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# Pollen-based quantitative reconstructions of Holocene regional vegetation cover (plant-functional types and land-cover types) in Europe suitable for climate modelling

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## Abstract

We present quantitative reconstructions of regional vegetation cover in north-western Europe, western Europe north of the Alps, and eastern Europe for five time windows in the Holocene [around 6k, 3k, 0.5k, 0.2k, and 0.05k calendar years before present (BP)] at a 1° × 1° spatial scale with the objective of producing vegetation descriptions suitable for climate modelling. The REVEALS model was applied on 636 pollen records from lakes and bogs to reconstruct the past cover of 25 plant taxa grouped into 10 plant-functional types and three land-cover types [evergreen trees,

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summer-green (deciduous) trees, and open land]. The model corrects for some of the biases in pollen percentages by using pollen productivity estimates and fall speeds of pollen, and by applying simple but robust models of pollen dispersal and deposition. The emerging patterns of tree migration and deforestation between 6k BP and modern time in the REVEALS estimates agree with our general understanding of the vegetation history of Europe based on pollen percentages. However, the degree of anthropogenic deforestation (i.e. cover of cultivated and grazing land) at 3k, 0.5k, and 0.2k BP is significantly higher than deduced from pollen percentages. This is also the case at 6k in some parts of Europe, in particular Britain and Ireland. Furthermore, the relationship between summer-green and evergreen trees, and between individual tree taxa, differs significantly when expressed as pollen percentages or as REVEALS estimates of tree cover. For instance, when *Pinus* is dominant over *Picea* as pollen percentages, *Picea* is dominant over *Pinus* as REVEALS estimates. These differences play a major role in the reconstruction of European landscapes and for the study of land cover–climate interactions, biodiversity and human resources.

*Keywords:* Europe, Holocene, plant-functional types, pollen data, quantitative past land cover, REVEALS model

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## Introduction

In this paper, we present an initial attempt at using the mechanistic 'Regional Estimates of VEgetation Abundance from Large Sites' model (REVEALS, Sugita, 2007a) to reconstruct past vegetation/land cover using Holocene pollen records at the sub-continental scale of Europe [north-western, western (north of the Alps), and eastern Europe]. This study is part of the research project 'LAND cover – CLIMate interactions in Europe during the Holocene (LANDCLIM)' that attempts to quantify the possible effects of anthropogenic land-cover change (ALCC) on the Holocene climate of Europe at the regional spatial scale using a regional climate model (Gaillard *et al*., 2010). Therefore, the primary objective of the REVEALS reconstructions discussed in this paper is to use them in climate-modelling studies of past land cover–climate interactions at selected time periods of the Holocene (6k, 3k, 0.5k, 0.2k, and 0.05k calibrated years BP) (Strandberg *et al*., 2014). Here, we present and discuss (i) the first generation of LANDCLIM maps of 10 plant-functional types (PFTs) and three land-cover types (LCTs) for the purpose of climate modelling within the project and (ii) the new insights provided by the REVEALS estimates of plant/vegetation cover on Holocene vegetation composition and their implications for (i) the evaluation of existing scenarios of past ALCC (e.g. HYDE, Klein Goldewijk *et al*., 2011), (ii) past land cover–climate interactions and climate modelling, and (iii) past biodiversity and human resources, and nature conservation/landscape management.

Quantitative reconstruction of past vegetation cover has long been a major objective for many palynologists (e.g. Davis, 1963; Prentice & Parsons, 1983; Sugita, 1993, 1994; Prentice *et al*., 1996, 1998; Gaillard *et al*., 1998, 2008). Vegetation cover on earth influences many aspects of the environment; climate, food resources, and water quality and availability being among the most important ones. If we can understand the processes involved over past centuries and millennia, we also have a better understanding of which processes should be included in environmental models (climate, dynamic vegetation, water-catchment models, etc.) for projections of future changes. The more accurate the model projections, the more appropriate the management strategies for our future environment can be (e.g. Anderson *et al*., 2006; Dearing, 2008, 2013; Gaillard *et al*., 2010). However, quantitative reconstruction of past land cover is not straightforward. Many methods have been developed in recent decades including biomization (e.g. Prentice *et al*., 1996, 1998; Prentice & Webb, 1998; Tarasov *et al*., 2013) and mechanistic models (e.g. Prentice & Parsons, 1983; Sugita, 2007a,b). The latest mechanistic models developed by Sugita (2007a, b) have the advantage of including both pollen productivity estimates (PPEs) and models of dispersal and deposition of small particles in the air, and they have been successfully tested in several areas of the world (e.g. Hellman *et al*., 2008a,b; Soepboer *et al*., 2010; Sugita *et al*., 2010).

Terrestrial vegetation is an important part of the earth system that is both influenced by climate and affects climate through biogeochemical and biogeophysical processes/feedbacks (e.g. Foley *et al*., 2003). Human-induced land-cover change may impact climate through similar processes and represents one of the many forcings of climate change (e.g. Pongratz *et al*., 2008; Pitman *et al*., 2009; de Noblet-Ducoudré *et al*., 2012; Gaillard *et al*., in press). Therefore, it is necessary to incorporate land-cover descriptions in climate models to better understand vegetation–climate interactions in the past, to test coupled vegetation–climate models, and to improve projections of future climate and related impacts. Dynamic vegetation models (DVMs) have been developed and coupled to climate models (e.g. Smith *et al*., 2011). However, these DVMs simulate climate-induced potential vegetation and do not take account of human-induced vegetation changes. During

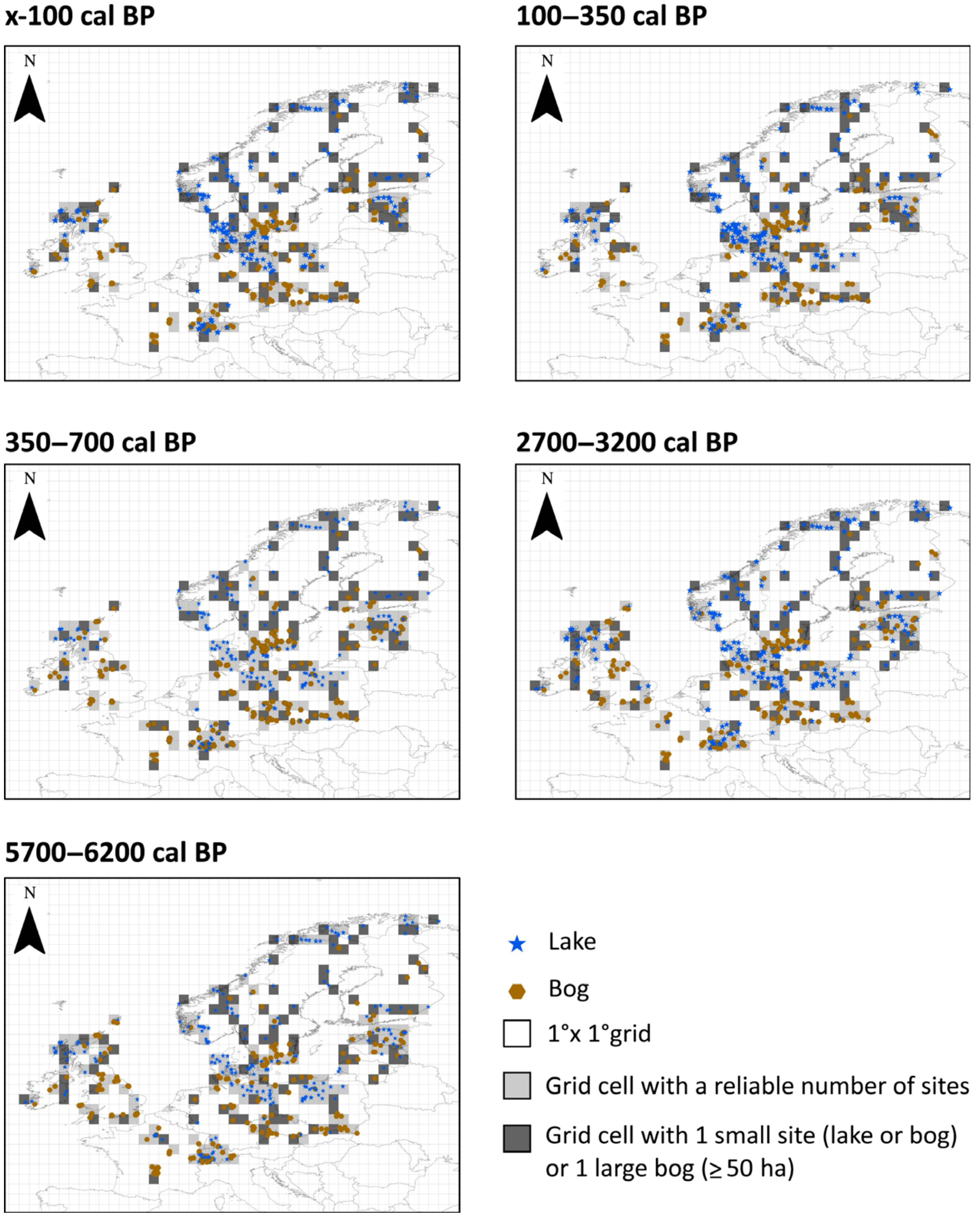

**Fig. 1** The LANDCLIM study area with all the sites (i.e. pollen records) used for the REVEALS reconstructions of land cover for each time window. Blue stars are pollen records from lakes and brown dots are pollen records from bogs. The uncertainties are based on the number and type of site(s) used for the REVEALS reconstruction in each grid cell and expressed by different shades of grey. Light grey: grid cells with a sufficient number of sites, i.e. the REVEALS estimates in these grid cells are regarded as reliable. Dark grey: grid cells where the REVEALS estimates are based on pollen data from one small site (lake or bog) or one large bog (≥50 ha), i.e. the REVEALS estimates in these grid cells are regarded as less reliable or even unreliable.

the last decade, several approaches have been developed to estimate past ALCCs to assess their possible effects on past climate (Ramankutty & Foley, 1999; Klein Goldewijk, 2001; Olofsson & Hickler, 2008; Pongratz *et al*., 2008, 2010; Kaplan *et al*., 2009, 2011, 2012; Lemmen, 2009; Klein Goldewijk *et al*., 2011). However, these ALCC scenarios exhibit significant differences between themselves (e.g. Gaillard *et al*., 2010; Boyle *et al*., 2011), which implies major differences in conclusions about past ALCC climate interactions (e.g. Kaplan *et al*., 2011; Strandberg *et al*., 2014). Thus, pollen-inferred quantitative reconstructions will become increasingly important (i) to evaluate the performance of different ALCC scenarios (J.O.Kaplan, unpublished data) and DVMs coupled to climate models (Strandberg *et al*., 2014) and (ii) as alternative descriptions of past land cover, for example for climate modelling (Strandberg *et al*., 2014; Pirzamanbein *et al*., in press).

## Materials and methods

### *Study region*

The region covering north-western Europe, western Europe north of the Alps, and eastern Europe (Fig. 1) is currently the part of the world with the largest number of PPEs for the major plant taxa of the area (Broström *et al*., 2008; Mazier *et al*., 2012) (Table 1). These PPEs were all calculated using Extended R-Value models (e.g. Prentice & Parsons, 1983; Sugita, 1993) and modern (historical in few cases) pollen data and related distance-weighted vegetation data (see review by Broström *et al*., 2008). It is therefore currently the most appropriate region in which to apply the REVEALS model for pollen-based quantitative reconstructions of past land cover at a large regional/sub-continental spatial scale, and to meet the objectives of the LANDCLIM project (Gaillard *et al*., 2010). Our study region covers the following present-day environmental zones (according to Metzger *et al*., 2005), Alpine North, Boreal, Nemoral, Continental, Atlantic North, Atlantic Central, and Alpine South (i.e. ca. 40°N to 75°N and 15°W to 35°E; Fig. 1).

### *Data sources*

The pollen records for the land-cover reconstructions are from 17 countries (Fig. 1). They were collected directly from the data contributors (co-authors and Tables S1 and S2) and from archives of pollen records (Ireland, Norway, Estonia) and databases, i.e. the European Pollen Database (EPD) (Fyfe *et al*., 2009; Giesecke *et al*., 2014), the Czech Quaternary Palynological Database (PALYCZ) (Kuneš *et al*., 2009), and the Alpine Pollen Database (ALPADABA) (University of Bern, Switzerland)

**Table 1** Land-cover types (LCTs) and plant-functional types (PFTs) according to Wolf *et al.* (2008) with modifications (see text)

| Land-cover types | PFT | PFT definition | Plant taxa/ Pollen-morphological types (25 taxa) | FSP (m s$^{-1}$) | PPE.st2 |
|---|---|---|---|---|---|
| Evergreen tree canopy (ET) | TBE1 | Shade-tolerant evergreen trees | *Picea* | 0.056 | 2.62 (0.12) |
| | TBE2 | Shade-tolerant evergreen trees | *Abies* | 0.120 | 6.88 (1.44) |
| | IBE | Shade-intolerant evergreen trees | *Pinus* | 0.031 | 6.38 (0.45) |
| | TSE | Tall shrub, evergreen | *Juniperus* | 0.016 | 2.07 (0.04) |
| Summer-green tree canopy (ST) | IBS | Shade-intolerant summer-green trees | *Alnus* | 0.021 | 9.07 (0.10) |
| | | | *Betula* | 0.024 | 3.09 (0.27) |
| | | | *Corylus* | 0.025 | 1.99 (0.20) |
| | | | *Fraxinus* | 0.022 | 1.03 (0.11) |
| | | | *Quercus* | 0.035 | 5.83 (0.15) |
| | TBS | Shade-tolerant summer-green trees | *Carpinus* | 0.042 | 3.55 (0.43) |
| | | | *Fagus* | 0.057 | 2.35 (0.11) |
| | | | *Tilia* | 0.032 | 0.80 (0.03) |
| | | | *Ulmus* | 0.032 | 1.27 (0.05) |
| | TSD | Tall shrub, summer-green | *Salix* | 0.022 | 1.22 (0.11) |
| Open land (OL) | LSE | Low shrub, evergreen | *Calluna vulgaris* | 0.038 | 0.82 (0.02) |
| | GL | Grassland – all herbs | *Artemisia* | 0.025 | 3.48 (0.20) |
| | | | Cyperaceae | 0.035 | 0.87 (0.06) |
| | | | *Filipendula* | 0.006 | 2.81 (0.43) |
| | | | Poaceae | 0.035 | 1.00 (0.00) |
| | | | *Plantago lanceolata* | 0.029 | 1.04 (0.09) |
| | | | *Plantago media* | 0.024 | 1.27 (0.18) |
| | | | *Littorella*-t | 0.030 | 0.74 (0.13) |
| | | | *Rumex acetosa*-t | 0.018 | 2.14 (0.28) |
| | AL | Agricultural land – cereals | Cerealia-t | 0.060 | 1.85 (0.38) |
| | | | *Secale cereale* | 0.060 | 3.02 (0.05) |

(Table S2). The pollen data and related metadata from the databases were checked for consistency in pollen-morphological taxonomy and nomenclature, pollen counts, and chronology in collaboration with the database managers, the EPD's working group MADCAP (Fyfe *et al.*, 2009), and/or the data contributors (for more information, see Appendix S2 and Table S2).

### *Time windows*

To maximize the number of samples with pollen counts (i.e. to maximize the overall size of pollen counts) within each time window, we chose to work with 500-year time windows around 6k and 3k years BP (in calibrated years before present; BP = before 1950), and 350-year, 250-year, and 100-year time windows around 0.5k, 0.2k, and 0.05k BP, respectively (see Table S2 and Appendix S2 for more explanations). They were selected for the purpose of climate modelling at times in the past with contrasting human impact on the vegetation cover (Gaillard *et al.*, 2010) and are as follows:

1. *x*–0.1k BP (ca. 0.05k BP, 'Present'/Recent past): industrial time (*x* = date of the core surface, e.g. AD 2005-100 BP if *x* = AD 2005)
2. 0.1k–0.35k BP (ca. 0.2k BP, end of the Little Ice Age): preindustrial time
3. 0.35k–0.7k BP (ca. 0.5k BP, Middle Ages): decreased human impact in parts of Europe
4. 2.7k–3.2k BP (ca. 3k BP, Early/Late Bronze Age transition): relatively strong human impact in several parts of the study region
5. 5.7k–6.2k BP (ca. 6k BP, Neolithic period/Mesolithic-Early Neolithic boundary in southern Scandinavia, northern Germany and northern Netherlands): low human activity.

### *The REVEALS model and the LANDCLIM protocol*

A short description of the REVEALS model (Sugita, 2007a) and a detailed presentation and discussion of the LANDCLIM protocol for the REVEALS runs using the pollen records described above are provided in Appendices S1 and S2, respectively. The LANDCLIM protocol was also used in studies published earlier by Mazier *et al.* (2012), Nielsen *et al.* (2012), and Fyfe *et al.* (2013).

Following tests of REVEALS runs using different parameter settings (Mazier *et al.*, 2012) and the LANDCLIM protocol (Appendix S2), we selected sites (lakes and bogs, large and small) with chronologies based on $\geq 3$ $^{14}$C dates (or other dates and chronological references listed in Table 2 of Appendix S2). Today, there are PPEs and Fall Speed of Pollen (FSP) values available for 35 European tree, shrub, and herb taxa (families, genus groups, genus, species groups, and species) (Broström *et al.*, 2008; Mazier *et al.*, 2012). Of these, we excluded the strictly entomophilous taxa (Mazier *et al.*, 2012). Therefore, we worked with 25 taxa that were then grouped into 10 PFTs and three LCTs (Table 1). The REVEALS model was run on one or multiple sites located within each cell of a common $1° \times 1°$ grid (Table S3). The bog and lake sites were run separately using the models of pollen dispersal and deposition for bogs (Prentice, 1985) and lakes (Sugita, 1993), respectively. A mean of both estimates was then calculated for each grid cell with pollen records and for each of the 25 plant taxa (i.e. Grid-based REVEALS estimate for each taxon, hereafter referred to as REVEALS taxon (e.g. REVEALS *Pinus*; see Appendix S2 for more details). The REVEALS taxa were then grouped into REVEALS PFTs (e.g. REVEALS AL for the PFT agricultural land) and REVEALS LCTs (e.g. REVEALS OL for the LCT open land). Independent estimates of variances and covariances of pollen counts and variances of relative PPEs were used to estimate the standard errors (SEs) of the REVEALS taxa, PFTs, or LCTs based on the Delta method (Stuart & Ord, 1994; Sugita, 2007a). The maximum distance of regional vegetation (*Zmax*, see Appendix S1) was set to 50 km, and the wind speed to 3 m s$^{-1}$ (Hellman *et al.*, 2008a,b; Mazier *et al.*, 2012; see Appendix S1).

## Results

Below, for the sake of simplicity and ease of readability, the REVEALS taxa, PFTs, and LCTs (see Methods above) are referred to as taxa (e.g. *Picea*), PFTs (e.g. ALs for agricultural land), and LCTs (e.g. OLs for open land), respectively, except when it may lead to confusion and REVEALS is added for clarification.

Given the main purpose of the LANDCLIM project, we describe in particular the results related to changes in (i) the vegetation openness [i.e. the LCT open land (OL) and PFTs agricultural land (AL), grassland (GL), and *Calluna vulgaris* (heather; low shrub evergreen (LSE)] and (ii) the relationship between the three LCTs [i.e. OL, summer-green (deciduous) trees (STs) and evergreen trees (ETs)]. We also describe the results for *Picea* (spruce; PFT shade-tolerant evergreen tree, TBE1) as one of the striking examples of the effect of the REVEALS model reconstructions when compared to pollen percentages and its implication for conservation and biodiversity issues. In the text below 6k, 3k, 0.5k, 0.2k, and 0.05k are the selected time windows in calibrated years BP as explained above.

### *Presentation of results and uncertainties*

The 10 PFTs and three LCTs are presented with their error estimates in a series of 13 × 5 maps (one map per time window) (LCTs: Figs 2, 6, 7; PFTs: Figs 3–5, 8 and S1–S6). Based on (i) an estimation of the reliability of the REVEALS estimates related to the available pollen records in each grid cell (Fig. 1) and (ii) the calculated error estimates on the REVEALS results (Figs 2–8 and S1–S6), we think that the southern part of the study region including Denmark, southern Sweden, southern Norway, southern Finland, northern Poland, and Estonia, as well as northernmost Sweden and Norway, have the most reliable REVEALS estimates, while large parts of mid-Norway, Sweden, and Finland have few grid

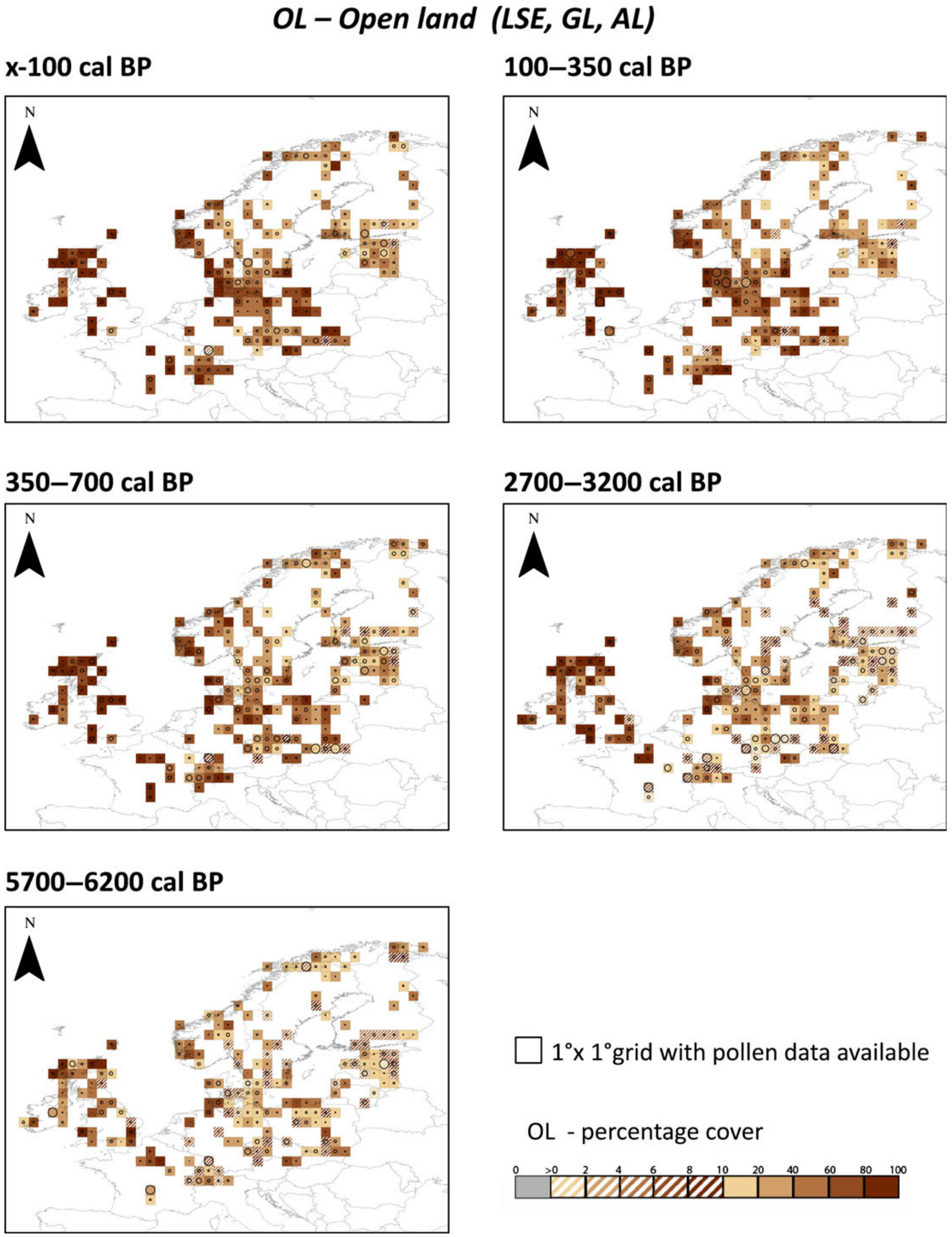

**Fig. 2** Grid-based REVEALS estimates for the land-cover type (LCT) open land (OL) for the five Holocene time-windows. The scale is percentage cover, with the different colours indicating different percentage intervals: >0–10% in 2% intervals, 10–20% in a 10% interval, and 20–100% in 20% intervals. The category 0 (grey) corresponds to the grid cells with pollen records but no pollen for the actual LCT and, therefore, no REVEALS estimates. The category >0–2 corresponds to REVEALS estimates different from zero (can be less than 1%) up to 2%. The uncertainties of the LCTs and REVEALS estimates for the plant-functional types (PFTs) (Figs 3–5 and 8) are shown by circles of various sizes in each grid cell with a REVEALS estimate. The circles represent the coefficient of variation (CV; the standard error divided by the REVEALS estimate). When SE ≥ REVEALS estimate, the circle fills the entire grid cell and the REVEALS estimate is considered unreliable. This occurs mainly where REVEALS estimates are low.

cells with more than one pollen record (from one small site) available and, therefore, these results should be interpreted with care; they are not necessarily representative of the regional vegetation.

### *Vegetation openness (LCT OL and PFTs AL, GL and LSE)*

The LCT OL (Fig. 2) includes the PFTs AL (i.e. Cereals; Fig. 3), GL (eight herbs with Poaceae and Cyperaceae often being the dominant taxa; Fig. 4), and LSE (one evergreen low shrub, *C. vulgaris*; Fig. 5).

Because cereals often have low pollen counts except *Secale* (rye), the AL REVEALS estimates (ALs; Fig. 3) often do not differ from zero (largest circle in the grid cells). At 6k, few grid cells have reliable values <2% in central Europe, Denmark, Poland, and the Baltic Countries. At 3k, there are a larger number of grid cells with ALs <2% in particular in Scotland, Ireland, northern Germany, and southern Scandinavia. Except in south-eastern Ireland and eastern Estonia, values >2% (up to 6%) are all reliable estimates (northern France, eastern Austria, northern Czech Republic, western Estonia). At 0.5k, ALs >0 are found in most of the grid cells and for a much larger area than at 3k. The values are also higher than at 3k, i.e. they reach 6–10% in a large number of grid cells, and >10% in northern Germany, Poland, southern Sweden and the eastern Baltic Countries. At 0.2k, the picture is very similar to the one at 0.5k. At 0.05k, an increase of ALs to values >10% is seen primarily in northern Germany and Poland. In contrast, a decrease in values is observed in north-eastern Germany, Britain, and Ireland.

The dominant taxon in GL is almost always Poaceae (grasses). Because the GLs (Fig. 4) are usually >2%, few grid cells have values that do not differ from zero. There is a clear trend of increased GLs from 6k until present. The highest reliable values at 6k (40–100%) are found in the western part of the study region, from northern Scotland to southern Scandinavia. Values >20–40% are found in the same areas and in central Germany (mountain area of Fichtelgebirge and Thuringerwald) and the Scandes mountains. GLs increase by 10–20% between 6k and 3k in most parts of the study region, except in areas with already high GLs at 6k and in northernmost Scandinavia. The regions with highest GLs are Ireland, Britain, north-central France, central (Harzgebirge) and northern Germany, southern Scandinavia and Poland. Between 3k and 0.5k, the GLs increase by 10–20% in particular from Switzerland to Estonia, as well as in southern Scandinavia and northernmost Norway and Sweden. At 0.2k, the picture is not much different from that at 0.5k except in southern and central Sweden and southernmost Finland where GLs increase by 10–20%. There is no major change between 0.2k and 0.05k, besides a further increase in GLs in western Switzerland, western Denmark, and Estonia.

The LSEs (*C. vulgaris*; Fig. 5) are generally low and do not differ from zero in most of the study region in many grid cells. At 6k, values are <10% except in a few grid cells where reliable REVEALS estimates up to 100% occur at bog sites of western Britain, in the Netherlands, and northern Germany, up to 60% in western Denmark, and up to 40% in southernmost Sweden. A general increase in the LSEs of 10–30% occurs between 6k and 3k in the areas with significant values at 6k. The picture does not change much at either 0.5k or 0.2k, except for some increase by 10–20% at 0.5k in the western part of the study region. At 0.05k, the LSEs decrease in most grid cells of the regions characterized by high values in the past, most significantly in Ireland, Britain, Denmark, southern Sweden, and northern Poland.

The open-land estimates (OLs; Fig. 2) exhibit a very similar picture to the one for GLs (above). This indicates that the overall trends seen in the OLs are primarily due to the values of GLs and their changes. The major differences between OLs and GLs can, therefore, be ascribed to the behaviour of LSEs (*C. vulgaris*) and ALs. The OLs are >2% in all but two grid cells at 6k and three grid cells at 3k. There are very few values that do not differ from zero for all time windows. There is a clear west–east division of Europe at 6k and 3k with higher OLs west of north-central France (Paris Basin), and in the Netherlands, north-western coastal Germany, and western Denmark. There is also a south–north division with higher OLs south of northern Poland in the Baltic area. These trends are also found in GLs (above), but they are less pronounced. The clear west–east division of OLs is due to the pattern of LSEs. The highest OLs at 6k (60–100%) are found in western Ireland and Britain across to northern Germany and western Denmark. The OLs increase by 40–60% between 6k and 3k in Ireland and Britain, and by 10–40% in most parts of the study region east of the west–east division mentioned above. The latter division is still very apparent at 3k, as well as the south–north division at the level of the Baltic Sea. Between 3k and 0.5k, a new increase by 10–40% occurs from Switzerland to Estonia, and in northernmost Norway and Sweden. At 0.2k, the picture is similar, except in southernmost Sweden and Finland where OLs increase by 10–20%. At 0.05k, OLs are higher in western Switzerland and lower in northern Germany, eastern Denmark, and southern Sweden.

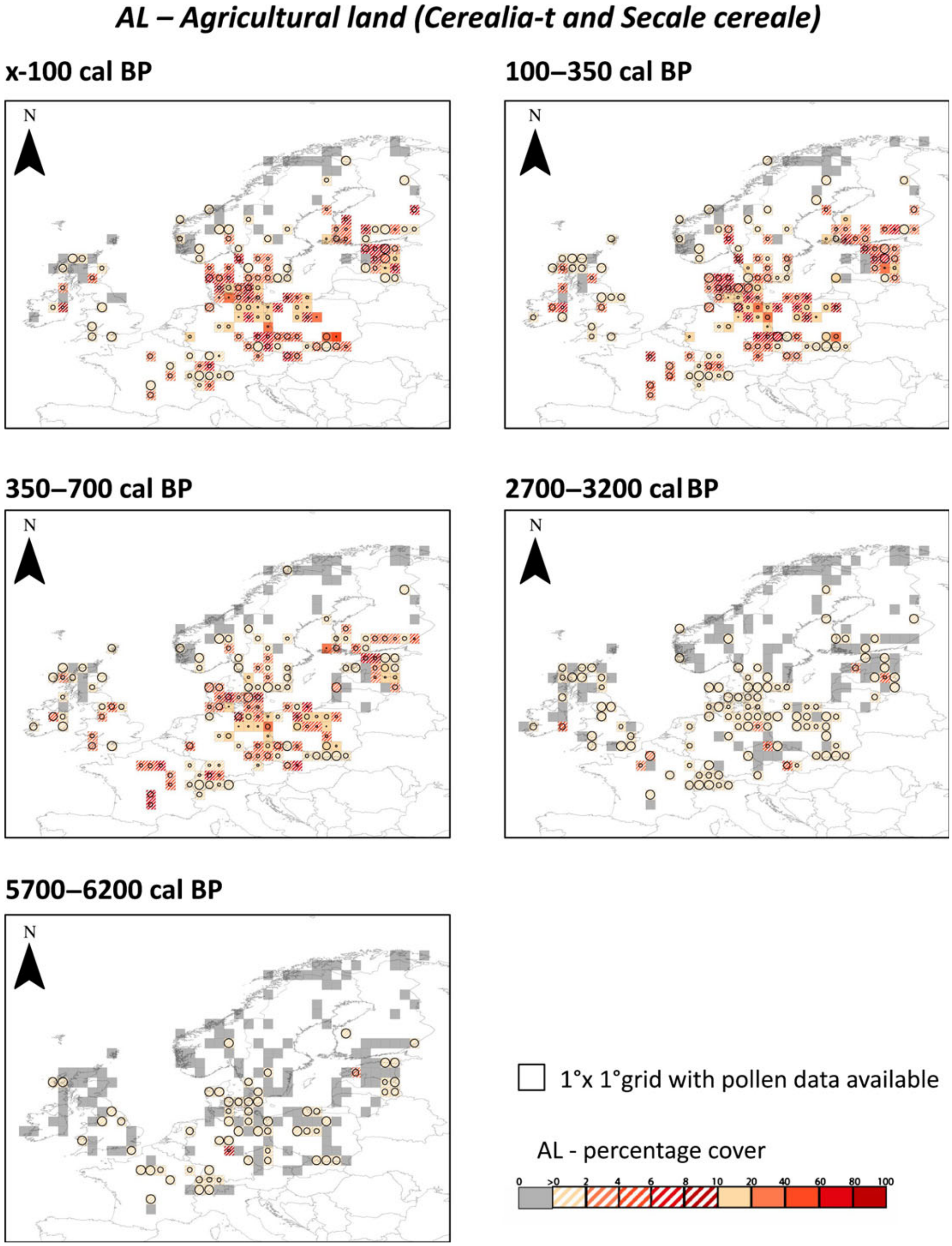

**Fig. 3** Grid-based REVEALS estimates for the plant-functional type (PFTs) agricultural land (AL) for five Holocene time-windows. Grey-coloured grid cells (category 0) indicate that pollen data exist for those cells, but the actual PFT is not present in that specific time window. The uncertainties of the REVEALS estimates for the plant-functional types (PFTs) are shown in the same way as those for REVEALS LCTs (see Fig. 2). For further figure interpretation, see Fig. 2.

### *Summer-green (deciduous) and evergreen trees (LCTs STs and ETs)*

The highest ST values are found at 6k, with 60–100% cover in the central parts of the study region, parts of Britain and Ireland, southern Scandinavia, and the Baltic Countries (Fig. 6). Between 6k and 0.05k, a general decrease in STs occurs. The largest decrease (by ca. 20–40%) is found between 6k and 3k in Britain, Ireland, Germany, Denmark, southern Scandinavia, Poland,

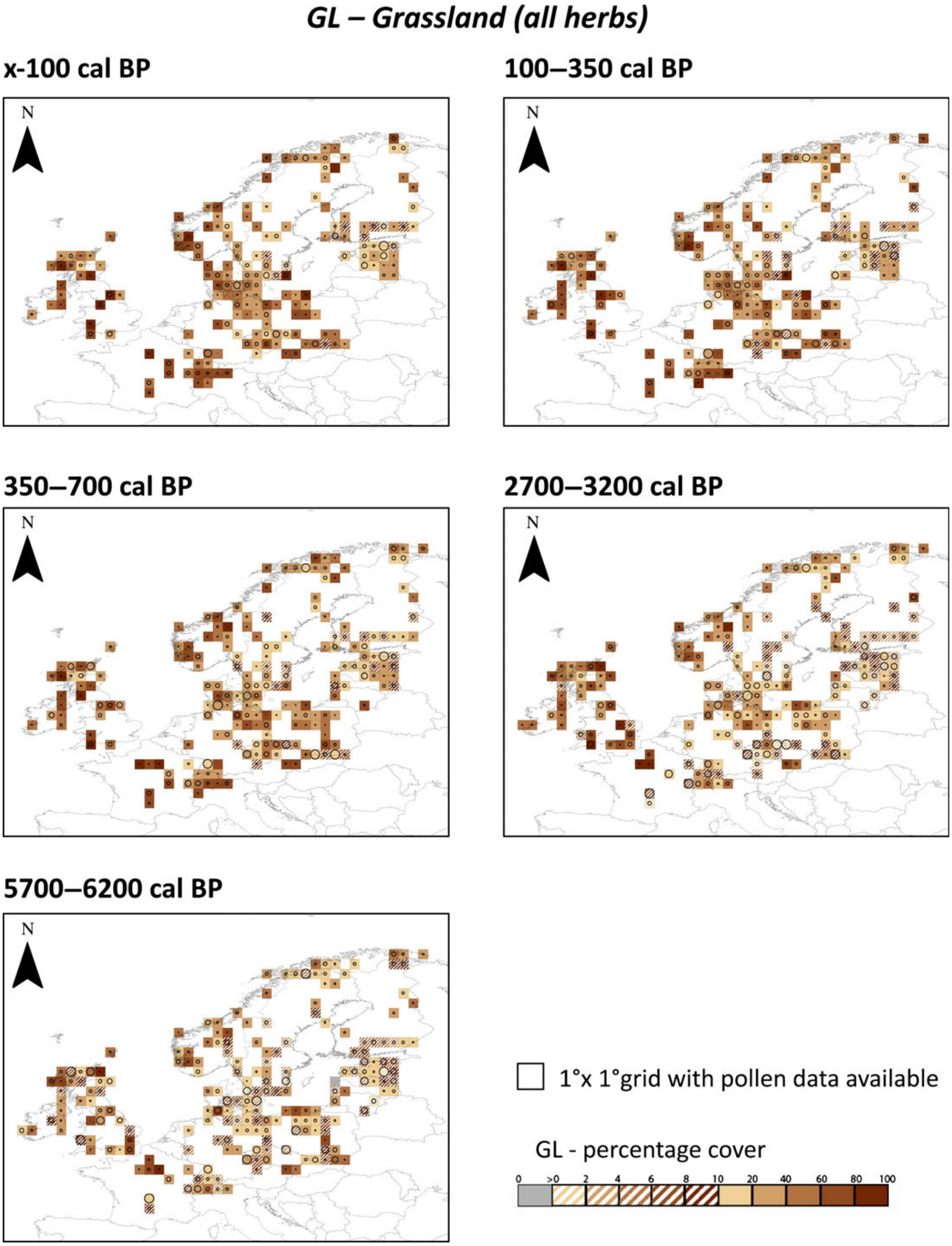

**Fig. 4** Grid-based REVEALS estimates for the plant-functional type (PFT) grassland (GL) for five Holocene time-windows. For further figure interpretation, see Figs 2 and 3.

and the Baltic Countries. Between 3k and 0.5k, a further decrease by 20–40% occurs in the entire western part of the study region north to southern Norway, while there are no significant changes in the Baltic Countries and southern Finland. The STs further decrease between 0.5k and 0.2k in the east and in southernmost Scandinavia. No significant changes occur between 0.2k and 0.05k.

Throughout the period between 6k and 0.05k there is a clear division in the study region between a western part (from Britain and Ireland to south-western Norway) with low evergreen tree values (ETs, i.e. sum of

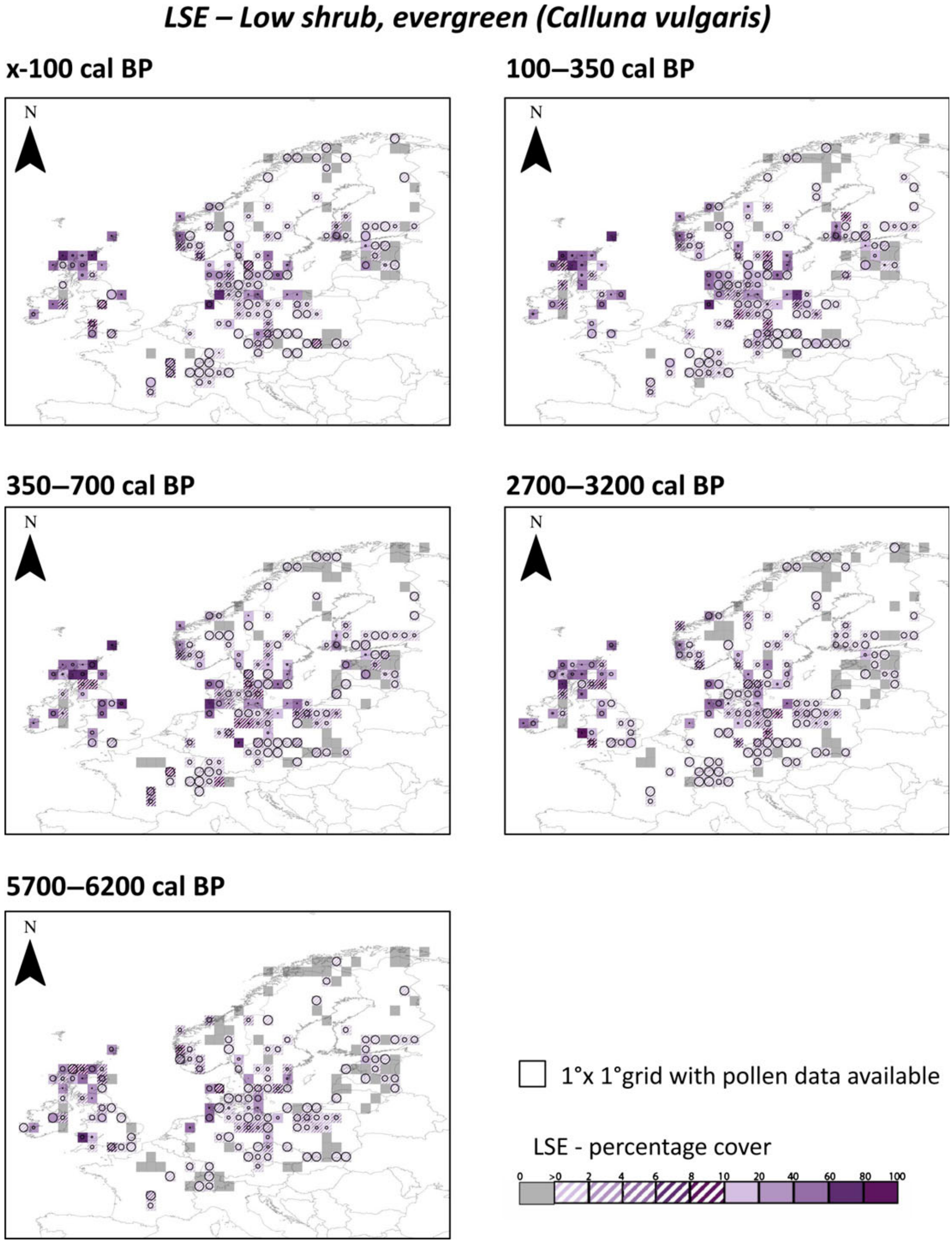

**Fig. 5** Grid-based REVEALS estimates for the plant-functional type (PFT) low shrub, evergreen *Calluna vulgaris* (LSE) for five Holocene time-windows. For further figure interpretation, see Figs 2 and 3.

the PFTs *Pinus*, *Picea*, *Abies*, and *Juniperus* ≤10%) and an eastern and northern part (from central-southern France to Poland and the northern part of Norway and Sweden, Finland and the Baltic Countries) with high ETs >10% (Fig. 7). It should be noted that *Pinus* includes *Pinus sylvestris*, *P. mugo*, and *P. cembra*, but *P. sylvestris* is generally dominant in the pollen counts except for a few records in the Alps. At 6k, the highest ETs (60–100%) are found in the Alps and the Carpathians. Between 6k and 3k, ETs increase by 10–40% from central-southern France to the Baltic Countries, southern and central Finland, and northern Sweden, with

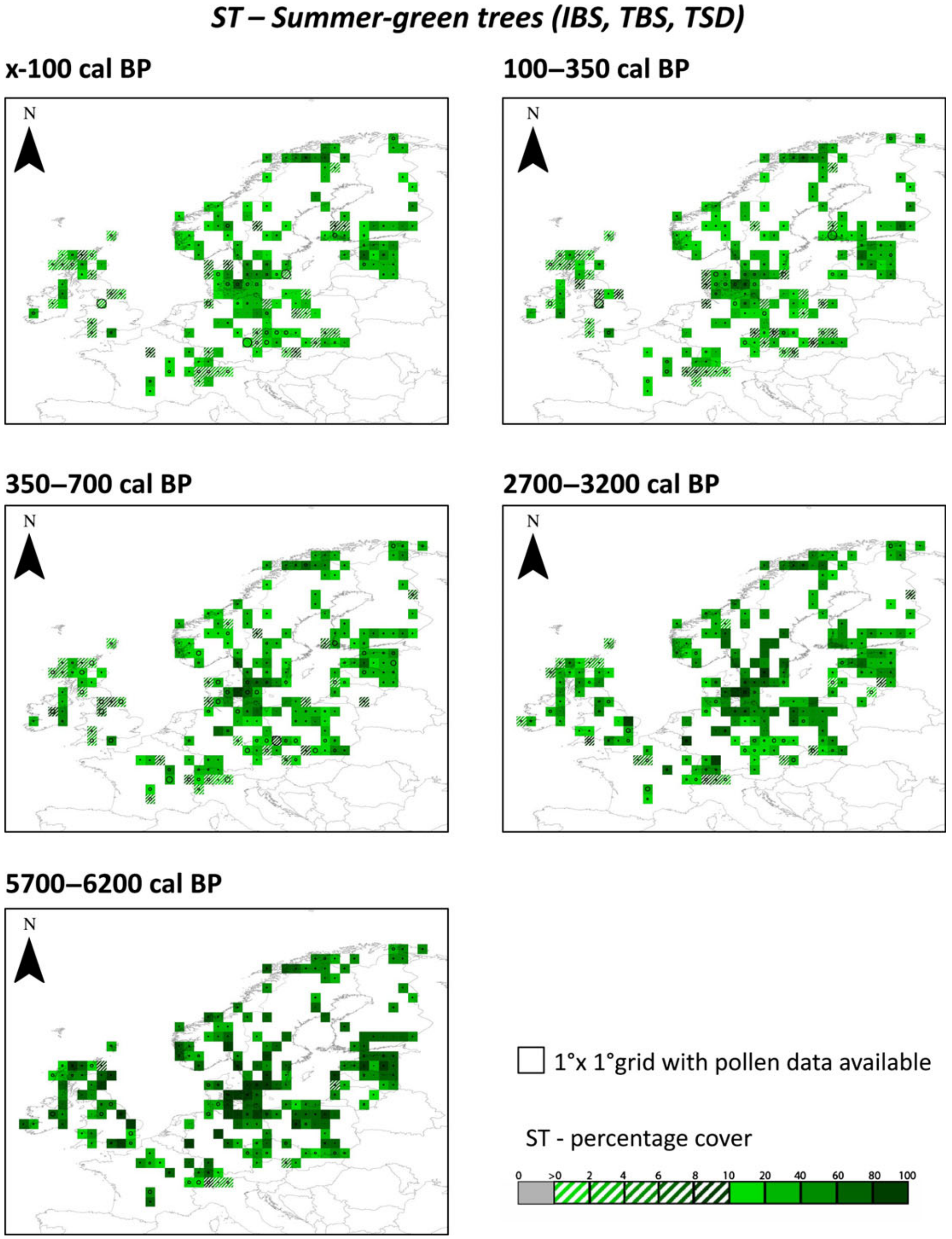

**Fig. 6** Grid-based REVEALS estimates for the land-cover type (LCT) summer-green trees (STs) for five Holocene time-windows. For further figure interpretation, see Figs. 2 and 3.

the highest values (60–100%) in the easternmost areas of the study region. At 0.5k, the pattern is very similar, but the ETs decrease by 20–50% in the easternmost parts of the study region and by 80% in central-southern France, while they increase by 10–20% (up to 20–80%) in Sweden (except its southernmost part) and Norway (except its south-western part). There is no significant change in ETs between 0.5k and 0.2k. At 0.05k, the pattern is very similar, except in southernmost Sweden where the ETs increase from ca. 2–4% to 10–20%, and in northern Poland from 8–10% to 20–40%.

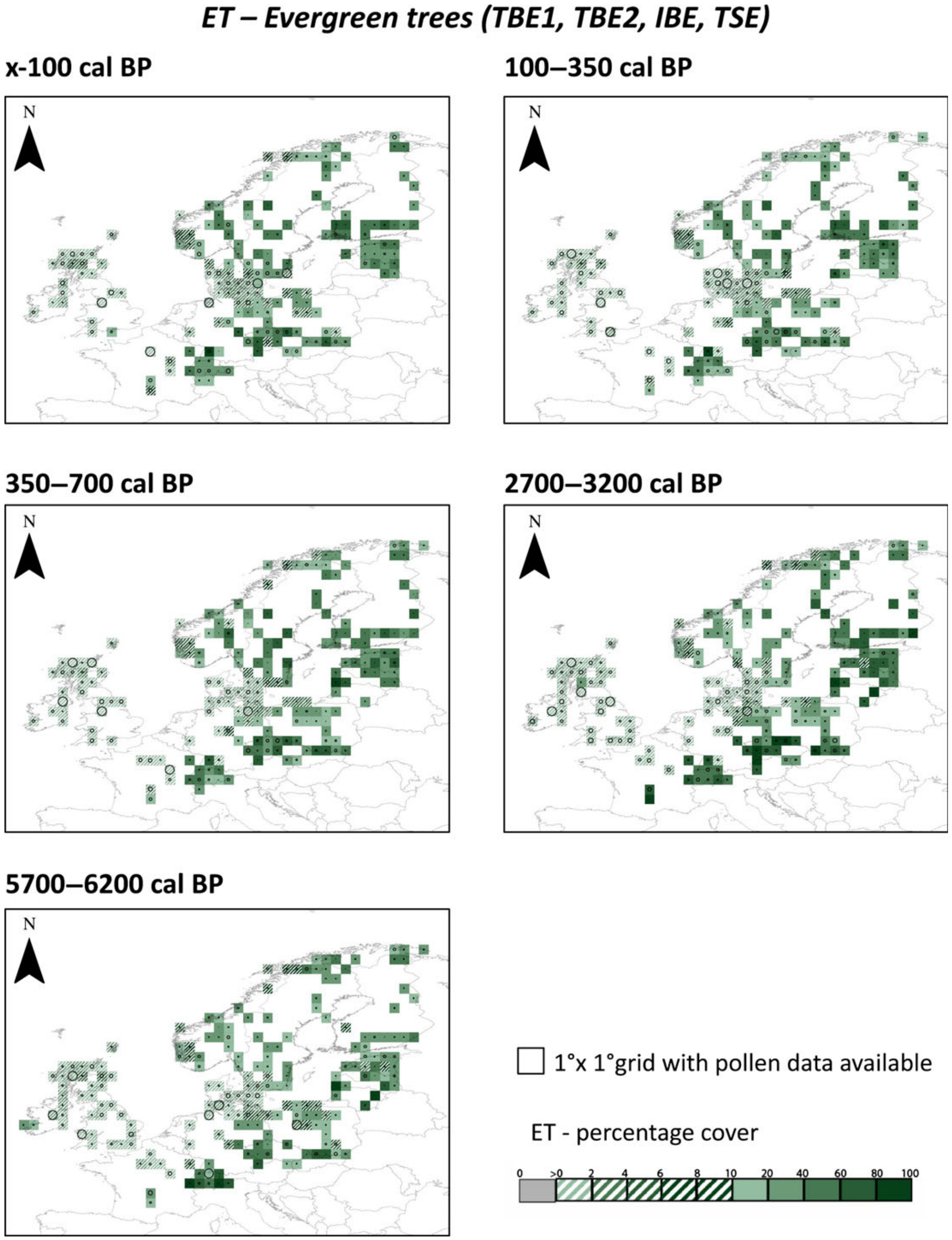

**Fig. 7** Grid-based REVEALS estimates for the land-cover type (LCT) evergreen trees (ETs) for five Holocene time-windows. For further figure interpretation, see Fig. 2.

### *Spruce (PFT TBE1 Picea)*

Because *Picea* (TBE1, Fig. 8) is part of the land-cover type ETs (Fig. 7), the patterns of TBE1s and ETs are very similar with an increase of values through time from south-east to north-west Europe and, from 3k, in northern Scandinavia from north-east to south-west. The difference between TBE1s and ETs is due to the history of *Pinus* (mainly *P. sylvestris*, see above) in western Europe and of *Abies* in continental Europe. The TBE1s at 6k represent up to 60% of the vegetation cover from eastern Switzerland to southern Poland,

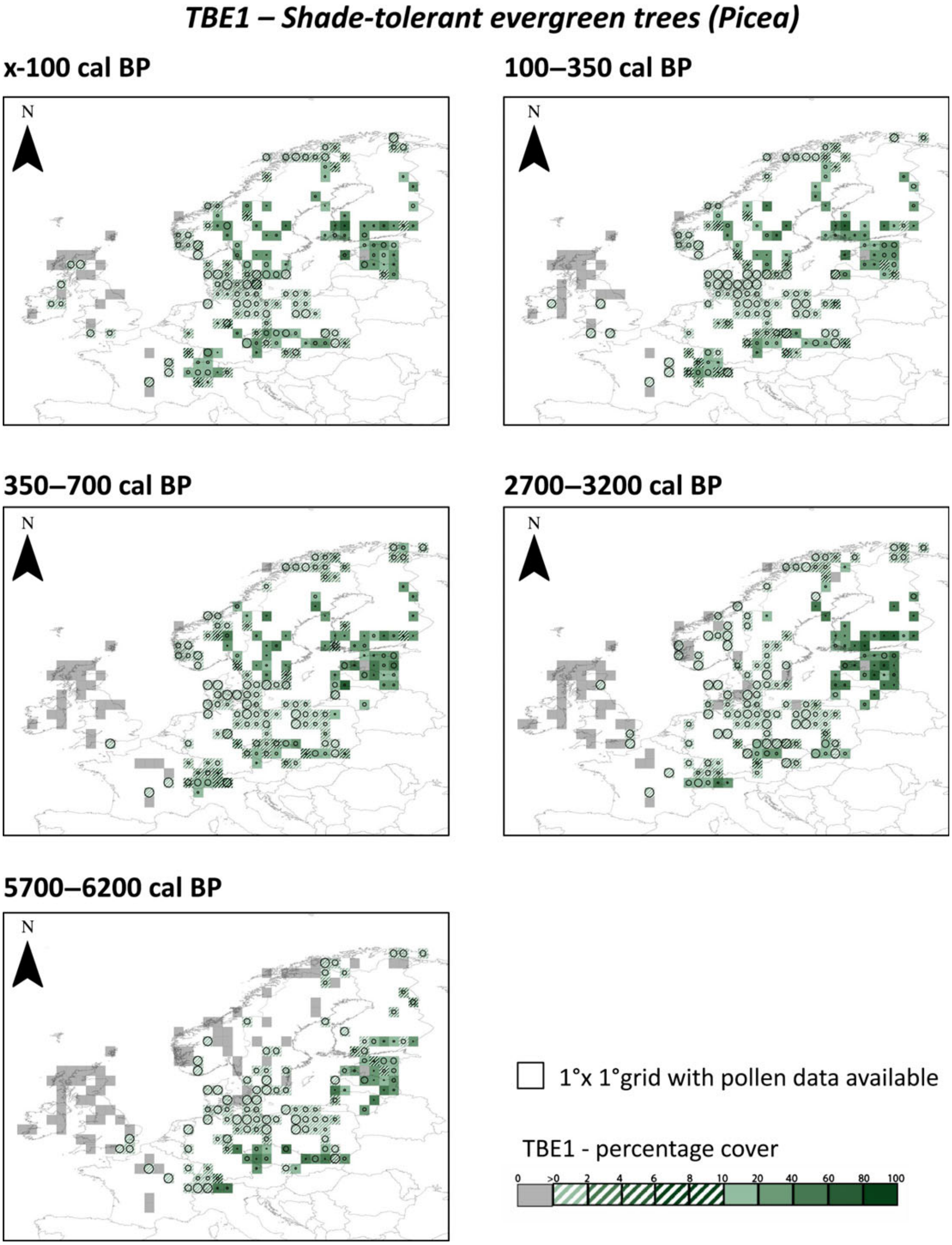

**Fig. 8** Grid-based REVEALS estimates for the plant-functional type (PFT) *Picea* (TBE1) for five Holocene time-windows. For further figure interpretation, see Figs 2 and 3.

the Baltic Countries, and southern Finland. At 3k, the TBE1s increase by ca. 10% in the western Alps, and by 20–60% in the Baltic Countries, and in southern and central Finland. TBE1s >10% occur for the first time in northern Sweden. In contrast, the TBE1s decrease in the Czech Republic and southern Poland. At 0.5k, the TBE1s decrease in most of the regions characterized by high values at 3k, except in the western part of the Baltic Countries and northern Sweden. Moreover, the values have increased in central Sweden and *Picea* now occurs with values >10% and up to 60% in southern Sweden (except the southernmost part) and Norway (except the westernmost part). The TBE1s do not change significantly between 0.5k and 0.05k, except increases of ca. 10–20% in western Switzerland, the Alps, south-western Germany, north-eastern Czech Republic, the Carpathians (S Poland), and southernmost Sweden.

## Discussion

In this discussion, we first evaluate the reliability of the REVEALS-based land-cover reconstructions and other methodological issues related to the selection of pollen types and their transformation to land-use/landscape units. We then synthesize and discuss the major differences between REVEALS estimates and pollen percentages described in earlier studies (e.g. Hellman *et al.*, 2008a,b; Sugita *et al.*, 2008; Gaillard *et al.*, 2010; Nielsen *et al.*, 2012; Fyfe *et al.*, 2013; Gaillard, 2013). We finally focus on the insights from the REVEALS estimates in terms of quantification of anthropogenic deforestation and composition of tree PFTs through time, and discuss the implications of the REVEALS results for the study of land cover–climate interactions and issues related to conservation biology and biodiversity.

### *Reliability, accuracy, and precision of the grid-based REVEALS estimates*

The reliability, accuracy and precision of the REVEALS estimates of past vegetation using pollen records depend on a large number of factors, of which the most important are:

- The type (bog or lake) and size (large or small) of the sites.
- The number of pollen records used and their distribution (homogenous or heterogeneous) in each grid cell.
- The accuracy of the pollen records' chronologies.
- The past regional vegetation (homogeneous or heterogeneous ecoclinal/ecotonal) in each grid cell.
- The applicability and reliability of the available PPEs in the study region.

The REVEALS model has been tested and validated for large lakes in southern Sweden (Hellman *et al.*, 2008a,b), the Swiss lowland (Soepboer *et al.*, 2010) and in Michigan and Wisconsin (Sugita *et al.*, 2010), and for multiple small sites (lakes and bogs) in the Czech Republic (Mazier *et al.*, 2012; Abraham *et al.*, 2014) and southern Sweden (A.-K. Trondman, unpublished data). It has not so far been tested for large bogs. Pollen records from bogs might be problematic as bogs do not meet the assumption of the REVEALS model that the surface of the deposition basin should not be covered by vegetation. When multiple small bogs are used, the violation of that assumption does not have a severe impact on the results when compared to multiple small lakes (Mazier *et al.*, 2012; A.-K. Trondman, unpublished data), while the results from a large bog differ significantly from those from a large lake (M.-J. Gaillard, unpublished data).

When REVEALS is applied to pollen records from multiple sites, the pollen counts from several pollen records and several sites are merged to estimate the vegetation abundance during a given time window. If the chronologies are not accurate, the pollen counts might not be synchronous, which would bias the estimates of vegetation abundance for the assumed time period.

The accuracy ('realism') of the REVEALS estimates was discussed earlier by, for example, Hellman *et al.* (2008a,b) and Sugita *et al.* (2010). Because PPEs are not available for all plant taxa and pollen assemblages only represent part of the plant taxa and vegetation cover existing at any time of the past, pollen-based REVEALS estimates of vegetation abundance never reflect the exact actual past vegetation. Although the 25 selected pollen taxa generally account for >90% of the total pollen assemblage and represent plants with the major share in the total vegetation, one should not forget that REVEALS reconstructions are an approximation of the actual plant cover in the past. Therefore, REVEALS estimates of the cover of large vegetation units, such as OL and ETs, may often be closer to 'reality' and more useful than REVEALS estimates of the cover of individual taxa (Hellman *et al.*, 2008a,b).

The precision of the grid-based REVEALS estimates is indicated by their SEs (Figs 2–8 and S1–S6). The larger the variability of the pollen counts between pollen records, the larger the SEs of REVEALS estimates (Sugita, 2007a). Extensive simulations (Sugita, 2007a) and empirical studies (A.-K. Trondman, unpublished data) show that REVEALS estimates based on pollen counts from multiple small sites have generally larger SEs than those based on large lakes. Furthermore, the larger the pollen counts, the smaller the SEs. The latter is explained by the decrease in variability of the pollen assemblages (taxon composition) with the amount of pollen counted, a well-known phenomenon since the early days of pollen analysis (Birks & Birks, 1980).

To summarize, REVEALS estimates obtained using pollen data from large bogs or few small sites, and/or pollen records with poor chronologies (≥3 to <6 dates, i.e. one date per millennium), should be considered with caution as they can potentially be unreliable. In this study, the REVEALS estimates can be considered as reliable when large lakes (one or several) or multiple (minimum two) small lakes (or small lakes and bogs) are used (A.-K. Trondman, unpublished data). The results should be regarded as potentially unreliable in the dark grey grid cells of Fig. 1 when the values do not show consistent patterns with adjacent grid cells with reliable results.

### *Other methodological issues*

The OL [OL: AL + GL + *C. vulgaris* (LSE); Fig. 2] values can be used as a measure of past vegetation openness. However, it is necessary to assess the AL, GL and LSE values separately before interpreting the OLs in terms of human-induced openness, because *C. vulgaris* (LSE), and Poaceae and Cyperaceae (dominant in GL) may represent natural openness in wetlands, mountains and high latitude areas. Moreover, these taxa may also occur in the field layer of woodlands and, therefore, comparison of GLs and LSEs with tree LCTs and taxa is useful.

AL (Fig. 3) represents only cereal cultivation. Other cultivated plants that can be identified from pollen are *Fagopyrum* (buckwheat), *Linum usitatissimum* (common flax), and cultivated trees such as *Castanea sativa* (chestnut) and *Juglans regia* (walnut). Many other cultivated crops are either difficult or impossible to identify from pollen such as *Setaria italica* (millet), *Lens culinaris* (lentils), and *Pisum sativum* (peas) (Gaillard, 2013). Therefore, the ALs might under-represent the cover of cultivated land in many cases. AL may on the other hand include large pollen grains from wild grasses characteristic of wet environments, e.g. *Glyceria fluitans* (floating sweet-grass), or other grasslands, e.g. the *Hordeum* (barley) pollen type may include pollen from the genus *Bromus* (brome) (Beug, 2004). This might be the case in particular for pollen records from bogs and small lakes with surrounding marshes or mires. In such cases, the ALs may instead over-represent the area of cultivated land. Except *Secale* (wind pollinated), cereals are largely self-pollinated, and pollen is first dispersed by wind when the cereal ears are threshed (Vuorela, 1970). Therefore, reliable PPEs for cereals other than *Secale* are difficult to obtain. Moreover, PPE values are mainly based on modern pollen-vegetation data (Broström *et al.*, 2008), and the modern varieties of cereals are not necessarily comparable to old varieties in terms of pollen productivity and dispersal; they usually produce and disperse less pollen than old varieties (Behre, 1981). Thus, cereal PPEs based on historical pollen and vegetation data (Nielsen, 2004) might be the best to use for fossil pollen (Hellman *et al.*, 2008a,b). However, because only one historical PPE value is available so far, we chose to use the mean of all available PPE values of cereals for Europe, i.e. including the PPEs calculated for modern varieties of cereals (Mazier *et al.*, 2012).

Besides the PFT AL (cereals), *Filipendula*, *Artemisia*, *Plantago* (in our case mainly *P. media* and *P. lanceolata*), and *Rumex acetosa*-type (all included in PFT GL, Fig. 4) are the best indicators of anthropogenic openness/deforestation. Most species belonging to these pollen-morphological types are characteristic of human-induced biotopes such as pastures, hay meadows, cultivated fields, paths, and settlements (Behre, 1981; Gaillard, 2013). However, the two *Filipendula* species are also represented in natural plant communities, in wetlands (*F. ulmaria*; meadowsweet) and dry meadows (*F. vulgaris*; fern-leaf dropwort). Similarly, many of the *Artemisia* species may occur in natural dry GLs, in particular in steppe areas (e.g. in the Czech Republic). These indicators of deforestation – if used alone – will strongly underestimate openness, because grasses, sedges, and *C. vulgaris* generally represent the largest part of the plant cover in most deforested areas of Europe. Therefore, although the latter pollen taxa may lead to over-estimation of deforestation, they need to be included in open-land REVEALS estimates to obtain a more realistic picture of the vegetation openness.

To summarize, the obtained ALs might underestimate or overestimate the actual cover of cereals and total AL (all cultivated lands) depending on which of the issues discussed above (basin type, pollen identification, PPE) are most critical in a particular case. We expect that under-estimation of cultivated land by ALs is probable, particularly at 6k before the expansion of cereal cultivation (millet and lentils are known to have been cultivated in Neolithic time in Switzerland and Germany; e.g. Behre, 1988) and at 3k before the introduction and increase in the cultivation of rye (from ca. 2k, e.g. Behre, 1988; Gaillard *et al.*, 1991).

### *Differences between REVEALS estimates and pollen percentages*

Earlier studies have presented and discussed the differences between REVEALS estimates of regional vegetation abundance and pollen percentages (e.g. Hellman *et al.*, 2008a,b; Sugita *et al.*, 2008; Gaillard *et al.*, 2010; Gaillard, 2013; Marquer *et al.*, 2014), and more specifically between the LANDCLIM grid-based REVEALS estimates and pollen percentages (Nielsen *et al.*, 2012; Fyfe *et al.*, 2013). Our results confirm the earlier observation that REVEALS estimates are generally very different from pollen percentages in terms of taxa proportions. They also indicate that the differences found in this study are of the same magnitude as those observed by Sugita *et al.* (2008), Nielsen *et al.* (2012), and Fyfe *et al.* (2013) for subregions of Europe. We describe and discuss here the most important differences that might significantly influence the interpretation of pollen records in terms of the relative abundance of individual plants or LCTs in past vegetation.

*Open land.* The OL [OL: AL + GL + *C. vulgaris* (LSE)] values (Fig. 2) are two to four times higher than pollen percentages (this study and earlier studies). Although it is well known that herbs are under-represented in comparison to trees in Quaternary pollen assemblages from the Northern Hemisphere, REVEALS estimates of OL imply a much larger share of OL in the Holocene vegetation of Europe than previously deduced from pollen percentages. For instance, over the last 1000 years, NAP values reach a maximum of 40% in north-east Germany and the south-east Czech Republic, 20–40% in southern Norway, and 40–50% in Britain and Ireland (Berglund *et al.*, 1996), while the OL REVEALS estimates are mostly >40% in those countries at 0.5k and may reach 60–80% (rarely 80–100%) (Fig. 2). Moreover, pollen percentages of Poaceae in modern lake sediments are <10–20% in southernmost Sweden (e.g. Berglund *et al.*, 1996; Broström *et al.*, 1998; Hellman *et al.*, 2008a), but the GL REVEALS estimates (dominated by Poaceae, Fig. 4) are generally >20% up to 40%. Similarly, even though the AL (cereals) REVEALS estimates Fig. 3 probably underestimate the true cover of cultivated land (see above), they are always significantly higher than the pollen percentages of cereals. For instance, the pollen percentages of Cerealia and *Secale* are generally ≤2% and reach a maximum of ca. 5% at 0.2k in southernmost Sweden (Berglund *et al.*, 1996), while the REVEALS ALs reach 10–20%.

*Pinus vs. Picea and summer-green vs. evergreen trees.* Besides landscape openness, the most spectacular differences between the REVEALS estimates and pollen percentages are (i) the inverted relationship between *Pinus* (Fig. S1) and *Picea* (Fig. 8), i.e. if *Pinus* is dominant over *Picea* in pollen percentages, *Picea* is generally dominant over *Pinus* in the REVEALS estimates (Hellman *et al.*, 2008a; this study), (ii) when the REVEALS landscape openness is higher than ca. 25%, the STs (deciduous) trees (Fig. 6) are dominant over ETs (Fig. 7), but the difference between the two is lower in the REVEALS estimates than in the pollen percentages, and (iii) when the landscape openness is lower than ca. 25%, the ETs are dominant over STs, but the difference between the two is higher in the REVEALS estimates than in pollen percentages.

The inverted relationship between *Pinus* and *Picea* is due to the fact that the PPE of *Pinus* is much higher than that of *Picea*, and the fall speed (FSP) of *Pinus* is almost half of that of *Picea* (Table 1 in Appendix S2; Broström *et al.*, 2008; Mazier *et al.*, 2012), which results in a strong under-representation of *Picea* in pollen percentages. For instance, in the modern vegetation of the province of Skåne (southern Sweden), when the pollen percentages of *Pinus* and *Picea* are 12% and 2.5%, respectively, the REVEALS estimates are 4% and 7%, respectively (Hellman *et al.*, 2008a). Similarly, in the modern vegetation of the province of Småland (southern Sweden), when the pollen percentages of *Pinus* and *Picea* are 40% and 15%, respectively, the REVEALS estimates are 12% and 55%, respectively (Hellman *et al.*, 2008a).

The relationship STs/ETs differs depending on the share of OL (herbs and *Calluna*). Moreover, the difference between STs and ETs is larger in pollen percentages than in REVEALS estimates when the REVEALS OL is higher than ca. 25%, while it is lower in pollen percentages than in REVEALS estimates when the REVEALS OL is lower than ca. 25%. These features are also observed in REVEALS estimates and pollen percentages of the past (Sugita *et al.*, 2008; Cui *et al.*, 2013). This is due to the effect of percentage calculations of the REVEALS estimates after the transformation of the pollen data by the model. PPEs and FSPs are the major parameters influencing that transformation (Hellman *et al.*, 2008a; Sugita *et al.*, 2010). For example, Hellman *et al.* (2008a) show that, when the REVEALS OL is 68% (modern vegetation of the province of Skåne, southern Sweden), the summer-green/evergreen relationship is 3.6 in pollen percentages and 1.3 in REVEALS tree cover; and when the REVEALS OL is 21% (modern vegetation of the province of Småland, southern Sweden), the summer-green/evergreen relationship is 0.7 in pollen percentages and 0.15 in REVEALS tree cover.

### *Changes in open-land (OL) cover from 6k to present*

*General patterns.* The geographical patterns of the REVEALS estimates of OL and GL in all time windows, and their changes over time, are comparable (Figs 2 and 4). However, the GLs exhibit a less clear division than the OLs between the western and eastern part of the study region (Fig. 4), i.e. the OLs are more clearly higher in the western part than in the eastern part of the region than the GLs are. The latter is due to the REVEALS estimates of *C. vulgaris* (LSEs, Fig. 5) that are highest in the western part of the study region at 6k and 3k. The LSEs are also high along the north-western coast of Poland at 3k. Although some LSEs are based on pollen records from bogs, many are based on records from lakes (Scotland, north-western and south-western Denmark, south-eastern Sweden) and/or a mix of bogs and lakes (northern Poland). Therefore, we interpret most of the high LSEs in the westernmost parts of Europe as a result of the development of *Calluna* heaths from the Neolithic time due to burning and grazing, in accordance with the interpretation of previous studies in the coastal areas of Denmark (e.g. Odgaard, 1994; Nielsen & Odgaard, 2010) and Norway (e.g. Prøsch-Danielsen & Simonsen, 2000), as well as in southern Sweden (e.g. Lagerås, 2000, 2002, 2007; Greisman & Gaillard, 2009), northwest Poland (Latałowa, 1992), and Scotland (Fyfe *et al.*, 2013).

At 0.5k, the contrast between west and east for the OLs is much less pronounced than earlier, which is due primarily to the increase in GLs (grasses and other herbs, Fig. 4), but also in ALs (cereals, Fig. 3) in the eastern part of the study region between 3k and 0.5k, while *C. vulgaris* does not increase much in the western part. However, Britain, Ireland, France, north-western Germany, Denmark, and south-western Norway remain among the most deforested landscapes in north-west Europe until the present day. The increase in OLs between 0.5k and 0.2k is due to a general increase in ALs. From 0.2k to 0.05k, there is an increase in GLs of 10–20% in some areas of Estonia, northern Poland, Switzerland, and Denmark, which is probably due to an increase in the cultivation of fodder or in the area of grazing land (e.g. Gaillard *et al.*, 1991). In parts of southern Sweden there is a decrease in GLs of ca. 10–40% due to land-use changes leading to an increase in coniferous forests, mainly *Pinus* and *Picea*, which is known to have occurred between the 19th and 20th centuries based on historical documents (Kardell, 2004; Cui *et al.*, 2014; Mazier *et al.*, in press). Lindbladh *et al.* (2014) demonstrate that the increase in *Picea* is first natural and followed by plantations from AD 1920, becoming massive in the 1950s.

*Open-land cover at 6k.* The REVEALS estimates of OL (Fig. 2) and GL (Fig. 4) are >2% in almost all grid cells already at 6k, although archaeological records from north-west Europe indicate that population density at that time cannot have been of such magnitude that anthropogenic deforestation occurred over the entire study region. Humans started fine-scale cultivation around 6k in many parts of Europe, but most of the continent is assumed to have been covered by natural woodland (e.g. Behre, 1988). Almost all reliable GLs are found in coastal or mountainous areas with natural open vegetation, i.e. the Norwegian mountains, the Alps and the Carpathians (Berglund *et al.*, 1996), the bog areas of Britain and Ireland (Fyfe *et al.*, 2013), and the steppe in the south-east of the Czech Republic (Berglund *et al.*, 1996). Therefore, we interpret these GLs as a representation of natural GL vegetation. The high values in north-central France (Paris Basin) might be due to a landscape dominated by flood-plains (David, 2014). The occurrence of cereals (ALs, Fig. 3) at 6k with a reliable percentage cover of >0–2% in northern France, the western Swiss lowland, the Czech Republic, northern Germany, and Poland is consistent with archaeobotanical evidence for cereal cultivation from that time (e.g. Behre, 1988; Berglund *et al.*, 1996).

*Open-land cover at 3k.* At 3k (Bronze Age), the REVEALS estimates of OL and GL, and the number of grid cells with REVEALS estimates of AL (i.e. cereals) >0 are higher than at 6k. The clear increase in OLs and GLs to >20%, reaching 60–100% in many areas of the western part of our study region including southern Scandinavia, suggests that the development of cattle breeding and, consequently, grazing land and hay meadows were important land-cover determinants. The latter agrees with the recent interpretation of the archaeological data of Europe for the Bronze Age (e.g. Krzywinkski & O'Connell, 2009; Kähler Holst *et al.*, 2013; Kristiansen, 2013), i.e. the likelihood that a combination of the increase in cattle numbers and a climate deterioration beginning ca. 4k (e.g. Hammarlund *et al.*, 2003) drove a requirement for both larger grazing areas and more hay meadows to provide winter feed (e.g. Berglund, 1991; Gaillard *et al.*, 1991; Krzywinkski & O'Connell, 2009).

*Open-land cover from 0.5k to present.* The major difference in the REVEALS estimates of OL (Fig. 2) between the periods 6k–3k and 0.5k–0.05k is the significant increase in the REVEALS estimates of GL cover (Fig. 4) east of Britain and northern France and the general increase in cereals (AL, Fig. 3) from 0.5k over most of the study region (in particular from Switzerland in the south-west to Estonia in the north-east, and in northernmost Norway and Sweden). The landscape openness of the study region is very similar at 0.2k and 0.05k to that at 0.5k (40–80% open-land cover), with the addition of a distinct increase in OLs in southern Scandinavia and the Baltic Countries at 0.2k. The 19th century is most probably the time of largest landscape openness in the entire study region, and in Europe in general, due to major population growth (e.g. Gaillard *et al.*, 2009; Krzywinkski & O'Connell, 2009; Mazier *et al.*, in press). In recent times, grazing decreased significantly in many parts of Europe, in particular in mountainous areas and in southern Scandinavia, as a result of socio-economic changes; large areas with traditional agriculture (crop cultivation and grazing) were abandoned and replaced by secondary tree vegetation and/or used for afforestation (e.g. Gaillard *et al.*, 2009;

Krzywinkski & O'Connell, 2009). Because of the spatial scale of the grid-based REVEALS reconstructions, this decrease in OL values is not very clear in this study, but it is seen in the Alps (OLs and GLs) and in southern Sweden (GLs).

### *Changes in woodland cover between 6k and present*

Some grid cells in all time windows have reliable REVEALS estimates of the cover of *Picea* >0–2(4) % (Fig. 8) and *Pinus* >0–10% (Fig. S1) in regions where these tree taxa are not expected to occur based on the absence of other proxies (e.g. seeds, needles, wood), for example at high elevations and latitudes (Alps, Norway, northern Sweden, and Finland). This is also the case for the REVEALS estimates of STs (deciduous) trees (Fig. 6), which is primarily due to the REVEALS estimates of *Betula* (IBS; Fig. S2). This phenomenon is most probably due to the well-known long-distance transport of conifer (*Pinus* in particular) and *Betula* pollen, a bias that the REVEALS model cannot entirely allow for at sites situated in vegetation zones that are dominated by OL. But it may also be a consequence of the spatial resolution of REVEALS reconstructions being too large (a minimum of ca. 50–100 km × 50–100 km; Hellman *et al.*, 2008b) implying that there is always part of the area represented by the pollen records that are located in wooded vegetation zones. Binney *et al.* (2011) used a simplified REVEALS approach (COBRA) and biomization (see discussion below) to test how the boreal tree-line is best described, given the propensity of *Pinus* and *Picea* pollen to be transported long distances into tundra landscapes. The square-root transformation was shown to perform reasonably well compared with the COBRA estimates. Although the COBRA method was not tested on other taxa and in other regions, it is assumed that it will be useful primarily to delimit more precisely the boundaries between biomes.

The highest values of STs (deciduous) trees are found at ca. 6k in most of the study region (Fig. 6). It is well known from pollen studies that Europe during the mid-Holocene was covered primarily by summer-green (deciduous) woodland, which was interpreted as a result of the prevalent climate conditions at that time (e.g. Huntley, 1988; Berglund *et al.*, 1996); at 6ka, the summers were warmer than present due to a positive Northern Hemisphere insolation anomaly (e.g. Braconnot, 2000). The major differences between pollen percentages and REVEALS estimates of STs are due to the significantly smaller STs/ETs relationship in the REVEALS estimates compared with that derived from pollen percentages (see above). As a consequence, the STs are much lower than pollen percentages in the eastern part of the study region (Fig. 6) where the REVEALS estimates of the ETs are higher (40–100%) than in its western part (Fig. 7). The high ETs in the east reflect the establishment, expansion, and migration of *Abies* (TBE2: Fig. S3) and *Picea* (TBE1: Fig. 8). The pollen percentages of *Picea* and *Abies* found in the pollen records from these regions (Berglund *et al.*, 1996; this study) significantly under-represent ETs in relation to STs compared to the REVEALS estimates. As a result, the STs are much more abundant than ETs (in comparison to their share in pollen percentages) in the western part of the study region, while STs are much lower in the eastern part, i.e. the Alps, the Czech Republic, the Carpathians, the eastern Baltic Countries, and eastern Finland.

Through the five time windows, a general decrease in STs (deciduous) trees (Fig. 6) is observed. In the eastern areas mentioned above, ETs increase at the expense of STs. The well-known pattern of migration of *Picea* from east to west in the northern part of the study region between 6k and 3k, and from north-western Sweden and Norway to southern Sweden and western south-west Norway between 3k and 0.5k (e.g. Giesecke & Bennett, 2004) is clearly seen in the REVEALS estimates of *Picea* (Fig. 8) and ETs (Fig. 7). However, the REVEALS estimates of *Picea* are much higher than the pollen percentages of that same taxon, which provides a new insight into the Holocene land cover of Europe (discussed below). From 0.5k and onwards, a general decrease in STs occurs in the entire study region, which is related primarily to the anthropogenic opening of the landscape (i.e. increase in OLs, Fig. 2; see discussion above). There is generally no significant change in the ETs during that time period, except in southern Sweden where they increase, which is explained by the increase of *Picea* at the end of the 19th century and the beginning of the 20th century (e.g. Björkman, 1996, 1997; Lindbladh *et al.*, 2000, 2014). *Picea* is today both natural (secondary rejuvenation) and planted (old and recent plantations) in the entire study region.

### *Major implications of the REVEALS estimates of Holocene land cover*

Below, we discuss the major implications of the REVEALS estimates of percentage cover of (i) OL vs. woodland, (ii) *Pinus* vs. *Picea*, and (iii) summer-green (deciduous, STs) vs. evergreen (ETs). The implications of the REVEALS estimates of other individual taxa of trees, shrubs, and herbs are discussed in A.-K. Trondman (unpublished data).

*Open land vs. woodland.* The increase in (i) the REVEALS estimates of ALs (6–40%, Fig. 3) and GLs (from >2–40% to 60–80%, Fig. 4) in large parts of the lowlands of our study region, and ii) the size of the distribution area of AL and GL between 6k and 0.2k correspond with an increase in pollen percentages of NAP [non-arboreal pollen, i.e. all taxa included in AL, GL, and *C. vulgaris* (LSE, Fig. 5), and less common herbs not included in the REVEALS reconstructions]. This increase in NAP% in Europe was interpreted by numerous palynologists as a result of increased grazing and cultivation in the lowlands (e.g. Behre, 1988; Berglund, 1991, 2000; Gaillard, 2013). Given that the NAP percentages, when compared to the NAP REVEALS estimates, severely under-represent the vegetation/landscape openness (by ca. 20–30% or more), the REVEALS results have major consequences on our understanding of the anthropogenic impact on land cover (landscape openness/deforestation in particular) and, in turn, on the possible effects of anthropogenic land-use change on climate (e.g. Strandberg *et al.*, 2014; Gaillard *et al.*, 2010, in press).

Several ALCC scenarios for the past have been developed over the last 10–15 years, and the differences between them are striking (see review in Gaillard *et al.*, 2010). In this respect, the REVEALS reconstructions have a great potential to serve as a means of evaluating these scenarios. The first comparison of the grid-based REVEALS estimates of open-land cover (OLs, this paper) with the KK10 scenarios of Kaplan *et al.* (2009) and HYDE (Klein Goldewijk *et al.*, 2011) is presented in J.O. Kaplan (unpublished data) and shows that the REVEALS OLs are closer to the KK10 than to the HYDE scenarios. This is due to differences in methodologies producing higher degrees of deforestation in pre-industrial times in the KK10 than in the to the HYDE scenarios. It should be stressed that neither KK10 nor HYDE incorporates archaeological and palaeoecological proxy data or historical descriptions of past land use. The KK10 and HYDE scenarios were used in combination with LPJ-GUESS-simulated potential vegetation to create descriptions of the past land cover at 6k and 0.2k for the study region of the LANDCLIM project to study the past land cover-climate relationships (Strandberg *et al.*, 2014). The results show that pre-industrial ALCCs according to KK10 influenced the climate of Europe through biogeophysical processes (primarily changes in albedo and evapotranspiration) causing differences in, for example, summer temperature due to deforestation ranging from −1 °C in south-western Europe to +1°C in eastern Europe. Therefore, ALCCs matter for climate change and the evaluation of past ALCCs is thus essential for climate modelling.

Prentice *et al.* (1996, 1998; Prentice & Jolly, 2000) developed the 'biomization' approach. The aim was to produce global palaeobiome maps based on empirical data (pollen), and to compare these maps with simulated palaeobiomes using General Circulation Models (climate models) to evaluate and improve these models (e.g. Braconnot, 2000). This method was initially used for the mid-Holocene (6k) and the last glacial maximum (LGM, 18k). Biomization includes a simple transformation of the pollen data (square root) that roughly corrects for over- and under-representation of pollen by different plant taxa. However, biomization does not achieve the actual cover of PFTs well because of the fuzzy logic approach involved in the method. Further, anthropogenic OL is not represented in the biomes that are climate-induced physiognomic vegetation classes. Fyfe *et al.* (2010) developed a new biomization methodology in which anthropogenic OL is included. It is a useful approach for rough estimates of the anthropogenic impact on European biomes, but it still cannot provide a more precise quantification of landscape openness and of the cover of individual PFTs and taxa. The advantage of the REVEALS reconstructions over biomization is their ability to quantify more precisely the cover of LCTs (used in climate modelling) and PFTs (used in DVMs). Moreover, the REVEALS estimates have the great advantage of including error estimates, which provides a means of evaluating the reliability and robustness of the reconstructions. Therefore, REVEALS reconstructions, by providing a more detailed and quantitative reconstruction of vegetation cover than ALCCs or biomization, are a valuable contribution to the evaluation of the performance of vegetation and climate models in data-model comparison studies.

*Pinus vs. Picea.* The relative percentage covers of *Pinus* and *Picea* are important if vegetation history is used to answer questions on past environmental issues related to the type of vegetation or the cover of vegetation units or individual plant taxa, such as past changes in biodiversity (plants and animals) and their relationships to, for example, vegetation characteristics such as taxonomic composition and/or vegetation structure. *Pinus* and *Picea* woodlands are usually very different in both structure and ecology, the former often being more open and more flammable than the latter. For instance, Cui *et al.* (2013) show that estimates of the cover of *Pinus* during the Holocene using the Landscape Reconstruction Algorithm (Sugita, 2007b) have a large difference between two sites, while the pollen percentages did not exhibit any clear between-site differences. The amount of *Pinus* cover was found to be the main cause of the contrasting fire histories at the two sites. The vegetation feedbacks on climate may also be different between the two woodland types, as the biogeophysical processes (such as albedo and snow-masking effects) are likely not the same for open pine or dense spruce woodland (e.g. Levis, 2010).

*Summer-green and evergreen trees.* The significant differences between the REVEALS estimates of percentage cover of STs (deciduous) and ETs and their composition interpreted from pollen percentages not only provide a different view of European landscapes and issues such as changes in past biodiversity and human resources, but they also strongly influence the interpretation of past land cover–climate interactions. The biogeochemical and biogeophysical processes between the land/vegetation surface and the atmosphere differ with the characteristics of the vegetation cover, in particular between wooded and OL (see above), but also between STs and ETs. Therefore, changes in the share of STs and ETs will affect climate change (e.g. Strandberg *et al.*, 2014). It will also influence biodiversity (e.g. Olsson & Lemdahl, 2009, 2010; Cui *et al.*, 2013, 2014).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Grid-based REVEALS estimates for the plant-functional type (PFT) shade-intolerant evergreen trees IBE.
**Figure S2.** Grid-based REVEALS estimates for the plant-functional type (PFT) shade-intolerant summer-green trees IBS.
**Figure S3.** Grid-based REVEALS estimates for the plant-functional type (PFT) shade-tolerant evergreen trees TBE2.
**Figure S4.** Grid-based REVEALS estimates for the plant-functional type (PFT) tall shrub, evergreen TSE.
**Figure S5.** Grid-based REVEALS estimates for the plant-functional type (PFT) shade-tolerant summer-green trees TBS.
**Figure S6.** Grid-based REVEALS estimates for the plant-functional type (PFT) tall shrub, summer-green TSD.
**Table S1.** Data contributors that are not co-authors.
**Table S2.** Metadata of all pollen records used for the REVEALS reconstructions.
**Table S3.** Additional information on the pollen records used for the REVEALS reconstructions.
**Appendix S1.** The REVEALS model.
**Appendix S2.** The LANDCLIM protocol.