

A modern pollen–climate calibration set from central-western Mongolia and its application to a late glacial–Holocene record

Fang Tian^{1,2}*, Ulrike Herzschuh^{1,2}, Richard J. Telford³, Steffen Mischke^{2,4}, Thijs Van der Meeren⁵ and Michael Krengel⁴

¹Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Research Unit Potsdam, Potsdam, Germany, ²Institute of Earth and Environmental Science, University of Potsdam, Potsdam, Germany, ³Department of Biology and Bjerknes Centre for Climate Research, University of Bergen, Bergen, Norway, ⁴Institute of Geological Sciences, Free University of Berlin, Berlin, Germany, ⁵Royal Belgian Institute of Natural Sciences, Freshwater Biology, Brussels, Belgium

ABSTRACT

Aim Fossil pollen spectra from lake sediments in central and western Mongolia have been used to interpret past climatic variations, but hitherto no suitable modern pollen–climate calibration set has been available to infer past climate changes quantitatively. We established such a modern pollen dataset and used it to develop a transfer function model that we applied to a fossil pollen record in order to investigate: (1) whether there was a significant moisture response to the Younger Dryas event in north-western Mongolia; and (2) whether the early Holocene was characterized by dry or wet climatic conditions.

Location Central and western Mongolia.

Methods We analysed pollen data from surface sediments from 90 lakes. A transfer function for mean annual precipitation (P_{ann}) was developed with weighted averaging partial least squares regression (WA-PLS) and applied to a fossil pollen record from Lake Bayan Nuur (49.98° N, 93.95° E, 932 m a.s.l.). Statistical approaches were used to investigate the modern pollen–climate relationships and assess model performance and reconstruction output.

Results Redundancy analysis shows that the modern pollen spectra are characteristic of their respective vegetation types and local climate. Spatial autocorrelation and significance tests of environmental variables show that the WA-PLS model for P_{ann} is the most valid function for our dataset, and possesses the lowest root mean squared error of prediction.

Main conclusions Precipitation is the most important predictor of pollen and vegetation distributions in our study area. Our quantitative climate reconstruction indicates a dry Younger Dryas, a relatively dry early Holocene, a wet mid-Holocene and a dry late Holocene.

Keywords

Central-western Mongolia, climate reconstruction, Lake Bayan Nuur, modern pollen, ordination, palaeoclimate reconstruction, palaeoecology, transfer functions, WA-PLSY, Younger Dryas.

INTRODUCTION

Mongolia lies in the transition zone between the westerlies and the East Asian Monsoon, making it a climatically sensitive area. We make use of this sensitivity via the information contained in climate proxy records to gain a better understanding of the vegetation and environmental changes of recent millennia and to predict future changes. With respect to climatic variability since the end of the last glacial period,

© 2014 John Wiley & Sons Ltd

*Correspondence: Fang Tian, Alfred Wegener

Telegrafenberg A5, 14473 Potsdam, Germany.

E-mails: Fang.Tian@awi.de; tfhebtu@sohu.com

Institute Helmholtz Centre for Polar and

Marine Research, Research Unit Potsdam,

two unanswered palaeoclimate problems exist. (1) Previous qualitative studies suggest that the Younger Dryas event exhibited both wet and dry conditions in north-western Mongolia (Herzschuh, 2006) and thus reliable quantitative estimates are necessary to discern whether these contradictory results originate from methodological shortcomings or whether they represent a true signal. (2) Was the early Holocene dry or wet? Although several publications focus on the Holocene climate changes of Mongolia, the general trend of moisture change is still under debate. For example, a compilation of palaeoclimate proxy data from Mongolia suggests a relatively dry early Holocene but a wet mid-Holocene (Herzschuh, 2006; Chen *et al.*, 2008), which is in contrast to most monsoon areas (Herzschuh, 2006). However, other publications propose a relatively wet early Holocene (Komatsu *et al.*, 2001; Prokopenko *et al.*, 2007), but a dry mid-Holocene (Fowell *et al.*, 2003; Wang *et al.*, 2011) in Mongolia.

Pollen records have been used to gain quantitative estimates of past climatic variations at millennial time-scales. As a prerequisite, the numerical relationships between modern pollen taxa and climate variables of interest need to be investigated and a transfer function developed. Often, modern pollen assemblages from various sources (soil surfaces, moss polsters, lake sediment-surfaces) are jointly used to interpret fossil pollen records, even though it is known that they have distinct differences in pollen taphonomy (Minckley & Whitlock, 2000; Zhao & Herzschuh, 2009). Ideally, a modern pollen-climate calibration set should be based on sediment samples from lakes of a similar taphonomy (deposition, preservation, source area) to the lake for which the resulting transfer functions will be applied (Birks, 2003). Pollen calibration sets based on lake sediments are available from, for example, the Tibetan Plateau (Herzschuh et al., 2010). Hitherto, modern pollen data are rare for Mongolia (e.g. Gunin et al., 1999; Ma et al., 2008) and none are from lake sediments.

Here we present a pollen–climate calibration set consisting of pollen assemblages from 90 lake sediment-surface samples. Our research aims were: (1) to determine the relationship between pollen taxa and selected climate variables in central and western Mongolia; (2) to identify those climate variables that are most likely to be responsible for the spatial variations of pollen assemblages; (3) to establish and assess pollen–climate calibration sets; (4) to apply the useful calibration models to a fossil pollen record from Bayan Nuur in western Mongolia covering the last 16 cal. kyr; and (5) to contribute to the important palaeoclimatic questions mentioned above.

MATERIALS AND METHODS

Study area

Mongolia is an upland country with about 85% of its area situated above 1000 m a.s.l., mostly between 1000 and 1500 m (Hilbig, 1995). Our study focuses on the semi-arid transition area (stretching from 46° to 52° N and from 88° to 106° E with an elevation of *c*. 550 to 4100 m a.s.l), which is most vulnerable to climate and vegetation change (Tian *et al.*, 2013). The climate in Mongolia is characterized by extreme continentality with cold and dry winters controlled mainly by the Siberian high-pressure system, and relatively warm and wet summers controlled by the Asian low-pressure system (Angerer *et al.*, 2008). The westerlies bring moisture to the mountain ranges of north-western Mongolia and there is a mean annual precipitation (P_{ann}) gradient from north to south, with more than 70% of $P_{\rm ann}$ occurring during summer (Ma *et al.*, 2008). The highest $P_{\rm ann}$ values of 300–400 mm (occasionally exceeding 600 mm) occur in the Khangai and Khentii mountainous region. The Gobi desert in south-west Mongolia has the lowest $P_{\rm ann}$ of 50–100 mm and has periods without precipitation lasting several years. Mean temperature of the coldest month ($T_{\rm Jan}$) is generally below –15 °C, and mean temperature of the warmest month ($T_{\rm Jul}$) is around 15 °C in the mountains and 20–30 °C in the southern semi-deserts and deserts (Paul & Horn, 2000; Ma *et al.*, 2008).

Mongolia is a transitional zone from Siberian taiga to dry steppe, steppe-desert and desert in Central Asia, and the major portion of its territory is in the steppe and foreststeppe zones. The study area includes mountain foreststeppe, mountain steppe, steppe and dry steppe, desert steppe and desert vegetation types (Fig. 1b; Hilbig, 1995; Saandar & Sugita, 2004). The forest-steppe and steppe zones have the highest density of population and livestock (Angerer *et al.*, 2008).

Bayan Nuur is located in the Uvs Nuur Basin in northwestern Mongolia (Fig. 1). The climate is highly continental with P_{ann} of 142 mm (around 66% falling between June and August) and is characterized by very cold, dry winters and relatively warm summers (Paul & Horn, 2000). Bayan Nuur is surrounded by desert steppe (Saandar & Sugita, 2004). A summary of the present-day climate, vegetation and limnological characteristics of Bayan Nuur is given in Table 1.

Collection and analysis of surface pollen samples and sediment core

Lake sediment-surface samples (Fig. 1, and see Appendix S1 in Supporting Information) were collected from the centres of 90 lakes from a variety of vegetation zones (mountain forest steppe, mountain steppe, steppe and dry steppe, desert steppe and desert) in central Mongolia (2005) and western Mongolia (2008) using a gravity corer or sediment grab. For pollen analysis, the top 2 cm of sediment was used. Fifty-one samples were collected from small lakes with a radius of less than 1000 m, 20 samples were collected from medium-sized lakes with a radius of 1000-5000 m, and the other 19 samples from lakes with a radius greater than 5000 m. Pollen preparation followed the modified acetolysis procedure (Faegri & Iversen, 1989), which included HCl, KOH, HF and acetolysis treatment and sieving in an ultrasonic bath to remove particles < 7 µm. A known quantity of Lycopodium spores was initially added to each sample (1 mL) for calculation of pollen concentrations (Maher, 1981). More than 400 terrestrial pollen grains were counted for each sample.

A 10.75-m-long sediment core was collected from the central part of Bayan Nuur by the study group of M. Walther of the Free University Berlin during 1995–97. Pollen data and accelerator mass spectrometry radiocarbon measurements for seven bulk sediment samples were originally published in



Figure 1 Maps showing (a) the topography of Mongolia and (b) the vegetation types and location of the 90 lakes used for sedimentsurface pollen samples in central and western Mongolia (the number of each site is used as its ID in Appendix S1). Bayan Nuur and Hoton-Nur are indicated with a black arrow and a red cross, respectively. The vegetation types are indicated with different colours, and samples collected from different vegetation types are indicated with different symbols (see the top-right legend).

Krengel (2000). We recalculated the age-depth model (Fig. 2) using the method of Blaauw & Christen (2011) in the BACON 2.2 package in R 3.0.2 (R Core Team, 2013). We used the parameters suggested for lake sediments by Blaauw & Christen (2011) and set the age of 0 cm depth to -45 cal. yr BP and adjusted the accumulation rate to 10 years cm⁻¹. The sampling resolution of the pollen spectra is, on average, 210 years/sample (75 samples).

Modern climate data screening

Modern climate data were interpolated for each site on the basis of climate data extracted from New_LocClim_1.10.exe (ftp://ext-ftp.fao.org/SD/Reserved/Agromet/New_LocClim/, data downloaded 1 June 2012) from 74 meteorological stations in Mongolia covering the period of 1961–90 at 1-km resolution and using the smoothing spline interpolation method (ANU-SPLIN 4.36; Hutchinson & Hancock, 2006) and the STRM 1-km digital elevation model (Farr *et al.*, 2007). P_{ann} , T_{Jan} , T_{Jub} mean annual temperature (T_{ann}) and continentality (T_{Jul} minus T_{Jan}) were calculated for each sampling site. The soil data needed in the calculation process were inferred from a global digital soil map at a 0.5° resolution (Kaplan, 2001). Continentality has a strong collinear relationship with T_{Jan} (r = 0.92); we therefore excluded T_{Jan} before data analysis.

Numerical analysis methods

Only pollen taxa with an abundance of at least 0.5% in at least three samples were included in all the statistical analyses (n = 20). Pollen percentages were recalculated based on a sum of these 20 pollen types and square-root transformed prior to numerical analysis [apart from Huisman–Olff–Fresco models (HOF, Huisman *et al.*, 1993) and modern analogue technique (MAT, Overpeck *et al.*, 1985)] to stabilize their variances. Pollen assemblage zones for fossil

Table 1 Summary of the meteorological and limnological
characteristics of Bayan Nuur, Mongolia.

Latitude	49.9829° N
Longitude	93.9531° E
Elevation (m a.s.l.)	932
P _{ann} (mm)*	142
$T_{\rm ann}$ (°C)*	-3.7
$T_{\rm Jul}$ (°C)*	19.5
T_{Jan} (°C)*	-32.5
Continentality	52
Vegetation type	Desert steppe
Human alterations	Grazing
Outflow	Yes
Open water area (km ²)	32
Catchment area (km ²)	730
Maximum water depth (m)	29.2
Mean water depth (m)	10.2
Water pH	8.9
Secchi depth (m)	5.4
Water source	Groundwater

*The climate data are from monthly means 1943–96, station Ulaangom (Paul & Horn, 2000).

 P_{ann} , mean annual precipitation; T_{ann} , mean annual temperature; T_{Jul} , mean temperature of the warmest month; T_{Jan} , mean temperature of the coldest month; continentality, mean temperature of the warmest month (T_{Jul}) minus mean temperature of the coldest month (T_{Jan}).



Figure 2 Age–depth model for the core collected from Lake Bayan Nuur, Mongolia. Dashed grey lines indicate the 95% probability intervals of the model and darker shading implies greater probability.

pollen assemblages were defined by stratigraphically constrained cluster analysis with incremental sum-of-squares partitioning (CONISS) and the squared chord distance (Gordon & Birks, 1972) using the software TILIA/TGVIEW 2.0.2 (Grimm, 2004).

As a preliminary detrended correspondence analysis (DCA) showed that the length of the first axis is 1.3 SD (standard deviation units), we performed redundancy analysis (RDA) on our modern pollen dataset using forward selection and checking the variance inflation factors (VIF) at each step (Birks, 1995). VIFs greater than 20 indicate that some variables are redundant, and we therefore simplified our model using ecological criteria until all VIF values were lower than 20 (ter Braak & Prentice, 1988). We used the ratio of the eigenvalue of the first constrained axis (λ_1) and the first unconstrained axis (λ_2) for each climate variable when included separately in an RDA to determine which climate variables could potentially be used in the reconstructions (Juggins, 2013). A higher $\lambda 1$: $\lambda 2$ ratio is better. These ordinations were performed using the R package VEGAN 2.0-4 (Oksanen et al., 2012).

The statistical relationship of each pollen taxon to significant climate variables was assessed by HOF response models using the R package GRAVY 0.2-0 (Oksanen, 2013), which selects between a null model of no specific response curve (I), a monotonically increasing (IIi) or decreasing (IId) sigmoidal response model, a plateau model (III), a symmetric Gaussian unimodal response model (IV), or a skewed unimodal response model (V).

We established and assessed modern pollen–climate calibration models using weighted averaging partial least squares (WA-PLS) regression (ter Braak & Juggins, 1993). Performance of each calibration model was evaluated using leaveone-out cross-validation (ter Braak & Juggins, 1993). The model with a high coefficient of determination between observed and predicted values (r^2), low maximum bias, and the smallest number of 'useful' components indicated by a decrease of at least 5% in RMSEP towards the lower component number for each climate variable was selected (Birks, 1998). The WA-PLS transfer functions were compared with MAT reconstructions using a weighted average of the five closest analogues identified using chi-squared distance. Both were implemented in C2 1.5.1 (Juggins, 2007).

We tested the extent to which single calibration models may be affected by spatial autocorrelation using the R package PALAEOSIG 1.1.2 (Telford, 2013). The statistical significance tests for quantitative palaeoenvironmental reconstructions were performed following the methods described in Telford & Birks (2011) using PALAEOSIG 1.1.2 (Telford, 2013). Fossil samples with squared residual distances higher than the 95th and 90th percentiles of all squared residual distances of the modern calibration data are defined as having a 'very poor fit' and 'poor fit', respectively, to each reconstructed climate factor (Birks et al., 1990). The uncertainty of individual reconstructed values was evaluated by the samplespecific error, which is estimated by bootstrap resampling using C2 1.5.1 (Juggins, 2007). More detailed information concerning these statistical methods can be found in Appendix S2.

RESULTS

Modern pollen data

Modern pollen assemblages are dominated by herbaceous taxa such as *Artemisia*, Chenopodiaceae, Cyperaceae and Poaceae, while *Betula*, *Larix* and *Pinus* are the major arboreal taxa (Fig. 3). The samples collected in the mountain forest-steppe, and steppe and dry steppe vegetation from central Mongolia have higher Cyperaceae and *Larix* abundances, and lower *Artemisia* abundances than the samples collected from western Mongolia in the same vegetation types (Table 2, Fig. 3).

Forward selection in RDA shows that all climate variables are statistically significant in relation to the variance in pollen data (P < 0.03), with $P_{\rm ann}$ capturing the largest proportion. As some VIFs for this RDA model were over 20, we removed $T_{\rm ann}$. The VIFs of the new model were all then below 20 (Table 3). The first RDA axis, which is highly correlated with $P_{\rm ann}$, divides the dataset into dry steppe and desert taxa such as *Artemisia*, Chenopodiaceae and *Ephedra distachya*-type, and steppe/meadow taxa such as Poaceae, Cyperaceae and Caryophyllaceae (Fig. 4). The second axis separates arboreal taxa from herbaceous taxa and is positively correlated with $T_{\rm Jul}$. The samples from mountain forest-steppe and mountain steppe are found in the lower part of the RDA plot, whereas samples from steppe and dry steppe, desert steppe and desert are located in the upper part (Fig. 4). In addition, the samples from mountain forest-steppe and steppe and dry steppe vegetation in central Mongolia characterized by relatively high P_{ann} are clearly separated from the samples from north-western Mongolia with lower P_{ann} by the first RDA axis (Fig. 4). When each climate variable is added separately in the RDA, all λ_1/λ_2 ratios are lower than 1, but P_{ann} has a higher λ_1/λ_2 ratio than other variables (Table 3).

The responses of the 20 taxa to climate variables are identified and shown by HOF models (Appendix S3). Brassicaceae, *Picea*, *Pinus* and Polygonaceae do not have statistically significant responses to any of the four climate variables. Arboreal taxa (apart from *Larix*, which shows a symmetric Gaussian unimodal response to P_{ann} and a sigmoidal decreasing response to T_{Jul}) do not have significant relationships with P_{ann} and T_{Jul} . Steppe and meadow taxa such as Cyperaceae and Poaceae show increasing sigmoidal responses to P_{ann} and decreasing sigmoidal responses to continentality, while desert taxa such as *Ephedra distachya*-type present the opposite features.



Figure 3 Pollen diagram for the central and western Mongolian lake sediment-surface samples, showing the percentages for selected pollen taxa and the modern environmental data. The samples are arranged according to vegetation type (C: samples from central Mongolia, W: samples from western Mongolia); pp, the pollen types from Asteraceae or Ranunculaceae but excluding *Artemisia* or *Thalictrum*, respectively. Climate variables are defined in Table 1.

	Mountain forest steppe		Steppe and dry steppe		
	Central Mongolia	Western Mongolia	Central Mongolia	Western Mongolia	
No. of samples	20	11	15	2	
Artemisia (%)	11.2-46.9 (27.3)	22.5-68.7 (51.8)	8.6-61.9 (26.3)	44.3, 54.9	
Cyperaceae (%)	4.1-51.1 (26.9)	1.7-13.7 (8.5)	3.1-43.6 (15.3)	1.2, 7	
Larix (%)	0.2-6.5 (3.5)	0-3 (0.3)	0-7.1 (1.4)	0, 0	
$P_{\rm ann} \ (\rm mm)$	249–328	202–265	201–265	171, 227	

Table 2 Comparison of percentages of dominant pollen taxa in the same vegetation type between samples from central Mongolia and western Mongolia (the numbers in brackets are the median values).

Table 3 Summary statistics for redundancy analysis (RDA), with 90 samples, 20 pollen species and four climate variables (see Table 1) used to select the main determinant of the pollen distribution in central and western Mongolia.

			Marginal contribution bas four climate variables	sed on	Each climate variable included in RDA separately			
Climate variables	VIF (excluding T_{ann})	VIF	Explained variance (%)	P-value	Explained variance (%)	<i>P</i> -value	λ_1/λ_2	
P _{ann}	1.6	1.7	17.0	0.005	19.8	0.001	0.65	
$T_{\rm ann}$	_	117	2.7	0.005	5.6	0.002	0.13	
$T_{\rm Jul}$	2.4	221	2.6	0.01	6.2	0.001	0.14	
Continentality	2.1	180	2.3	0.02	13.0	0.001	0.35	

VIF, variance inflation factors.



Figure 4 Redundancy analysis of the surface samples with climate variables shown by black arrows and pollen taxa shown by grey arrows ($\lambda_1 = 0.275$, $\lambda_2 = 0.049$). Climate variables are defined in Table 1.

Pollen-climate calibration models and evaluation

Model performances with sites deleted at random, or from geographical or environmental neighbourhoods, indicate that WA-PLS is slightly less influenced by spatial autocorrelation

6

than MAT, and that models for P_{ann} and continentality are slightly less influenced by spatial autocorrelation than models for T_{ann} and T_{Jul} (Fig. 5).

A two-component WA-PLS model for P_{ann} and a one-component model for continentality were selected. The residuals (predicted values minus observed values) of the calibration models show slight trends of overestimation at low P_{ann} and low continentality (Fig. 6).

Fossil record and transfer-function application

Pollen spectra of Bayan Nuur (Fig. 7) are dominated by non-arboreal taxa, such as Artemisia, Chenopodiaceae, Poaceae, Cyperaceae and Ephedra distachya-type. Tree pollen such as Pinus, Betula, Larix, Alnus, Picea, Salix and Ulmus are common but occur at low percentages. The pollen diagram of Bayan Nuur is divided into four major zones. The first two pollen zones (15.8–15.2 cal. kyr BP and 15.2– 12.4 cal. kyr BP) are characterized by relatively low Pinus, Betula and Chenopodiaceae pollen percentages but high Alnus, Picea, Salix and Artemisia percentages, which is in contrast to zone 3 (12.4-5.2 cal. kyr BP) and zone 4 (5.2-0 cal. kyr BP; Fig. 7). Moreover, the significance test shows that P_{ann} has a better correlation between weighted average optima and the first axis species scores of the RDA than continentality, although none of them are significant (Fig. 8). Finally, P_{ann} WA-PLS was selected to be used in the reconstructions based on the results of RDA, spatial autocorrelation, significance test and transfer function performance.

Analogue quality analysis shows that 57% of fossil samples have 'good' and 33% have 'close' modern analogues. High dissimilarities between fossil and modern samples occur in



Figure 5 The effect on transfer function r^2 when deleting modern pollen sites in central and western Mongolia at random (mean of 10 trails, open circles); from the geographical neighbourhood of the test site (filled circles); and from the most similar environment (grey crosses) during cross-validation for our modern pollen data, using weighted averaging partial least squares regression (WA-PLS) and the modern analogue technique (MAT) with five analogues. Climate variables are defined in Table 1.



Figure 6 Weighted averaging partial least squares regression (WA-PLS) inferred models obtained from the pollen–climate calibration set in central and western Mongolia, showing (a) predicted mean annual precipitation (P_{ann}) versus observed P_{ann} (mm); (b) residuals versus observed P_{ann} (mm); (c) predicted continentality versus observed continentality (°C); and (d) residuals versus observed continentality (°C). RMSEP, root mean squared error of prediction.

pollen zones 1, 2c and 3b due to the high percentages of *Ephedra distachya*-type, *Salix* and *Alnus* (Fig. 9a). For goodness-of-fit analysis, all fossil samples have squared residual distances lower than the 90th percentile for $P_{\rm ann}$, except for one sample (around 8.6 cal. kyr BP) that is lower than the 95th percentile (Fig. 9b).

The application of the P_{ann} WA-PLS model to the Bayan Nuur pollen record suggests pronounced changes in precipitation, with P_{ann} varying between 85 and 223 mm during the late glacial and Holocene (Fig. 9c). Sample-specific errors range from 41.7 to 51.7 mm. They are slightly higher (mean 46 mm) for late glacial and early Holocene samples than for mid- and late Holocene samples (mean 43 mm) during 7–0 cal. kyr $_{\rm BP.}$

DISCUSSION

Pollen–climate relationships

Statistically significant relationships between the modern pollen spectra and four climate variables are found with RDA. P_{ann} explains the highest amount of pollen spectra variance (Table 3), suggesting P_{ann} is the decisive environmental variable and has the largest influence on pollen composition, as



Figure 7 Pollen percentage diagram from Lake Bayan Nuur, Mongolia. The black infilled silhouettes show pollen relative abundances; the abundances of rare species are shown with a fivefold exaggeration (unfilled silhouettes).



Figure 8 Redundancy analysis (RDA) axis 1 species scores against weighted averaging (WA) optima for (a) mean annual precipitation (P_{ann}) and (c) continentality (bigger circle size indicates higher pollen percentage) in central and western Mongolia. Histogram of absolute weighted correlation of RDA species scores against WA optima for 999 random variables for (b) P_{ann} and (d) continentality. The observed weighted correlation is shown by the vertical black line, the 95 percentile of the absolute weighted correlations is shown by the vertical black line, the 95 percentile of the absolute weighted correlations is shown by the vertical black line, the 95 percentile of the absolute weighted correlations is shown by the vertical black line, the 95 percentile of the absolute weighted correlations is shown by the vertical black line, the 95 percentile of the absolute weighted correlations is shown by the vertical black line, the 95 percentile of the absolute weighted correlations is shown by the vertical black line, the 95 percentile of the absolute weighted correlations is shown by the vertical black line, the 95 percentile of the absolute weighted correlations is shown by the vertical black line, the 95 percentile of the absolute weighted correlations is shown by the vertical dotted line.

also found for Mongolia by Ma et al. (2008) and for northern China by Zhao & Herzschuh (2009). This result is not surprising because most samples come from arid and semi-arid areas where vegetation cover and composition are strongly related to the seasonal and geographical distribution of precipitation (Gunin *et al.*, 1999; Ma *et al.*, 2008). The



Figure 9 The feasibility analysis for mean annual precipitation (P_{ann}) reconstructions for Lake Bayan Nuur using the modern pollen dataset from central and western Mongolia and the reconstructed P_{ann} . (a) Nearest modern analogues for the fossil samples in the calibration dataset; (b) goodness-of-fit of the fossil samples with P_{ann} ; and (c) summary diagram for Bayan Nuur with weighted averaging partial least squares regression (WA-PLS) inferred P_{ann} reconstructions together with LOWESS smoother (grey line, span: 0.1).

separation of vegetation along the first axis of the RDA plot explains markedly more variance than the second axis and is correlated with P_{ann} . It indicates that pollen assemblages and thus vegetation types are more sensitive to precipitation than to temperature in our study area.

In our study, 10 of the 20 pollen taxa have statistically significant response patterns with Pann as inferred by HOF models, among them steppe/meadow taxa such as Cyperaceae and Poaceae with sigmoidal increasing models, the typical desert taxon Ephedra distachya-type with sigmoidal decreasing models, as well as forest taxa such as Larix showing an optimum at the wetter end of the gradient. These main features are also seen in the modern pollen assemblages in studies focusing on northern and western China (Luo et al., 2010). Picea and Pinus have no relationship with any of the tested climate variables, which is probably because they are extra-regional components and thus their input is related to lake size and wind conditions. Furthermore, Fowell et al. (2003) found Larix pollen can be used as an indicator taxon of relatively humid conditions in the Lake Telmen basin. A typical characteristic of the vegetation distribution in the Altai and Khangai mountains is that the major tree taxon, Larix, is always restricted to the northern side of the slopes, because of the lower solar radiation input and thus

lower transpiration than on the southern slopes. In some permafrost areas with better soil-water supply due to the seasonal melt from permafrost, *Larix* can grow on sites with P_{ann} less than 200 mm (Klinge *et al.*, 2003). This confirms our field findings. However, this ecological response to local soil conditions complicates the climatic interpretation of fossil pollen signals in lake sediments.

Our study area is too far from the oceans to receive heavy monsoonal rains. Thus incoming moisture originated mainly from the Atlantic and is transported by westerlies (Gillespie et al., 2003). The lower Pann in some areas in western Mongolia, especially in the Valley of Lakes between the Altai and Khangai mountains, in comparison to central Mongolia may be caused by their locations on the lee side of mountain chains where vegetation types with lower moisture requisites develop due to the specific geomorphological setting (Hilbig, 1995; Klinge et al., 2003). This pattern can be used to interpret the differences in pollen assemblages from the same vegetation type between central and western Mongolia, although the number of steppe and dry steppe vegetation samples in western Mongolia is too small to show the differences in pollen assemblages. In arid and semi-arid areas in China, vegetation cover and composition are also mostly controlled by moisture availability (Luo et al., 2010).

Mongolia shows a broad south–north temperature gradient (Ministry of Nature & the Environment of Mongolia, 2006). However, in our study, more than half of the pollen taxa do not show a significant relationship with T_{Jul} or T_{ann} , which is possibly a result of our sampling design and its relatively small range in the south–north direction and the relatively low temperature gradient between the mountains and the plain.

HOF models show that 12 pollen taxa are significantly correlated with continentality. Although several plant taxa in our dataset seem to have ecological responses towards shifts in summer warmth and winter coldness, the autecological information is limited: within one pollen taxon, different plant species may have conflicting ecological responses. Thus a final conclusion about the impact of continentality on the pollen spectra is not possible because in the modern environmental setting continentality is slightly correlated with moisture so that the relationships of the taxa with this variable might be an artefact.

Assessment of the calibration set and obtained models

The evaluation of our pollen–climate calibration models based on 90 modern lake sediment-surface samples yielded the following strengths and weaknesses that need to be considered when the calibration models are applied to fossil datasets.

Lake size

Most of the samples (79%) were collected from small and medium-sized lakes, thus, the model's application to fossil spectra from large lakes needs to be interpreted with caution because of differences in the relevant source area (Birks, 2003).

Environmental gradients

With respect to Holocene changes inferred from pollen records from arid Mongolia, the dataset covers the relevant vegetation. In contrast to the relatively large precipitation and continentality gradients, the T_{Jul} gradient is narrow and glacial-interglacial temperature variability is probably not fully covered.

Correlation among environmental variables

Although RDA revealed that the four selected variables independently explain a significant portion of the modern pollen dataset, the weak correlation among the variables hampers the reliable reconstruction of several climate variables. The addition of selective samples from Mongolia and adjacent areas from hitherto unrepresented climatic space could solve this problem.

Method of climate reconstruction

In this study, the diagnostic statistics of MAT (Fig. 5) for $P_{\rm ann}$ are similar to those of WA-PLS based on leave-one-out cross-validation. Because of the spatial structure in the environmental variable when the gradient is correlated, MAT always produces over-optimistic diagnostic statistics when cross-validation is limited to leave-one-out (Telford & Birks, 2005). In this study, MAT shows stronger spatial autocorrelation than WA-PLS for $P_{\rm ann}$, in agreement with previous work (Telford & Birks, 2005). Therefore, WA-PLS was selected to develop the final transfer functions in this study. The low r^2 for $P_{\rm ann}$ is probably related to the relatively narrow climate span.

Comparison between transfer functions in Eurasia

No comparable pollen–climate transfer function is available from Mongolia, so we have to compare our model's performance with those pollen calibration sets from other regions in Eurasia. The RMSEP for P_{ann} (41 mm) is the lowest among the studies listed in Table 4, whereas the RMSEP as a percentage of the gradient length (15.5%) is higher than for most of these studies. The RMSEP for continentality has the highest percentage of 21.1%, which is probably because of the short gradient in our dataset or because continentality is not ecologically important.

Table 4 Comparison of the performance statistics between	n different quantitative pollen-based	climate transfer functions.
--	---------------------------------------	-----------------------------

Study	Area	Variables	Range	Comp.	r^2	RMSEP	RMSEP % of grad.	Max. bias
Lotter <i>et al.</i> (2000)	Switzerland	P _{ann}	756–2018 mm	2	0.57	194 mm	9.9	405 mm
Birks et al. (2000)	Norway	Pann	300–3234 mm	2	0.68	417 mm	14.2	952 mm
Seppä & Birks (2001)	Norway, Finland	P_{ann}	300–3234 mm	2	0.73	334 mm	11.6	951 mm
Birks & Seppä (2004)	Finland	P_{ann}	395–717 mm	2	0.77	58 mm	18.0	80 mm
Shen et al. (2006)	Tibetan Plateau	P_{ann}	66–910 mm	3	0.87	61 mm	7.2	81 mm
Li et al. (2007)	North China	P_{ann}	40–800 mm	4	0.89	69 mm	9.1	39 mm
Herzschuh et al. (2010)	Tibetan Plateau	$P_{\rm ann}$	31–1022 mm	1	0.75	104 mm	10.6	205 mm
Lu et al. (2011)	Tibetan Plateau	P_{ann}	12–1843 mm	2	0.8	143 mm	7.8	_
This study	Mongolia	$P_{\rm ann}$	65–328 mm	2	0.58	41 mm	15.5	98 mm
This study	Mongolia	conti	26.5–54.2 °C	1	0.35	6 °C	21.1	9 °C

Comp., component; RMSEP, root mean squared error of prediction; grad., gradient; Max., maximum; P_{ann} , mean annual precipitation; conti, continentality.

Assessment of quantitative reconstruction from Bayan Nuur

Besides the low sample-specific errors of bootstrapping, the reliability of a reconstruction can also be assessed by comparison with the modern pollen–climate relationship from the surrounding area. The extremely high $P_{\rm ann}$ reconstructions around 15.6 cal. kyr BP are caused by the high *Salix* values and extremely low *Ephedra distachya*-type percentages from the lowermost part of the core, which is, according to our modern pollen dataset, typical for rather moist vegetation. The peak of *Ephedra distachya*-type percentages occurs between 12.4 and 11.9 cal. kyr BP, which causes the lowest $P_{\rm ann}$ reconstructions in the pollen spectra. An *Ephedra* expansion at the end of the last glacial is also known from other central Asian records (Herzschuh *et al.*, 2006).

Considering the error range, the Holocene precipitation reconstruction of Bayan Nuur does not show significant changes. However, we assume that at least the Holocene trend (indicating a mid-Holocene precipitation optimum and rather dry conditions for the early and late Holocene) is still a reliable feature as it is related to characteristic changes in the pollen signal, i.e. high Chenopodiaceae abundances in early and late Holocene spectra, and high Cyperaceae and Caryophyllaceae values in mid-Holocene spectra. These taxa are sensitive indicators for P_{ann} as revealed by HOF modelling (this study) and are generally considered to be reliable precipitation indicators in Central Asia (Herzschuh & Birks, 2010; Luo *et al.*, 2010).

Neither the pattern nor the range of our reconstructed precipitation anomaly is consistent with pollen-based precipitation inferences from Lake Hoton-Nur located in western Mongolia (48.62° N, 88.35° E, 2083 m; Rudaya et al., 2009). These P_{ann} reconstructions were performed using MAT using a subcontinental-scale modern pollen dataset mostly derived from soil surfaces. In such a dataset each pollen taxon reflects a large number of plant species, which can obscure the local taxon-climate relationship and may reduce the reliability of reconstruction (Williams & Shuman, 2008). Despite the small gradient of our calibration set, both analogue quality and goodness-of-fit results show that fossil pollen assemblages can be represented by modern analogues, and that fossil samples generally have 'good fit' with our calibration set for Pann. Thus the relatively narrow range of reconstructed P_{ann} for Bayan Nuur might be a more reliable signal, although it might slightly overestimate Pann at the lower end as indicated by the trends in the residuals obtained from leave-one-out cross-validation (Fig. 6).

Contribution to central research questions concerning Mongolia's climate since the late glacial

Shakun & Carlson (2010) conclude that the magnitude of Younger Dryas (YD) temperature/precipitation changes increase with latitude in the Northern Hemisphere based on a synthesis of palaeoclimate records globally, but records from

central arid Asia were lacking. Our record, in accordance with a pollen-based Pann reconstruction from Lake Kotokel in southern Siberia (Tarasov et al., 2009), reveals a marked dry event during the YD. In monsoonal East and Central Asia, most proxy-records exhibit dry YD climatic conditions too (Herzschuh, 2006; Ma et al., 2012). However, there are several records with the opposite or no clear signals. For example, no marked climatic response was found in arid areas of the north-eastern Tibetan Plateau (Herzschuh et al., 2010; Wischnewski et al., 2011) and Fedotov et al. (2004) could not infer significant climate change for the YD using geochemical proxies from Lake Khubsugul (50.94° N, 100.36° E, 2267 m a.s.l., located 450 km to the north-east of Bayan Nuur). These contrasting results may either suggest differing regional responses or are caused by differences in the sensitivity of proxies to the YD signal. Vegetation, for example, might be much more sensitive to the YD event because in addition to precipitation the CO₂ levels dropped, which should further support the expansion of drought-resistant vegetation and thus cause an overestimation of the real YD precipitation decrease (Herzschuh et al., 2011). In contrast, the YD temperature decrease and resulting evaporation decline may have compensated slightly for the precipitation-related reduced runoff and thus related proxy records may overestimate real precipitation.

Compared to the early (11.5-8.5 cal. kyr BP) and late Holocene (3.0 cal. kyr BP-present), reconstructed Pann at Lake Bayan Nuur is high for the mid-Holocene (8.5-3 cal. kyr BP), which is consistent with the average changes of sites from westerlies-dominated areas in Central Asia (Herzschuh, 2006; Chen et al., 2008) and also with the mid-Holocene climate optimum in mid- to high-latitude Eurasia (Koshkarova & Koshkarov, 2004; Bezrukova et al., 2011). However, palynological records from Lake Telmen (Fowell et al., 2003) and Lake Ugii Nuur (Wang et al., 2011) in central Mongolia reveal a relatively dry mid-Holocene compared to the early and late Holocene. It is probable that the increased mid-Holocene westerlies moisture supply did not compensate the strong evaporative moisture loss during the time of Holocene maximum warmth in these regions, which are further inland than Bayan Nuur (Bush, 2005). Furthermore, it is likely that central Mongolia was then more frequently impacted by the complex Asian monsoonal circulation than it is today and in comparison to north-western Mongolia in the mid-Holocene.

CONCLUSIONS

The numerical analyses of the relationship between modern pollen spectra and climate variables from 90 lakes in centralwestern Mongolia reveal that $P_{\rm ann}$ is the dominant climate variable. The transfer function for $P_{\rm ann}$ based on WA-PLS has a good statistical model performance, although our model possibly overestimates $P_{\rm ann}$ in dry periods owing to insufficient modern analogues in arid areas. Relative to present-day conditions, reconstructed $P_{\rm ann}$ for Bayan Nuur in north-western Mongolia is drier during the Younger Dryas and wetter during the mid-Holocene (8.5–3 cal. kyr BP). Although we made a state-of-the-art $P_{\rm ann}$ reconstruction for Bayan Nuur, the interpretation of the results highlights the complexity of the Holocene climate history of Mongolia rather than providing answers to the major palaeoclimatic questions.

ACKNOWLEDGEMENTS

The doctoral research of Fang Tian has been funded by the 'Helmholtz–China Scholarship Council (CSC) Young Scientist Fellowship' (No. 20100813030). This research has been supported by the German Research Foundation (Deutsche Forschungsgemeinschaft, DFG). We thank Cathy Jenks for language corrections.

REFERENCES

- Angerer, J., Han, G.D., Fujisaki, I. & Havstad, K. (2008) Climate change and ecosystems of Asia with emphasis on Inner Mongolia and Mongolia. *Rangelands*, **30**, 46–51.
- Bezrukova, E.V., Belov, A.V. & Orlova, L.A. (2011) Holocene vegetation and climate variability in North Pre-Baikal region, East Siberia, Russia. *Quaternary International*, 237, 74–82.
- Birks, H.J.B. (1995) Quantitative palaeoenvironmental reconstructions. *Statistical modelling of Quaternary science data*, Vol. 5, *Technical guide* (ed. by D. Maddy and J.S. Brew), pp. 161–254. Quaternary Research Association, Cambridge, UK.
- Birks, H.J.B. (1998) Numerical tools in quantitative palaeolimnology – progress, potentialities, and problems. *Journal of Paleolimnology*, **20**, 301–332.
- Birks, H.J.B. (2003) Quantitative palaeoenvironmental reconstructions from Holocene biological data. *Global change in the Holocene* (ed. by A. Mackay, R.W. Battarbee, H.J.B. Birks and F. Oldfield), pp. 107–123. Edward Arnold, London.
- Birks, H.J.B. & Seppä, H. (2004) Pollen-based reconstructions of late-Quaternary climate in Europe – progress, problems, and pitfalls. *Acta Palaeobotanica*, **44**, 317–334.
- Birks, H.J.B., Line, J.M., Juggins, S., Stevenson, A.C. & ter Braak, C.J.F. (1990) Diatoms and pH reconstruction. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **327**, 263–278.
- Birks, H.H., Battarbee, R.W. & Birks, H.J.B. (2000) The development of the aquatic ecosystem at Kråkenes Lake, western Norway, during the early Holocene and late glacial – a synthesis. *Journal of Paleolimnology*, **23**, 91–114.
- Blaauw, M. & Christen, J.A. (2011) Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Analysis*, **6**, 457–474.
- ter Braak, C.J.F. & Juggins, S. (1993) Weighted averaging partial least squares regression (WA-PLS): an improved method for reconstructing environmental variables from species assemblages. *Hydrobiologia*, **269/270**, 485–502.
- ter Braak, C.J.F. & Prentice, I.C. (1988) A theory of gradient analysis. *Advances in Ecological Research*, **18**, 271–317.
- Bush, A.B.G. (2005) CO₂/H₂O and orbitally driven climate variability over central Asia through the Holocene. *Quaternary International*, **136**, 15–23.

- Chen, F.H., Yu, Z.C., Yang, M.L., Ito, E., Wang, S.M., Madsen, D.B., Huang, X.Z., Zhao, Y., Sato, T., Birks, H.J.B., Boomer, I., Chen, J.H., An, C.B. & Wünnemann, B. (2008) Holocene moisture evolution in arid central Asia and its out-of-phase relationship with Asian monsoon history. *Quaternary Science Reviews*, **27**, 351–364.
- Faegri, K. & Iversen, J. (1989) *Textbook of pollen analysis*. John Wiley & Sons, Chichester, UK.
- Farr, T.G., Rosen, P.A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burnamk, D. & Alsdorf, D. (2007) The shuttle radar topography mission. *Review of Geophysics*, 45, RG2004. doi:10.1029/2005RG000183.
- Fedotov, A.P., Chebykin, E.P., Yu, S.M., Vorobyova, S.S., Yu, O.E., Golobokova, L.P., Pogodaeva, T.V., Zheleznyakova, T.O., Grachev, M.A., Tomurhuu, D., Oyunchimeg, T., Narantsetseg, T., Tomurtogoo, O., Dolgikh, P.T., Arsenyuk, M.I. & Batist, M.D. (2004) Changes in the volume and salinity of Lake Khubsugul (Mongolia) in response to global climate changes in the upper Pleistocene and the Holocene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 209, 245–257.
- Fowell, S.J.B., Hansen, B.C.S., Peck, J.A., Khosbayar, P. & Ganbold, E. (2003) Mid to late Holocene climate evolution of the Lake Telmen Basin, North Central Mongolia, based on palynological data. *Quaternary Research*, **59**, 353–363.
- Gillespie, A., Ruffer, S. & Roe, G. (2003) *Climatic interpretation from mountain glaciations in Central Asia*. XVI IN-QUA Congress, Programs with Abstracts, Desert Research Institute, Reno, NV.
- Gordon, A.D. & Birks, H.J.B. (1972) Numerical methods in Quaternary palaeoecology I. Zonation of pollen diagrams. *New Phytologist*, **71**, 961–979.
- Grimm, E.C. (2004) *Tgview. Version 2.0.2.* Illinois State Museum Research Collection Center, Springfield, IL.
- Gunin, P.D., Vostokova, E.A., Dorofeyuk, N.I., Tarasov, P.E.& Black, C.C. (1999) *Vegetation dynamics of Mongolia*.Kluwer Academic Publishers, Dordrecht.
- Herzschuh, U. (2006) Palaeo-moisture evolution at the margins of the Asian monsoon during the last 50 ka. *Quaternary Science Reviews*, **25**, 163–178.
- Herzschuh, U. & Birks, H.J.B. (2010) Evaluating the indicator value of Tibetan pollen taxa for modern vegetation and climate. *Review of Palaeobotany and Palynology*, **160**, 197–208.
- Herzschuh, U., Kürschner, H. & Mischke, S. (2006) Temperature variability and vertical vegetation belt shifts during the last ~50,000 yr in the Qilian Mountains (NE margin of the Tibetan Plateau, China). *Quaternary Research*, **66**, 133–146.
- Herzschuh, U., Birks, H.J.B., Mischke, S., Zhang, C.J. & Böhner, J. (2010) A modern pollen–climate calibration set based on lake sediments from the Tibetan Plateau and its application to a Late Quaternary pollen record from the Qilian Mountains. *Journal of Biogeography*, **37**, 752–766.

- Herzschuh, U., Ni, J., Birks, H.J.B. & Böhner, J. (2011) Driving forces of mid-Holocene vegetation shifts on the upper Tibetan Plateau, with emphasis on changes in atmospheric CO₂ concentrations. *Quaternary Science Reviews*, **30**, 1907– 1917.
- Hilbig, W. (1995) *The vegetation of Mongolia*. SPB Academic Publishing, Amsterdam.
- Huisman, J., Olff, H. & Fresco, L.F.M. (1993) A hierarchical set of models for species response analysis. *Journal of Vegetation Science*, **4**, 37–46.
- Hutchinson, M. & Hancock, P.A. (2006) Spatial interpolation of large climate data sets using bivariate thin plate smoothing splines. *Environmental Modelling and Software*, 21, 1684–1694.
- Juggins, S. (2007) C2 version 1.5 user guide. Software for ecological and palaeoecological data analysis and visualisation. Newcastle University, Newcastle upon Tyne, UK.
- Juggins, S. (2013) Quantitative reconstructions in palaeolimnology: new paradigm or sick science? *Quaternary Science Reviews*, **64**, 20–32.
- Kaplan, J.O. (2001) *Geophysical applications of vegetation modeling*. PhD Thesis, Lund University, Lund, Sweden.
- Klinge, M., Böhner, Ü. & Lehmkuhl, F. (2003) Climate pattern, snow- and timberlines in the Altai Mountains, Central Asia. *Erdkunde*, **57**, 296–307.
- Komatsu, G., Brantingham, P.J., Olsen, J.W. & Baker, V.R. (2001) Paleoshoreline geomorphology of Böön Tsagaan Nuur, Tsagaan Nuur and Orog Nuur: the Valley of Lakes, Mongolia. *Geomorphology*, **39**, 83–98.
- Koshkarova, V.L. & Koshkarov, A.D. (2004) Regional signatures of changing landscape and climate of northern central Siberia in the Holocene. *Russian Geology and Geophysics*, **45**, 717–729.
- Krengel, M. (2000) Discourse on history of vegetation and climate in Mongolia – palynological report of sediment core Bayan Nuur I (NW-Mongolia). State and dynamics of geosciences and human geography in Mongolia: extended abstracts of the international symposium (Berliner Geowissenschaftliche Abhandlungen) (ed. by M. Walther, J. Janzen, F. Riedel and H. Keupp), pp. 80–84. Selbstverlag Fachbereich Geowissenschaften, Free University of Berlin, Germany.
- Li, Y.C., Xu, Q.H., Liu, J.S., Yang, X.L. & Nakagawa, T. (2007) A transfer-function model developed from an extensive surface-pollen data set in northern China and its potential for palaeoclimate reconstructions. *The Holocene*, **17**, 897–905.
- Lotter, A.F., Birks, H.J.B., Eicher, U., Hofmann, W., Schwander, J. & Wick, L. (2000) Younger Dryas and Allerød temperatures at Gerzensee (Switzerland) inferred from fossil pollen and cladoceran assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **159**, 349–361.
- Lu, H.Y., Wu, N.Q., Liu, K.B., Zhu, L.P., Yang, X.D., Yao, T.D., Wang, L., Li, Q., Liu, X.Q., Shen, C.M., Li, X.Q., Tong, G.B. & Jiang, H. (2011) Modern pollen distributions in Qinghai-Tibetan Plateau and the development

of transfer functions for reconstructing Holocene environmental changes. *Quaternary Science Reviews*, **30**, 947– 966.

- Luo, C.X., Zheng, Z., Tarasov, P., Nakagawa, T., Pan, A.D., Xu, Q., Lu, H. & Huang, K.Y. (2010) A potential of pollen-based climate reconstruction using a modern pollenclimate dataset from arid northern and western China. *Review of Palaeobotany and Palynology*, **160**, 111–125.
- Ma, Y.Z., Liu, K.B., Feng, Z.D., Sang, Y.L., Wang, W. & Sun, A.Z. (2008) A survey of modern pollen and vegetation along a south–north transect in Mongolia. *Journal of Bio*geography, 35, 1512–1532.
- Ma, Z.B., Cheng, H., Tan, M., Edwards, R.L., Li, H.C., You, C.F., Duan, W.H., Wang, X. & Kelly, M.J. (2012) Timing and structure of the Younger Dryas event in northern China. *Quaternary Science Reviews*, **41**, 83–93.
- Maher, L.J. (1981) Statistics for microfossil concentration measurements employing samples spiked with marker grains. *Review of Palaeobotany and Palynology*, **32**, 153– 191.
- Minckley, T. & Whitlock, C. (2000) Spatial variation of modern pollen in Oregon and southern Washington, USA. *Review of Palaeobotany and Palynology*, **112**, 97–123.
- Ministry of Nature and the Environment of Mongolia (2006) *Climate change and sustainable livelihood of rural people in Mongolia.* Ministry of Nature and the Environment of Mongolia (MNE). Netherlands Climate Change Studies Assistance Programme. Project report, Ulaanbaatar, Mongolia.
- Oksanen, J. (2013) gravy: gradient analysis of vegetation. Version 0.2-0. Available at: https://r-forge.r-project.org/R? group_id=68.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2012) *vegan: community ecology package. Version 2.0-4.* Available at: http://cran.r-project. org/web/packages/vegan/index.html.
- Overpeck, J.T., Webb, T., III & Prentice, I.C. (1985) Quantitative interpretation of fossil pollen spectra: dissimilarity coefficients and the method of modern analogs. *Quaternary Research*, **23**, 87–108.
- Paul, M. & Horn, W. (2000) Lakes in the Uvs Nuur Basin: ecosystem features and typology. State and dynamics of geosciences and human geography Mongolia: extended abstracts of the international symposium (Berliner Geowissenschaftliche Abhandlungen) (ed. by M. Walther, J. Janzen, F. Riedel and H. Keupp), pp. 131–138. Selbstverlag Fachbereich Geowissenschaften, Free University of Berlin, Germany.
- Prokopenko, A.A., Khursevich, G.K., Bezrukova, X.B., Kuzmin, M.I., Boes, X., Williams, D.F., Fedenya, S.A., Kulagina, N.V., Letunova, P.P. & Abzaeva, A.A. (2007) Paleoenvironmental proxy records from Lake Hovsgol, Mongolia, and a synthesis of Holocene climate change in the Lake Baikal watershed. *Quaternary Research*, 68, 2–17.
- R Core Team (2013) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.

- Rudaya, N., Tarasov, P., Dorofeyuk, N., Solovieva, N., Kalugin, I., Andreev, A., Daryin, A., Diekmann, B., Riedel, F., Tserendash, N. & Wagner, M. (2009) Holocene environments and climate in the Mongolian Altai reconstructed from the Hoton-Nur pollen and diatom records: a step towards better understanding climate dynamics in Central Asia. Quaternary Science Reviews, 28, 540–554.
- Saandar, M. & Sugita, M. (2004) Digital atlas of Mongolian natural environments, (1) Vegetation, soil, ecosystem and water. CD-ROM, Monmap Engineering Service, Ulaanbaatar, Mongolia.
- Seppä, H. & Birks, H.J.B. (2001) July mean temperature and annual precipitation trends during the Holocene in the Fennoscandian tree-line area: pollen-based climate reconstructions. *The Holocene*, **11**, 527–537.
- Shakun, J.D. & Carlson, A.E. (2010) A global perspective on Last Glacial Maximum to Holocene climate change. *Quaternary Science Reviews*, **29**, 1801–1816.
- Shen, C.M., Liu, K.B., Tang, L.Y. & Overpeck, J.T. (2006) Quantitative relationships between modern pollen rain and climate in the Tibetan Plateau. *Review of Palaeobotany and Palynology*, **140**, 61–77.
- Tarasov, P.E., Bezrukova, E.V. & Krivonogov, S.K. (2009) Late Glacial and Holocene changes in vegetation cover and climate in southern Siberia derived from a 15 kyr long pollen record from Lake Kotokel. *Climate of the Past*, **5**, 285–295.
- Telford, R.J. (2013) palaeoSig: significance tests for palaeoenvironmental reconstructions. Version 1.1-2. Available at: http:// cran.r-project.org/web/packages/palaeoSig/index.html.
- Telford, R.J. & Birks, H.J.B. (2005) The secret assumption of transfer functions: problems with spatial autocorrelation in evaluating model performance. *Quaternary Science Reviews*, 24, 2173–2179.
- Telford, R.J. & Birks, H.J.B. (2011) A novel method for assessing the statistical significance of quantitative reconstructions inferred from biotic assemblages. *Quaternary Science Reviews*, **30**, 1272–1278.
- Tian, F., Herzschuh, U., Dallmeyer, A., Xu, Q., Mischke, S. & Biskaborn, B.K. (2013) High environmental variability in the monsoon-westerlies transition zone during the last 1200 years: lake sediment analyses from central Mongolia and supra-regional synthesis. *Quaternary Science Reviews*, 73, 31–47.
- Wang, W., Ma, Y., Feng, Z., Narantsetseg, T., Liu, K.B. & Zhai, X. (2011) A prolonged dry mid-Holocene climate

revealed by pollen and diatom records from Lake Ugii Nuur in central Mongolia. *Quaternary International*, **229**, 74–83.

- Williams, J.W. & Shuman, B. (2008) Obtaining accurate and precise environmental reconstructions from the modern analog technique and North American surface pollen dataset. *Quaternary Science Reviews*, **27**, 669–687.
- Wischnewski, J., Mischke, S., Wang, Y. & Herzschuh, U. (2011) Reconstructing climate variability on the northeastern Tibetan Plateau since the last Lateglacial – a multi-proxy, dual-site approach comparing terrestrial and aquatic signals. *Quaternary Science Reviews*, **30**, 82–97.
- Zhao, Y. & Herzschuh, U. (2009) Modern pollen representation of source vegetation in the Qaidam Basin and surrounding mountains, north-eastern Tibetan Plateau. *Vegetation History and Archaeobotany*, **18**, 245–260.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Site information for the 90 lake sediment-surface samples from central and western Mongolia.

Appendix S2 Additional explanation for statistical methods.

Appendix S3 The response models of major pollen taxa to P_{ann} , T_{ann} , T_{Jul} and continentality.

BIOSKETCH

Fang Tian's research interests include relationships between modern pollen and climate and vegetation, quantitative past climate reconstructions, palaeovegetation reconstructions, and the human–nature relationship based on pollen data from Mongolia and arid central Asia.

Author contributions: U.H., S.M. and T.V.d.M. collected the modern pollen samples in the field; F.T. performed the palynological analyses for modern pollen samples; M.K. contributed the fossil pollen data of B.N.; F.T. and U.H. led the writing; R.T. helped with the statistical analysis. All authors contributed to the discussion.

Editor: James Richardson