Patterns in recent and Holocene Pollen Accumulation Rates across Europe; the Pollen Monitoring Programme Database as a tool for vegetation reconstruction

Vojtěch Abraham[1], Sheila Hicks[2], Helena Svobodová-Svitavská[1, 3], Elissaveta Bozilova[4], Sampson Panajiotidis[5], Mariana Filipova-Marinova[6], Christin Eldegard Jensen[7], Spassimir Tonkov[4], Irena Agnieszka Pidek[8], Joanna Święta-Musznicka[9], Marcelina Zimny[9], Eliso Kvavadze[10], Anna Filbrandt-Czaja[11], Martina Hättestrand[12], Nurgül Karlıoğlu Kılıç[13], Jana Kosenko[14], Maria Nosova[15], Elena Severova[14], Olga Volkova[14], Margrét Hallsdóttir[16], Laimdota Kalniņa[17], Agnieszka M. Noryśkiewicz[18], Bożena Noryśkiewicz[19], Heather Pardoe[20], Areti Christodoulou[21], Tiiu Koff[22], Sonia L. Fontana[23, 24], Teija Alenius[25], Elisabeth Isaksson[26], Heikki Seppä[27], Siim Veski[28], Anna Pędziszewska[9], Martin Weiser[1], and Thomas Giesecke[29]

[1]Department of Botany, Faculty of Science, Charles University; Benátská 2; CZ-128 01; Prague; Czech Republic

[2]P.O. Box 8000, FI-90014 University of Oulu, Finland

[3]Institute of Botany v.v.i.; Czech Academy of Sciences; Zámek 1; CZ-252 43 Průhonice; Czech Republic

[4]Laboratory of Palynology, Department of Botany, Faculty of Biology, Sofia University, 8 Dragan Tsankov blvd., Sofia 1164, Bulgaria

[5]Lab. of Forest Botany, Faculty of Forestry and Natural Environment, Aristotle University of Thessaloniki, P.O. Box 270, 54124 Thessaloniki, Greece

[6]Museum of Natural History Varna, 41 Maria Louisa Blvd. 9000 Varna; Bulgaria

[7]University of Stavanger, Museum of Archaeology, Peder Klows gate 31A, PB 8600 Forus, NO-4036 Stavanger, Norway

[8]Institute of Earth and Environmental Sciences, Maria Curie-Sklodowska University; al. Krasnicka 2d; 20-718 Lublin; Poland

[9]University of Gdańsk, Faculty of Biology, Department of Plant Ecology, Laboratory of Palaeoecology and Archaeobotany, ul. Wita Stwosza 59, 80-308 Gdańsk, Poland

[10]Georgian National Museum, Purtseladze Str.3, Tbilisi 5, Georgia 0105.

[11]Faculty of Biological and Veterinary Sciences, Geobotany and Landscape Planning, Nicolaus Copernicus University in Toruń, 87-100 Toruń, ul. Lwowska 1; Poland

[12]Department of Physical Geography, Stockholm University, SE-106 91 Stockholm, Sweden

[13]Department of Forest Botany, Faculty of Forestry, Istanbul University-Cerrahpaşa; Bahçeköy; TR-34473; Istanbul; Turkey

[14]Depertament od Higher Plants, Moscow State University; Leninskie Gory, 1, 12, Moscow, 119234, Russia

[15]Main Botanical Garden RAS; Botanicheskaya, 4, Moscow, 127276, Russia

[16]Laugarnesvegi 87 íbúð 105, 105 Reykjavík, Iceland

[17]Department of Geography and Earth Sciences, University of Latvia; Jelgavas Street 1, LV-1004; Riga, Latvia

[18]Institute of Archeology, Faculty of History, Nicolaus Copernicus University in Toruń; Szosa Bydgoska 44/48; 87-100 Toruń; Poland

[19]Faculty of Earth Sciences and Spacial Managment, Nicolaus Copernicus University in Toruń; Lwowska 1, 87-100 Toruń; Poland

[20]Department of Natural Sciences, National Museum Wales, Cathays Park, Cardiff, CF10 3NP, U.K.

[21]Department of Forests, Ministry of Agriculture, Rural Development and Environment, P. Box 24136, 1701 Nicosia, Cyprus

[22]Tallinn University, School of Natural Sciences and Health, Institute of Ecology, senior researcher. Uus Sadama 5, 10120 Tallinn, Estonia

[23]Cátedra de Palinilogía, Facultad de Ciencias Naturales y Museo, UNLP, Calle 64 n°3, 1900 La Plata, Argentina

[24]Faculty of Resource Management, HAWK University of Applied Sciences and Arts, Büsgenweg 1a, 37077 Göttingen, Germany

[25]Turku Institute for Advanced Studies (Department of Archaeology), FI-20014 University of Turku

[26]Norwegian Polar Institute, Fram Centre, N-9296 Tromsø, Norway

[27]Department of Geosciences and Geography, University of Helsinki, Gustav Hällströmin katu 2, 00014, Helsinki, Finland

[28]Department of Geology, Tallinn University of Technology, TalTech, Ehitajate tee 5, 19086 Tallinn, Estonia

[29]Palaeoecology, Department of Physical Geography, Faculty of Geosciences, Utrecht University, P.O. Box 80115, 3508 TC Utrecht, The Netherlands.

Correspondence: Vojtěch Abraham (vojtech.abraham@gmail.com)

Abstract. The collection of modern spatially extensive pollen data is important for the interpretation of fossil pollen diagrams. Such datasets are readily available for percentage data but lacking for pollen accumulation rates (PAR). Filling this gap has been the motivation of the pollen monitoring network, whose contributors monitored pollen deposition in modified Tauber-traps for several years or decades across European latitudes. Here we present this monitoring dataset consisting of 351 trap locations with a total of 2742 annual samples covering the period from 1981 to 2017. This dataset shows that total PARs are influenced by forest cover and climate parameters, which determine pollen productivity and correlate with latitude. Pollen traps situated beyond 200 km of the distribution of a given tree species are still collecting occasional pollen grains of that species. PAR's of up to 30 grains cm^{-2} y^{-1} in fossil diagram should therefore be interpreted as long distance transport from beyond 200 km from the area of distribution. Comparisons between modern and fossil PAR from the same regions show comparable values. Comparisons often demonstrate that similar high values for temperate taxa in fossils sites are found further south or downhill. While modern situations comparable to high PAR values of some taxa (e.g. *Corylus*) do not occur, CO_2 fertilization and land use may cause high modern PAR's that are not documented in the fossil record. The modern data is now publically available in the Neotoma Paleoecology Database (https://apps.neotomadb.org/explorer/) and serves improving interpretations of fossil PAR data.

1 Introduction

1.1 The need for a dataset of modern absolute pollen deposition

Pollen analytical results are usually reported as percentages, which are a simple and robust representation of the data, while they have a number of well-known biases. The problem of separating locally produced from long distance transported pollen has received attention from the very beginning of modern pollen analysis (Davis, 2000). Particularly at the tree-line the interpretation from pollen percentage data may be misleading as local treeless vegetation (e.g. tundra) is often low pollen procuring, while distant woodlands (e.g. consisting of boreal trees) may produce much pollen. In such situations absolute pollen data are

very informative. Pollen accumulation rates (PAR) or the number of pollen grains deposited on the sediment surface over a set period of time is better suited to differentiate between long distance transported and locally produced pollen as already realized by (Hesselman, 1919) and (Malmström, 1923). In a seminal publication (Davis and Deevey, 1964) document the power of using absolute pollen deposition for the interpretation of vegetation change during the postglacial afforestation around Rogers Lake in Connecticut, USA. Another bias in percentage data is the interdependence of values obscuring the quantification in the amount of change of a single taxon. PARs are therefore required when studying the population dynamics of individual trees (Bennett, 1983).

However, obtaining PAR from sediments cores requires accurate chronologies. While sedimentation in lakes occurs generally without abrupt changes, lake internal processes such as re-deposition and sediment focusing and also catchment erosion may bias the resulting values [Davis and Brubaker (1973); (1984); Giesecke and Fontana (2008); (Bennett and Buck, 2016). These are some reasons why advances in interpreting PAR have been slow. The other reason is that collecting modern PAR values is not as simple as collecting mosses, soil litter or the top sediment of lakes for obtaining modern pollen percentages for a particular vegetation type. Modern rates of pollen accumulation can be obtained from monitoring pollen deposition using pollen traps (Hicks, 1994) as well as from carefully sampling the top sediments of lakes that are either annually laminated or precisely dated (Matthias and Giesecke, 2014). Due to the high inter-annual variability in pollen production (Andersen, 1980; Haselhorst et al., 2020) it is necessary to conduct pollen monitoring over several years to enable comparisons with estimates from sediment cores (Hicks, 1974; Hicks and Hyvärinen, 1999).

For these reasons there are numerable studies investigating the pollen vegetation relationship using percentage data and comparably few using absolute pollen deposition. Nevertheless, investigations using pollen traps yielded invaluable insights in the mode of pollen transport (Tauber, 1967). Also the construction of representation factors for common Europe trees by Andersen (1970), which are still used, were based on pollen monitoring data from pollen traps. In this way pollen monitoring studies have contributed to the development of models of pollen dispersal and deposition (Gaillard et al., 2008).

More recent investigations demonstrate the linear response of the absolute pollen deposition to absolute tree abundance (Seppä et al., 2009, Sugita et al. (2009), Matthias and Giesecke (2014)), which may be used to reconstruct past standing tree biomass of different trees. However, rather than changes in tree biomass, changes in PAR at an annual time resolution correspond to weather conditions of the previous, as well as the year of flowering (Hicks, 1999, van der Knaap et al. (2010), Nielsen et al. (2010)). Thus the question arises: If weather is determining annual pollen production, could climate or site conditions not determine average rates? Comparing *Pinus* PAR between two pine dominated forest regions in central Sweden and north east Germany shows much higher values in the south, suggest that PAR may not correspond to tree biomass alone (Matthias and Giesecke, 2014). The relationship between pollen production and weather suggests that more pollen is produced when the primary productivity of the tree is higher. Therefore, climate, soil fertility and even the amount of CO_2 in the atmosphere may determine the pollen productivity of a tree at a given site. Already Welten (1944) interpreted the first fossil PAR in this way, suggesting that climate deteriorations may not immediately lead to a decline in forest cover but to the amount of pollen produced. This interpretation of changing PAR was however forgotten. If climate and CO_2 determine pollen productivity than the postglacial increase in PAR at Rodgers Lake could also be due to a change in these parameters. It is therefore impotent

to investigate the possible relationship between climate and average PAR in more detail. Also the initial question on the amount of pollen that may arrive at a site from long distance sources has not been addressed in a systematic way using modern absolute pollen deposition data.

Spatially extensive modern pollen percentage datasets provide the possibility of searching for modern analogues for fossil pollen proportions and in this way reconstructing past vegetation and environmental conditions assemblages (Davis et al., 2013; Jackson and Williams, 2004; Overpeck et al., 1985). Modern datasets of absolute pollen deposition are hitherto rarely used as references helping to reconstruct past tree abundances or environmental conditions. By using a network of pollen traps across the latitudinal tree-line in Finland Hicks et al. (2001) show that average modern PAR values can be obtained representing the gradual transition from the boreal forest to tundra. These "modern analogues" were successfully applied reconstructing Holocene shifts of the latitudinal tree line (Seppä and Hicks, 2006). This idea of building a modern dataset of absolute pollen deposition that can be used as a reference to interpret fossil PAR was the motivation for the establishment of the Pollen Monitoring Programme (PMP, Hicks et al., 1996; 1999; 2001)).

1.2 The Pollen Monitoring Program (PMP)

The program was launched in August 1996 at a meeting in Finland, bringing mainly European researchers together. Members of the network changed over the years and monitoring experiments were discontinued or newly started. Although pollen monitoring studies were and are carried out on other continents (e.g. Jantz et al., 2013) the PMP had little success in attracting researchers working outside Europe. The standardisation of the monitoring protocol allowed for easy comparisons between the results in different regions which were discussed at INQUA in 1999 and led to a special volume published in 2001 (Tinsley and Hicks, 2001) collecting results based on several initial time series (van der Knaap et al., 2001; Koff, 2001; Tinsley, 2001; Tonkov et al., 2001) as well as a first comparative study (Hicks et al., 2001). More individual results were published in the following years (e.g. Gerasimidis et al., 2006; Giesecke and Fontana, 2008; Hättestrand et al., 2008; Jensen et al., 2007; Kvavadze, 2001; Pidek, 2007) and comparative studies followed in a second special volume published in 2010 (Giesecke et al., 2010). The data produced by contributors to the PMP were analysed for different questions, including weather parameters determining the amount of pollen production (van der Knaap et al., 2010) and its correlation to masting years in *Fagus* (Pidek et al., 2010). The programme established a database collecting the original data for individual years, as well as general information on the pollen traps installed in the different regions (Fig. 1). The database was developed offline and was thus difficult to access by individual researchers. The paleoecology database Neotoma (Williams et al., 2018) offers a platform to store the PMP data and make it available to researchers worldwide, allowing them to interrogate the data and potentially identify modern analogues to interpret fossil pollen accumulation rates.

The overall purpose of this manuscript is to present an overview of the data in the PMP database and to interrogate this continental scale dataset of modern PAR with the following aims:

a) Examine the hypothesis that climate as well as regional forest cover explain the variability in PAR.
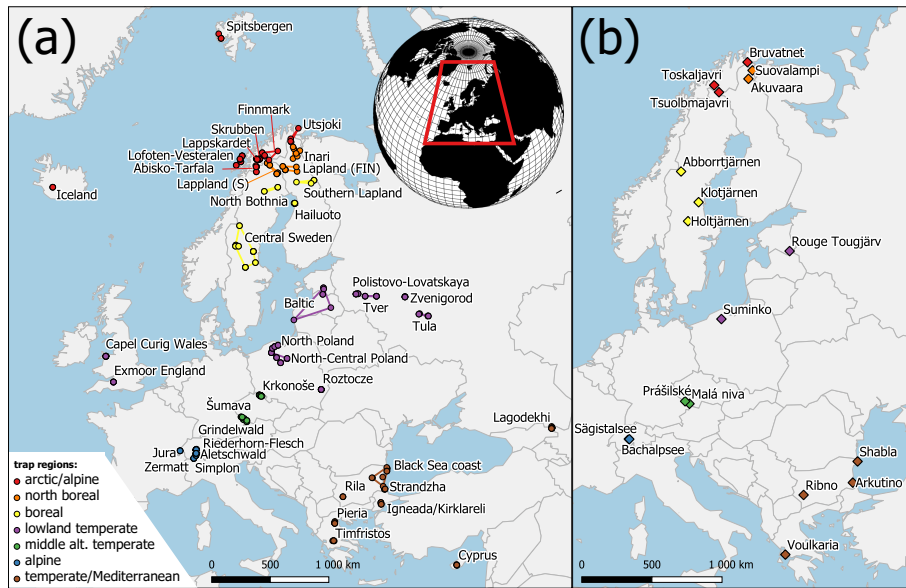
Figure 1. Map of the study area with trap areas (a) and Holocene pollen sites (b). Both datasets are divided into trap regions (colours). – Colours correspond to Fig. 5.

b) Study the absolute amount of long distance dispersed pollen encountered in pollen traps beyond the known distribution limits of the parent trees.

c) Compare modern and fossil pollen accumulation rates by collecting fossil datasets with estimates of PAR from the same regions where the pollen traps were installed. For the most abundant pollen types we explore how the modern situations can provide a reference for the interpretation of the fossil data.

2 Methods

2.1 Study area

Sites in the PMP database were divided into 7 'trap regions' according to the latitude and altitude. These regions were further divided into 'trap areas', by grouping 2-10 trap locations according to their spatial proximity. The arctic/alpine region includes distant trap areas in Spitsbergen and Iceland, northernmost traps in Finland (Utsjoki) and Norway (Lofoten-Vesterålen) and traps in the Scandinavian mountains above the local tree-line (Finnmark, Abisko-Tarfala, Skrubben and Lappskardet). The landscape around these traps is often treeless or covered by sparse birch shrubland with *Betula nana* and *B. pubescens* in some locations. The north boreal region includes traps in Northern Lapland in Finland, Norway and Sweden with a vegetation dominated by *Betula* and *Pinus sylvestris*. The northern limit of *P. sylvestris* occurs between traps from this region, which are situated at altitudes below 500 m a.s.l. The boreal region includes trap areas situated in Southern Lapland, around the

Bay of Bothnia and in Central Sweden. The vegetation is dominated by *Picea abies*, *P. sylvestris* and *Betula* species, with the occurrence of *Alnus incana*. Northernmost populations of *Alnus glutinosa* occur near some sites and the southernmost traps in Central Sweden are situated near northern outpost populations of *Corylus avellana* and *Ulmus glabra*. Traps from the temperate lowland region have the widest longitudinal extent including the British Isles, Poland, the Baltic countries and European Russia. Vegetation at trapping locations below 500 m a.s.l. is characterised by *Quercus* and *Fraxinus excelsior* in the West and *P. sylvestris*, *P. abies* and *Betula* with an admixture of *Quercus*, *Tilia*, *Ulmus* and *C. avellana* in the East. *Fagus sylvatica* and *Carpinus betulus* occur in Poland, *Abies alba* only in south-eastern Poland. Trapping locations in the temperate region at elevations above 500 m (mid elevation) were separated and include the Krkonoše and Šumava Mountains. Traps in both areas are placed on an elevation gradient from 500 m and 1200 m a.sl. The lower slopes of the mountains are dominated by *F. sylvatica*, while the traps are situated on a gradient from *P. abies*-dominated forest to the onset of alpine vegetation in Krkonoše. In the Alps and Jura Mountains, traps were placed at even higher elevations, between 1200 m to 3000 m, crossing the altitudinal treeline. Trapping locations in the Southeast represent diverse landscapes and vegetation types including grasslands, evergreen and deciduous forests. Some traps are situated in high mountain regions around treeline situations or within the upper mountain forests including Rila (Bulgaria), Pieria (Greece), Timfristos (Greece), Lagodheki (Georgia) and Cyprus. Traps at lower elevations are situated near the Black Sea coast, within the low Strandzha Mountains and European Turkey.

2.2 Data collection

The pollen traps used in the PMP network generally consist of a bucket or bottle large enough to contain the annual surplus in precipitation on a surface of usually 19.6 cm^2 (5 cm diameter opening) or similar. Many traps had a sloping collar inspired by the design of pollen traps by Tauber (1974), although few collars were truly aerodynamic. The collection of the trap content was generally carried out annually and any special circumstances potentially affecting the annual pollen deposition were noted and stored in the database. For the analyses presented here and data overview we excluded traps where the pollen record is 2 years or less, as averages may be affected by high inter-annual variability. The only exception is the trap situated in Spitsbergen where there is a two-year record. Pollen accumulation from the two-year record shows little variation and, being the only analogue for a truly arctic and treeless environment, provides important information on long distance pollen transport. We also excluded annual samples with records shorter than 8 months and, in addition, traps or years with spurious values due to particular events or local conditions (Table S1).

Most of the traps in the PMP network were placed in the open vegetation or in forest openings in order to avoid an unrepresentative contribution of individual trees e.g. due to anthers dropping into the traps. Traps were generally installed at ground level mimicking collection conditions relevant for sedimentary archives. In consequence tall herbs or grasses might overgrow or cover some of the traps potentially leading to higher pollen deposition. Traps not equipped with a mesh occasionally trapped pollen collecting insects, leading to enormous counts of insect pollinated taxa e.g. *Calluna*, *Erythranthe guttata*. The presence of insects in the traps is usually noted for the collection year so that careful evaluation of the information in the database can also inform on herbaceous pollen types (Jensen et al., 2007). Including this information in comprehensive database queries is currently not possible and a manual screening of datasets is required when analysing herbaceous pollen types. This problem

does not seem to occur in tree pollen taxa. The occurrence of phytophagous insects in the traps were not accompanied by unusual peaks in tree pollen taxa, indicating that the insects inadvertently trapped were primarily collecting pollen from the herbaceous vegetation around the traps. Comprehensive database queries restricted to tree pollen, Poaceae and Cyperaceae should therefore not be affected by the occurrence of insects in the trap and mainly represent pollen transport via wind, the rainout of pollen from the atmosphere and the gravity component.

Concentrating the content of the traps was carried out either using filter paper or centrifugation and decanting the supernatant. In many cases the trap content was washed onto a paper filter, which was later digested using acetolysis. Pollen quantity was assessed by adding *Lycopodium* spore tablets (Stockmarr, 1971) to each trap before processing. Pollen concentration was obtained from the ratios between pollen grains counted to *Lycopodium* spike counted and *Lycopodium* spike added. Details about *Lycopodium* spike data, as well as details of the pollen trap such as the exact size of the opening are stored in the database. The PMP database was created in the PostgreSQL database system. Names of pollen taxa were unified using the accepted variable names from the European Pollen Database (Giesecke et al., 2019).

2.3 Investigated taxa and environmental parameters

We selected the common tree and shrub taxa of Europe. Pollen taxa generally refer to all the species within the genus. Pollen taxa allowing higher taxonomical resolution, which were consistently separated and excluded from the genus in the whole dataset are marked as "excl.". Pollen taxa potentially including pollen grains from another genus are indicated by "incl.": *Abies*, *Alnus* (excl. *A. viridis*), *Betula* (excl. *B. nana*-type), *Carpinus*-type (incl. *C. orientalis/Ostrya*-type), *Corylus*, *Fagus*, *Fraxinus* (incl. *F. ornus*), *Juniperus*-type (incl. *Cupressus*, *Tetraclinis*, *Thuja*), *Picea*, *Pinus* (excl. *P. cembra*-type), *Tilia*, *Quercus* (incl. *Q.robur*-type, *Q. cerris*-type and *Q. ilex*-type). Pollen accumulation rates of trees and shrubs were summed as arboreal pollen accumulation (hereafter as "tree PAR"). We also included pollen from the plant families Cyperaceae and Poaceae (excluding cereals). For the purpose of the analysis in this paper we refer to sum of tree PAR plus Cyperaceae and Poaceae as "total PAR".

The climate parameters Mean Annual Temperature (MAT) and Annual Precipitation (APrecip) for the trapping locations were obtained from WorldClim 2 (Fick and Hijmans, 2017). For site altitude we used the information supplied by the individual investigator. Comparisons between PAR and forest cover were conducted using the data of the Forest Map of Europe (Kempeneers et al., 2012), which has a grid resolution of 1 km^2. Forest cover was extracted as a mean of all grid cells within a 10 km radius. We used regression analysis to explore whether individual or combinations of these environmental parameters describing the trapping location can explain the variance in average pollen accumulation of the traps. To balance the contribution of high and low pollen producers in the assessment of the total PAR we applied correction factors (Table S2, Andersen, 1970).

Pollen deposition beyond the distribution area of the parent plant was studied by merging the distribution maps of the relevant species included in the pollen type described above (Caudullo et al., 2017; San-Miguel-Ayanz et al., 2016). These comparisons were not suitable for *Alnus*, *Betula*, Cyperaceae, *Juniperus*, *Pinus* and Poaceae as these taxa are widely distributed in Europe and few traps are located beyond their distribution area. We compared the amount of pollen accumulating from these taxa in

pollen traps at 200 km from their mapped distribution limits. Pollen traps in the UK are situated beyond the natural distribution limits of several of these trees but were excluded from the comparison as the taxa considered may be planted in the area.

For each trap location and each pollen taxon we calculated the distance to the nearest area of distribution using GIS (GRASS Development Team, 2018). Linear regression between this distance and the decadic logarithm of PAR was used to predict the
5   threshold of long-distance transport (hereafter also as "LDT").

2.4   Comparison between modern and Holocene PAR

To enable the comparison of modern with fossil PAR values the pollen trap data was extracted from the PMP database with above described constraints and all annual samples were averaged within traps. Per each trap region we selected at least one and a maximum of three Holocene PAR records (Table 1). Holocene PAR estimates often show high variation between samples due
10   to changes in the sedimentary environment. To reduce this effect in this comparison Holocene data were averaged in 500-year bins. Site and sample compilation resulted in a fossil dataset containing 354 Holocene samples.

We compared trap and fossil PAR datasets in two ways. First, we compared the distribution of logged PAR values and their mean for all taxa in all regions. Differences were measured by t-test at 5% level of alpha. Second, we searched for Holocene pollen records containing estimates of PAR in proximity to the locations of pollen traps, so we compared trap and fossil PAR
15   at level of individual sites or trap areas. Average trap and fossil PAR values per taxon were submitted to one-dimensional clustering using the R-package Ckmeans.1d.dp (Song and Wang, 2011). The classes produced were used to facilitate the comparison between trap and fossil data and to match the trap values with analogous situations in the past. The aim of this comparison was to find traps with similarly high values for individual taxa that compared to the highest average fossil PAR. However, averaging did not smooth out all spuriously high values variation, thus we need to ignore individual high fossil values
20   (Table S3). Thus, we aimed to find modern analogues for fossil situations represented by several bins (more than 500 years). We linked these periods with high fossil PARs to the closest pollen trap, using a matrix of distances between fossil sites and pollen traps. We selected the comparisons for the 8 most abundant taxa to be presented in the main text and show the remaining 7 taxa in the supplementary. All statistical analysis and data visualizations were produced in R (R Core Team, 2019).

3   Results and interpretations

25   ### 3.1   Overview of the PMP database and the environments sampled

The PMP database version 02.02.2020 contains data from 351 trap locations with a total of 2742 annual samples covering the period from 1981 to 2017. Considering the trap record with 3 years and more we obtained 271 mean trap assemblages. Trapping sites cover a range of altitudes from 0 to 3000 m a.s.l. with annual precipitation ranging from 402 to 1549 mm. Mean annual temperature (MAT) for the sites fall between -5.7 to 14.1 °C. The forest cover within a 10 km radius of the trapping
30   sites ranges from 0 to 98%. This range of environmental situations has yielded tree pollen accumulation rates from 5 to 86000 grains cm^{-2} y^{-1}, with a median value of 5400 grains cm^{-2} $year^{-1}$ (Fig. 2). An overview of the taxonomic composition of the

Table 1. Fossil sequences including type and size of the deposit.

country	region	site	deposit	latitude	longitude	(m) a.s.l.	area (ha)	reference
FIN	arctic/alpine	Bruvatnet	lake	70.17933	28.39998	119	60	(Hyvärinen, 1975)
FIN	arctic/alpine	Toskaljavri	lake	69.19177	21.44841	704	100	(Seppä et al., 2002)
FIN	arctic/alpine	Tsuolbmajavri	lake	68.68915	22.05235	256	14	(Seppä and Weckström, 1999)
FIN	north boreal	Suovalampi	lake	69.58333	28.83333	104	16	(Hyvärinen, 1975)
FIN	north boreal	Akuvaara	lake	69.125	27.68333	170	4	(Hyvärinen, 1975)
SWE	boreal	Abborrtjärnen	lake	63.88333	14.45	387	3	(Giesecke, 2005c)
SWE	boreal	Klotjärnen	lake	61.81667	16.53333	235	1	(Giesecke and Fontana, 2008)
SWE	boreal	Holtjärnen	lake	60.65	14.91667	232	1	(Giesecke, 2005a)
EST	lowland temp	Rõuge Tõugjärv	lake	57.73904	26.90515	114	4.2	(Veski et al., 2012)
POL	lowland temp.	Suminko	lake	53.72556	17.77278	115	0.12	(Pędziszewska et al., 2015)
CZE	middle alt. temp.	Prášilské	lake	49.07551	13.40002	1079	3.7	(Carter et al., 2018)
CZE	middle alt. temp.	Malá niva	peatbog	48.90789	13.81982	754	65	(Svobodová et al., 2002)
CHE	mountain temp.	Sägistalsee	lake	46.68139	7.9775	1935	7.2	(van der Knaap et al., 2000)
CHE	mountain temp.	Bachalpsee	lake	46.66944	8.020833	2265	8	(van der Knaap et al., 2000)
BGR	temp/medit.	Shabla	lake	43.58333	28.55	1	1.51	(Filipova-Marinova, 1985)
BGR	temp/medit.	Arkutino 2	lake	42.3299	27.72363	0	40	(Bozilova and Beug, 1992)
BGR	temp/medit.	Ribno	lake	42.20682	23.32346	2184	3.5	(Tonkov et al., 2002)
GRC	temp/medit.	Voulkaria	lake	38.866667	20.833333	0	10000	(Jahns, 2004)

traps (Fig. S1) shows a dominance of pollen from *Pinus* and *Betula* in the traps from boreal and hemiboreal environments, with *Betula* as the taxon with the highest PARs overall. In most northern traps from open environments Cyperaceae is the dominant NAP pollen type while Poaceae are dominant in traps from open environments in the south, where they also contribute much higher absolute amounts. The diversity of landscapes and forest types in central and southern Europe is well represented in the pollen composition of traps from this area. Differences in pollen composition and abundance between the high mountain forests of central and southern Europe and the boreal forest in the north are also noticeable(Fig. S2).

3.2 Dependence of variation in PAR on regional forest cover and climate

Total PAR is generally lower at high latitudes, with the lowest values in the arctic alpine region (trap area Spitsbergen). However, the highest absolute values are not from the southernmost traps but from the lowland temperate region (trap area Tver; Fig. 2). Nevertheless, latitude alone explains about 11% of the variance in log transformed tree PAR, while MAT and forest cover within 10 km explain 21% and 19% respectively. In combination, these three variables explain 37% of the variation in log-transformed absolute tree pollen deposition. The addition of elevation increased the amount of variance explained to 50% (Table S4a).
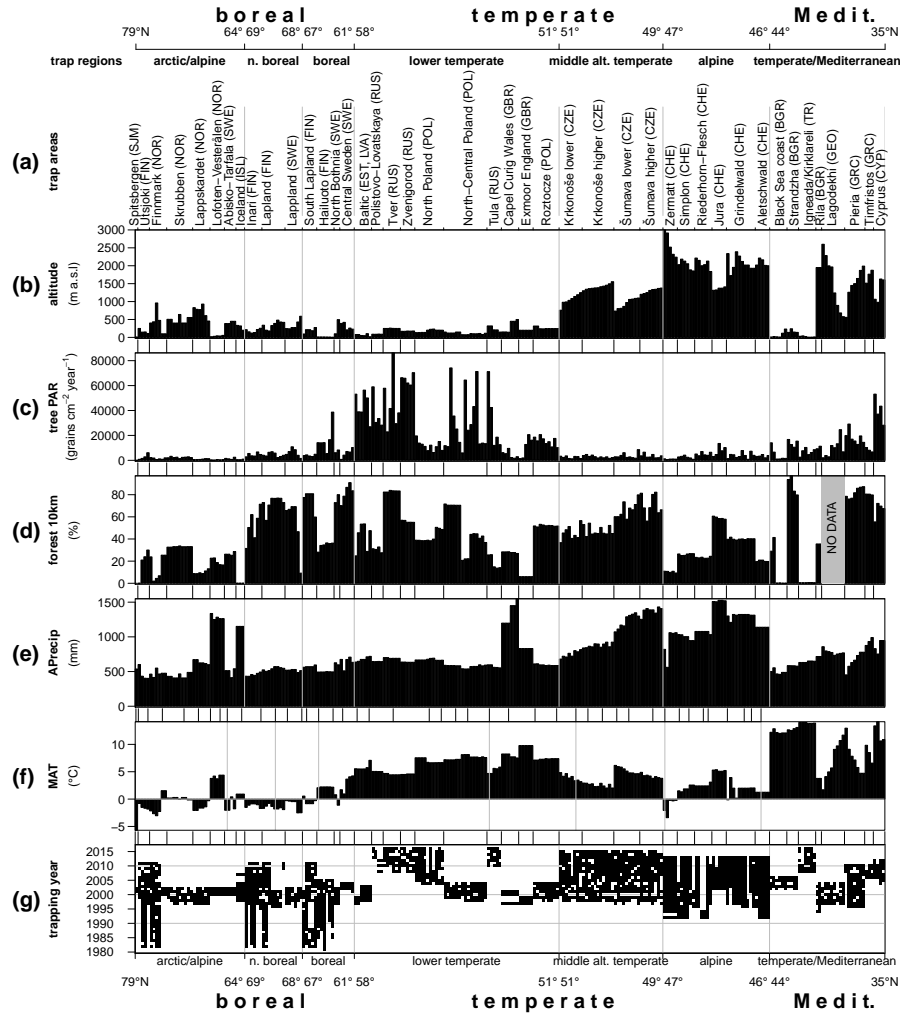
Figure 2. Environmental setting of the trap dataset. (a) trap areas ordered from north (left) to south (right), (b) altitude, (c) mean annual tree PAR, (d) forest cover within 10 km radius, (e) annual precipitation, (f) temperature: MAT - Mean Annual Temperature, (g) temporal coverage of the PMP database.

Large differences in the pollen productivity between different trees effect this relationship. Adjusting the PAR from individual taxa by Andersen factors reduces the bias of differential pollen production between different plants and makes it possible to consider the total amount of pollen deposition including grasses. This adjustment increases the amount of variance explained by the regression model with all 4 explanatory variables to 56% (Table S4b). Due to the inclusion of grasses the explanatory

5   power of forest cover within 10 km is reduced, while latitude alone explains 37% of the Andersen adjusted log transformed total PAR (Fig. 3a, Table S4b).

The regression models consider the full range of the data, while due to local factors there is often a spread of average trap values for different traps in the same region. The traps with the highest regional values do not follow a latitudinal pattern, the distribution of the minimum average trap values are more informative (Fig. 3a). These lower values closely follow a latitudinal

10   trend. The average PAR south of 62° latitude and below the altitudinal treeline or close to forests are generally higher than 1000 grains cm^{-2} y^{-1}. An area with low PAR in the south is the coastal grassland in northern Bulgaria. The generally low PAR in this area can be explained by the sparse vegetation cover on thin rendzina soils formed on limestone rock. Adjusting the PAR values by Andersen factors increases the values for this region so that they fit the general latitudinal trend (Fig. 3a). Traps with minimum average PAR values per region also correspond well to the forest cover within 10 km (Fig. 3b). Considering 3%

15   wide bins of the forest cover, traps with the lowest PAR per each bin of the forest cover provide a regression model predicting a tree PAR of 3200 grains cm^{-2} year^{-1} at 80% forest cover within 10 km of the trap.

3.3   Long distance dispersed pollen

The comparison of PAR with the distribution limit of different tree taxa shows that PAR generally decline with distance (Fig. 4). A gradual decline is best documented for *Quercus* where average values at the distribution limit scatter around 100 grains

20   cm^{-2} y^{-1}. This analysis also documents the long-distance transport of many tree pollen, including the heavy pollen of *Picea*. For better comparison of the absolute values between taxa we used regression analysis to estimate the amount of pollen at 200 km from the distribution limit (Fig. 4b). This comparison indicates that less than 30 grains cm^{-2} y^{-1} of *Carpinus, Corylus, Fagus, Fraxinus, Quercus* and *Tilia* are deposited beyond 200 km of the distribution of the parent trees. Only *Picea* shows less than 1 grain cm^{-2} y^{-1} at 200 km of the distribution range.

25   ### 3.4   Ranges of modern and fossil PAR values

The here presented comparison of modern and fossil PAR values shows good agreement in tree PAR. The highest frequency of tree PAR values ranges between 2000 and 10000 grains cm^{-2} y^{-1} in both datasets (Fig. 5). Maximum PARs of the trap dataset are higher (often ten times) for all species compared to maximum PARs in the fossil dataset, with the exception of *Corylus*. The frequency distribution of PARs is log normal for *Alnus*, *Tilia* and *Fraxinus*. A bimodal distribution of values occurs for some

30   taxa, which is particularly clear for the fossil values of *Abies*, *Picea* and Poaceae. In the modern samples such a bimodality can be recognized for *Pinus* with a trough at around 1000 grains cm^{-2} y^{-1}. The frequency distribution of modern and fossil PARs corresponds best for *Corylus*, with most values falling between 100 - 300 grains cm^{-2} y^{-1} and recent and fossil maxima at around 3000 grains cm^{-2} y^{-1}. The greatest difference in the distribution of modern versus fossil PARs occurs for *Juniperus*,
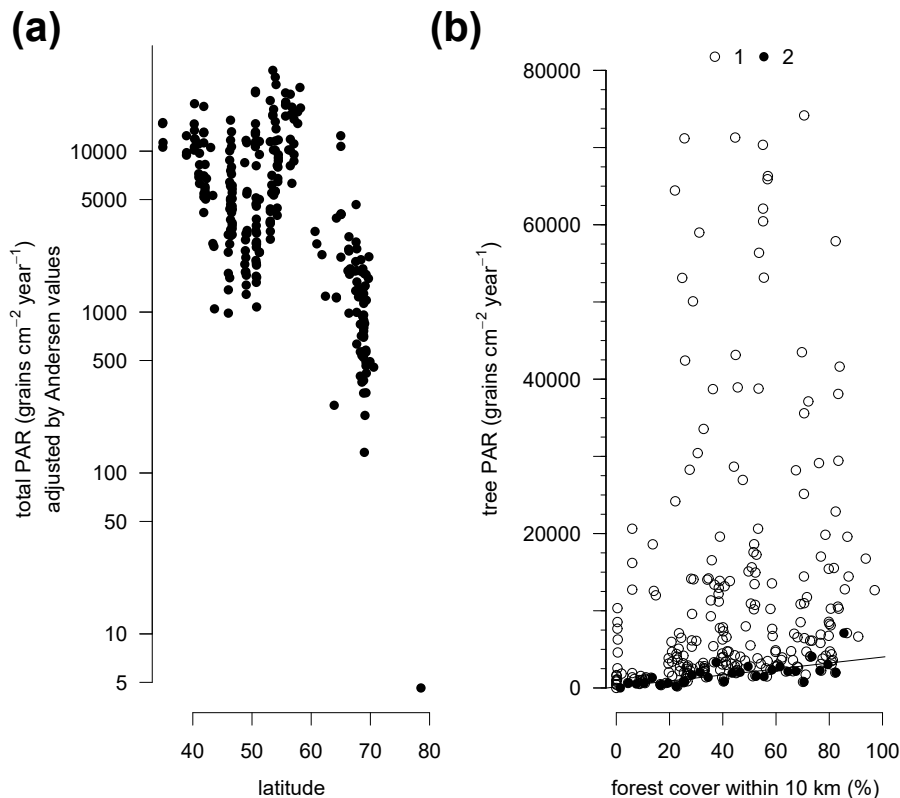
Figure 3. Latitudinal gradient in pollen accumulation rates of major tree taxa and Poaceae and Cyperaceae (total PAR) adjusted by Andersen values (see Tab S2) of pollen representation (a). Relationship between forest cover within 10 km radius and tree PAR (b). All trap sites (1) and minimum tree PAR per every 3 % of forest cover (2).

where maximum values are around a hundred times larger in the traps. Minimal PARs are about ten times higher in the traps for Poaceae and Cyperaceae in particular and the right side of the distribution is shifted upwards. For *Fagus, Quercus* and *Carpinus* the fossil PARs show a local maximum in the frequency of low values, which does not occur in the traps. These frequent low values range below the threshold indicating long distance transported pollen.

5   Using the 15 selected taxa in seven trap regions and the occurrence of the pollen types we obtained 92 pairs; of these 31 pairs are similar based on a t-test and a p-value > 0.05 (Fig. 5, Table S5). In this regional comparison *Betula* shows the best agreement between modern and fossil values. Values are similar in four regions across the gradient, with highest values of 5400 grains cm^{-2} y^{-1} in the lowland temperate region and the lowest values of 34 grains cm^{-2} y^{-1} in the temperate/Mediterranean region, where the parent trees are generally absent. Modern and fossil PARs generally correspond well for the lowland temperate region where,

10   in addition to *Betula*, *Alnus*, *Carpinus*, Cyperaceae, *Fraxinus*, *Picea*, *Pinus* and *Quercus* also have similar values. Although *Corylus* has a good overall agreement, the regions with similar modern to fossil data are shifted, with Holocene values in the boreal region corresponding to modern PARs in the lowland temperate region.
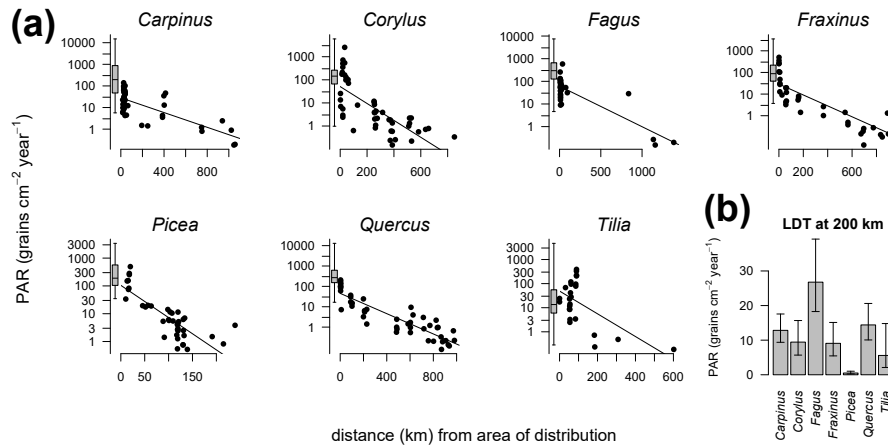
Figure 4. Relationship between the distance from the trap site to the nearest area of species distribution and PAR for selected trees. Zero distance represents edge of distribution area. Traps within the distribution area are aggregated in boxplots (a). PARs of the long-distance transport (b) calculated from linear regression at 200 km (Fig. 4a).

3.5 Taxa specific linkage of the highest average PAR at fossil sites with individual trap values

3.5.1 Introductory notes

To facilitate the comparison of modern and fossil PAR the combined taxa specific values were submitted to a one-dimensional cluster analysis, which resulted in between 5 and 9 classes of PAR values per taxon (Fig. S1-S2). Comparing the maximum averages of fossil PARs to modern trap data on a site by site basis shows that it is possible to find modern comparisons for all fossil situations. We demonstrate the linkage of the highest PAR clusters per each fossil site with individual trap records for the example of selected tree taxa (*Abies*, *Betula*, *Corylus*, *Fagus*, *Picea*, *Pinus*, *Quercus*, *Tilia*; Fig. 6). Detailed description of the remaining of taxa are presented in the supplementary (*Alnus*, *Carpinus*, Cyperaceae, *Fraxinus*, *Juniperus*, Poaceae, arboreal pollen; Fig. S3).

3.5.2 *Abies*

Modern PAR of 490-3900 grains cm^{-2} y^{-1} are observed in Roztocze, Jura, Rila and Timfristos. These values are produced by the different species: *Abies alba* in Roztocze and the Jura mountains and *A. cephalonica* in the Rila mountains and on Timfristos. Generally high fossil values occur in the two Alpine lakes Sägistalsee and Bachalpsee around 7000 years, in Ribno in the Rila mountains around 5000 years and in the two sites in Šumava between 4000 and 1000 years. In all these regions with fossil evidence of high *Abies* populations the modern PAR values in pollen traps are comparably low documenting that the populations have much declined. The *Abies alba* populations in Roztocze provide modern analogues for how dense *Abies* forests may have been in the Alps and Šumava although the forests in Roztocze occur at much lower elevations. Pollen traps on Timfristos mountain provide analogues of the density of Middle Holocene *Abies* forests in the Rila mountains. Pollen traps
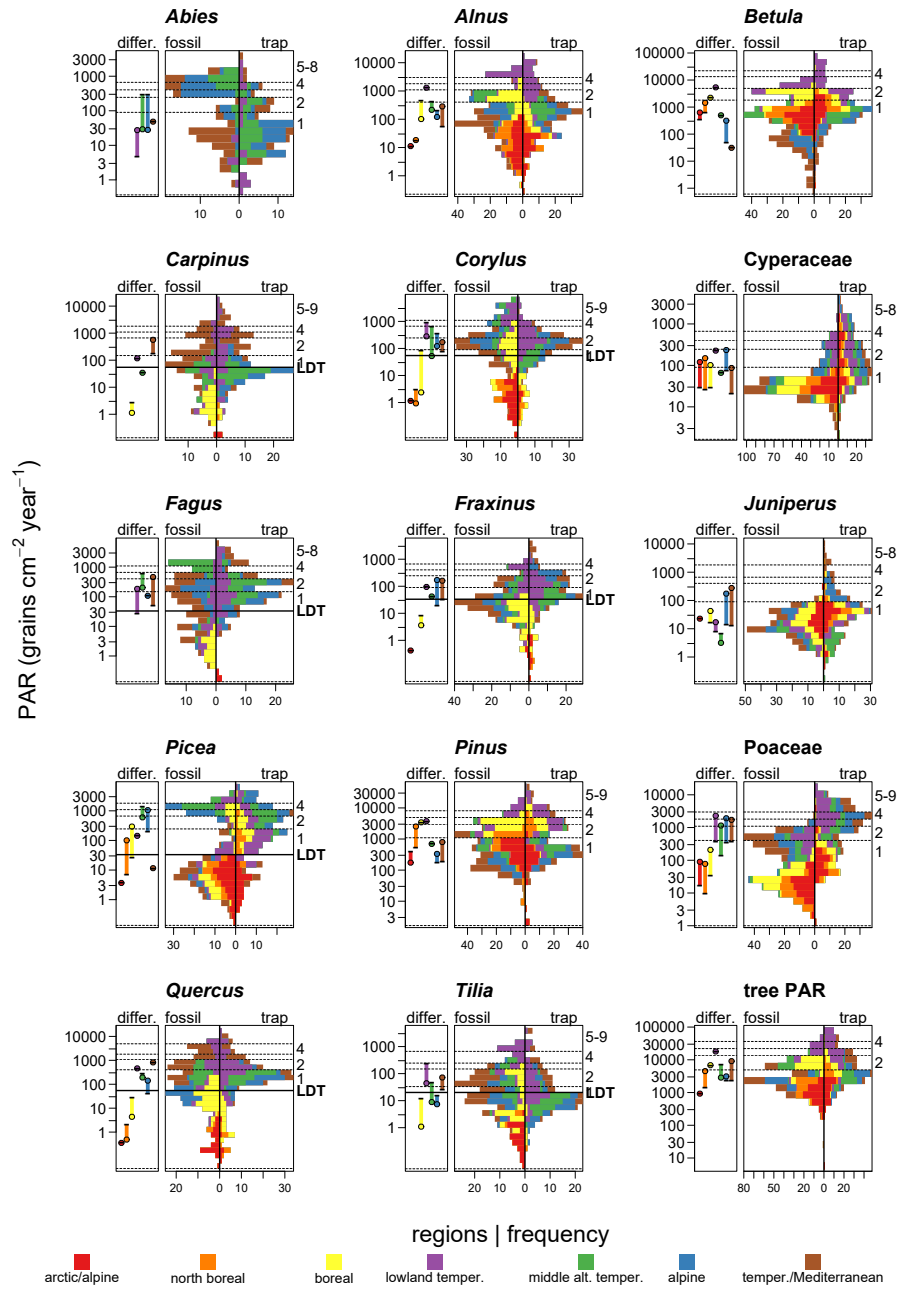
Figure 5. Difference (differ.) between the mean fossil (-) and the mean trap (o) PAR per trap region is shown by length of the vertical segment. Paired histograms of mean annual PAR from fossil record (on the left) and from traps (on the right). Colours denote different trap regions and correspond to Fig. 1. Note logged y-axis. Horizontal lines and numbering on the secondary y-axis denote classes of PAR, for more detail see Fig. 6b) and d). LDT is threshold for long distance transport.
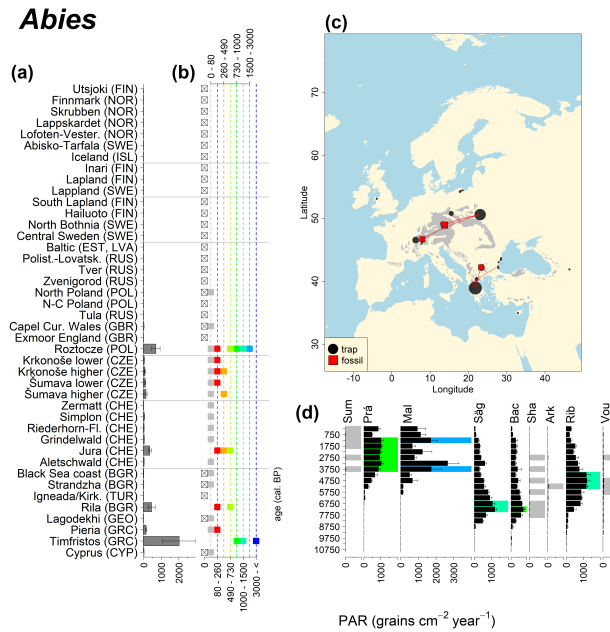
Figure 6. Mean modern PARs averaged for each trap area (a). b) Range of mean individual trap values classified by one-dimensional clustering. Crossed squares indicate that pollen of the taxon was not found in any trap from the area. c) Map of Europe with the distribution of the species (gray, Caudullo et al., 2017, San-Miguel-Ayanz et al. 2016) falling within the pollen taxa, size of symbols shows classes of PAR in recent and the highest PAR per each fossil record. Arrows show the closest trap with the same class of PAR. d) Fossil PAR values with the highest PAR class per each record (see Table 1 for full name) highlighted by the corresponding colour for the class (see b) Note the scale of the x-axis corresponds to the x-axis scale of graph a).

located far from the distribution limits of *Abies* in Wales, northern Poland, Georgia and Cyprus registered occasional *Abies* pollen grains with PARs of up to 80 grains cm^{-2} y^{-1}.

3.5.3 *Betula*

Letting aside traps from the Caucasus and Turkey, trap sites cover the distribution of *Betula pendula* and *B. pubescens*. The highest modern values between 11900-73900 grains cm^{-2} y^{-1} are found in Estonia and Russia as well as in one pollen trap from Hailuoto. These modern PARs exceed values from fossil examples. The highest fossil PAR of around 10000 grains cm^{-2} y^{-1} in this comparison come from northern Poland and Estonia and are thus consistent with the area of high modern values. Whether high abundance of *Betula* is a characteristic of the eastern European forests or a result of frequent disturbance at the forest ecotone or due to recent land-use change is difficult to evaluate based on the available data. Modern and fossil values agree for the sites in central Sweden at PARs between 1900-5600 grains cm^{-2} y^{-1}.
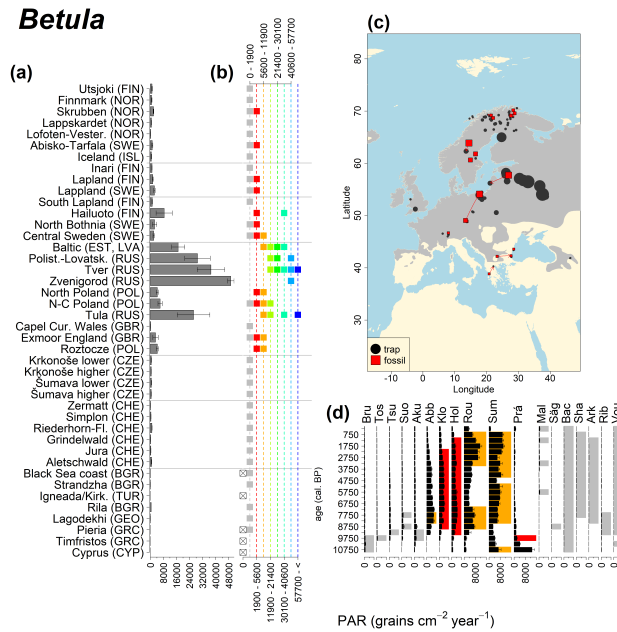
Figure 7. See caption Fig. 6

3.5.4 *Corylus*

Modern PARs stay below 2800 grains cm^{-2} y^{-1} except for two traps in north-central Poland. Values above 610 grains cm^{-2} y^{-1} are also found in pollen traps from the Baltic, Wales, Turkey and Georgia. The pollen type mainly comes from *Corylus avellana*, while *C. maxima* occurs in Greece, *C. colchica* in Georgia and *C. colurna* in Turkey and in plantations or as ornamental trees

5 in the rest of the Europe. As discussed in the main text, the selection of fossil sites did not include studies from western and lowland central Europe where values of 10000 grains cm^{-2} y^{-1} are common for the Early Holocene. The highest fossil PARs from the chosen examples were estimated for the Early Holocene from Prášilské situated at 1000 m a.s.l. Thus the high modern values in north-central Poland provide analogues for several fossil situations. Occasional grains and small PARs of *Corylus* pollen are common in traps from boreal regions as well as two traps from the arctic region.

10 ### 3.5.5 *Fagus*

PARs of more than 3300 grains cm^{-2} y^{-1} are found in pollen traps in Poland and Georgia and values above 2100 occur in traps from the Strandza, Šumava and Jura mountains, in southern Bulgaria, Czechia and Switzerland respectively. Two species of *Fagus* contribute to the pollen type with *Fagus sylvatica* as the dominant tree across much of Europe and *F. orientalis* occurring in southern Bulgaria, Turkey and Georgia. Fossil PAR increase around 8000 cal. BP at the Bulgarian Black Sea coast, around

15 7000 in the Šumava Mountains and 1500 years ago in northern Poland. High values in Šumava and northern Poland match the values in adjacent traps. Hardly any *Fagus* pollen occurs in pollen traps outside its modern distribution except sporadic
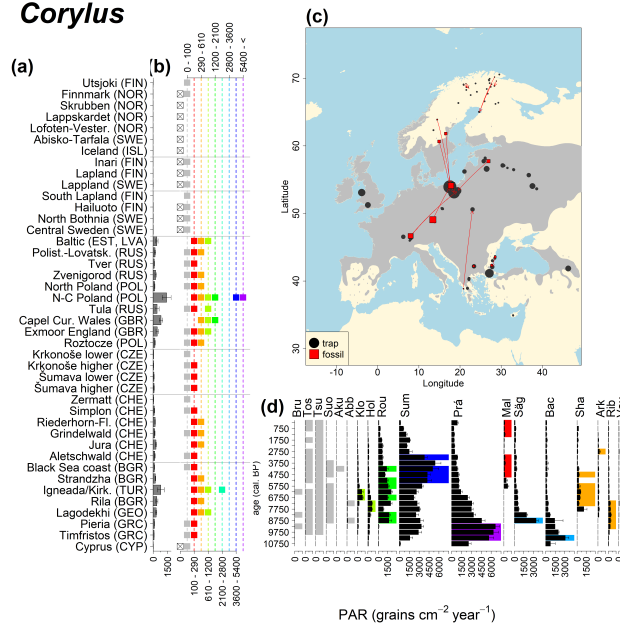
Figure 8. See caption Fig. 6

appearances in Tula and the two northernmost trap areas. However, *Fagus* pollen occurs regularly at fossil sites that were assumed to have never been within the distribution of the tree, such as the sites in central Sweden, where *Fagus* grains occurred regularly over the last 3000 years.

3.5.6 *Picea*

5 Modern *Picea* PARs above 2800 grains cm^{-2} y^{-1} are present in traps from Central Sweden, the Baltic region, Russia, Šumava mountains and the Alps. While some of the modern *Picea* pollen may be released by planted non-native *Picea sitchensis* and *P. pungens*, most of the pollen comes from Picea abies, which is also planted in many European regions outside its natural distribution. The highest fossil values in the selection of sites come from the Šumava mountains and are comparable to high trap values from the same region although at lower elevations. Noteworthy are also the generally low fossil *Picea* PARs for

10 sites in Central Sweden and Tver region, where the tree is dominating or co-dominating the forest for the last 2000 years. Most pollen traps from beyond the distribution area of *Picea* collect individual *Picea* pollen.

3.5.7 *Pinus*

Highest modern PARs exceeding 43600 grains cm^{-2} y^{-1} are observed in traps on Cyprus, while the values in traps from the northern boreal forest often stay below 5400 grains cm^{-2} y^{-1}. *Pinus* PAR values increase from Finnmark (2000 grains cm^{-2} y^{-1})

15 and central Sweden (5000 grains cm^{-2} y^{-1}) to the Baltic and north-central Poland with 35000 grains cm^{-2} y^{-1}. In northern Europe nearly all *Pinus* pollen comes from *P. sylvestris*, while southern European trapping sites have a higher diversity of trees within

Fagus

Figure 9. See caption Fig. 6

Picea

Figure 10. See caption Fig. 6
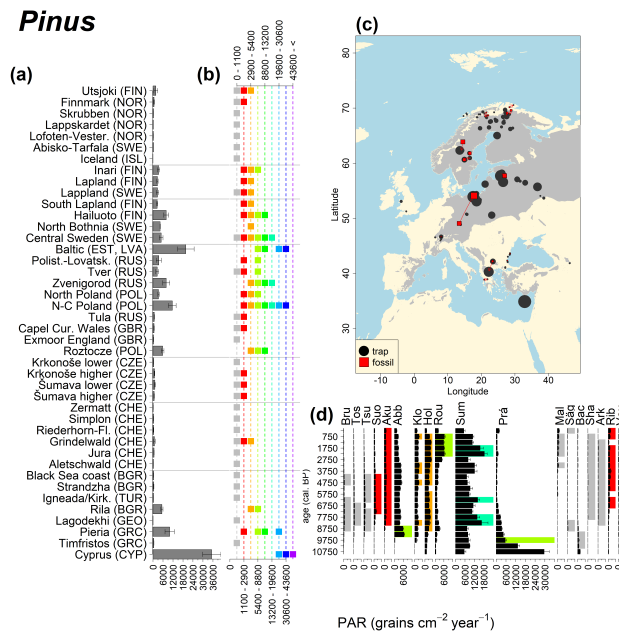
Figure 11. See caption Fig. 6

the subgenus Diploxylon including *P. mugo*, *P. nigra*, *P. brutia* and *P. halapensis*. Pollen of both Haploxylon pines *P. cembra* in Alps and *P. peuce* in Rila was separated. High fossil *Pinus* PAR values are estimated for Suminko in northern Poland, matching modern trap values from the same region. In the Šumava mountains *Pinus* was possibly the dominant forest tree during the Early Holocene and declined thereafter, so that modern values from north-central Poland provide the nearest analogue to the

5 Early Holocene situation. The lowest *Pinus* PARs (<125 grains cm^{-2} y^{-1}) are found in taps from Iceland (2-5 grains cm^{-2} y^{-1}), Lagodheki and most of the traps from Lofoten-Vesterålen (38-125 grains cm^{-2} y^{-1}) and single traps from Lappskardet, Exmoor England and Zermatt.

3.5.8   *Quercus*

Modern PARs of *Quercus* within the area of distribution of a parent tree in the genus range between 620-15000 grains cm^{-2}

10 y^{-1}. Highest modern values (6000-15000 grains cm^{-2} y^{-1}) are found in the traps from the UK, Poland and the southern Balkan. The first two areas host only species belonging to the *Q. robur*-type, whereas the two latter also include species from *Q. cerris*-type and *Q. ilex*-type. The highest fossil values from Suminko seem too high for the region compared to other fossil samples, nevertheless modern values in pollen traps from the region provide comparable high PARs. Also, PARs in recent sediments from some lakes in north-eastern Germany show similar values (Matthias and Giesecke, 2014). PARs to about 1300 grains cm^{-2}

15 y^{-1} are estimated for Rõuge Tõugjärv near the distribution limit of *Quercus robur* where the tree only became abundant after 7000 years ago. *Quercus robur* reached its maximum abundance even later in central Sweden where the PAR at Holtjärnen around 3200 years ago suggest its presence. The pollen seems to disperse well and is found in small amounts in most pollen
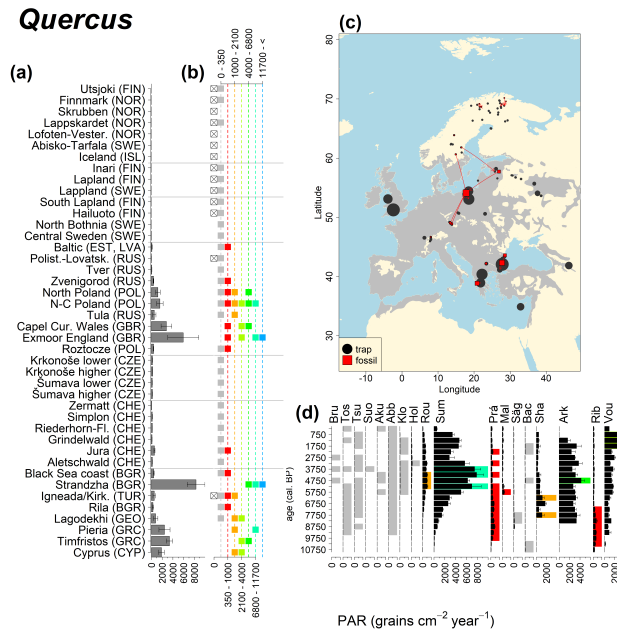
Figure 12. See caption Fig. 6

traps beyond its distribution area and fossils samples far to the north of the distribution have also collected *Quercus* pollen during the Holocene, which may be partly due to the abundance of trees of this genus in Europe.

3.5.9 *Tilia*

The highest modern PAR 1500-4700 grains cm^{-2} y^{-1} was measured in Poland, European Russia (Tula) and Lagodheki in Georgia, however, this high range has no comparison in the fossil record. Lower values 120-1500 grains cm^{-2} y^{-1} were found in traps from European Turkey and the Alps. Highest fossil PAR 270-1500 was measured in middle altitude and lowland temperate zone during the Middle Holocene. The closest trap analogues to them are in North Poland. Sites on the current edge of *Tilia* distribution and in the mountains (Central Sweden, Alps and Rila) show highest PAR range 120-270 grains cm^{-2} y^{-1}, also during the Middle Holocene. Trap records corresponding to the lowest class and above the LDT (5-40 grains cm^{-2} y^{-1}) appear in sites within distribution limit of *Tilia* (Baltic, European Russia, Poland), on its edge (Central Sweden, Wales, Black Sea Coast, Greece) or in the mountains (Šumava, Alps).
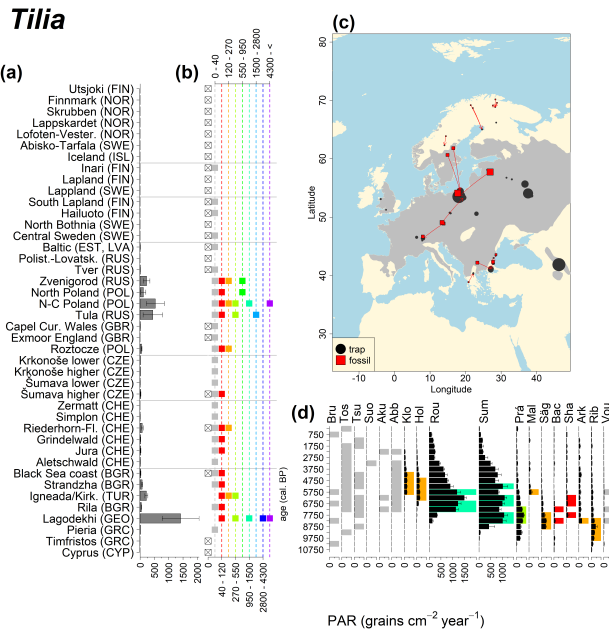
Figure 13. See caption Fig. 6

4 Discussion

4.1 Trap PARs and environmental conditions

This overview of European pollen trap data collected by the PMP network demonstrates that modern PARs provide comparable values to fossil records and can thus help interpreting the fossil signal in spite of different taphonomic processes that influence

5 PAR values in pollen traps versus lake sediments. The dataset extends across the European latitudinal and altitudinal range and documents general patterns. The latitudinal gradient in PAR is clearly visible in this dataset. Although data on plant biomass and primary productivity are not available for all trapping locations the regression analysis indicates that mean annual temperature has an influence on the quantity of pollen deposition. The July temperature of the previous year determines the amount of pollen production in *Pinus* near the tree-line (Autio and Hicks, 2004; McCarroll et al., 2003). Evidence from other European

10 regions (van der Knaap et al., 2010; Nielsen et al., 2010) suggests that also growing season warmth and other climate variables explain the interannual variability of pollen deposition. On the regional scale PAR corresponds to plant biomass of the parent tree (Matthias and Giesecke, 2014; Seppä et al., 2009). However, differences in forest cover cannot explain the latitudinal gradient in PAR described here, which may, at least in part, result from the latitudinal gradient in primary productivity of trees (Gillman et al., 2015). An increase in primary productivity and pollen production has been shown in a carbon dioxide

15 fertilization experiment (Wayne et al., 2002), which supports the interpretation that PAR of the same species may vary due to environmental parameters determining its productivity.

4.2 Long Distance Transport

Modern PARs from traps near the latitudinal limit of *Pinus* and *Betula* have been used previously to reconstruct past changes in the northern distribution limits of these trees (Seppä and Hicks, 2006). Here we evaluated larger distances and therefore had to ignore *Pinus* and *Betula*, while suggesting some general thresholds for other dominant European trees. The upper value of around 30 grains cm^{-2} y^{-1} for *Picea* agrees well with the fossil PAR value for the tree of 50 *Picea* grains cm^{-2} y^{-1} found in a sample at Klotjärnen just after the occurrence of the first *Picea* bud scale (Giesecke, 2005b). However, these modern thresholds estimated here are likely to depend on the abundance of the parent tree in the larger region rather than properties of the pollen types. A larger threshold would be expected for *Corylus* compared to *Fagus*, based on the fall speed of pollen. However, *Corylus* is not very abundant near its northern limit in these more continental areas, while *Fagus* often dominates forests near its presumed limits. Similarly, the occurrences of taxa outside the mapped natural distribution can bias this estimate.

Characteristic radius is a useful measure showing pollen transport predicted by pollen dispersal models. It represents theoretical proportion of pollen loading at different distances from the source plants (Prentice, 1988) and thus can be easily compared with our empirical values. PAR of *Carpinus*, *Corylus*, *Fraxinus* and *Quercus* at 200 km from the distribution area represent 5-10 % of the median PAR within the distribution area (Fig. 4). Considering the range of standard terminal velocities of those taxa and Gaussian Plume model with wind speed 3 m.s^{-1} (Abraham et al., 2014), we get 2-13% of pollen loading at the characteristic radius 200 km (Table S6).

4.3 Analogues for vegetation reconstruction

While the dataset of modern PARs presented here provides analogues for the selection of fossil sites, reliable fossil PAR records were not available from the trapping locations in the UK. Moreover, no sites with fossil PAR from western Europe or from low elevations in the Alps are included in this comparison. Consequently, the large quantities of *Corylus* pollen deposited in many west European sites during the early Holocene was not considered. There are limited modern analogues forthe highest early Holocene values of around 7000 *Corylus* grains cm^{-2} y^{-1} at Prášilské. Average Early Holocene *Corylus* PAR at Soppensee in northern Switzerland are 12000 grains cm^{-2} y^{-1} (Lotter, 1999) and at Meerfelder Maar (Kubitz, 2000) in western Germany 18000 grains cm^{-2} y^{-1}. Judging from pollen percentages even higher Early Holocene values should be found in more oceanic situations and the *Corylus* PAR at Hockham Mere in eastern England may be as high as 40000 grains cm^{-2} y^{-1} for the early Holocene (Bennett, 1983). Modern values in pollen traps from Wales at around 2000 grains cm^{-2} y^{-1} are far below these early Holocene figures and it is likely that modern analogues of sites with high *Corylus* PARs no longer exist in Europe.

Conversely, the high modern PAR values for *Pinus* and *Betula* from Poland and Latvia are not found in the fossil examples. *Pinus* PAR values around 30000 grains cm^{-2} y^{-1} were also obtained from [210] Pb dated modern lake sediment samples in north eastern Brandenburg (Matthias and Giesecke, 2014). This study evaluated the PARs for the years 1993 and 2009. The increase in *Pinus* PAR values between the first and the second sampling period corresponded with an increase in the amount of standing pine volume in the region. Forestry practices aimed at increasing yield could account for the high *Pinus* values. *Pinus* was extensively planted after the 1950s, even on soils where trees with a lower pollen production would have grown

naturally. The fertilization due to increased nitrogen deposition, as well as increased atmospheric carbon dioxide, increase the pollen production not only of *Pinus*. A carbon dioxide enrichment experiment of 19-year old *Pinus taeda* resulted in a twofold probability of reproductive maturity after 3 years (LaDeau and Clark, 2001). The continued experiment also showed that carbon dioxide fertilization increased the number of pollen cones and therefore pollen grains produced per tree (LaDeau and Clark, 2006).

In the case of *Pinus*, the modern dataset includes trap data from Cyprus, where *Pinus brutia* dominates at 1600 m a.s.l., resulting in even higher *Pinus* PAR values compared to those found in the Polish and Baltic regions. The highest *Betula* values come mainly from Russia, where values frequently exceed 30000 grains cm^{-2} y^{-1}. We previously discussed such high fossil PAR values for *Corylus*, which is assumed to produce a similar amount of pollen. However, fossil *Betula* PARs in the examples considered here are consistently below 6000 grains cm^{-2} y^{-1} and published early Holocene values rarely exceed 6000 grains cm^{-2} y^{-1} (but see Theuerkauf et al., 2014). Pollen diagrams from the forest steppe ecotone in European Russia are often characterized by high *Betula* percentage (Nosova et al., 2019; Shumilovskikh et al., 2018). However, there are no suitable diagrams with reliable PAR estimates from that region. It is thus difficult to judge whether high modern trap values are associated with recent land-use change or are characteristic of eastern European forests.

The comparison of regional PARs between traps and fossil estimates indicates higher fossil PAR of *Picea*, *Fagus* and *Abies* in middle altitudes of the temperate zone (Fig. 5), which, in the case of *Abies*, represents the Europe-wide decline in *A. alba* (Tinner et al., 2013). *Picea* and *Fagus* dominate central European forests today and *Picea* is planted much beyond its natural range. However, both trees start flowering rather late in their lives and harvesting the trees at a young age may contribute to lower modern PAR values. Fossil and modern PARs for these trees in Šumava are similar, while only the highest trap values match the Holocene high values. On average there are lower modern PAR values; this may be explained by a lowering of the treeline over the last millennia. This interpretation agrees with REVEALS reconstructions for this region, indicating a decline in the cover abundance of *Picea* and *Fagus* (Abraham et al., 2016; Carter et al., 2018). Within a 60 km radius of the fossil sites *Picea* decreased in abundance from 70% during the Middle Holocene to 43%, compared to modern abundance. *Fagus* and *Abies* declined from Late Holocene values of 22% and 3% to currently 20% to 1% respectively (Abraham et al., 2016). The abundance of *Abies* in the Roztocze region (SE Poland; Fig. 6) provides a good analogue for the past abundance of the tree in Šumava with maximum PAR of 1000-3000 grains cm^{-2} y^{-1}. *Abies* disappeared from the Czech Republic during the Mediaeval Age due to forest management methods (Kozáková et al., 2011), which were not practiced in SE Poland.

Linking the fossil to modern PAR values facilitates interpretation of the fossil record of individual sites. Unfortunately, the details cannot be discussed here. However, the central Swedish sites Holtjärnen and Klotjärnen provide excellent examples. These sites are situated north of the modern distribution of *Tilia*, *Corylus*, *Quercus* and near the limit of *Alnus glutinosa*. The fossil PAR values are higher for these taxa than those found in pollen traps at or near these lakes (Giesecke, 2005a; Giesecke and Fontana, 2008). Modern reference values for the PARs of these taxa can be found in northern Poland and Estonia. Moreover, this analogue matching indicates that 3000 years ago the PAR values for *Quercus* at Holtjärnen were sufficiently high to indicate the occurrence of small populations near the lake. Those taxa at both sites also nicely illustrate the potential use of

LDT for the interpretation of the fossil record. Fossil PAR values of *Tilia*, *Corylus* and *Quercus* in boreal region result above LDT threshold, whereas all trap PAR values are below (Fig. 5).

4.4 Limitations and problems

There are significant differences between the accumulation of pollen in traps and on peatlands and lakes (Lisitsyna et al., 2011; Pardoe et al., 2010). Differences in pollen trap design and placement in the landscape will influence the values. Trap values are also affected by modern processes that have no impact on the fossil signal. These biases appear minor as indicated by the large consistency of the data collected in the PMP database. Also the comparison of values over this large environmental gradient result in the signal being stringer than the noise. Nevertheless, some traps or individual years have unusual values and were removed from the comparison (Table S1). Despite this, the uncertainty of fossil PAR values is much greater than pollen traps, which is primarily due to the added uncertainty coming from sampling a sediment core, combined with the uncertainty of the age model (Maher, 1981). PAR from lake sediments has additional biases due to differential sedimentation of pollen grains in lakes (Davis and Brubaker, 1973), sediment re-deposition, focussing and catchment erosion (Davis et al., 1984; Pennington, 1979). Although we carefully selected the best available fossil sites, PARs especially from lake Suminko and Rõuge Tõugjärv may be biased by lake internal processes and the addition of stream borne pollen respectively. Nevertheless, their fossil PAR estimates are in the range of values found in pollen traps. Where detailed knowledge on the sedimentation process is available the bias of sediment focussing may be reduced as in the example of Hockham Mere cited above (see also Bennett and Buck, 2016; Bennett, 1983). Peatlands may thus seem the better choice for obtaining fossil PAR, which may be the case in northern Scandinavia (Barnekow et al., 2007; Finsinger et al., 2013), but frequent changes in the rate of peat growth lead to difficulties assessing the time represented in individual samples at many sites.

The problem of traps collecting high amounts of herbaceous pollen brought by insects and small animals was discussed in the method section and for this reason only Poaceae and Cyperaceae are the only herbs selected for our analyses. However, pollen from these two families is also often overrepresented in the pollen traps (Lisitsyna et al., 2011), as the plants may overhang the trap opening and their pollen may fall directly into the trap. Reduced PARs in the trap may be caused by overgrowth of the vegetation or leaves temporally blocking the opening, while proximity to the forest edge would increase values compared to large open peatlands or lakes. These effects have not been systematically evaluated so far.

Detailed comparisons of vegetation data to PARs hold potential for a better understanding of the spatial representation and processes shaping the pollen signal (Matthias and Giesecke, 2014) and allow estimates of absolute pollen productivity (Sugita et al., 2009) or test pollen dispersal models. However, for this continental scale dataset available vegetation data have limited precision. Forest inventory data with the detail essential for this type of study is not available for all traps. The forest cover data presented here has a resolution of 1 km^2, which is insufficient as the abundance of trees within hundreds of meters of the traps is important. Moreover, without information on standing volume or age structure, the percentage cover used here is a crude measure of the vegetation producing the pollen. Forestry practices like harvesting trees that start flowering at a later age (e.g. *Picea* 30-40 years) reduce the number of trees producing pollen (Matthias et al., 2012) and bias the search for modern

analogues. Also, the available mapped distribution limits of trees have large uncertainties precluding more detailed assessments of the quantity of long distance transported pollen using this continental dataset.

5 Conclusions

Comparison of the mean annual PAR from traps and fossil sites showed similar ranges for *Abies*, *Alnus*, *Betula*, *Carpinus*,
5 *Corylus*, *Fagus*, *Fraxinus*, *Picea*, *Pinus, Quercus* and *Tilia* at the continental scale. This indicates that there are no major biases hampering the application of the PMP Database data as a modern reference to interpret the fossil record. The dataset clearly shows that climate parameters that correlate with latitude determine pollen productivity. The effect of regional forest cover is discernible. Minimum values suggest that an 80% forest cover within 10 km of the trap results in PARs above 3200 tree pollen grains cm^{-2} year^{-1}.

10 Assessment of long-distance transport indicates that values below 30 grains cm^{-2} y^{-1} for *Carpinus*, *Corylus*, *Fagus*, *Fraxinus*, *Picea*, *Quercus* and *Tilia* may originate from beyond 200 km of a sampling site. This number of 30 grains cm^{-2} y^{-1} may therefore be used as a general threshold indicating long distance origin of pollen. The application of these threshold values holds potential to refine and adjust reconstructions of tree distributions.

Code availability. Primary trap and fossil pollen data are availible in Neotoma Palaeoecology Database https://www.neotomadb.org/. Anal-
15 ysis are based on the WorldClim 2 dataset of Fick and Hijmans (2017), Chorological data for the main European woody species, version 2 by Caudullo et al. (2018), European atlas of forest tree species, 2016th ed. by San-Miguel-Ayanz et al. (2016), which are availible online: http://worldclim.org/version2 , https://data.mendeley.com/datasets/hr5h2hcgg4/2 and http://www.euforgen.org/, respectively. Forest Map of Europe of Kempeneers et al. (2012) is availible on request on authors.
Code for analysis, derived data and code for figures are available in the https://github.com/vojtechabraham/PMPdatabase.

20 *Author contributions.* Design of the analysis: TG and VA. Data analysis: VA, TG and MW. Manuscript draft: VA and TG. Manuscript comments: HP, SH, CEJ, HSS, HS, SV, SH, MN, MW, SP, ST, TK, AMN and JŚM. Data collection: all authors except VA and MW.

Competing interests. The authors declare no competing interests.

Acknowledgements. We thank to all collaborators of pollen trapping, especially to those who contributed to the PMP dataset: Pim van der Knaap, Jacqueline van Leeuwen, Karl-Dag Vorren, Heather Tinsley, Lena Barnekow, Małgorzata Latałowa, Enikő Magyari, Larissa
25 Savelieva, Elena Pavlova, Heidi Hyyppä, Mari Kuoppamaa and Gunhild Rosqvist.

References

Abraham, V., Oušková, V., and Kuneš, P.: Present-Day Vegetation Helps Quantifying Past Land Cover in Selected Regions of the Czech Republic, PLoS ONE, 9, e100 117, https://doi.org/10.1371/journal.pone.0100117, http://dx.plos.org/10.1371/journal.pone.0100117, 2014.

Abraham, V., Kuneš, P., Petr, L., Svitavská-Svobodová, H., Kozáková, R., Jamrichová, E., Švarcová, M. G., and Pokorný, P.: A pollen-based
5   quantitative reconstruction of the Holocene vegetation updates a perspective on the natural vegetation in the Czech Republic and Slovakia, Preslia, 88, 409–434, 2016.

Andersen, S.: The relative pollen productivity and representation of north European trees, and correction factors for tree pollen spectra., Danmarks Geologiske Undersøgelse Række II, 96, 1–99, 1970.

Andersen, S. T.: Influence of Climatic Variation on Pollen Season Severity in Wind-Pollinated Trees and Herbs, Grana, 19, 47–52,
10   https://doi.org/10.1080/00173138009424986, 1980.

Autio, J. and Hicks, S.: Annual variations in pollen deposition and meteorological conditions on the fell Aakenustunturi in northern Finland: Potential for using fossil pollen as a climate proxy, Grana, 43, 31–47, https://doi.org/10.1080/00173130310017409, 2004.

Barnekow, L., Loader, N. J., Hicks, S., Froyd, C. A., and Goslar, T.: Strong correlation between summer temperature and pollen accumulation rates for Pinus sylvestris, Picea abies and Betula spp. in a high-resolution record from northern Sweden, J. Quaternary Sci., 22, 653–658,
15   https://doi.org/10.1002/jqs.1096, 2007.

Bennett, K. and Buck, C. E.: Interpretation of lake sediment accumulation rates, Holocene, 26, 1092–1102, https://doi.org/10.1177/0959683616632880, 2016.

Bennett, K. D.: Devensian Late-Glacial and Flandrian Vegetational History at Hockham Mere, Norfolk, England, New Phytol., 95, 489–504, https://doi.org/10.1111/j.1469-8137.1983.tb03513.x, 1983.

20 Bozilova, E. and Beug, H.-J.: On the Holocene history of vegetation in SE Bulgaria (Lake Arkutino, Ropotamo region), Veg. Hist. Archaebot., 1, 19–32, https://doi.org/10.1007/BF00190698, 1992.

Carter, V. A., Chiverrell, R. C., Clear, J. L., Kuosmanen, N., Moravcová, A., Svoboda, M., Svobodová-Svitavská, H., Leeuwen, V., N, J. F., Knaap, V. D., O, W., and Kuneš, P.: Quantitative Palynology Informing Conservation Ecology in the Bohemian/Bavarian Forests of Central Europe, Front. Plant Sci., 8, https://doi.org/10.3389/fpls.2017.02268, 2018.

25 Caudullo, G., Welk, E., and San-Miguel-Ayanz, J.: Chorological maps for the main European woody species, Data in Brief, 12, 662–666, https://doi.org/10.1016/j.dib.2017.05.007, http://www.sciencedirect.com/science/article/pii/S2352340917301981, 2017.

Davis, B. A. S., Zanon, M., Collins, P., Mauri, A., Bakker, J., Barboni, D., Barthelmes, A., Beaudouin, C., Bjune, A. E., Bozilova, E., Bradshaw, R. H. W., Brayshay, B. A., Brewer, S., Brugiapaglia, E., Bunting, J., Connor, S. E., de Beaulieu, J.-L., Edwards, K., Ejarque, A., Fall, P., Florenzano, A., Fyfe, R., Galop, D., Giardini, M., Giesecke, T., Grant, M. J., Guiot, J., Jahns, S., Jankovská, V., Juggins, S.,
30   Kahrmann, M., Karpińska-Kołaczek, M., Kołaczek, P., Kühl, N., Kuneš, P., Lapteva, E. G., Leroy, S. A. G., Leydet, M., Guiot, J., Jahns, S., Jankovská, V., Juggins, S., Kahrmann, M., Karpińska-Kołaczek, M., Kołaczek, P., Kühl, N., Kuneš, P., Lapteva, E. G., Leroy, S. A. G., Leydet, M., López Sáez, J. A., Masi, A., Matthias, I., Mazier, F., Meltsov, V., Mercuri, A. M., Miras, Y., Mitchell, F. J. G., Morris, J. L., Naughton, F., Nielsen, A. B., Novenko, E., Odgaard, B., Ortu, E., Overballe-Petersen, M. V., Pardoe, H. S., Peglar, S. M., Pidek, I. A., Sadori, L., Seppä, H., Severova, E., Shaw, H., Święta Musznicka, J., Theuerkauf, M., Tonkov, S., Veski, S., van der Knaap, W. O., van
35   Leeuwen, J. F. N., Woodbridge, J., Zimny, M., and Kaplan, J. O.: The European Modern Pollen Database (EMPD) project, Veg. Hist. Archaebot., 22, 521–530, https://doi.org/10.1007/s00334-012-0388-5, 2013.

Davis, M. B.: Palynology after Y2K–Understanding the Source Area of Pollen in Sediments., Annual Review of Earth & Planetary Sciences, 28, 1, https://doi.org/Article, 2000.

Davis, M. B. and Brubaker, L. B.: Differential Sedimentation of Pollen Grains in Lakes, Limnol. Oceanogr., 18, 635–646, https://doi.org/10.4319/lo.1973.18.4.0635, 1973.

5   Davis, M. B. and Deevey, E. S.: Pollen Accumulation Rates: Estimates from Late-Glacial Sediment of Rogers Lake, Science, 145, 1293–1295, https://doi.org/10.1126/science.145.3638.1293, 1964.

Davis, M. B., Moeller, R., and Ford, J.: Sediment focusing and pollen influx, in: Lake sediments and environmental history: studies in palaeolimnology and palaeoecology in honour of Winifred Tutin, edited by Haworth, E. Y., Lund, J. W. G., and Tutin, W., pp. 261–293, Leicester University Press, 1984.

10   Fick, S. E. and Hijmans, R. J.: WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas, Int. J. Climatol., 37, 4302–4315, https://doi.org/10.1002/joc.5086, 2017.

Filipova-Marinova, M.: Palaeoecological investigations of lake Shabla-Ezeretz in NE Bulgaria, Ecologia Mediterranea, 11, 147–158, 1985.

Finsinger, W., Schoning, K., Hicks, S., Lücke, A., Goslar, T., Wagner-Cremer, F., and Hyyppä, H.: Climate change during the past 1000 years: a high-temporal-resolution multiproxy record from a mire in northern Finland, J. Quaternary Sci., 28, 152–164,
15   https://doi.org/10.1002/jqs.2598, 2013.

Gaillard, M.-J., Sugita, S., Bunting, M. J., Middleton, R., Broström, A., Caseldine, C., Giesecke, T., Hellman, S. E. V., Hicks, S., Hjelle, K., Langdon, C., Nielsen, A.-B., Poska, A., Stedingk, H., Veski, S., and members, P.: The use of modelling and simulation approach in reconstructing past landscapes from fossil pollen data: a review and results from the POLLANDCAL network, Veget Hist Archaeobot, 17, 419–443, https://doi.org/10.1007/s00334-008-0169-3, http://www.springerlink.com/content/1tpg426573513vqg/, 2008.

20   Gerasimidis, A., Panajiotidis, S., Hicks, S., and Athanasiadis, N.: An eight-year record of pollen deposition in the Pieria mountains (N. Greece) and its significance for interpreting fossil pollen assemblages, Rev. Palaeobot. Palyno., 141, 231–243, https://doi.org/10.1016/j.revpalbo.2006.04.004, 2006.

Giesecke, T.: Holocene dynamics of the southern boreal forest in Sweden, Holocene, 15, 858–872, https://doi.org/10.1191/0959683605hl859ra, 2005a.

25   Giesecke, T.: Moving front or population expansion: How did Picea abies (L.) Karst. become frequent in central Sweden?, Quaternary Sci. Rev., 24, 2495–2509, https://doi.org/10.1016/j.quascirev.2005.03.002, 2005b.

Giesecke, T.: Holocene forest development in the central Scandes Mountains, Sweden, Veg. Hist. Archaebot., 14, 133–147, https://doi.org/10.1007/s00334-005-0070-2, 2005c.

Giesecke, T. and Fontana, S. L.: Revisiting pollen accumulation rates from Swedish lake sediments, Holocene, 18, 293–305,
30   https://doi.org/10.1177/0959683607086767, 2008.

Giesecke, T., Fontana, S. L., Knaap, W. O., Pardoe, H. S., and Pidek, I. A.: From early pollen trapping experiments to the Pollen Monitoring Programme, Veg. Hist. Archaebot., 19, 247–258, https://doi.org/10.1007/s00334-010-0261-3, 2010.

Giesecke, T., Wolters, S., Leeuwen, J. F. N. v., Knaap, P. W. O. v. d., Leydet, M., and Brewer, S.: Postglacial change of the floristic diversity gradient in Europe, Nat. Commun., 10, 1–7, https://doi.org/10.1038/s41467-019-13233-y, 2019.

35   Gillman, L. N., Wright, S. D., Cusens, J., McBride, P. D., Malhi, Y., and Whittaker, R. J.: Latitude, productivity and species richness, Global Ecol. and Biogeogr., 24, 107–117, https://doi.org/10.1111/geb.12245, 2015.

GRASS Development Team: Geographic Resources Analysis Support System (GRASS GIS) Software, Open Source Geospatial Foundation, 2018.

Haselhorst, D. S., Moreno, J. E., and Punyasena, S. W.: Assessing the influence of vegetation structure and phenological variability on pollen-vegetation relationships using a 15-year Neotropical pollen rain record, Journal of Vegetation Science, 31, 606–615, https://doi.org/https://doi.org/10.1111/jvs.12897, https://onlinelibrary.wiley.com/doi/abs/10.1111/jvs.12897, _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/jvs.12897, 2020.

5 Hesselman, H.: Om pollenregn på hafvet och fjärrtransport af barrträdspollen., Geologiska Föreningens i Stockholm Förhandlingar, 41, 89–99, 1919.

Hicks, S.: A method of using modern pollen rain values to provide a timescale for pollen diagrams from peat deposits, Memorana Societas Fauna Flora Fennica, 49, 21–33, 1974.

Hicks, S.: Present and past pollen records of Lapland forests, Rev. Palaeobot. Palyno., 82, 17–35, https://doi.org/10.1016/0034-
10 6667(94)90017-5, 1994.

Hicks, S.: The relationship between climate and annual pollen deposition at northern tree-lines, Chemosphere - Global Change Science, 1, 403–416, https://doi.org/10.1016/S1465-9972(99)00043-4, http://www.sciencedirect.com/science/article/pii/S1465997299000434, 00034, 1999.

Hicks, S. and Hyvärinen, H.: Pollen influx values measured in different sedimentary environments and their palaeoecological implications,
15 Grana, 38, 228–242, https://doi.org/10.1080/001731300750044618, 1999.

Hicks, S., Ammann, B., Latałowa, M., Pardoe, H. S., and Tinsley, H.: European Pollen Monitoring Programme: Project Description and Guidelines, Oulu University Press, 1996.

Hicks, S., Tinsley, H., Pardoe, H. S., and Cundill, P. R.: European Pollen Monitoring Programme: Supplement to the Guidelines, Oulu University Press, 1999.

20 Hicks, S., Tinsley, H., Huusko, A., Jensen, C., Hättestrand, M., Gerasimides, A., and Kvavadze, E.: Some comments on spatial variation in arboreal pollen deposition: first records from the Pollen Monitoring Programme (PMP), Rev. Palaeobot. Palyno., 117, 183–194, https://doi.org/10.1016/S0034-6667(01)00086-0, 2001.

Hättestrand, M., Jensen, C., Hallsdóttir, M., and Vorren, K.-D.: Modern pollen accumulation rates at the north-western fringe of the European boreal forest, Rev. Palaeobot. Palyno., 151, 90–109, https://doi.org/10.1016/j.revpalbo.2008.03.001, 2008.

25 Hyvärinen, H.: Absolute and relative pollen diagrams from northernmost Fennoscandia, Fennia - International Journal of Geography, 142, 1975.

Jackson, S. T. and Williams, J. W.: Modern analogs in Quaternary paleoecology: Here Today, Gone Yesterday, Gone Tomorrow?, Annu. Rev. Earth Pl. Sc., 32, 495–537, https://doi.org/10.1146/annurev.earth.32.101802.120435, 2004.

Jahns, S.: The Holocene history of vegetation and settlement at the coastal site of Lake Voulkaria in Acarnania, western Greece, Veg. Hist.
30 Archaebot., 14, 55–66, https://doi.org/10.1007/s00334-004-0053-8, 2004.

Jantz, N., Homeier, J., León-Yánez, S., Moscoso, A., and Behling, H.: Trapping pollen in the tropics — Comparing modern pollen rain spectra of different pollen traps and surface samples across Andean vegetation zones, Rev. Palaeobot. Palyno., 193, 57–69, https://doi.org/10.1016/j.revpalbo.2013.01.011, 2013.

Jensen, C., Vorren, K.-D., and Mørkved, B.: Annual pollen accumulation rate (PAR) at the boreal and alpine forest-line of
35 north-western Norway, with special emphasis on Pinus sylvestris and Betula pubescens, Rev. Palaeobot. Palyno., 144, 337–361, https://doi.org/10.1016/j.revpalbo.2006.08.006, 2007.

Kempeneers, P., Sedano, F., Seebach, L. M., Strobl, P., and San-Miguel-Ayanz, J.: Data Fusion of Different Spatial Resolution Remote Sensing Images Applied to Forest-Type Mapping, IEEE T. Geosci. Remote, 49, 4977 – 4986, https://doi.org/10.1109/TGRS.2011.2158548, 2012.

Koff, T.: Pollen influx into Tauber traps in Estonia in 1997–1998, Rev. Palaeobot. Palyno., 117, 53–62, https://doi.org/10.1016/S0034-6667(01)00076-8, 2001.

Kozáková, R., Šamonil, P., Kuneš, P., Novák, J., Kočár, P., and Kočárová, R.: Contrasting local and regional Holocene histories of Abies alba in the Czech Republic in relation to human impact: Evidence from forestry, pollen and anthracological data, Holocene, 21, 431–444, https://doi.org/10.1177/0959683610385721, 2011.

Kubitz, B.: Die holozäne Vegetations- und Siedlungsgeschichte in der Westeifel am Beispiel eines hochauflösenden Pollendiagrammes aus dem Meerfelder Maar [History of Holocene vegetation and settlement of the Western Eifel region (Germany) using a high resolution pollenprofile from the Meerfeld Maar], no. 339 in Dissertationes botanicae, Borntraeger, 2000.

Kvavadze, E.: Annual modern pollen deposition in the foothills of the Lagodekhi Reservation (Caucasus, East Georgia), related to vegetation and climate, Acta Palaeobotanica, 41, 355–364, 2001.

LaDeau, S. L. and Clark, J. S.: Rising CO2 Levels and the Fecundity of Forest Trees, Science, 292, 95–98, https://doi.org/10.1126/science.1057547, 2001.

LaDeau, S. L. and Clark, J. S.: Pollen production by Pinus taeda growing in elevated atmospheric CO2, Funct. Ecol., 20, 541–547, https://doi.org/10.1111/j.1365-2435.2006.01133.x, 2006.

Lisitsyna, O. V., Hicks, S., and Huusko, A.: Do moss samples, pollen traps and modern lake sediments all collect pollen in the same way? A comparison from the forest limit area of northernmost Europe, Veg. Hist. Archaebot., 21, 187–199, https://doi.org/10.1007/s00334-011-0335-x, 2011.

Lotter, A. F.: Late-glacial and Holocene vegetation history and dynamics as shown by pollen and plant macrofossil analyses in annually laminated sediments from Soppensee, central Switzerland, Veg. Hist. Archaebot., 8, 165–184, https://doi.org/10.1007/BF02342718, 1999.

Maher, L. J.: Statistics for microfossil concentration measurements employing samples spiked with marker grains, Rev. Palaeobot. Palyno., 32, 153–191, https://doi.org/10.1016/0034-6667(81)90002-6, 1981.

Malmström, C.: Degerö Stormyr—en botanisk, hydrologisk och utvecklingshistorisk undersökning över ett nordsvenskt myrkomplex., Meddelanden från Statens Skogsförsöksanstalt, 20, 1–2, 1923.

Matthias, I. and Giesecke, T.: Insights into pollen source area, transport and deposition from modern pollen accumulation rates in lake sediments, Quaternary Sci. Rev., 87, 12–23, https://doi.org/10.1016/j.quascirev.2013.12.015, 2014.

Matthias, I., Nielsen, A. B., and Giesecke, T.: Evaluating the effect of flowering age and forest structure on pollen productivity estimates, Veg. Hist. Archaebot., 21, 471–484, https://doi.org/10.1007/s00334-012-0373-z, 2012.

McCarroll, D., Jalkanen, R., Hicks, S., Tuovinen, M., Gagen, M., Pawellek, F., Eckstein, D., Schmitt, U., Autio, J., and Heikkinen, O.: Multiproxy dendroclimatology: a pilot study in northern Finland, Holocene, 13, 829–838, https://doi.org/10.1191/0959683603hl668rp, 2003.

Nielsen, A. B., Møller, P. F., Giesecke, T., Stavngaard, B., Fontana, S. L., and Bradshaw, R. H. W.: The effect of climate conditions on inter-annual flowering variability monitored by pollen traps below the canopy in Draved Forest, Denmark, Veg. Hist. Archaebot., 19, 309–323, https://doi.org/10.1007/s00334-010-0253-3, 2010.

Nosova, M. B., Novenko, E. Y., Severova, E. E., and Volkova, O. A.: Vegetation and climate changes within and around the Polistovo-Lovatskaya mire system (Pskov Oblast, north-western Russia) during the past 10,500 years, Veg. Hist. Archaebot., 28, 123–140, https://doi.org/10.1007/s00334-018-0693-8, 2019.

Overpeck, J. T., Webb, T., and Prentice, I. C.: Quantitative interpretation of fossil pollen spectra: Dissimilarity coefficients and the method of modern analogs, Quaternary Res., 23, 87–108, https://doi.org/10.1016/0033-5894(85)90074-2, 1985.

Pardoe, H. S., Giesecke, T., Knaap, W. O., Svitavská-Svobodová, H., Kvavadze, E. V., Panajiotidis, S., Gerasimidis, A., Pidek, I. A., Zimny, M., Święta Musznicka, J., Latałowa, M., Noryśkiewicz, A. M., Bozilova, E., Tonkov, S., Filipova-Marinova, M. V., Leeuwen, J. F. N., and Kalniņa, L.: Comparing pollen spectra from modified Tauber traps and moss samples: examples from a selection of woodlands across Europe, Veg. Hist. Archaebot., 19, 271–283, https://doi.org/10.1007/s00334-010-0258-y, 2010.

Pędziszewska, A., Tylmann, W., Witak, M., Piotrowska, N., Maciejewska, E., and Latałowa, M.: Holocene environmental changes reflected by pollen, diatoms, and geochemistry of annually laminated sediments of Lake Suminko in the Kashubian Lake District (N Poland), Rev. Palaeobot. Palyno., 216, 55–75, https://doi.org/10.1016/j.revpalbo.2015.01.008, 2015.

Pennington, W.: The Origin of Pollen in Lake Sediments: An Enclosed Lake Compared with One Receiving Inflow Streams, New Phytol., 83, 189–213, https://doi.org/10.1111/j.1469-8137.1979.tb00741.x, 1979.

Pidek, I. A.: Nine-year record of Alnus pollen deposition in the Roztocze region (SE Poland) with relation to vegetation data, Acta Agrobot., 60, 57–64, 2007.

Pidek, I. A., Svitavská-Svobodová, H., van der Knaap, W. O., Noryśkiewicz, A. M., Filbrandt-Czaja, A., Noryśkiewicz, B., Latałowa, M., Zimny, M., Święta Musznicka, J., Bozilova, E., Tonkov, S., Filipova-Marinova, M., Poska, A., Giesecke, T., and Gikov, A.: Variation in annual pollen accumulation rates of Fagus along a N–S transect in Europe based on pollen traps, Veg. Hist. Archaebot., 19, 259–270, https://doi.org/10.1007/s00334-010-0248-0, 2010.

Prentice, I. C.: Records of vegetation in time and space: the principles of pollen analysis., in: Vegetation history, Handbook of vegetation science., edited by Huntley, B. J. and Webb, T., pp. 17–42, Kluwer Academic Publishers, 00182, 1988.

R Core Team: R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, 2019.

San-Miguel-Ayanz, J., Rigo, D. d., Caudullo, G., Durrant, T. H., and Mauri, A.: European atlas of forest tree species, Publication Office of the European Union, 2016 edn., 2016.

Seppä, H. and Hicks, S.: Integration of modern and past pollen accumulation rate (PAR) records across the arctic tree-line: a method for more precise vegetation reconstructions, Quaternary Sci. Rev., 25, 1501–1516, https://doi.org/10.1016/j.quascirev.2005.12.002, 2006.

Seppä, H. and Weckström, J.: Holocene vegetational and limnological changes in the Fennoscandian tree-line area as documented by pollen and diatom records from Lake Tsuolbmajavri, Finland, Écoscience, 6, 621–635, https://doi.org/10.1080/11956860.1999.11682562, 1999.

Seppä, H., Nyman, M., Korhola, A., and Weckström, J.: Changes of treelines and alpine vegetation in relation to post-glacial climate dynamics in northern Fennoscandia based on pollen and chironomid records, J. Quaternary Sci., 17, 287–301, https://doi.org/10.1002/jqs.678, 2002.

Seppä, H., Alenius, T., Muukkonen, P., Giesecke, T., Miller, P. A., and Ojala, A. E.: Calibrated pollen accumulation rates as a basis for quantitative tree biomass reconstructions, Holocene, 19, 209–220, https://doi.org/10.1177/0959683608100565, 2009.

Shumilovskikh, L. S., Novenko, E., and Giesecke, T.: Long-term dynamics of the East European forest-steppe ecotone, J. Veg. Sci., 29, 416–426, https://doi.org/10.1111/jvs.12585, 2018.

Song, J. and Wang, H.: Ckmeans.1d.dp: Optimal and Fast Univariate Clustering, Holocene, 3, 29–33, 2011.

Stockmarr, J.: Tablets with spores used in absolute pollen analysis, Pollen et Spores, 13, 615–621, 1971.

Sugita, S., Hicks, S., and Sormunen, H.: Absolute pollen productivity and pollen-vegetation relationships in northern Finland, J. Quaternary Sci., 25, 724–736, https://doi.org/10.1002/jqs.1349, 2009.

Svobodová, H., Soukupová, L., and Reille, M.: Diversified development of mountain mires, Bohemian Forest, Central Europe, in the last 13,000 years, Quatern. Int., 91, 123–135, https://doi.org/10.1016/S1040-6182(01)00106-9, 2002.

5   Tauber, H.: Investigations of the mode of pollen transfer in forested areas, Review of Palaeobotany and Palynology, 3, 277–286, https://doi.org/10.1016/0034-6667(67)90060-7, http://www.sciencedirect.com/science/article/pii/0034666767900607, 00198, 1967.

Tauber, H.: A Static Non-overload Pollen Collector, New Phytol., 73, 359–369, https://doi.org/10.1111/j.1469-8137.1974.tb04770.x, 1974.

Theuerkauf, M., Bos, J. A. A., Jahns, S., Janke, W., Kuparinen, A., Stebich, M., and Joosten, H.: Corylus expansion and persistent openness in the early Holocene vegetation of northern central Europe, Quaternary Sci. Rev., 90, 183–198,
10   https://doi.org/10.1016/j.quascirev.2014.03.002, 2014.

Tinner, W., Colombaroli, D., Heiri, O., Henne, P. D., Steinacher, M., Untenecker, J., Vescovi, E., Allen, J. R. M., Carraro, G., Conedera, M., Joos, F., Lotter, A. F., Luterbacher, J., Samartin, S., and Valsecchi, V.: The past ecology of *Abies alba* provides new perspectives on future responses of silver fir forests to global warming, Ecol. Monogr., 83, 419–439, https://doi.org/10.1890/12-2231.1, 2013.

Tinsley, H.: Modern pollen deposition in traps on a transect across an anthropogenic tree-line on Exmoor, southwest England: a note sum-
15   marising the first three years of data, Rev. Palaeobot. Palyno., 117, 153–158, https://doi.org/10.1016/S0034-6667(01)00083-5, 2001.

Tinsley, H. and Hicks, S.: Preface, Rev. Palaeobot. Palyno., 117, vii–x, https://doi.org/10.1016/S0034-6667(01)00073-2, 2001.

Tonkov, S., Hicks, S., Bozilova, E., and Atanassova, J.: Pollen monitoring in the central Rila Mountains, Southwestern Bulgaria: comparisons between pollen traps and surface samples for the period 1993–1999, Rev. Palaeobot. Palyno., 117, 167–182, https://doi.org/10.1016/S0034-6667(01)00085-9, 2001.

20   Tonkov, S., Panovska, H., Possnert, G., and Bozilova, E.: The Holocene vegetation history of Northern Pirin Mountain, southwestern Bulgaria: pollen analysis and radiocarbon dating of a core from Lake Ribno Ban derishko, Holocene, 12, 201–210, https://doi.org/10.1191/0959683602hl535rp, 2002.

van der Knaap, W. O., van Leeuwen, J. F. N., Fankhauser, A., and Ammann, B.: Palynostratigraphy of the last centuries in Switzerland based on 23 lake and mire deposits: chronostratigraphic pollen markers, regional patterns, and local histories, Rev. Palaeobot. Palyno., 108,
25   85–142, https://doi.org/10.1016/S0034-6667(99)00035-4, 2000.

van der Knaap, W. O., van Leeuwen, J. F. N., and Ammann, B.: Seven years of annual pollen influx at the forest limit in the Swiss Alps studied by pollen traps: relations to vegetation and climate, Rev. Palaeobot. Palyno., 117, 31–52, https://doi.org/10.1016/S0034-6667(01)00075-6, 2001.

van der Knaap, W. O., van Leeuwen, J. F. N., Svitavská-Svobodová, H., Pidek, I. A., Kvavadze, E., Chichinadze, M., Giesecke, T., Kaszewski,
30   B. M., Oberli, F., Kalniņa, L., Pardoe, H. S., Tinner, W., and Ammann, B.: Annual pollen traps reveal the complexity of climatic control on pollen productivity in Europe and the Caucasus, Veg. Hist. Archaebot., 19, 285–307, https://doi.org/10.1007/s00334-010-0250-6, 2010.

Veski, S., Amon, L., Heinsalu, A., Reitalu, T., Saarse, L., Stivrins, N., and Vassiljev, J.: Lateglacial vegetation dynamics in the eastern Baltic region between 14,500 and 11,400 cal yr BP: A complete record since the Bølling (GI-1e) to the Holocene, Quaternary Sci. Rev., 40, 39–53, https://doi.org/10.1016/j.quascirev.2012.02.013, 2012.

35   Wayne, P., Foster, S., Connolly, J., Bazzaz, F., and Epstein, P.: Production of allergenic pollen by ragweed (Ambrosia artemisiifolia L.) is increased in CO2-enriched atmospheres, Ann. Allerg. Asthma Im., 88, 279–282, https://doi.org/10.1016/S1081-1206(10)62009-1, 2002.

Welten, M.: Pollenanalytische, stratigraphische und geochronologische Untersuchungen aus dem Faulenseemoos bei Spiez., vol. 21 of *Veröffentlichungen des Geobotanischen Instituts RübeI in Zürich*, Verlag H. Huber, 1944.

Williams, J. W., Grimm, E. C., Blois, J. L., Charles, D. F., Davis, E. B., Goring, S. J., Graham, R. W., Smith, A. J., Anderson, M., Arroyo-Cabrales, J., Ashworth, A. C., Betancourt, J. L., Bills, B. W., Booth, R. K., Buckland, P. I., Curry, B. B., Giesecke, T., Jackson, S. T., Latorre, C., Nichols, J., Purdum, T., Roth, R. E., Stryker, M., and Takahara, H.: The Neotoma Paleoecology Database, a multiproxy, international, community-curated data resource, Quaternary Res., 89, 156–177, https://doi.org/10.1017/qua.2017.105, 2018.