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Late-glacial and Holocene European pollen data

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ABSTRACT

The European Pollen Database (EPD) is a community effort to archive and make available pollen sequences from across the European continent. Pollen sequences provide records that may be used to infer past vegetation and vegetation change. We present here maps based on 828 sites from the EPD giving an overview of changes in postglacial pollen assemblages in Europe over the past 15,000 years. The maps show the distribution and abundance of 54 different pollen taxa at 500 year intervals, supported by new age-depth models and associated chronological uncertainty analysis. Results show the individualistic patterns of spread of different pollen taxa, and provide a standardized dataset for further analysis, defining a spatial context for the study of past plant and vegetation changes and other aspects of environmental history in Europe.

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1. Introduction

1.1. Fossil pollen analysis

Current vegetation and land-use has developed progressively through time, and knowledge of this long-term development is a requirement for understanding the present spatial distributions of plants and projecting future changes in these patterns. Further, this knowledge allows for hypothesis testing of reasons for the changes in the distribution and abundance of individual plant taxa.

Pollen preserved in sedimentary environments, e.g. lake beds and peat bogs, provide the main source of information on long-term changes in vegetation and land-use for the pre-industrial period. A proportion of the pollen released by different plants during their reproductive cycle will fall in sedimentary environments, e.g. lakes and peat bogs, where it becomes preserved if anaerobic conditions are present. The quantity of deposited pollen is related to the abundance of the parent plant at the time of deposition (Matthias & Giesecke, 2014). Pollen analytical results are generally expressed as percentages, which combined with the differential production and dispersal of pollen leads to a complex and non-linear relationship between pollen proportions and plant abundance (Prentice & Webb, 1986). However, this bias may be reduced using estimates of relative pollen productivity and models of pollen dispersal (Sugita, 2007a, 2007b; Sugita, Parshall, Calcote, & Walker, 2010).

Sediment cores from these environments can be readily extracted and their pollen content identified and counted, yielding individual pollen diagrams. Chronological control can then be obtained from radiocarbon dating and other means (see Giesecke et al., 2014 for an overview). The combination of the pollen data and dating information results in a time series of changing pollen composition over several hundreds to thousands of years. As the majority of pollen found in these sediments is wind transported, information from individual sites contains a strong regional component (Prentice, 1985; Sugita, 1994) and comparisons between sites from adjacent regions reveal spatial aspects of vegetation development and land-use change (Fyfe, Woodbridge, & Roberts, 2015; Marquer et al., 2014; Nielsen et al., 2012; Trondman et al., 2015).

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1.2. History of pollen maps

The first maps depicting pollen analytical results for selected time periods were constructed within a few years after the development of modern pollen analysis in different European regions (von Post, 1924; Rudolph, 1930; Szafer, 1935). These early maps predated the development of radiocarbon dating and suffered from a lack of independent chronological control of the individual pollen diagrams, as time scales were based mostly on the observed vegetation development from the same diagrams. The maps therefore summarized distributions and abundance gradients of pollen deposition over long time periods (e.g. Firbas, 1949), but the dating problem hampered interpretations of spatially dynamic processes on shorter time scales. This changed with the development of radiocarbon dating (Libby & Arnold, 1949), which allowed the mapping of diachronous changes in pollen assemblages which could then be interpreted as vegetation change (Davis, 1976).

These developments eventually led to continental scale syntheses, and in 1983, Brian Huntley and John Birks published an atlas of pollen maps for the European continent (Huntley & Birks, 1983), detailing changes in the spatial distribution of pollen taxa between the last glacial maximum (~21,000 years ago) and the present day. This atlas influenced a number of disciplines, including phylogeography (e.g. Hewitt, 1999; Petit et al., 2002), paleoclimatology (e.g. Huntley & Prentice, 1988) and the debate over the natural controls of plant dispersal (Huntley, 1991; Saltré et al., 2013). The maps presented in the Huntley and Birks atlas were based on 423 sites across the European continent, but in many cases the original data were not available to the authors, so were extracted from published diagrams. While Huntley and Birks (1983) provided insights into the dynamics of vegetation over broad temporal and spatial scales, it quickly became apparent that further work should be based on the original data, rather than digitized or inferred estimations. Chronologies of individual pollen diagrams were based on un-calibrated radiocarbon dates as the consensus calibration curve at that time only covered the last 8000 years (Klein, Lerman, Damon, & Ralph, 1982). Therefore, the chronology of the maps was in radiocarbon years before present, rather than calendar years. In addition, the chronology was limited by a scarcity of independent chronological control, with 35% of the sites remaining undated other than by biostratigraphic correlation (Guiot, Harrison, & Prentice, 1993).

1.3. The European Pollen Database

The work published by Huntley and Birks (1983) stimulated the development of a continental scale database of pollen records, the European Pollen Database (EPD) (Fyfe et al., 2009; Grimm et al., 2013). This community effort to archive pollen sequences is continually extended to include new records (http://www.europeanpollendatabase.net/). The EPD has been used more recently to map late Quaternary changes in the distribution and abundance of individual taxa (e.g. Brewer, Cheddadi, de Beaulieu, Reille, & Data Contributors, 2002; Giesecke & Bennett, 2004; Magri et al., 2006). However, new sets of maps for common species for a standard region and set of time periods are not generally available, and many regions have new independently dated pollen diagrams. Further, a recent compilation of new standardized chronologies for the pollen datasets in the EPD allows querying and mapping pollen data on a linear calendar timescale (Giesecke et al., 2014).

Continental scale maps of taxon-specific fossil pollen deposition document past gradients in species abundance and their change through time. These maps have been combined with range-wide genetic surveys to better understand postglacial colonization of forest trees (Magri et al., 2006; Petit et al., 2002). They also provide examples to help understand the effects of future changes, by providing scenarios of past vegetation changes. These may be used for testing process-based vegetation models, by hindcasting vegetation distributions in the past and comparing against the pollen syntheses (Giesecke, Hickler, Kunkel, Sykes, & Bradshaw, 2007; Henne, Elkin, Reineking, Bugmann, & Tinner, 2011), allowing an estimation of their predictive skill outside of the modern period. The information underlying the individual taxa maps can be further analyzed. For example combining the data for multiple taxa permits reconstruction of past biomes, allowing study of changes in the composition and structure of terrestrial ecosystems (Jackson & Williams, 2004; Prentice, Guiot, Huntley, Jolly, & Cheddadi, 1996) and the services they provide (Dearing et al., 2012; Jackson & Hobbs, 2009). Applying relative pollen productivities and models adjusting for the differential transport of pollen allows quantitative assessments of the relative magnitude of anthropogenic-induced environmental changes (Trondman et al., 2015) compared to changes prior to the Anthropocene (Rockström et al., 2009). The underlying pollen data (Brewer, Guiot, & Barboni, 2013) also represent a key source of information for reconstructions of past climates at regional or continental scale (Bartlein et al., 2011; Davis, Brewer, Stevenson, Guiot, & Contributors, 2003), by linking modern pollen assemblages with climate variables, then attributing these to past assemblages.

Since the work of Huntley and Birks (1983), mapping applications using the EPD have largely been driven by projects based on individual pollen taxa (Brewer et al., 2002; Cheddadi et al., 2006; Magri et al., 2006),

and have had limited scope. However, given the potentially broad range of applications of these maps, and the continuing expansion and development of the EPD, an effort has been made to produce new, general pollen maps for Europe. The maps presented here are a result from this process and represent the first substantial update of the 1983 European Pollen Atlas (Huntley & Birks, 1983). Significantly, this new set of maps is based on the original count data of a substantially larger set of 828 sites, and more robust chronological information.

2. Methods

2.1. Study area

The EPD contains sites over a broad geographic area, from Iceland to Russia and from Northern Scandinavia to North Africa. For this mapping project, we have restricted site selection to sites west of a line running from the White Sea to the Black Sea (approximately 25° east), with a southern limit that includes the Aegean Islands (approximately 35° North). The western and northern limits are formed by the Atlantic Ocean and the northern limits of the Scandinavian countries respectively (Figure 1). These limits were chosen to maintain a reasonable spatial coverage of sites; available sites are sparsely distributed outside of this area. We have excluded pollen sequences from marine cores, as the source area contributing to the pollen signal is unclear. The only exceptions to this are a set of cores from the western shelf of the Black Sea, that provide general information on past vegetation in the coastal and lowland region of the western Black Sea that is otherwise scarce.

2.2. Data

The current version of the database contains in excess of 1500 sequences from more than 1300 sites, although this includes data that are not suitable for the current project, for example, sites in North Africa and Eurasia, or samples that are older than the time period of interest (0–15,000 years before present). The database also contains extensive metadata describing each site, age controls, researcher and publications. The database was initiated at a time before digital data exchange was common practice and contains datasets produced before computers were commonly available. Original data often had to be entered by hand, and a number of errors occurred during the process. The database has recently undergone a thorough quality control check, and errors and inconsistencies, where found, have been corrected (Fyfe et al., 2009).

While calibrated ages have been used elsewhere for continental scale mapping of pollen taxa (e.g. Williams, Shuman, & Webb, 2001; Williams, Shuman, Webb, Bartlein, & Leduc, 2004), previous efforts in Europe have used radiocarbon time scales. Time scales based on radiocarbon may deviate from calendar years by as much as 2000 years during the late-glacial period, due to variations in the atmospheric production of the heavy carbon isotope (^{14}C) (Reimer et al., 2009). New models relating the depth of sediments recovered to their calendar age have been developed for all sites for which independent chronological controls, mainly radiocarbon dates, exist (Giesecke et al., 2013). These are used here to facilitate map production on an absolute, calendar time-scale, and to improve subsequent analysis of the observed vegetation dynamics. While constructing these new age-depth models, the uncertainty of assigned sample ages was computed in two ways. First, individual dates have uncertainty arising from the precision of the radiocarbon estimation, and the subsequent conversion to calendar ages. This was quantified for each date used in an age-depth model, then propagated to the ages attributed to each pollen sample. Second, an error class was given based mainly on the distance to the nearest age-control point. These uncertainties are then retained for each pollen sample and may be used to select samples for different mapping and analytical purposes according to different criteria. Further information on the development of these chronological models and uncertainties is given in Giesecke et al. (2013). The new age-depth models were based on the version of the EPD released 2 August 2012 and we restrict the mapping of pollen taxa to datasets for which this age information and uncertainty was computed.

We limited the mapping to samples where the age uncertainties were less than 1000 years, and to samples classified to the minimum error class assigned during the development of the sites chronology, which limits extrapolations of the age-depth models beyond 2000 years from the nearest age-control point. The density of pollen samples varies over time, and declines severely prior to 15,000 years BP (Giesecke et al., 2013; 0 BP (before present) = AD 1950). We have therefore further restricted our dataset to only include samples that are younger than this time. The final subset for mapping based on these criteria was 828 sediment cores with 49,660 pollen samples for the European continent over the past 15,000 years. Figure 2 outlines the site and sample selection process.

2.3. Taxa selection

Pollen types can usually be identified to genus level of the parent plant. Identification to species level is rare and in some cases identification cannot be resolved beyond the plant family level. Pollen assemblages capture a large proportion of floristic diversity, however they tend to be insensitive to plants that are not abundant in the vegetation or are insect pollinated (e.g.

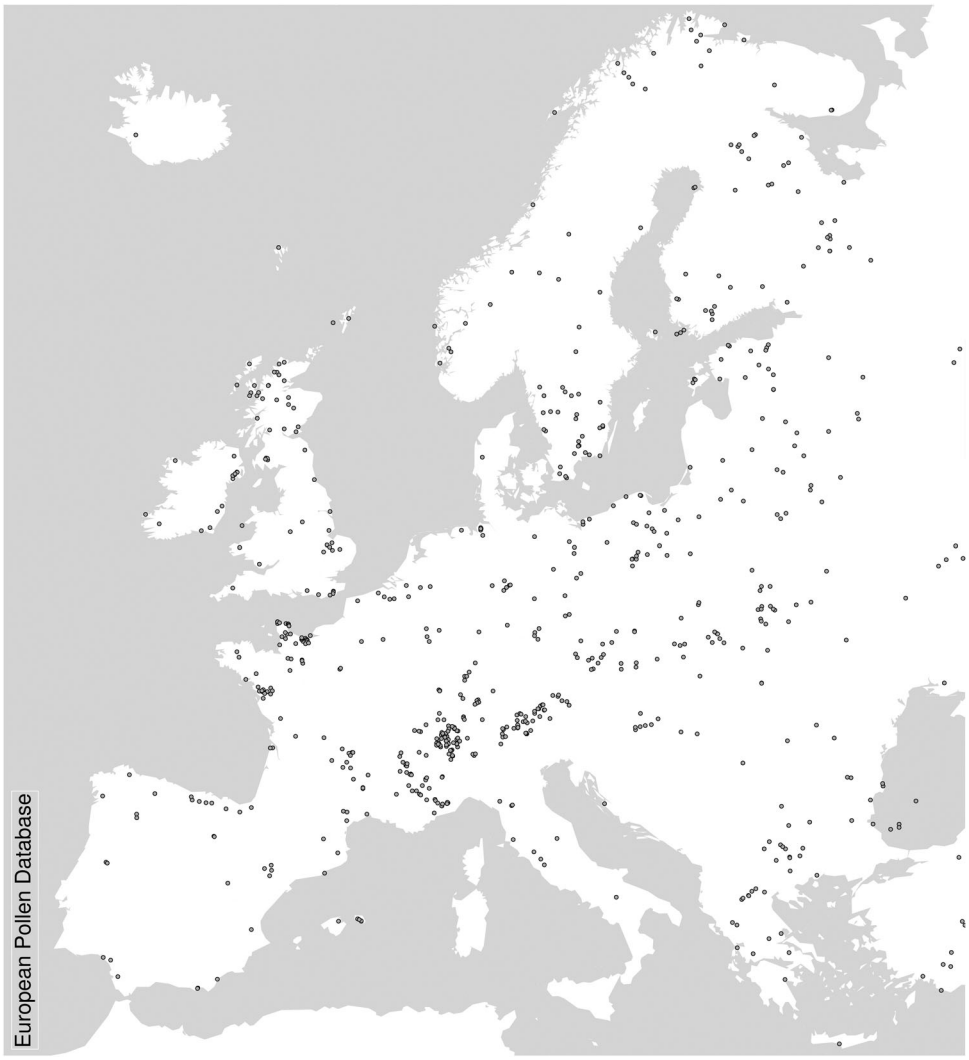

Figure 1. Distribution of the 828 pollen sequences from the EPD used in production of the pollen maps.

Giesecke, Wolters, Jahns, & Brande, 2012). We therefore only map common woody plants as well as a selection of herbs with anemophilous pollination. Due to the fact that pollen analysis is often carried out on lake sediments, pollen data frequently also represent aquatic and telmatic species and a selection of these taxa is also mapped.

A further problem in the mapping of pollen types is related to differences in the taxonomy and nomenclature used for pollen morphological types by different investigators, and by different levels of identification. This is resolved by the use of a synonym table that cross-links taxa which are identified with different names into the same group. A full description of this is given in Giesecke et al. (2013). Here we generally map higher order taxonomic levels that may be linked to a single plant species in some parts of Europe but may include several species in other areas. In cases where two hierarchical levels including the same pollen type are used for mapping (e.g. Ericaceae and *Calluna*) the higher level includes the abundances of the lower (e.g. abundances of *Calluna* are included in Ericaceae). The names of plant species included in each pollen taxon are according to Flora Europaea (Tutin, 1964) and are shown with each map.

The original raw data give the number of pollen grains for a taxon counted in a given sample. These are converted to percentage data to avoid biases due to different sample counts. Percentages are calculated based on the sum of pollen from terrestrial plants counted for that sample. As these are compositional data, the representation of any one taxon at a site may be affected by changes in the other taxa. Using multiple sites to map the changes in these values limits this problem, by emphasizing spatial coherent changes.

2.4. Mapping of time slices

The maps are produced in time steps of 500 years between 15,000 years and the present, each representing a 'snap-shot' distribution of a taxon for a target age. As the dataset consists of irregular time series of pollen abundances, samples for each target age are taken within a half-window of 250 years around the target age (e.g. for the target age of 10,000 years BP, samples are taken between 9750 and 10,250 years

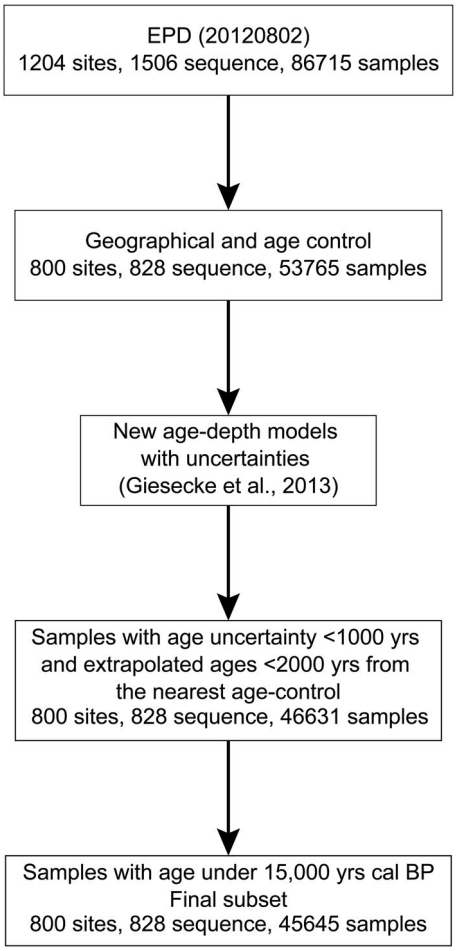

Figure 2. Workflow displaying the selection process of the site and sample data from the original full database.

BP). The value attributed to each site is the weighted average of all abundances within that window, where weights are taken as a linear function of the distance in time between a sample and the target age. Age uncertainties were used to exclude samples, but were not used in the weights.

Maps were produced using the Lambert Azimuthal Equal-Area projection, centered on 12°E, 48°N.

3. The maps

For each pollen taxon, we prepared a set of 16 maps from 15,000 years ago to the present day Main Map. Each circle represents the location of a site, and its diameter represents the pollen abundance at that site for that time period. Pollen percentages are split into five taxon-specific classes, which are used to derive the circle diameter. The breaks used for these classes were chosen manually for each taxon. As the values for any given taxon vary quite widely, both in range and in skewness, classes were selected to best visualize the data. While this limits direct comparison between the different taxa maps, using the same set of classes for all taxa would mean that all variation in low represented taxa (e.g. *Abies*) would be forced into 1 or 2 classes.

Black dots represent locations where no pollen for a given type falls in the 500-year search window. One additional class, portrayed as small grey circles, represents low pollen abundances, which may signify anything between long distance dispersal and chance encounter due to low population densities around a site, rather than the distinct evidence for the nearby presence of the parent plant. This threshold value is more critical for abundant taxa with high pollen production and dispersal, where it is used as an attempt to describe the distributional limits of the parent plant (Lisitsyna, Giesecke, & Hicks, 2011). The values applied here for common trees are derived from a comparison of modern pollen spectra with plant distribution data on the European scale (Lisitsyna et al., 2011).

The decay of ice sheets is illustrated for Scandinavia, the British Isles and Ireland as an aid for the interpretation of past vegetation development. The ice limits are based on generalized information summarized by Ehlers, Gibbard, and Hughes (2011) and Lundqvist (2002), and should be taken as a general guide rather than exact spatial information. Sites falling onto the ice result from inherent temporal and spatial uncertainties and these points should be interpreted as locations at the edge of the ice or established within a few hundred years of deglaciation. Ice sheets and glacier extent in the Alpine and Pyrenean mountain chains are not represented.

The sea level rise and isostatic rebound connected with deglaciation changed both the topography and coastline of Western Europe, most notably in the north-west. However, compiling the available information for these maps lay beyond the scope of this project and the maps are therefore displayed using the modern shoreline configuration.

4. Discussion

The maps presented here provide a substantial update of the atlas of past and present pollen maps by Huntley and Birks (1983): they are based on approximately double the number of pollen diagrams, using the original data recorded by each researcher and the maps are based on calendar time scales supported by over 3600 radiocarbon dates and other types of independent chronological information, e.g. volcanic (tephra) layers. Our goal with this set of maps is to spatially visualize the pollen percentage information contained in the database, and have not carried out any further analysis for this paper. Other forms of visualization exist, including isopollen maps (e.g. Huntley & Birks, 1983), in which the abundance values are interpolated for a given time step, or isochrone maps, in which the time at which some abundance threshold is passed at each site is interpolated (e.g. Birks, 1989). However, these may smooth out or obscure small-scale spatial

variability, which is apparent in non-interpolated maps. We note that in areas with a high density of sites, the maps presented here give a similar visual impression as an interpolated isopollen map, while retaining the variability.

The results show the substantial differences in post-glacial history among this set of taxa presented. Some (e.g. *Artemisia*) reach maximum abundance in the late-glacial and subsequently decline, while others expand at the end of the last glacial period to continental-wide distributions during the Holocene (e.g. *Quercus*). Among the latter, the rate at which abundance values rise varies, with some showing rapid, range-wide expansion (e.g. *Corylus*), and others a slower expansion across a latitudinal or longitudinal gradient (e.g. *Fagus*).

The maps presented here are a visualization of the content of the EPD. Although much work has gone into reviewing the content of the database (Fyfe et al., 2009) and establishing new age-depth models (Giesecke et al., 2013), it is important to note that the data carry a number of uncertainties, particularly with the attribution of ages to samples. Further, the high taxonomic level of many of the pollen taxa used may conflate the dynamics of several lower level taxa, for example, Box (*Buxus*) includes Balearic Box (*Buxus balearica*) and Common or European Box (*Buxus sempervirens*). However, these maps present the major aspects of European vegetation history as reported in pollen diagrams, and the broad-scale patterns are comparable to previous mapping studies (Brewer et al., 2002; Giesecke & Bennett, 2004; Huntley & Birks, 1983; Magri et al., 2006).

While the main objective in the construction of the maps was to represent the raw data, the abundance values needed to be classified to facilitate visual interpretation. In this respect, the threshold values proposed by Lisitsyna et al. (2011) and used in our mapping are critical values, and were chosen to minimize both false presence and false absence. As such, the values may be too conservative in some regions and time periods, causing an underestimation of the distributional limits, while in other situations they may not sufficiently constrain these limits.

5. Concluding remarks

The mapping of data in the EPD represents a moving target as the database is constantly updated to include new sites. It is envisaged that this type of mapping will be developed into a web-based application linked directly to the database, giving the user more freedom to select time slices and species. However, the current work presents a set of pollen maps using standardized techniques and parameters, giving both an overview of the history of European pollen assemblages and their changes in time and space, and a high-quality dataset for further analysis and use in a number of different applications, including climate and land cover reconstructions and tests of process-based models. In addition, these maps are based on a publicly available dataset with a high number of individual sites, and include information for some regions that were not previously available.

A notable feature of the maps is the uneven spatial distribution of the sites. In order to improve the visualization of the spatial dynamics of the vegetation and to prepare a dataset that may be more easily used for spatial analyses, we are currently preparing a second set of maps based on interpolated abundance values for a subset of the taxa presented here. However, the current set of maps remain important in that they allow an examination of the underlying dataset, and, despite the varying site density, still provide a clear picture of postglacial pollen deposition in lakes and bogs of Europe, and information that may be used to infer the spatial dynamics and compositional changes of European vegetation through time.

Software

All data processing was carried out using Perl and R version 3.0 (R Core Team, 2013), and maps were produced using the Generic Mapping Tools version 5.1.0 (Wessel & Smith, 1991).

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