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

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Abstract. The collection of modern, spatially extensive pollen data is important for the interpretation of fossil pollen assemblages and the reconstruction of past vegetation communities in space and time. Modern 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 Europe. 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 PAR are influenced by forest cover and climate parameters, which determine pollen productivity and correlate with latitude. ~~Regional forest cover >80% is indicated by >3200 tree pollen grains grains cm^{-2} y^{-1}~~ ~~In treeless vegetation PAR values of at least 140 grains cm^{-2} year^{-1} are found and with each 10% of forest cover tree PAR increases by 400 grains cm^{-2} year^{-1} at least,~~ Pollen traps situated beyond 200 km of the distribution of a given tree species still collect occasional pollen grains of that species. ~~PAR's of up to 30~~ The threshold of this long distance transport ~~for individual species is~~ generally below 60 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 similar values. ~~Comparisons for temperate taxaoften demonstrate that similar trap values are found further south or downhill~~For temperate taxa, modern analogues for fossil PARs are generally found downslope or southward of the fossil sites. While we do not find modern situations comparable to fossil PAR values of some taxa (e.g., *Corylus*). CO_2 fertilization and land use may cause high modern PAR that are not documented in the fossil record. The modern data ~~is~~ are now publicly available in the Neotoma Paleoecology Database and aids interpretations of fossil PAR data.

1 Introduction

1.1 The need for a dataset of modern absolute pollen deposition

Pollen analysis ~~became the~~ has became the most widely used method for the reconstruction of the Holocene vegetation. Pollen percentages are a simple representation of pollen analytical results, but have a number of well-known limitations and biases that are often ignored. One of these is separating locally produced from long distance transported pollen (Davis, 2000), which is paramount for mapping past changes in plant distributions. Also reconstructing the position of tree-lines from pollen percentage data may be misleading as local treeless vegetation (e.g., tundra) produces few pollen grains, while distant woodlands (e.g., consisting of boreal trees) produce much pollen. In such situations absolute pollen data are very informative as was already realized by Hesselman (1919) and Malmström (1923). Pollen accumulation rates (PAR) or the number of pollen grains deposited on the sediment surface over a set period of time, are in theory superior to pollen percentages as they do not suffer the closure effect of percentage data. Thus by using absolute data it is possible to differentiate between ~~low amounts~~ small quantities of long distance transported ~~versus high amounts~~ pollen versus large quantities of locally produced pollen. In a seminal publication Davis et al. (1964) document the power of using absolute pollen deposition for the interpretation of the spread of trees 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. PAR are therefore required when studying the population dynamics of individual trees (Bennett, 1983). While absolute pollen data do not share the artefacts of percentage data, they are often difficult to obtain and subject to a different set of limitations.

One limitation for obtaining reliable PAR from sediment cores is the requirement for accurate chronologies. Lake internal processes such as re-deposition and sediment focusing and also catchment erosion may bias the resulting values ~~(Davis and Brubaker, 1973;~~ (Bennett and Buck, 2016; Davis and Brubaker, 1973; Giesecke and Fontana, 2008; Davis et al., 1984). 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 sediment 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 only a few investigations of the pollen vegetation relationship using absolute pollen deposition, while there are numerous studies using percentage data. Nevertheless, investigations using pollen traps yielded invaluable insights into the mode of pollen transport (Tauber, 1967). Also the construction of representation factors for common ~~Europe~~ European trees by Andersen (1970), which are still used, was 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).

Several aspects of PAR data have not been exhaustively explored in modern comparison studies and here we will focus on the following three: 1) the influence of climate in combination with forest biomass; 2) the application of PAR to indicate the local presence of trees versus long distance transport of pollen; 3) using modern PAR values of single taxa to interpret fossil situations.

1.2 Climate and biomass

Recent investigations demonstrate the linear response of absolute pollen deposition to absolute tree abundance ~~(Seppä et al., 2009, Sugita et~~ (Matthias and Giesecke, 2014; Seppä et al., 2009; Sugita et al., 2009), which may be used to reconstruct past standing tree biomass of different trees. However, at an annual time resolution, variability in PAR can be explained by weather conditions during the time of flowering as well as during the previous year ~~(Hicks, 1999, van der Knaap et al. (2010), Nielsen et al. (2010))~~ (Hicks, 1999; Nielsen et al., 2010; van der Knaap et al., 2010). Thus the question arises: If weather is determining annual pollen production, could climate ~~in addition to determining biomass~~ determine average PAR? Comparing *Pinus* PAR between two pine dominated forest regions in central Sweden and north east Germany shows much higher values in the south, suggesting 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. This is also true for fertilization with CO_2 (LaDeau and Clark, 2006). Therefore, climate and even the amount of CO_2 in the atmosphere may determine the pollen productivity of a tree at a given site. Welten (1944) already 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~~ then the postglacial increase in PAR at Rodgers Lake could also be due to a change in these parameters. It is, therefore, important to investigate the possible relationship between climate and average PAR in more detail.

1.3 Local presence versus long distance transport

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. ~~Occasional reports of PAR values for~~ Identification of the local presence of taxa in the past by comparison of different proxies, produces ambiguous results. Some studies show that the rise of PAR is able to mirror the first occurrence of a macrofossil ~~indicating local presence exist (e.g. Giesecke, 2005a), but modern comparisons are lacking~~(e.g. Giesecke, 2005a), others show an increase in PAR and percentage values thousands years after the first appearance of stomata (Froyd, 2005; Parshall, 1999). So, the modern comparisons of PAR thresholds and recent vegetation are needed. While percentage data are not well suited for detecting distribution limits, a continental scale comparison (Lisitsyna et al., 2011a) provides some guidance on values that can be used for mapping past distribution changes (Giesecke et al., 2017). The PMP dataset presented here provides a continental scale dataset permitting such a comparison with PAR data.

1.4 Modern ~~analogies~~analogues

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 an~~ (Jackson and Williams, 2004; Overpeck et al., 1985; Davis et al., 2013). Modern datasets of absolute pollen deposition are hitherto rarely used 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) showed that average modern PAR values can be obtained, representing the gradual transition from the boreal forest to tundra. These "modern analogues" were successfully applied to 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).

1.5 The Pollen Monitoring Programme (PMP)

The programme 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 in 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., 200~~ (Koff, 2001; Tinsley, 2001; Tonkov et al., 2001; van der Knaap 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; Hättestran~~ (e.g. Kvavadze, 2001; Pidek, 2007; Giesecke and Fontana, 2008; Gerasimidis et al., 2006; Jensen et al., 2007; Hättestrand et al., 2008) 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~~ To examine the hypothesis that climate as well as regional ~~forest cover~~ biomass explain the variability in PAR.

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

c) ~~Compare~~ To 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.

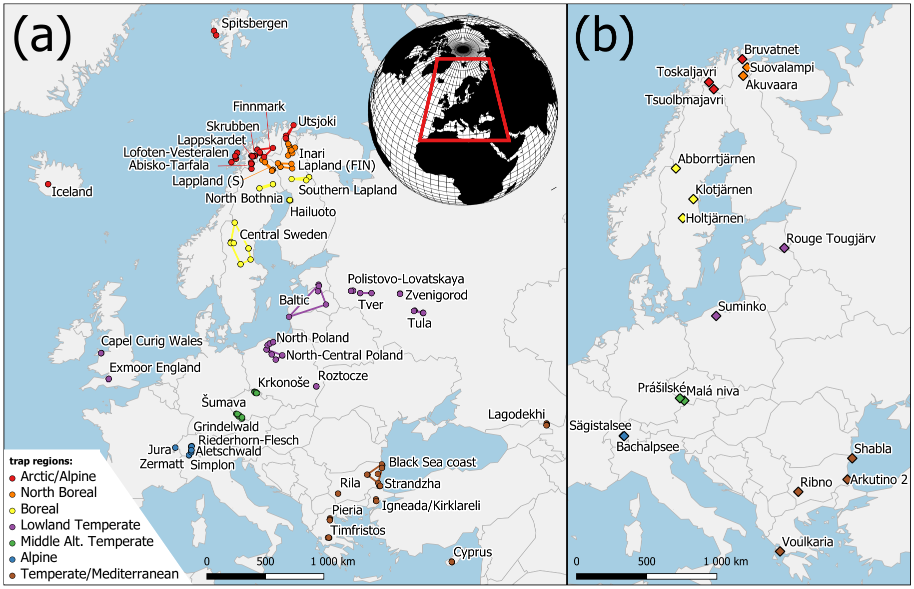


Figure 1. Map of the study area with trap areas (a) and Holocene pollen sites (b). Both datasets are divided into trap regions (colours). – Colours correspond to Fig. 5.

2 Methods

2.1 Study area

Sites in the PMP database were divided into 7 ‘trap regions’ according to their 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~~. The traps 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~~ The northernmost populations of *Alnus glutinosa* occur near some sites and the southernmost traps in Central Sweden are situated near the 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 Mid Altitude Temperate region were separated from the Temperate Lowland sites and include the Krkonoše and Šumava Mountains. Traps in both areas are placed on an elevation gradient from 500 m and 1200 m a.s.l. The lower slopes of the mountains are dominated by *Fagus sylvatica*, while the traps are situated on a gradient from *Picea abies*-dominated forest to the onset of alpine vegetation in Krkonoše. In the Alps and Jura Mountains (Alpine region), traps were placed at even higher elevations, between 1200 m to 3000 m a.s.l., crossing the altitudinal treeline. Trapping locations in Temperate/Mediterranean region in the southeastern Europe 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~~ Lagodekhi (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~~ with an opening of 19.6 cm^2 usually (5 cm diameter opening)~~or similar~~.
The bottle or bucket must be large enough to hold the annual surplus precipitation that falls into the trap. 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. Consequently, tall herbs or grasses might have overgrown or covered some of the traps potentially leading to higher pollen deposition of grasses and reduced pollen deposition of trees caused by leaves temporally blocking the opening. 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 were restricted to tree pollen, Poaceae and Cyperaceae~~should therefore~~ .

Those taxa should 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 (Tauber, 1967).

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, climate and forest cover

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~~ tree 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 the 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 total and tree PAR. To balance the contribution of high and low pollen producers in the assessment of the PAR, we applied correction factors (Table S2, Andersen, 1970). Average modern PAR have a large variance of values between traps of the same region, with the smaller numbers often being the focus of information. For this reason, we often log-transformed PAR values in the different analyses.

2.4 Distribution limits and PAR

Pollen deposition beyond the distribution area of the parent plant was studied by merging the distribution maps of the relevant species included in each of the pollen types listed above ~~(Caudullo et al., 2017; San-Miguel-Ayanz et al., 2016)~~(San-Miguel-Ayanz et al., 20
. These comparisons were not possible 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.

For each trap location and each pollen taxon we calculated the distance to the nearest area of distribution using GIS (GRASS Development Team, 2018). Initial observations showed that PAR dropped rapidly away from the distribution of the parent tree and did not decline at the same rate at larger distances. We therefore compared distance to the decadic logarithm of PAR, applying linear regression to explore thresholds of long-distance transport (hereafter also as “LDT”) at 200 km from their mapped distribution limits. This distance was chosen as a compromise accounting for uncertainties in the information on distribution limits and available pollen trap data. 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 target taxa may be planted in the area.

~~We compare LDT with the characteristic radius for the same taxa. Characteristic radius is a useful measure showing pollen transport predicted by pollen dispersal models. It represents the theoretical proportion of pollen loading at different distances from the source plants (Prentice, 1988) and can thus be easily compared with our empirical values. We used Gaussian Plume model with wind speed 3 $m.s^{-1}$ (Prentice, 1985).~~

2.5 Comparison between modern and Holocene PAR

To enable the comparison of modern with fossil PAR values the pollen trap data ~~was~~ were extracted from the PMP database with above described constraints and all annual samples were averaged within traps. For each trap region we selected at least one and a maximum of three Holocene PAR records (Table 1). This distance was chosen as a compromise accounting for uncertainties in the information on distribution limits and available pollen trap data. Holocene PAR estimates often show high variation between samples due 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. For a general comparison of the distribution of fossil and modern values, we plotted the frequency of log-transformed PAR values over all regions and traps per taxon. ~~Per~~ For each region and taxon we compared the frequency distribution of fossil and modern PAR values using a t-test at 5% level of alpha to identify situations where modern and fossil values are comparable. Secondly, we compared trap and fossil PAR at the level of individual sites or trap areas. To facilitate this comparison average trap and fossil PAR values per taxon were submitted to one-dimensional clustering using the R-package Ckmeans.1d.dp (Wang and Song, 2011). This method splits the univariate data in ~~the~~ such a way that the total of within-cluster sums of squares is always kept to a minimum. These classes helped us compare trap and fossil data and to link the highest fossil PARs with the trap PARs. We dealt only with the highest class in each fossil sequence because maximum abundance of several our target taxa was used as a stratigraphic marker of the Holocene period and thus their timing is well known. However, time windows did not smooth out all spuriously high values variation. In order to remove this remaining variation of individual time windows, we ignored some high fossil values (Table S3). Thus, we aimed to find modern analogues for fossil situations represented by several bins (more than 500 years). We linked these periods containing high fossil PAR to the closest pollen trap, using a matrix of geographical distances between fossil sites and pollen traps. All statistical analysis and data visualizations were produced in R (R Core Team, 2019).

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	Alpine	Sägistalsee	lake	46.68139	7.9775	1935	7.2	(van der Knaap et al., 2000)
CHE	Alpine	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)

3 Results and interpretations

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 records 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 temperatures (MAT) for the sites fall between -5.7 to 14.1 °C. The forest cover within a 10 km radius of the trapping 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 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 PAR 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 (Fig. S1b). Dominance of oak and hornbeam at Temperate/Mediterranean sites in the

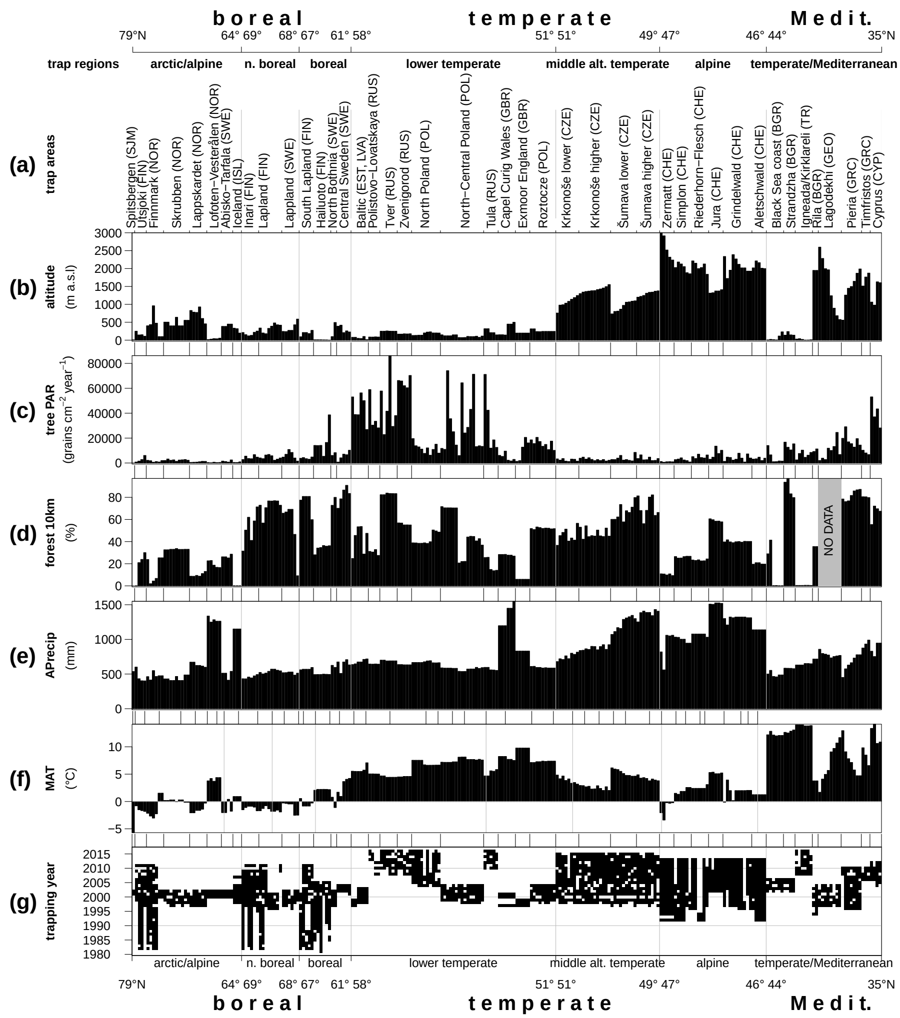


Figure 2. Environmental setting of the trap dataset. (a) trap areas ordered from north (left) to south (right), (b) altitude, (c) mean annual tree PAR, (d) forest cover within 10 km radius, (e) annual precipitation, (f) temperature: MAT - Mean Annual Temperature, (g) temporal coverage of the PMP database.

lowland and pine and birch at Arctic/Alpine and North Boreal sites show similar stability ~~in the~~ from a Holocene perspective. Vegetation history at the rest of the fossil sites shows a more dynamic development (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), where no trees can grow. However, the highest absolute values of tree PAR are not from the southernmost traps but from the Lowland Temperate region (trap area Tver; Fig. 2). 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).

Large differences in the pollen productivity between different trees affect 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 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, so the distribution of the minimum average trap values is more informative (Fig. 3a). These lower values closely follow a latitudinal trend. The average PAR south of 62° latitude and below the altitudinal treeline or close to forests is generally higher than 1000 grains cm^{-2} y^{-1}. ~~An area with low PAR in the south is the~~ The coastal grassland in northern Bulgaria ~~. The generally low PARin this area can be explained by the sparse vegetation cover on thin~~ is a southern area with a particularly low PAR. The rendzina soils formed on limestone rock in this area host only sparse vegetation which produces generally low PAR. 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~~ with the forest cover within 10 km (Fig. 3b). ~~Exploring the data showed that a 3% wide bins of the forest cover,~~ The traps with the lowest PAR per each ~~bin of the~~ 3%-wide bin of forest cover provide a regression model~~predicting a tree PAR of 3200~~. The relationship predicts a PAR of at least 140 grains cm^{-2} year^{-1} ~~at 80%~~ in a treeless vegetation. With each 10% of forest cover within 10 km of the trap, tree PAR increases at least by 400 grains cm^{-2} year^{-1}.

3.3 Long distance dispersed pollen

The comparison of PAR with the distribution ~~limit~~ limits of different tree taxa shows that PAR generally declines with distance (Fig. 4). A gradual decline is best documented for *Quercus* where traps cover different distances from the distribution area. 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 fitted a linear relationship, also to compare the amount of pollen at 200 km from the distribution limit (Fig. 4b). This comparison indicates that less than 80 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~~ of *Carpinus, Corylus, Fagus, Fraxinus, Quercus* and *Tilia*. For *Picea* ~~shows~~ alone the values drop rapidly so that less than 1 grain cm^{-2} y^{-1} ~~at~~ may be expected beyond 200 km of the distribution range. In the case of *Fagus* ~~it has to be noted that~~ the interpolation yielded the highest values for the distance of 200 km~~,~~ however, this is based on few data points and the interpolation procedure. Only one trap beyond 200 km of the distribution of the tree recorded more than 30 grains cm^{-2} y^{-1}. ~~The general threshold of 80 grains~~ Three remaining traps beyond 1000 km have PAR of *Fagus* < 1 grain cm^{-2} y^{-1} ~~suggested here is near the detection limit and the~~

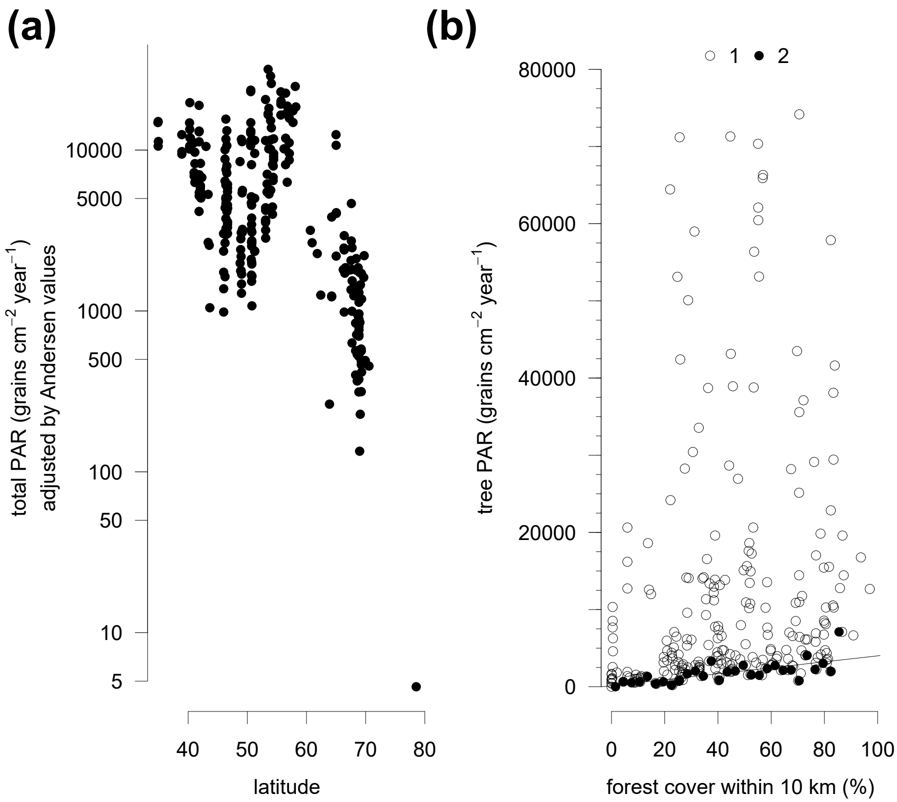


Figure 3. Latitudinal gradient in pollen accumulation rates of major tree taxa and Poaceae and Cyperaceae (total PAR) adjusted by Andersen values (see Tab S2) of pollen representation (a). Relationship between forest cover within 10 km radius and tree PAR (b). All trap sites (1) and minimum tree PAR per every 3 % of forest cover (2).

~~PAR value may be~~ and such values are biased by the size of the pollen count~~in cases where only one grain was encountered.~~, while still influencing the regression.

~~PAR at 200 km from the distribution area represent 0.002-36% of the median PAR within the distribution area (Fig. 4), which is 0.2% of pollen loading in average for those seven taxa (Table S5).~~

3.4 Ranges of modern and fossil PAR values

The comparison of modern and fossil PAR values shows good agreement ~~in~~ for 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 PAR of the trap dataset are higher (often ten times) for all species compared to maximum PAR in the fossil dataset, with the exception of *Corylus*. The frequency distribution of PAR is log-normal for *Alnus*, *Tilia* and *Fraxinus*. A strong bimodal distribution of values can be recognized for fossil samples of *Picea* and Poaceae (Fig. 5). Such a bimodality, but less clear, occurs for the modern samples of *Pinus* and for fossil samples of *Abies* and *Fagus*. The highest frequency of trap values for *Carpinus*, *Fagus* and *Tilia* is very close to the line

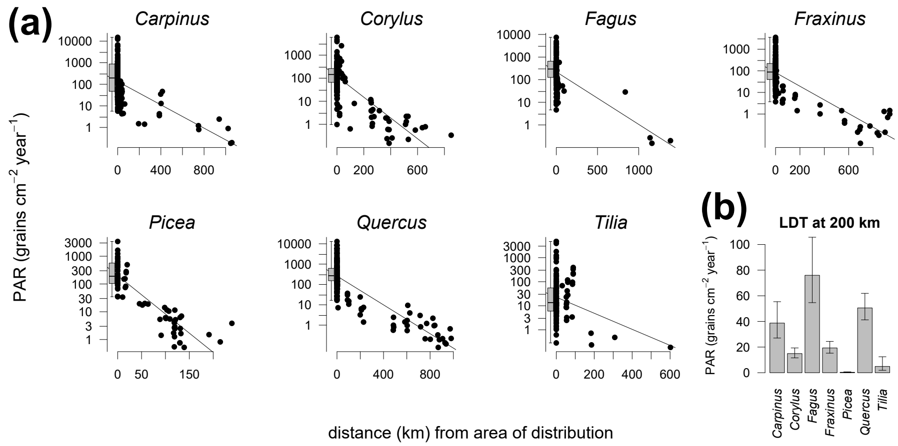


Figure 4. Relationship between the distance from the trap site to the nearest area of species distribution and PAR for selected trees. Zero distance represents edge of distribution area. Traps within the distribution area are aggregated in boxplots (a). PAR of the long-distance transport (b) calculated from linear regression at 200 km (Fig. 4a).

of the LDT threshold. The LDT threshold for *Corylus*, *Fraxinus* and *Quercus* separates values of the three boreal regions from the rest of the regions. The trap values of *Picea* from the Arctic/Alpine region are above the LDT threshold. The frequency distribution of modern and fossil PAR ~~corresponds best~~ shows the best correspondence 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 PAR occurs for *Juniperus*, where maximum values are around a hundred times larger in the traps. Minimum PAR are about ten times higher in the traps for Poaceae and Cyperaceae, in particular, and the right side of the distribution is shifted upwards.

Using the 15 selected taxa in seven trap regions and the occurrence of the pollen types, we obtained 92 pairs of trap and fossil data. The frequency distribution of PAR values is similar between modern and fossil samples in 31 of these pairs based on a t-test and a p-value > 0.05 (Fig. 5, Table S6). 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 PAR generally correspond well for the lowland Temperate region where, 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 PAR in the Lowland Temperate region.

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

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. Comparing the highest class of fossil PAR

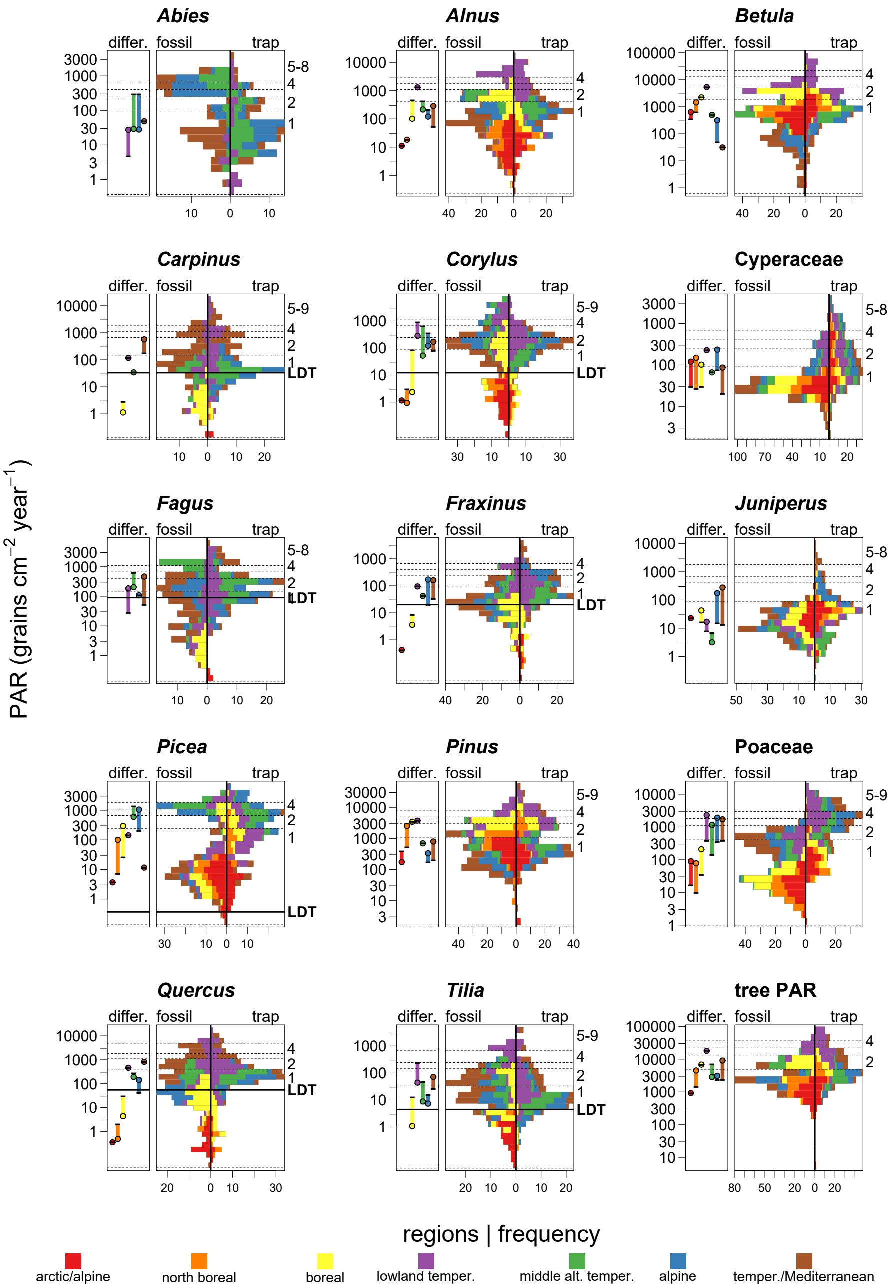


Figure 5. Difference (differ.) between the mean fossil (-) and the mean trap (o) PAR per trap region is shown by length of the vertical segment. Paired histograms of mean annual PAR from the fossil record (on the left) and from traps (on the right). Colours denote different trap regions and correspond to Fig. 1. Note log-transformed y-axis. Horizontal lines and numbering on the secondary y-axis denote classes of PAR~~, for~~. For more detail see Fig. 6b) and d). LDT is threshold for long distance transport.

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 main linkage. Detailed descriptions are presented in the supplement (Fig. S3).

Abies declined in most of the populations, thus ~~Roztoce~~ Roztocze is the only ~~analogous trap area with PAR for~~ trap area analogous to fossil sites in central Europe and similarly the Timfristos trap area is analogous for fossil sites in southern Europe (Fig. 6). *Alnus* retreated from Scandinavia, thus the fossil sites ~~have the closest linkage southwards~~are most closely related to the more southerly sites, on the island of Hailuoto or in North Poland. *Corylus*, *Quercus* and *Tilia* (Fig. 7) also declined, thus modern values in North Poland provide analogues for fossil situations in central and northern Europe. Poaceae and Cyperaceae exceed values from fossil examples, thus analogous traps are close to the fossil site. Similarly, *Betula* and *Juniperus* have high PAR at only a few trap sites (11900-73900 and 870-8300 grains cm^{-2} y^{-1}, respectively), whereas the fossil PAR and the rest of the trap dataset are lower, fitting within the two or three first classes. Both taxa find an analogous trap record within the same area~~,~~ ; most of the distant links are for the lowest classes (0-5600 and 0-90 grains cm^{-2} y^{-1} respectively). Fossil PAR of *Carpinus* in North Poland and the Black Sea coast fall within the range of trap records from the same area. Trap areas in the Baltics, Šumava and Central Sweden indicate higher fossil than trap PAR of *Carpinus*. All fossil sites within the recent distribution of *Fagus* and *Picea* have the closest analogous trap in the same or adjacent trap area and fossil-trap links are short. Fossil and trap PAR of ~~arboreal~~ tree pollen and *Pinus* are comparable within the trap areas, ~~except for~~ with exception of the Baltics and Rila mountains, respectively, where the fossil is lower than the trap record. On the other hand, their record from the Early Holocene at Prášilské Lake is higher than any trap record from the Šumava mountains.

4 Discussion

4.1 Trap PAR and environmental conditions

This overview of European pollen trap data collected by the PMP network ~~demonstrates that modern PAR provide comparable values to fossil records and can thus help in interpreting the fossil signal in spite of the different taphonomic processes that~~ provides an important reference to investigate continental scale patterns in absolute pollen deposition. Different taphonomic processes influence PAR values in pollen traps versus lake sediments ~~(Lisitsyna et al., 2011b). The~~ or moss surface samples (Giesecke and Fontana, 2008; Pardoe et al., 2010; Lisitsyna et al., 2011b). Processes involving differences in the efficiency of capture and deposition of pollen on a surface are important explaining local variability, while the added uncertainty is generally smaller than the overall signal. On the other hand lake internal processes like focusing, bank erosion or riverine pollen input may alter the fossil signal substantially and here careful site selection and site specific interpretation are needed to allow comparisons (Giesecke and Fontana, 2008). The pollen trap 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 regions ~~(van der Knaap et al., 2010; Nielsen et al., 2010)~~ (Nielsen et al., 2010; van der Knaap et al., 2010) suggests

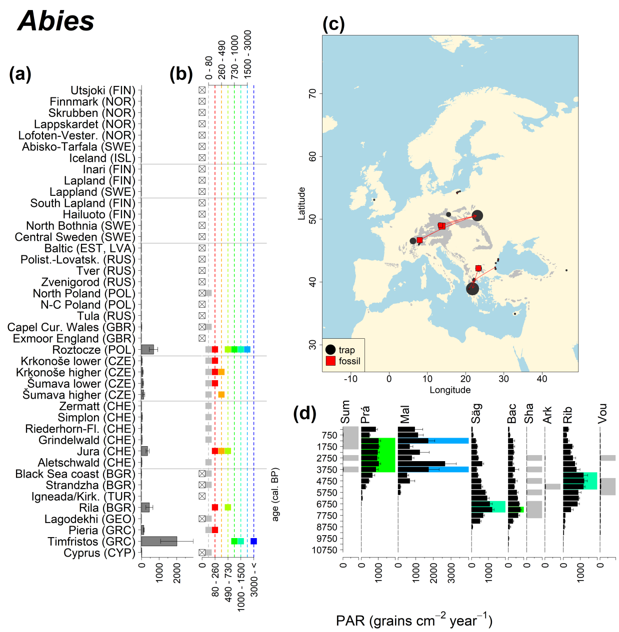


Figure 6. a) Mean modern PAR for selected tree taxa averaged for each trap area~~(a)~~. b) Range of mean individual trap values classified by one-dimensional clustering. Crossed squares indicate that pollen of the taxon was ~~not found~~ absent from at least in ~~any~~ one trap from the area. c) Map of Europe with the distribution of the species (gray, ~~Caudullo~~ San-Miguel-Ayanz et al. 2016, ~~2017, San-Miguel-Ayanz~~ Caudullo et al.~~2016~~, 2017) ~~falling within~~ from the pollen taxa~~, size~~. 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).

that the ~~growing season warmth~~ warmth of the growing season and other climate variables also explain the interannual variability of pollen deposition. On a 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 fertilization experiment (Wayne et al., 2002) ~~, which supports the~~ and in an increase of the temperature due to global warming (Frei and Gassner, 2008). Both factors support the interpretation that average PAR of the same species may vary due to environmental parameters determining ~~its~~ productivity.

4.2 Long Distance Transport (LDT)

Modern PAR 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). ~~Our LDT result~~ The maximum LDT estimate 80

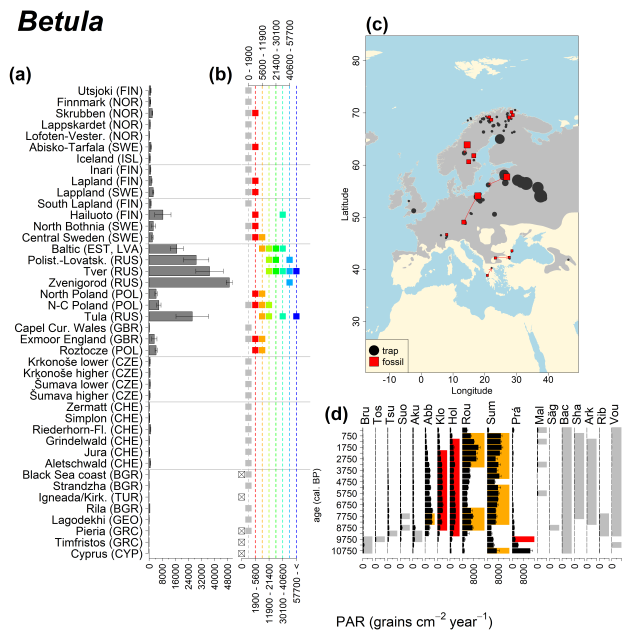
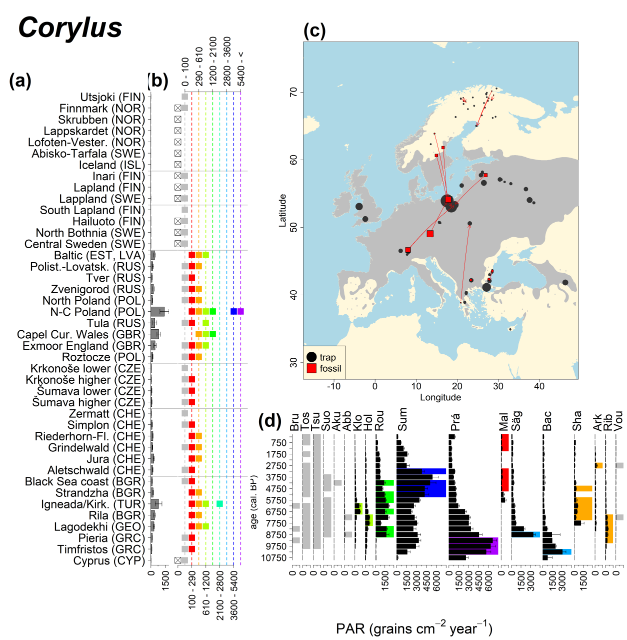


Figure 7. See caption Fig. 6



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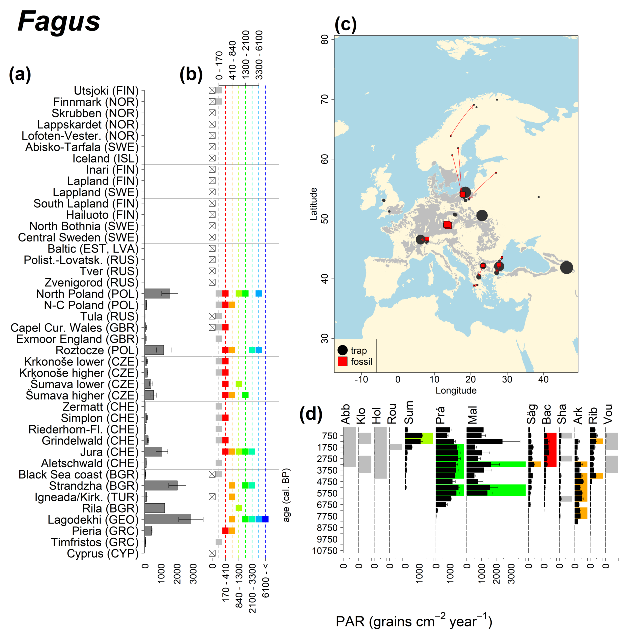

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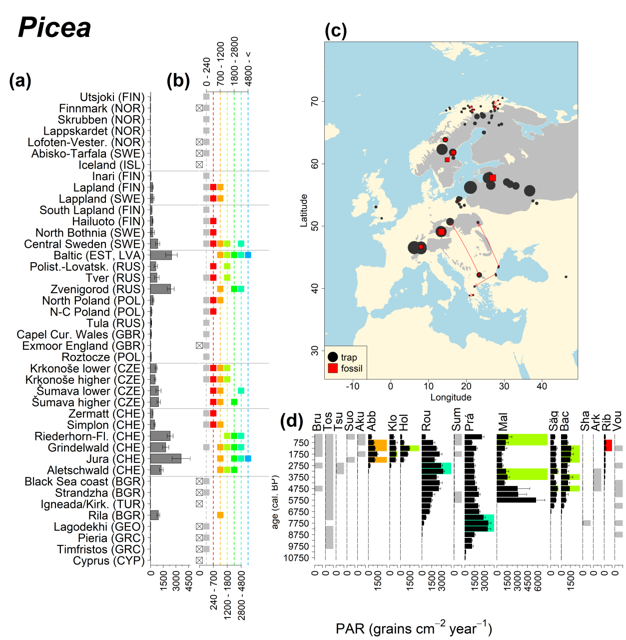

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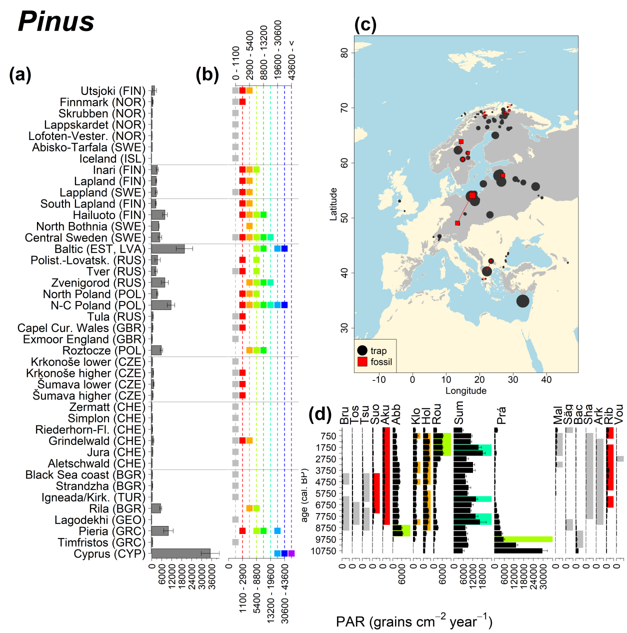

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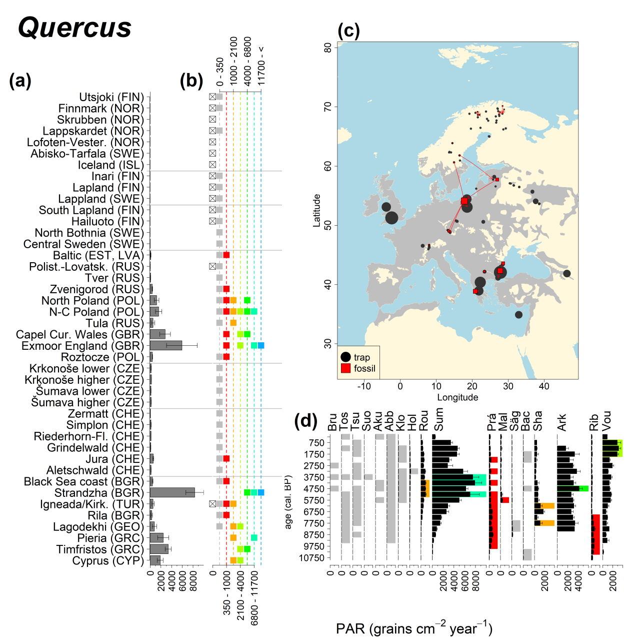

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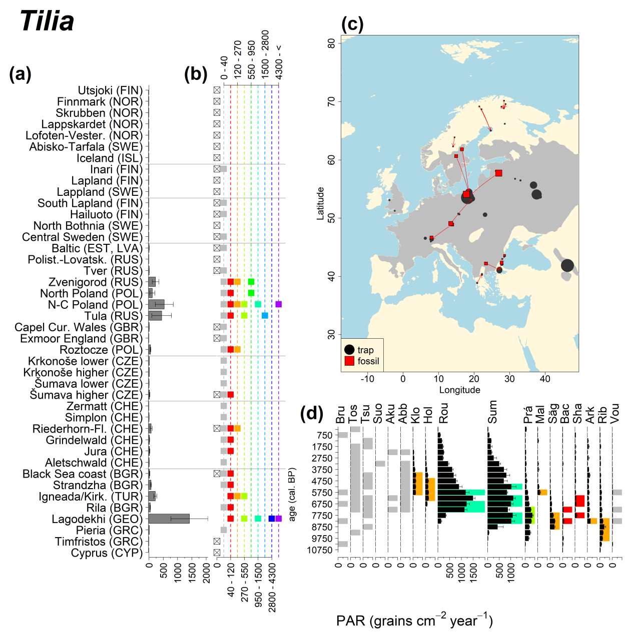

Figure 13. See caption Fig. 6

grains cm^{-2} y^{-1} presented here is slightly lower than the range of PAR values for *Pinus* and *Betula* in ~~aretic-apline~~ arctic-alpine zone 100-200 grains cm^{-2} y^{-1} ~~(Seppä and Hicks, 2006). Here we evaluated greater distances and, therefore, had to ignore both species, while indicating some general thresholds for other~~. This analysis investigated PAR values of a given taxon in traps located several hundred kilometers away from the distribution limit of the parent tree. Therefore, *Pinus* and *Betula* had to be ignored as all traps are within or close to their distribution limits. Using approximate distribution data in combination with a large distance of 200 km provides thresholds for most dominant European trees. ~~The suggested threshold of 80 grains~~

The lowest LDT threshold was obtained for *Picea* (0.3 grain cm^{-2} y^{-1} ~~may be used to differentiate local from long distance transport for most wind pollinated trees. However, this value may still lead to false negatives as the absence of a plant cannot be proven by the absence of evidence for presence. The value of~~) and with a good number of traps documenting the decline of *Picea* PAR values away from the distribution limit. The most distant trap for *Picea* is only 250 km from the distribution limit so that no elevated values in traps at even larger distances influenced the regression. On the other hand, the highest values of 80 ~~grains cm~~grains cm^{-2} y^{-1} for ~~*Picea* agrees well with the fossil PAR value for the tree of 50 *Picea*~~ *Fagus* may be biased by the availability of only limited data. While three traps from beyond 1000 km of the distribution limit of *Fagus* registered less than 1 grain cm^{-2} y^{-1}, these traps strongly influence the regression due to the large distance. Consequently, the value of 80 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~~ may be an overestimate. Also, the ~~larger region rather than properties~~ threshold for *Fagus* is high in comparison to the size of the pollen ~~types~~grain and associated fall speed. A higher threshold would be expected for *Corylus* compared to *Fagus*. *Corylus* ~~has a lighter pollen grain~~

pollen is lighter than *Fagus* ~~, which can travel more easily over large~~ pollen and able to travel greater distances (Table S5). ~~However, LDT~~

The LDT threshold for *Picea* ~~results too low and *Fagus* too high. They do not cover the same distance ranges as the *Corylus* results. LDT estimate of~~ seems low in comparison to the fossil PAR value of ~~*Fagus*~~*Picea* ~~is based on a few traps, very distant from the distribution area. Similarly, the occurrences of taxa outside the mapped natural distribution can bias this estimate. Considering *Carpinus*, *Corylus*, *Fagus*, *Fraxinus*,~~ (50 grains cm^{-2} y^{-1}) found in a sample at Klotjärnen just after the occurrence of the first *Picea* ~~, *Quercus* and *Tilia*, the proportion of pollen loading within the area of distribution and~~ bud scale (Giesecke, 2005b). However, the thresholds suggested here represent long distance transport at 200 km~~from the source plants measured empirically by our PAR results (0.002-36%, in average 0.2%) is wider and higher than the theoretical range (0.005-13%, in average 0.05%; Table S6). This mismatch can be caused by too leptokurtic character of the Gaussian Plume model with windspeed 3 m.s^{-1} and fits with previous indication that it underestimates dispersal of pollen with a large grain (Abraham et al., 2014, Theuerkauf et al. (2016)).~~ , while macrofossil evidence indicates local presence.

Pollen ~~rain~~ deposition beyond the area of distribution is analogous with high elevations~~with sparse vegetation. However, with the increasing altitude, PAR decreases independently from the actual growth density, because of the worse climatic conditions and low pollen productivity (Markgraf, 1980)~~. Decreasing temperatures with elevation cause a reduction in the pollen production of trees (Markgraf, 1980; van der Knaap et al., 2010).

4.3 Analogues for vegetation reconstruction

The comparisons of modern and fossil PAR values show that pollen traps can characterize the population density of particular taxa in modern situations and thus provide analogues aiding in the interpretation of fossil situations. One caveat of the comparisons conducted here is the lack of fossil sites in the oceanic climate of western Europe. Reliable fossil PAR records were not available from the areas of trapping locations in the UK and pollen trapping locations from northern France or Spain are not available. Moreover, no sites with fossil PAR from western Europe or from low elevations in the Alps are included in this comparison. This omission has consequences for some of the comparisons. A particular case where PAR could in theory aid in the interpretation of the fossil situation are the large quantities of *Corylus* pollen in early Holocene samples of west European sites. However, there are no or limited modern analogues for the highest Early Holocene values. Among the fossil sites considered here the highest values are 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* PAR 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 PAR 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~~ Pollen production, including that of *Pinus*, could be increased by fertilization due to increased nitrogen deposition (Pers-Kamczyc et al., 2020), 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* PAR 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* percentages ~~(Nosova et al., 2019; Shumilovskikh et al., 2018)~~(Shumilovskikh et al., 2018; Nosova et al., 2019) . 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 PAR 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 well 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 PAR 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~~ Period due to forest management methods (Kozáková et al., 2011), which were not ~~practiced~~ practised in south-east Poland.

~~Linking the fossil to~~ Directly comparing fossil and modern PAR values facilitates the interpretation of the fossil record of individual sites. ~~Unfortunately, the details cannot be discussed here. However, the~~ For instance, 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 PAR 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 of *Quercus* trees near the lake. Those taxa at both sites of the paired histogram (Fig. 5) also nicely illustrate the potential use of LDT for the interpretation of the fossil record. Fossil PAR values of *Tilia*, *Corylus* and *Quercus* in the Boreal region are above LDT threshold, whereas all trap PAR values ~~result below~~ are well below the threshold (Fig. 5).

4.4 Limitations and problems

~~Nevertheless, there~~ There are significant differences between the accumulation of pollen in traps and on peatlands and lakes ~~(Lisitsyna et al., 2011b; Pardoe et al., 2010)~~(Pardoe et al., 2010; Lisitsyna et al., 2011b). 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, such as ~~pollen from~~ the inclusion of pollen brought into the trap by trapped insects. These biases appear minor as indicated by the large consistency of the data collected in the PMP database. ~~Also the~~ The comparison of values over this large environmental gradient results in the signal being stronger than the noise. ~~Nevertheless, some~~ Some traps or individual years have unusual values and were removed from the comparison (Table S1). ~~Despite this, the~~ The uncertainty of fossil PAR values is much greater than pollen traps, which is primarily due to the added uncertainty ~~coming from~~ caused by sampling a sediment core, combined with the uncertainty of the age model (Maher, 1981). PAR from lake sediment 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)~~(Pennington, 1979; Davis et al., 1984). Although we carefully selected the best available fossil sites, PAR especially from ~~lake Suminko~~ the Suminko lake and Rõuge Tõugjärv may be biased by ~~lake internal~~ internal lake processes and the addition of stream borne pollen~~respectively. Nevertheless, their~~. Here fossil PAR estimates are still in the range of values found in pollen traps~~.~~, while lake internal processes often lead to PAR values exceeding modern ranges. Such biased fossil PAR estimates can in turn be used to elucidate the sedimentation history. Where detailed knowledge of 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)~~ (see also Bennett, 1983; Bennett and Buck, 2016). 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 large amounts of herbaceous pollen brought by insects and small animals was discussed in the method section and for this reason 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., 2011b), as the plants may overhang the trap opening and their pollen may fall directly into the trap. Reduced PAR 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 PAR hold the 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 are 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~~ metres 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, there are large uncertainties associated with 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, Corylus, Fagus, Fraxinus, Picea, Pinus, Quercus* and *Tilia*~~ the common European trees 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~~ Fossil PAR values can be linked to modern analogues in Europe, opening up possibilities for using fossil PARs to ~~inform on~~ past changes in plant biomass and primary productivity. However, careful selection of fossil sites is necessary to a avoid biases of absolute pollen deposition in the fossil record, which may be caused by lake internal processes such as focusing or the addition of pollen from the catchment or bank erosion.

Modern absolute pollen deposition values clearly show that climate parameters correlate with latitude~~in determining~~ , supporting earlier findings that growing season warmth determines pollen productivity. The effect of regional forest cover is discernible ~~. Minimum values suggest that an 80%~~ in the data. Minimum PAR values rise with increasing forest cover within 10 km of the trap~~results in PAR above 3200 tree pollen~~ , while the maximum values are determined by local site conditions. ~~Fossil PAR data may therefore be of limited use when aiming to reconstruct regional forest cover.~~ At least 140 grains cm^{-2} year^{-1} of tree pollen may be found in treeless vegetation and ~~with each 10% of forest cover~~ tree PAR increases by at least by 400 grains cm^{-2} year^{-1}.

~~Assessment of long-distance transport indicates that values below 80~~ Absolute pollen deposition decreases gradually away from the distribution limit of common trees. Generally, less than 60 grains cm^{-2} y^{-1} ~~for~~ are found at a distance of 200 km from the distribution limit. The following thresholds of PAR for were obtained for a distance of 200 km from a distribution limit: *Quercus* (50), *Carpinus* ~~, *Corylus, Fagus*,~~ (39), *Fraxinus* ~~,~~ (20), ~~*Picea*, Quercus *and*~~ *Corylus* (15), *Tilia* ~~may originate from beyond 200 km of a sampling site. This number~~ (5) and *Picea* (0.3). The obtained threshold of 80 grains cm^{-2} y^{-1} ~~may therefore be used as a general threshold indicating long distance origin of pollen~~for *Fagus* is likely too high. The application of these ~~threshold values holds~~ taxon-specific values holds the potential to refine and adjust reconstructions of tree distributions.

Code availability. Primary trap and fossil pollen data are available in Neotoma Palaeoecology Database https://www.neotomadb.org/. Analysis 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 available 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 available on request on authors.
Code for analysis, derived data and code for figures are available in the https://github.com/vojtechabraham/PMPdatabase.

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.

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