

**The impact of  
land-use change on  
floristic diversity**

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# The impact of land-use change on floristic diversity at regional scale in southern Sweden 600 BC–AD 2008

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## Abstract

This study explores the relationship between land-use and floristic diversity between 600 BC and AD 2008 in the uplands of southern Sweden. 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. Floristic richness and evenness are estimated using palynological richness and REVEALS-based evenness, respectively. We focus on the period AD 350 to 750 to investigate the impact of an inferred, short-lived (< 200 yr) period of land-use expansion and subsequent land abandonment on vegetation composition and floristic diversity. 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 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 yr. However, REVEALS-based evenness shows much lower values during the last century compared to the previous ca. 2600 yr, 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 yr. We show the importance of traditional land-use to attain high biodiversity and suggest that ecosystem management should include a regional landscape perspective.

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# 1 Introduction

One of the main ecological challenges during this century is to mitigate the expected loss of species due to rapid land-use and climate changes (MacDonald et al., 2008; Anton et al., 2010; Barnosky et al., 2011). To make adequate priorities and implement realistic nature conservancy efforts, we need a range of methods to understand how these processes may impact on biodiversity (Dawson et al., 2011). Because ecosystem responses may occur over decades or centuries, making them difficult to observe, palaeobotanical records provide important information about past responses relevant to on-going and future changes in vegetation and biodiversity (Jackson and Hobbs, 2009; Haslett et al., 2010; Willis and Bhagwat, 2010; Willis et al., 2010).

In many areas, such as northwest Europe, agricultural land-use has influenced vegetation and biodiversity for thousands of years (Berglund et al., 2008; Emanuelsson, 2009; Willis et al., 2010). Many herbs originate from steppe areas where natural disturbances such as wind and drought have allowed these species to exist. The traditional agriculture functioned as a substitute for these disturbances which made it possible for plants that not naturally grow in northwest Europe to survive also in these areas (Emanuelsson, 2009). The rapid land-use changes during the last ca. 100 yr, towards a modern agriculture based more on crop cultivation and forestry, have led to a decrease in available habitats, such as semi-open grasslands, that many species are restricted to.

Land-use transitions have occurred throughout agricultural history (Berglund, 1969; Lagerås, 2007; Froyd and Willis, 2008). By studying these transitions, using high-resolution palaeobotanical records, we may reconstruct the rate and degree of change in land-use and vegetation. This allows us to better understand how current ecosystems will respond to present and future land-use changes and provide information useful for ecosystem management.

The Landscape Reconstruction Algorithm (LRA) enables new ways to study past land-use and biodiversity changes (Sugita, 2007a, b). Based on pollen counts extracted

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from sediments, LRA, with submodel Regional Estimates of Vegetation Abundance from Large Sites (REVEALS), compensates for differences in pollen productivity and dispersal characteristics between taxa and makes it possible to quantify past vegetation composition (Broström et al., 1998; Sugita et al., 1999; Sugita, 2007a, b; Hellman et al., 2009). Moreover, it makes it now possible to reconstruct past floristic diversity using the two parameters richness and evenness. Richness is the number of species within a specific area, which may be estimated using palynological richness, i.e. the number of different pollen taxa found in a sediment sample (Birks and Line, 1992; Odgaard, 1999; Van Dyke, 2008; Meltsov et al., 2011). Evenness is a measure of the relative abundance of the different species that are present within an area, which may be estimated for common taxa by applying evenness indices to the REVEALS output (Magurran, 2004; Sugita, 2007a; Fredh et al., 2012). High evenness describes situations when all species within an area are represented by similar spatial coverage, whereas low evenness characterizes landscapes where a few species cover large areas and other species cover small areas.

Fredh et al. (2012) analyzed the relationship between land-use and floristic diversity during the transition from traditional to modern land-use management AD 1800–2008, using the uplands of southern Sweden as an example. In this study, the record is extended back to 600 BC, using a similar approach and the same sediment sequence from Lake Fiolen. The aims are to:

- Build a robust chronology to enable quantification of rate of change.
- Analyze the relationship between land-use and floristic diversity during the last 2600 yr at a regional scale (50 km radius) using fossil pollen assemblages and the REVEALS model.
- Specifically study the period AD 350–750 as an example of the impact of a short-lived (< 200 yr) period of land-use expansion followed by abandonment on vegetation composition and floristic diversity.

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- Compare the vegetation responses during the inferred agricultural expansion and regression period AD 350–750 with the previous study of the transition from traditional to modern land-use management AD 1800–2008 (Fredh et al., 2012).
- Provide quantitative estimates of long-term (century to millennial scale) impacts of land-use changes on floristic diversity, useful for ecosystem management.

## 2 Study area

The study area is located in the uplands of southern Sweden, above 200 m a.s.l., in the central part of the province of Småland (Fig. 1). The bedrock consists mainly of crystalline bedrock of granite and gneiss, which is covered by sandy till and some glaciofluvial deposits (Fredén, 1994). The tree cover consists of a mixture of coniferous and deciduous forest, which is typical for the boreo-nemoral zone (Sjörs, 1963). The tree cover is 72 %, shrubs 1 %, herbs 21 % and Cerealia 6 %, with *Picea* and *Pinus* as the dominant trees (Hellman et al., 2008b). Mean annual temperatures are 5–7 °C, and mean annual precipitation varies from ca. 600 to ca. 1200 mm along an east-west gradient (Raab and Vedin, 1995).

Because of their relatively poor soils and climatic conditions, the uplands of southern Sweden are usually less suitable for agriculture compared to lower areas and therefore colonized relatively late, although human remains can be found at some places since the Neolithic and before (Hyenstrand, 1979; Berglund et al., 2002; Poschlod et al., 2005). Pollen records and archaeological evidence show that there has been a pattern of expansion and regression phases during the last 6000 yr and that land-use was dominated by grazing (Hyenstrand, 1979; Berglund et al., 2002). During the Iron Age, 500 BC to AD 1050, some settlements became organized in hamlets and villages but single farms dominated (Welinder et al., 2004).

From ca. AD 1000, agriculture in the upland area was dominated by permanently farmed land, with clear separation between cultivated fields, meadows and common

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land around the farms used for grazing (Berglund et al., 2002). The medieval expansion, ca. AD 900–1200, was interrupted by the late medieval agrarian crisis, when marginal areas were abandoned for better soils (Berglund et al., 2002; Myrdal, 2003; Emanuelsson, 2005; Lagerås, 2007). The uplands have been subject to slash- and burn agriculture documented from the 17th century which was used for temporal cultivation in addition to more permanent fields (Larsson, 1974). During the agricultural revolution (ca. AD 1700–1900) arable fields were combined to form larger units, and the common land was split up and divided between farmers (Gadd, 2000). The maximum extent of agricultural land-use occurred in the late 19th century. Since then *Picea* plantations and cultivated fields have expanded and dominate the land-use today (Morell, 2001).

### 3 Methods

#### 3.1 Field work and core correlation

During fieldwork in June 2008, overlapping sediment cores were retrieved from Lake Fiolen (160 ha) using Kajak (core K; Renberg and Hansson, 2008), Russian (core C and D; Aaby and Digerfeldt, 1986) and piston (core P) corers (Fig. 2a). Correlations between the cores were carried out using mineral magnetic properties (Thompson et al., 1980) and element compositions based on X-ray fluorescence measurements (Boyle, 2000). For more details on methods used for core correlation see Fredh et al. (2012). All analyses were carried out on core K and P, except for a few radiocarbon datings performed on core C and D.

## 3.2 Dating

### 3.2.1 Radiocarbon

<sup>14</sup>C dating was used to date organic remains in the sediment sequence. Thirteen macrofossil samples and eight bulk gyttja samples were dated using accelerator mass spectroscopy (AMS) at the Radiocarbon Dating Laboratory at Lund University (Table 1). Three of the macrofossil samples were taken from correlated parallel cores, introducing an estimated depth uncertainty of < 2 cm. 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. Only six of the dated macrofossil samples were used to construct the age-depth model (see below). The OxCal program (v. 4.1.7) and the CaliBomb program were used for calibration of <sup>14</sup>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 Lead-210 and Caesium-137

<sup>210</sup>Pb dating was used to date the uppermost part of the sediment sequence. 26 samples (21 from core K and five from core P) between 0 and 44 cm depth were analysed for the activity of <sup>210</sup>Pb, <sup>137</sup>Cs and <sup>226</sup>Ra. The samples were analysed via gamma-spectrometry at the Gamma Dating Centre, Institute of Geography at the University of Copenhagen, Denmark. The fraction of total <sup>210</sup>Pb that is deposited on the lake surface from the atmosphere, i.e. the unsupported <sup>210</sup>Pb, was calculated based on the <sup>226</sup>Ra data obtained. The irregular profile of <sup>210</sup>Pb below 15 cm allows for different calculation options using the Constant Rate of Supply (CRS) model (Fig. 2e; Appelby 2001). Fredh et al. (2012) included 20 samples in the CRS model, whereas in this study we only included the nine samples above 15 cm (Fig. 2). Below 15 cm the activity of

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$^{210}\text{Pb}$  was calculated by assuming a constant sedimentation rate. Variations in  $^{137}\text{Cs}$  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 history

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 ( $^{206}\text{Pb}/^{207}\text{Pb}$ ), 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. The 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 at 1 cm intervals in the upper sediment core (core K) and at between 1 and 11 cm intervals in the lower sediment core (core P) using X-ray Fluorescence (XRF) to estimate total lead concentration (Boyle, 2000), and at ca. 5 cm intervals using Acid Dissolution (EPA 3052) and Quadrapole ICP-MS to estimate 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,

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we used an approximation of 50 yr uncertainty for all markers except the modern maximum at AD 1975, which was assigned an uncertainty of 5 yr.

### 3.2.4 Age modelling

Because of inconsistencies within and between the chronological data provided by the different methods applied, we had to make some selections of these data points in the final age-depth model. We chose to include all pre-treated macrofossils and as many small macrofossil samples and lead pollution markers as possible. However, using this option we had to exclude most of the samples analyzed for  $^{210}\text{Pb}$ -activity used in the CRS-model and most of the small macrofossil samples. We also assumed that our interpretations of the total lead and lead isotopes data used for time markers are correct.

Using our preferred chronological data, the OxCal program (v. 4.1.7) was used to establish a chronology for the entire sediment sequence using Bayesian analysis (Bronk Ramsey, 2009). The age model was established using a P-sequence which takes the stratigraphic levels of dated samples into account and allows for fluctuations in sedimentation rate (Bronk Ramsey, 2008). The degree of fluctuation allowed for by the program may be modified by varying the k-value (the number of accumulation events per unit depth). This parameter was chosen as high as possible to obtain an agreement index  $\geq 60\%$  for the entire age model (Bronk Ramsey, 2008). Two polynomial functions, one above and one below 60 cm, with a polynomial order of seven and two, respectively, were fitted to the midpoints of the calibrated  $2\sigma$  intervals provided by OxCal and used to calculate age estimates for the sequence at 0.5 cm intervals.

### 3.3 Quantitative reconstruction of land cover

Material for pollen analysis was subsampled at 0.5 to 10 cm intervals from the sediment cores from Lake Fiolen and prepared using standard methods (Berglund and Ralska-Jasiewiczowa, 1986). Pollen grains were identified using a light microscope,

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identification keys (Beug, 1961; Punt, 1976–2003; Moore et al., 1991; Beug, 2004) and the reference collection at the Department of Geology, Lund University. Subsequently, pollen counts from several levels were pooled together to attain at least 1,000 grains for each time window, varying in width between 20 and 60 yr as inferred from the chronology. The use of time windows, in sequences when sedimentation rate and sample resolution are high, allows us to capture vegetation changes rather than weather conditions because pollen productivity may change between individual years when sedimentation rate and sample resolution are high (Hicks, 1999; Autio and Hicks, 2004).

Based on pollen counts for each time window, we used the REVEALS program (v. 4.2.2, Sugita, unpublished) to provide quantitative estimates of vegetation composition at a regional scale (within a 50 km radius) between 600 BC and AD 2008. The REVEALS model is an objective way to estimate vegetation composition by compensating for known biases in how vegetation is represented in the pollen record (Sugita, 2007a). 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; Sugita et al., 1999; Davis, 2000; Sugita, 2007a). 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; Sugita et al., 1999; Davis 2000).

The REVEALS model requires various parameter inputs. We used pollen productivity estimates (PPEs), including their standard errors (SEs), obtained for 26 taxa (Table 2) from southern Sweden and Denmark and fall speed estimates of pollen from the literature (Eisenhut, 1961; Sugita et al., 1999; Broström et al., 2004; Nielsen, 2004; Broström et al., 2008). The REVEALS version used in this study (v. 4.2.2) assumes neutral atmospheric conditions and wind speed  $3\text{ms}^{-1}$  as in Prentice (1985) and Sugita (1993, 1994, 2007a, b). We used a mean radius of 714 m for Lake Fiolen, calculated from the total lake surface area, assuming this is the area of a circular basin. The maximum spatial extent of the regional vegetation ( $Z_{\text{max}}$ ) was set to 50 km as most of the pollen grains found originate from within this area (Hellman et al., 2008a, b).  $Z_{\text{max}}$  can

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in theory be 50–400 km (Sugita, 2007a), but Mazier et al. (2012) showed that different values of this parameter (i.e. 50, 100 and 200 km) do not affect the REVEALS output.

We used the pollen dispersal-deposition function appropriate for lakes, 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 vegetation abundance were calculated in the REVEALS program using a hybrid of the delta method (Stuart and Ord, 1994) and Monte Carlo simulations (Sugita, 2007a).

### 3.4 Reconstruction of floristic diversity

In this study we used palynological richness and REVEALS-based evenness as proxies for floristic diversity and floristic evenness, respectively (Birks and Line, 1992; Fredh et al., 2012). Palynological richness is the number of different pollen and spore taxa identified in each sample, whereas REVEALS-based evenness is the relative abundance between the taxa reconstructed by the REVEALS model (Birks and Line, 1992; Magurran, 2004; Sugita et al., 2007a; Fredh et al., 2012).

Due to different total pollen counts between time windows the palynological richness was recalculated using rarefaction (Birks and Line, 1992). We therefore present the results of palynological richness as the expected number of pollen taxa for a specific pollen sum. The calculation was based on all terrestrial taxa, in total 17 trees, 66 herbs and 9 ferns. We are aware of that the relationship between pollen identified in sediments and the surrounding vegetation is complex, and that the pollen grains found in sediments only represent a small portion of all species in surrounding vegetation (Odgaard, 1994, 2007; Peros and Gajewski, 2008; van der Knaap, 2009). However, as a relative measure of floristic diversity, palynological richness has shown to be reliable (Meltsov et al., 2011, 2013).

Based on the proportional abundances estimated by the REVEALS model we calculated the Shannon index, which combines the number of taxa and the relative abundance between taxa to estimate floristic diversity (Magurran, 2004; Odgaard, 2007; van Dyke, 2008). Subsequently, we calculated floristic evenness using the ratio between

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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 proportion within the 50 km radius. We estimated REVEALS based evenness for all 26 taxa (14 trees and 12 herbs) used in the REVEALS model, but also for trees and herbs separately. These 26 taxa represent about 70–90 % of the total vegetation cover in the upland area of southern Sweden today (Broström et al., 2004).

## 4 Results

### 4.1 Chronology

The radiocarbon dated macrofossil samples show rather scattered ages (Table 2, Fig. 2b). Most of the macrofossil samples were smaller than two milligram and therefore not pre-treated. This means that any contamination with modern material during extraction, storage and identification, that would have a relatively strong influence on the dating results of these small samples, was not removed. An extreme case of this effect is probably illustrated by sample LuS8602 from a depth of 63.75 cm, which yielded a modern or close to modern age (Table 2). Because of unexpectedly young ages due to suspected contamination, most of the small macrofossil samples were rejected and not used to construct the age model. We included all pre-treated macrofossil samples that were considered to be most reliable. We also included three small macrofossil samples that were in agreement with the pre-treated macrofossil samples and our interpretation of the lead pollution time markers. The bulk dates show a rather well defined slope with increased age at greater depth, indicating that the sediments have not been subject to major mixing or disturbance. The absolute ages for these samples are,

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however, likely affected by a lake reservoir age and therefore assumed to be too old (ca. 200 to 400 yr) and not used for the chronology.

The activity of unsupported  $^{210}\text{Pb}$  in the sediment sequence generally decreases exponentially with depth down to about 15 cm (Fig. 2e), while below this depth the activity data are rather irregular. As explained above, we therefore only included the nine lead dates above 15 cm in the CRS-model calculation. However, using only the lead dates from above 15 cm we have to assume that some mixing has occurred and/or that some of the measured elements are mobile in this particular sediment below this depth. This is supported by the high activity of  $^{137}\text{Cs}$  at depths below 14 cm that correspond to ages older than ca. AD 1950 according to the CRS-model (Fig. 2f).  $^{137}\text{Cs}$  is normally only found in sediments younger than AD 1950 (Appelby, 2001).

Time markers were inferred from the total lead concentrations and lead isotope ratios based on comparison with the typical pattern of pollution lead though time for southern Sweden (Brännvall et al., 2001; Renberg et al., 2001). For our age model we used time markers at 110 cm, 55 cm, ca. 38 cm, and 11 cm interpreted to represent AD 0, AD 1000, AD 1200 and AD 1975, respectively (Fig. 2b–d). At 110 cm total lead concentration increases to  $16\ \mu\text{g g}^{-1}$  and the lead isotope ( $^{206}\text{Pb}/^{207}\text{Pb}$ ) ratio decreases with 0.12. Between 100 and 55 cm depth the lead isotope ratio increases and the total concentration decreases which may reflect the decline in mining activities between AD 400 and 900. Between 55 and 38 cm total lead concentration increases to  $53\ \mu\text{g g}^{-1}$  and the lead isotope ratio decreases with 0.13 compared to background values. At 11 cm the highest total concentration of  $189\ \mu\text{g g}^{-1}$  is recorded which we interpret to reflect the pollution maximum at AD 1975. The lead isotope ratio close to or below 1.17 above 19 cm indicates that a large proportion of the lead found in this interval is derived from pollution from leaded petrol during the 20th century, which has an isotope ratio of ca. 1.15.

Because of inconsistencies within and between the chronological data provided by the different methods applied, dating of the Lake Fiolen sequence is not straightforward. Our preferred age-depth model is based on six macrofossil samples (three pre-treated),

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a CRS-model (based on nine  $^{210}\text{Pb}$  samples) and four lead pollution markers (Fig. 2b). We therefore rejected eight small macrofossil samples and 17  $^{210}\text{Pb}$  measured samples below 15 cm that were considered unreliable.

Consequently, the proposed age model is tentative, in particular between AD 1200 and AD 1950. It should also be pointed out that our age model for the interval between 0 and 48 cm differs from that used by Fredh et al. (2012), resulting in deviating age estimates in the lower part of this interval.

## 4.2 Long-term ecological changes 600 BC–AD 2008

Vegetation coverage was quantified using REVEALS for the 26 taxa (14 trees and 12 herbs) for which PPEs are available (Fig. 3). The differences between the REVEALS-based reconstruction and pollen percentages reflect corrections by REVEALS for differences in e.g. pollen productivity and dispersal characteristics. Although the relative importance of taxa is different between the two datasets, their trends are similar. The importance of *Picea*, *Acer*, *Corylus*, *Fagus*, Poaceae, *Cerealia* type, *Carpinus*, *Fraxinus*, *Salix*, *Tilia*, *Ulmus*, *Calluna vulgaris*, Compositae SF. Cichorioideae, Cyperaceae, *Plantago lanceolata* and *Secale* type is underestimated by pollen percentages, while *Pinus*, *Alnus*, *Betula*, *Quercus*, *Juniperus*, *Filipendula*, *Ranunculus acris* type and *Rumex acetosa* type are overestimated by pollen percentages compared to REVEALS-based vegetation coverage.

According to the herb taxa coverage estimated by REVEALS, landscape openness varies between 5 and 34 % throughout the studied period (Fig. 4). However, we may assume that *Corylus* and *Juniperus* mainly grew on open lands. When including these shrubs openness varies between 18 and 60 % (Fig. 4). In either case, maximum openness is recorded between AD 350 and 550, mainly due to the increase in Poaceae coverage during this time.

During the studied period palynological richness varies between 21 and 38, with the highest value at AD 1600 (Fig. 4). REVEALS-based evenness varies between 0.83

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and 0.54, with maximum evenness between AD 500 and 1600. Evenness for trees is almost identical to total evenness, which shows that the tree evenness dominate the total evenness calculation. Evenness for herbs was generally higher the last 1400 yr, but rather variable.

Several major vegetation changes occurred during the last 2600 yr according to the REVEALS reconstruction (Fig. 3). However, the period between 600 BC and AD 350 was relatively stable with a vegetation cover dominated by *Corylus* and *Betula* with 23–39 % and 12–23 % coverage, respectively. Palynological richness varies between 22 and 27 during this period, and REVEALS-based evenness shows values between 0.71 and 0.78.

Between AD 350 and 750 changes in vegetation coverage indicate land-use expansion followed by regression. We divided this interval into three parts, one expansion period and two regression phases (Fig. 5), based on changes in coverage of open land taxa such as Poaceae, *Cerealia* type, early successional taxa such as *Betula* and late successional taxa such as *Carpinus*, *Quercus*, *Tilia* and *Ulmus*. We also took into account “other herbs”, which include *Calluna vulgaris*, Compositae SF. Cichorioideae, Cyperaceae, *Plantago lanceolata*, *Ranunculus acris* type, *Rubiaceae* and *Rumex acetosa* type.

At the beginning of the expansion period AD 350 the coverage of *Cerealia* type, Poaceae and other herbs increased significantly from 0 to 3 %, 9 to 18 % and 3 to 8 %, respectively, which suggests a regional agricultural land-use expansion (Fig. 5). Simultaneously, *Corylus* decreased significantly in coverage from 39 to 28 %. Poaceae shows maximum abundance at AD 450 with 26 % coverage and decreased thereafter, whereas *Cerealia* type in general remained at higher values at least until AD 550. Both palynological richness and REVEALS-based evenness increased AD 350 to 550 and varied between 27 and 34 and between 0.74 and 0.82, respectively. Also evenness for trees and herbs generally increased during this period.

At AD 550 we can observe an opposite pattern. The coverage of Poaceae significantly decreased from 20 to 14 %, *Cerealia* type was only recoded in some samples

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and other herbs decreased in most samples, indicating an agricultural land-use regression (Fig. 5). At the same time *Betula* increased significantly in coverage from 13 to 18 %. Between AD 650 and 750 the late-successional trees *Carpinus*, *Quercus*, *Tilia* and *Ulmus* increased significantly in coverage from 16 to 22 % and *Betula* decreased. Between AD 550 and 750, REVEALS-based evenness remained at higher values between 0.77 and 0.83, whereas palynological richness decreased to generally lower values between 21 and 29. Evenness for herbs and trees also remained at generally higher values.

At AD 750 late successional trees such as *Carpinus*, *Quercus*, *Tilia* and *Ulmus* decreased in coverage from 20 to 16 % (Figs. 3 and 5). Between AD 750 and 1000 *Alnus* shows a decreasing trend, whereas *Betula* increased. During the last 1000 yr *Betula*, *Quercus*, *Tilia* and *Ulmus* show decreasing trends, while *Picea* increases in coverage from 6 to 61 %. Also *Fagus* increased gradually in coverage starting at AD 1000 from 3 to 10 %, but decreased rapidly at ca. AD 1900 from 8 to 2 % coverage. *Alnus* had less coverage between AD 1000 and 2008 compared to earlier periods. *Corylus* decreased during the last ca. 500 yr and *Juniperus* was highest during the last 500 yr but variable. *Calluna vulgaris* and *Rumex acetosa* type decreased in coverage during the last ca. 150 yr from 3 to 1 % and from 1 to 0.5 %, respectively. REVEALS-based evenness decreased gradually from AD 1600 until today from 0.82 to 0.54. Evenness for trees followed the same pattern as total evenness, but evenness for herbs remained at a higher level.

## 5 Discussion

We applied the study design suggested by Fredh et al. (2012), which includes high-resolution pollen analysis, quantitative vegetation reconstruction and estimates of both floristic richness and evenness. The quantification of taxa coverage related to human impact allows us to estimate the extent of agricultural land-use at different times and its relation to floristic diversity.

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Between 600 BC and AD 350 human impact was relatively low, but pollen grains of *Cerealia* and herbs related to human agriculture show that some land-use occurred. The relatively large portion of *Corylus*, which requires some degree of openness, was possibly caused by widespread grazing (Berglund et al., 2002; Fyfe, 2008).

In general, *Cerealia* and most herbs had a higher coverage during the last ca. 1650 yr, which suggests an increased agricultural land-use and/or more focus on crop cultivation during this period. Palynological richness is generally higher during the same time, which suggests that traditional agriculture favors floristic diversity. REVEALS-based evenness was highest between AD 500 and 1600, indicating more equal distribution among taxa during this time. An increase in palynological richness is usually recorded at AD 1100 to 1200 in the uplands of southern Sweden as a consequence of increased land-use (Lindbladh and Bradshaw, 1995; Sköld et al., 2010), although maximum palynological richness has been recorded at earlier times, between 500 BC-AD 1000, in other areas in southern Sweden (Berglund et al., 2008).

Maximum openness, based on herb taxa coverage dominated by Poaceae, was recorded AD 350 to 550. This suggests a maximum extent of agricultural land-use at this time, estimated at 26 to 34 % of the area. The increase in open-land taxa at AD 350 is interpreted as a regional land-use expansion and correlates with high values of both palynological richness and increase in evenness for both herbs and trees, which suggests that many plants were favoured by this land-use expansion. This could reflect an increased establishment of farms and permanent fields, which possibly resulted in higher openness. Land-use expansions and regressions, similar to the one at AD 350, have been observed throughout the last 6000 yr in several pollen diagrams and may be related to periods of human population expansion and decline (Berglund, 1969; Lagerås, 2007).

This expansion was followed by a 200 yr long interval of regression, which was recorded by decreased herb coverage and increased tree coverage (Fig. 4). The increased tree cover was recorded in two steps, first by early successional tree taxa such as *Betula* followed by late successional tree taxa such as *Carpinus*, *Quercus*, *Tilia*

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and *Ulmus*. This succession indicates that some areas were abandoned after AD 550, which allowed the vegetation to expand on areas previously used for agricultural land-use. During this land-use regression palynological richness decreased, which indicates that this type of land-use regression is unfavourable for herbs. However, evenness for both trees and herbs remained at a higher level, and increased somewhat in the later part of the period, which mainly reflect that several herbs and trees remained in the area while Poaceae decreased in coverage. This regression period may be correlated to the Migration period AD 400–600, which was a period of general decline and societal change in Europe (Frezel et al., 1994).

Connell (1978) suggested the “Intermediate disturbance hypothesis”, which states that the highest biodiversity is created and maintained where disturbance is intermediate in frequency and intensity. Similarly, Emanuelsson (2005) suggested that discontinuous management, like that observed at AD 550 in this study, is essential for biodiversity by allowing species groups favoured by traditional management, succession and old growth forest to coexist. Fredh et al. (2012) suggested that floristic diversity was favoured during the initial ca. 40 yr of the transition from traditional to modern land-use management. 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. In the present study, the regression at AD 550 was accompanied by land abandonment, which allowed succession of shrubs and trees to occur. In this case, palynological richness declined simultaneously with land-use, which suggests that species richness is not favoured during this type of succession, possibly due to rapid land abandonment. However, REVEALS-based increased during this period, which indicates that floristic evenness increased for these taxa despite a decline in agricultural land-use.

During the last ca. 100 yr land-use gradually changed from a small-scaled agriculture towards a modern land-use based more on crop cultivation and forestry (Myrdal, 1997; Morell, 2001). This is supported in our record by decreased coverage of most herbs, such as *Calluna vulgaris* and *Rumex acetosa* type, and some trees, such as *Fagus*,

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*Corylus* and *Betula*, during the last ca. 100–150 yr, while *Picea* and *Cerealia* type increased. A decrease in palynological richness during the last ca. 100 yr is sometimes observed in pollen records (Lindbladh and Bradshaw, 1995; Lindbladh, 1999; Sköld et al., 2010). In this study palynological richness decreased at AD 1700, but remained within the range observed during the last 1650 yr. REVEALS-based evenness gradually decreased from AD 1600 until today, which suggests a decrease in habitats related the traditional agricultural. Evenness for herbs remained at a higher level probably by the increase in *Cerealia*, which compensated for the decline of herb coverage in general.

Previous pollen records, as well as archaeological/historical records, from the region suggest maximum openness during the last ca. 1000 yr, often including a prominent expansion at ca. AD 900–1200 (Lindbladh and Bradshaw, 1995; Björkman, 1996; Lagerås, 1996; Lindbladh, 1999; Lindbladh et al., 2000; Andersson Palm, 2001; Berglund et al., 2002), which is not consistent with our record. However, some pollen diagrams do show equally high, and sometimes higher, openness between AD 0 and 500 compared to the last 1000 yr (Lagerås, 1996; Björkman, 1996). Most previous pollen studies were based on small lakes and bogs, which partly reflect the local vegetation, since approximately 35 to 50 % of the pollen assemblage originates from within few kilometers from small sites (< 1–100 ha) (Sugita, 1994). Therefore, it is not straightforward to compare these records with our pollen record reflecting regional vegetation. There are a few pollen-analytical studies based on medium sized lakes (approximately 75 ha) from the region, but the chronologies in these studies are based on bulk gyttja samples, which makes detailed dating of events difficult (Digerfeldt, 1972; Jacobson, unpublished). Furthermore, Russian and Livingstone corers sometimes fail to recover the uppermost part of a sediment sequence, which may explain why a late 19th century maximum in land-use is only recorded in a few pollen diagrams. Our study is also one of the first in the region using the Landscape Reconstruction Algorithm to correct for biases in pollen representation of vegetation.

When relating our record to earlier studies in the region, it should be kept in mind that establishing a chronology for the Lake Fiolen sediment sequence was not

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straightforward despite our rather ambitious dating program involving a range of methods. The age-depth relationship in the interval between 160 and 40 cm is almost linear and in general parallel to the slope of the bulk dates. However, the interval between 40 and 20 cm reflects a more variable and generally lower sedimentation rate compared to the sections above and below. Possibly, there are other options to construct an age-depth model. However, given the available data, we consider our age-depth model the most probable one.

Fredh et al. (2012) studied land-use and floristic diversity during the last 200 yr in detail using the same sediment sequence but based on a different chronology. Although pollen percentages for some taxa do not differ so much between the chronologies covering the last 200 yr, the overall interpretation of the pollen record would be different using the chronology in this study. The main differences are in the interval AD 1800 to 1950 when *Pinus*, *Betula*, *Corylus*, have significantly larger coverage, while *Picea* have significantly less coverage in this study compared to Fredh et al. (2012). Also, *Fagus* has both significantly higher and lower coverage during this time in comparison. Palynological richness is similar between the two chronologies, but between AD 1800 and 1920 REVEALS-based evenness is higher with 0.75 to 0.83 compared to Fredh et al. (2012) with 0.63 to 0.73.

Fredh et al. (2012) interpreted the increase in Poaceae and many herbs at AD 1880 as an increase in biomass rather than an increase in coverage. This biomass increase was proposed to be connected to a reduction in grazing and mowing promoting flowering of grasses and herbs, i.e. a change to less intense agricultural land-use. According to the chronology used in this study this transition occurred at AD 1500, which is a known period of expansion in the uplands of southern Sweden (Lagerås, 2007). Therefore, the change in coverage of Poaceae and other herbs at this time could possibly be interpreted both as an expansion and a regression. This is not obvious since Poaceae includes a large number of species which may react differently to land-use changes (Broström et al., 2008). During the last ca. 150 yr, grass cultivation increased,

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which may explain the relatively small change in Poaceae coverage during this time, despite a decrease in extent of meadows and pastures.

Since long we are aware of that the traditional agriculture land-use promote floristic diversity (e.g. Emanuelsson, 2009), however, this study is one of first that have quantified the effect modern land-use has had on the landscape on a regional scale. REVEALS based evenness for our modern landscape is 0.54 compared to 0.70–0.83 between 600 BC and AD 1700 i.e. unusually low in a millennial perspective. For the palynological richness the differences are not as striking, however, lower today than between AD 1500 and 1700. Our results also makes it possible to quantify the rate of diversity changes in a traditionally managed landscape moving from expansion to regression with two successional phases. We show that the impact on diversity is different from the transition to modern land-use (Fredh et al., 2012). During the expansion of agricultural land-use AD 350–550 both palynological richness and REVEALS based evenness increased less than 20–50 yr after the first sign of expansion. In the early succession of the regression, dominated by the significant increase in birch, there is a rapid reaction (less than 20 yr) in palynological richness. In the late succession of the regression there is a slight increase in palynological richness, however, not to the same numbers as before the regression. REVEALS based evenness also increased to the highest values (0.83) in the late successional phase because of the increased coverage of several of the broadleaved trees.

How are our results useful for ecosystem management? On a regional landscape scale the evenness is strikingly higher in traditional than in modern agricultural land-use. This suggests that ecosystem management should also include a regional landscape perspective in addition to the management of the small fragments of traditional agricultural land-use left. Also we provided an estimate of reaction time of richness and evenness to expansion and regression of traditional agricultural land-use.

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## 6 Conclusions

Because of inconsistencies within and between the chronological data provided by a range of different methods applied, the absolute chronology of this study is tentative, in particular between AD 1200 and AD 1950. However, given the available data, we consider our age-depth model the most probable one.

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 more equal distribution among taxa during this time. We identified a period of land-use expansion followed by regression between AD 350 and 750.

At the beginning of the expansion period at AD 350, land-use, palynological richness and REVEALS-based evenness for herbs increased simultaneously, which suggests that floristic diversity was favored by this land-use expansion. In contrast, during the land-use regression at AD 550, palynological richness and REVEALS-based evenness for herbs decreased at the same time as land-use. Maximum openness was recorded during the expansion period AD 350 to 550, with 27 to 34 % open land taxa coverage.

The regression period AD 550 to 750 was initially characterised by early successional tree taxa such as *Betula*, followed by a shift towards late successional tree taxa such as *Carpinus*, *Quercus*, *Tilia* and *Ulmus*, indicating that areas were abandoned and allowed the vegetation to develop in a natural succession. REVEALS-based evenness for trees increased at this time, which suggests that tree cover expanded and tree vegetation became more diverse.

Values of palynological richness for the last few decades are within the range observed during the last ca. 1650 yr. However, REVEALS-based evenness shows much lower values during the last century than during the previous ca. 2600 yr, which indicates that the distribution of present day vegetation is unusual in a millennial perspective.

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Our data suggest that floristic diversity responds within 20 to 50 yr to changes in land-use on a regional scale, as illustrated by the inferred land-use expansion and regression at AD 350 and 550, respectively. Our results show the importance of traditional land-use to attain high biodiversity and suggest that ecosystem management should include a regional landscape perspective.

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**Table 1.** Fall speed of pollen, relative pollen productivity estimates (PPE) and associated standard error estimates (SE) for 26 taxa obtained for southern Sweden (Sugita et al., 1999; Broström et al., 2004) and Denmark (numbers in bold; Nielsen et al., 2004) used in the REVEALS model run.

Pollen taxa	Fall speed (ms <sup>-1</sup> )	PPE	SE
<i>Acer</i>	0.056	1.267	0.452
<i>Alnus</i>	0.021	4.200	0.140
<i>Betula</i>	0.024	8.867	0.134
<i>Calluna vulgaris</i>	0.038	<b>1.102</b>	<b>0.054</b>
<i>Carpinus</i>	0.042	2.533	0.070
Cereal-t	0.060	<b>0.747</b>	<b>0.039</b>
Comp. SF. Cichorioideae	0.051	0.244	0.065
<i>Corylus</i>	0.025	1.400	0.042
Cyperaceae	0.035	1.002	0.164
<i>Fagus</i>	0.057	6.667	0.173
<i>Filipendula</i>	0.006	2.480	0.821
<i>Fraxinus</i>	0.022	0.667	0.027
<i>Juniperus</i>	0.016	2.067	0.036
<i>Picea</i>	0.056	1.757	0.000
<i>Pinus</i>	0.031	5.663	0.000
<i>Plantago lanceolata</i>	0.029	<b>0.897</b>	<b>0.235</b>
Poaceae	0.035	1.000	0.000
<i>Potentilla-t</i>	0.018	2.475	0.377
<i>Quercus</i>	0.035	7.533	0.083
<i>Ranunculus acris-t</i>	0.014	3.848	0.718
Rubiaceae	0.019	3.946	0.589
<i>Rumex acetosa-t</i>	0.018	<b>1.559</b>	<b>0.089</b>
<i>Salix</i>	0.022	1.267	0.313
<i>Secale-t</i>	0.060	3.017	0.052
<i>Tilia</i>	0.032	0.800	0.029
<i>Ulmus</i>	0.032	1.267	0.050

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**Table 2.** Radiocarbon dates on macrofossils and bulk sediment samples. Calibrated age intervals are those provided by the OxCal program when calculated for each sample individually (not in a sequence). The  $^{14}\text{C}$  age for sample LuS8602 is younger than AD 1950 and therefore expressed as percent modern carbon (pMC). Sample weights are those reported by the laboratory for material used for graphitization (after any pre-treatment). Weights for the first dated sample batches (LuS8XXX) were reported as mg organic material, while weights for samples dated later were reported as mg C.

Macrofossils							
Lab-ID	Depth (cm)	$^{14}\text{C}$ age BP $\pm 1\sigma$	Calibrated age BP (1 $\sigma$ interval)	Sample weight (mg)	Pre-treatment	Type of material	Core
LuS9161	33.75	260 $\pm$ 50	429– –1	3.1 (C)	HCl, NaOH	Twig	P
LuS9103	44.50	950 $\pm$ 50	925–796	2.1 (C)	HCl, NaOH	Plant remains	C
LuS9105	58.00	1160 $\pm$ 45	1170–1000	1.29 (C)	-	Plant remains	D
LuS9104	59.50	1255 $\pm$ 50	1274–1141	0.52 (C)	-	Plant remains	C
LuS8602	63.75	105.5 $\pm$ 0.7 pMC	3– –57	0.39 (org. mtrl)	-	Leaf + <i>Betula</i> catkin scale	P
LuS8603	73.75	750 $\pm$ 60	734–658	0.15 (org. mtrl)	-	<i>Betula</i> catkin scale	P
LuS8061	83.75	1070 $\pm$ 120	1169–803	0.15 (org. mtrl)	-	<i>Alnus</i> fruit	P
LuS8604	87.50	1260 $\pm$ 60	1279–1095	0.57 (org. mtrl)	-	Plant remains + <i>Betula</i> catkin scale	P
LuS8605	99.50	300 $\pm$ 60	456–299	0.29 (org. mtrl)	-	Moss + <i>Betula</i> catkin scale + plant remains	P
LuS8606	115.50	1095 $\pm$ 60	1060–937	0.53 (org. mtrl)	-	Leaf + <i>Betula</i> catkin scale + plant remains	P
LuS8062	121.75	1995 $\pm$ 50	1995–1887	3.8 (org. mtrl)	HCl, NaOH	Leaf	P
LuS8607	134.75	1475 $\pm$ 60	1408–1306	0.34 (org. mtrl)	-	Plant remains	P
LuS8608	158.25	2440 $\pm$ 60	2695–2359	0.17 (org. mtrl)	-	Leaf + <i>Betula</i> fruit	P
Bulk sediments							
Lab-ID	Depth (cm)	$^{14}\text{C}$ age BP $\pm 1\sigma$	Calibrated age BP (1 $\sigma$ interval)	Sample weight (mg)	Pre-treatment	Type of material	Core
LuS9616	29.75	995 $\pm$ 50	961–800	4.1 (C)	HCL	Bulk	P
LuS9617	44.75	1165 $\pm$ 50	1171–1005	4.3 (C)	HCL	Bulk	P
LuS9618	59.75	1415 $\pm$ 50	1353–1290	4.3 (C)	HCL	Bulk	P
LuS9619	79.75	1975 $\pm$ 50	1988–1878	5.0 (C)	HCL	Bulk	P
LuS9620	99.75	2110 $\pm$ 50	2146–2004	5.3 (C)	HCL	Bulk	P
LuS9621	119.75	2220 $\pm$ 50	2320–2156	5.0 (C)	HCL	Bulk	P
LuS9622	139.75	2590 $\pm$ 50	2771–2546	5.0 (C)	HCL	Bulk	P
LuS9623	157.75	2700 $\pm$ 50	2845–2761	5.3 (C)	HCL	Bulk	P

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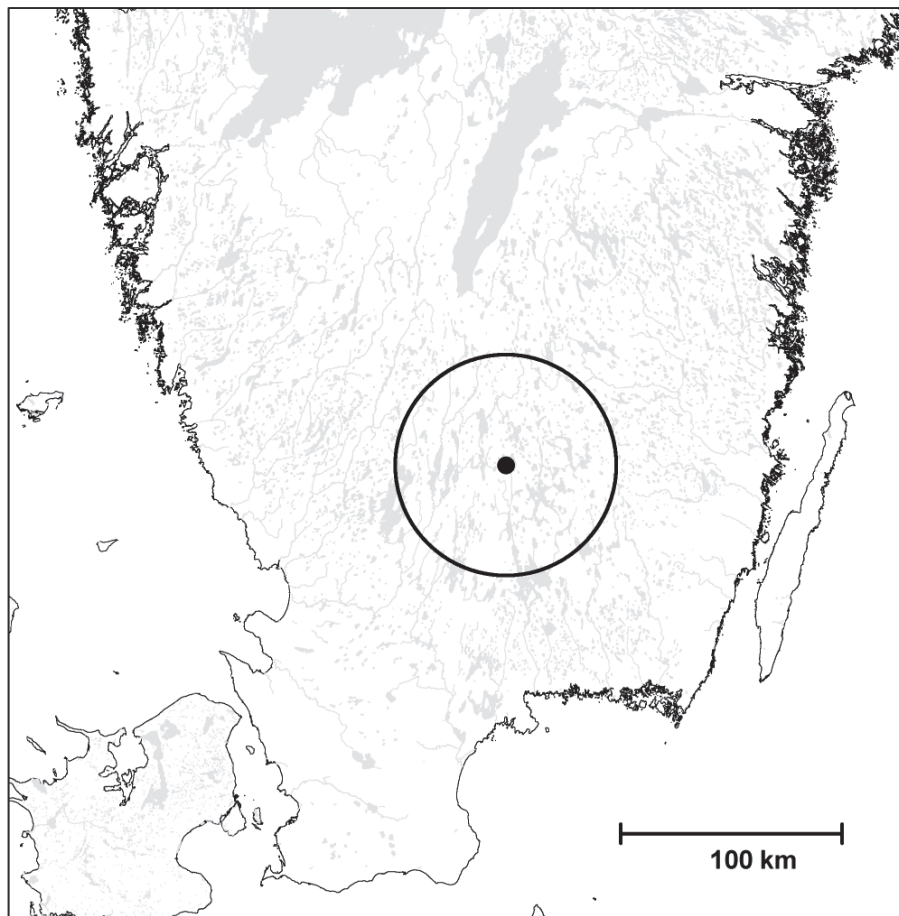
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**Fig. 1.** Study area in the south-Swedish Uplands. The circle represents the reconstructed area within a 50 km radius from Lake Fiolen which is situated in the centre.

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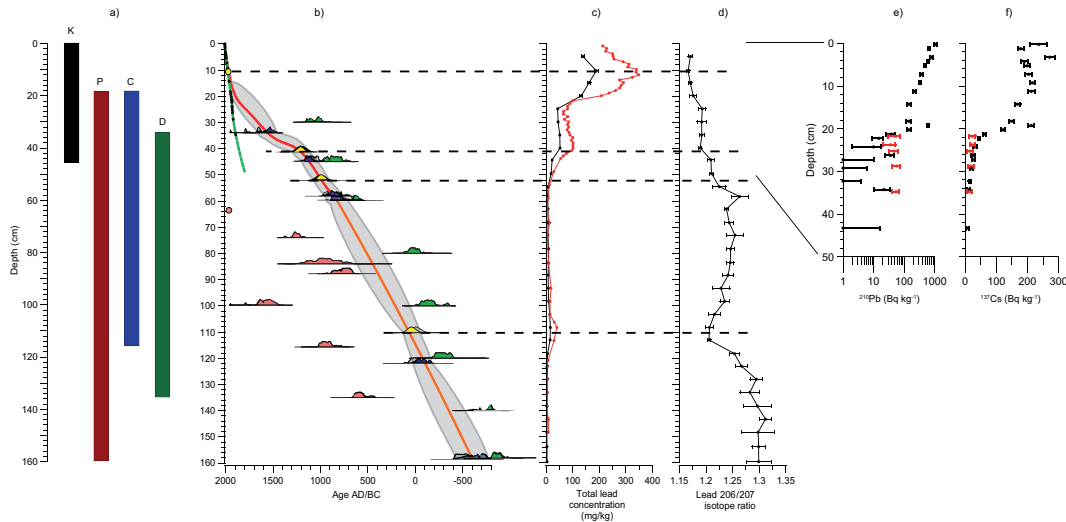
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**Fig. 2.** (a) Cores used in this study. (b) Age model established by the OxCal program when including six radiocarbon dates based on three large (> 2 mg) macrofossils (dark blue) and three small (< 2 mg) macrofossils (light blue), a CRS-model based on nine  $^{210}\text{Pb}$  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  $^{210}\text{Pb}$  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  $2\sigma$  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). (c) Total lead concentrations measured using Quadrapole ICP-MS (black line) and XRF (red line), respectively. (d) Lead 206/207 ratio. (e), (f) Unsupported  $^{210}\text{Pb}$  and  $^{137}\text{Cs}$  concentrations measured on core K (black) and core P (red).

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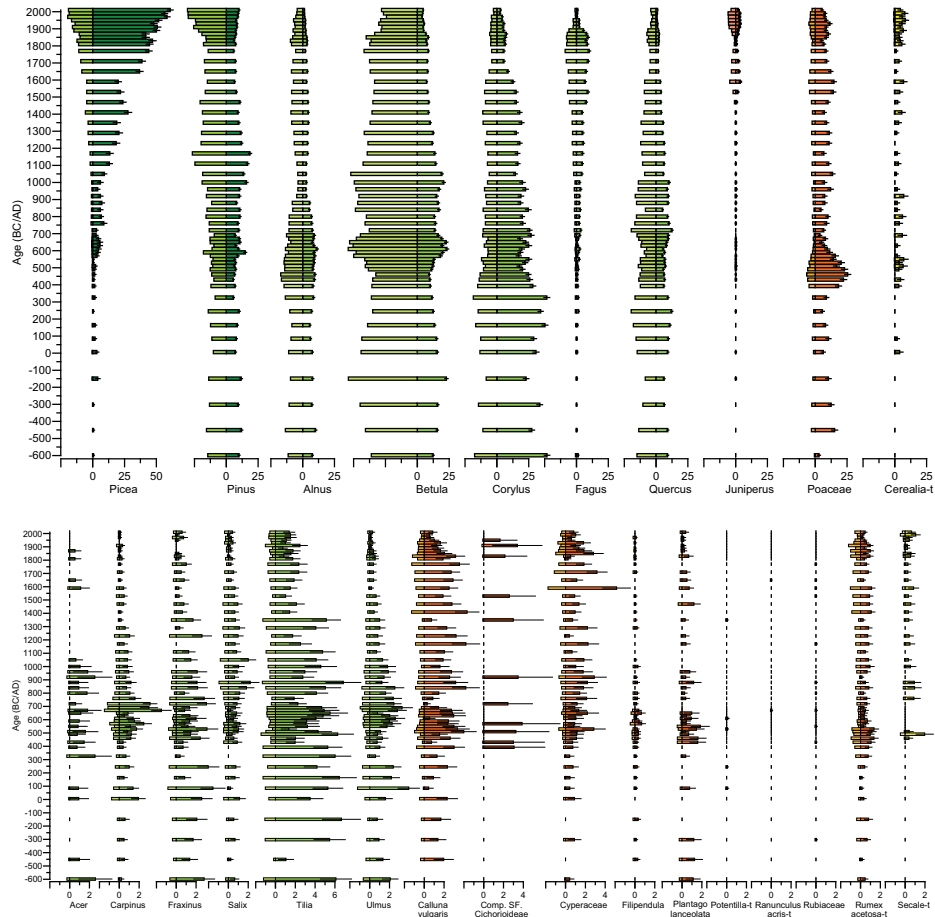
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**Fig. 3.** Pollen percentage diagram (left side) and estimated regional vegetation cover using the REVEALS model (right side) for 26 taxa for the period 600 BC to AD 2008. Note the different scales for the upper and lower parts of the figure.

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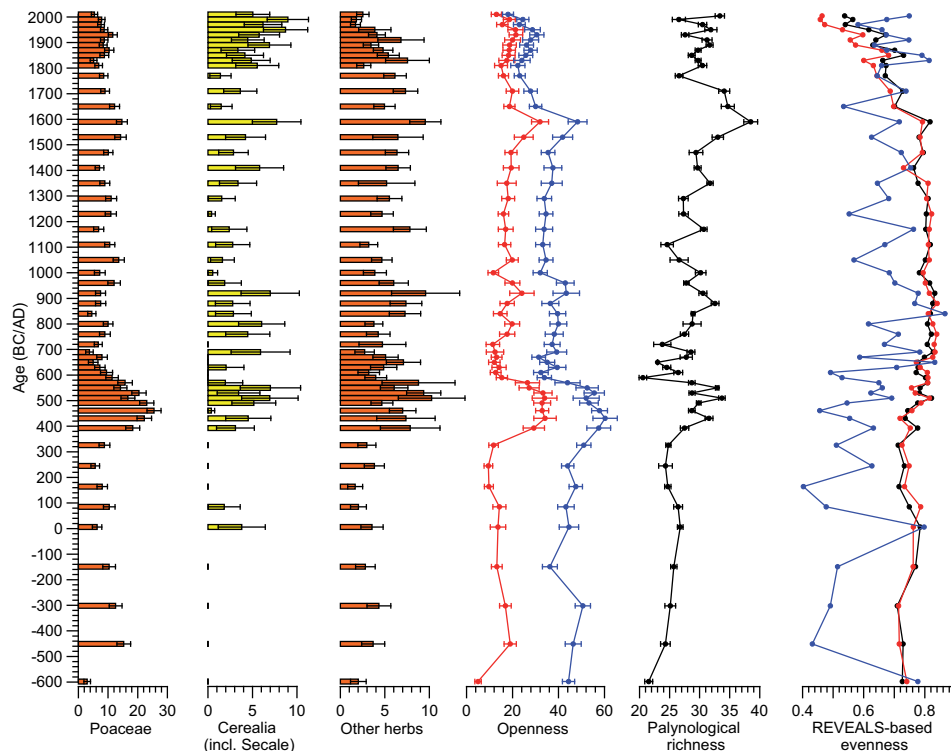
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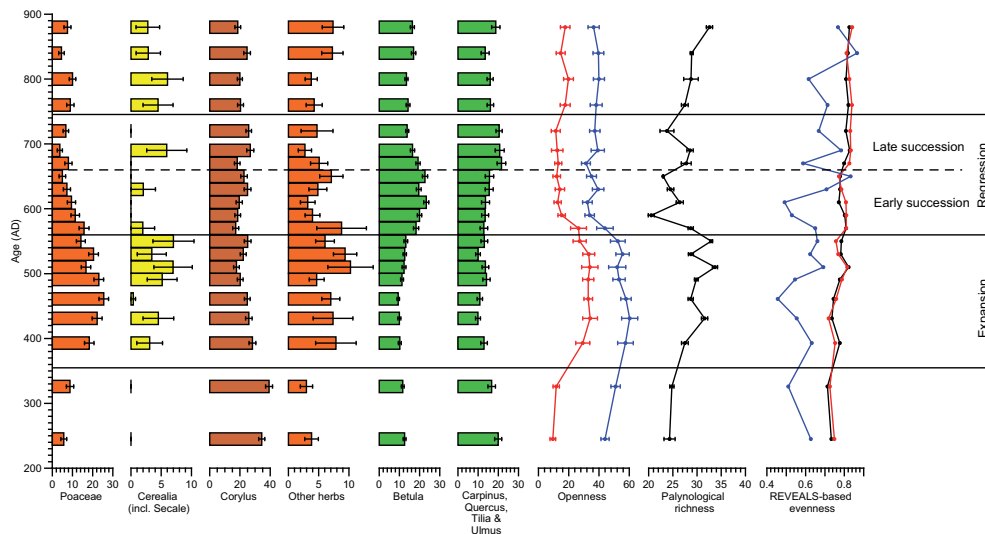
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**Fig. 4.** Regional vegetation cover for selected taxa/taxa groups, openness, palynological richness and REVEALS-based evenness between 600 BC to AD 2008. Openness was estimated both including and excluding bushes shown by blue and red line, respectively. REVEALS-based evenness was calculated for all 26 reconstructed taxa (black line), but also for trees (red line) and herbs (blue line) separately.

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**Fig. 5.** Regional vegetation cover for selected taxa/txa groups, openness, palynological richness and REVEALS-based evenness at the transition from expansion to regression AD 350 to 750. Openness was estimated both including and excluding bushes shown by blue and red line, respectively. REVEALS-based evenness was calculated for all 26 reconstructed taxa (black line), but also for trees (red line) and herbs (blue line) separately. The transition was divided into one expansion and two regression phases.

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