quaternary

Review

Using Annual Resolution Pollen Analysis to Synchronize Varve and Tree-Ring Records

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Abstract: Fossil wood and varved lake sediments allow proxy analysis with exceptionally high, (sub-)annual resolution. Both archives provide dating through ring and layer counting, yet with different accuracy. In wood, counting errors are small and can be eliminated through cross-dating because tree-rings show regionally synchronous patterns. In varved sediments, counting errors are larger and cross-dating is hampered by missing regional patterns in varve parameters. Here, we test whether annual pollen analysis is suited to synchronize varve records. To that end, annual pollen deposition was estimated in three short cores from two lakes in north-eastern Germany for the period 1980–2017 CE. Analysis has focused on *Fagus sylvatica* and *Picea abies*, which show the strongest annual variations in flowering (mast). For both tree taxa, annual flowering variations recorded by forest and pollen monitoring are well represented in varved lake sediments, hence indeed allow us to synchronize the records. Some pollen mast events were not recognized, which may relate to sampling uncertainties, redeposition or regional variations in flowering. In *Fagus sylvatica*, intense flowering limits wood growth in the same year. Peaks in pollen deposition hence correlate with minima in tree-ring width, which provides a link between varved lake sediments and fossil wood.

Keywords: annually laminated lake sediments; dating; mast; pollen analysis; tree-rings; varves

1. Introduction

Annually laminated (varved) lake sediments, like tree-ring records, are invaluable archives for palaeoecological and palaeoclimatological research with annual or even seasonal resolution. They allow the study of, for example, short-lived effects of volcanic eruptions, pathogen outbreaks, forest fires, landscape clearing, species migration or weather extremes. Accurate dating provided, the study of multiple sites along climate gradients and comparison with other accurately dated, high resolution proxies from, e.g., ice cores or tree-ring studies, has the potential to explore leads and lags of climate and environmental change.

However, such time-sensitive applications rely on accurate dating, ideally to the year, which is commonly achieved in tree-ring but not in varve studies. In tree-ring studies, counting errors are commonly small because ring boundaries are usually well-defined. Errors can occur when under very harsh and unfavourable growing conditions trees have only developed very narrow or occasionally no rings at all, the so-called missing rings [1]. On the other hand, intra-annual density fluctuations may be mistaken for annual ring boundaries, so-called false rings [2]. Such counting errors can be detected/eliminated by careful cross-dating against other, overlapping tree-ring records from the region. Cross-dating is possible because variations in tree-ring width are largely determined by weather conditions during or before the growing season and hence are synchronous across regions, at least for each species [3]. Tree-ring patterns may differ between species because the ecological niches, climatic requirements and physiological strategies of tree species differ. For example, in north-central Europe the main limiting factor for radial growth of many broadleaved species including beech (*Fagus sylvatica*) is summer moisture availability whereas pine (*Pinus sylvestris*) growth is sensitive to late winter/spring temperatures. Cross-dating is also used to match tree-ring sequences from living trees with sequences from fossil wood preserved in, e.g., lakes, peatlands or buildings. With sufficient fossil wood available, long tree-ring chronologies spanning several millennia can be constructed [4–7].

Errors in varve counting are clearly higher than errors in tree-ring counting because the seasonal layers are usually less well defined. Furthermore, varve formation is more easily disturbed either due to changes in seasonal sedimentation or to oxygenation of bottom waters. Seasonal deposition, e.g., diatoms in spring and carbonates in summer, may change by orders of magnitude from year to year due to variable weather conditions [8]. Sedimentation may also vary due to fluctuations in lake mixing. Other than in tree-rings, sediments may be redeposited. As a result, the presence of poorly visible, missing or wrong varves is much higher than similar problems in wood. Hence, errors in varve counting may approach 5% even in well-preserved laminations [9], and higher errors are to be expected with poor varve preservation. Validation with parallel cores from the same site may reduce errors but is rarely applied because of the high work load [9]. Cross-dating between sites is hampered because varve thickness (or other varve parameters), unlike tree-ring width, does not show regionally synchronous variations. While the formation of seasonal layers may well be influenced by weather conditions [8], overall sedimentation is determined by complex interactions between water circulation, lake stratification, biomass productivity, food webs, erosion, etc. Variations in varve thickness are hence site specific. Accurate synchronization of varve records is possible with tephra layers, yet only a limited number of tephra layers, often less than one per millennium, is available even in well studied areas, e.g., Europe [10–12], Japan [13] or New Zealand [14]. Furthermore, recently proof has been provided for ^{10}Be as a novel synchronization tool for varved lake sediments [8,15].

Here, we explore whether annual pollen analysis can improve synchronization and finally dating of varved lake records. The idea is based on the observation that annual pollen deposition of beech in pollen traps, which measure atmospheric pollen deposition, varies by three orders of magnitude [16,17]. The observed variations in pollen deposition relate to annual variations in flowering and seed production (mast), which are an adaption to reduce seed predation and hence to optimize sexual reproduction. Mast years, i.e., years with strong flowering and high seed production, are commonly related to particular weather conditions. Among major European forest trees, such weather cues are spatially consistent only for beech, and to a more limited extent, spruce (*Picea abies*) [18]. For beech, the occurrence of mast years is related to summer temperatures in the two previous years, i.e., intense flowering is triggered by a sequence of a cool–wet summer followed by a warm–dry summer [19–21]. Similarly, for spruce, summer temperatures in the two previous years can explain some variation in seed production, again with a cool summer followed by a warm and dry one triggering cone production in year three [22].

The primary question of the present study is whether the high annual variations in pollen deposition from beech and spruce observed in pollen traps are also recognizable and hence useful in varved lake sediments. To this end we apply annual pollen analysis in three short cores from two lakes in north-eastern Germany. Furthermore, we compare annual pollen deposition with tree-ring records from the same area. Intense flowering and seed production require a substantial amount of resources, so that in mast years fewer resources are available for radial growth, and even less when mast years coincide with summer droughts [23]. In long time series, this effect is visible as an inverse correlation between mast years and ring-width chronologies [24]. We explore whether such a relationship is also recognizable between annual pollen deposition and tree-ring width.

2. Materials and Methods

The present study explores whether annual variations in flowering of beech and spruce are represented and recognizable in varved lake sediments. To that end we study pollen deposition in three cores from surface sediments of two lakes in north-eastern Germany. Our primary study site is Lake Tiefer See, because here modern varve formation has been recently studied in several research projects [8,25,26]. Lake Arendsee was selected for comparison as the nearest site with suitable contemporary varves. The pollen records are compared with forest monitoring data of flowering and seed production, pollen trap data and tree-ring data.

2.1. Study Sites and Coring

Lake Tiefer See, in the centre of Mecklenburg-Western Pomerania, is a deep lake in a glacial meltwater valley (Figures 1 and 2). The lake is part of the Klocksin lake chain. In the north, it receives inflow during wet periods from Lake Flacher See. In the south, a permanent connection exists towards Lake Hofsee. Lake Tiefer See has a surface area of ~0.75 km^2 and a maximum water depth of 62.5 m, which makes it one of the deepest lakes in the lowlands of Northern Germany. The lake is surrounded by a narrow fringe of trees and bushes dominated by *Alnus glutinosa*, *Fraxinus excelsior*, *Quercus petraea*, *Q. robur* and *Corylus avellana*. Beyond that fringe, the lake is surrounded by arable land and open wetlands. Forests in the vicinity of the lake are dominated by *Pinus sylvestris*, while both *Fagus sylvatica* and *Picea abies* are rare within a 10 km distance. The Holocene sediments of Lake Tiefer See show several sections with well-preserved annual laminations (=varves), which however cease during the Medieval period around 1200 CE [26]. Varves are again recognizable in the surface sediments starting at about the year 1924 CE. Dating and monitoring have proven that these varves are indeed annual layers [25,26]. Modern varve formation was probably triggered by the construction of a railway-dam that modified the inflow from Lake Flacher See, and by higher nutrient loads from artificial fertilizers. Higher nutrient loads increase primary production of mainly diatoms and other single-celled algae in the epilimnion of the lake. The decomposition of dead algae leads to increased oxygen consumption and finally the formation of anoxic zones in the deepest part of the lake during summer, which is a precondition for varve formation [8]. The modern varves in Lake Tiefer See are calcite varves with a diatom layer deposited in spring, a calcite layer deposited in summer and an organic layer deposited in autumn [25,26]. Due to higher biomass production, the modern varves are much thicker (~4 mm) than varves deposited before the Medieval period (~1–2 mm).

Lake Arendsee is a karstic lake in northern Saxony-Anhalt (Figures 1 and 2). The main lake basin formed already during the Late Glacial period, and was reshaped in further collapses in 822 CE and 1685 CE [27]. Today, the lake has a surface area of 5.14 km^2, a maximum depth of 48.7 m and a mean depth of 29 m. The lake is mostly surrounded by arable land in the south and west and by pine forests and wetlands in the north and east. *Fagus sylvatica* and *Picea abies* are again rare in the vicinity of the lake. Like in Lake Tiefer See, high nutrient loads and the subsequent appearance of bottom water anoxia has induced the formation of varves since the mid-20th century [27]. The varves are characterized by a calcareous layer, precipitated in June to July, embedded in the algal gyttja [27]. A particular feature of the surface sediments is a massive, ~5 cm thick calcareous layer about 10 cm below the sediment surface during coring in 2017. The layer originates from artificial dispersion of calcareous lake marl extracted from the littoral zone across the lake in the autumn of 1995, which aimed to reduce internal phosphorus release by capping of the sediment [28]. However, lake marl application did not result in any significant decrease of phosphorus loads and the trophic level [29]. We counted 22 calcareous layers above this artificial layer, which indicates that each layer corresponds to one summer between 1996 and 2017, confirming that the varves are indeed annual layers.

Figure 1. Map of the study area, indicating Lake Tiefer See and Lake Arendsee, and position of the pollen traps in Delmenhorst, Vilm, Eldena and Lüssow, as well as position of tree-ring study sites. Green areas indicate forest regions, for which flowering data are recorded.

For the present study we analysed pollen deposition in three short cores, two from Lake Tiefer See and one from Lake Arendsee. Sediment cores of 60 mm diameter were taken with a gravity corer (UWITEC, Mondsee, Austria). The two cores from Lake Tiefer See (TSK15-K1, TSK15-K7) were taken in the deepest lake basin at about 62.5 m water depth in 2015. The core from Arendsee (ARS17A) was taken in the northern part of the main basin at a water depth of about 40 m in 2017.

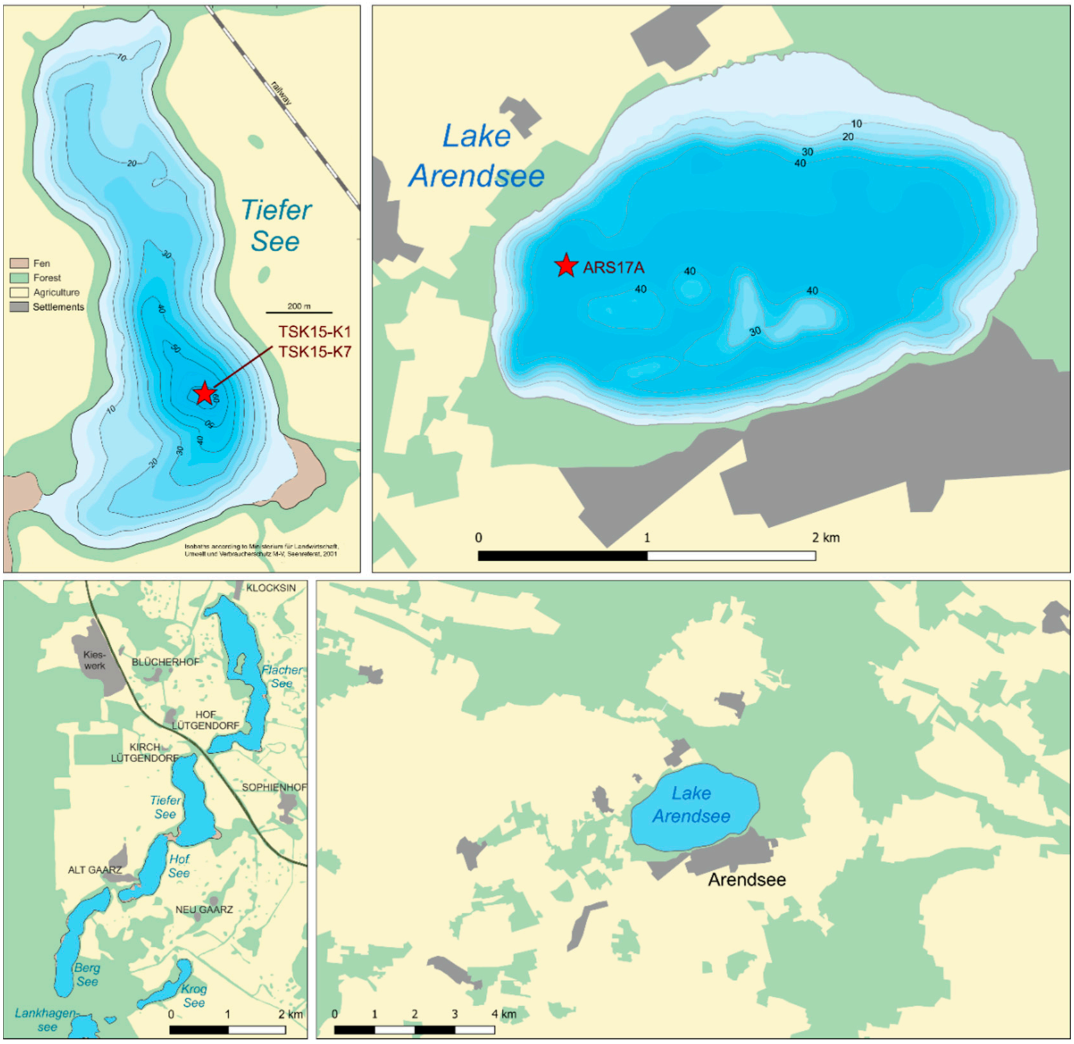

Figure 2. Detailed maps of Lake Tiefer See and Lake Arendsee.

2.2. Pollen Sampling, Preparation and Analysis

Sampling annual layers in lake sediments is difficult for common varves with less than 1 mm thickness. The varves in our surface sediments are instead mostly 2–4 mm thick and allowed us a simple sampling strategy.

Cores from Tiefer See remained in the field for some weeks before transport to the lab to allow sediments to consolidate. The cores were opened and kept cool and dry for about one week before sampling to allow further consolidation. Finally, a 1 × 1 cm longitudinal section was extracted from both cores using a u-channel. From this strand, samples were cut off with a sharp blade directly above the calcareous layer of each varve. In the study area, beech flowers in April and May, spruce in May and June. The calcareous layer is deposited from April to July or longer [25]. Hence by cutting just above the calcareous layer we aimed for samples that include the total pollen deposition of Fagus and Picea from the respective year. In all cores, the chronology is based on layer counting during sampling, performed by two analysts (Table 1). For core TSK15-K7, dating is supported by microscopic varve counts on thin sections from the same core [26].

Table 1. Lake surface sediment cores sampled for annual resolution pollen analysis.

Core	Location	Sample Period
TSK15-K1	Lake Tiefer See (53.59° N, 12.53° E)	1981–2015
TSK15-K7	Lake Tiefer See (53.59° N, 12.53° E)	1980–2007
ARS17A	Lake Arendsee (52.8891° N, 11.4598° E)	1983–2017

Pollen sample preparation followed the standard procedure described by Fægri et al. (1989) and includes treatment with 25% HCL, 10% KOH and 7 min acetolysis at 100 °C. One or two tablets with exotic marker grains (*Lycopodium clavatum* spores, Batch Nr. 3862) were added to estimate pollen accumulation. Treatment with hydrofluoric acid (HF) was only applied for samples of core TSK15-K7. Finally, samples were washed with either ethanol or 2-propanol (isopropyl) and transferred to glycerin (TSK15-K7) or silicon oil (TSK15-K1, ARS17A), respectively. Pollen samples were analysed at 400× magnification with a Zeiss-Axiolab microscope. In samples from core TSK15-K7 complete pollen spectra were analysed. Pollen percentages were calculated on the basis of an upland pollen sum. In samples from TSK15-K1 and ARS17A only FAGUS (and PICEA) pollen as well as exotic marker grains were counted until a minimum of 50 marker grains. The results are presented as annual pollen accumulation rates. To clearly separate between data from plant observations and pollen analysis we set names of pollen types in capital letters [30].

2.3. Identifying Pollen Mast Years

To identify mast intensity in the study area since 1980, we compiled information from three monitoring sources: pollen trap records, flowering intensity observations and fructification observations.

Pollen trap data appear to be the best reference for pollen deposition in lakes. For beech, the longest record available from northern Germany is the 32-year record (1982–2014) from Delmenhorst, about 200 km west of our study sites (Figure 1). Here, atmospheric pollen concentration is measured with a Hirst volumetric trap. The record is published as an annual pollen index, which for each year is calculated as the sum of all daily means of FAGUS pollen grains per cubic metre of air [17]. In our study area of north-eastern Germany, pollen trapping has been ongoing since 2005 at several locations. Here, we use data from three modified Tauber traps [31] (Table 2). In addition to the original design, a galvanized wire mesh with 1-cm grid size is added below the opening to prevent larger animals from entering the trap. The trap in Lüssow is attached to a tree 80 cm above the ground. The traps Eldena and Vilm are installed on the ground, with the opening 12 cm above the surface. The traps are harvested yearly in late September/early October. Samples were sieved (1-mm mesh size) and prepared following the above protocol. HF was applied for samples with high mineral content. Pollen values for these traps are presented as relative values related to a sum of PINUS and QUERCUS.

Table 2. Location and details of the pollen trap records used in the present study.

Trap	Location	Site Type	Sampling Period
Delmenhorst	53.05° N 8.63° E	roof top in the city centre, 17.5 m above street level	1982–2014 (1992 missing)
Lüssow	53.8911° N 13.4781° E	Alder (*Alnus glutinosa*) carr (100 ha) in a large river valley mire	2005–2016 (2006 and 2007 missing)
Eldena	54.0784° N 13.4767° E	old-growth forest with *Fagus sylvatica*, *Quercus robur*, *Acer* spp. and *Carpinus betulus*	2014–2018
Vilm	54.3273° N 13.5396° E	old-growth forest with *Fagus sylvatica*, *Quercus robur*, *Acer* spp. and *Carpinus betulus*	2015–2018

Flowering intensity of the major forest trees, including beech and spruce, has been reported for forest regions across Germany since 1992 [32]. Flowering is classified into four categories, from 1 (no or very weak flowering) to 4 (rich flowering). To explore regional variations, here we include data from three forest regions in northern Germany (Figure 1), as well as mean values for northern and southern Germany.

Finally, extensive and long observations exist for fructification, i.e., the seed production of trees. However, fructification is not a fully accurate proxy for flowering and pollen production in the same year because seed development may be interrupted during and after flowering by calamities, late frosts or other weather extremes. Hence, fructification data is primarily used to fill gaps in the other proxies. We used data compiled by federal forest monitoring from the MASTREE database [32].

2.4. Tree-Ring Chronologies

For comparison we use composite tree-ring chronologies of beech from the Müritz area, close to Lake Tiefer See, and from Boizenburg/Schwerin, about 100 km north of Lake Arendsee (Figure 1). The Müritz composite chronology is created from eight sites of mature closed canopy forest stands. Sample replication is 160 trees with a minimum age of 80 years. The Boizenburg/Schwerin chronology comprises 45 trees from two sites with a strong common signal. All chronologies were detrended using flexible spline curves to remove the inherent age trend and possible influences of disturbances or forest management. The resulting index chronologies are thought to best represent the inter-annual variations in tree-growth caused by climate and allocation to reproduction (mast).

2.5. Meteorological Data

The flowering intensity of beech in one year has been attributed to summer temperatures in the two previous years [19–21]. To validate this relationship for the study sites, we compare flowering data with the July temperature offset ($\Delta_{temp}July_{1-2}$), i.e., mean July temperature one year ago minus mean July temperatures two years ago. Mean July temperatures were obtained from Deutscher Wetterdienst (DWD) for the weather station Waren, about 10 km south-east of Lake Tiefer See.

2.6. Statistical Analyses

To compare the pollen records with monitoring data and the tree-ring chronologies we tested for gleichläufigkeit (glk) and correlation using the R environment for statistical computing (R Core Team 2018). Gleichläufigkeit was calculated with the glk function from the 'dplR' package, version 1.6.6 [33–35].

3. Results

3.1. Pollen Mast Years between 1980 and 2018

In this section we compare all monitoring data to identify years with widespread intense flowering and pollen emission. For beech, the pollen traps from Delmenhorst, Lüssow, Eldena and Vilm show sharp, and largely synchronous variations in annual pollen deposition (Figure 3). Since 1982, the Delmenhorst record shows seven years with very high pollen deposition (pollen index > 500: 1983, 1995, 2000, 2004, 2007, 2009, 2011), and five years with intermediate pollen deposition (pollen index between 250 and 500: 1987, 1990, 1998, 2006 and 2014). The pollen traps from north-eastern Germany show very high pollen deposition in 2014 and 2016, so that we overall assume nine years with very high and four years with intermediate pollen deposition. The trap data correspond well to monitoring data of flowering intensity across northern Germany—in all years with intermediate to high pollen deposition since 1995, mean flowering intensity is higher than 2.5 in all sub-regions, indicating intermediate to strong flowering (Figure 3). Flowering intensity is also high in the year 1992, which is missing from the pollen trap record, hence adding a year with presumed high pollen deposition to the record. In only two years we do observe regional variation in the flowering data. In 2002, only region 2 and 3 indicate intense flowering, in 2018 only region 3 indicates intense flowering.

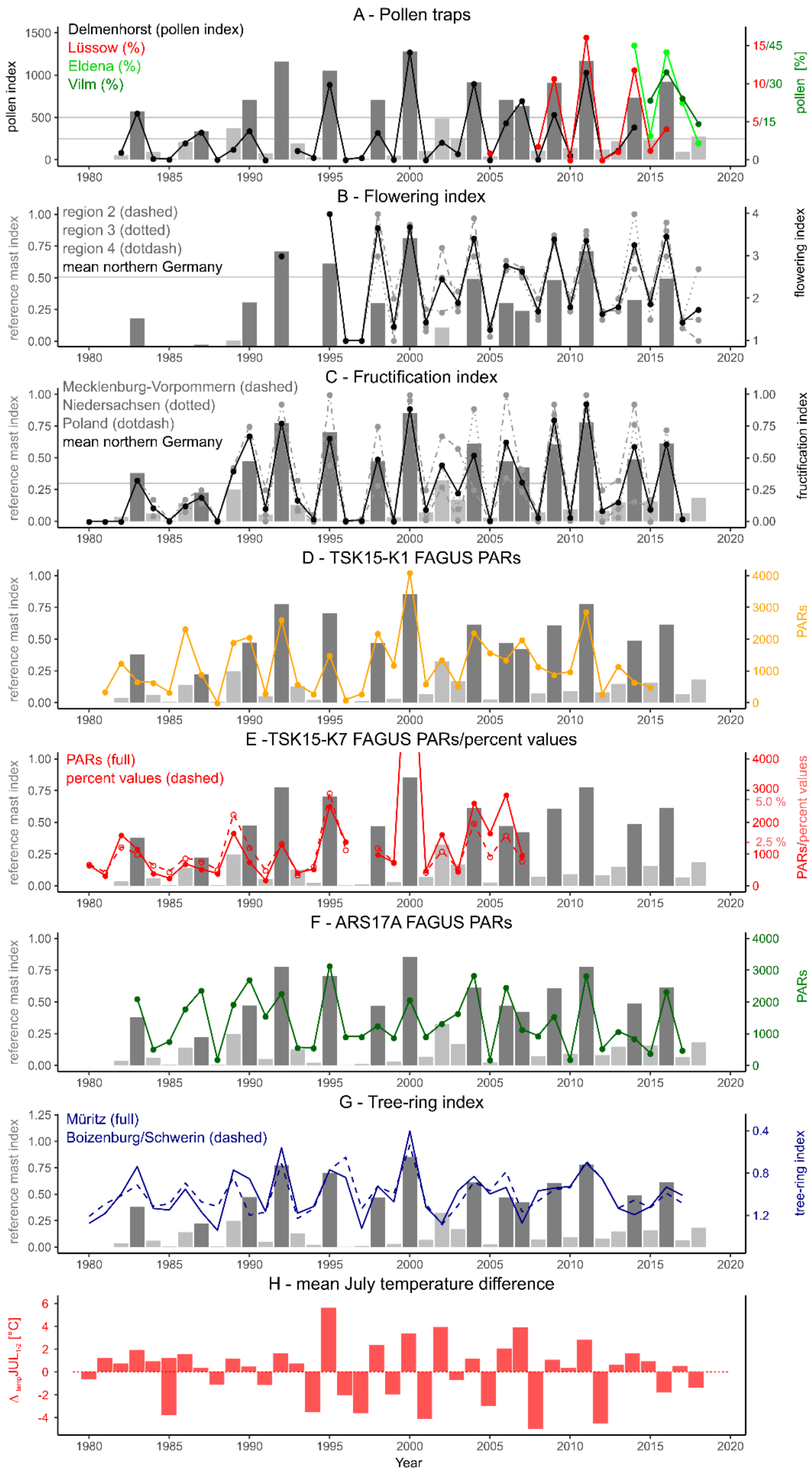

Figure 3. Pollen and forest monitoring data for beech (**A**–**C**), annual pollen deposition in three sediment cores (**D**–**F**), ring width index from the Müritz and Boizenburg/Schwerin composite (**G**) and difference in mean July temperature one year ago minus mean the value two years ago (**H**). Grey bars: reference mast index, dark bars indicate supposed pollen mast years. The pollen index (**A**) for each year is the sum of all daily means of Fagus pollen grains per cubic metre of air. Flowering and fructification index (**B**,**C**) are assigned by forest monitoring. The reference index is calculated as a mean of pollen, flowering and fructification index. Pollen accumulation rates (PARs) (**D**–**F**) are given in pollen grains cm^{-2} yr^{-1}.

Finally, observed fructification also corresponds well to pollen deposition and flowering: in all years with intermediate to high pollen deposition and flowering (except 1987), the fructification index is higher than 0.3 (Figure 3). Such a high index is also observed in 1989, with pollen index and flowering index being low, and 2002, with pollen index and flowering index just below the threshold for intermediate flowering. Again, the regional records are closely correlated. Only in 1998, 2006 and particularly in 2014, the index is clearly lower in Mecklenburg-Vorpommern than in the other regions.

Overall, we observe ten years with supposedly strong, four years with intermediate and two years with possibly also elevated flowering and hence pollen deposition. Flowering and pollen production has been highly synchronous across northern Germany, and intense flowering in almost all cases resulted in strong fructification. Only in 2014, fructification was low in north-eastern Germany although strong flowering is recorded. For this year, late frost was reported, which may have hampered fructification [36]. For further analysis we use a mean mast index composed of pollen, flowering and fructification index as a reference. For calculation of this mean index, all indices were rescaled to the range 0 to 1.

Comparison with mean July temperatures largely confirms the earlier observation that intense flowering in beech is related to a positive July temperature difference in the two previous years, i.e., when mean July temperatures were low two years ago and high one year ago (Figure 3). However, in 2016 intense flowering is observed although the July temperature difference was negative. This observation may indicate that flowering intensity is influenced by further factors.

For spruce, only short pollen trap records are available. They show high pollen deposition in 2009, 2011, and 2015, and somewhat elevated values in 2013 and 2014. Monitoring of flowering intensity started in 1995 and shows more regional variation for spruce than for beech. In several years, intermediate to intense flowering (index > 2.5) is only recorded in one of the three regions: only in region 4 in 2000 and 2003, only in region 3 in 2008 and only in region 2 in 2013 and 2017. In eight years, all regional records indicate intermediate to strong flowering: 1992, 1998, 2004, 2006, 2009, 2011, 2015 and 2018. For the overlapping period, intense flowering matches high pollen deposition in the pollen traps. However, pollen deposition was low in 2018 although intense flowering was reported. Spring and summer of 2018 were exceptionally dry, which may have limited pollen production per single flower. In another four years, the mean flowering index is above 2.5: 2000, 2003, 2014 and 2016. For fructification, only a mean German record and a record from north-eastern Poland are available. Both largely match the flowering index, with the exception that the mean German record indicates strong fructification in 1993 and 2007, although flowering has been low. The Polish record shows strong fructification also in 1990, which hence may have been a year with intense flowering as well. Widespread intermediate to intense flowering is indicated in seven years, regional flowering in another nine years. As a reference, widespread flowering years are indicated in Figure 4 with a value of 1, regional flowering years with a value of 0.5.

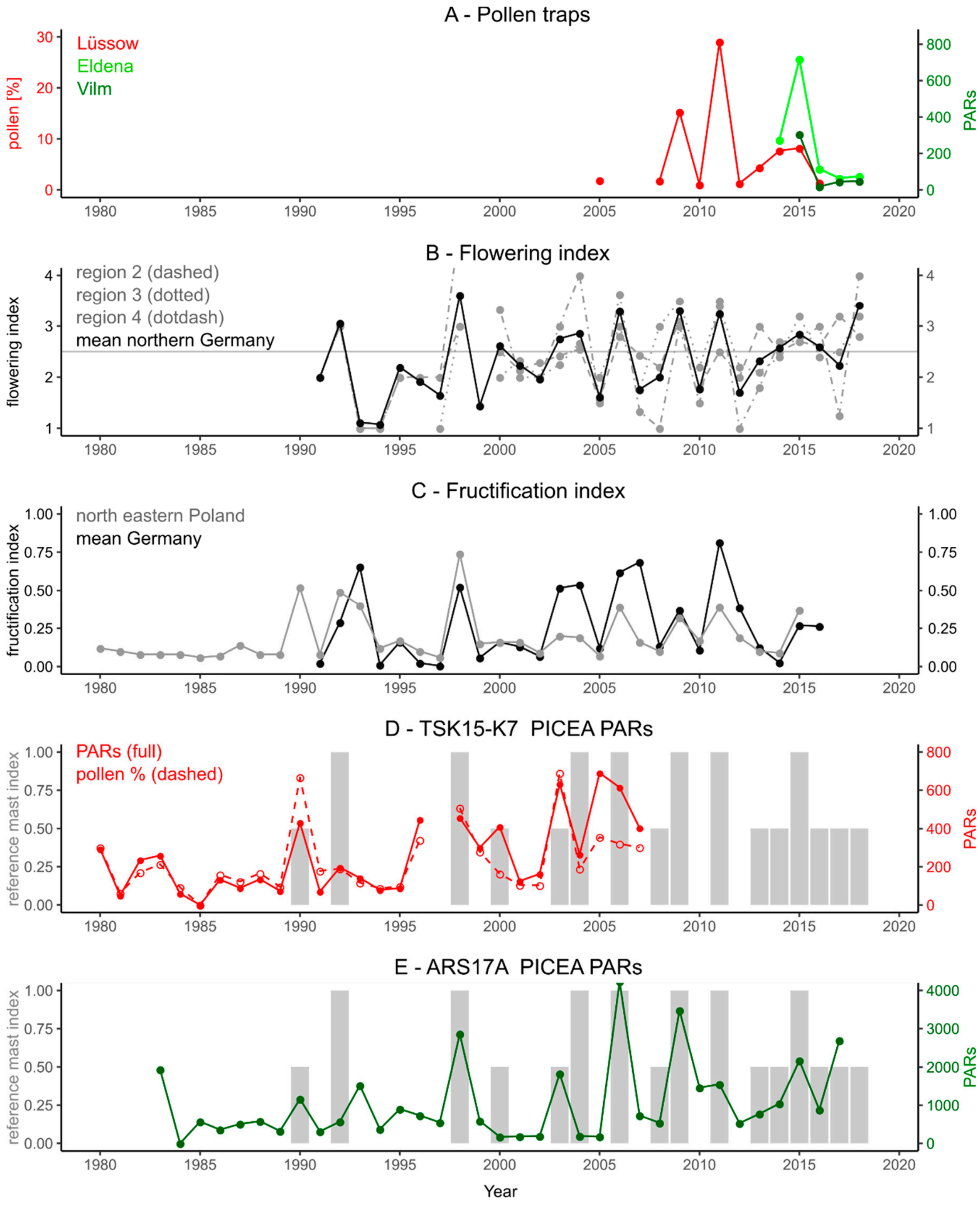

Figure 4. Pollen and forest monitoring data for spruce (**A**–**C**), annual pollen deposition in three sediment cores (**D**–**E**). Grey bars: Long bars indicate supposed intense, short bars intermediate flowering years.

3.2. Pollen Mast Years in the Lake Records

3.2.1. Fagus

Annual pollen accumulation rates (PARs) of Fagus in the three lake pollen records show high annual variations mostly between ~100 and ~4000 grains cm^{-2} year^{-1} (Figure 3). An exceptionally high value of 9300 grains cm^{-2} year^{-1} is observed in TSK15-K7 for the sample of the year 2000. Also other pollen types in that sample have exceptionally high values, which may indicate a sampling error or an error in PAR estimation. All three lake pollen records closely correlate with the reference mast index, with correlation being strongest for ARS17A (Figure 5, Table 3). To compare the number of pollen mast years detected in the lake records with those observed in the monitoring data, ad-hoc classification was applied: A sample is classified as a pollen mast year if the PAR value in this sample is higher than the PAR value in the sample above or below plus the median over all samples in that record. The pollen mast years identified in this way correspond well to the monitoring data; all pollen mast years identified in the monitoring data, except 2007, were recorded in at least one of the lake pollen records (see Supplementary Materials). However, in each record several pollen mast years have not been identified (false negatives): six in TSK15-K1 (1983, 1987, 2006, 2007, 2009 and 2014), four in TSK15-K7 (1987, 1990, 1998 and 2007) and three in ARS17A (1998, 2014 and 2007). On the other hand, only three pollen mast years have been wrongly detected (false positives), one in TSK15-K1 (1986) and two in TSK15-K7 (1982, 2002).

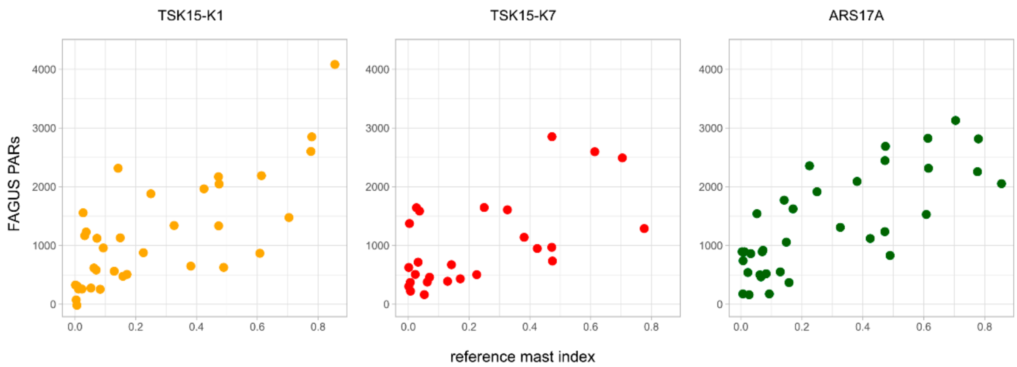

Figure 5. Scatter plots of annual Fagus PARs over the reference mast index.

Table 3. Correlation coefficients and gleichläufigkeit between annual pollen deposition of Fagus and Picea in three lake pollen records and the reference mast index as well as the tree-ring records.

Relationship Tested	TSK15-K1	TSK15-K7	ARS17A
Fagus PARs ~ reference mast index	r = 0.73 $p = 1.124 \times 10^{-6}$ glk = 0.79 (33 a)	r = 0.63 p = 0.00074 glk = 0.79 (25 a)	r = 0.77 $p = 6.133 \times 10^{-8}$ glk = 0.90 (35 a)
Picea PARs ~ reference mast index	-	r = 0.36 p = 0.1702 glk = 0.66 (15 a)	r = 0.56 p = 0.002192 glk = 0.73 (27 a)
Tree-ring index ~ Fagus PARs	r = −0.67 $p = 1.129 \times 10^{-5}$ 1-glk = 0.65 (35 a)	r = −0.67 p = 0.00014 1-glk = 0.85 (25 a)	r = −0.44 p = 0.0082 1-glk = 0.72 (35 a)

In TSK15-K7, full pollen spectra were counted so that pollen percentages of Fagus are also available. PARs and pollen percentages show parallel variations, and hence suggest that either data type is suitable to recognize pollen mast years in the pollen record (Figure 3).

3.2.2. Picea

Annual pollen deposition of Picea in TSK15-K7 and ARS17A shows similarly high variations as pollen deposition of Fagus (Figure 4). Furthermore, pollen deposition in Lake Arendsee is ~5 times higher (maximum = 4200 grains cm^{-2} $year^{-1}$) than in Lake Tiefer See (maximum = 700 grains cm^{-2} $year^{-1}$). The higher values in Llake Arendsee probably reflect the smaller distance to extended spruce forests. Spruce is a rare forest tree in Mecklenburg-Vorpommern. Larger stands occur in Lower Saxony, about 75 km west of Lake Arendsee and 200 km south-west of Lake Tiefer See, and in the Harz Mountains, about 150 km south of Lake Arendsee and 250 km south-west of Lake Tiefer See.

Of the seven mast years indicated by the monitoring data, five are recognizable in the pollen record of ARS17A (1998, 2006, 2009, 2011 and 2015) while two years (1992, 2004) do not show elevated PARs.

A similar situation with intense flowering but low pollen deposition in the pollen traps is observed in 2018. The growing season of this year has been exceptionally dry. So, a possible explanation for lower than expected pollen deposition is that pollen development was hampered by the drought. Precipitation has been at average levels in 2004, so that lower than expected pollen deposition in this year may relate to another effect. Already 2003 was a year with elevated flowering and fructification. Due to resource depletion, spruce may not produce abundant pollen in two subsequent years, even if flowers are present. Both effects are only speculative and need verification. On the other hand, pollen deposition of PICEA was elevated in 1993 despite low observed flowering in northern Germany. However, high values of the mean German fructification record suggest intense mast in central and southern Germany. Mast is also indicated in north-eastern Poland. The higher than expected pollen deposition in Lake Arendsee may hence relate to long-distance transport of pollen from these areas. Similarly, pollen deposition was elevated in 2017 although intense flowering was only recorded in region 2. Finally, pollen deposition was high in 2010, although low flowering and fructification was reported in all areas. The high PARs for PICEA in 2010 may represent redeposition from 2009, which was a strong flowering year. No redeposition is indicated for beech pollen; PARs were high in the mast year 2009 and very low in 2010. However, redeposition may here play a larger role in spruce pollen because this species flowers about four weeks later than beech and the pollen grains float longer. Both effects increase chances that some pollen is deposited at the lake bottom later in the year and hence within the detrital layer that due to the chosen sampling procedure is attributed to the next year.

Only two of the seven mast years indicated in monitoring data are detected in the Lake Tiefer See pollen record TSK15-K7 (1992 and 2006). High deposition is also observed in three years with regional flowering (1990, 2000 and 2003) and three years with only weak flowering (1996, 2005 and 2007). We suggest that the weak link between monitoring data and pollen deposition in Lake Tiefer See is related to the rareness of spruce in the area. Due to the overall low pollen deposition, localized flowering events and random, long distance transport events may strongly influence pollen deposition in that lake.

3.3. Tree-Ring Records

The tree-ring indices from the Müritz area and Boizenburg/Schwerin are closely correlated during the study period 1980–2017, showing very similar growth trends in both areas (Figure 3). The index ranges from 0.4 to 1.4, with the lowest values being observed during the years with most intense flowering and highest fructification: 1993, 1995, 2000 and 2010 (Figure 3). Correlation between monitoring data of fructification and the Müritz tree-ring index (1991–2016) is high ($r = -0.67$) and significant. Similarly we found close negative relationships between annual pollen deposition in the three pollen records and the tree-ring indices (Figure 6, Table 3). The correlation is somewhat closer between the two Tiefer See pollen records and the Müritz tree-ring index ($r = -0.67$ for both records) than between the Arendsee pollen record and the Boizenburg/Schwerin tree-ring index ($r = -0.44$). These results indicate that tree growth is depressed during years of high pollen production. Such a negative relationship between reproduction and growth is well known for beech stands across Europe [19,21,37]. It has been interpreted as a trade-off in resource allocation between reproduction on the one side and radial tree growth on the other [19,37,38]. In addition, beech as a flowering masting species [39] shows a high coherence between flowering intensity and final seed production, i.e., the number of seeds produced is largely controlled by the flowering effort. In fruit-maturation masting species like oak (*Quercus* spp.), fruit production is instead more strongly controlled by the variable ripening of a more constant flower crop [39]. For flowering masting species, a high coherence between pollen production and final seed crop can thus be expected, which is supported by our results. Only in years with unfavourable spring/early summer conditions (strong drought) or in years with late frost events massive flowering will not result in high seed crops [40,41].

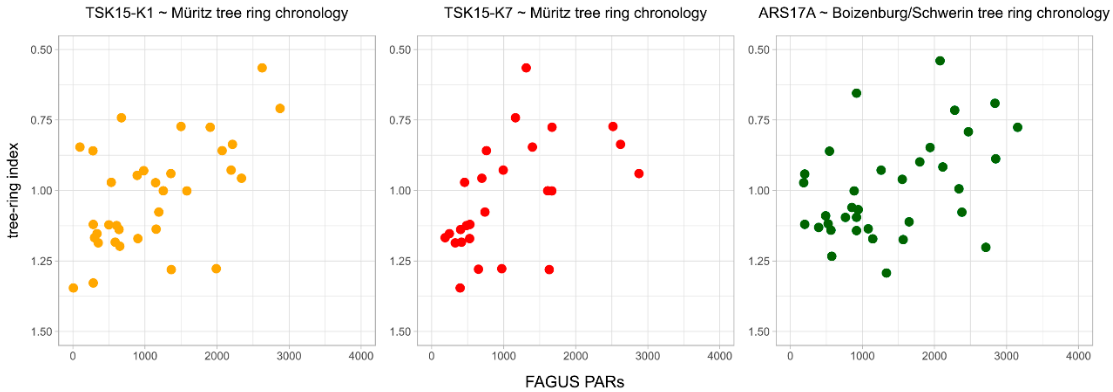

Figure 6. Scatter plots of tree-ring width in the Müritz and Boizenburg/Schwerin composite chronologies over annual Fagus PARs.

4. Discussion

4.1. Annual Pollen Data

The close correlation between the mean masting index and annual pollen deposition in varved lake sediment cores shows that annual variations in pollen production of beech and spruce are indeed recognizable in annually laminated sediments, although not in all cases. For beech all the years with strong flowering have been well identified, yet some of the years with intermediate flowering are missing in one or several lake records, e.g., 2007 and 2014. Only in 2006 and 2007 is intermediate flowering observed in two consecutive years. In 2007, pollen production may have been low despite a high number of observed flowers, e.g., due to resource depletion. For spruce, a similar situation is observed in 2003 and 2004. Alternatively, pollen production and later seed production may have been disturbed by the exceptionally warm and dry conditions during the summer of 2003. In 2018, intense flowering in spruce was recorded yet pollen deposition in the pollen traps remained low. In 2014, fructification in beech was regionally low although flowering was widespread and high. In this case, however, pollen deposition in the pollen traps was also high. Hence, seed production may have been disturbed after flowering, at least in particular areas.

Lower than expected pollen deposition in the lakes, as in 2014, may also be related to sampling uncertainties. The varves in the studied sections were mostly 2–4 mm thick, which allowed us a simple slicing approach. However, particularly in the Lake Tiefer See cores, not all varves are clearly recognizable by the naked eye, and seasonal layers tend to be undulating. Moreover, the surface sediments in both lakes are still soft. Hence, despite the rather large varve thickness, separation of single years may not have been fully successful in all cases. Finally, the pollen signal in lake bottom sediments may be disturbed by redeposition of pollen. In the study area, the main pollen season of beech and spruce occurs between April and June. We have separated samples directly above the distinctive calcareous layer, which is observed to be deposited from April until at least July, but often longer [25]. Hence, the pollen deposition of beech and spruce from one season is expected to be present in the sample of that year. However, pollen initially deposited at the lake margins or in its surroundings may be later redeposited and hence end up in sediments attributed to the following year. In our records, pollen deposition of both trees mostly declines sharply after a year with peak pollen deposition, suggesting that redeposition has only minor effects. Ref. [42] correspondingly found little indication of redeposition in lakes with a large, deep basin and a small littoral zone, like our study sites. Only in some cases, PARs remain high in the year after a mast year, e.g., for Fagus in 1991 (ARS17A) and 2005 (both cores from Tiefer See) and for Picea in 2010 (ARS17A). Redeposition thus may be relevant in some years.

4.2. Outlook

4.2.1. Application of Annual Pollen Records

Flowering and pollen production in beech and spruce vary sharply from year to year. These variations are well represented in pollen traps, and also preserved and recognizable in annually laminated lake sediments. We suggest that such annual pollen counts are potentially useful in three ways.

1. Synchronization and Dating of Varved Sediments

As the main application, we consider annual pollen counts as useful to synchronize varved sediment sections from sites across a region. Annually laminated lake sediments are valuable climate and environmental archives, because they provide up to sub-annual resolution. Exploiting the full potential of varved records requires dating to the exact year, which is potentially provided through layer counting. In reality, however, invisible, blurred, or duplicate layers cause dating errors [9]. Furthermore, many varve records include poorly or non-varved sections, hence creating floating varve sections. So far only tephra layers allow exact synchronization of varve sections for, e.g., transect studies, yet only a few tephra layers are recorded in central Europe [10]. Annual pollen counts instead may provide continuous synchronization. If a sufficient number of long records are available, continuous pollen mast chronologies may be established. Like tree-ring chronologies, they will allow the dating of further (floating) varve sections.

The primary question, however, is whether the pollen mast signal is indeed sufficient to synchronize records. In northern Germany, pollen mast years have occurred regularly since 1990, often every second year. Such a regular pattern provides limited links for synchronization. Long mast records instead show more variation, i.e., clusters of regular flowering and long pauses well suited for synchronization [24]. Robust synchronization requires records with a minimum length. In tree-ring science, typically overlaps of 50 years or more are considered to give reliable cross-dating results. Similar values may apply for mast records. Longer overlap may be necessary in periods with very regular masting. On the other hand, further marker horizons, such as tephra layers, will reduce the necessary overlap. Also analysis of pollen mast in several taxa may reduce the necessary overlap. In addition to *Fagus sylvatica* and *Picea abies*, *Carpinus betulus* and *Abies alba* also show higher flowering variability (Table 4). Whether they provide a meaningful pattern in annually laminated pollen records still needs to be tested. *Quercus robur* and *Q. petraea*—although well known for pronounced seed mast—show low variation in flowering intensity and probably provide no robust pattern in annual pollen deposition. As mentioned before, variable fruit production in *Quercus* is more strongly controlled by the variable fruit ripening rather than by variable flowering.

Table 4. Standard deviation (SD) in the mean flowering index of major forest trees in Germany during the period 1992–2018.

Species	SD
Abies alba	0.52
Alnus glutinosa	0.39
Betula pendula	0.29
Carpinus betulus	0.62
Fagus sylvatica	0.82
Picea abies	0.81
Pinus sylvestris	0.41
Qercus petraea	0.41
Qercus robur	0.39
Tilia cordata	0.37

Synchronization itself may be applied in different ways. Records may be either synchronized using a binary approach, in which each annual sample is classified as mast or non-mast, e.g., in a higher-than-neighbour approach as in the present study. Alternatively, records may be synchronized using their gleichläufigkeit, correlation or the T-values approach. The latter method is used for cross-dating tree-rings. Calculation is based on correlation coefficients between two records, weighted by the length of the overlapping period. Thus, the same correlation values indicate a more reliable match when found in longer records. Although there is no commonly agreed threshold, T-values above 4 are often considered as reliable for cross-dating. For a 50 year overlap a T-value of 4 would correspond to a correlation coefficient of 0.5. The T-value approach will be particularly useful when annual variation in pollen deposition is overlaid by longer term changes in pollen deposition due species expansion or decline.

Synchronization with annual pollen data has spatial limits defined by the area over which trees flower simultaneously. Forest and pollen monitoring show that flowering of beech is indeed synchronous across northern Germany and probably also northern/north-western Poland. Over longer distances, i.e., between northern and southern Germany/Switzerland, several mast years are synchronous (2009, 2011 and 2016), while others were limited to the north (2000, 2004, 2014) or south (2003, 2006, 2018). Hence, both areas would probably need separate pollen mast chronologies. Also Ref. [16], on a N-S transect from Poland to Bulgaria, shows some widely synchronous mast years but also regional differences. Further monitoring data, e.g., those compiled for pollen forecast, will allow defining areas with synchronous variations in flowering and pollen production/deposition.

Application of flowering chronologies will also have temporal limits. In central Europe, beech and spruce show the most prominent variations in annual flowering among all major tree taxa and hence are most suited for the approach. However, in the northern part, beech became an abundant tree only ~2500 years ago while spruce is not native to the area and has only been planted over the past 150 years. To the south both taxa have been present for much longer, so that probably longer mast chronologies covering 6000 years or more may be established. Whether strong mast years in the south are also reflected in pollen records from northern Germany due to long distance transport of pollen still needs to be tested. Such long-distance transport is indicated by continuous yet rare presence of Fagus and Picea in pollen records from northern Germany since about 6000–8000 cal. BP.

Finally, the observed close link between annual pollen accumulation of beech and tree-ring width suggests that varve sequences may be dated through direct linking with tree-ring records. The present sequences are too short to fully validate this option. We therefore aim to extend analysis to past periods with overlapping varve and tree-ring records. For northern Germany, the tree-ring record for beech goes back about 1040 years until 980 CE [43]. In Lake Tiefer See, well varved sections exist before 1200 CE, hence the overlap is about 200 years [26].

2. Tree-Ring Studies

Our results confirm that radial growth in beech is strongly influenced by allocation of carbohydrates to reproduction, i.e., flowering and fructification, which itself is triggered by weather parameters [38,44]. This interplay of climate, reproduction and tree growth implies that climate controls on tree growth are partly indirect and delayed. At least in beech, mast can explain the often-observed influence of weather conditions in the previous year on current year's growth [37]. Disentangling the climatic from the reproduction effect in the analysis of tree-ring width would enhance the quality of tree-ring-based climate reconstructions. The relationship between annual PARs in varves and tree-ring chronologies is therefore a mutual one: First, long tree-ring chronologies can provide a link for long annual PAR records before the era of forest monitoring data, hence help to date varve records. Second, varve-derived records of strong flowering events can help to "clean" tree-ring records from the mast effect—by identifying narrow rings related to mast events—in order to strengthen the inherent climate signal.

3. Climate Reconstruction

In several European tree species, most prominently beech and spruce, masting is highly synchronous and has shown to be triggered by large scale weather patterns, e.g., such as that represented by indices of the north Atlantic circulation (NAO) [45,46]. Reconstructions of mast years may hence be an additional proxy for those indices in the past. For beech, the closest correlation exists between mast and a high positive offset in July temperatures in the two years before mast [18,19,47]. A high mast frequency hence points at high inter-annual variations in summer temperatures while absence of mast instead indicates low variation.

4.2.2. Practical Issues

From previous experience the main practical challenge of annual pollen analysis is sediment sampling. Here, we sampled rather thick varves but even then, sampling was not easy because of several not well-defined varves and soft sediments. In older, more consolidated sediments, varves are commonly as thin as 0.5 mm or less. In this case, different sampling strategies using magnification will be required. We sliced actual samples from a longitudinal core section of about 1.5 × 1.5 cm across, but also smaller sections (e.g., 0.5 × 0.5 cm) would contain a sufficient number of pollen grains while at the same time providing higher sampling accuracy. Using such narrow core sections would also simplify parallel sampling for validation.

A second limitation derives from the large number of pollen samples. Full spectrum pollen analysis is time consuming, and certainly limits analysis of many hundreds or thousands of annual samples. Here, we applied simplified analysis, i.e., only Fagus pollen, Picea pollen and the exotic marker were counted. The exotic marker counts were as high as ~500 for samples from Tiefer See but as low as ~50 in samples from Arendsee, which appears to be sufficient for reliable PAR values because of the high variations. Thus, analysis time was reduced to about 20 min per sample, i.e., analysis of 10–15 samples per day is feasible. These efforts will often remain too high for complete analysis of long varve sections, but may be worth doing when the focus is on shorter time periods.

Supplementary Materials: The following is available online at http://www.mdpi.com/2571-550X/2/3/23/s1, Figure S1: Identification of mast years in monitoring data and lake sediments.

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