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RESEARCH ARTICLE

Influence of plant coverage and environmental variables on pollen productivities: evidence from northern China

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Abstract Pollen productivity is a critical parameter in the interpretation of pollen-vegetation relationships, and in the quantitative reconstructions of past vegetation from fossil pollen records. One-year monitoring records were collected for 143 pollen traps in various parts of northern China, together with modern vegetation data. Absolute Pollen Productivity Estimates (APPE) were calculated for 11 taxa using the ratio of pollen influx to plant coverage at each applicable sampling site, in which the plants of the target taxon were present. Relative Pollen Productivity Estimates (RPPE) were calculated for the 11 taxa (taking Poaceae as the reference taxon) at those sites in which each taxon occurred together with Poaceae. *Artemisia* and Chenopodiaceae were found to have the highest RPPEs and the largest RPPEs ranges, while *Pinus* and *Quercus* also had higher RPPEs than Poaceae; *Abies*, *Betula*, *Larix*, *Picea* and Cyperaceae had relatively low RPPEs. Variations in RPPE between different areas may be explained by variations in climatic conditions, plant coverage and land use practices which might influence plant growing situation. Marked effect that variations in pollen productivity can have on vegetation reconstructions was demonstrated by applying these distinct RPPEs to reconstructions of Holocene vegetation in the Lake Daihai area (northern China), such as a large range of RPPE produces a large range of plant coverage. Variations in RPPEs within a single taxon, related to vegetation coverage and climatic conditions, therefore need to be considered in future vegetation reconstructions.

Keywords pollen influx, pollen productivity, vegetation reconstruction, REVEALS model, northern China

1 Introduction

The quantitative reconstruction of vegetation compositions is a primary objective in Quaternary palaeoecology and palynology, and such information on local, regional and global scales is a prerequisite for vegetation model validation and environmental archeology. Pollen-based quantitative vegetation compositions can be modeled on the basis of taxa-specific pollen transport characteristics, lake size and Relative Pollen Productivity Estimates (RPPE; Sugita, 2007a and 2007b). The reliability of these approaches has been demonstrated in North America (Sugita et al., 2010a), Denmark (Nielsen and Odgaard, 2010), Sweden (Hellman et al., 2008a and 2008b), the Swiss Plateau (Soepboer et al., 2010), the Tibetan Plateau (Wang and Herzschuh, 2011), northern Asia (Cao et al., 2019) as well as temperate China (Li et al., 2020). The results of these quantitative vegetation reconstructions rely heavily on RPPE for the plant taxa involved (Sugita, 2007a

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and 2007b; Broström et al., 2008; Trondman et al., 2015; Cao et al., 2019; Li et al., 2020). Pollen productivities have consequently been estimated for many taxa (Sugita et al., 1999; Broström et al., 2004; Bunting et al., 2005; Soepboer et al., 2007; Räsänen et al., 2007; Mazier et al., 2008; Sjögren et al., 2008; von Stedingk et al., 2008; Grindean et al., 2019), but most of these investigations have been restricted to Europe. In eastern Asia, studies on pollen productivities have increased sharply in recent years, particularly in temperate regions of China (e.g., Wang and Herzschuh, 2011; Xu et al., 2014; Li et al., 2015; Han et al., 2017; Li et al., 2017a; Li et al., 2017b), and these RPPEs have already been incorporated quantitatively into land-cover reconstruction (Li et al., 2020). However, the reliability of RPPE need to be further confirmed because, for example, one pollen taxon might have quite different RPPEs among different regions.

It is usually assumed that the RPPEs which the vegetation is based on have remained constant throughout the entire period covered by the vegetation reconstruction. However, the RPPEs derived for major plant types are only broadly consistent between different regions, and it has been suggested that pollen productivity for a particular plant taxon can vary regionally as a result of environmental factors such as climate, edaphic parameter and vegetation composition (Calcote, 1995; Hicks, 2001; Pardoe, 2001; Schofield et al., 2007; Hättestrand et al., 2008; Bunting et al., 2013; Chen et al., 2019). For example, Cyperaceae and *Empetrum* plants in northern Finland are characterized by vegetative reproduction rather than prolific flowering because of the severe climatic conditions. Furthermore, the lower RPPE obtained for *Fagus* on the Swiss Plateau than in the Swiss Jura, southern Sweden and Denmark may be simply due to a reduced representation of this taxon in the vicinity of lakes (Broström et al., 2008). However, differences in RPPEs may also arise as a result of different methodologies in the collection of pollen samples and/or vegetation data (Broström et al., 2008; Bunting and Hjelle, 2010; Ge et al., 2015; Niemeyer et al., 2015). For example, the RPPE obtained for *Filipendula* based on lake sediment surface samples from Estonia are markedly higher than those based on moss polster samples from southern Sweden and Norway, and non-distance-weighted vegetation data from Norway resulted in lower herbaceous RPPEs than for southern Sweden (Broström et al., 2008). *Larix* and Cyperaceae obtained higher representation in the lacustrine than in terrestrial moss samples (Niemeyer et al., 2015). In addition, the poor taxonomic resolution of pollen identification renders it impossible to estimate the productivity of a single plant species. Hence, productivity estimates at higher taxonomic levels can be biased if pollen productivities vary within a single taxon (Watrin et al., 2007).

Hitherto, pollen productivity estimation is mainly restricted to the ratio between productivity of the target taxon to that of the reference taxon, named by the RPPEs, and all corresponding models and software are prepared for the RPPEs and land-cover reconstruction based on RPPEs (e.g., Sugita, 2007a and 2007b). Besides the RPPEs, the APPE is quite important in pollen-based vegetation reconstruction. Since absolute measures of pollen deposition in sediments are more effective than pollen percentages for distinguishing plant communities near the limits of trees as well as in the areas of sparsely occurring trees (Hicks, 2001; Sugita et al., 2010b). On the Tibetan Plateau, pollen samples from the last glacial period harbours were with quite low pollen concentration but abundant arbor pollen grains, which is generally considered to be transported by wind from a long distance, while there is no direct evidence (e.g., Sun et al., 1993; Zhu et al., 2015); absolute pollen deposition could be a potential solution to separate the local or regional pollen grains. Sugita et al. (2010a) employed the slope of the linear relationship between pollen loading and distance-weighted plant abundance to represent APPE, which supports us a new approach to investigate the pollen-plant relationship.

The main objective of this study was to derive APPEs for six major tree types (*Abies*, *Betula*, *Larix*, *Picea*, *Pinus*, *Quercus*), one shrub type (*Ostryopsis*) and four types of herbs (*Artemisia*, Chenopodiaceae, Cyperaceae, Poaceae) in northern China, on the basis of pollen influx data from one-year pollen traps, in order to address the following questions: 1) What are the ranges and median values of the APPEs and RPPEs for these taxa in northern China? 2) How are APPEs related to plant coverage and climate parameters? 3) How do the different RPPEs based on Holocene pollen records from Lake Daihai in northern China affect vegetation reconstructions?

2 Study area

To investigate variations in pollen productivity with different environmental settings we collected modern pollen traps and vegetation data from a large area (Fig.1) (33.97°N–43.98°N, 104.54°E–117.58°E) covering steep environmental gradients, particularly in terms of mean annual temperature (ranging from −4.4°C to 9.2°C) and mean annual precipitation (ranging from 150 to 800 mm). This region encompasses major forest, steppe and desert vegetation zones. Forest trap sites were mainly located in mountainous areas which had a mean annual precipitation between 400 and 800 mm and were dominated by *Larix*, *Pinus*, *Picea*, *Abies*, *Quercus* and *Betula* plant communities. Steppe trap sites were located in areas with a mean annual precipitation ranging from 200 to 450 mm, where the dominant plant species included *Stipa*, *Aneurolepidium chinense*, *Festuca ovina*, *Artemisia frigida*, *Cleistogenes squarrosa* and *Thymus mongolicus*. The key plants in desert steppe areas, which have annual mean precipitation of 150–200 mm, include herbaceous plants such as *Stipa gobica*, *Stipa breviflora*, *Stipa glareosa* and *Stipa*

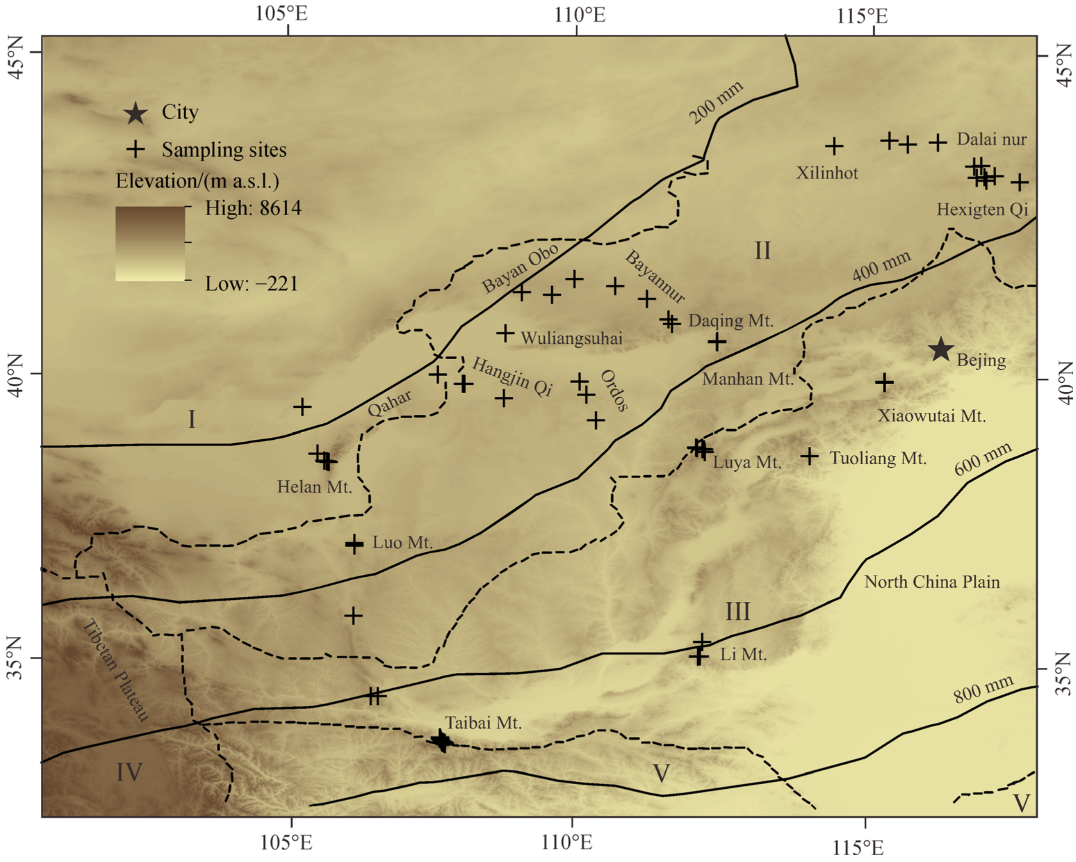


Fig. 1 Locations of 120 Tauber traps and location of the study area relative to the Tibetan Plateau, the Loess Plateau, the Inner Mongolia Plateau and the North China Plain. Black dashed lines represent the boundaries of different vegetation types and solid black lines are annual precipitation isolines. I: Temperate desert zone; II: Temperate steppe zone; III: Warm temperate broad-leaved forest zone; IV: Tibetan plateau zone; V: Sub-tropical broad-leaved forest zone.

klemenzii, and shrubby species such as *Ajania*, *Hippolytia* and *Artemisia salsoloides*. Cyperaceae are dominant in alpine meadow vegetation. Shrub communities are characterized by *Ostryopsis*, *Caragana* and *Nitraria* (Wu, 1980; The Inner Mongolia and Ningxia Investigation Group of the Chinese Academy of Sciences, 1985; Gao and Dai, 1988). In the eastern part of the study area, the original vegetation had been substantially modified by human activities, and for this reason, the less impacted mountainous areas were chosen for sampling. The western and northern parts of the study area mainly belong to the steppe vegetation zone used only as pastures, and consequently have been less impacted by human activities than the eastern area. The pollen traps were nevertheless placed in sparsely populated areas to reduce human impact as much as possible.

Lake Daihai is situated on the eastern edge of the Ordos Plateau in Inner Mongolia (112°33′E–112°46′E, 40°29′N–40°37′N, 1221 m a.s.l.). It has a surface area of 133.5 km^2, a maximum water depth of about 14 m (in the year of 1999), a catchment area of 2289 km^2, and several rivers providing seasonal inflow. The lake is located in the transition zone between semi-humid and semi-arid areas in the middle temperate zone of China, and is surrounded by temperate steppe.

3 Materials and methods

Some 143 pollen traps were deployed between July 2004 and July 2005, including 56 traps in forested areas, 16 in shrublands, 28 in steppes, 21 in alpine meadows and 22 in desert areas, thus covering the major vegetation types in northern China. The traps consisted of a bucket 10 cm in diameter and 30 cm deep, with a lid that had a 5.2 cm diameter aperture surrounded by a sloping collar. The traps were sunk into the ground at each site so that the opening was 5–10 cm above the ground surface to minimize the risk of surrounding surface soil getting into the trap. The original pollen data were published by Li et al. (2008) and Xu et al. (2009) yet the representation of different pollen taxa has not been discussed then. The vegetation components in a 50 m radius surrounding forest traps and a 5 m radius surrounding steppe traps were recorded as percentages of plant coverage. The species compositions, the total coverage of each plant community and the coverage percentages of different plant species were recorded for each of these sites. Unfortunately, the vegetation surveying data are infeasible to calculate the plant abundance at different distances around the sampling sites, which is essential for the Extended R-Value (ERV) model; thus, we had to select another reliable approach to estimate pollen productivity.

Daily weather records from 1961 to 1990 measured at 243 meteorological observatories in northern China were obtained from the China Meteorological Statistical Annals (supplied by the China National Weather Service), and averages were calculated. The mean annual precipitation (P_{ann}), mean annual temperature (T_{ann}), mean temperature of the warmest month (Mt_{wa}) and mean temperature of the coldest month (Mt_{co}) for each trap site were calculated by parabolic interpolation using the Polation 1.0 program (Nakagawa, The Polation 1.0 program), with the inverse square distance as the weighting factor.

Pollen influx was reflected in the pollen sedimentation patterns and recorded as grains per cm^2 per annum. We calculated the APPEs using the ratio of pollen influx (grains $\mathrm{cm}^{-2}\ \mathrm{a}^{-1}$) to plant coverage (%) for individual taxa (*Abies*, *Betula*, *Larix*, *Picea*, *Pinus*, *Quercus*, *Ostryopsis*, *Artemisia*, Chenopodiaceae, Cyperaceae and Poaceae) based on those applicable sampling sites in which the target taxa were present in the vegetation communities; then each individual taxon obtains series of APPE values based on individual sampling sites. The ranges of APPEs for each pollen taxon are presented in box-plots produced using SPSS 11.5 software (Fig. 2). To explore which climatic factors (P_{ann}, T_{ann}, Mt_{co} or Mt_{wa}) affect the pollen productivity of individual taxa, we fitted univariate tree models using the Brodgar software package (Highland Statistics Ltd., available at Brodgar website). The determination of tree size was guided by cross-validation; the smallest tree was selected using the one standard deviation rule (Breiman et al., 2015). A LOESS smoother was then applied to highlight pollen productivity correlations with climate, using a default smoother span of 0.67 in the CanoDraw program. The thresholds obtained from univariate tree analysis are presented in the LOESS plots (Fig. 3).

We calculated the RPPEs for the 11 taxa by comparing the influxes per unit of plant coverage for the target taxa with those for the inference taxon. Poaceae was chosen as the reference taxon because it is common in the present-day vegetation of northern China as well as in both modern and fossil pollen records, and it has well defined pollen morphology, an intermediate pollen productivity, and has been used in previous studies (e.g., Herzschuh et al., 2003; Broström et al., 2008; Mazier et al., 2008; Zhao and Herzschuh, 2009; Wang and Herzschuh, 2011; Li et al., 2017a). It is, however, not an ideal taxon since it includes more than one species and different areas are likely to contain different species.

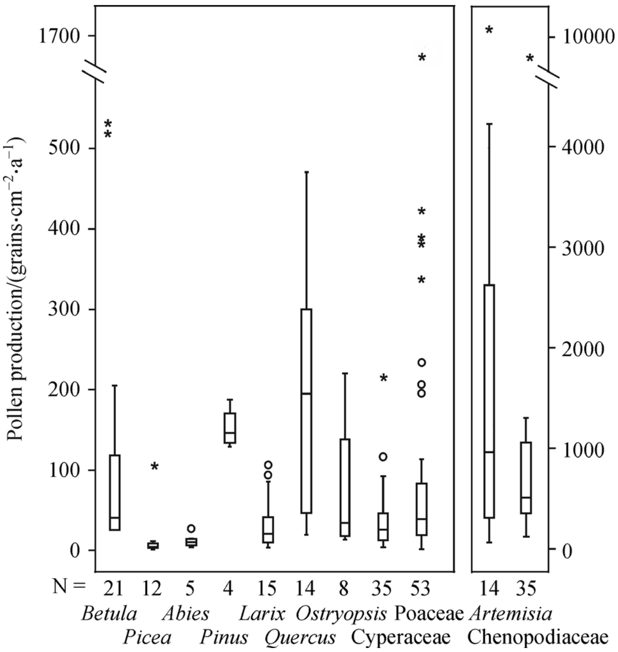
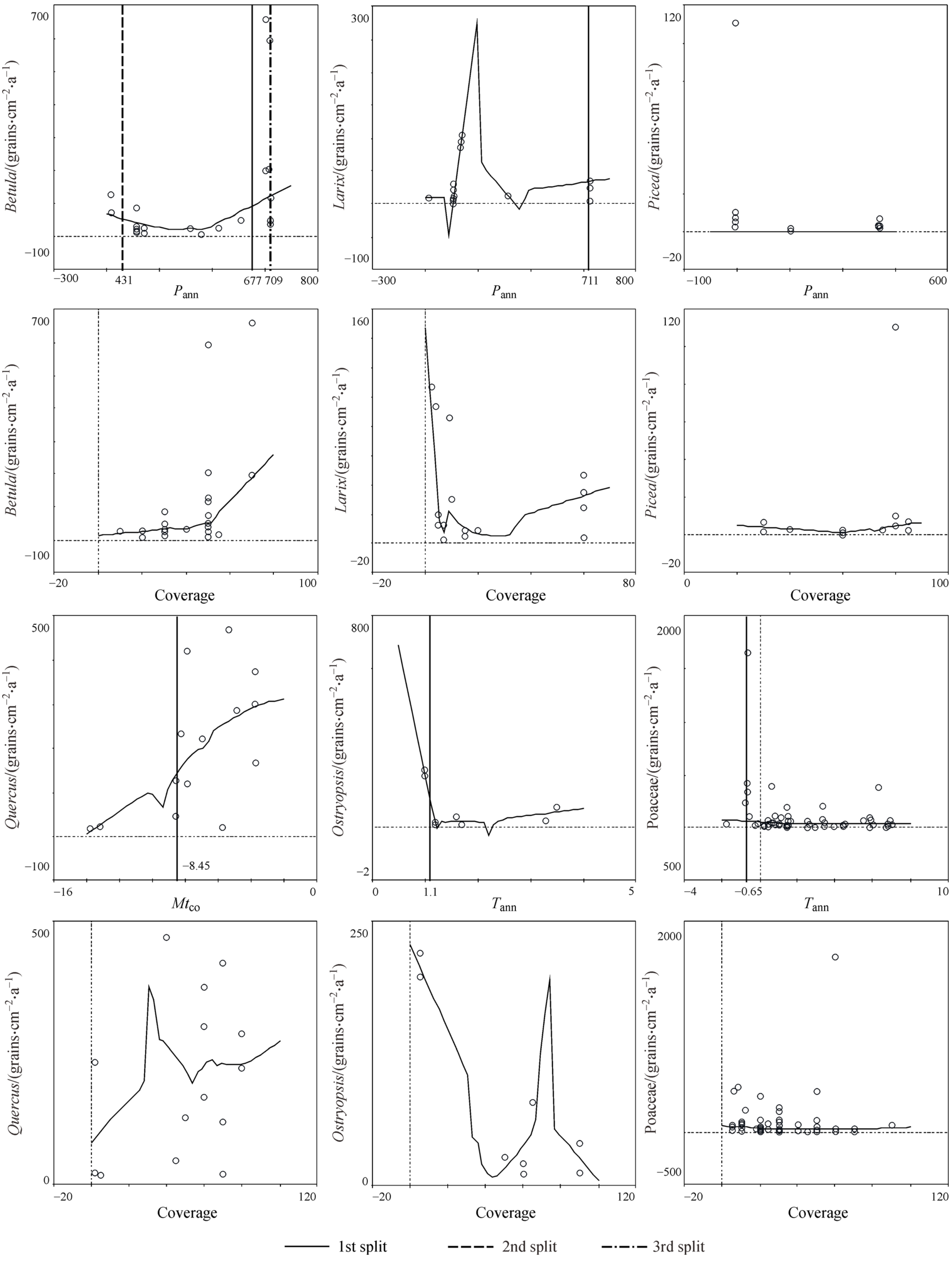


Fig. 2 Box plots of absolute pollen productivity estimates for the 11 major taxa in northern China. (N: number of samples, *: Extremes, °: Outliers).

To demonstrate the impact of differences of pollen productivity on vegetation modeling, we set up a series of 100 REVEALS (version 3.9) model runs using Sugita's lake model (Sugita, 1993 and 2007a) involving 100 randomly selected RPPE subsets and fossil pollen data from the DH99a Lake Daihai sediment core (Xiao et al., 2004). The eight taxa (*Betula*, *Pinus*, *Quercus*, Ostryopsis, *Artemisia*, Chenopodiaceae, Cyperaceae and Poaceae) that were used in the model, make up between 72.1% and 98.1% (median: 93.4%) of the pollen assemblages in the fossil record. To establish the 100 RPPE data sets for model running, RPPE values for each taxon were selected randomly for 100 times respectively using the sample function in REVEALS. The fall speed used for the calculation draws on information from Sugita et al. (1999), Broström et al. (2004) and Tian (2010), and is shown in Table 1. Approximate error ranges (due to variations in the present-day RPPEs) could thus be obtained for each taxon and each sample. To be able to directly compare the original pollen percentages with the model-based reconstructed vegetation percentages, the pollen percentages for the eight taxa included in the pollen totals were recalculated.


Betula/(grains·cm^{-2}·a^{-1})
700
−100
−300
431
677
709
800
P_{ann}
Larix/(grains·cm^{-2}·a^{-1})
300
−100
−300
711
800
P_{ann}
Picea/(grains·cm^{-2}·a^{-1})
120
−20
−100
600
P_{ann}
Betula/(grains·cm^{-2}·a^{-1})
700
−100
−20
100
Coverage
Larix/(grains·cm^{-2}·a^{-1})
160
−20
−20
80
Coverage
Picea/(grains·cm^{-2}·a^{-1})
120
−20
0
100
Coverage
Quercus/(grains·cm^{-2}·a^{-1})
500
−100
−8.45
−16
0
Mt_{co}
Ostryopsis/(grains·cm^{-2}·a^{-1})
800
−2
0
1.1
5
T_{ann}
Poaceae/(grains·cm^{-2}·a^{-1})
2000
500
−4
−0.65
10
T_{ann}
Quercus/(grains·cm^{-2}·a^{-1})
500
0
−20
120
Coverage
Ostryopsis/(grains·cm^{-2}·a^{-1})
250
0
−20
120
Coverage
Poaceae/(grains·cm^{-2}·a^{-1})
2000
−500
−20
120
Coverage
1st split
2nd split
3rd split

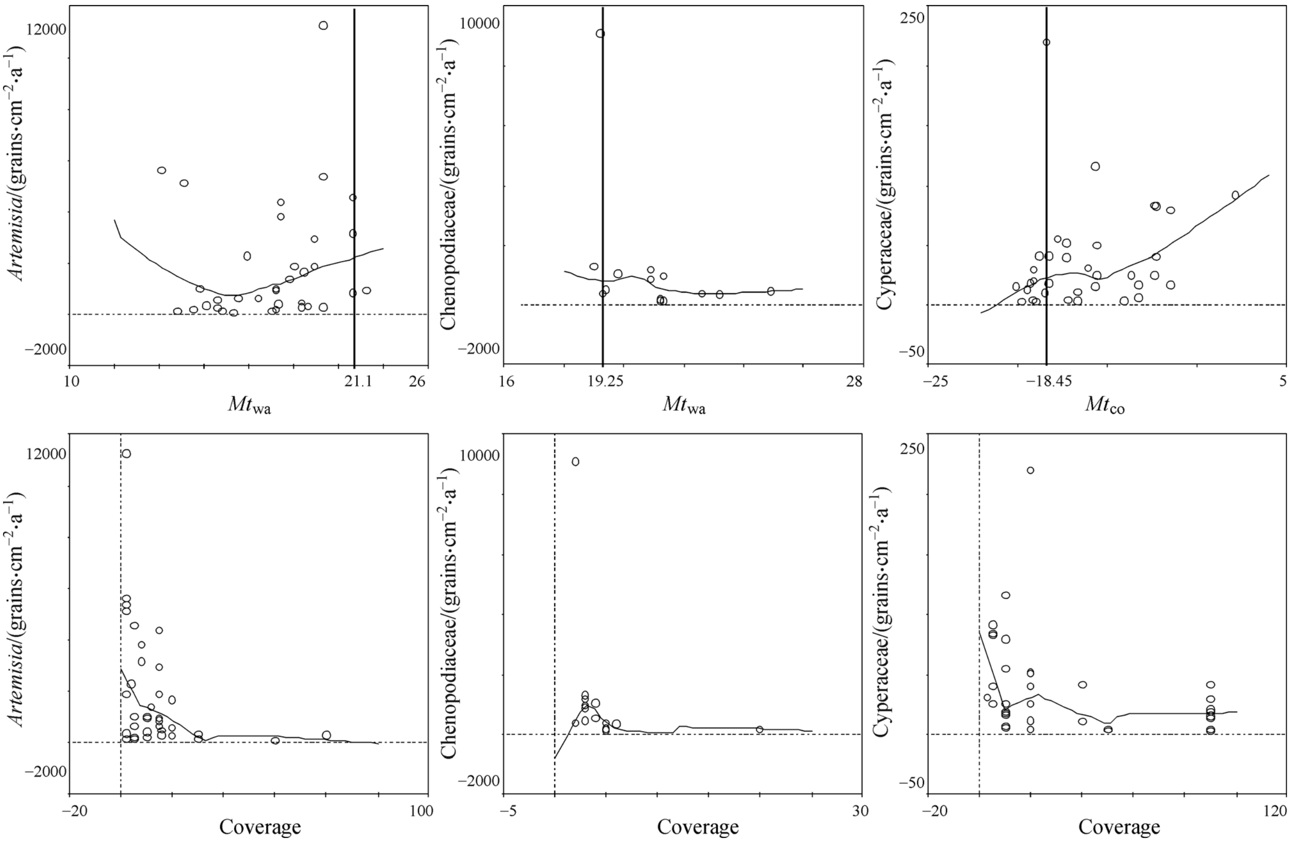


Fig. 3 LOESSs Smoothed curves for variations in the APPEs (grains cm^{-2}·a^{-1}) of nine pollen taxa with plant coverage and key climatic factors (smoother span: 0. 67).

Table 1 Fall speeds for the eight species used in the REVEALS model

Species	Fall speed/(m·s^{-1})
Betula	0.031[a]
Pinus	0.031[b]
Quercus	0.042[a]
Ostryopsis	0.025[a]
Artemisia	0.015[a]
Chenopodiaceae	0.029[a]
Cyperaceae	0.035[c]
Poaceae	0.035[b]

Note: [a]Tian 2010; [b]Sugita et al.,1999; [c]Broström et al., 2004.

4 Results

4.1 Calculation of APPEs and RPPEs

The PPE ranges and median values for the 11 taxa investigated are shown in Fig. 2 and Table 2, which also includes the main climatic factors affecting these values. *Artemisia* and Chenopodiaceae had the highest APPEs and the largest ranges. *Artemisia* recorded one APPE (grains ·cm^{-2}·a^{-1}, unit for APPE omitted below) value higher than 10000 and 21 values below 1020, with the other 13 values falling between 1400 and 5600; six of the sites for which RPPEs were available had values between 152 and 690, while all other sites had values less than 62. The maximum APPE for Chenopodiaceae was 9122, with three sites ranging between 1000 and 1300 and 10 sites ranging between 140 and 970; its two highest RPPEs were 830 and 517, while other values were all less than 50. The highest APPE for Poaceae was 1658, with 42 sites below 100 and 10 sites between 108 and 427. *Pinus* and *Quercus* had higher PPEs than Poaceae, and *Pinus* had the smallest range of PPEs out of all the 11 taxa. *Abies*, *Betula, Larix*, *Picea* and Cyperaceae all had relatively low PPEs. The fact that *Ostryopsis* has a low APPE median but a relatively high RPPE median value is a methodological artifact: there were eight traps applicable for APPEs, but only three of these could be used for *Ostryopsis* RPPEs as they were the only ones in which *Ostryopsis* and Poaceae occurred together in the surrounding vegetation. No traps were applicable for calculating RPPEs for the *Abies*, *Pinus* and *Quercus* taxa, but since they are common taxa in fossil pollen records as well as in the modern vegetation of mountain areas in northern China we used the ratios of

Table 2 APPE and RPPE values and their associated major climatic factors in northern China

Species	APPEs/($\text{grains}\cdot\text{cm}^{-2}\cdot\text{a}^{-1}$)			RPPEs (related to Poaceae)			Key Factor
	Number of traps	Range	Median	Number of traps	Range	Median	
Abies	5	4–26	9	0*	0.10–0.69*	0.24*	—
Betula	21	8–660	40	5	0.13–2.14	0.29	P_{ann}
Larix	15	2–106	20	6	0.03–3.81	0.12	P_{ann}
Picea	12	0.65–111	3	3	0.07–0.13	0.09	P_{ann}
Pinus	4	128–188	145	0*	3.32–4.9*	3.78*	—
Quercus	14	18–471	194	0*	0.46–12.23*	5.05*	Mt_{co}
Ostryopsis	8	11.6–220	34	3	0.3–9	6	T_{ann}
Artemisia	35	65–11,265	963	30	0.74–690	25.38	Mt_{wa}
Chenopodiaceae	14	140–9,122	514	10	1.79–830	25.7	—
Cyperaceae	35	3–220	25	9	0.04–15	0.13	—
Poaceae	53	1–1,658	38	53	1	1	T_{ann}

Note: * Due to the absence of sites in which these taxa co-occurred with Poaceae, their RPPEs were calculated using the median influx for Poaceae.

their APPEs to the APPE median for Poaceae to calculate their individual RPPEs.

4.2 The relationship of APPEs to plant coverage and key climatic factors

Variation in plant coverage has a systematic effect on the APPEs for *Larix*, *Picea*, *Ostryopsis*, *Artemisia*, Chenopodiaceae, Cyperaceae and Poaceae. The plant coverages for *Betula* and *Quercus* have a positive correlation with their respective APPEs (Fig. 3).

Of all the environmental factors the APPEs for *Betula*, *Larix* are revealed by univariate tree modeling to be the most strongly related to P_{ann}, while the APPEs for *Quercus* and Cyperaceae are related to Mt_{co}, those for *Ostryopsis* and Poaceae are related to T_{ann}, and those for *Artemisia* and Chenopodiaceae are related to Mt_{wa}. The APPEs for *Betula*, *Quercus*, *Artemisia* and Cyperaceae have a positive correlation with their key climatic factors, but no obvious trends have been found for *Larix* and *Picea*. The APPE for Poaceae remains consistent with increasing T_{ann}, while a reduction in the APPE for Chenopodiaceae is mainly due to the effect of a single outlier (Fig. 3).

4.3 Holocene vegetation reconstructions for the Lake Daihai area

The vegetation composition reconstructed on the basis of a series of 100 runs of the REVEALS model on randomly selected RPPE schemes is markedly different from that based on the original pollen percentages. For example, extremely high proportions of *Artemisia* (up to 77%) and Chenopodiaceae (up to 48%) were found in the pollen spectra throughout the entire Holocene, but the proportions appear much lower (less than 40% and 16%, respectively) in the reconstructed vegetation (Fig. 4). In contrast, the abundance of Cyperaceae (0%–2.5%, median: 0.3%) in pollen assemblages is extremely low compared to the abundance of Cyperaceae plants (between 0%–55%, median: 9%) in the reconstructed vegetation because of its low RPPE. *Pinus*, *Quercus* and *Ostryopsis* are present in similar proportions in both the pollen and vegetation data. As indicated by the large error ranges, particularly for *Betula* and Cyperaceae (Fig. 4), the individual reconstruction results vary greatly depending on the RPPEs involved.

Fossil pollen records indicate a steppe vegetation during the early Holocene (before 8 cal ka BP) dominated by herbs, with forest patches probably growing around the lake. However, according to the quantitative vegetation reconstruction, the regional vegetation around Lake Daihai was, at this stage, dominated by open birch forests rather than by steppe vegetation. Between 8 and 2.4 cal ka BP, the vegetation reconstruction indicates that the presence of pines and oaks showed a distinct and synchronous increase at the expense of birches, which is in accordance with the inferences based on pollen percentages; however, Cyperaceae is one of the main herbaceous taxa in the vegetation reconstruction while *Artemisia* and Chenopodiaceae are the dominant herbs in the original pollen percentage data. After 2.4 cal ka BP, pollen data indicates a scrub-steppe environment in which the forests almost disappeared, and that since that time the mountain slopes were composed mainly of *Artemisia* and Poaceae, with Chenopodiaceae growing in the valleys and depressions. However, the reconstruction indicates that birches began to recover during this period, although *Artemisia*, Chenopodiaceae, Cyperaceae and Poaceae reached their highest coverage while the *Pinus* and *Quercus* coverage began to decrease. The most significant difference between pollen data and the REVEALS-based vegetation reconstruction is that *Betula* and Cyperaceae were dominant taxa in the vegetation but contributed very little to the total pollen.

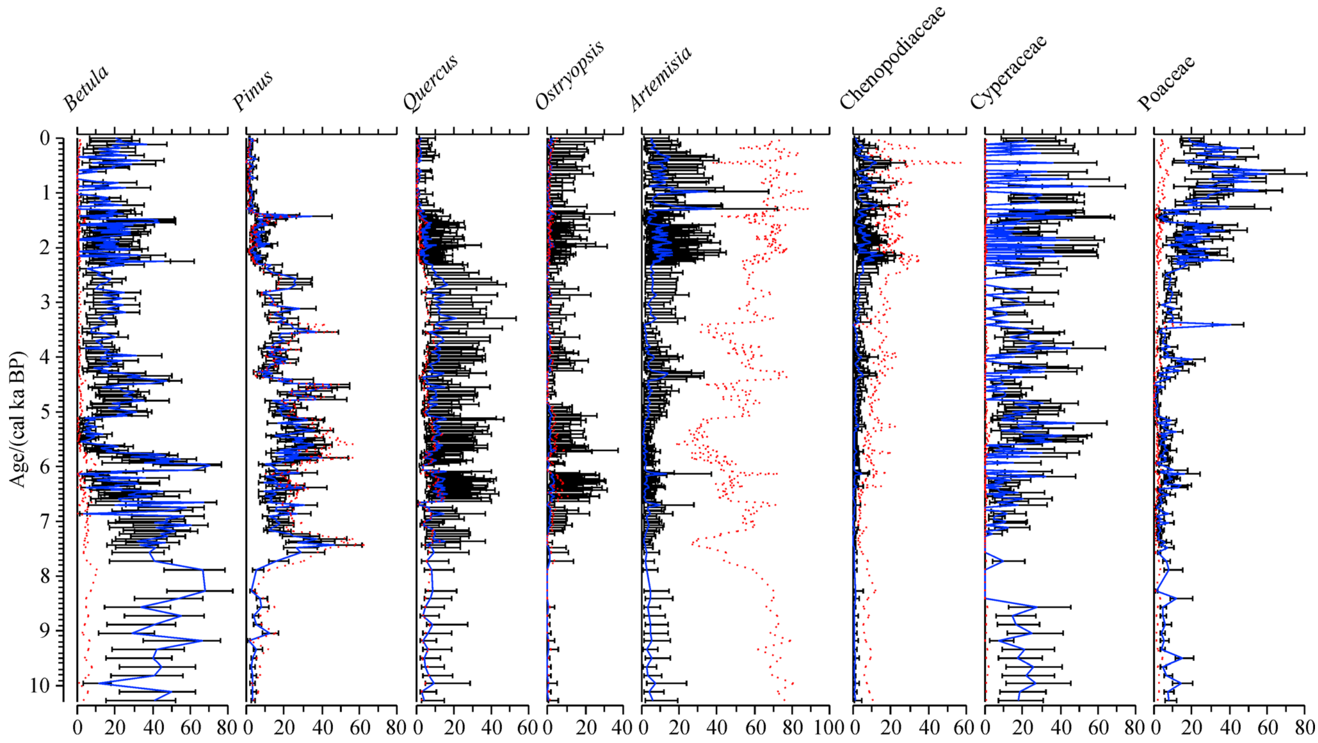


Fig. 4 Holocene vegetation compositions deduced from the original pollen count data and REVEALS models. The blue line represents median vegetation reconstructions (from 100 reconstructions), with the lower limits of error bars marking the 25% quartiles and their upper limits the 75% quartiles. The broken red lines indicate total pollen percentages for the eight reconstructed taxa.

The sample-specific relative vegetation coverage reconstruction ranges for *Betula* and Cyperaceae are large, while those for *Artemisia* and Chenopodiaceae are much smaller. Poaceae only has a large range in reconstructed vegetation coverage during the late Holocene.

5 Discussion

5.1 PPE variations between different areas

The highest productivity estimates were for *Artemisia* and Chenopodiaceae (median APPEs of 963 and 514, and median RPPEs of 25.38 and 25.7, respectively), while lower estimates were obtained for Cyperaceae and Poaceae (median APPEs of 25 and 38, and median RPPEs of 0.13 and 1, respectively), which is consistent with the over-representation of *Artemisia* and Chenopodiaceae relative to Poaceae and Cyperaceae reported by Li et al. (2011). However, in contrast to our results, Li et al. (2011) obtained markedly higher productivity for *Artemisia* than for Chenopodiaceae. In our study, Cyperaceae shows consistently low PPEs, which is consistent with studies from the Alashan Plateau (Herzschuh et al., 2003 and 2006a), the Tibetan Plateau (Herzschuh et al., 2006b; Zhao and Herzschuh, 2009; Wang and Herzschuh, 2011; Wei et al., 2011), and southern Sweden (Sugita et al., 1999; Broström et al., 2004), but contrary to a study from Estonia (Poska et al., 2011). In addition, *Pinus* (median APPE/RPPE: 145/3.78) and *Quercus* (median APPE/RPPE: 194/5.05) have generally higher PPEs than Poaceae, which is in agreement with results from Europe (Sugita et al., 1999; Räsänen et al., 2007; Soepboer et al., 2007; von Stedingk et al., 2008; Poska et al., 2011).

Although the RPPEs for some taxa are more or less consistent between regions, some differences do exist. The largest differences are recognized in *Abies* and *Picea*, which have distinctly lower RPPEs in northern China than those obtained from several European areas. The RPPEs for *Artemisia* and Chenopodiaceae in northern China are also markedly higher than on the Tibetan Plateau (alpine meadow), where the cold climate might be not optimum for *Artemisia* and Chenopodiaceae; and *Betula* has a lower RPPE in northern China than in other regions (Table 3). The differences in RPPEs between our study and other studies could be caused by (at least to some extent) the different pollen source areas between the small (5.2 cm diameter) opening-area of traps and the surface-soil or lake-surface samples.

Some older studies assumed that *Larix* had a pollen productivity as high as other boreal conifers and concluded that its under-representation in pollen spectra was mainly due to the poor preservation and dispersal abilities of its pollen (Gunin et al., 1999). However, our own results for *Larix* (median APPE/RPPE: 20/0.12) support the conclusions of, for example, Gunin et al. (1999) and Ma et al.

Table 3 Relative pollen production for the 9 major taxa in countries or regions

Species	This study	Inner Mongolia[1]	Tibetan Plateau[2]	Denmark[3]	England[4]	Estonis[5]	Finland[6]	Norway[7]	Central Sweden[8]	Southern Sweden[9]	Swiss Jura[10]	Swiss Plateau[11]	Xilinhot[12]	Shandong Province[13]	Changbai Mt. [14]	Forest-steppe ecotone[15]	Loess Plateau[16]
Abies	0.237										3.34	9.92	0.39	1.06		0.19	1.00
Betula	0.29				8.06	1.81	4.6		2.24	8.94		2.42			24.65	1.16	6.20
Picea	0.09			4.75		4.73			2.78	1.77	7.1	0.57					11.70
Pinus	3.777			1.41		5.07	8.4		21.58	5.71		1.35		8.96	15.21	20.07	29.80
Quercus	5.049				7.6	7.39				7.6		2.56		4.89		58.05	0.6
Artemisia	25.375	53.625	3.267			3.48							11.21	24.70		1.29	2.3
Chenopodiaceae	25.7	12.5	5.379										6.74			50.49	
Cyperaceae	0.13		0.66		0.002	1.23		0.29	0.89	0.67	0.68		0.94	0.21		0.01	
Poaceae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Note: *PPEs were estimated using the Extended R-value (ERV) Model 3, with Poaceae as the reference taxon, except for northern China, Norway, England, Estonia, and the Swiss Jura, for which ERV Model 1 was used, and the Tibetan Plateau for which ERV Model 2 was applied. [1]Li et al., 2011; [2]Wang and Herzschuh, 2011; [3]Nielsen, 2003; [4]Bunting et al., 2005; [5]Poska et al., 2011; [6]Räsänen et al., 2007; [7]Hjelle, 1998; [8]von Stedingk et al., 2008; [9] Sugita et al., 1999; Broström et al., 2004; [10]Mazier et al., 2008; [11]Soepboer et al., 2007; [12] Xu et al., 2014; [13]Li F et al., 2017; [14]Li et al., 2015; [15]Han et al., 2017; [16]Li Y et al., 2017.

(2008), that *Larix* has a low pollen productivity as well as poor pollen dispersal. The PPE values for *Larix* obtained in our study should be reliable since all four of the *Larix* traps were located in pure *Larix* forest and since glycerin was added to each trap at the time of installation to preserve the pollen grains.

5.2 The dependence of PPEs on taxa coverage and climate

5.2.1 Critical assessment of the data and method

The correlations between APPEs and the environmental variables were found to be complex for most of the pollen taxa. The following methodological limitations might have enhanced the natural ambiguity.

1) Low number and limited distributions of sites.

Although 120 traps were included in this study, only very few traps were useable for some of the pollen taxa and their distribution was very limited. For example, only four traps were applicable for the *Pinus* APPEs, which were located on the Manhan and Li Mountains, but none of these traps could be used to calculate RPPEs for *Pinus* since Poaceae was not present in the vegetation at these sites. Due to the small number of available traps, the obtained PPE-range may have been underestimated.

2) Taxonomic resolution

In most cases, a single pollen taxon corresponds to several plant species or genera, with variable reproduction strategies, life forms, habitats and climatic requirements, which can have a marked effect on the PPEs and the associated vegetation reconstructions (Watrin et al., 2007). Within our study area *Artemisia* and Chenopodiaceae have many more species than the arboreal taxa (*Abies*, *Betula*, *Larix* and *Picea*) investigated (How, 1998), which, together with the larger sampling area for *Artemisia* and Chenopodiaceae than for arboreal taxa, may explain their larger PPE ranges. Clearly taxonomic resolution presents a challenge to quantitative vegetation reconstruction and needs further investigation.

3) Pollen source area and vegetation data

The source area of pollen has important implications for the interpretation of pollen-vegetation relationships and palaeoecological records (Bunting et al., 2004; Niemeyer et al., 2015). However, Li et al. (2008) concluded that the pollen source radius is less than 50–100 m for forest sites and other studies have also concluded that the plants in the immediate vicinity of a trap supply most of the pollen in the trap (Jackson and Kearsley, 1998; Sugita et al., 1999; Pérez et al., 2009; Xu et al., 2009; Sugita et al., 2010b). Therefore, we surveyed vegetation components within a radius of 50 m for the forest traps and 5 m for steppe traps, aiming to account for the different dispersal mechanisms of arborous and herbaceous taxa. The background pollen was not included in the calculations but may have contributed a substantial proportion of the pollen load in the traps, and the proportion of this load may vary between the sites which is even more problematic.

4) Temporal variations in pollen productivity

The inter-annual variability in PPEs for the same taxon is well documented (Andersen, 1974; Saito et al., 1984; Hicks et al., 1994; Hicks, 2001; Sugita et al., 2010b; McLauchlan et al., 2011) and hence monitoring records of pollen influxes over 5 to 10 years is required to obtain average pollen productivities (Hicks, 2001). The observed spatial differences in productivity estimates may, to some extent, be due to the same factors that cause differences between the years.

5.2.2 Possible reasons for PPE variances

Differences in vegetation structure and vegetation cover density, both between and within species, have been found to influence pollen productivity (Hicks, 2001; Broström et al., 2008; von Stedingk et al., 2008; Sugita et al., 2010b; Baker et al., 2016). In this study, the APPEs for *Betula* and *Quercus* clearly increase when the forest coverage exceeds 40%, which may be a result of optimal growth conditions. In contrast, higher APPEs for non-arboreal taxa (*Ostryopsis*, *Artemisia*, Chenopodiaceae and Cyperaceae) occur in sites with lower plant coverage while lower APPEs appear in sites with higher plant coverage. It is possible that these species expend less energy on sexual reproduction (but more on vegetative reproduction) at sites with high coverages (Cresswell et al., 2011). The response of PPEs to plant coverage clearly differs between arboreal and non-arboreal species.

It has been suggested in previous studies that differences in vegetation structure, vegetation cover, reproduction strategy, age class, and growth behavior, both between and within species, might influence pollen productivity (Hicks, 2001; Broström et al., 2008; von Stedingk et al., 2008; Sugita et al., 2010b; Han et al., 2017). The higher APPEs for *Betula* and *Quercus* in sites with higher coverages might have resulted from the optimal growing conditions, while the lower PPEs for *Artemisia* in forest zones (median APPE/RPPE: 299/4) than in non-forest zones (median APPE/RPPE: 962/34) may have been due to lower plant coverage and less suitable growing conditions in forest areas.

The impact of climate conditions on pollen productivity is complicated and is likely to vary from different pollen taxa (Autio and Hicks, 2004; Broström et al., 2008; van der Knaap et al., 2010). And vegetation evolution is sensitive to temperature (Wu et al., 2016). In our study, the PPEs for *Larix* are related to the mean annual precipitation, while those for *Quercus* and Cyperaceae may be affected by the mean temperature of the coldest month. The productivity of *Ostryopsis* and Poaceae may be related to the mean annual temperature and those of *Artemisia* and Chenopodiaceae to the mean temperature of the warmest month.

The major climatic factors affecting the PPEs for an individual taxon also vary from one region to another. For example, in northern China, the PPEs for *Betula* and *Picea* have been shown to be related to the mean annual precipitation, while in the Swiss Jura Mountains the PPE for *Betula* responds positively to both winter and spring temperature (Sjögren et al., 2006), and in northern Finland and the Caucasus the PPE for *Picea* is affected by the summer temperature of the previous year (Autio and Hicks, 2004; van der Knaap et al., 2010). A possible explanation for these differences could be that moisture is the climatic factor controlling vegetation distribution in northern China, particularly in the relative dry steppe and desert areas, while temperature is the controlling factor in western and northern Europe. Sjögren et al. (2008) suggested that the pollen productivity of trees growing close to the tree line in mountain areas might be climatically limited. Our RPPE for *Betula* (range: 0.13–2.14, median: 0.29) is far lower than those for European areas (Table 3), possibly because our traps were located in the transition zone between forest and alpine meadow, close to the upper tree limit.

Although we tried to avoid human impact as much as possible when positioning the traps, the selected areas would have still been impacted by grazing. The pollen productivity of herb species in pasture-lands are likely to be lower than in non-pasture areas as a result of grazing disturbing the flowers and thus reducing the pollen productivities (Groenman-van Waateringe, 1993; Dahlström, 2008). Since Poaceae is one of the favorite forages for livestock species, the lower APPE for Poaceae in non-forested areas (median: 31) than in forested areas (median: 112) may be related to human impacts, which would unfortunately also affect the RPPEs for other taxa since Poaceae was used as the reference taxon in our study.

5.3 Implications of differences in RPPEs for vegetation reconstruction

The basic assumption of the REVEALS model (Sugita, 2007a) is that wind is the dominant agent of pollen transport. Lake Daihai has several inflowing rivers that originate from the surrounding mountains; and previous studies on sediment-surface pollen distribution for Lake Daihai revealed that the pollen assemblages represent regional vegetation surrounding Lake Daihai well and the influence of background pollen transported by wind is quite weak (Xu et al., 2005; Tian et al., 2008). As taphonomy did not change substantially, we assume that the vegetation reconstruction should represent the regional vegetation coverage well. In addition, the drainage catchment area may be overrepresented in the Daihai pollen record compared to areas that only receive contributions from air-borne pollen (Xu et al., 2012). This may explain the high contributions of arboreal taxa to the early and middle Holocene fossil pollen spectra despite the fact that the lake was surrounded by steppe vegetation.

In the present-day vegetation, *Betula* and *Pinus* are the main tree taxa in forest communities on the northern slopes of the mountains in the Lake Daihai area, accompanied by *Ostryopsis* in the forest under-storey. However, the vegetation reconstructions indicated by REVEALS modeling suggest that birches were the main component in forests throughout the entire Holocene. Previous studies found that both *Betula* and *Pinus* are over-represented in the pollen taxa (Xu et al., 2007). In our reconstruction the proportion of *Pinus* in the vegetation is slightly lower than it is in the pollen, which agrees with the previous conclusion that it is over-represented (Xu et al., 2007). The contribution of *Betula* in the vegetation is markedly higher than in the pollen, which disagrees with the previously interpreted over-representation, hence we argue that the birch coverage could be over-estimated, because *Betula* RPPE in this study is lower than previous RPPE studies in north China.

Artemisia is widely distributed within the Lake Daihai area, occurring in both steppes and alpine meadows, while the Chenopodiaceae species are only common on hilly steppes (Xiao et al., 2004). Liu et al. (1999) found that *Artemisia* and Chenopodiaceae are dominant components in modern pollen samples from temperate-steppe areas in northern China, even in sites with low plant coverage. In our reconstructions their vegetation coverage percentages are substantially lower than their pollen percentages due to their high pollen productivities. In contrast, Cyperaceae and Poaceae plants are major components of halophilic meadows and patches of boggy meadow that are predominant along the lake shores and on the leading edges of diluvial fans (Wang et al., 1990; Xiao et al., 2004). Their high proportions in the reconstructed vegetation are consistent with those in present-day vegetation.

Large ranges in reconstructed vegetation estimates were found for the individual samples, for almost all species, indicating that the vegetation reconstructions are strongly affected by the large ranges of the pollen productivity estimates. Taxa with large RPPE ranges such as *Artemisia*, Chenopodiaceae, Cyperaceae and *Quercus* are reconstructed to behave in large ranges in plant coverage; while taxa with narrow RPPE ranges such as *Pinus* are estimated to have small coverage-ranges (Table 2; Fig. 4). Our experiment reveals the importance of RPPE in the vegetation reconstruction. We found that the pollen productivity of individual species varied with different climatic conditions. If only one PPE-set for the investigated species is applied throughout the entire period covered by the vegetation reconstruction (as is commonly the case), the effect of climatic variations on the vegetation reconstruction would be obscured, especially for a series of strong climatic fluctuations. Further investigations into pollen productivity under various climatic conditions are required to reveal the relationships between pollen productivity and environmental factors; the application of different PPE-sets for different climatic periods might then be expected to produce more accurate reconstructions of past vegetation.

6 Conclusions

1) Pollen influxes per unit plant coverage can be used as an index to scale pollen productivity for different taxa. In this study, *Artemisia* and Chenopodiaceae had the highest pollen productivity estimates and the largest ranges, while *Pinus* and *Quercus* were moderate pollen producers and *Abies*, *Betula*, *Larix*, *Picea*, *Ostryopsis*, Cyperaceae and Poaceae were all low pollen producers.

2) We found that environmental factors, climatic conditions and plant coverage could all produce variations in the PPEs for individual taxa.

3) Using REVEALS modeling to reconstruct Holocene vegetation in the Lake Daihai area of northern China, we found that the large range of taxa-specific PPEs produced a large variability in the vegetation reconstructions, which could even prevent the recognition of major changes in vegetation. Further investigations into the relationship between pollen productivity and climatic conditions are required to improve the reconstructions of Holocene vegetation changes.

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