Local versus extra-local representation of Holocene vegetation change in North-East Germany

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Acknowledgements

Summary

Projected climate change is expected to put increasing pressure on already fragile European forest ecosystems. This provides a challenge for future forest management and calls for sustainable forest management strategies based on knowledge of natural forest dynamics. Especially the European beech, one of the most dominant trees in central Europe that is of great economic importance, is expected to be threatened by the projected increasing severity of droughts. While conservation of (near)-natural beech forests is high on the political agenda, with 94 beech forests in 18 countries being listed as UNESCO World Heritage Sites, the status of beech forests as a natural vegetation-type in northern Europe has been questioned by paleoecologists. Numerous studies on pollen records from northern European lowlands reveal that the expansion of beech here was facilitated by human activities which generated openings in forests that were densely occupied by elm, linden, hazel, birch, oak and pine trees. Contrasting results from central and southern European pollen records suggest that not human activities, but rapid cooling events facilitated the establishment of beech. These contrasting results have been a subject of debate and may be the result of methodological differences between these studies, as the pollen records studied in northern Europe originate from small forest hollows while the pollen records from central and southern Europe originate from larger lakes.

Pollen assemblages from differently sized basins have been shown to reflect the vegetation at a different spatial resolution as large lakes collect pollen from a larger area than smaller basins such as forest hollows. The exact differences remain difficult to quantify as they also depend on site-specific characteristics such as the heterogeneity of the landscape and specific properties of the pollen types in the record. To explore the differences between pollen records from differently sized basins and specifically the reflection of the establishment of beech, a pollen record was obtained from a lake in NE Germany nearby a forest hollow that was previously studied. The pollen record from the forest hollow shows that the expansion of beech around 3000 years ago was preceded by a disturbance of the vegetation, possibly caused by human activities in this area.

Comparison of the pollen record from the forest hollow to the newly obtained pollen record from the lake provides the context of the disturbance but a direct causal link between these disturbances and the expansion of beech, which occurs around 2100 years ago in the pollen record from the lake, is more difficult to establish. Although this is in line with the hypothesis that discrepancies in causative relations may arise from differences in the spatial resolution of pollen records, a comparison to other lakes in the area reveals that the timing of population expansion was not synchronous in NE Germany and thus climate change was rejected as the main trigger on a larger scale. These findings contribute to the debate on underlying processes connected to the establishment of beech in northern Europe by revealing a different signal in a pollen record from a lake compared to a forest hollow, but also suggest that the trigger for beech establishment in northern Europe may have been different than for central and southern Europe.

The facilitation of beech establishment by human activities challenges the view of beech being a naturally dominant tree in northern European forests and seriously questions the validity of nature-based forest management strategies in these 'man-made' forests. In this light, true nature-based forest management may entail active promotion of more drought-resistant trees such as lime that was disadvantaged by human activities in forests and indirectly by the facilitation of the establishment of beech.
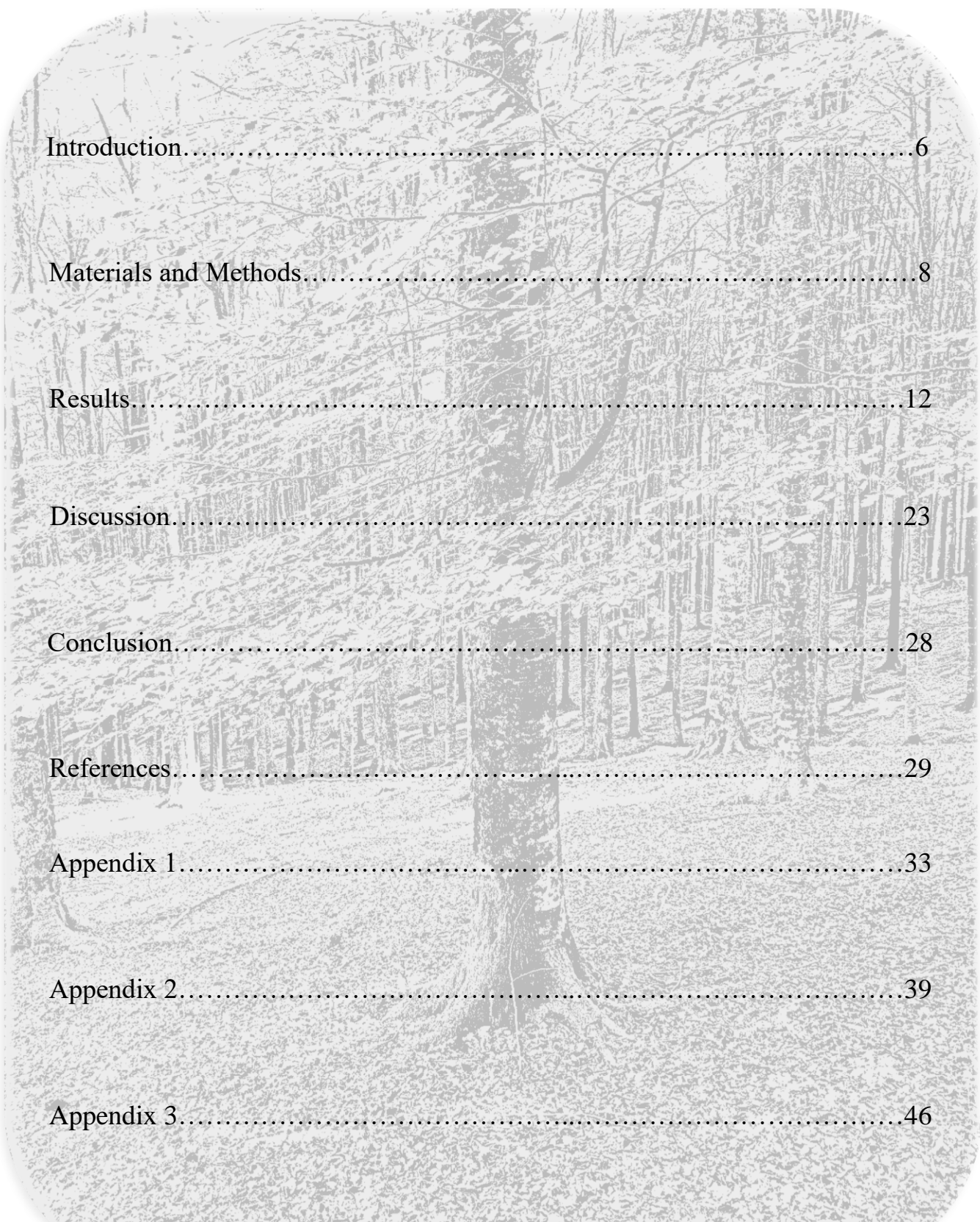
Abstract

The current successful establishment of the European beech (*Fagus sylvatica)* in northern European lowlands that contrasts with previous interglacials has been a subject of debate among palynologists. It is argued that disturbance by anthropogenic activities facilitated its expansion during the current interglacial and strong evidence from pollen diagrams from forest hollows, documenting local vegetation change, supports this theory. Contrasting results from central and southern European pollen diagrams that document regional vegetation change, however, show that the expansion of *F. sylvatica* was triggered by a short-term climate event. These contrasting finds imply that either the processes connected to the establishment of *F. sylvatica* were different throughout Europe or that multiple processes connected to the expansion of *F. sylvatica* were acting on different spatial scales.

Combining a vegetation reconstruction from a forest hollow with one from a lake makes it possible to understand the spatial versus temporal dynamics of these processes connected to the establishment of *F. sylvatica.* The area of terminal moraines in NE-Germany offers a high density of lakes as well as forest hollows, allowing this type of combination. Pollen data from a forest hollow in the Peutscher forest document that the population expansion of *F. sylvatica* at the site was triggered by a disturbance event. To place this event in a broader context, a core was obtained from a nearby lake, Stribbowsee.

Results show that the expansion of *F. sylvatica* and the processes that triggered the to the expansion are differently recorded in a the pollen diagram from a lake versus a forest hollow. This supports the theory that the processes connected to the establishment of *F. sylvatica* were differently recorded in lake records from central and southern Europe than in records from forest hollows in northern Europe. However, comparison to other lake records reveals that on a large scale, climate was probably not the most important trigger for the expansion of *F. sylvatica* in NE Germany and that human activities may have impacted the expansion here also on this larger scale.

Contents

1. Introduction

Increasing severity of droughts are expected to put additional pressure on already fragile European ecosystems. Especially the European beech (*Fagus sylvatica*), one of the most dominant trees of Central Europe, is very sensitive to drought and therefore, models project growth declines in the range of 20-50 % by 2090 (Martinez del Castillo et al., 2022). With 94 beech forests in 18 countries being listed as UNESCO World Heritage Sites (https://whc.unesco.org/), these projections call for appropriate forest management strategies based on knowledge of forest dynamics. The information that can be gained from experiments and observations, however, is limited to short-term processes that do not entail the full extent of these dynamics as trees often have long life-spans and reproduction periods. Therefore, palynological research based on pollen grains deposited in lakes and wetlands that give an indirect record of vegetation development through time is needed to provide additional information on long-term forest dynamics.

The processes involved in the establishment and expansion of beech populations have been a subject of debate among palynologists. Its widespread success contrasts with previous interglacials, where the tree played only a minor role in forests North of the Alps (Pott, 1997; Magri et al., 2006). Therefore, is argued that large-scale anthropogenic activities during this interglacial contributed to the expansion of *F. sylvatica*. This theory is supported by numerous studies from northern European lowlands (Björkman & Bradshaw, 1996; Björkman 1999; Bradshaw & Lindbladh, 2005; Bradshaw et al., 2010; Bradley et al., 2013) that show establishment and expansion of *F. sylvatica* after anthropogenically caused disturbance events such as forest clearings. The facilitation of the expansion of *F. sylvatica* by anthropogenic activities challenges the validity of the view that *F. sylvatica* is the naturally dominant tree species in forests of northern European lowlands. With this, it contrasts with ecological descriptions of for example Leuschner & Ellenberg (2017) that state that *F. sylvatica* "will eventually outcompete all other central European tree species on soils that are not too dry, too nutrient-rich or too cold." However, it is supported by the notion that advanced *F. sylvatica* recruits require canopy disturbance to develop into mature trees (Janik et al., 2016).

A yet different perspective developed from studies on lake records from central and southern Europe that attribute the expansion of *F. sylvatica* to short-term climate events such as the 8.2 kyr event that describes the sudden decrease of temperatures and increasing availability of moisture around 8.2 k years ago (Tinner & Lotter, 2006). Climate as a driving factor for the expansion of *F. sylvatica* during the Holocene is also valid in the montane area of South-western Bulgaria according to Tonkov (2003). It has been a subject of debate whether these differing finds are indicating that underlying processes connected to the establishment of beech in central and southern Europe were different from the processes involved in northern Europe or if these discrepancies result from methodological differences between the studies from these areas (Bradshaw, 2005; Tinner & Lotter, 2006).

The main methodological difference between the studies from central and southern Europe versus northern Europe is the use of pollen records from small forest hollows in northern Europe versus the use of pollen records from lakes in central and southern Europe. Jacobson & Bradshaw (1981) developed a model that visualises the effect of basin size on the spatial resolution of pollen records (Figure 1). This model reflects the increasing proportion of pollen from regional origin in larger basins and the increasing proportion of pollen from local origin in smaller basins. Other than basin size, taxon-specific properties of pollen such as fall speed determine the pollen source area (Jacobson & Bradshaw, 1981). High fall speeds are observed for large and heavy pollen grains such as *Fagus* but also for pollen that tend to form larger clumps such as *Tilia,* that is not adapted to wind dispersal but to dispersal by insects.

Nonetheless, pollen records from lakes generally reflect the vegetation development on a larger scale than pollen records from a forest hollow and thus their spatial resolutions must be differently interpreted.
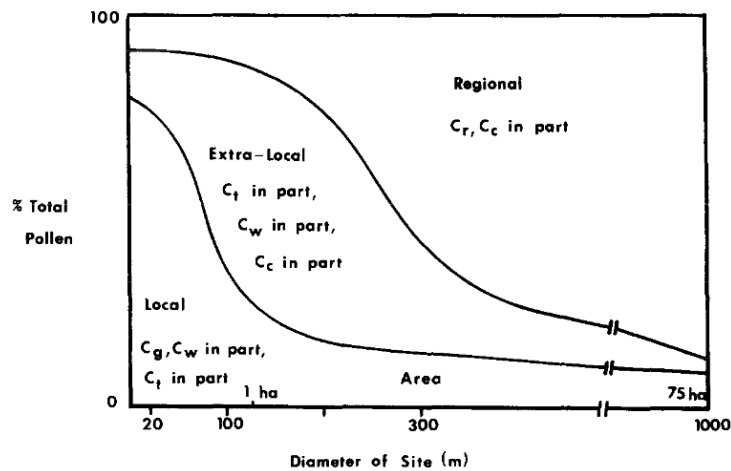

Figure 1: Relationship between basin-size and the relative proportions of pollen originating from different areas around the site with the relevant components per area: Cg=gravity, Cw=surface runoff, Cc= above the canopy, Cr=rainfall (Jacobson & Bradshaw, 1981)

The spatial resolution of hollows versus lakes may also determine the signal of underlying processes and for example Kuosmanen et al. (2016) show that the impact of climate change on the vegetation was more significant in pollen diagrams from lakes compared to forest hollows reflecting stand-scale forest dynamics. At the local scale, changes were found to be more dependent on small-scale disturbances and local site characteristics. Similar results are found in a study on the importance of basin size for the detection of local human activities in Scotland (Davies & Tipping, 2004). In this study area, it appears that the fragmentary distribution of soils that were suitable for agricultural activities hampered signals of agricultural activities in pollen records from large basins while more clear signals were prevalent in small basins. These findings support the hypothesis that the processes connected to the establishment of beech may have been the same throughout Europe but that the signals picked up by pollen records from differently sized basins reflect the processes on a different spatial scale.

In this study, this hypothesis is tested by comparing the signals captured in a forest hollow with signals that were captured in a nearby lake. The terminal moraines of NE-Germany allow such a comparison as this area has a high density of lakes as well as forest hollows. Bradley et al. (2013) studied a small forest hollow in the Peutscher forest and found that the expansion of *F. sylvatica* was triggered by a disturbance event. To compare these findings to the vegetation change in the larger area, in 2012, two cores were retrieved from Stribbowsee, a small lake in the proximity of the hollow. This comparison contributes to the debate on the underlying processes connected to the establishment of beech since the last ice-age by exploring the role of spatial resolution for the interpretation of disturbance versus climate signals in pollen records. The comparison started in Göttingen in 2012 as a student project but was never finished. Thus, the study presented here is based on existing data that was obtained in Göttingen combined with new data, resulting in a high-resolution pollen record for Stribbowsee that allows for the interpretation of the reflection of vegetation development and underlying processes in pollen records with a different spatial resolution.

2. Materials and Methods

2.1 Site description

Peutscher forest is situated north of Neustrelitz and east of the Muritz National Park in Mecklenburg-Vorpommern, NE Germany. The location of the Peutscher forest with respect to the natural distribution of *F. sylvatica* in Europe is indicated in Figure 2. The landscape was formed by the glaciers of the last ice age, leaving many lakes, kettle holes and valleys within terminal moraines. Stribbowsee is situated in the northern part of the Peutscher forest at 53°25'54.8"N 13°04'38.5"E about 8 km north of the city of Neustrelitz. The lake is about 220 meter in length and 154 meter wide at its broadest part. Carlshof forest hollow is situated about 530 meters Southeast of Stribbowsee as shown in Figure 2.

   The forest surrounding the hollow is currently dominated by *F. sylvatica* and *Pinus sylvestris* trees next to managed stands of *Picea abies.* The forest composition of the wider areas of the lake also includes *Alnus glutinosa, Quercus robur, Quercus petraea* and *Larix decidua*, with *A. glutinosa* trees surrounding the lake (J. Brockhaus, 2014).

   Annual mean temperatures in this region were 8 ℃ during the period of 1961-1990 with the lowest monthly averages in January (-1.1 ℃) and the highest monthly averages in July (16.9 ℃). Mean annual precipitation during this period was 584 mm/y (www.dwd.de).

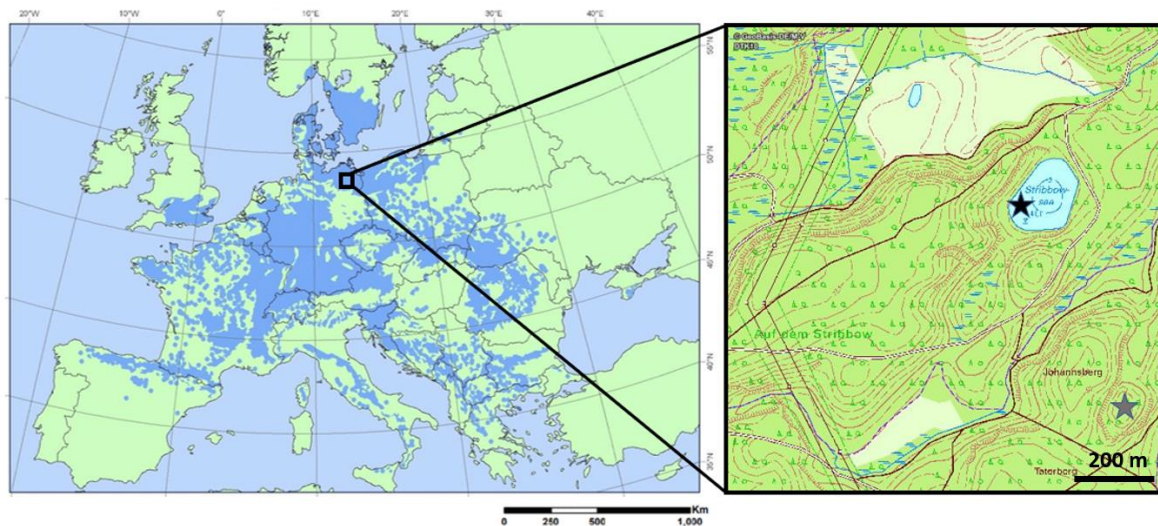*Figure 2: Natural distribution of the European beech (F. sylvatica; image slightly adapted from www. Euforgen.org) and the location of Stribbowsee (black star) and Carlshof forest hollow (grey star) in the Peutscher forest (Map retrieved from: https://www.wald-mv.de/landesforst-mv/Forststruktur/)*

2.2 Sampling

Sediment was collected in the autumn of 2012 from two locations in the lake Stribbowsee (Figure 3) with a 1 meter long Livingston-Piston corer. A total of 8 m were taken from the centre of the lake at a depth of 5.8 meters (hereinafter referred to as Upper core). Pushing through the upper 4 meters of sediment, another 3.58 meters of core were taken from the south-western edge of the lake (hereinafter referred to as Lower core). The cores were stored in a dark cooling cell at 4 ℃ at the Georg-August University in Göttingen, Germany and transported to Utrecht University, the Netherlands in 2021 for further study.

The initial analysis and coring of Stribbowsee was part of a student project of Göttingen University. For this project, 94 samples were taken from the Lower core, of which 45 were analysed and an additional 15 samples from the Upper core, of which 2 were analysed. Most of the already available samples were analysed for this study and, since the Upper core is the focus of this study as it contains the pollen signals for the establishment and rise of *F. sylvatica*, this core was resampled at a high resolution in Utrecht. In total, 65 additional samples were taken, 62 of which originated from the Upper core and a total of 110 samples were analysed to combine with the available data from the initial project in Göttingen. A detailed overview of the sampling/processing location and the analyst per sample is provided in Table 1 for the Upper core and Table 2 for the Lower core (Appendix 1).

Figure 3: Location of the cores that were taken from Stribbowsee, NE Germany. The blue star indicates the location of the Upper core and the red star indicates the location of the Lower core.
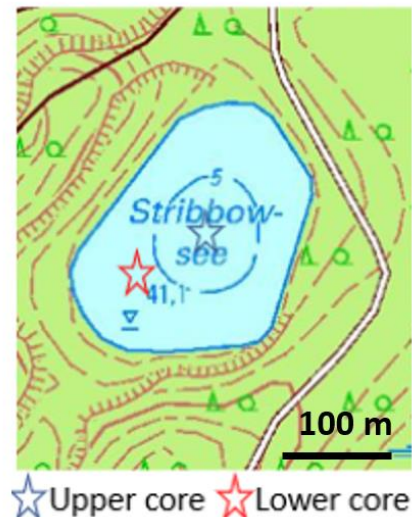
2.3 Pollen preparation

After the sampling, that occurred in 2012/2013 in Göttingen and in 2021 in Utrecht, samples were prepared for pollen analysis. *Lycopodium* spore tablets were added as a marker grain to allow for the calculation of pollen concentrations. The approximate amount of *Lycopodium* spores added per sample is depicted in Table 1 (Appendix 1). Unfortunately, the amount of *Lycopodium* spores that was added to the samples in Göttingen was not documented. The procedures that were followed differed between the two different labs where the samples were prepared (Table 3).

Table 3: Preparation methods of pollen samples in Göttingen and Utrecht

GÖTTINGEN	UTRECHT
1) After the addition of the marker spores, humic compounds were removed from the samples by treatment with a 10% KOH solution. Hereafter, samples were heated in a water bath to 90 degrees 10 minutes. These steps were followed by the addition on 10 % HCL to remove carbonates. **2)** 40% HF solution was added to the samples to remove silicates and the samples with the solution were heated in a water bath at 90 degrees for 30 minutes. Hereafter HCL solution was added . **3)** The samples were washed with acidic acid to remove water and acetolysis was done for 2 minutes. **4)** Samples were stained with safranine and transferred to Eppendorf tubes. Finally, the samples were dried in the stove and glycerine was added.	**1)** After the addition of the marker spores, humic compounds were removed from the samples by treatment with a 5% KOH solution. Hereafter, samples were heated to 70 degrees 60 minutes and subsequently sieved with a 200 μ mesh to remove large organic particles. These steps were followed by the addition of 10 % HCL to remove carbonates. **2)** The samples were washed with acidic acid to remove water and acetolysis was done for 4 minutes. **3)** A solution of sodium polytungstate (density=2) was added to the samples. Samples were vortexed to mix well, after which they were centrifuged and decanted. **4)** Samples were transferred to Eppendorf tubes. Finally, the samples were dried in the stove and glycerine was added.

After the pollen preparation, slides were prepared from the resulting substances in the Eppendorf tubes. Per slide, ~500 terrestrial pollen were counted under 400x magnification and identified using pollen identification keys of Beug (1961) and Moore & Webb (1991). In addition, the pollen reference collection at the University of Utrecht was used aiding identification.

2.4 Loss on ignition

In Göttingen, samples were taken for LOI analysis at the same intervals as the samples that were taken for pollen analysis for the Lower core. For the Upper core, samples were taken separately at ~10 cm intervals. The samples were dried in an oven at 105 ºC and subsequently at 500 ºC and 950 ºC while the weight of the samples was taken after each step of drying to assess the dry content, organic matter content and carbonate content respectively. In addition to this data, which consists of 228 datapoints describing the carbon and carbonate content, organic matter content of 23 samples from the Upper core was determined in Utrecht by drying the samples at 105 ºC and 550 ºC, taking the weight of the samples after each step.

2.5 Age determination

For age determination, terrestrial macrofossils from 6 depths from the Lower core were radiocarbon dated at CHRONO, Queens University of Belfast, United Kingdom (Table 5 in Appendix 1). Due to the scarcity of macrofossils in the Upper core, 4 bulk samples and 1 terrestrial macrofossil (*Alnus glutinosa* inflorescence) were sent for radiocarbon dating to the Poznań Radiocarbon Laboratory, Poland (Table 4 in Appendix 1). Additionally, the Laacher See tephra that was observed near the bottom of the Lower core (Figure 4) was used for the construction of the age model. As an age, the newly published age correction of Reinich et al. (2021) was used. The construction of an age depth model for the two cores was executed with the Clam package (Blaauw, 2010) in the statistical software R (R Development Core Team 2014). Overlap in the path that the pollen assemblages of the Upper and Lower core followed in the plane of the first two principle components was used to link the cores together and provide an age-depth model for the entire pollen sequence from Stribbowsee.

Figure 4: Laacher See tephra in core S-A4 at 816 cm depth (bottom of the Lower core). The depth of this tephra was used as an additional dating point with the age set at the newly published date for the Laacher see eruption of 13,006 ± 9 cal yr. BP (Reinig et al., 2021).

2.6 Data visualization

The obtained pollen counts were converted to percentages, using only pollen of terrestrial origin in the pollen sum. For Stribbowsee and Carlshof forest hollow, the same pollen sums were used to allow the comparison. Cyperaceae, that is known to grow on site in the forest hollow, and *Humulus*, that was found to be overrepresented in the Upper core of Stribbowsee most likely due to the use of the lake for hennep retting, were therefore excluded from both pollen sums. Percentages were visualized using Tilia software version 3.0.1. Ordinations were based on the covariance matrix after square root transformation of the data using the vegan package (R package version 2.5- 7; https://CRAN.R-project.org/package=vegan; Oksanen et al., 2013) in the statistical software R (R Development Core Team 2014). A zonation was made with CONISS in Tilia software and statistical significance of the zones was determined with the broken stick method using the rioja package (R package version 0.9-26; https://CRAN.R-project.org/package=rioja; Juggins & Juggins, 2020) in R.

3. Results and Interpretations

3.1 Ordinations and age-depth model

PCA analysis was performed on the two datasets from Stribbowsee and the dataset from the forest Hollow. The broken stick method indicates that the first 4 principal components are significant, explaining 36 %, 22%, 11% and 9% of the variance respectively. Figure 5 shows scores of the first two principal components PC 1 and PC 2 with the succession in time visualised by the connection of successive points with line segments. The loadings of the principal components are shown in Figure 6.
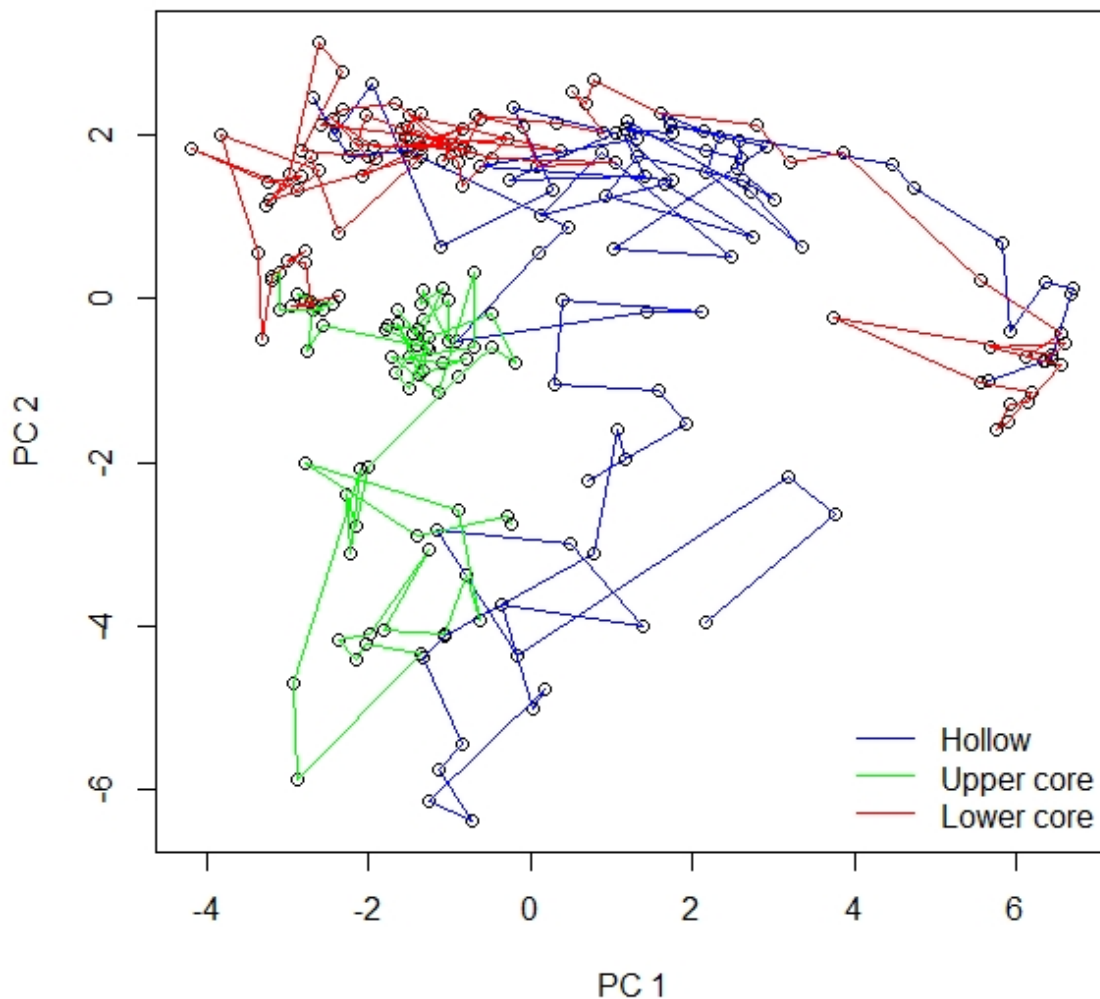

Figure 5: Scores of the PCA that was performed on the datasets from Stribbowsee and Carlshof forest hollow. The loadings of PC1 and PC2 are given in Figure 6.

The development of the pollen assemblages both in the samples from Carlshof forest hollow and from Stribbowsee follows a path from right to left in the figure first, reflecting a shift from pollen assemblages dominated by *Pinus, Betula* and *Juniperus* to increasing values of *Ulmus, Corylus, Tilia, Fraxinus, Alnus* and *Quercus*. From around the time where the Upper and Lower core overlap in the PCA-plane onwards, a shift from dominance of *Corylus* to *Fagus* and *Carpinus betulus* is clear. This same development is occurring in the pollen assemblages from

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Carlshof forest hollow, but a clear distinction between the two sites is visible due to structurally higher values of PC1 for the pollen assemblages from Carlshof forest hollow, caused by the overrepresentation of *Alnus* and *Quercus* in the Stribbowsee record relative to the forest hollow record and the overrepresentation of *Pinus* in the hollow record relative to the Stribbowsee record.
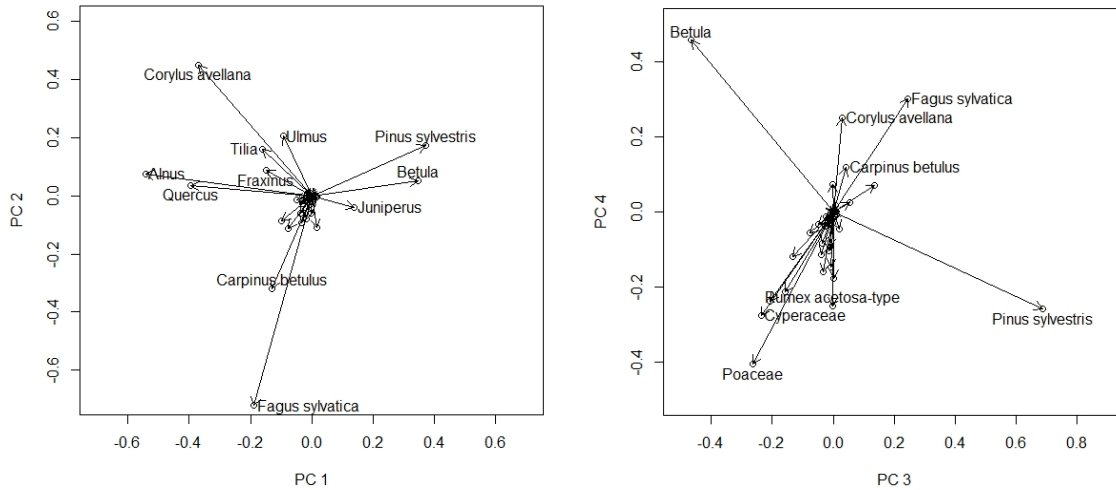

Figure 6: Loadings for PC 1 & 2 (left) and PC 3 & 4 (right). Labels are only provided for the most important taxa in the loadings figure. PC1-4 are significant, explaining 36 %, 22%, 11% and 9% of the variance respectively.

The PCA reveals an overlap in the path along the plane of the first two principal components of the Upper and Lower core from Stribbowsee (Figure 7). The similarity of the path of the two cores from Stribbowsee in the plane of the first two principal components was used to combine the two sequences into one so that depths 781 and 761 (Upper core) respectively coincide with depths 487 and 467 (Lower core).

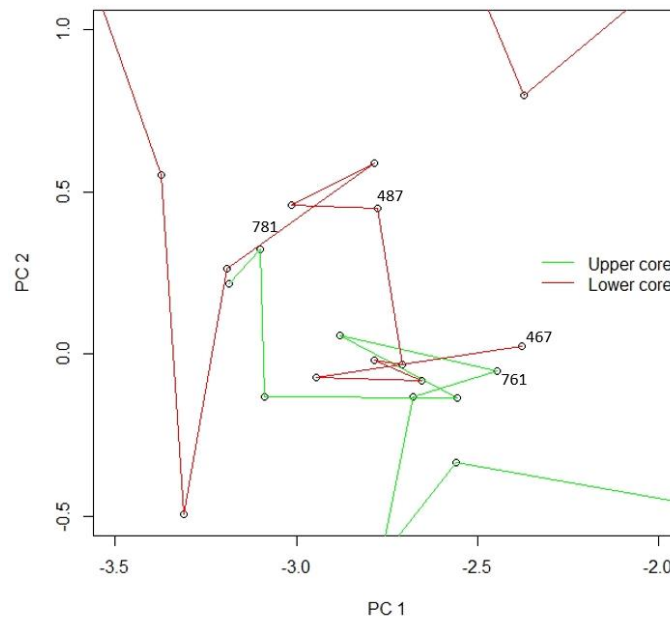*Figure 7: Overlap in the path followed by the Upper and Lower core from Stribbowsee along the plane of the first two principal components. From this it appears that the pollen assemblages between 781 and 761 (Upper core) and the assemblages of 487 and 467 (Lower core) have a similar development in the plane, although the values of the pollen assemblages from the Lower core for PC1 appear to be structurally higher by 0.1-0.4.*
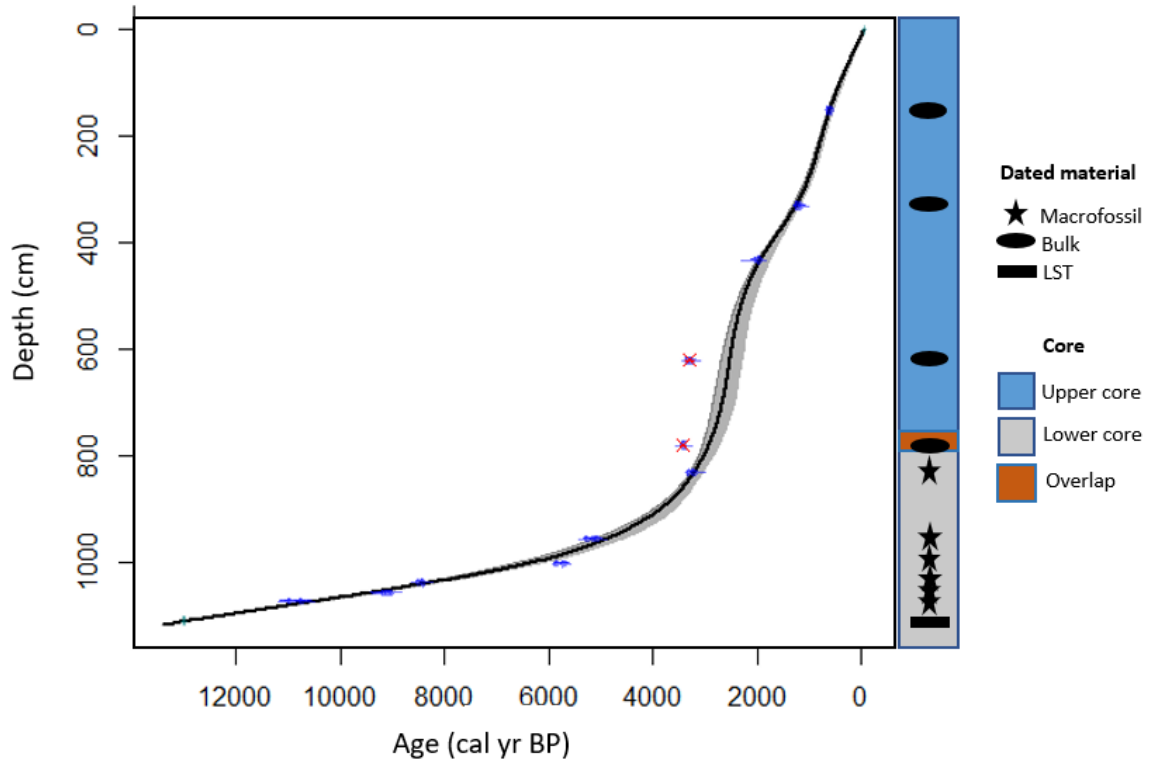
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Figure 8: Age model for cores from Stribbowsee. Sediments from the Lower core have been deposited from 13400 to 2841 cal. BP and the sediment from the Upper core can be dated to 2986 to -60 cal. BP. Two dates from the Upper core were marked as outliers as these are perceived as less reliable than the surrounding dates that originate from macrofossils of terrestrial origin.

3.2 Loss on ignition

LOI data is shown in Figure 9. The top part of the figure shows the LOI for the Upper and Lower core as an entire sediment sequence through time, using the matched part of the PCA as a reference for the overlap in time. The LOI data for the overlapping parts of the cores is given in Figure 10. Although the organic matter content of the Lower core is higher, possibly as a result of sediment focussing in the lake, the general trend appears to be similar. The organic matter content of the samples that were analysed in Utrecht also show a similar trend compared to the samples that were analysed in Göttingen but percentages are lower, possibly due to methodological differences.
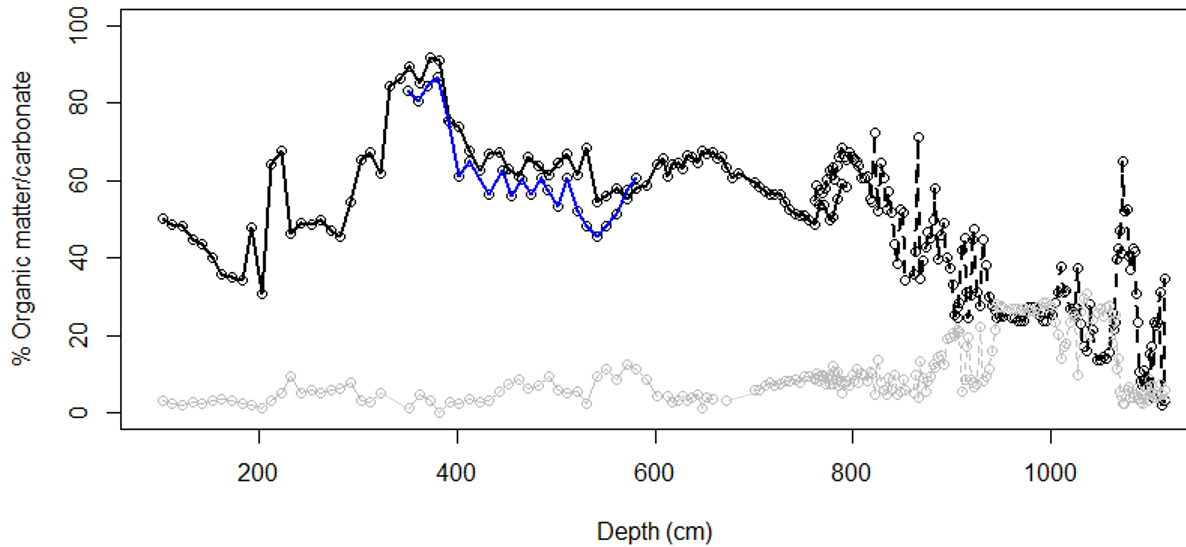
*Figure 9: Organic matter content (**black/blue**) and carbonate content (**grey**) for the Upper (**solid line**) and Lower (**dashed line**) core from Stribbowsee. The sequence is displayed as if the sediments from the two cores were deposited in one place. Data from Göttingen is shown in (**black/ grey**), additional data from Utrecht, also describing the organic matter content, is shown in **blue**.*
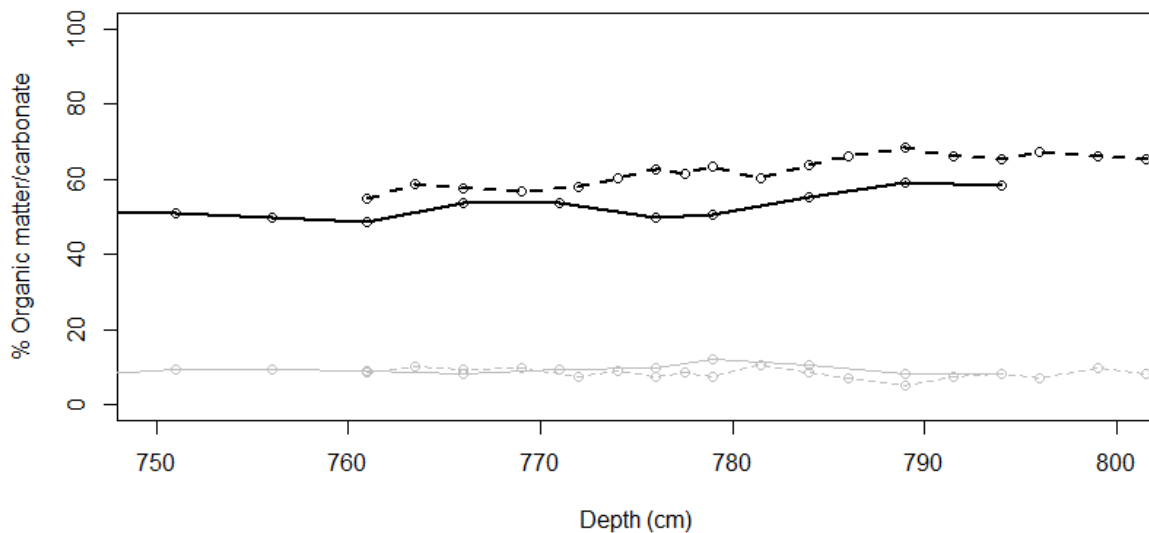
*Figure 10: Organic matter content (**black**) and carbonate content (**grey**) for the Upper (**solid line**) and Lower (**dashed line**) core from Stribbowsee. The overlap between the Upper core (originating from the centre of the lake) and the Lower core (originating from the southwestern edge of the lake) is based on the analysis of the principal components of the pollen assemblages throughout the cores. The organic matter content of the Lower core appears to be higher, although the general trend is similar to the matching part of the Upper core.*

3.3 Pollen diagram Stribbowsee

A pollen diagram was constructed based on the pollen counts of the combined Upper and Lower core from Stribbowsee (Figure 11). The broken stick method indicates that 8 zones are statistically significant. The development of the pollen diagram during the last 4000 year is shown in Figure 12. An additional zone boundary was added at the timing of the known transition from the Bølling-Allerød to the Younger Dryas at the newly published date for the onset of the Younger dryas of 12807 BP (Reinig et al., 2021).
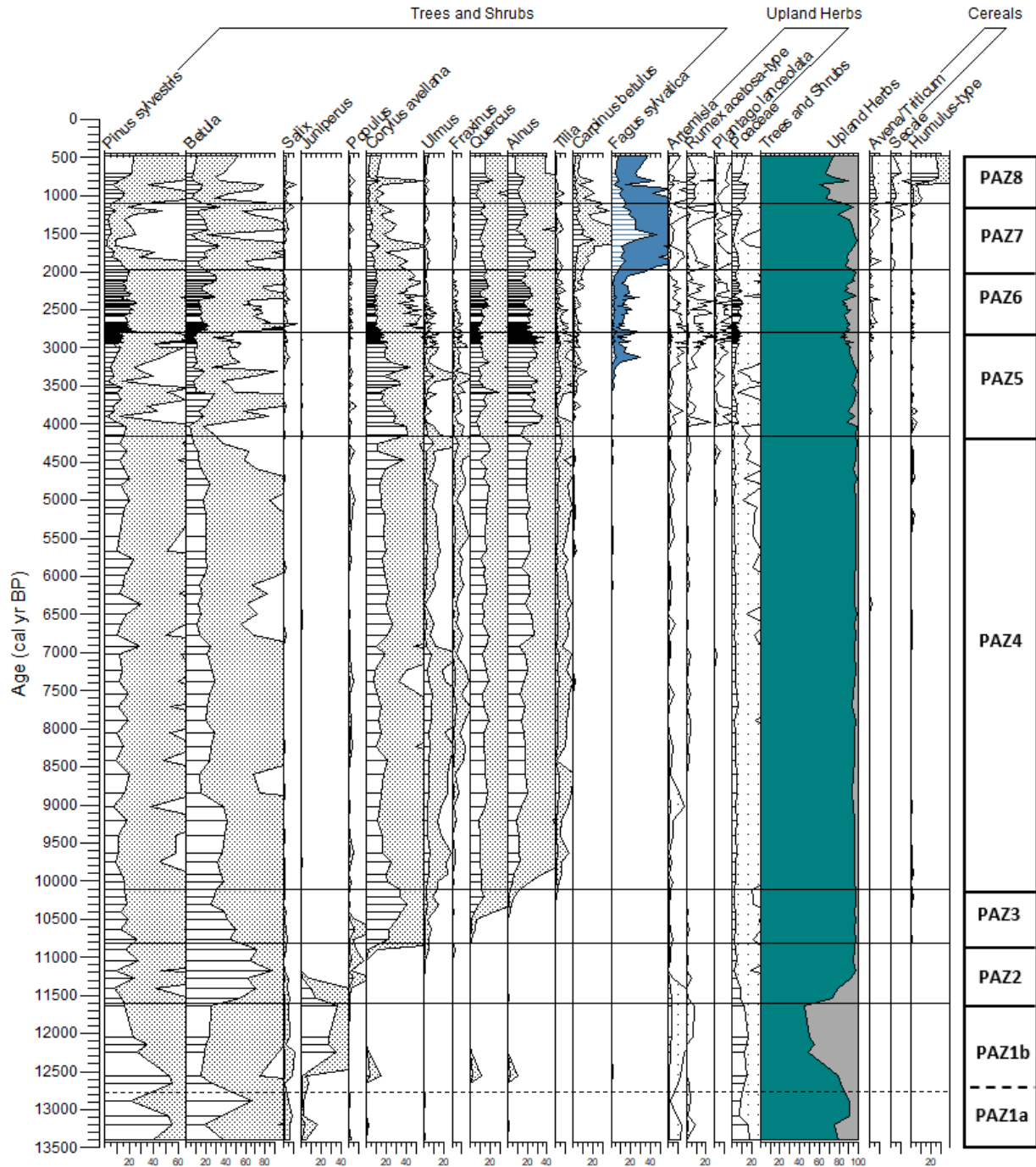
Figure 11: Pollen diagram for Stribbowsee, NE Germany. In total, 8 Pollen Assemblage Zones were found to be statistically significant. An additional zone boundary is added at the timing of the transition from the Bølling-Allerød to the Younger Dryas. The pollen record covers the last ~13400 years. A total of 153 samples were analysed with the highest resolution from 4000 cal. BP onwards. The pollen diagram of Fagus is indicated in blue.

PAZ 1a (Bølling-Allerød; 13395-12807 BP): The oldest pollen zone of the Stribbowsee record is characterized by dominance of *Pinus* and *Betula* in the pollen record, with NAP percentages around 15%. *Juniperus* pollen are part of the pollen assemblages in the oldest half of the zone, but not in the upper half of the zone, where NAP pollen percentages decrease from 20% to 10%. This transition in the pollen record is also reflected in a shift from dominance of *Pinus* to *Betula*.

The Laacher See Tephra is visible as a 1-1.5 cm thick light-gray band in the Stribbowsee core at 1105 cm depth (816 cm in Lower core), a representation that was also found in other lake sediments from NE Germany (Theuerkauf, 2003; De Klerk et al., 2008). The Laacher See eruption occurred towards the end of the Allerød warm period, at the end of a minor cooler episode when temperatures had started to rise (de Klerk et al., 2008). Theuerkauf (2003) describes an increase in Poaceae, Cyperaceae and *Salix* right after the LST in pollen diagrams from lake records from Mecklenburg-Vorpommern NE Germany, possibly as a result of eutrophication after the input of sulphuric acid from the volcanic acid rain. This increase is not visible in the Stribbowsee diagram, possibly because the resolution in this part of the pollen diagram is too low to record this. Increasing values of *Betula* pollen at the end of the Lateglacial *Betula*/*Pinus* forest phase are also recorded in other records from NE Germany although the timing is not synchronous, possibly because it reflects the expansion of birch carrs along the margins of many basins, which depended for a large part on the local hydrological conditions around the basin (Theuerkauf, 2003; De Klerk et al., 2008).

PAZ1b (Younger Dryas; 12807-11600 BP): The lowest samples of this zone capture the increase in NAP percentages and an increasing dominance of *Pinus* relative to *Betula.* Increases of *Equisetum* and *Sphagnum* pollen in the assemblages possibly reflect increased moisture levels. *Juniperus* pollen dominate the assemblages from 12300 cal. BP onwards. Other taxa that are represented in this zone include species of the families of Caryophyllaceae, Asteraceae, Rubiaceae Amaranthaceae and Apiaceae, *Helianthemum*, *Empetrum* and *Filipendula.*.

The sediments that were deposited in the part of the core corresponding to this zone are relatively sandy/silty, which is in accordance with sediments from other lake cores from this time and region and indicates that sedimentation was for a large part controlled by erosion (De Klerk, 2008b). This is also supported by relatively low LOI values of the samples from this period. Finds of thermophilous tree pollen around the start of the rise of *Juniperus* may indicate that older pollen washed into the lake sediments with these eroding soils. Although pollen and charcoal finds of thermophilous taxa in sediments from this period do occur, these finds are still debated (Giesecke, 2016; Robin et al., 2016). The sudden appearance and disappearance of these pollen types in this pollen records is more suggestive that they originate from washed in sediments than that these trees were actually present nearby Stribbowsee during this time. High percentages of NAP, the occurrence of heliophilous pollen types such as *Empetrum* and *Helianthemum* and erosion of the surrounding soils suggest a relatively open landscape, but probably, scattered stands of trees still existed according to Theuerkauf et al. (2014), allowing for a fast recolonization of the open land in the next zone.

PAZ2 (Colonization of open land; 11600-10820 BP) The start of this zone is characterized by a rapid decline of *Juniperus* percentages and an increase in *Betula* pollen percentages, that show a peak around 11200 cal. BP. Pollen percentages of Poaceae*, Artemisia and* Cyperaceae start to decline. Amaranthaceae pollen disappear completely from the pollen assemblages around this time while *Populus* pollen become more frequent. The zone boundary of this zone occurs at 11.600. cal. BP, which roughly coincides with the onset of the Holocene at 11703 cal. BP (Björck et al., 1998). The development of the vegetation during the Younger Dryas-Holocene transition has been well documented for NE Germany (Theuerkauf et al., 2014). Amelioration of the climate allowed both *Betula* and *Pinus* to rapidly expand, although *Betula* generally expanded faster than *Pinus*. This is also visible in the pollen diagram from Stribbowsee, where

Betula pollen percentages rise from ~11600 cal. BP onwards while *Pinus* percentages only increase (temporarily) around 11400 cal. BP.

PAZ3 (Corylus expansion; 10820-10100 BP): *Betula* pollen percentages decline rapidly at the start of this zone while *Corylus* becomes the most dominant constituent of the pollen assemblages. Around the same time as the rise of *Corylus*, *Ulmus* and *Fraxinus* percentages become a constant factor. This is followed by a rise in *Quercus* and *Alnus*. The end of the zone is marked by the appearance of *Tilia.* According to Theuerkauf et al., (2014), *Corylus* replaced *Betula* on intermediately wet to wet gleyic and loamy soils, where *Betula* established previously. In contrast, *Pinus* populations, mostly growing on podzolic sandy soils, were less affected by the expansion of *Corylus*. Only minor stands of *Pinus*, growing on gleyic, wet soils were outcompeted. This is also reflected in the Stribbowsee pollen diagram as *Betula* pollen percentages decrease drastically from the moment that *Corylus* expands, while *Pinus* pollen percentages only show a small decrease.

PAZ4 (Mixed forest; 10100-4160) From this zone onwards, the assemblages are mixed with *Betula, Pinus, Corylus, Quercus, Tilia, Ulmus, Fraxinus* and *Salix* all being constantly present. Percentages of Poaceae and other herbs are consistently relatively low. *Alnus* grows in dominance from ~7000 cal. BP onwards. Pollen from *Fagus* and *Carpinus betulus* are sporadically found throughout the zone with the first count of *Fagus* around 7700 BP. *Corylus* shows a sharp peak at the end of the zone. Such remarkably high percentages of *Corylus* have also been observed in other pollen diagrams from NE Germany as well and have been attributed to coppicing and/or recolonization of openings in the forest related to human activities (Sadovnik et al., 2014)

PAZ5 (Increased human impact; 4160-2800 BP): This zone is more dynamic than the previous zone, with sharp peaks of *Corylus,* and a single sharp peak of *Quercus. Fagus* percentages become consistently >1% from 3200 cal. BP onwards while *Carpinus betulus* also becomes a consistent presence in the assemblages. Around the same time, *Salix,* Poaceae*, Artemisia* and *Rumex* percentages gradually increase. *Corylus* displays a dynamic curve at the first part of the zone but its percentages drop gradually from 3300 cal. BP onwards. This decline of *Corylus* was also found in many other pollen diagrams from Poland and Germany around this time and its cause has been ascribed to cattle grazing and/or the expansion of *Carpinus betulus* and *Fagus* (Ralska-Jasiewiczowa et al., 2003). In the core sediments of Stribbowsee, the lamination stops around the same time as the decline of Corylus, indicating increased circulation of lake water. In the lake sediment of Lake Tiefer See that was studied by Dräger et al. (2017), lamination is also disrupted from ~3940–3100 and 2700–2200 cal. BP, which the authors relate to increased openness of the vegetation due to anthropogenic activities. *Tilia, Fraxinus* and *Ulmus* decrease at the beginning of the zone and reach a minimum around 3750 cal. BP, whereafter their percentages recover. At the same time, *Plantago lanceolata, Rumex, Artemisia* and Poaceae increase in abundance and decrease after 3750 cal. BP. *Betula* increases from the beginning of the zone until ~3600 cal. BP. These series of events corresponds well with a typical landnám phase *sensu* Iversen (1973) that describes forest clearance and subsequent recovery of the forest as observed in Danish pollen diagrams. A similar pattern was observed in the pollen diagram for the Großer Krebssee (Jahns, 2000) around ~4400 cal. BP and here, the event was also identified as a landnám phase by the author.

PAZ6 (Open forest; 2800-1970 BP): *Fagus* pollen percentages are consistent throughout this zone, with a range between 1.2-6.4 %. In the second half of the zone, *Betula* percentages rise to a peak after which they decline again twice. Cereals occur sporadically while herbs such as *Plantago lanceolata*, *Rumex* and Amaranthaceae are more consistently present in the pollen assemblages. Relatively high percentages of NAP and the low abundance of *Tilia* and *Ulmus* may indicate that the forest remained relatively open after deforestations in the previous zone. Seemingly, the forest did not fully recover as shade tolerant trees such as *Tilia, Ulmus* but also

the newly established *Fagus* did not expand yet. Ongoing human activities are a probable reason for this. Iversen (1973) describes that secondary woodland regeneration can be hampered by grazing or soil degradation. Alternatively, consistent deforestations may have prevented the forest from developing a closed canopy again.

PAZ7 (Rise of Fagus and Carpinus; 1970-1100 BP): From the beginning of the zone, pollen percentages of *Pinus* decrease and remain low. *Fagus* increases stepwise from 2100 cal. BP onwards with the second step of increase around 1650 cal. BP. During these periods of expansion, is seems that the forest was less open than previously as herbaceous taxa such as Poaceae, *Plantago lanceolata, Rumex* and *Artemisia* were less abundant. Possibly, grazing intensity in the forest decreased during this time, allowing *F. sylvatica* trees to expand in the area. After *Fagus* reaches its peak, with a pollen percentage around 40% in the pollen record, percentages drop again while herbaceous pollen become more abundant. *Carpinus betulus* percentages also rapidly increase to a short-lived peak right before *Fagus* and decrease hereafter. Such a rapid increase in the presence of herbaceous taxa and a decrease of tree pollen suggest that humans significantly deforested the landscape around Stribbowsee from 1300 cal. BP onwards.

PAZ8 (1100-485 BP; Deforestation and hemp retting): *Carpinus betulus* percentages drop to very low values while *Fagus* percentages remain around 6%. Increasing percentages of Cereals, *Plantago lanceolata, Urtica,* Amaranthaceae and *Rumex* but also sporadic finds of *Centaurea cyanus* and *Agrostemma githago* indicate that agricultural activities in the area intensified. *Humulus/Cannabis* becomes the most abundant pollen-type in the pollen record. This drastic increase of hemp pollen in the Stribbowsee pollen assemblages corresponds with records from lakes that were used for hemp retting, a method of fibre extraction (Bradshaw et al., 1981). Therefore, this increase in hemp pollen was likely a sign of anthropogenic activities rather than an actual change in the vegetation composition.
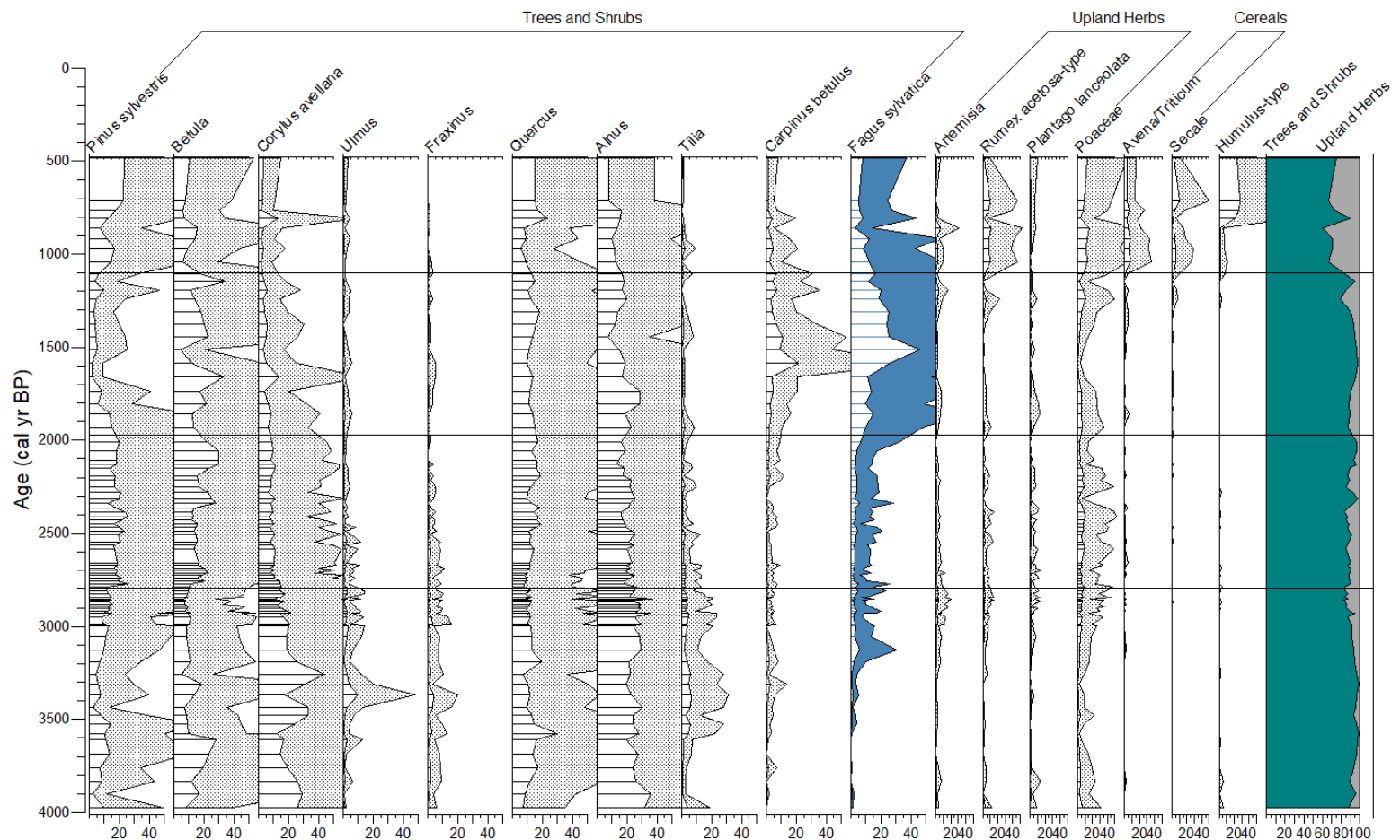
Figure 12: Pollen diagram for the last 4000 years that are represented in the Stribbowsee core. The pollen percentage curve of Fagus is indicated in blue.

3.4 Comparison to Carlshof forest hollow

Figure 13 shows the pollen diagrams for Carlshof forest hollow and Stribbowsee on the same time scale to visualize how the development of the vegetation on a stand-scale compares to the wider area of the Peutscher forest. Additional graphs, comparing separate taxa, are provided in Appendix 2. The development of the first 4 principal components through time is visualised in Figure 14.

The PCA reveals that a consistent difference between the pollen assemblages of Carlshof forest hollow and Stribbowsee is captured in PC1, which is mainly driven by variance in *Pinus, Alnus* and *Quercus* pollen percentages. This is clearly visible in a direct comparison of the pollen percentage development through time of these taxa (Appendix 2). Stribbowsee has consistently higher percentages of *Alnus* and *Quercus* which indicates that these taxa occurred locally around Stribbowsee as they do currently. In contrast, the pollen record from Carlshof forest hollow shows higher percentages for *Pinus.* This is also in accordance with the current pattern of a relatively high proportion of *P. sylvestris* in the area around the forest hollow. Differences can also be noticed in the pollen diagrams for the development of NAP such as *Plantago lanceolata, Rumex* and Poaceae which show a clear increase from ~4000 cal. BP onwards in the Stribbowsee pollen diagram but only two short-lived increases in the Carlshof hollow pollen diagram. These differences are mainly captured by PC 3 and 4.

20
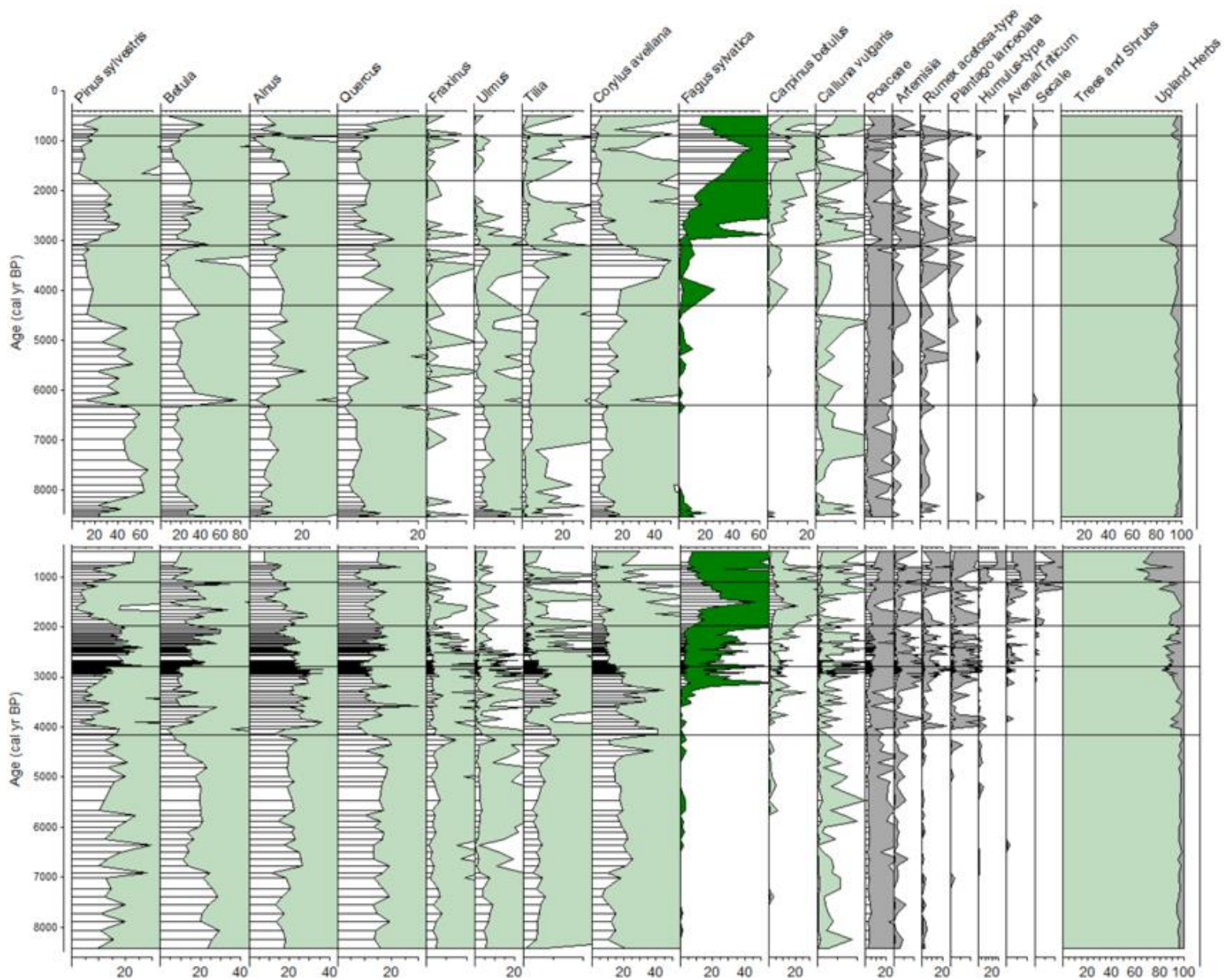
Figure 13: Comparison of the pollen percentage diagrams of Carlshof forest hollow (top) and Stribbowsee upper core (bottom). Tree species are indicated in green (Fagus darkgreen), herbal species are indicated in grey. Statistically significant zone boundaries are marked by the black horizontal lines.

21
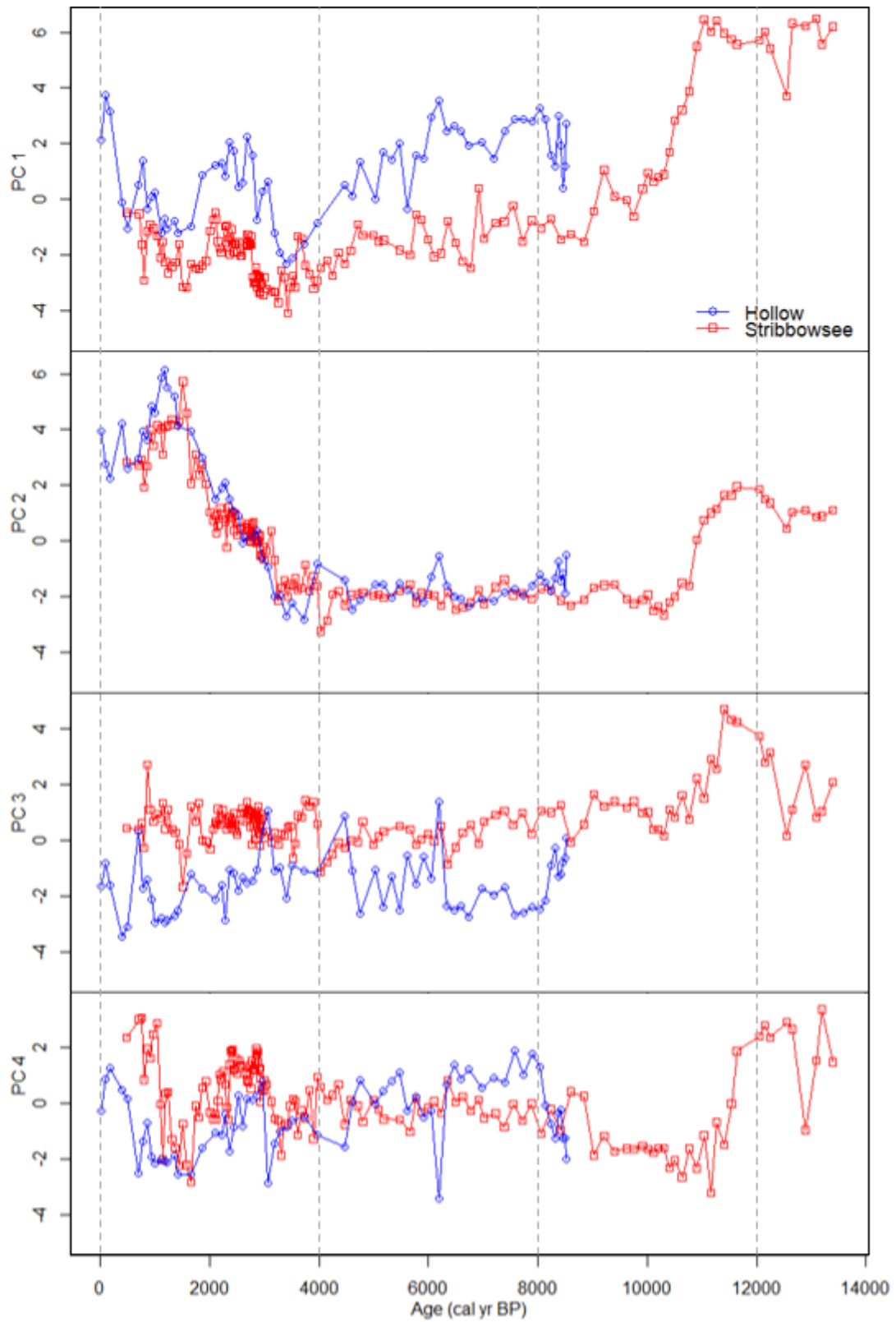
Figure 14: Development of the first 4 principal components through time. Samples from Carlshof forest hollow are indicated by blue circles and samples from the nearby Stribbowsee by red squares. The first 4 principal components are significant and explain respectively 36 %, 22%, 11% and 9% of the variance. Loadings of the PC1-4 are shown in Figure 6.

4. Discussion

4.1 Expansion of F. sylvatica

Based on the 1% threshold that is found to be a good indicator of its local presence (Lisitsyna et al., 2011), *F. sylvatica* established in the Peutscher forest around 3200 cal. BP, about 200-300 years before its establishment around the forest hollow. When *F. sylvatica* established around the hollow, it seems that the population expanded here almost immediately, as the pollen record from Carlshof forest hollow shows an almost continuous rise of *Fagus* pollen percentages from 3000 onwards with two small relapses to lower pollen percentages around 2800 and 2200 cal. BP. This expansion was local, as it is not visible in the Stribbowsee record, where *Fagus* pollen percentages remain around 4% until they increase around 2100 cal. BP (Figure 15).

Bradley et al (2013) describe several signals that are suggestive of a disturbance event prior to the expansion of *Fagus* such as a decline in *Corylus, Ulmus* and *Tilia* and a peak in *Betula* pollen percentages. Simultaneously, NAP pollen show a short-lived increase in the pollen diagram (Figure 17). LOI data reveals several erosion events, indicating instability of the slopes around the hollow.

In the Stribbowsee record, signals of human activities in the area occur already from ~4000 cal. BP, with forest dynamics reflecting Iversens landnám model. At the time of the disturbance event around the hollow, the pollen diagram of Stribbowsee also reveals a decline in percentages of *Tilia, Ulmus* and *Fraxinus,* possibly reflecting a phase of forest clearings. Here, however, these trends are followed by a small increase in *Fagus* pollen percentages, that only increase further ~1000 years later (Figure 17). These observations suggest that *F. sylvatica* established in the area around Stribbowsee ~3200 cal. BP at a location that was relatively close to the hollow, but its population did not expand further into the forest yet. Both in the hollow and in Stribbowsee, the increase of *Fagus* appears to follow a step-wise pattern. The second step of increase in the Stribbowsee records matches the timing of the third step of increase in the forest hollow record.

A step-wise increase of *Fagus* pollen percentages was also noted by Tinner & Lotter (2006), and they attribute this pattern to gradual climatic changes or a stepwise successive reaching of the age of blooming. Bradshaw & Lindbladh (2005) describe that the spreading of *F. sylvatica* in southern Scandinavia was patchy rather than a smooth migrating front, which would also explain a stepwise increase in pollen diagrams. Other than gradual climatic change and intrinsically slow population growth rates, the expansion of *F. sylvatica* could also have been delayed by grazing or soil degradation that prevents secondary succession of the forest (Iversen, 1973). The latter explanation is supported by the observation that not only *Fagus* percentages do not increase, but also pollen percentages of *Tilia* and *Ulmus* do not recover yet during this period, like they did previously in the pollen diagram. Furthermore, NAP pollen percentages including *Plantago lanceolata,* which is known to grow on disturbed grounds such as pastures, remain relatively high throughout the period between the first and second step of increase of *Fagus*, suggesting that the forest remained relatively open during this time.

Comparison to other lake records from NE Germany (Figure 16) reveals that the expansion of *F. sylvatica* in NE Germany did not occur synchronously across the region. Its expansion occurred relatively early around Großer Krebssee (~3500 BP; Jahns & Kirleis 2013), Felchowsee (~3600 BP; Jahns & Kirleis, 2013) and Carlshof forest hollow (~3000 BP; Bradley et al., 2013) but later around Löddigsee (~2750 BP; Jahns, 2007) and Stribbowsee (~2100 BP), that was analysed in this study. This pattern does not appear to correlate with the climate cooling phases at 2750-2350 BP and 3800-3400 BP (Haas et al., 1998), but this is difficult to assess

because of the uncertainties of the age models and a possible lagged response. However, it clearly contrasts with the uniform expansion of *Fagus* in Central Europe around 8200 BP, where the increase of *Fagus* in lake pollen diagrams occurs almost simultaneously within a timeframe of 200 years after the 8.2 kyr event across a region of 500 km (Tinner & Lotter, 2006). Therefore, it is unlikely that climate was the most important trigger for the expansion of *F. sylvatica* in NE Germany across the entire region. However, in these other lake records from NE Germany, like in the Stribbowsee record, secondary human impact indicators such as *Plantago lanceolata* and *Rumex* were already present in the record for more than 1000 years before the expansion of *Fagus,* so a direct link between the expansion of *F. sylvatica* and anthropogenic activities is also not evident.
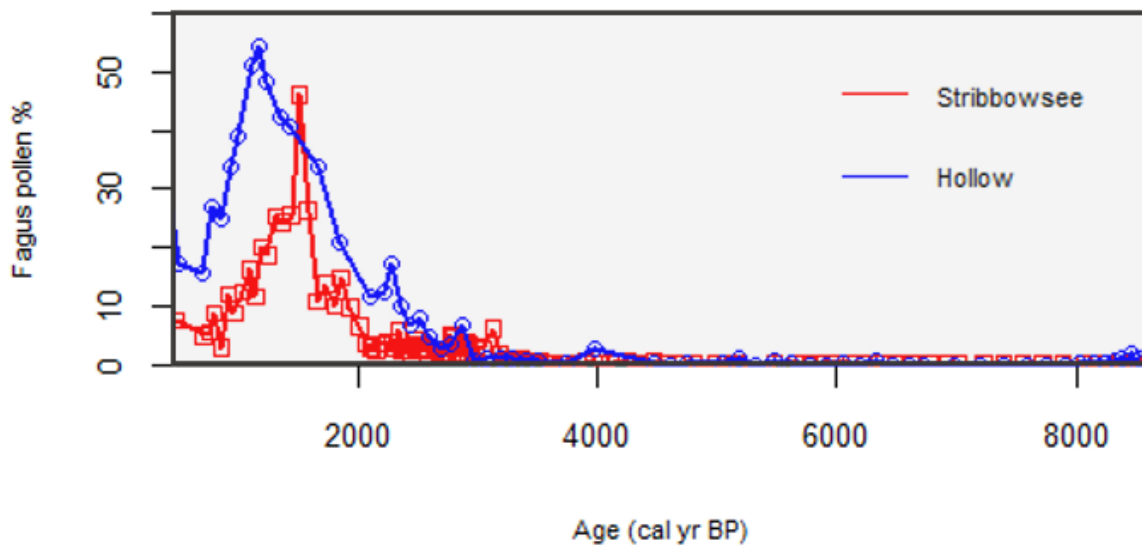
Figure 15: Pollen percentage curves for Fagus from Stribbowsee and Carlshof forest hollow. The increase of pollen percentages starts sooner in the hollow record while the decline starts earlier in the Stribbowsee record. The increase of Fagus pollen percentages occurs stepwise in both curves.

Figure 16: Locations of the lakes Löddigsee (Jahns, 2007), Großer Krebssee (Jahns & Kirleis, 2013), Felchowsee (Jahns & Kirleis, 2013) and Stribbowsee (this study) in NE Germany.
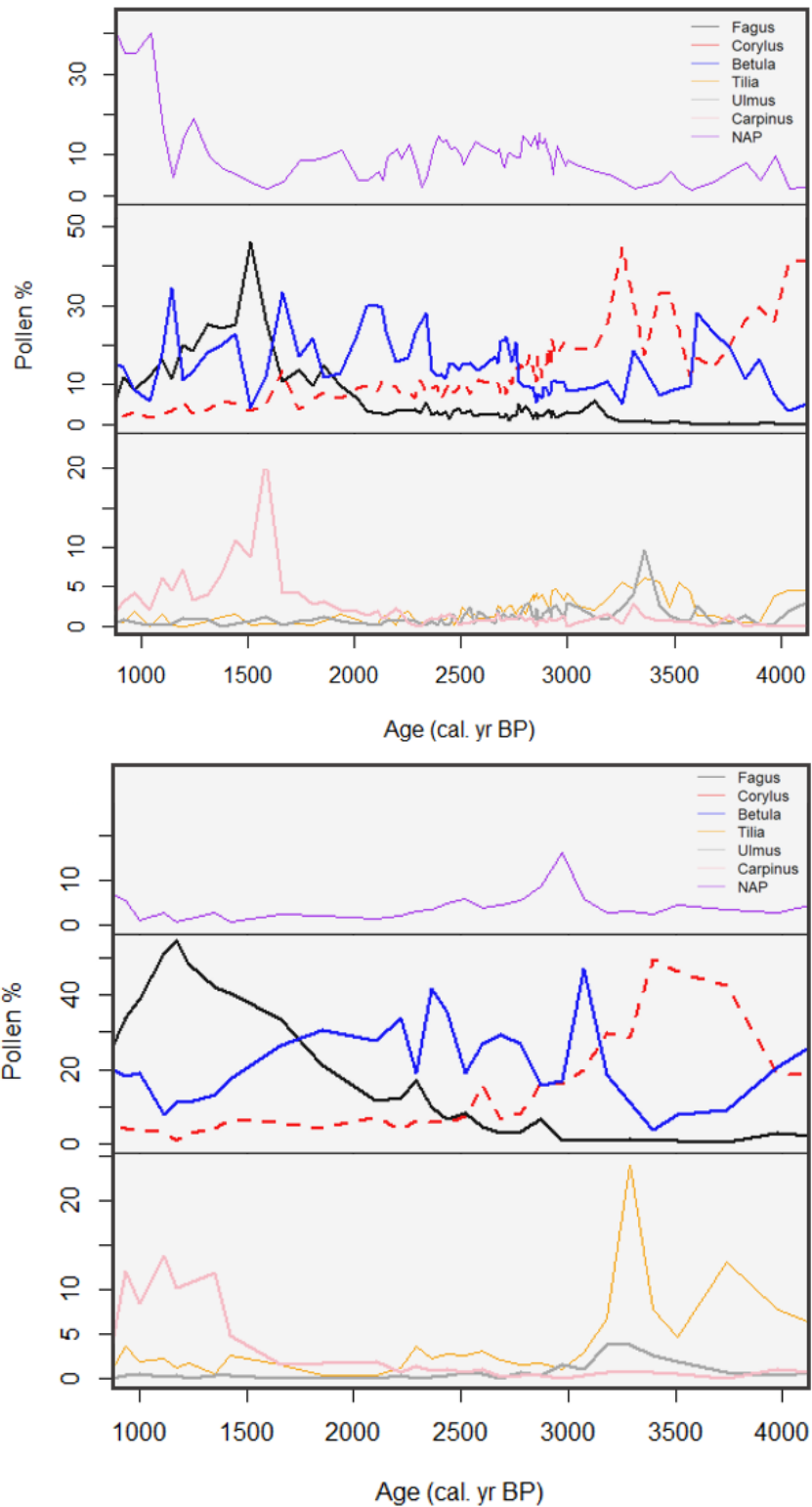
*Figure 17: Pollen percentages of **Fagus**, **Corylus**, **Betula**, **Tilia**, Ulmus, **Carpinus betulus** and **NAP** in the Stribbowsee and Carlshof forest hollow records. A disturbance event is followed by the expansion of Fagus in the record from the hollow. In the Stribbowsee record, Fagus pollen percentages only increase slightly after this disturbance. The event itself is also different between the hollow and the lake records, being more pronounced in the hollow record and supported by a short-lived increase in NAP while this is not the case for the Stribbowsee record.*

4.2 Chronology and preparation method

For the construction of the age model, the two cores from Stribbowsee were combined based on the overlap of their path along the plane of the first two principal components. Since the Upper core originates from the centre of the lake and the Lower core from the south-western corner of the lake, they possibly have different accumulation rates due to sediment focussing in the centre of the lake (Blais & Kalff, 1995) which is also indicated by the LOI values of the Lower core, that are slightly higher than those of the Upper core at their overlapping depths (Figure 11). From the PCA, it seems that the overlap occurred between the section of 467-487 cm in the Lower core and 761-781 cm in the Upper core. Both these sections are 20 cm, indicating that the discrepancy between the accumulation rates in the two cores was not large, so this would not be problematic for the age model.

Other than a possible difference in accumulation rate, pollen deposition is not homogeneous in a lake, since more buoyant pollen types such as *Pinus* do not sink to the bottom of the lake as fast as other smaller and denser pollen types (Hopkins, 1950). During the time that *Pinus* pollen are floating in the upper part of the lake water, winds can move them to the sides of the lake, resulting in an overrepresentation of this pollen type in cores taken from the side of a lake and an underrepresentation in cores taken from the centre of a lake. Furthermore, herbaceous pollen types are more common in littoral sediments than in deep-water sediments (Davis & Brubaker, 1973). This difference is slightly visible in Appendix 2, with *Pinus* pollen percentages from the Upper core being lower than percentages of the Lower core during their time overlap. NAP percentages are very similar both in abundance and in their trend in the parts of the cores that were matched so these effects appear to be negligible. A rapid decrease of *Corylus* pollen around 3300 cal. BP and later an increase of *Pinus* pollen occurs simultaneously in the Carlshof forest hollow and in the Stribbowsee record. This suggests that these events were not local to the hollow and supports the validity of the age model of the Stribbowsee record close to the time of overlap.

Due to differences in lab protocol in Utrecht vs. Göttingen, not all samples in this study were given the exact same treatment. The main difference between the sample preparation in Utrecht vs. Göttingen was the method that was used for the separation of clastic sediment from the pollen. While the HF method was used in Göttingen, heavy liquid separation with a sodium polytungstate solution was used in Utrecht. Although the preparation method would ideally be the same for all samples, the impact of this difference in preparation method as well as the difference of the analyst was checked by resampling three samples that were prepared and analysed in Götingen in Utrecht and comparing the analyses (Appendix 3). This comparison showed that the results were similar and this is further supported by a comparison study by Campbell et al. (2016) that reveals no significant differences between samples that are given HF treatment vs heavy liquid separation.

4.3 Climate or anthropogenic disturbance?

From the comparison of the records of Stribbowsee and Carlshof forest hollow it becomes clear that while the expansion of *F. sylvatica* around the hollow clearly follows a disturbance event that was probably caused by anthropogenic activities, based on the context of the event that is given by the Stribbowsee record, this is not the case in the Stribbowsee record. Here, disturbances by anthropogenic activities are evident from 4000 BP cal. BP onwards but not followed directly by the expansion of *F. sylvatica*. It is difficult to assess what process actually triggered the expansion of *F. sylvatica* around Stribbowsee. Possibly it took several cycles of forest clearings for *F. sylvatica* to establish and consequently expand in the area because of its

slow maturation and competition with other species such as *Tilia* and *Ulmus* or its expansion was delayed by grazing or soil degradation. Another explanation could be that the climate was not yet suitable for *F. sylvatica* to expand and therefore it established first in small densities at patches where the microclimate compensated for the lack of moisture and it expanded on a large scale only after a 8.2-ky type event around 2600 BP. Disentangling the effects of settlement activities and climate on the expansion of *F. sylvatica* is hampered by a strong dependence of these settlement activities on the regional climate (Ralska-Jasiewiczowa et al., 2003). However, comparison to other lake records in NE Germany reveals that the expansion of *F. sylvatica* here was less synchronous across a larger region than it was in Central Europe (Tinner & Lotter, 2006) or in the Bulgarian mountains (Tonkov, 2003). This lack of spatial and temporal synchrony was also found by Bradshaw and Lindbladh (2005) for the spread of beech in southern Scandinavia, thus it is plausible that also on a larger scale, the expansion of *F. sylvatica* was influenced by anthropogenic activities in forests of the northern lowlands and not driven solely by climate change.

A problematic aspect of the debate whether climate change or anthropogenic disturbance facilitated the expansion of *F. sylvatica* is that disturbance by anthropogenic activities could describe many types of activities that do not all have the same effect on forest communities. These activities could include slash-and-burn agriculture, coppicing, leaf fodder collection and cattle grazing to name a few. Tinner & Lotter (2006) state that cross-correlations of anthropogenic indicator species and *Fagus* pollen percentages are an objective method to determine whether the expansion of *F. sylvatica* was facilitated by anthropogenic activities and thus that this is the way forward for future research. While it is true that this method is objective, it captures the term anthropogenic activities as a static term which is not. It is clear that not all anthropogenic activities affect the expansion of *F. sylvatica* in the same way. While forest clearings may be beneficial, grazing and soil degeneration after agricultural activities might hamper secondary forest regeneration (Iversen, 1973). *F. sylvatica* expansion may even be favoured or disfavoured by selective cuttings. These different types of activities may be culturally different and may change through time. Therefore, the facilitation of the expansion of *F. sylvatica* by anthropogenic activities was probably a complicated process that cannot be easily captured by cross-correlations. In this light, studies reflecting the expansion on different scales combined with archaeological data providing insights into neolithic land-use practises may be more valuable for the understanding of the complex impact of human activities on forest dynamics.

4.4 *Implications*

The results of this study challenge the idea that *F. sylvatica* is the naturally dominant tree in forests of northern European lowlands. If anthropogenic activities facilitated the expansion of *F. sylvatica* in northern Europe, the interpretation of nature-based management of these forests may have to be reviewed. As was also proposed by Stobbe & Gumnior (2021), perhaps management practises that favour *Ulmus* and *Tilia* over *F. sylvatica* have a stronger claim of being nature-based since *F. sylvatica* would not have been the dominant tree in these forests without human interference. Especially in the context of climate change, which is expected to severely affect the drought-sensitive European beech, such considerations must not be overlooked.

5. Conclusion

The results presented in this study show that the expansion of *F. sylvatica* is recorded differently in the pollen record from a lake versus a forest hollow. Other than the expansion itself, the processes connected to the expansion are difficult to establish on the larger scale that is reflected in the lake record, while disturbance seems to be a clear trigger for the expansion at the stand-scale that is reflected in the forest hollow record. This confirms the hypothesis that the spatial resolution of pollen records is essential for recording these type of event-chains, which may be the reason that the expansion of *F. sylvatica* cannot be linked to disturbance events in lake records from central and southern Europe whereas this link is well established in hollow records from northern Europe. However, comparison of lake records in a central Europe show a synchronous expansion of *F. sylvatica* likely caused by climate change while the timing of expansion of *F. sylvatica* in lake records in northern Europe lacks synchrony. Thus, although scale differences could have contributed to the apparent discrepancy between processes connected to the expansion of *F. sylvatica* in central and southern Europe versus northern Europe, the processes acting on a larger scale were probably also different.

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Appendix 1

Table 1: Sampling data Stribbowsee-Upper core. Batch 1=grey, Batch 2=darkgrey, Batch 3= white, Batch 4 = lightgreen; C= counted by Catrien Hoffman, T= counted by Thomas Giesecke, ND= Not Documented

Depth (cm)	Core	Analist (X = Not analysed)	Sample volume (cm³)	Sampling location	Sampling date	Amount of Lycopodium added (~number of spores)
20	S-1	X	1	Utrecht	June 2021	33333
40	S-1	X	1	Utrecht	June 2021	33333
60	S-1	X	1	Utrecht	June 2021	33333
75	S-1	X	1	Utrecht	June 2021	33333
90	S-1	X	1	Utrecht	June 2021	33333
108	S-2	X	1	Utrecht	June 2021	33333
120	S-2	C	0.5	Göttingen	October 2012	ND
137	S-2	X	1	Utrecht	June 2021	33333
155	S-2	X	1	Utrecht	June 2021	33333
170	S-2	C	0.5	Göttingen	October 2012	ND
188	S-2	C	1	Utrecht	June 2021	33333
205	S-3	C	1	Utrecht	June 2021	33333
220	S-3	C	0.5	Göttingen	October 2012	ND
237	S-3	C	1	Utrecht	June 2021	33333
255	S-3	C	1	Utrecht	June 2021	33333
270	S-3	C	0.5	Göttingen	October 2012	ND
288	S-3	C	1	Utrecht	June 2021	33333
302	S-4	C	1	Utrecht	June 2021	33333
311	S-4	C	1	Utrecht	June 2021	33333
320	S-4	C	0.5	Göttingen	October 2012	ND
329	S-4	C	1	Utrecht	June 2021	33333
340	S-4	C	1	Utrecht	June 2021	33333
350	S-4	C	1	Utrecht	June 2021	33333
360	S-4	C	1	Utrecht	June 2021	33333
370	S-4	C	0.5	Göttingen	October 2012	ND
380	S-4	C	1	Utrecht	June 2021	33333
391	S-4	C	1	Utrecht	June 2021	33333
402	S-5	C	0.3	Utrecht	June 2021	10000
412	S-5	C	0.3	Utrecht	June 2021	10000
420	S-5	C	0.5	Göttingen	October 2012	ND

432	S-5	C	0.3	Utrecht	June 2021	10000
446	S-5	C	0.3	Utrecht	June 2021	10000
455	S-5	C	0.3	Utrecht	June 2021	10000
465	S-5	C	0.3	Utrecht	June 2021	10000
470	S-5	C	0.5	Göttingen	October 2012	ND
475	S-5	C	0.3	Utrecht	June 2021	10000
485	S-5	C	0.3	Utrecht	June 2021	10000
491	S-5	C	0.3	Utrecht	June 2021	10000
501	S-6	C	0.3	Utrecht	June 2021	10000
511	S-6	C	0.3	Utrecht	June 2021	10000
521	S-6	C	0.3	Utrecht	June 2021	10000
531	S-6	C	0.3	Utrecht	June 2021	10000
541	S-6	C	0.3	Utrecht	June 2021	10000
551	S-6	C	0.3	Utrecht	June 2021	10000
561	S-6	C	0.3	Utrecht	June 2021	10000
571	S-6	C	0.3	Utrecht	June 2021	10000
581	S-6	C	0.3	Utrecht	June 2021	10000
591	S-6	C	0.3	Utrecht	June 2021	10000
606	S-7	C	0.3	Utrecht	June 2021	10000
615	S-7	C	0.3	Utrecht	June 2021	10000
628	S-7	C	0.5	Göttingen	March 2013	ND
640	S-7	C	0.3	Utrecht	June 2021	10000
650	S-7	C	0.3	Utrecht	June 2021	10000
660	S-7	C	0.3	Utrecht	June 2021	10000
678	S-7	C	0.5	Göttingen	March 2013	ND
701	S-8	C	0.3	Utrecht	April 2021	20000
706	S-8	C	0.3	Utrecht	April 2021	20000
711	S-8	C	0.3	Utrecht	April 2021	20000
716	S-8	C	0.3	Utrecht	April 2021	20000
721	S-8	C	0.5	Göttingen	March 2013	ND
726	S-8	C	0.3	Utrecht	April 2021	20000
731	S-8	C	0.3	Utrecht	April 2021	20000
736	S-8	C	0.3	Utrecht	April 2021	20000
741	S-8	C	0.5	Göttingen	March 2013	ND
746	S-8	C	0.3	Utrecht	April 2021	20000
751	S-8	C	0.3	Utrecht	April 2021	20000
756	S-8	C	0.3	Utrecht	April 2021	20000
761	S-8	C	0.5	Göttingen	March 2013	ND
767	S-8	C	0.3	Utrecht	April 2021	20000
773	S-8	C	0.3	Utrecht	April 2021	20000
779	S-8	C	0.5	Göttingen	March 2013	ND
781	S-8	T	0.3	Utrecht	April 2021	20000
794	S-8	T	0.5	Göttingen	March 2013	ND

Table 2: Sampling data Stribbowsee-Lower core. Batch 1=lightorange, Batch 2=orange, Batch 3= darkorange, Batch 4 = lightgreen; C= counted by Catrien Hoffman, T= counted by Thomas Giesecke

Depth (cm)	Core	Analist (X = Not analysed)	Sample volume (cm³)	Sampling location	Sampling date
467	S-A	C	0.5	Göttingen	March 2013
470	S-A	C	0.5	Göttingen	October 2012
472	S-A	C	0.5	Göttingen	March 2013
477	S-A	C	0.3	Utrecht	April 2021
482	S-A	C	0.5	Göttingen	March 2013
487	S-A	C	0.3	Utrecht	April 2021
492	S-A	T	0.5	Göttingen	March 2013
502	S-A	C	0.5	Göttingen	March 2013
512	S-A	C	0.5	Göttingen	October 2012
525	S-A	C	0.5	Göttingen	March 2013
535	S-A	T	0.5	Göttingen	March 2013
545	S-A	C	0.5	Göttingen	October 2012
552	S-A	C	0.3	Utrecht	April 2021
559	S-A2	T	0.5	Göttingen	March 2013
567	S-A2	T	0.5	Göttingen	March 2013
572	S-A2	C	0.5	Göttingen	March 2013
577	S-A2	C	0.5	Göttingen	March 2013
582	S-A2	T	0.5	Göttingen	March 2013
585	S-A2	C	0.5	Göttingen	October 2012
592	S-A2	C	0.5	Göttingen	March 2013
598	S-A2	T	0.5	Göttingen	March 2013
604	S-A2		0.5	Göttingen	March 2013
609	S-A2	T	0.5	Göttingen	March 2013
614	S-A2	C	0.5	Göttingen	March 2013
618	S-A2	C	0.5	Göttingen	October 2012
625	S-A2	T	0.5	Göttingen	March 2013
631	S-A2	C	0.5	Göttingen	March 2013
637	S-A2	C	0.5	Göttingen	March 2013
643	S-A2	T	0.5	Göttingen	March 2013
648	S-A2	C	0.5	Göttingen	October 2012
654	S-A2	C	0.5	Göttingen	March 2013
658	S-A2	T	0.5	Göttingen	March 2013
666	S-A3	C	0.5	Göttingen	January 2013
669,5	S-A3	C	0.5	Göttingen	January 2013
673	S-A3	T	0.5	Göttingen	January 2013

675,5	S-A3	X	0.5	Göttingen	January 2013
679	S-A3	X	0.5	Göttingen	October 2012
683	S-A3	T	0.5	Göttingen	January 2013
686	S-A3	X	0.5	Göttingen	January 2013
689	S-A3	T	0.5	Göttingen	January 2013
692	S-A3	C	0.5	Göttingen	January 2013
695	S-A3	C	0.5	Göttingen	January 2013
698	S-A3	T	0.5	Göttingen	January 2013
701	S-A3	C	0.5	Göttingen	January 2013
704	S-A3	T	0.5	Göttingen	January 2013
707	S-A3	C	0.5	Göttingen	January 2013
710	S-A3	T	0.5	Göttingen	January 2013
713	S-A3	C	0.5	Göttingen	January 2013
716	S-A3	T	0.5	Göttingen	October 2012
719	S-A3	C	0.5	Göttingen	January 2013
721	S-A3	C	0.5	Göttingen	January 2013
725	S-A3	T	0.5	Göttingen	January 2013
728	S-A3	T	0.5	Göttingen	January 2013
731	S-A3	C	0.5	Göttingen	January 2013
734	S-A3	T	0.5	Göttingen	January 2013
737	S-A3	C	0.5	Göttingen	January 2013
740	S-A3	T	0.5	Göttingen	January 2013
743	S-A3	C	0.5	Göttingen	January 2013
746	S-A3	T	0.5	Göttingen	January 2013
749	S-A3	C	0.5	Göttingen	October 2012
753	S-A3	T	0.5	Göttingen	January 2013
756	S-A3	T	0.5	Göttingen	January 2013
759	S-A3	T	0.5	Göttingen	January 2013
762	S-A3	T	0.5	Göttingen	January 2013

765,5	S-A4	T	0.5	Göttingen	January 2013
767,5	S-A4	T	0.5	Göttingen	January 2013
770	S-A4	T	0.5	Göttingen	October 2012
771,5	S-A4	T	0.5	Göttingen	January 2013
773	S-A4	T	0.5	Göttingen	January 2013
774,5	S-A4	T	0.5	Göttingen	January 2013
776	S-A4	T	0.5	Göttingen	January 2013
777,5	S-A4	T	0.5	Göttingen	January 2013
779	S-A4	T	0.5	Göttingen	January 2013
781	S-A4	T	0.5	Göttingen	January 2013
783	S-A4	T	0.5	Göttingen	January 2013
785	S-A4	T	0.5	Göttingen	January 2013
787	S-A4	T	0.5	Göttingen	January 2013
789	S-A4	T	0.5	Göttingen	October 2012
790,5	S-A4	T	0.5	Göttingen	January 2013
792,5	S-A4	T	0.5	Göttingen	January 2013
794,5	S-A4	T	0.5	Göttingen	January 2013
796	S-A4	T	0.5	Göttingen	January 2013
797,5	S-A4	X	0.5	Göttingen	January 2013
800,5	S-A4	X	0.5	Göttingen	October 2012
802	S-A4	T	0.5	Göttingen	January 2013
803,5	S-A4	C	0.5	Göttingen	January 2013
805	S-A4	C	0.5	Göttingen	January 2013
806,5	S-A4	X	0.5	Göttingen	January 2013
808	S-A4	X	0.5	Göttingen	January 2013
809,5	S-A4	C	0.5	Göttingen	January 2013
811	S-A4	C	0.5	Göttingen	January 2013
812,5	S-A4	X	0.5	Göttingen	October 2012
814,5	S-A4	C	0.5	Göttingen	January 2013

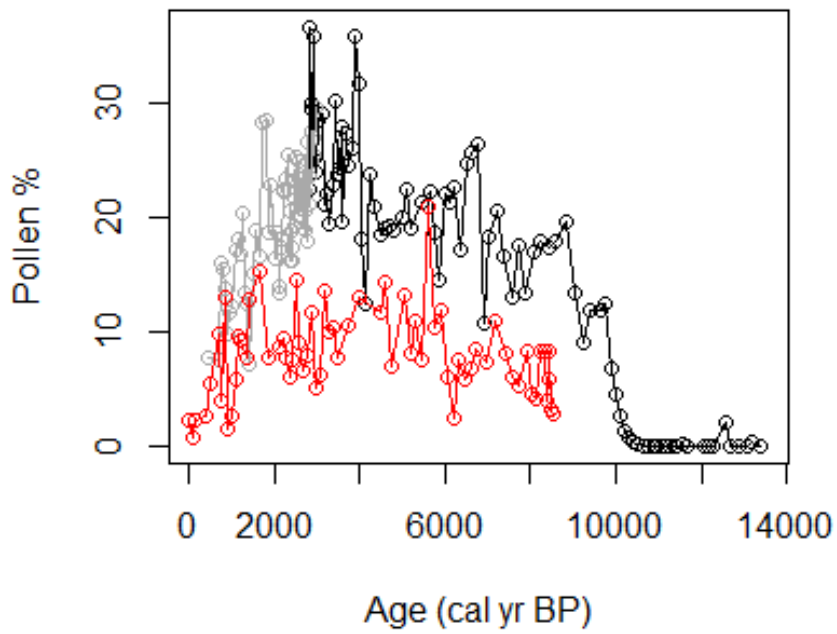|					
817,5	S-A4	C	0.5	Göttingen	January 2013
819	S-A4	C	0.5	Göttingen	January 2013
821	S-A4	X	0.5	Göttingen	October 2012
822	S-A4	C	0.5	Göttingen	January 2013

Table 4: Radiocarbon data Stribbowsee-Upper core. Bulk material=white, Terrestrial macrofossil=orange

Depth	Core	Type of material	Laboratory	Age (cal yr)	Estimated error (yr)
120	S-2	Bulk	Poznan	630 BP	30
330	S-4	Bulk	Poznan	1265 BP	30
432	S-5	*Alnus glutinosa* inflorescence	Poznan	2035 BP	30
620	S-7	Bulk	Poznan	3080 BP	30
780	S-8	Bulk	Poznan	3200 BP	30

Table 5: Radiocarbon data Stribbowsee-Lower core. Clastic material=white, Terrestrial macrofossil=orange

Depth	Core	Type of material	Laboratory	Age (cal yr)	Estimated error (yr)
537,5	S-A	Terrestrial macrofossil	CHRONO, Queens University	3032 BP	29
661	S-A3	Terrestrial macrofossil	CHRONO, Queens University	4503 BP	31
707,5	S-A3	Terrestrial macrofossil	CHRONO, Queens University	5010 BP	32
743	S-A3	Terrestrial macrofossil	CHRONO, Queens University	7660 BP	43
762,5	S-A3	Terrestrial macrofossil	CHRONO, Queens University	8183 BP	41
778	S-A4	Terrestrial macrofossil	CHRONO, Queens University	9508 BP	47
816	S-A4	Laacher See tephra	-	13006 BP	9

Appendix 2

Figures 18-31: Pollen percentages for the 13 most common taxa from Carlshof forest hollow, Stribbowsee Upper core and Stribbowsee Lower core
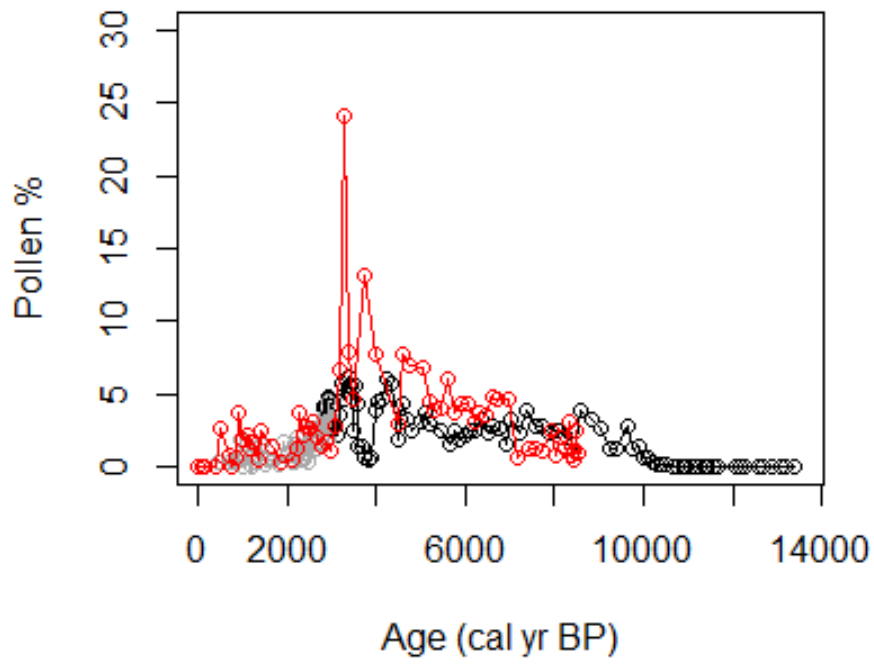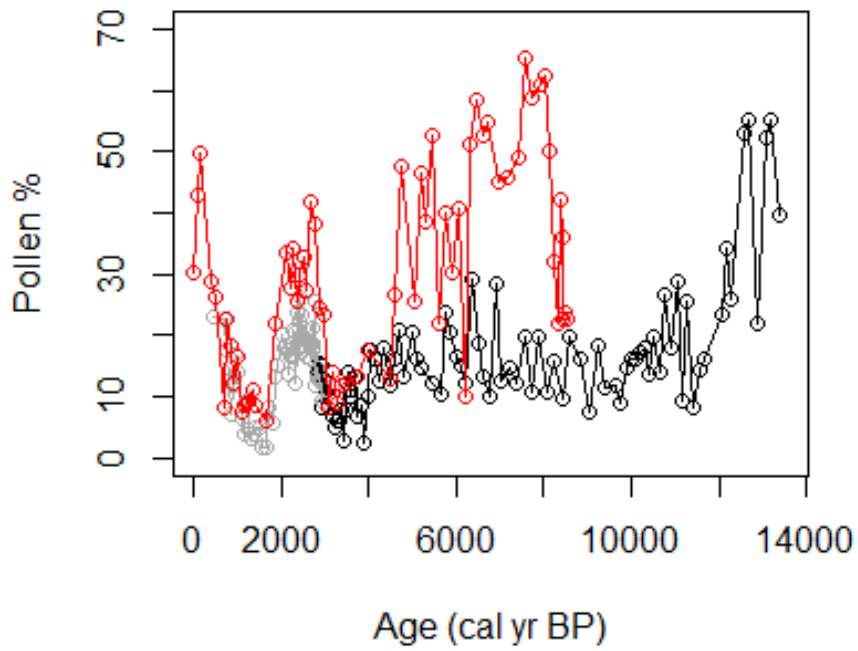
Alnus

Corylus

Quercus

Age (cal yr BP)

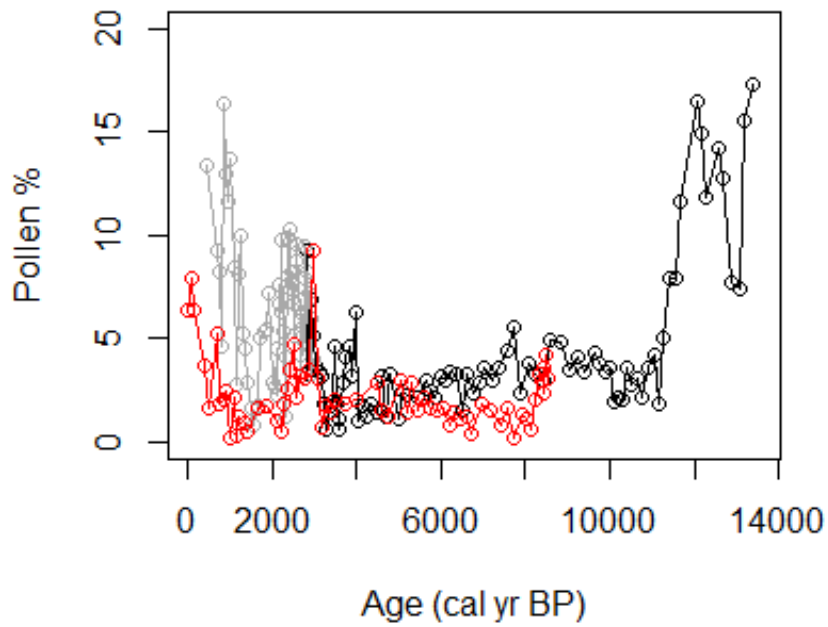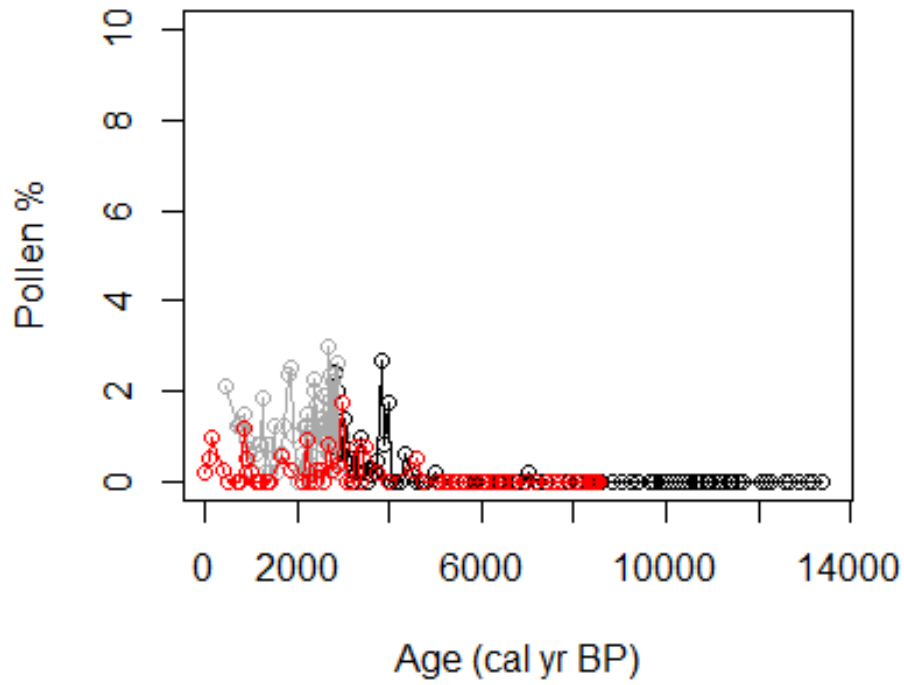# Ulmus

Age (cal yr BP)
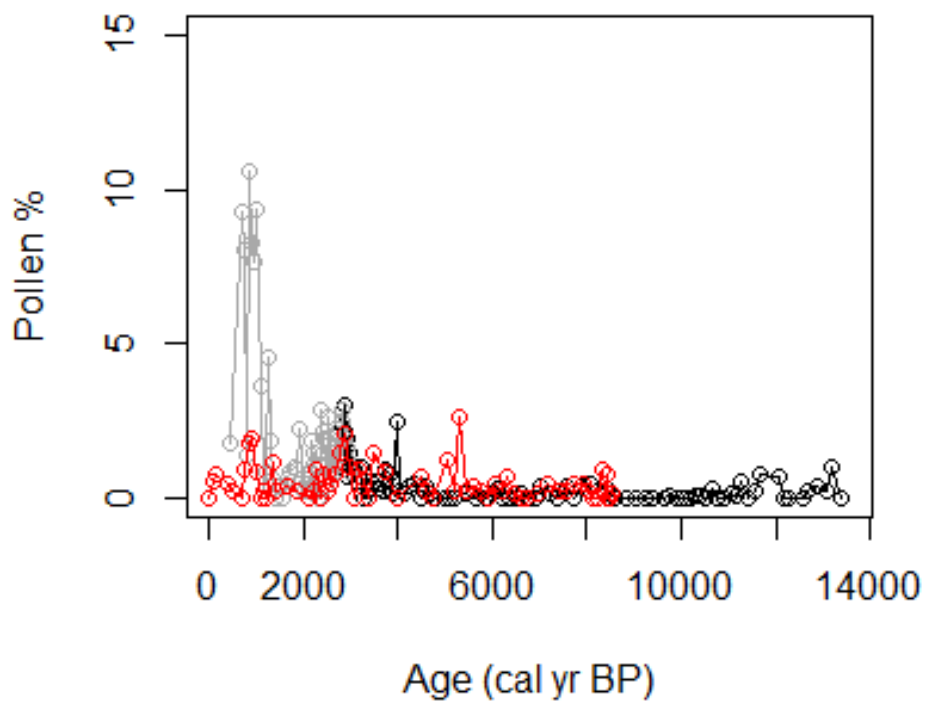
Tilia
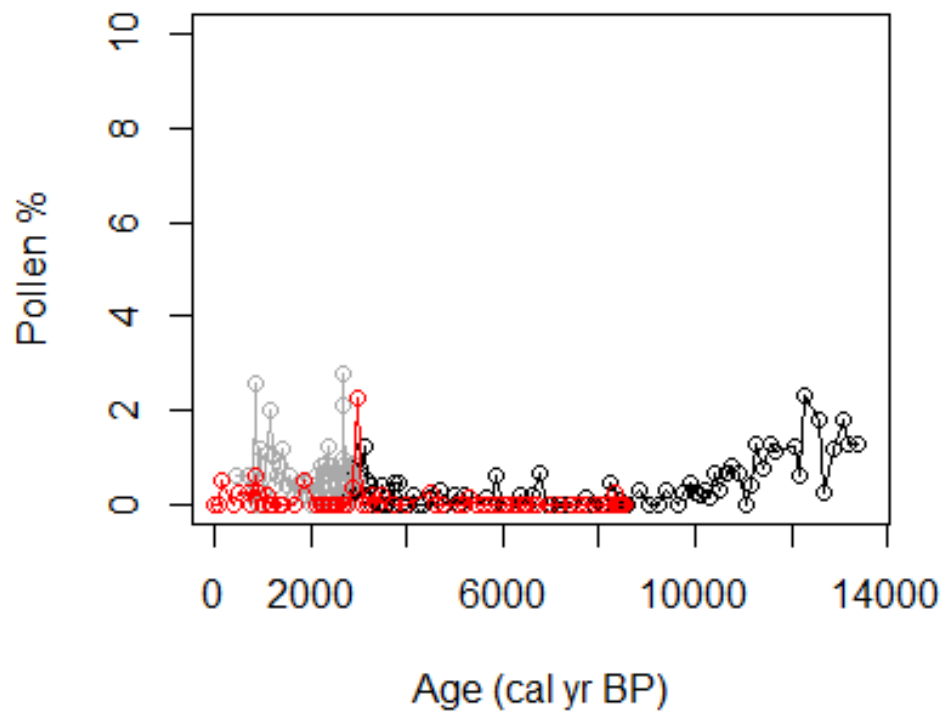

Age (cal yr BP)
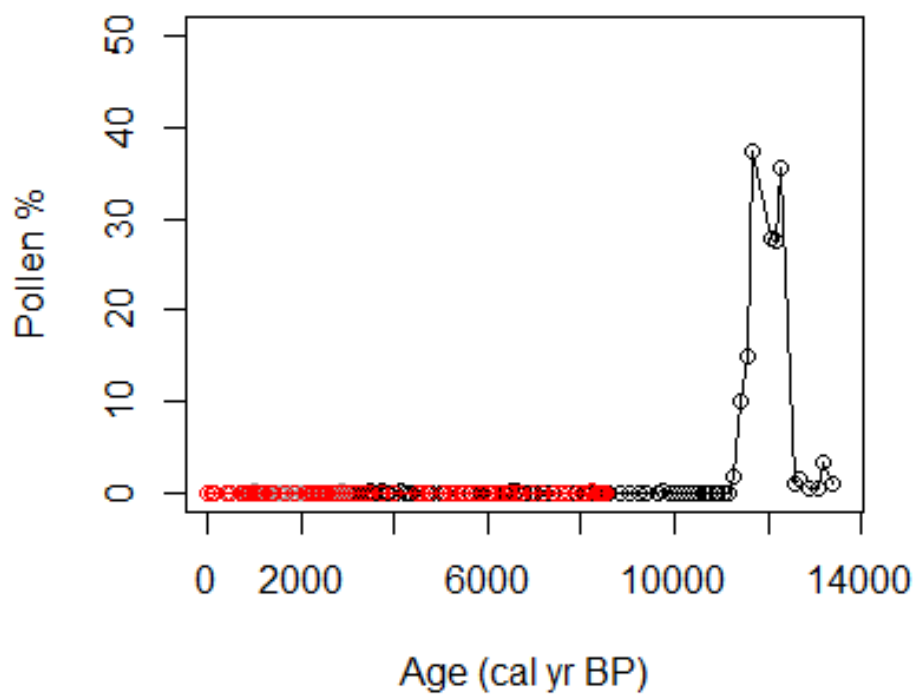
Pinus
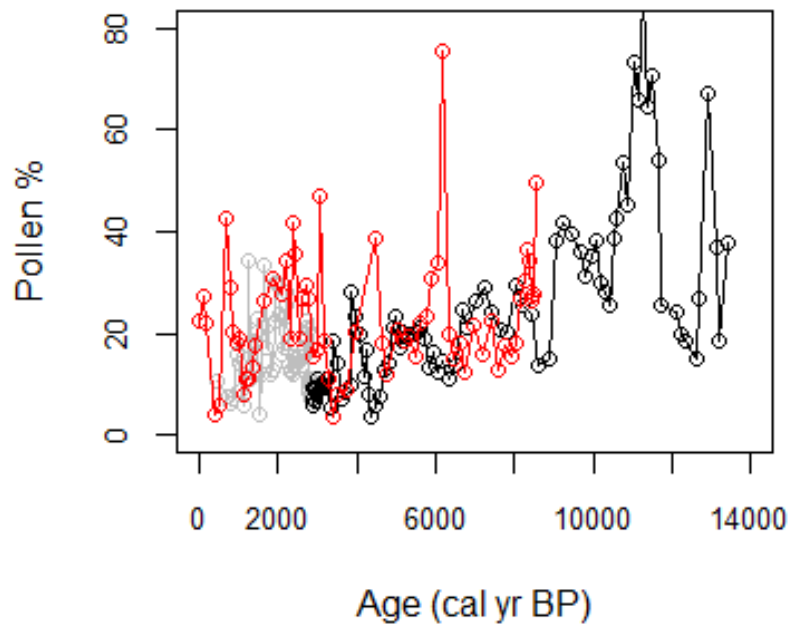

Age (cal yr BP)
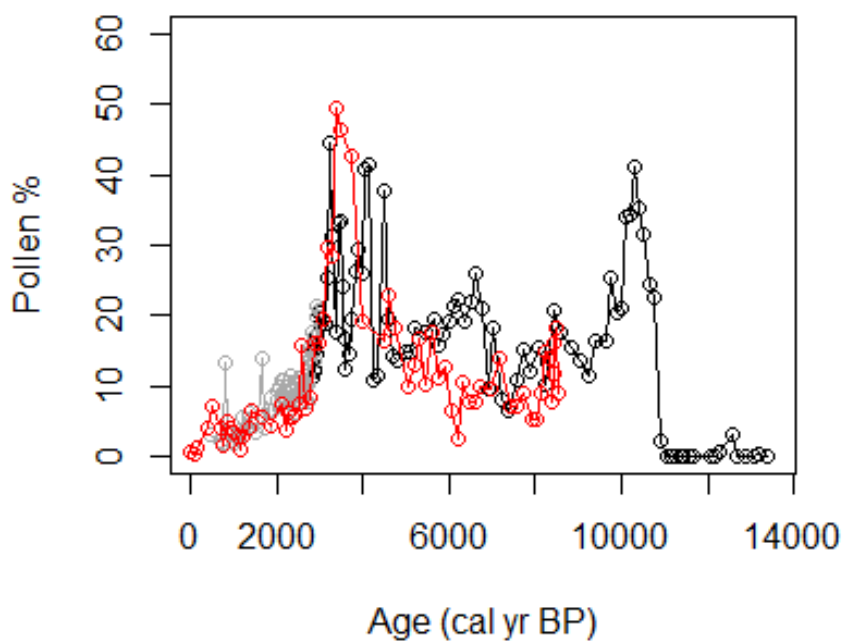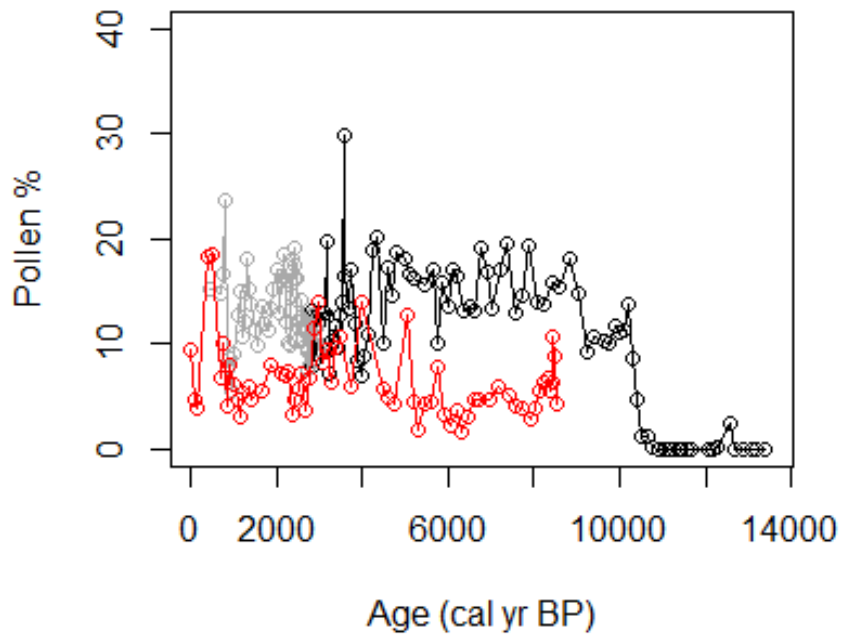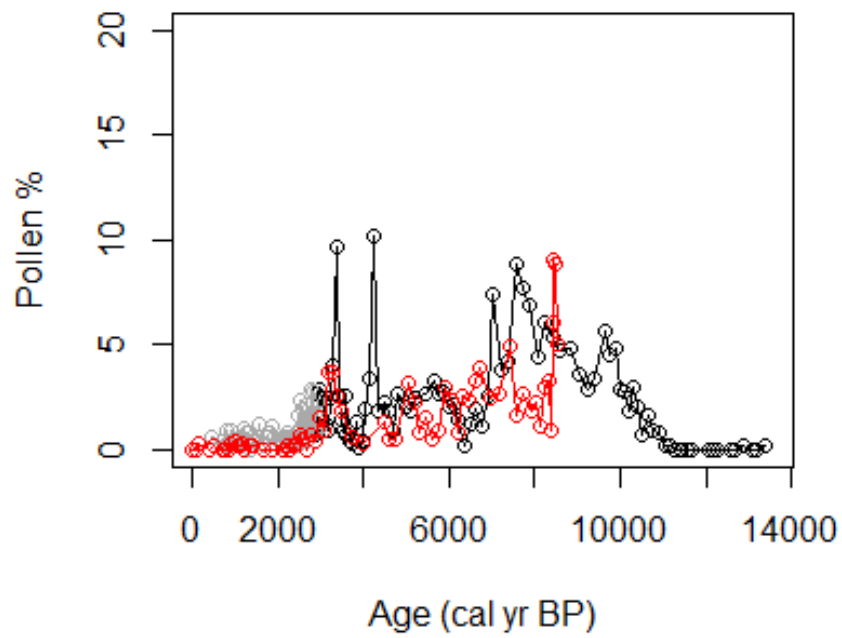
Artemisia
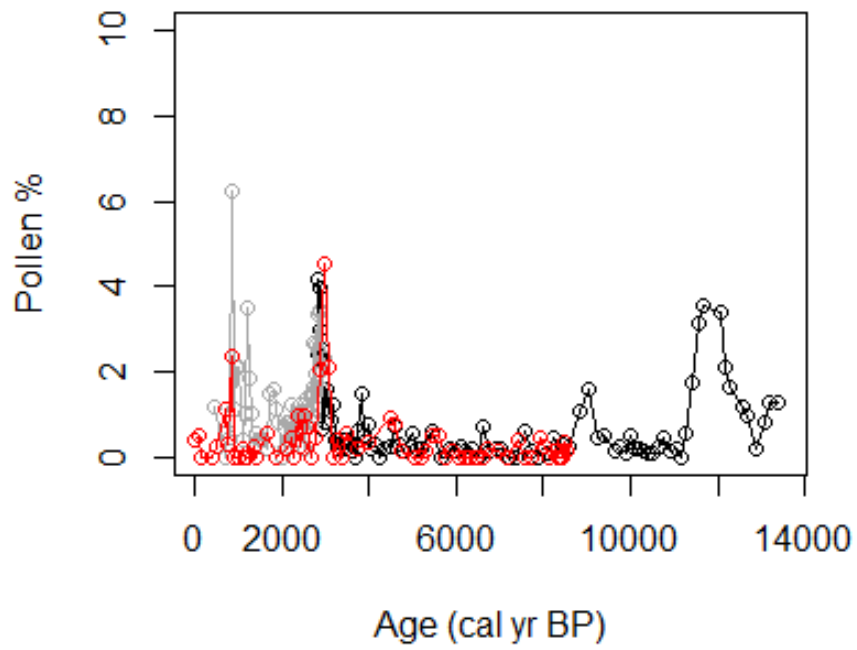
Poaceae

Plantago lanceolata

Rumex

Salix

Juniperus

Betula

Age (cal yr BP)
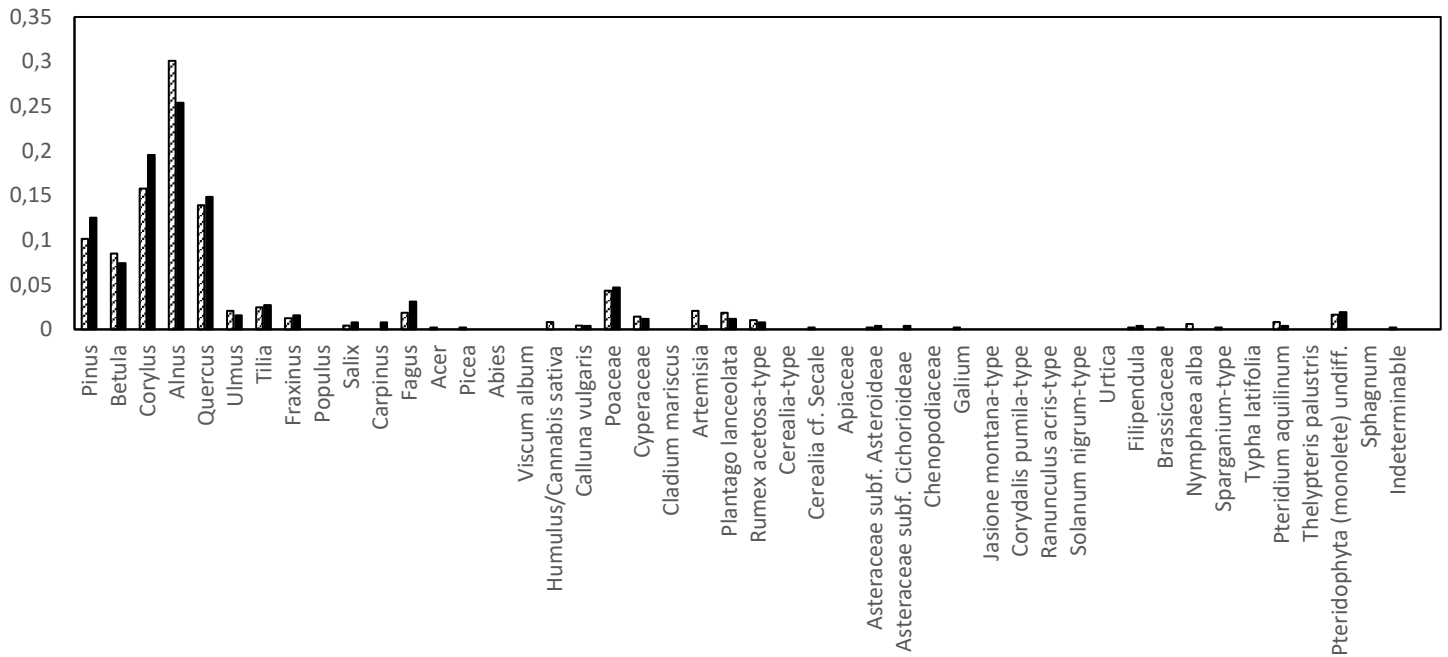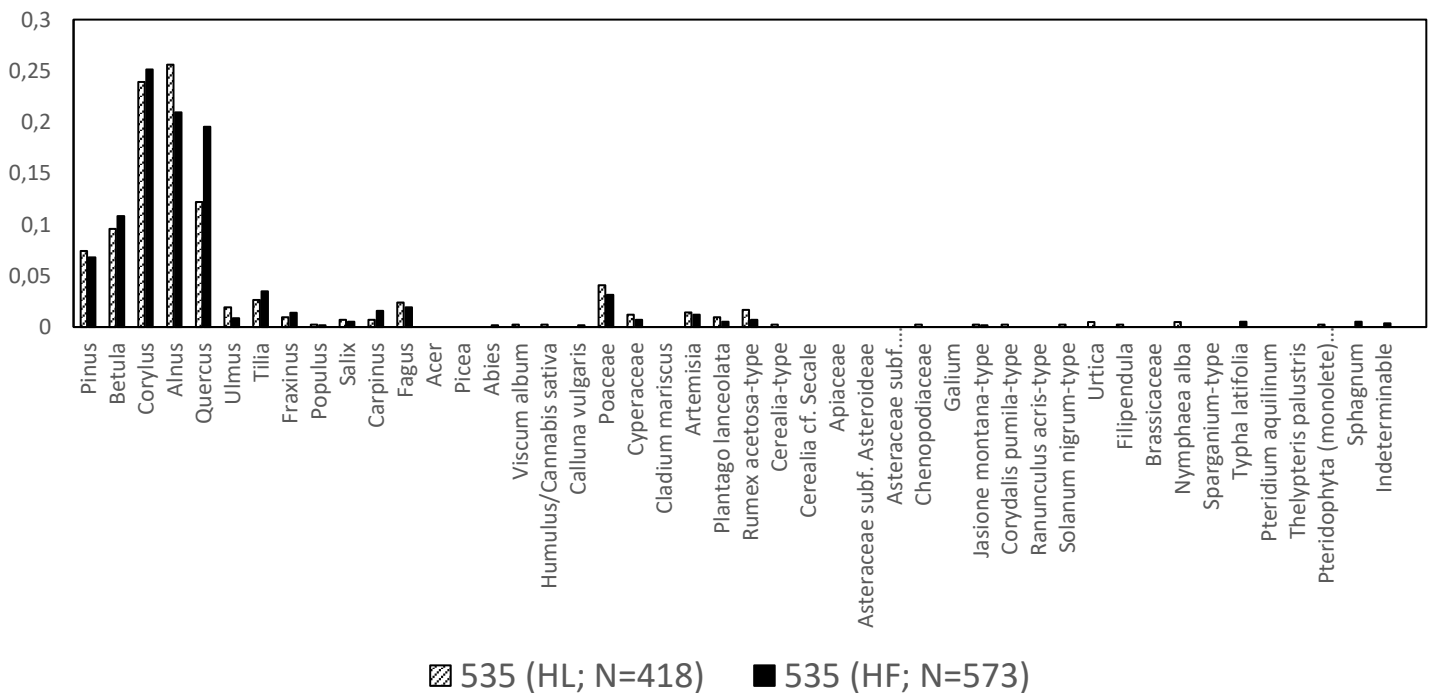
Appendix 3

Figures 32-25: Comparison of pollen proportions from samples prepared and analysed in Göttingen (HF) vs Utrecht (HL) at depths 512, 535 and 743 cm of the Stribbowsee Lower core.

512 HL vs. HF

535 HL vs. HF

◨ 535 (HL; N=418)　■ 535 (HF; N=573)

743 HL vs. HF

743 (HL; N=248)   743 (HF; N=230)