial photographs

Land-use changes during the last few centuries can also be inferred from historical maps and aerial photographs. Local-scale historical maps were produced in Sweden from the 17th century, mainly to estimate the economic value of the lands. These maps separated between cultivated fields, meadows and common lands, but rarely contained any information about vegetation composition (Myrdal and Morell, 2011). The common lands were mainly used for grazing and for wood collection, but the ratio between these land-use types is usually unknown. In contrast, separation between tree coverage and open land in aerial photographs is straight forward. Although historical maps and aerial photographs are heterogeneous in temporal and spatial coverage, they can provide estimates of land-use changes, and in combination with LOVE reconstructions they provide a more complete picture of land-use and vegetation changes.

In this study historical maps and aerial photographs from four time periods were compiled within a two kilometre radius, and used for comparison with LOVE model over the last 200 years on local scale (Appendix III). The main difficulty was to assign taxa composition in the land-use categories and to estimate tree-cover in meadows and common lands. The comparison was made on land-use level, i.e. the taxa from the LOVE output had to be grouped to match the land-use categories: cultivated fields, meadows/grasslands, wetland and common land/woodland. Each taxon was assigned to a unique land-use category although most taxa can potentially grow in several land-use types. The land-use categories from the historical maps and aerial photographs were distance weighted to enable comparison with the LOVE output. However, the historical maps were not available in all areas within the two kilometre radius and the storskifte and laga skifte reform maps were produced AD 1769-1826 and 1837-1895, i.e. over a time period of 57 and 58 years, respectively. For several time intervals the NSAP is larger than two kilometre radius from where maps were compiled, and the comparison is therefore not ideal. But the historical maps and the aerial photographs also provide a result of their own and show the amount and distribution of the land-use categories which are not possible based on the LOVE model alone. In general the LOVE model gives broadly similar results to those obtained with historical maps around Åbodasjön and Lindhultsgöl. However, at some time periods the croplands, wetlands, meadows are overestimated and outlands and woodlands are underestimated by the LOVE model compared to historical maps and aerial photographs.

5.3 Reconstructing floristic diversity

Palynological richness (the number of different pollen and spore taxa identified in a sample) and rarefaction analysis were used in this study as proxies for floristic richness (Birks and Line, 1992). However, the pollen grains found in sediments only represent a small portion of all species in surrounding vegetation, which is mainly due to the low taxonomic resolution possible in pollen identification for the large families Poaceae and Cyperaceae (Meltsov et al., 2011; Odgaard, 2007). Meltsov et al. (2011) suggested that the correlation between palynological richness and floristic richness may be a result of more effective pollen dispersal in open areas due to better connection between open areas, which allows more rare pollen to enter the lake. Furthermore, total pollen productivity is lower in open areas which allow pollen grains from low pollen producers to be better represented in the pollen assemblage (Odgaard, 1999; Peros and Gajewski, 2008; van der Knaap, 2009). These may partly explain the increased palynological richness during periods of increased openness, in addition to the fact that unfertilized grasslands are species rich (Meltsov et al., 2011).

In this study we have introduced REVEALS-and LOVE-based evenness (Appendix I-IV), which are new ways of estimating floristic evenness at regional and local scales based on the REVEALS and LOVE outputs (Magurran, 2004; Sugita 2007b). This approach has clear advantages compared to using raw pollen data for evenness calculations because it involves correction for a number of major biases related to pollen dispersal and deposition (Odgaard, 1999; Sugita, 2007a; 2007b). However, when using LOVE-based evenness we have to assume that the DWPA represents actual vegetation cover. Because this is not always the case, our LOVE-based evenness values should be considered tentative. REVEALS- and LOVE-based evenness is also limited to taxa for which pollen productivity estimates are available. The 26 taxa for which PPEs are currently available in southern Sweden represent about 70-90% of the total vegetation cover in the upland area of southern Sweden today (Broström et al., 2004). Because these taxa are generally dominated by trees, evenness mainly reflects tree evenness. However, in combination with richness estimates the use of evenness gives new possibilities to study past diversity changes. Some indirect information can also be gained from the REVEALS- and LOVE-based evenness records. Because REVEALS- and LOVE-based evenness reflects changes in landscape composition, this parameter indicates to which extent different habitats are available through time.

5.4 Constructing absolute chronologies

To study land-use and biodiversity development at high temporal resolution requires robust chronologies. In this study we used a number of different approaches to establish such chronologies, including ^{14}C, ^{210}Pb and ^{137}Cs dating and identification of time markers related to human activities (lead pollution and SCP).

To construct reliable ^{14}C chronologies for lake sediment sequences that contain only few and small (<2 mg) macrofossils is challenging. Small macrofossils cannot be fully pre-treated and are therefore prone to modern contamination. Terrestrial macrofossils can also remain on the ground for some time before deposition on the lake floor and therefore yield too old ages. Furthermore, radiocarbon dates obtained on macrofossils with a lacustrine origin or on bulk sediments are likely to be associated with a reservoir age related to the non-balance between the ^{14}C activity of the atmosphere and the lake water.

^{210}Pb dating uses a series of down-core measurements of ^{210}Pb-activity to create an age/depth model for the uppermost part of a sediment sequence (the last c. 150 years). ^{210}Pb is formed both within the sediment and derived from the atmosphere, and the separation between these two sources is calculated based on the ^{226}Ra-activity of the samples (Appelby, 2001). The subsequent modelling is depended on accurate calculation of these portions and that the elements have not been transported vertically in the sediment. ^{137}Cs can potentially be used to verify the age/depth model based on the ^{210}Pb measurements.

Measurements of total lead concentrations and lead isotope ($^{206}Pb/^{207}Pb$) ratios can be used to identify time markers at specific levels in a sediment column. Variations in these parameters are related to historical mining and have been studied in detail using varved lake sediments in northern Sweden. This pattern is similar in southern Sweden although not known in the same detail. In some sediment sequences the interpretation of these variations may be difficult, especially the separation of the Roman and the Medieveal peaks in lead concentrations.

In this study, it was surprisingly difficult to establish a detailed absolute chronology for Lake Fiolen, as reflected by the two alternative chronologies used in Appendix I-IV (Fig. 5). In Appendix I, the chronology was based on ^{210}Pb and extrapolated back to AD 1800. This option was supported by higher SCP and total lead concentration in the upper part used as time markers in sediment younger than AD 1940. However, during the course of this study more chronological data further back in time became available, and all of these were not consistent with the ^{210}Pb chronology and not in agreement with each other. Therefore, a number of OxCal runs were made (Bronk Ramsey, 2008; 2009), including

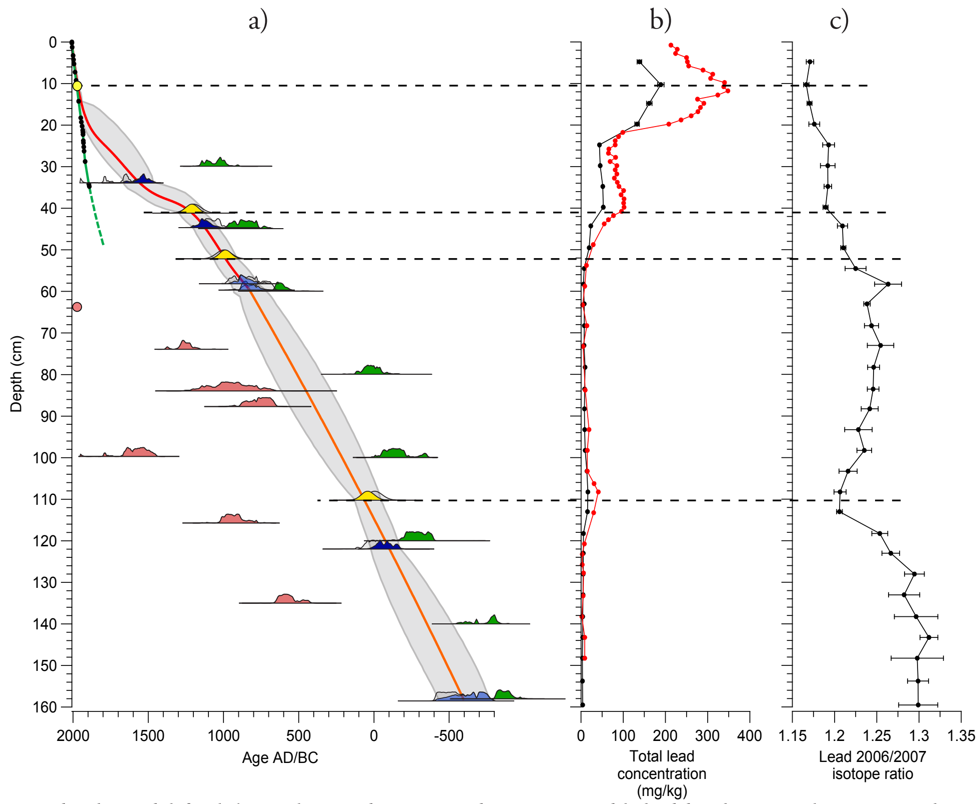


Figure 5. (a) Age-depth model for lake Fiolen used in Appendix II-IV, established by the OxCal program when including six radiocarbon dates based on three large (>2 mg) macrofossils (dark blue) and three small (<2 mg) macrofossils (light blue), a CRS-model based on nine ²¹⁰Pb samples (black dots above 15 cm), and four lead pollution markers (yellow, Brännvall et al., 2001). Seven radiocarbon dates based on small macrofossils (red), eight bulk radiocarbon dates (green) and all ²¹⁰Pb samples below 15 cm were excluded when constructing the model. Two polynomial functions, one above (red line) and one below 60 cm (orange line), with a polynomial order of seven and two, respectively, were fitted to the midpoints of the calibrated 2σ intervals (grey) provided by OxCal and used to calculate ages for the sequence at 0.5 cm intervals. Green line represents the age/depth model used in Fredh et al. (2012, Appendix I). (b) Total lead concentrations measured using Quadrapole ICP-MS (black line) and XRF (red line), respectively. (c) Lead isotope 206/207 ratio.

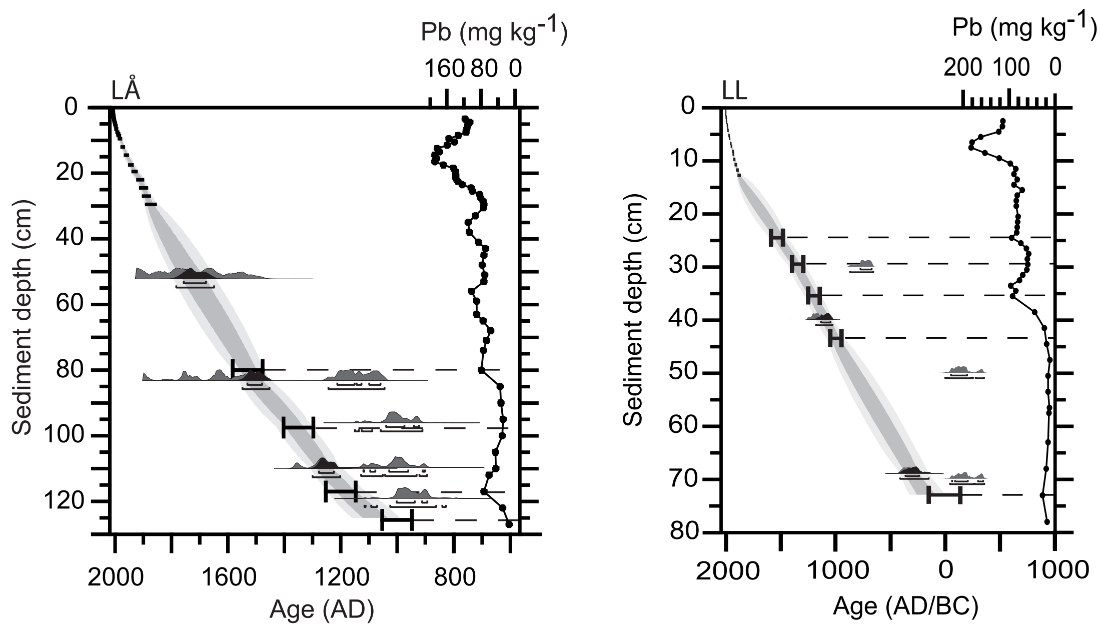


Figure 6. Age-depth models for Åbodasjön and Lindhultsgöl used in Appendix III-IV, based on radiocarbon dated macrofossils, ²¹⁰Pb and lead pollution markers (Bragée et al., in prep).

various sets of chronological data, based on different assumptions of which chronological data that were most reliable and with different interpretations of lead concentration and lead isotope ($^{206}Pb/^{207}Pb$) ratios. The preferred chronology used in Appendix II-IV included most large dated macrofossils samples and four inferred time markers from lead pollution. However, using this option a number of small macrofossil and ^{210}Pb measured samples had to be rejected.

One possible alternative was to choose a chronology that follows the trajectory of the ^{210}Pb-based chronology, which however includes a lower amount of dated macrofossil samples and requires a different interpretation of the lead concentration and lead isotope ($^{206}Pb/^{207}Pb$) ratios.

The inconsistencies in the chronological data provided by the different methods for Lake Fiolen means that the suggested chronology is tentative and that the absolute age for land-use and floristic diversity changes at a regional scale is uncertain. However, the relative changes in land-use and floristic diversity are certain and detailed, i.e. many densely spaced pollen samples were analysed levels and reveal no obvious mixing of sediments. Therefore the Fiolen record provides useful examples of vegetation change and timing of landscape processes, such as succession from open land to woodland and response times, even though the absolute ages are uncertain.

The difficulty with establishing a chronology for Fiolen means that the use of pollen data from this lake is not ideal to estimate the background pollen loading input for the LOVE model. However, Appendix IV showed that, when combining two lakes for background pollen loading, the differences in the LOVE output are very similar no matter which chronology is used.

For Lake Åbodasjön and Lake Lindhultsgöl, the described dating methods were more consistent and therefore provided relatively reliable chronologies for the sediment sequences, used in Appendix III and IV (Fig. 6).

6. Relationships between land-use and floristic diversity: implications for ecosystem management

This study provides some examples of long-term (decadal to millennial scale) impacts of land-use changes on floristic diversity at regional and local scales that can be useful for ecosystem management. Land-use changes were identified based on REVEALS and LOVE output, mainly for land-use indicators, such as Cerealia, Poaceae and herbs. Historical maps and aerial photographs were used in combination with the LOVE output over the last 200 years. Floristic diversity was estimated using the two components richness and evenness, inferred from palynological richness and REVEALS/LOVE-based evenness, respectively.

6.1 Regional scale

Based on pollen counts from Lake Fiolen sediments and the REVEALS model, regional (50 km radius) land-use and floristic diversity were estimated for the last 2600 years (Appendix I-II). These reconstructions show that floristic diversity can react rapidly to regional land-use changes. During the inferred agricultural expansion at AD 350-550, both palynological richness and REVEALS based evenness increased within 20-50 years after the first sign of expansion (Fig. 7). During this period, the coverage of Cerealia, Poaceae and herbs increased was more than doubled, which suggests that many plants are favoured by expansion of cultivated fields and grasslands at regional scale. Similarly, during the agricultural regression at AD 550 there was a rapid decline (within less than 20 years) in palynological richness. These response times show how fast and to what extent ecosystems may respond to regional land-use changes.

The land-use decline at AD 550 was identified by the succession from open land taxa to more tree coverage, first by early successional trees such as *Betula* followed by late successional trees such as *Carpinus*, *Quercus*, *Tilia* and *Ulmus* (Appendix II). REVEALS-based evenness increased to their highest values (0.83) in the late successional phase (AD 650-750) because of the increased coverage of several of the broadleaved trees, despite that

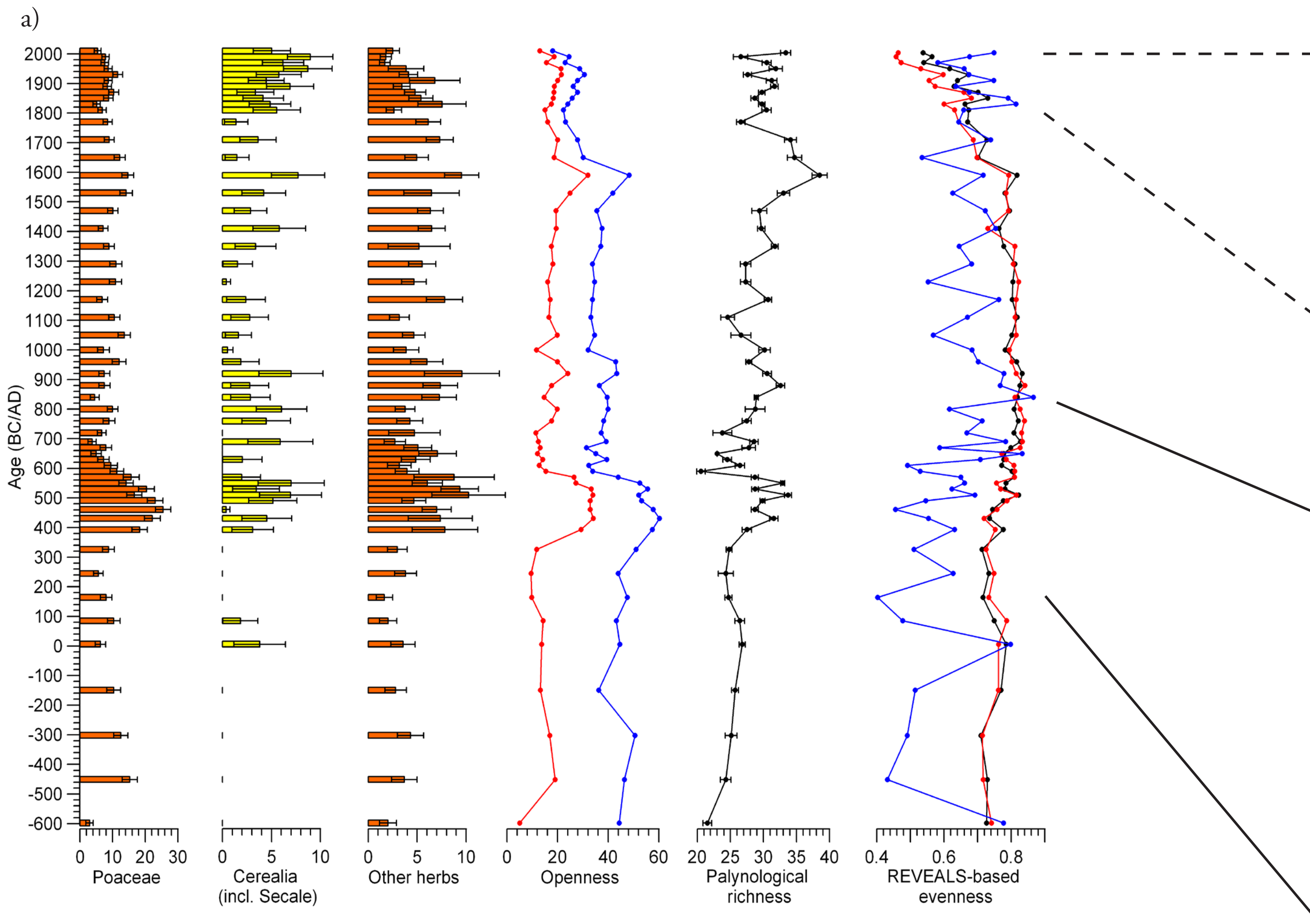
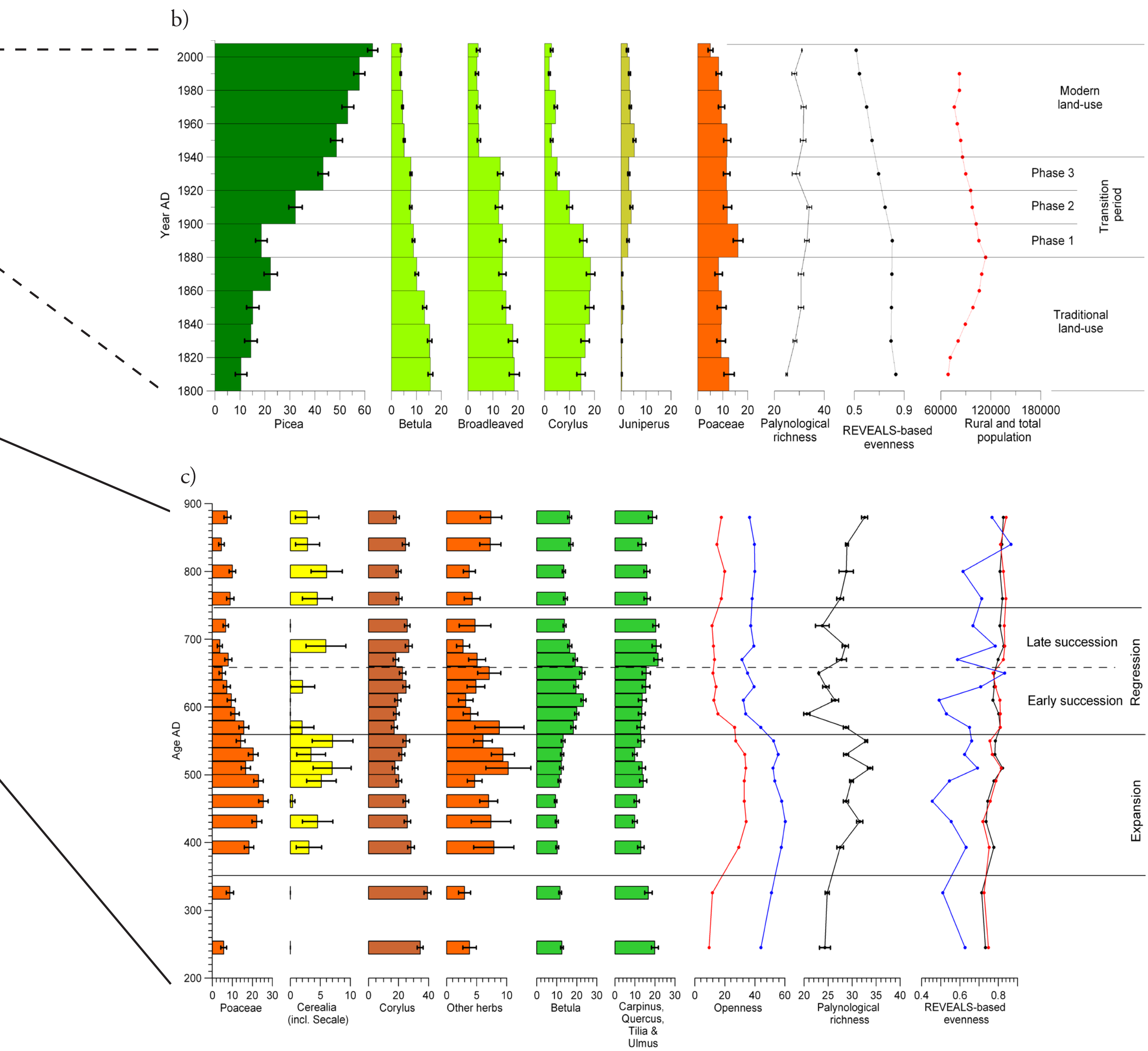


Figure 7. Quantitative estimates of regional vegetation cover for selected taxa/taxa groups, openness, palynological richness and REVEALS-based evenness based on pollen counts from Lake Fiolen, for a) the entire sequence studied 600 BC-AD 2008, b) the last 200 years, and c) the period AD 200-900. The dashed lines illustrate that a different chronology was used for b), making the records not directly comparable. Openness includes all herbs (red line) and all herbs including Corylus and Juniperus (blue line). REVEALS-based evenness was calculated for 26 taxa (black line), but also for trees (red line) and herbs (blue line) separately. Regional rural population data for the last 200 years is also shown. The sequence was divided into different land-use periods described in detail in Appendix I and II.

palynological richness declined. This deviation between palynological richness and REVEALS-based evenness indicates that habitat diversity can increase despite a decline in agricultural land-use and floristic richness.

The transition from traditional to modern agriculture shows a somewhat different pattern than previous transitions (Appendix I). The results suggest that the succession from open grasslands to more tree-covered habitats at AD 1880 initially favours floristic richness at a regional scale (Fig. 7). Palynological richness reached its highest values during the first 40 years of the transition period. During this transition the land was used to a similar extent as before but with more focus on crop cultivation and commercial forestry. Note that the transition from traditional to modern land-use may initially have promoted floristic diversity.

In general, Cerealia and most herbs had a higher coverage during the last c. 1650 years, which suggests a more widespread agriculture with more focus on crop cultivation during this period. The evenness is strikingly higher in traditional compared to modern agricultural land-use at regional scale (Appendix I-II). REVEALS-based evenness for our modern landscape is about 0.5 compared to 0.7-0.8 between 600 BC and AD 1700. For the palynological richness the differences are not as striking, although they are lower today than between AD 1500 and 1700. This shows that the evenness



in the modern landscape is unusually low in a millennial perspective, which indicates that the present land-use management may not support a high floristic diversity in the long-term perspective. This landscape change is supported by historical data with increased in *Picea* plantations and increased fragmentation during the last c. 100 years, which may have implications, e.g. for seed dispersal (Antonsson and Jansson, 2011). The regional landscape composition may be important for floristic diversity, i.e. for connectivity between the small fragments of traditional agricultural land-use that remain.

6.2 Local scale

Based on pollen counts from Lake Åbodasjön and Lindhultsgöl, the LOVE model and historical maps, local land-use (within a few kilometres) and floristic diversity were estimated for the last 1000 years (Appendix III and IV). The continuous presence of Cerealia, Poaceae and herbs suggests that crop cultivation and grazing occurred within a few kilometres radius of both lakes throughout the last 1000 years (Fig. 8). However, the agricultural extent was rather variable. Rapid agricultural expansions were recorded at AD 1260 and 1560 at Åbodasjön

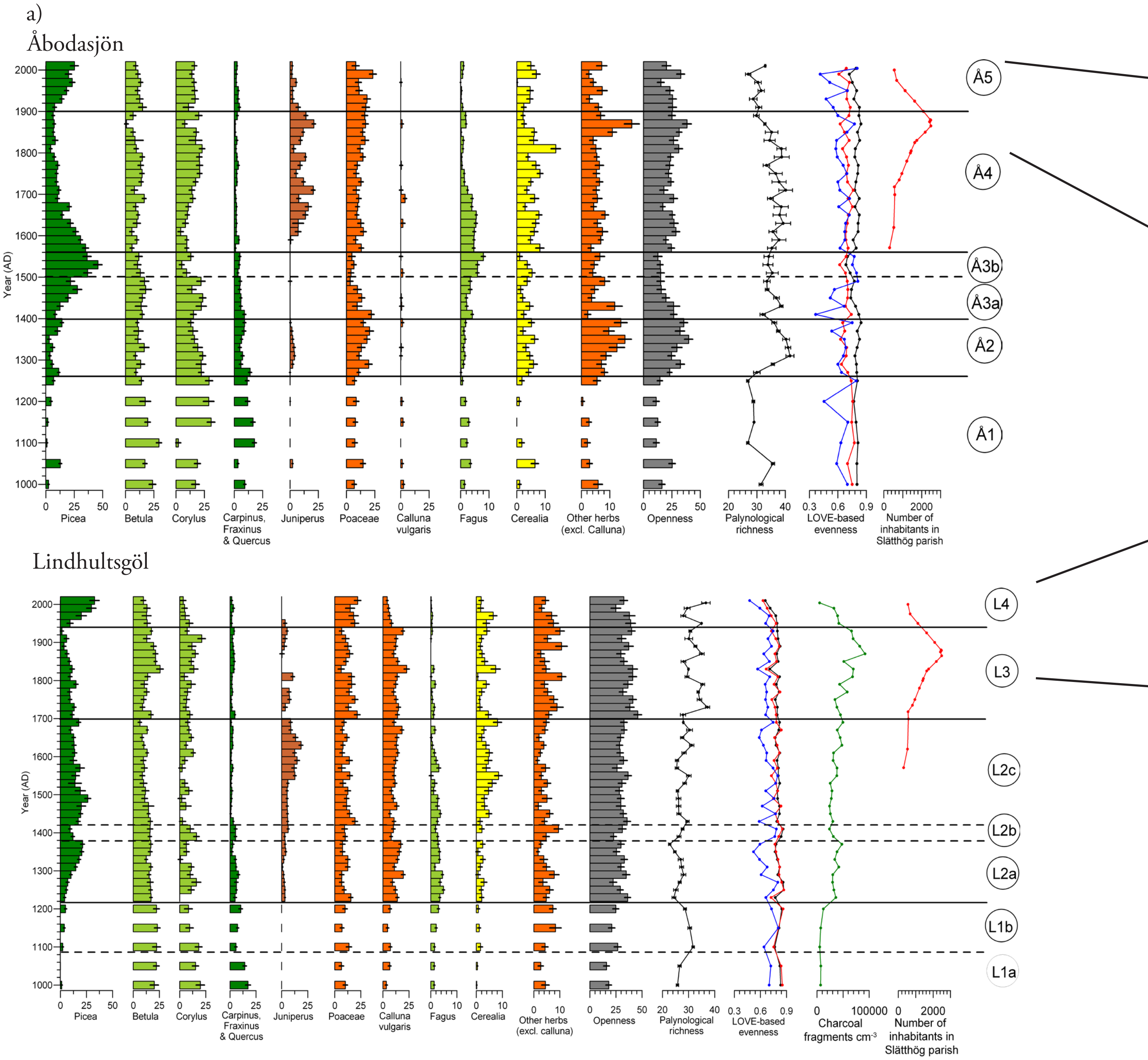
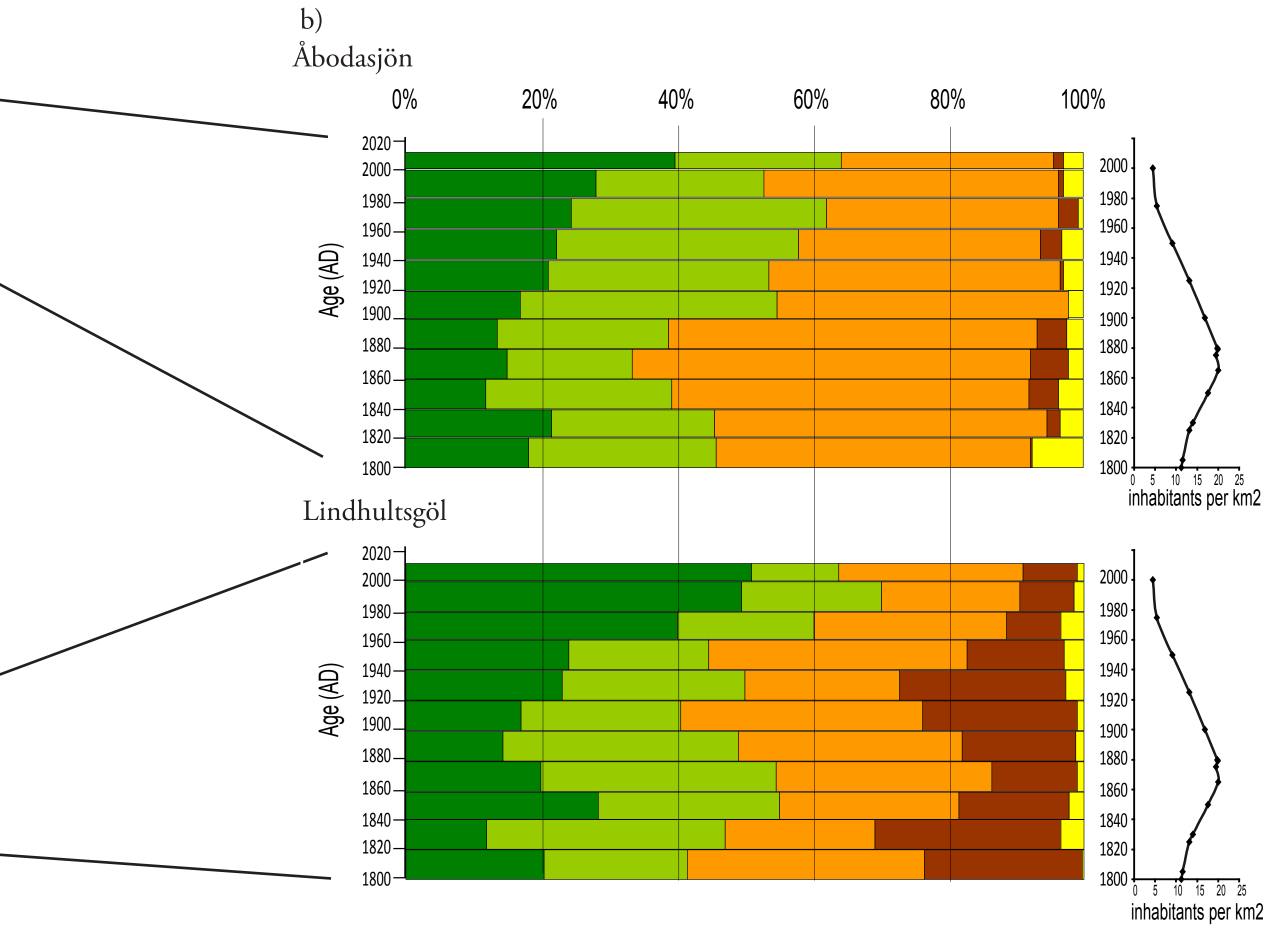


Figure 8. Quantitative estimates of local vegetation cover for selected taxa/taxa groups, openness, palynological richness and LOVE-based evenness based on pollen counts from Åbodasjön and Lindhultsgöl, and population changes in Slätthög parish, for a) the entire sequence studied AD 1000-2008 and b) the last 200 years. Openness includes all herb taxa. LOVE-based evenness was calculated for all 26 reconstructed taxa (black line), but also for trees (red line) and herbs (blue line) separately. The sequences were divided in land-use periods (Å1-Å5 and L1-L4) described in detail in Appendix IV. In b), dark green indicates coniferous woodland, light green deciduous woodland, orange meadows (Corylus and Juniperus included), brown wetland and yellow cropland.

and at AD 1700 at Lindhultsgöl, which were closely followed by increases in palynological richness. The response time was about 20 years at AD 1260 and 1700, but more gradual at 1560. These response times indicate how fast plants can spread across areas that have been cleared. The positive impact of increased agricultural land-use on palynological richness suggests that floristic richness is favoured when crop cultivation and grazing becomes more widespread. From c. AD 900-1200, agriculture with permanent fields was introduced, which could have contributed to increased floristic richness. This land-use system was more gradual in land-use intensity from the central part of the farm towards



pastures and woodlands further away (Myral and Morell, 2011; Emanuelsson, 2009). The generally higher concentrations of charcoal during periods of high palynological richness at Lindhultsgöl suggest that fire was also important to achieve high floristic diversity (Fig. 8).

At the late 14th century and late 19th century palynological richness decreased at Åbodasjön without any indications of declining agricultural land-use (Appendix IV). Possibly, the disturbance regime was too intense during these times, which only favoured a limited number of species (Huston, 1994). We know that the late 19th century was a period of maximum agricultural land-use in Sweden (Myrdal and Morell, 2011). Furthermore, there are many plant species that are favoured during the succession from open land to woodlands, which could have been common in the traditional agricultural landscape (Emanuelsson, 2009). Possibly this type of habitats in the succession from open land to more tree cover habitats decreased in extent during periods of more intense agricultural land-use, for example as an effect of more grazing animals.

The decline in agricultural land-use c. AD 1400 at Åbodasjön was followed by an expansion of *Picea*, *Fagus* and *Corylus* (Fig. 8). At this time probably relatively large areas were in succession from open land to woodland. Although palynological richness was generally lower during this period, slightly elevated values occurred initially (AD 1420 to 1480). Total LOVE-based evenness decreased at the beginning of this period, probably due to the expansion of *Picea*, while openness declined, which suggests that some habitats related to open land decreased in extent. However, after this initial phase at AD 1500-1560, evenness for herbs increased again, which reflects that many plants remained at similar levels while the extent Poaceae decreased. These changes indicate that many species can survive during periods of succession from open land to woodlands. However, the overall floristic diversity was generally lower than during periods of expansion.

This succession at AD 1400 differs from the one recorded at a regional scale at AD 550, mainly in terms of the taxa favoured during land abandonment (Fig. 7 and 8). At AD 550 and at a regional scale

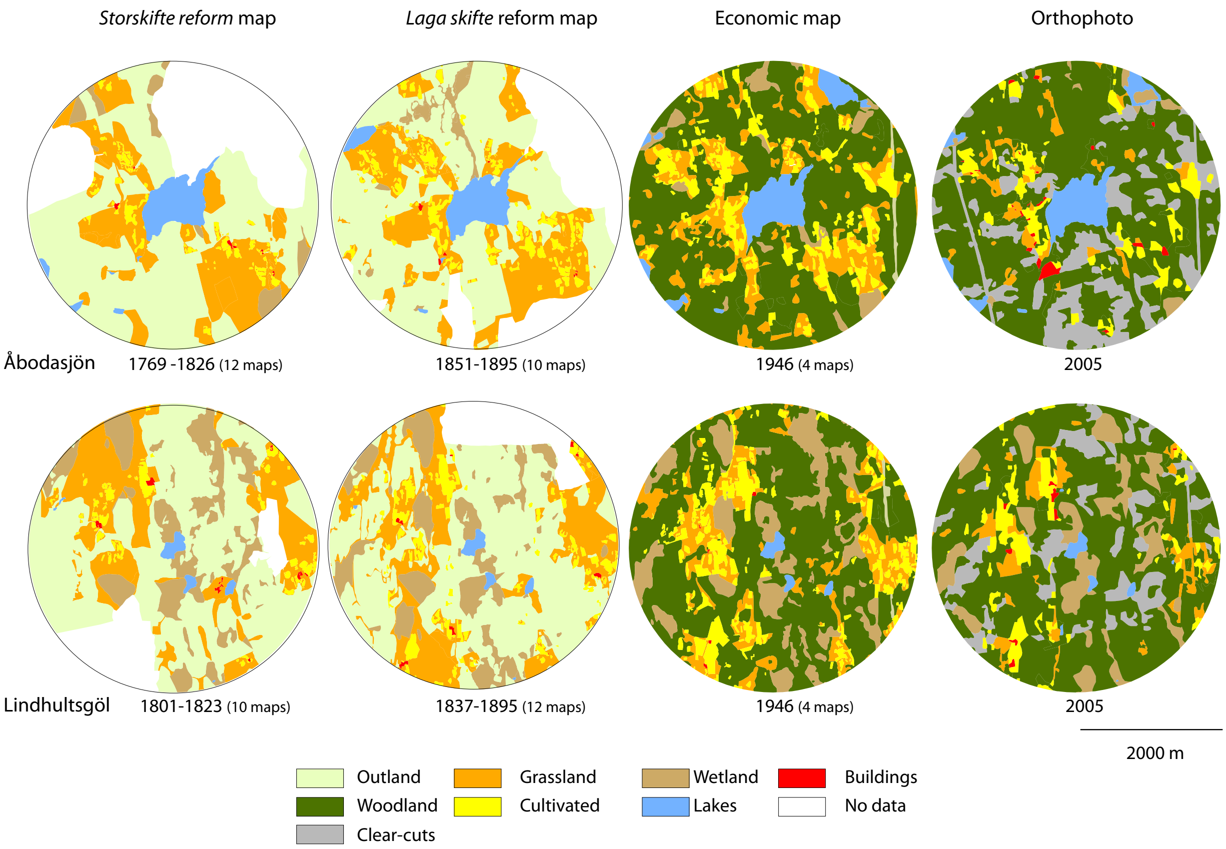


Figure 9. Digitalized historical maps and aerial photographs within 2-km radii around Åbodasjön and Lindhultsgöl.

Betula, and later *Carpinus*, *Quercus*, *Tilia* and *Ulmus*, expanded on abandoned lands, whereas at AD 1400 and at a local scale *Corylus* and *Picea* and *Fagus* expanded. Possibly, *Picea* was not present in the landscape during the earlier regression, which allowed broadleaved trees to expand. During the later regression palynological richness remained at an intermediate level. Possibly people remained in the area to some extent, which is shown by almost continuous presence of Cerealia-type. During the earlier regression, there might have been a more widespread abandonment which led to a more pronounced decline in floristic richness.

In the early 19th century, according to the historical maps, the areas around Åbodasjön and Lindhultsgöl were covered by 2 and 3% cultivated fields, 21 and 21% mowed meadows, 3 and 15% wetland, and 42 and 49% common land, respectively (Fig. 9). In the late 19th century the croplands had doubled around both lakes at the expense of meadows and common lands.

The transition from traditional agriculture to modern land-use occurred, according to the LOVE output, at c. AD 1900 and 1940 at Åbodasjön and Lindhultsgöl, respectively (Appendix III-IV). During this type of transition the landscape was probably used to a similar extent as before, but changed from small-scale agriculture towards domination of tree plantations and crop cultivation (Myrdal and Morell, 2011). At both lakes, openness changed only slightly during the modern land-use period, and a decrease in palynological richness related to this transition was only recorded at Åbodasjön and started slightly earlier. There were probably enough open land left and areas in succession from open land to woodland for the floristic diversity to remain at a higher level, at least at Lindhultsgöl.

Comparison with the historical maps from the late 19th to the mid-20th century more that 60% of the land-use changed, mainly from grassland and common lands to woodlands (Appendix III). However, the common lands were probably already tree covered, but to an unknown extent. The area of cropland was again doubled around to 12% around both lakes.

At both lakes total LOVE-based evenness decreased during the modern land-use period (Appendix IV). Also evenness for herbs and trees at Lindhultsgöl decreased, and evenness for herbs at Åbodasjön. This mainly reflects the increased dominance of *Picea* during this time while many taxa remained at lower levels, which suggests a development towards more habitats related to coniferous woodland and fewer habitats related to deciduous and open land taxa. Our reconstructions show that the areas around Åbodasjön and Lindhultsgöl has not more tree coverage today compared to a few hundred years ago, but taxa composition has changed. Probably the division between different land-use types, such as woodlands and arable land also became more distinct (Cousins, 2011). At Åbodasjön the modern land-use has probably resulted in a generally decreased floristic diversity, while the palynological richness has remained at a similar level since AD 1700 at Lindhultsgöl, which indicates that the modern land-use has not yet affected floristic diversity in this area. Åbodasjön has more agricultural land-use in its immediate surroundings which can explain these differences.

The aerial photographs between mid-20th century and 2005 approximately 40 % of the area around the lakes changed from mainly clear cut, grassland, wetland and cropland to woodland. The cropland area decreased to half the size around both lakes.

6.3 Implication for ecosystem management and future prospects

Because the remaining areas with high biodiversity are few and fragmented, we need to optimise ecosystem management to preserve species in the future. The landscape provides many ecosystem services, related to production of food and natural resources, but also recreational and aesthetic values which are important for human well-being (Millennium Ecosystem Assessment, 2005). Therefore, the modern land-use system must be capable of combining production targets with preservation and promotion of biodiversity (Emanuelsson, 2009). The impact on past land-use on floristic diversity provides information that can be useful in this context, although this needs to be combined with information from other methods and sources (Harrison et al., 2010).

In this study we have developed and applied a palaeoecological methodology for long-term ecological analysis and provided some examples of how the results can contribute to ecosystem management. We know that the traditional agriculture land-use promotes floristic diversity, but this study is one of first that has quantified the impact of modern and past land-use on the landscape at regional and local scales. The variability of the past agricultural landscape provides information on which type of land-use that promotes floristic diversity. Because REVEALS- and LOVE-based evenness reflects changes in landscape composition, this parameter indicates to which extent different habitats are available through time. Comparisons with the present landscape provide knowledge on what impact the present land-use may have on floristic diversity in the future. The response times of floristic diversity to past land-use changes provide quantitative estimates of the ecosystem resilience to land-use change. Reconstructions at regional scale (50 km radius) provide information about the overall landscape development. The local scale reconstructions (10 -50 km^2) are similar in size to a lake-catchment, large nature reserve or a small parish. This potentially makes it a useful tool for nature conservancy when planning the management within a specific area.

The adopted approach has the potential to be used also in other study areas with different vegetation and land-use history. However, to make the knowledge about long-term processes more useful for ecosystem management it requires an active strategy to merge paleaoecology and modern records, as well as developing methods how to implement this kind of data in ecosystem management.

The Swedish biodiversity strategies and action plans aim are integrated into several of the 16 environmental quality objectives a A Rich Diversity of Plant and Animal Life, Thriving Wetlands, A Varied Agricultural Landscape and Sustainable Forests. The authorities responsible to implement these plans may use the knowledge about the historical land-use and its effect on floristic diversity as one component to make adequate priorities within nature conservancy efforts. The BECC (Biodiversity and Ecosystem services in a Changing Climate) strategic research area at Lund University 2010-2019 has a commitment to continuously interact with stakeholders. Their stakeholder reference group includes among others representatives from the Swedish Environmental Protection Agency, the Swedish Forestry Agency and the Swedish Board of Agriculture, County administrative boards and municipalities. These organizations are responsible for implementing environmental objectives. One potential step would be to communicate the results from present study and get feedback from practitioners within these organizations.

More details are needed on how floristic richness and evenness are reflected in palynological richness and REVEALS/LOVE-based evenness. A potential advancement would be to develop new approaches to quantify vegetation cover and how taxa are distributed based on the LOVE output. This would require some kind of simulations, e.g. using GIS modelling, including different parameters such as topography, hydrology, soil type and spatial distribution of archaeological finds (Bunting and Middleton, 2009).

This study has used the uplands of southern Sweden as a case study of landscape processes relevant for North-west Europe. Probably upland areas in other parts of Europe have experienced similar developments during periods of expansion and regression with similar impacts on floristic diversity. Comparisons with other upland areas in Europe could provide more information useful for ecosystem management at different spatial scales.

7. Main conclusions

- The study design used in this thesis includes high-resolution pollen analysis, a combination of detailed chronological methods, quantitative vegetation reconstruction, historical maps/aerial photographs and quantitative estimation of floristic richness and evenness, which enables estimates of the rate of change in land-use coverage characterizing past periods of high floristic diversity.
- The agricultural land-use was most widespread AD 350-1850 at regional scale, and a period of land-use expansion followed by regression AD 350-750 was identified. The land-use patterns are similar around the local study sites, with agricultural expansion during the 13th century, partly abandoned landscape around AD 1400, re-establishment during the 15-16th century and a transition from traditional to modern land-use during the 20th century.
- Floristic richness responds within 20 to 80 years during agricultural expansion and regression both at regional scale and local scales, which provides quantitative estimates of the ecosystem resilience to land-use change. During succession from open lands to more tree covered habitats, floristic richness may increase temporary during c. 40 years. The REVEALS and LOVE-based evenness introduced in this thesis reflects changes in landscape composition and the extent of available habitats.
- The more widespread agriculture from the 13th to 19th century was of substantial importance for achieving the high floristic diversity that characterizes the traditional landscape which can allow species favoured by traditional management, succession and woodlands to coexist. The modern landscape is unusual in a centennial to millennial perspective with more habitats related to coniferous woods and fewer habitats related to deciduous trees and open land taxa, which may not be sustainable to preserve floristic diversity in the future.
- This thesis provides some examples of long-term (decadal to millennial scale) impacts of land-use changes on floristic diversity at regional and local scales. The adopted approach is potentially a useful tool for conservation strategies when planning the management within specific areas.

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Svensk sammanfattning

Det traditionella jordbruket i nordvästra Europa har gynnat förekomsten av många arter under tusentals år och den snabba övergången till modernt jord- och skogsbruk har lett till försämrade förutsättningar för dessa arter.

Både internationellt och nationellt finns strategier för att bevara biologisk mångfald. I Sverige är dessa strategier integrerade i miljömål med ansvar fördelade mellan olika myndigheter. Dock är naturvården inte optimerad för att i ett längre tidsperspektiv bevara de fragmenterade områden med hög biologisk mångfald som återstår.

För att möjliggöra en hållbar samhällsutveckling och ett bevarande av biologisk mångfald behövs många olika metoder och källor för att förstå hur ekosystem påverkas av olika typer av markanvändning. Eftersom ekosystem förändras över tid (decennier till århundraden) är det nödvändigt att öka kunskapen om den historiska markanvändningen och hur den har påverkat den biologiska mångfalden.

Paleoekologiska undersökningar baserade på sediment från naturliga arkiv är den viktigaste metoden för att studera vegetationsförändringar i ett långt tidsperspektiv. Men för att göra de paleoekologiska resultaten och tolkningarna tillgängliga för naurvården krävs en aktiv strategi där de sammanfogas och jämförs med observationer av ekologer och forskare som arbetar med biologisk mångfald i det moderna landskapet.

Under det senaste decenniet har det skett en väsentlig utveckling av metoder för att studera historisk vegetationsutveckling, som bland annat innefattar matematiska modeller som möjliggör objektiva tolkningar av pollendata. Dessa modeller kompenserar för växters olika produktion och spridning av pollen, vilket gör det möjligt att kvantifiera vegetationssammansättningen på regional och lokal nivå för specifika tidsintervaller. Denna metod gör det också möjligt att beskriva den historiska mångfalden av växter mer detaljerat, både hur antalet arter har varierat och hur ytmässiga fördelningen av dessa har varit. Det sistnämnda är av stor betydelse för att beskriva den biologiska mångfalden, eftersom det visar om olika arter har förekommit i lika antal eller om några få har dominerat i utbredning.

Denna avhandling utforskar hur markanvändningen har påverkat växters mångfald på Sydsvenska höglandet under de tre senaste millennierna, på både regional (100 x 100 km) och lokal (2-20 km^2) nivå. Vi använder pollenanalys med hög tidsupplösning (20-150 år), modeller för att kvantifiera vegetationens yttäckning under olika perioder, historiska kartor/flygfoton, samt beräkning av hur artrikedomen och dess ytmässiga fördelning har förändrats över tid. Med denna metodik kan vi uppskatta hur snabbt vegetationen reagerar på förändringar i markanvändningen och hur stora dessa förändringar har varit.

Resultaten visar att jordbruket hade störst utbredning 350-1850 e.Kr., sett på regional nivå. Dessutom identifierades en period av agrar expansion följd av tillbakagång 350-750 e.Kr. På lokal nivå skedde en agrar expansion under 1200-talet men den jordbruksmark som då etablerades övergavs delvis kring år 1400. En agrar återetablering skedde sedan under 1400- och 1500-talen och under 1900-talet introducerades modern markanvändning med ett industrialiserat jordbruk och skogsplantering.

Vidare visar våra resultat att artrikedomen förändras inom 20 till 80 år efter en agrar expansion eller regression på både regional och lokal nivå, vilket speglar ekosystemens motståndskraft mot förändringar i markanvändningen. Vid igenväxning av öppen mark kan artrikedomen öka tillfälligt under ca 40 år. Fördelningen mellan arterna, baserat på en beräkningsmetod som introducerats i denna avhandling, reflekterar förändringar i landskapets sammansättning och utbredningen av olika habitat.

De olika typer av agrar markanvändning som förekom när jordbruket hade sin största utbredning mellan 1200-talet och 1800-talet bidrog starkt till en hög biologisk mångfald, bland annat genom att arter som gynnades av såväl traditionell markanvändning som succession och skog kunde samexistera. I detta långa tidsperspektiv är det moderna landskapet ovanligt, med fler habitat kopplade till barrträd och färre habitat kopplade till lövträd och öppen mark, vilket förmodligen inte är hållbart för att bevara och främja den biologiska mångfalden på en hög nivå i framtiden.

Denna avhandlig bidrar med exempel på hur förändringar i markanvändning påverkar vegetationens mångfald på regional och lokal nivå. De metoder som används har potential att tillämpas vid planering av naturvård inom specifika geografiska områden.

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