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Vegetation change and human-environment interactions in the Qinghai Lake Basin, northeastern Tibetan Plateau, since the last deglaciation

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A R T I C L E I N F O

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A B S T R A C T

The nature of the interaction between prehistoric humans and their environment, especially the vegetation, has long been of interest. The Qinghai Lake Basin in North China is well-suited to exploring the interactions between prehistoric humans and vegetation in the Tibetan Plateau, because of the comparatively dense distribution of archaeological sites and the ecologically fragile environment. Previous pollen studies of Qinghai Lake have enabled a detailed reconstruction of the regional vegetation, but they have provided relatively little information on vegetation change within the Qinghai Lake watershed. To address the issue we conducted a pollen-based vegetation reconstruction for an archaeological site (YWY), located on the southern shore of Qinghai Lake. We used high temporal-resolution pollen records from the YWY site and from Qinghai Lake, spanning the interval since the last deglaciation (15.3 kyr BP to the present) to quantitatively reconstruct changes in the local and regional vegetation using Landscape Reconstruction Algorithm models. The results show that, since the late-glacial, spruce forest grew at high altitudes in the surrounding mountains, while the lakeshore environment was occupied mainly by shrub-steppe. From the lateglacial to the middle Holocene, coniferous woodland began to expand downslope and reached the YWY site at ~ 7.1 kyr BP. The living environment of the local small groups of Paleolithic-Epipaleolithic humans (during 15.3–13.1 kyr BP and 9–6.4 kyr BP) changed from shrub-steppe to coniferous forest–steppe. The pollen record shows no evidence of pronounced changes in the vegetation community corresponding to human activity. However, based on a comparison of the local and regional vegetation reconstructions, low values of biodiversity and a significant increase in two indicators of vegetation degradation, Chenopodiaceae and Rosaceae, suggest that prehistoric hunters-gatherers likely disturbed the local vegetation during ~ 9.0–6.4 kyr BP. Our findings are a preliminary attempt to study human-environment interactions at Paleolithic-Epipaleolithic sites in the region, and they contribute to ongoing environmental archaeology research in the Tibetan Plateau.

1. Introduction

The Tibetan Plateau (TP) is a harsh environment for humans due to its high elevation, low oxygen concentration and sparse fauna and flora resources (Beall, 2001); in addition, the ecosystems of the region are sensitive to climate change and human impacts (Li et al., 2019). Hence,

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it is a unique and important location for the study of the adaptation of prehistoric humans to environmental changes (Brantingham and Gao, 2006; Brantingham et al., 2003; Brantingham et al., 2010; Chen et al., 2015, 2019; Huerta-Sánchez et al., 2014; Madsen et al., 2006; Yi et al., 2010; Zhang et al., 2016, 2018). The northeastern TP (including the Qinghai Lake Basin) is especially significant in this context because it was a major early corridor of human migration to the inner TP (Chen et al., 2015; Madsen et al., 2006; Wei et al., 2020a). Archaeological research has documented well-dated Paleolithic and Epipaleolithic sites in the northeastern TP, including Jiangxigou 1 (JXG 1), Heimahe 1 (HMH 1), HZYC 1, Locality 93–13, 10HTHS 1, and Bronze Wire Canyon 3 (BWC 3), dating to ~ 12.5–4.2 kyr BP and distributed mainly in the Qinghai Lake Basin (Brantingham and Gao, 2006; Hou et al., 2016a; Madsen et al., 2006, 2017; Rhode, 2016; Rhode et al., 2007a, 2014; Sun et al., 2012). Therefore, the Qinghai Lake Basin is well-suited for studying vegetation change and human impacts in the TP.

Over the past few decades >100 papers have been published on the Lake Qinghai Basin, focusing mainly on environmental and climate changes (Chen et al., 2016). Two sediment cores from Qinghai Lake (Du et al., 1989; Liu et al., 2002; Shen et al., 2005) have revealed high pollen percentages of woody plants in the middle Holocene. In addition, charcoal from woody plants has been discovered at middle Holocene Epipaleolithic sites and in soil sections around Qinghai Lake (Kaiser et al., 2007; Rhode, 2016). However, only very low percentages of the pollen of woody plants were detected at the Jiangxigou site and in the LGR section in the Qinghai Lake Basin (Hou et al., 2016a; Wei et al., 2020a). The vegetation background of Paleolithic-Epipaleolithic foragers around Qinghai Lake and the source of the woody materials used by them are controversial. Some have suggested that the prehistoric foragers occupied a mixed forest-steppe environment and utilized nearby wood resources (Brierley et al., 2016; Rhode, 2016; Wang et al., 2016); whereas others have suggested that they occupied a steppe/meadow environment and collected woody materials from the surrounding valleys (Wei et al., 2020a). Thus, it is important to clarify the nature of the vegetation environment of prehistoric foragers in the region, and how they adapted to it.

Both climate change and human activity can exert major impacts on ecosystems, including changes in vegetation composition (Huang et al., 2017; Miehe et al., 2014; Schlütz and Lehmkuhl, 2009) and diversity (Klein et al., 2004; Pauli et al., 2012), and the tree-line position (Harsch et al., 2009). However, it remains unclear whether or not the modern largely treeless landscape of the TP (including the Qinghai Lake Basin) was the product of a drying climate or of enhanced human impacts. Several researchers have contended that the low human population densities could not have triggered extensive vegetation changes across the TP (Chen et al., 2013; Herzschuh et al., 2005; Ji et al., 2005a; Tang et al., 2009); however, others have found evidence that prehistoric humans did indeed impact the local vegetation at different times and locations in the TP (Huang et al., 2017; Kaiser et al., 2007; Miehe et al., 2009, 2014; Rhode, 2016; Schlütz and Lehmkuhl, 2009; Wei et al., 2020a). Therefore, it is unclear whether, when, and how prehistoric foragers impacted the local vegetation in the TP; and in particular the spatial and temporal scales of human disturbance (local and regional) are poorly addressed in previous studies (Herzschuh et al., 2010b).

Pollen analysis is a well-established and powerful tool for investigating past changes in vegetation composition and human impacts on vegetation. However, because of differences in pollen productivity among taxa, pollen percentages may over- or under-estimate changes in vegetation composition (Cao et al., 2019; Wang and Herzschuh, 2011), especially where high pollen producers such as *Pinus*, *Artemisia*, Chenopodiaceae and *Betula* (Liu et al., 1999; Mazier et al., 2012) invade areas dominated by low pollen producers such as *Picea*, Poaceae, Cyperaceae and Asteraceae (Liu et al., 1999). For example, a high *Artemisia* pollen representation does not always correspond to a high areal coverage of *Artemisia* in woodland and shrub communities because *Artemisia* is over-represented in pollen spectra (Herzschuh et al., 2003; Liu et al., 1999). Thus, it is necessary to provide more accurate quantitative vegetation reconstructions. The Landscape Reconstruction Algorithm (LRA, comprising a series of models) considers several factors, such as pollen productivity, the pollen source area in relation to basin size, and the background pollen loading (Sugita, 2007a, 2007b), in order to transform pollen data to a quantitative representation of the corresponding vegetation. The LRA makes it possible to transform pollen percentages into quantitative plant cover estimates at regional and local scales. In addition, LRA estimates of plant abundance have clearly demonstrated the effectiveness of pollen-based on studies of Holocene vegetation change and plant diversity in Europe (Marquer et al., 2014, 2017). Li et al. (2018) and Cao et al. (2019) concluded that pollen-based REVEALS estimates of plant abundances reliably reflect changes in plant cover in northern Asia and considered that LRA is more suitable than biomization for evaluating human-induced landscape change.

For these reasons we used the LRA approach to reconstruct the local and regional vegetation at the YWY site (an abbreviation for the Yaowuyao site, which is also called site 151, indicating its location ~ 151 km from Xining City) and in the Qinghai Lake area. The results provide a clarification of landscape change and information on human impacts on different spatial and temporal scales during the lateglacial and Holocene. The specific research questions we addressed are as follows: (1) What was the quantitative composition of the vegetation at the YWY site and at Qinghai Lake during the lateglacial and the Holocene? (2) How did the vegetation change in the Qinghai Lake Basin on the local and regional scales? (3) How were prehistoric foragers adapted to the vegetation of the area, and to what extent did they transform it?

2. Study region and site

The Qinghai Lake Basin, is centered on Qinghai Lake in the northeastern TP (Fig. 1) and has a watershed area of ~ 30,000 km^2. Several seasonal streams, such as the Buha, Shaliu and Ha'ergai rivers, feed the lake (Fig. 1). The topography of the basin is complex, with elevations varying from 3,194 to 5,174 m.a.s.l. (meters above sea level). Annual precipitation is ~ 373 mm, with ~ 65% falling from June to August, and the mean annual temperature is −0.1 ℃ (An et al., 2012). The region is dominated by two atmospheric circulation systems: the Asian Summer Monsoon (ASM) and the westerlies (Chen et al., 2016). A previous study indicated that westerly winds dominated the climate of the Qinghai Lake Basin during the last glacial, while the ASM was dominant during the Holocene (An et al., 2012).

The modern vegetation of the Qinghai Lake Basin is diverse (Chen and Peng, 1993). In the terrace and piedmont areas, the vegetation is temperate grassland dominated by Poaceae (including *Achnatherum splendens*, *Stipa sareptana* and *Stipa breviflora*), and alpine grassland dominated by Cyperaceae (including *Agropyron cristatum* and *Carex infuscate*). In the surrounding mountains, alpine meadow and alpine shrub (dominated by *Salix oritrepha* and *Potentilla fruticosa*) are widespread. In areas of low-lying topography and sandy land, swamp meadow and psammophytes are common. Today, the Qinghai Lake Basin is essentially treeless (Rhode, 2016), and there only a few patches of *Sabina przewalskii* forest in the gully zone within the altitudinal range of 3,350–3,600 m, adjacent to the Qieji River in the western part of the Qinghai Lake Basin, and sporadic patches of *Picea crassifolia* in the eastern part (Chen and Peng, 1993).

The YWY archaeological site (36.560°N, 100.475°E, 3397 m a.s.l.) is located in the foothills of the northern slopes of Qinghainanshan Mountain in the southern Qinghai Lake Basin. The site is ~ 3.5 km from Qinghai Lake and lies 203 m above the modern lake level (Wang et al., 2020). It was first discovered in 2007 (Yi et al., 2011) and was excavated in 2014 by the Qinghai Provincial Institute of Cultural Relics and Archaeological Research and Lanzhou University. Two cultural layers have been found at the site, and several hearths, stone artifacts, abundant charcoal, and numerous animal bones have been found (Wang et al., 2020). Based on surveys and archaeological remains, it was

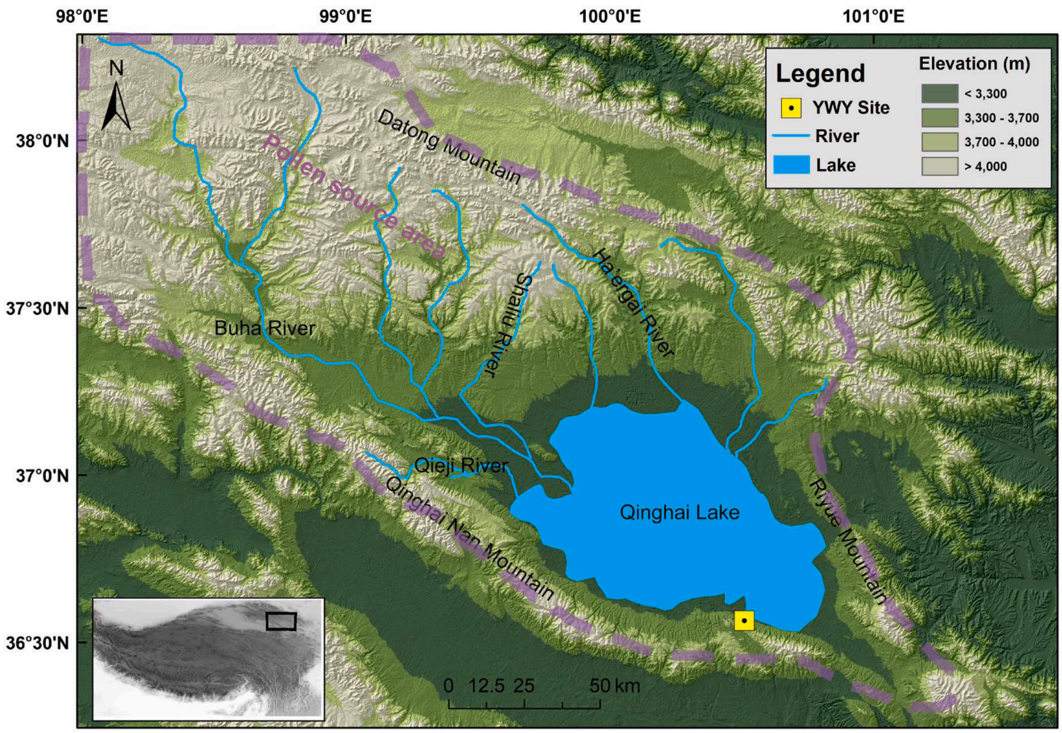

Fig. 1. Location of Qinghai Lake and the YWY archaeological site. The main rivers (Buha, Shaliu, Ha'ergai, and Qieji) are indicated by blue lines. The purple dotted line indicates the pollen source area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

determined to be a Paleolithic-Epipaleolithic site which was occupied for short intervals by hunter-gatherers who hunted ungulates such as *Bos*, wild horse/ass (Wang et al., 2020), and used willow (*Salix*) and spruce (*Picea*) as fuel for fires (Rhode, 2016). The YWY area is located in the alpine shrub zone, and the vegetation is dominated by *Salix oritrepha*, *Potentilla fruticosa*, Poaceae (including *Helictotrichon tibeticum, Roegneria nutans* and *Ptilagrostis dichotoma*), Cyperaceae (including *Kobresia capillifolia, K. bellardii, K. royleana* and *Carex atrofusca*), Asteraceae (*Aster farreri*), *Thalictrum alpinum,* and *Oxytropis ochrocephala* (Chen and Peng, 1993).

3. Methods

3.1. Lithology and chronology

The YWY profile sampled in this study is ~ 300-cm thick (Fig. 2). Based on the lithology, the profile can be divided into the following intervals. (1) 0–26 cm: modern soil layer. (2) 26–86 cm: dark grayish brown paleosol layer, containing more roots. (3) 86–136 cm: relatively weakly-developed grayish-brown paleosol layer; stone tools and charcoal are common. (4) 136–190 cm: dark grayish brown soil, with occasional fine gravels and charcoal. (5) 190–234 cm: light brownish gray

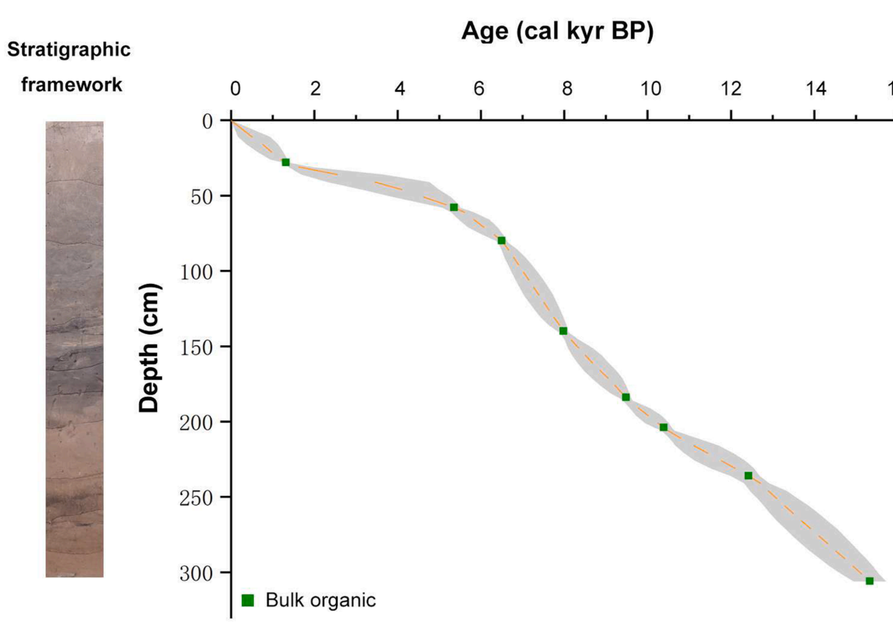

Fig. 2. Stratigraphic framework (left) and age-depth model (right) for the YWY profile.

loess layer. (6) 234–278 cm: dark grayish brown paleosol layer with multi-layered grayish-brown soil stripes, the boundaries of which are poorly defined; charcoal is present. (7) 278–306 cm: pale brown loess with silty sand. The chronology of the profile is based on eight calibrated accelerator mass spectrometry (AMS) ^{14}C dates of bulk organic matter (see Table 1), pre-treated at Lanzhou University and measured at Peking University, China. Before constructing the age-depth model for the profile, the mean estimated reservoir effect (610 years; (Liu, 2018)) was subtracted from the sample ages. The final age-depth model was built using the Bacon model (Blaauw and Christen, 2011) using R software (Fig. 2). Based on the archaeological evidence, the age range of the lower cultural layer is 15.4–13.1 kyr BP (Wang et al., 2020) and that of the upper cultural layer is 9.0–6.4 kyr BP (Liu, 2018).

In order to place the results within the context of the regional vegetation history, we used previously published pollen spectra from a sediment core from Qinghai Lake (Shen et al., 2005), the lithology of which is described in the original publication. The chronology of the sediment core is based on AMS ^{14}C dating of total organic carbon and the ages were corrected for a reservoir effect of 1,039 years (Shen et al., 2005).

3.2. Pollen extraction and identification

A total of 60 samples were collected for pollen analysis from the profile at a 5-cm interval. The ~ 200 g samples were treated using the standard procedures outlined in Faegri et al. (1989). One *Lycopodium* tablet containing 27,637 ± 593 spores was added before chemical treatment in order to calculate pollen concentrations. Carbonates were removed with 36% HCl, humic components with 10% NaOH, and siliceous materials with 30% HF, and any remaining mineral material was then removed using gravity separation with $ZnCl_2$ (specific gravity of 1.9). Pollen identification was based on pollen atlases for the arid and semi-arid areas of China (e.g., Wang et al. (1995); Xi and Ning (1994)). All of the pollen grains were identified and counted at 400 × magnification with a Leica DM5500B microscope. For each sample, a minimum of 5 slides were examined and generally >300 terrestrial pollen grains were counted for each sample. The percentages of terrestrial pollen were calculated based on the sum of total terrestrial pollen and the percentages of fern spores and aquatic pollen were calculated based on the sum of total terrestrial pollen plus aquatic pollen and fern spores, respectively. Pollen diagrams were drawn using Tilia software (version 2.02). Pollen zones were assigned using stratigraphically-constrained cluster analysis (CONISS) based on terrestrial pollen taxa with an occurrence > 2% in at least one sample (Grimm, 1987). We selected 241 pollen assemblages from the Qinghai Lake pollen spectra within the last 15.3 kyr BP to reconstruct the regional landscape, and the detailed experimental methods are described in Liu et al. (2002).

3.3. Pollen-based quantitative landscape reconstruction

3.3.1. Landscape reconstruction Algorithm (LRA)

The LRA is a quantitative approach for past landscape reconstruction based on fossil pollen spectra. It was developed by Sugita (2007a, 2007b) and is based on the theories of pollen representation proposed by Davis (1963), Prentice (1985, 1988) and Sugita (1994). It consists of two models: REVEALS (Regional Estimates of VEgetation Abundance from Large Site) and LOVE (LOcal Vegetation Estimate). The REVEALS model is used to estimate the regional vegetation abundance in areas of 10^4–10^5 km^2 using pollen counts from a large lake or bog (area > 10^2 ha) (Sugita, 1994), or from multiple pollen spectra from small sites (Cui et al., 2015; Trondman et al., 2016). The LOVE model is used for estimating the local vegetation abundance within the relevant source area of pollen (RSAP) (Sugita, 1994) using pollen counts from a small lake or bog (a few ha) within the same region where the vegetation is similar (Sugita, 2007b). Beyond the RSAP, the background pollen component supplied by the local vegetation is relatively constant (Sugita, 2007b). Tests of the REVEALS model have shown that LRA estimates of vegetation abundance provide more accurate estimates of landscape than unadjusted pollen percentages (Hellman et al., 2008; Sugita et al., 2010; Trondman et al., 2015).

Because pollen grains at the YWY site originate from near-source vegetation and are transported by wind, the LRA reconstruction obtained from the site reflects changes in vegetation at the local scale. The pollen assemblages from the sediment core from Qinghai Lake are not only wind-transported from the near-source vegetation but are also supplied from the entire drainage basin by inflowing rivers (Shang et al., 2009). Thus, the LRA reconstruction obtained from Qinghai Lake reflects vegetation change at the regional scale.

3.3.2. Parameter settings for the LRA model

Pre-existing models of pollen dispersal and deposition for lakes (Sugita, 1993) and bogs (Prentice, 1985) in REVEALS version 5 and LOVE version 5 (Shinya Sugita, unpublished data) were used for Qinghai Lake and the YWY site, respectively. Qinghai Lake was a large lake continuously from the lateglacial to the present (Liu et al., 2015), with an area of 4,256 km^2. The radius of the lake was set based on the assumption that the lake was circular; hence a radius of 36.8 km was used. It was impossible to accurately measure the dimensions of the YWY site using Google Earth and therefore we set the radius to 1 m. We used neutral atmospheric conditions and a constant wind speed of 3 m/s, which is the modern mean annual wind speed in the Qinghai Lake area (Li et al., 2008). Z_{max} (the maximum distance within which most pollen

Table 1
AMS ^{14}C dates for the YWY profile.

Sample no.	Depth/ cm	Material	Laboratory no.	Conventional radiocarbon age/ yr BP	Reservoir effect calibrated age/ cal. yr BP	95% confidence intervals/ cal. yr BP
YWY14-20	26	bulk organic matter	LZU14291	2040 ± 20	1430 ± 20	945.2–1362
YWY14-52	58	bulk organic matter	LZU14293	5240 ± 25	4630 ± 25	5084.2–5504
YWY14-74	80	bulk organic matter	LZU14294	6290 ± 30	5680 ± 30	6367.4–6627
YWY14-134	140	bulk organic matter	LZU1553	7715 ± 30	7105 ± 30	7834.8–8099.9
YWY14-178	184	bulk organic matter	LZU1554	9035 ± 35	8425 ± 35	9303.7–9598
YWY14-198	204	bulk organic matter	LZU14295	9840 ± 30	9230 ± 30	10167.9–10580.5
YWY14-230	236	bulk organic matter	LZU1555	11135 ± 30	10525 ± 30	11991.4–12686.6
YWY14-300	306	bulk organic matter	LZU1556	13420 ± 45	12810 ± 45	14941.8–15722.1

originates) was set to 200 km because a previous study found that > 90% of pollen comes from the area within a 200-km radius (Hellman et al., 2008). We selected the same time window for the REVEALS and LOVE reconstruction, according to the time resolution of the samples from the YWY site. For the REVEALS reconstruction, the pollen counts for each time window were calculated by averaging the pollen counts of all available samples within the corresponding period. We used the mean REVEALS estimates from Qinghai Lake as input regional vegetation estimates for the LOVE model.

The LRA model assumes that the PPEs of pollen taxa are temporally constant. The raw pollen count data from Qinghai Lake (Liu et al., 2002) and site YWY (this study) were used. In order to represent the main changes in vegetation composition, we selected the dominant pollen taxa (with average percentages > 0.61% and with a total frequency of occurrence > 13%). For these taxa, there are 19 reliable and available PPE predictions provided by previous studies (Cao et al., 2019; Li et al., 2018; Qin et al., 2019; Wieczorek and Herzschuh, 2020), mainly of Eurasia (Appendix 1). The 13 taxa (Fig. 4) out of the total of 19 taxa (Table 2 of Appendix 1) can represent > 95% of the terrestrial pollen counts per time window for Qinghai Lake, and 15 taxa (Fig. 5) can represent > 84% for the YWY site. The pollen productivity estimates, standard error, and fall speed settings are given in the appendix.

3.4. Biodiversity index

To minimize biases caused by the representation of the dominant pollen taxa, the main pollen counts were transformed using the LRA models (Sugita, 2007a, 2007b) before estimating the diversity, following the description given in Felde et al. (2016). The LRA-generated taxa proportions were converted back to pollen counts using the original pollen sum, and we used the new pollen counts and the original pollen counts of the minor taxa to estimate the diversity. Prior to the diversity calculation, we conducted rarefaction analysis of the pollen counts using R software (https://github.com/StefanKruse/R_Rarefaction). Rarefaction analysis minimizes the unavoidable bias in biodiversity estimates caused by differing count sizes among samples. The count normalization cannot be done by simple linear interpolation because the relationship between richness and count size is non-linear. Rarefaction analysis calculates the minimum variance unbiased estimates (Birks and Line, 1992) of the expected number of t taxa in a random sample of n individuals taken from a collection of N individuals containing T taxa. In this way, the counts are standardized. Simpson's Biodiversity Index was calculated using MVSP3.1 software. A smoothed version of the biodiversity index was calculated using the adjacent averaging method in Origin software.

4. Results

4.1. Pollen spectra from the YWY archaeological site

A total of ~ 80 pollen and spore taxa were identified in the 60 samples from the YWY profile. The terrestrial pollen counts for each sample range from 151 to 642 and the average count is 322. Here, we focus on the dominant terrestrial pollen taxa (Fig. 3). *Picea, Pinus*, Ephedraceae, Tamaricaceae and Rosaceae are the dominant pollen types of woody plants, and the major herbaceous pollen types are *Artemisia*, Asteraceae, Chenopodiaceae and Poaceae.

Based on the CONISS results, the percentage pollen diagram was divided into four zones (Fig. 3), which are described as follows:

Zone 1 (306–199 cm; 15.3–10.1 kyr BP): The pollen assemblages are dominated by herbaceous taxa, including Asteraceae (1–68%), *Artemisia* (15–59%), Chenopodiaceae (1–35%), Poaceae (0–13%). The pollen concentration is low (average of 72 grains/g).

Zone 2 (199–134 cm; 10.1–7.8 kyr BP): Asteraceae (2–21%) and Chenopodiaceae (0–6%) are greatly decreased compared to zone 1, while *Artemisia* (51–95%) and the average pollen concentration (average of 617 grains/g) are greatly increased.

Zone 3 (134–44 cm; 7.8–3.8 kyr BP): The proportion of tree pollen (predominantly *Picea* and *Pinus*) is considerably increased and the tree pollen percentages reach the maximum of 71% (average = 25%). Zone 3 is divided into two subzones. The characteristics of subzone 3a (7.8–6.7 kyr BP) are relatively high tree pollen percentages but still high herbaceous pollen percentages; and the characteristic of subzone 3b (6.7–3.8 kyr BP) is a further increase in tree pollen, which reaches levels equal to or slightly higher than the sum of total herbaceous pollen. The average pollen concentration is increased to 1,003 grains/g.

Zone 4 (44–0 cm; 3.8 kyr BP to the present): Compared to Zone 3, there is a significant decrease in tree pollen abundance. Asteraceae (9–73%), *Artemisia* (9–28%), Chenopodiaceae (2–11%), and Poaceae (2–22%) are the dominant taxa. The average pollen concentration is

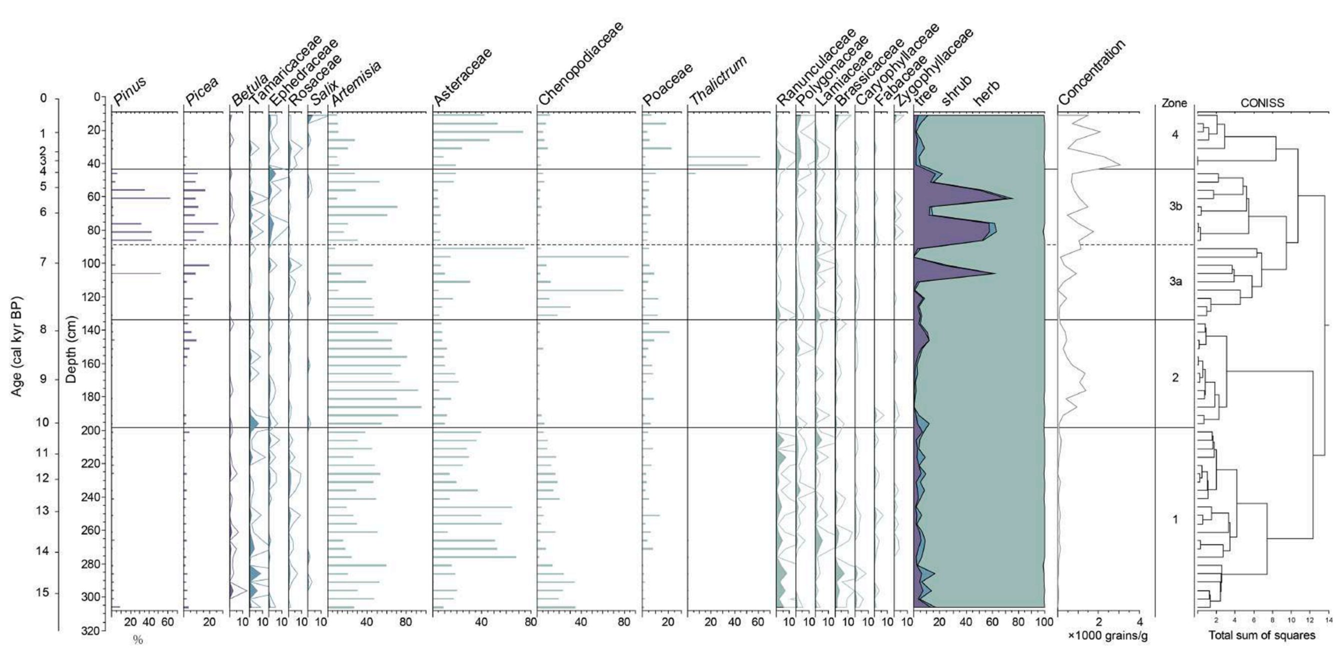

Fig. 3. Pollen percentage diagram of the main taxa and the pollen concentration for the YWY profile. The hollow curves represent 5 × exaggeration of scale.

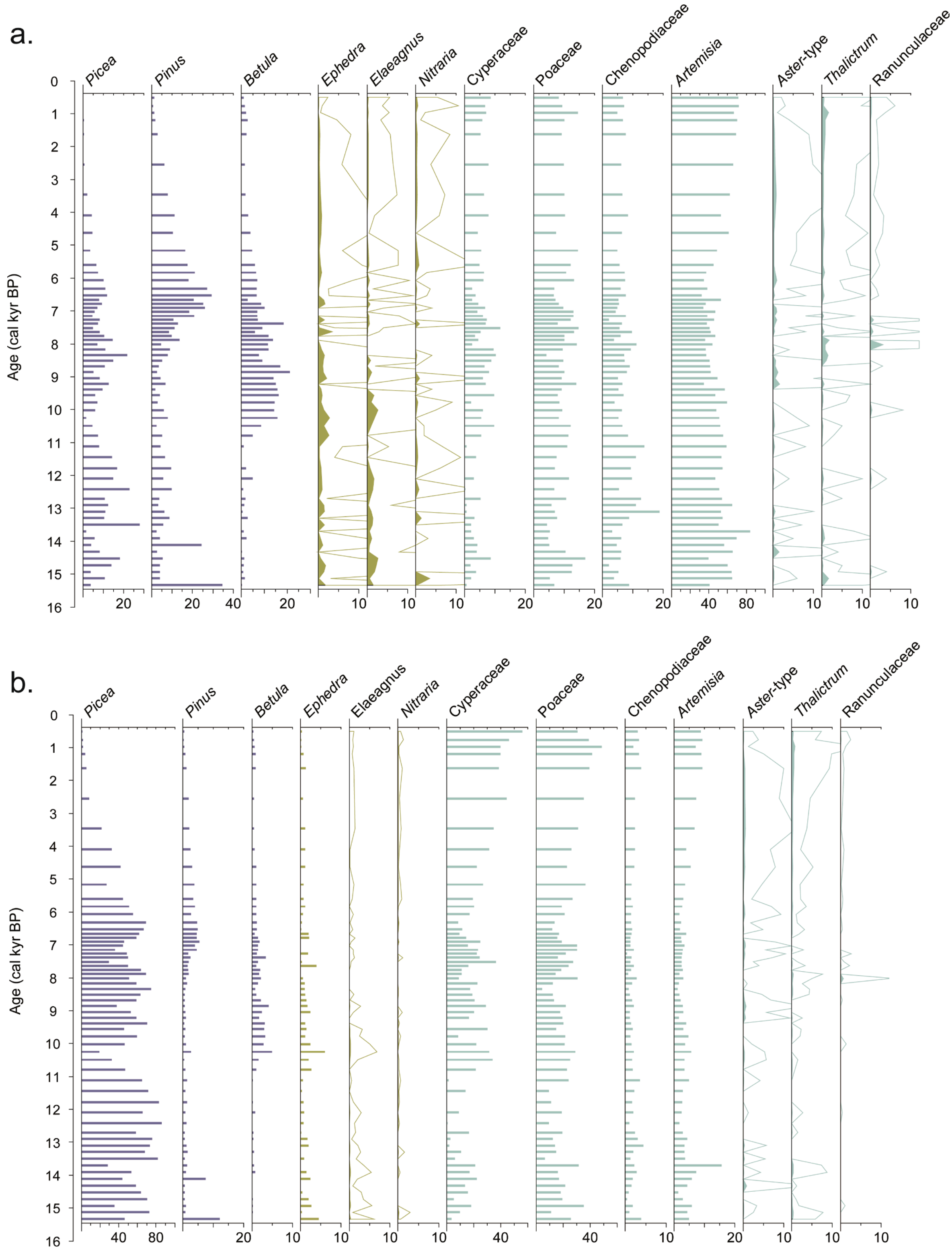

Fig. 4. The original pollen percentage and quantitative reconstruction of Qinghai Lake. a. Pollen percentages. b. REVEALS-based regional vegetation abundance based on the mean pollen productivity estimates from review studies (Cao et al., 2019; Li et al., 2018; Wieczorek and Herzschuh, 2020) for the 13 predominant taxa (with average pollen percentages > 0.61% and with a total frequency of occurrence > 13%). The time window setting is based on the time interval of the YWY site. The hollow curve represents 20 × exaggeration of scale.

relatively high (1,577 grains/g).

4.2. *Model estimates of vegetation abundance in the Qinghai Lake watershed and at the YWY archaeological site*

The estimates of vegetation cover, especially landscape/woodland

Table 2
Radiocarbon dates from wood charcoal at sites in the Qinghai Lake Basin sorted by age.

Profile	Dating method	Radiocarbon Age (yr BP)	Charcoal origin	Reference
JXG1/F2	AMS	12420 ± 50	Willow, Peashrub	Rhode, 2016
HMH1	AMS	11160 ± 50	Willow	Rhode, 2016
HZYC1/ F2	AMS	11010 ± 60	Willow	Rhode, 2016
TH1/F11, F2	AMS	10470 ± 60, 10360 ± 60	Willow	Rhode, 2016
BWC3/ F17	AMS	10280 ± 50	Sea buckthorn	Rhode, 2016
BWC3/ F15, F18,F2	AMS	10170 ± 50, 10050 ± 50, 10000 ± 50	Sea buckthorn	Rhode, 2016
BWC3/ F9	AMS	9510 ± 50	Willow	Rhode, 2016
BWC3/F3	AMS	8430 ± 30	Spruce	Rhode, 2016
QIL 5	AMS	8220 ± 67	Spruce	Kaiser et al., 2007
JXG 2	AMS	8170 ± 50	Spruce	Rhode, 2016
YWY1/F6	AMS	7770 ± 40	Spruce, Willow	Rhode, 2016
YWY1/F7	AMS	7760 ± 40	Spruce, Willow	Rhode, 2016
YWY1/F8	AMS	7713 ± 38	Spruce, Willow	Rhode, 2016
YWY1/F5	AMS	6990 ± 60	Spruce	Rhode, 2016
BWC3/ F12	AMS	6870 ± 40	Spruce	Rhode, 2016
JXG1/F4	AMS	5960 ± 40	Spruce	Rhode, 2016
BWC4/F1	AMS	4780 ± 40	Spruce	Rhode, 2016
WBT1	AMS	4280 ± 40	Spruce	Rhode, 2016
QIL 3	AMS	4095 ± 57	Spruce	Kaiser et al., 2007
QIL 3	AMS	4016 ± 51	Spruce	Kaiser et al., 2007
CDH	AMS	2890 ± 70	Spruce, Sea buckthorn, False tamarisk	Rhode, 2016

openness, vary considerably between the regional and local scales (Fig. 4 and Fig. 5). The mean REVEALS estimates suggest that from the lateglacial to the early Holocene (Zone 1 and Zone 2; 15.3–7.8 kyr BP) the woodland comprised *Picea* (up to 93% cover), *Pinus* (up to 14%) and *Betula* (up to 5%) (Fig. 4b). During the middle Holocene (Zone 3; 7.8–3.8 kyr BP), it comprised *Picea* (up to 84%), *Pinus* (up to 10%) and *Betula* (up to 4%). During the late Holocene (Zone 4; 3.6–0 kyr BP), there was an increase in meadow and steppe, with Cyperaceae (up to 73%), Poaceae (up to 64%), *Artemisia* (up to 32%), while *Picea* decreased slightly and then reached extremely low values (Fig. 4b).

The RSAP result from the LOVE model indicates the range of 6–431 m. The reconstructed abundance diagram for alpine shrub indicates a shrub-steppe community (with Rosaceae, Ephedraceae, Asteraceae, Chenopodiaceae, *Artemisia* and Poaceae), which changed to a coniferous forest–steppe community (with *Picea*, *Pinus*, Rosaceae, Ephedraceae and Asteraceae) after 7.3 kyr BP (Fig. 5b). After 5.2 kyr BP, the coniferous forest–steppe community changed to a shrub-steppe community (with Asteraceae, Rosaceae, Ephedraceae, *Salix, Thalictrum* and Polygonaceae). Compared with the regional vegetation abundance, the local vegetation composition was as follows: (1) woodland (*Picea* up to 35%, *Pinus* up to 35%) during ~ 7.1–5.2 kyr BP; (2) a lower abundance of woodland from the lateglacial to the early Holocene and late Holocene; (3) higher abundances of shrubs, including Rosaceae (up to 34%), *Salix* (up to 11%) and Ephedraceae (up to 29%) (Fig. 5b).

4.3. Plant biodiversity at the YWY archaeological site and Qinghai Lake

The smoothed Simpson's Biodiversity Index from Qinghai Lake is shown in Fig. 7a. A major decrease occurred during ~ 15.3–12.1 kyr BP; however, after ~ 12.1 kyr BP, biodiversity gradually recovered to reach its highest value at ~ 8.2 kyr BP. The values fluctuated during ~ 7.0–2.6 kyr BP, while after ~ 2.6 kyr BP, they fluctuated but with a generally increasing trend. The smoothed values of Simpson's Biodiversity Index from the YWY archaeological site are shown in Fig. 7b. The first low value occurred at ~ 14.7 kyr BP, and at ~ 7.9 kyr BP, the diversity index decreased to its lowest level.

5. Discussion

5.1. Vegetation changes at the YWY archaeological site and Qinghai Lake: Pollen percentages versus quantitative estimates of vegetation cover

In this study, the LRA is used to provide a quantitative reconstruction of the vegetation history of the YWY site and Qinghai Lake. Traditionally, pollen percentage data are used to provide qualitative estimates of taxa coverage, which is facilitated by a gradual increase in our understanding of the relationship between pollen percentages and vegetation coverage, based on studies of modern pollen productivity (e.g., Parsons and Prentice, 1981; Sugita, 1994). Overall, however, such efforts rely heavily on subjective empirical judgment, leading to uncertainties in research results. However, the LRA can provide a quantitative reconstruction of the vegetation by taking factors such as the spatial distribution of pollen sources, basin size and type, pollen loading and dispersal characteristics into account to correct abundance values, in addition to considering pollen productivities and transportation characteristics (Sugita, 2007a, 2007b).

In the present study the LRA provides a modeled estimate of the uppermost sample from Qinghai Lake and the YWY site which is good agreement with modern vegetation data. The modeled vegetation of the uppermost sample (31 yr BP) from Qinghai Lake indicates the dominance of Cyperaceae and Poaceae–dominated meadow and steppe communities around Qinghai Lake. In comparison, the modern vegetation around Qinghai Lake is mainly temperate steppe (dominated by *Agropyron cristatum* and *Stipa breviflora*), alpine meadow (dominated by *Kobresia humips*), and alpine shrub (dominated by *Potentilla fruticosa*, *Salix oritrepha* and *Caragana jubata*) (Huai and Zhou, 1997), with the first two categories occupying most of the surrounding area (http://www.nsii.org.cn/mapvege). The modeled vegetation of the uppermost sample (506 yr BP) from the YWY archaeological site indicates a sparse shrub community (with *Salix oritrepha*, *Potentilla fruticosa* and *Caragana jubata*). In comparison, the modern vegetation around the site is an alpine shrub community (Huai and Zhou, 1997). The reconstruction is superior to the original data owing to the higher shrub percentages (Rosaceae, Ephedraceae and *Salix*). In summary, compared with the traditional pollen percentage results, the quantitative reconstruction of the plant cover is more consistent with the true vegetation composition. This comparison indicates that the application of LRA can provide more accurate information about the relative abundances of trees, shrubs, grasses, and landscape openness since the lateglacial.

Briefly, for taxa with a high pollen productivity (e.g., Chenopodiaceae, *Artemisia*, and *Pinus*), the reconstructed vegetation abundance is lower than the corresponding pollen percentages; whereas for taxa with a low pollen productivity (e.g., Rosaceae, Ephedraceae, Cyperaceae, and Poaceae), their representation in the reconstructed vegetation is higher than the pollen percentages.

For Qinghai Lake, the vegetation composition and taxa proportions show large differences following the quantitative reconstruction. From the lateglacial to the early Holocene, the reconstructed tree proportions are much greater than the corresponding original tree pollen

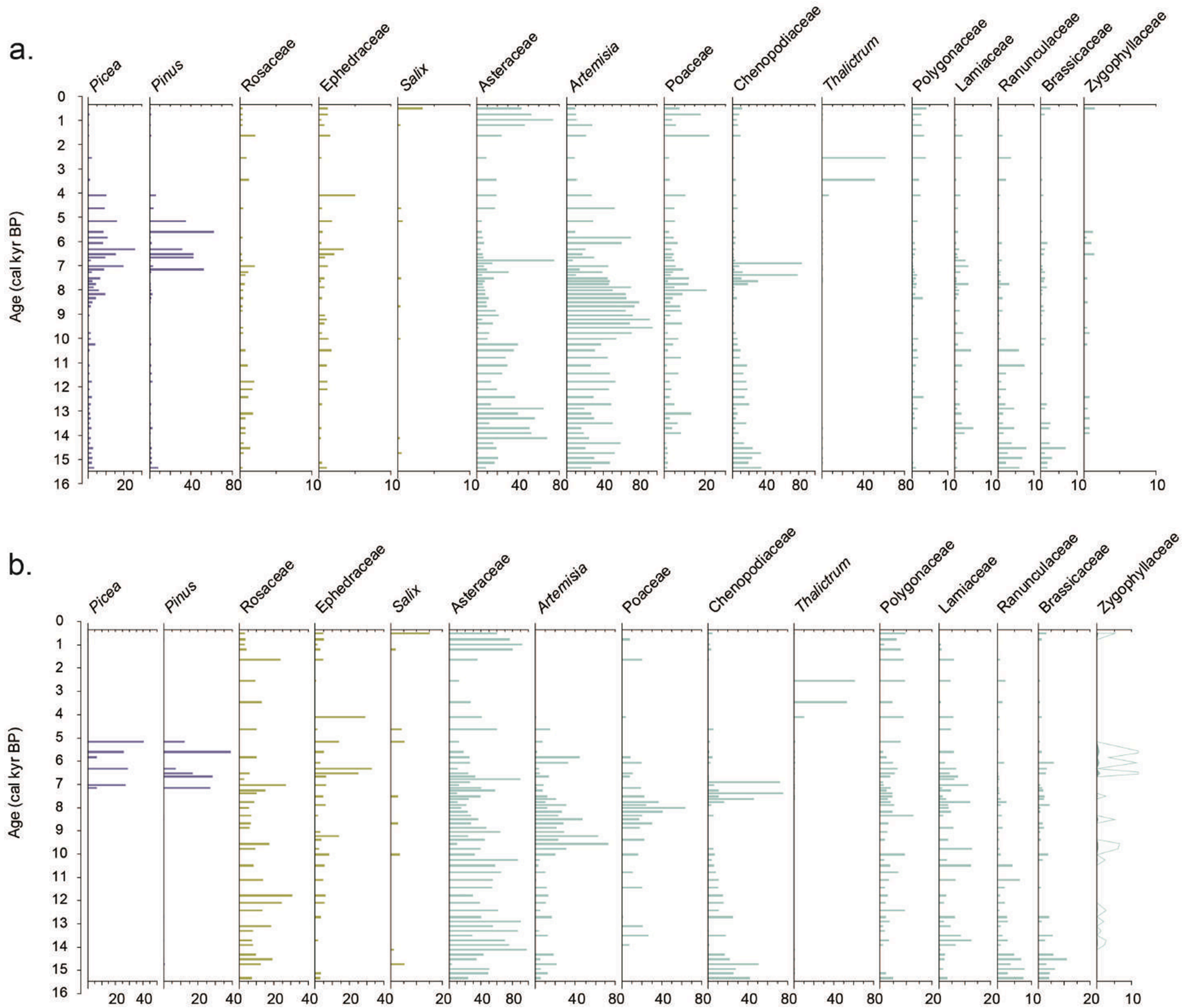

Fig. 5. Pollen assemblages and quantitative vegetation cover based on the 15 predominant taxa (with average pollen percentages > 0.61% and with a total frequency of occurrence > 13%) for the YWY profile. a. Pollen percentages. b. LOVE-based local vegetation abundance based on the mean pollen productivity estimates from review studies (Cao et al., 2019; Li et al., 2018; Wieczorek and Herzschuh, 2020) within a 6–431 m radius (relevant source area of pollen; RSAP) around the sampling site. The hollow curves represent 20 × exaggeration of scale.

percentages (Fig. 4). This is especially so for *Picea*, which is greatly increased after the quantitative estimation because of the low *Picea* PPE and high PPE of other taxa such as *Artemisia*. In the middle Holocene, the quantitative reconstruction indicates that *Picea* was the main tree taxon and it fluctuated throughout the middle Holocene. However, the original pollen percentage data indicate that *Pinus* was the main tree taxon with highest values at ~ 6.4 kyr BP. In the late Holocene, the reconstruction indicates that trees (mainly *Picea*) decreased and the major herbaceous taxa (Cyperaceae and Poaceae) increased. While the original pollen percentages show the same trend, the tree component is mainly *Pinus* and the herb component is mainly *Artemisia*.

For the YWY site, there is also a difference between the original pollen percentages and the quantitative reconstruction: (1) The reconstruction indicates the presence of coniferous woodland in the vicinity of the site during ~ 7.1–5.2 kyr BP, while the original pollen percentages indicate coniferous woodland during ~ 8.7–4.1 kyr BP. (2) The reconstruction indicates that shrubs (Rosaceae, Ephedraceae and *Salix*) were a significant component of the vegetation while the original pollen percentages indicate a very low shrub pollen representation. (3) The reconstruction indicates that *Artemisia* essentially disappeared after ~ 4.6 kyr BP, while the original pollen data show that *Artemisia* was frequently present during the late Holocene. (4) In the original pollen percentage data, herbs such as Polygonaceae, Fabaceae, Lamiaceae are poorly represented, while in the reconstruction these taxa are more abundant in the vegetation and their under-representation is obvious.

5.2. *Vegetation change on different spatial and temporal scales within the Qinghai Lake Basin*

Although the environment of the Qinghai lake area has been studied intensively, the vegetation dynamics on different spatial and temporal scales are unclear. Comparison of the regional vegetation reconstruction from Qinghai Lake with the local reconstruction from the YWY site reveals important information about spatiotemporal changes in the vegetation, such as upslope and downslope shifts in forest, representing expansion and contraction. Since the lateglacial, spruce forest grew at high altitudes in the mountains, which can be inferred from the significant proportion of spruce in Fig. 4 and the record of *Picea* pollen in the

Qinghai Lake catchment area (Du et al., 1989; Liu et al., 2002; Shen et al., 2005). However, the pollen record and the quantitative vegetation reconstruction for site YWY suggest that neither pine nor spruce grew in the mountain foothills, and the independent charcoal record from the Qinghai Lake Basin (Table 2) supports this conclusion. Wind and water are the main agents for pollen transport into Qinghai Lake. The upward transmission of pollen at low altitudes from outside the Qinghai Lake Basin could potentially influence the pollen spectra from high-altitude sites; however, long-distance transport of spruce pollen, which is the dominant arboreal pollen type in the area, is not as common as for *Pinus*. According to research on modern surface soil, spruce pollen is not easily dispersed (Lu et al., 2004; Zhu, 2002); for example, in the low-altitude vegetation zone in eastern Oregon, USA, the long-distance transmission of spruce pollen is less than 2–3% (Minckley and Whitlock, 2000). Thus, the tree pollen in the Qinghai Lake sediments is mainly transported from high altitudes to the pollen catchment area by rivers, and thus it is reasonable to conclude that spruce forest grew at high altitudes in the mountains.

In the early Holocene, it can be seen that the change in *Betula* was different from that of *Picea* and *Pinus* (Fig. 4b). *Betula* was higher in the early Holocene and decreased in the mid-Holocene. *Picea* and *Pinus* were less in the early Holocene compared with the mid-Holocene. After the reduction in the coniferous forest from ~ 12.3 kyr BP, recovery within a short time was difficult, which conforms to the known successional pattern of Qinghai coniferous forest. The increase in *Betula* during the early Holocene was possibly due to the significant improvement in temperature and precipitation because it preferred light and moisture (Ministry of Forestry, 1993). As birch is fast-growing, the upper canopy develops rapidly and the resulting shaded conditions are conducive to the growth of spruce and pine seedlings beneath. Once the height of coniferous trees exceeds that of birch and they form a tall forest layer, the birch is gradually reduced. Therefore, from the early Holocene to the middle Holocene, the gradual increase in the abundance of coniferous forest would have inhibited the growth of birch, resulting in the gradual decrease in *Betula*.

We interpret the gradual increase in *Picea* pollen from the early to the middle Holocene to indicate that spruce woodland began to expand downslope and that the forest edge on the mountains shifted closer to the YWY site (see Fig. 6a and 6b). During this interval, a pronounced wetting trend is evident across the entire northeastern TP (Ji et al., 2005b; Li et al., 2017b), which was the result of the humid Asian Summer Monsoon penetrating into the Qinghai Lake area of the TP (An et al., 2012), which continuously supplied sufficient moisture to support the growth of dense spruce forest on the mountain slopes until the Holocene climatic optimum (An et al., 2012; Herzschuh, 2006, 2019; Ji et al., 2005b; Shen et al., 2005; Zhao et al., 2007; Zhou et al., 2010). After ~ 8.7 kyr BP there was a gradual increase in *Picea* representation in the pollen assemblages at the YWY site (Fig. 5a). Since most of the *Picea* pollen at the site is thought to be derived from local sources rather than by long-distance transport (Herzschuh et al., 2010a; Liu et al., 1999; Lu et al., 2008; Yu et al., 2001), we interpret the gradual increase in *Picea* pollen to indicate that spruce woodland began to expand downslope and the forest edge on the mountains moved closer to the YWY site (see Fig. 6a and 6b). In short, the persistent occurrence of

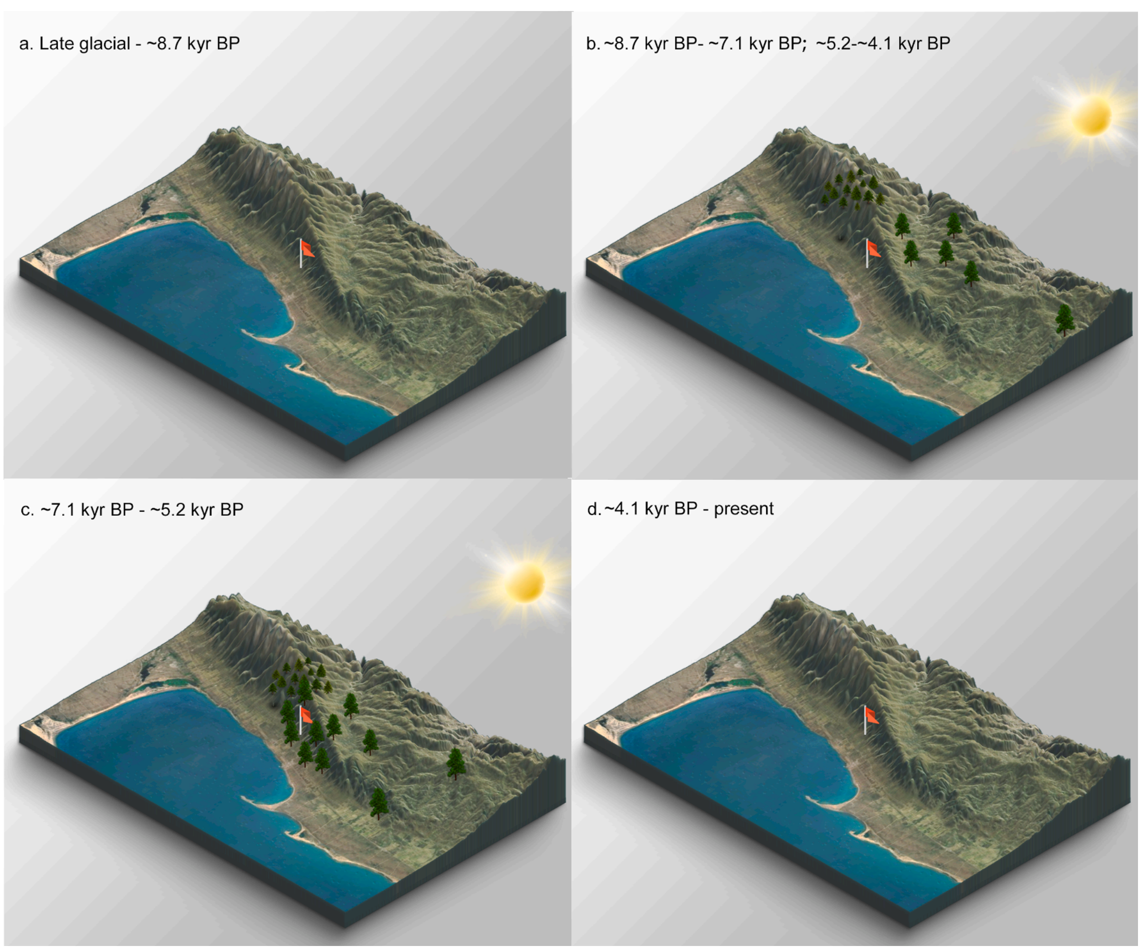

Fig. 6. Conceptual model of the vegetation dynamics of the YWY area on varying spatial and temporal scales. a. Late glacial to ~ 8.7 kyr BP. b. ~ 8.7–7.1 kyr BP and ~ 5.2–4.1 kyr BP. c. ~ 7.1–5.2 kyr BP. d. ~ 4.1 kyr BP to the present. The climatic optimum during the middle Holocene contributed to the expansion of the forest belt to the foothills.

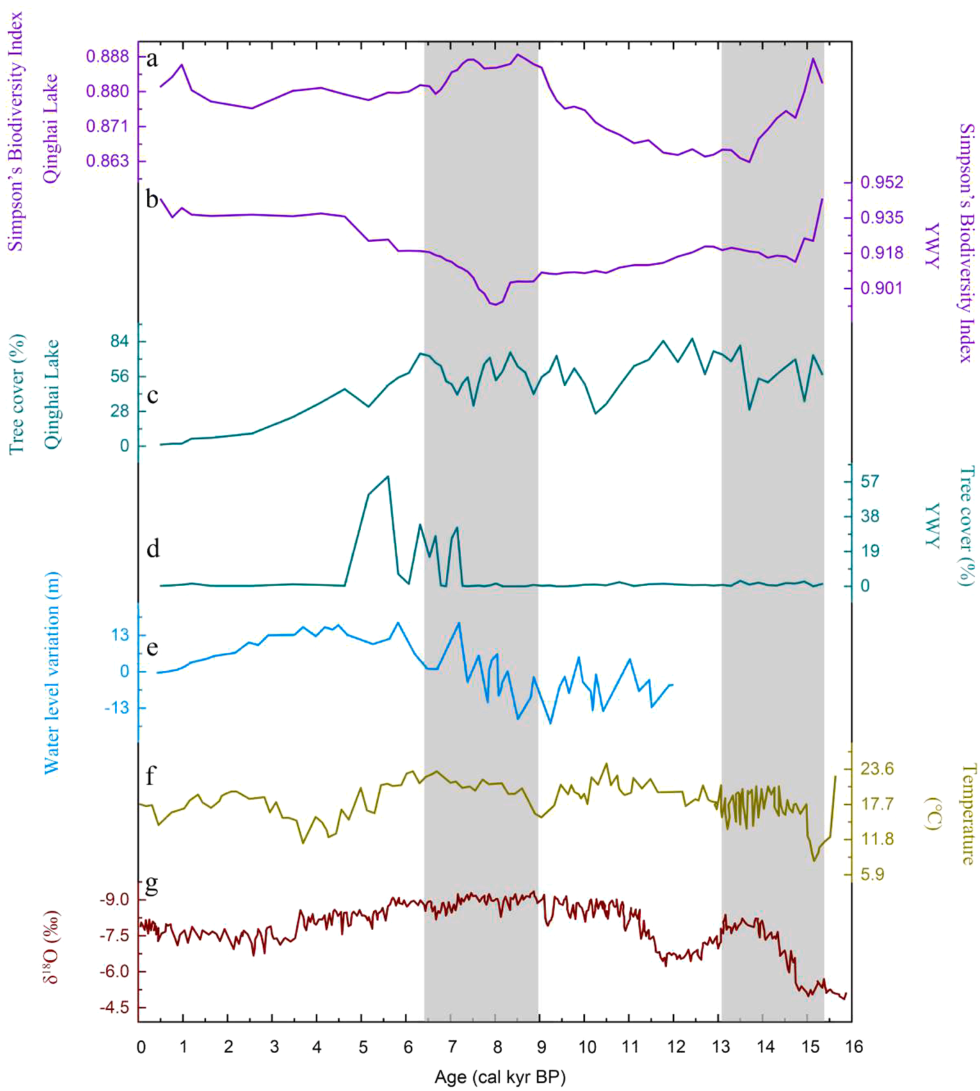

Fig. 7. Comparison of tree cover and biodiversity for the YWY site and Qinghai Lake with climate records from other studies. a. Adjacent averaged smoothed curves of Simpson's Biodiversity Index for Qinghai Lake (this study). The time interval of Qinghai Lake is set according to that of the YWY site. b. Adjacent averaged smoothed curves of Simpson's Biodiversity Index for the YWY site (this study). c. REVEALS-based tree cover percentages from Qinghai Lake (this study). d. LOVE-based tree cover percentages from the YWY site (this study). e. Record of water-level variations of Qinghai Lake (Zhang et al., 1994) reflecting changes in effective humidity. f. Temperature reconstruction for Qinghai Lake (Hou et al., 2016b). g. Stalagmite $\delta^{18}O$ record from Dongge cave, indicating Asian monsoon strength (Dykoski et al., 2005) and precipitation.

wetter conditions resulted in the expansion of the forest belt.

After ~ 7.1 kyr BP, woody plants including spruce and pine reached the YWY site (see Fig. 6c); the quantitative reconstruction results indicate the occurrence of both at Qinghai Lake and the YWY site and that they comprised a substantial proportion of the vegetation (Fig. 4b, 5b). In addition, archaeological and soil charcoal records (Table 2) further demonstrate that dense forest was universally present in the foothills in the middle Holocene. Thus, the vegetation of the Qinghai Lake area at this time was mixed spruce and pine forest, which grew both at high elevations in the mountains and at low elevations within the Qinghai Lake Basin. The vegetation at this time was quite different from that of the modern Qinghai Lake Basin, which is dominated by alpine meadow–steppe. Notably, at Luanhaizi Lake in the northeastern TP, tree pollen was represented from 16 kyr BP to the middle Holocene (Herzschuh et al., 2006). Forest in the northeastern TP expanded to higher altitudes than at present, which indicates that winter temperatures were not as cold as today when the occurrence of forest is restricted.

After ~ 5.2 kyr BP, forest almost disappeared from the YWY area. This was because of a decrease in the strength of the Asian monsoon which was accompanied by a fall in the level of Qinghai Lake (Fig. 7e, 7g) (An et al., 2012; Liu et al., 2015). No trees are evident in the quantitative vegetation reconstruction for the YWY site after ~ 5.2 kyr BP (Fig. 5b), which is also the case for most of the archaeological and soil charcoal records from the low-altitude vegetation zone of the Qinghai Lake area after ~ 4 kyr BP (Table 2). However, the quantitative vegetation reconstruction for Qinghai Lake does indicate the limited occurrence of trees, and therefore we conclude that the extent of the forest decreased and the tree-line moved upslope (see Fig. 6b and 6d). In addition, shrubs and herbs expanded within the low-altitude vegetation zone.

The results for the YWY site provide new information about the vegetation dynamics on different spatial and temporal scales within the Qinghai Lake basin. Previously, pollen analysis had only been conducted on the Jiangxigou and LGR profiles in the Qinghai Lake Basin (Hou et al., 2016a; Wei et al., 2020a), which indicated the occurrence of grassland but not forest. The difference is because of the relatively large contrasts in elevation, geology and geomorphology, corresponding to differences in water availability and water–table depth, heating, soil conditions and other natural ecological factors (Chen and Peng, 1993). Notably, the archaeological and soil charcoal records from several different sites (Kaiser et al., 2007; Rhode, 2016) support the quantitative vegetation reconstruction for the YWY site.

5.3. *Vegetation background of Paleolithic-Epipaleolithic hunter-gatherer subsistence at the YWY site and human impacts on the vegetation*

Since the lateglacial period, technological innovation in the production of microliths resulted in the increased movement of small, mobile bands of hunter-gatherers from low-altitude regions into the Qinghai Lake Basin (Lee, 1997; Wang et al., 2020; Zhang et al., 2016). During 15.3–13.1 kyr BP, prehistoric foragers occupied the YWY area on a seasonal basis, as indicated by archaeological evidence (Wang et al., 2020). The shrub-steppe vegetation of the area was dominated by Rosaceae, Asteraceae, Chenopodiaceae and *Artemisia* (Fig. 5), which would have provided small hunter-gatherer groups with abundant subsistence resources. The Rosaceae would have provided plant food resources for humans (Ju et al., 2013; Şerban et al., 2008), while the grassland vegetation near the YWY site would have been an important food source for *Bos* sp. and *Equus* which were the most important large animals hunted by prehistoric humans (Wang et al., 2020). The shrub vegetation would also have been a source of fuel for heating and food processing, as indicated by the hearths and charcoal discovered at the YWY site. The contemporaneous hunting groups at the HMH1 and JXG1 sites at Qinghai Lake also burned scrub and hunted the gazelle and wild sheep which occupied the steppe (Madsen et al., 2006; Rhode, 2016).

According to the archaeological evidence (Liu, 2018), prehistoric hunter-gatherers reappeared and seasonally occupied long-term camps in the YWY area during ~ 9.0–6.4 kyr BP. During most of the interval of 9.0–7.3 kyr BP, humans at the YWY site occupied a shrub-steppe environment which was dominated by Asteraceae, *Artemisia*, Poaceae, Chenopodiaceae, Rosaceae, and Ephedraceae (Fig. 5b). However, after 7.3 kyr BP they occupied forest steppe, dominated by Asteraceae, *Artemisia*, Chenopodiaceae, *Pinus, Picea*, Rosaceae, and Ephedraceae. The increasing temperature and precipitation during this period (Fig. 7e, 7f, 7g) promoted the expansion of the forest belt which gradually spread to the foothills, and the forest-steppe ecotone would have provided a wider range of resources (Chen, 2006a). The inhabitants of the YWY site and the contemporaneous hunting groups at the JXG2, BWC3 and HMH3 sites in the Qinghai Lake Basin (Table 2) were in close proximity to forest or patches of trees and thus they not only used scrub such as willow for fuel, but also trees such as spruce which would have provided longer-lasting fires for warmth and food processing. In addition, the ecotone environment would have attracted a wider variety of animals. Foragers occupied the mountain margins and hunted a diverse range of animals, including deer, which would have tended to be located in the boundary zone between forest and steppe (Chen, 2006a, 2006b; Wang et al., 2016). Prehistoric humans at several contemporaneous archaeological sites in the Qinghai Lake Basin hunted montane forest animals such as red deer (Cervidae), grassland animals such as gazelle (*Gazella* sp.), and animals typical of alpine slopes such as bharal (*Pseudois nayaur*) and Tibetan argali (*Ovis ammon*) (Rhode, 2016).

Although the onset of a warmer and wetter climate at 6.4 kyr BP might have been expected to have promoted the movement of humans to the high-elevation TP, the YWY site was abandoned. This may have been because of the change in the vegetation from steppe to forest steppe, with an increased proportion of trees (Fig. 7d). During the Paleolithic period, hunting and gathering were limited by the quantity of edible wild animals and plants (Elston et al., 2011). As a result of the more substantial changes in the vegetation compared to previously (Fig. 5), prey animals that were adapted to the steppe environment may have migrated outside the area and would have been followed by the hunter-gatherers who tended to specialize in hunting specific resources in locations where they were relatively concentrated and vulnerable (Madsen and Elston, 2007). Another possibility is that small mobile hunting parties were competitively replaced by farming groups that exploited an expanded habitat at lower elevations during the Holocene climatic optimum and subsequently moved to the higher Plateau (Madsen et al., 2006; Rhode et al., 2007b). Thus, although the climate was optimal, hunter-gatherers evidently elected to abandon the YWY site.

One of our research aims was to determine whether or not the activities of prehistoric humans had an impact on the local vegetation, and we now address this issue. During 15.3–13.1 kyr BP when the YWY site was occupied, the similarities in the changes in plant diversity and tree cover (Fig. 7a-7d) at Qinghai Lake and at the YWY site indicate a common driving factor. Given that few archaeological sites have been found dating to this period, human impacts on the local environment were likely limited, and it is unlikely that the vegetation cover and biodiversity in the Qinghai Lake area were affected by human activity during this early period. This inference is supported by the absence of a clear signal of anthropogenic disturbance at the YWY site in this early period. However, during ~ 9.0–6.4 kyr BP, human activity may indeed have affected the vegetation of the YWY area. Although the biodiversity in the entire Qinghai Lake area during this period remained high, as indicated by the lake sediment record (Fig. 7a), the lowest biodiversity at the YWY site occurred at this time (Fig. 7b). Biotic diversity is influenced by various factors, including biological and abiotic influences (Birks et al., 2016; Miras et al., 2015). According to the 'water-energy dynamics hypothesis', diversity is controlled by the levels of environmental heat and humidity (Field et al., 2005; Kreft and Jetz, 2007). However, there is no evidence of an abrupt event in quantitative climatic reconstructions for the Qinghai Lake area during 9.0–6.4 kyr BP in the Qinghai Lake area in the northeastern TP (Dykoski et al., 2005; Hou et al., 2016b; Zhang, 1994). Therefore, it is possible to conclude that human activities were the main influence on plant diversity in the YWY area at this time. The low biodiversity may have been the result of damage to the vegetation by trampling by Paleolithic hunter-gatherers. Compared with other regions with more favorable conditions of heat and precipitation, the harsh environment of the Qinghai Lake area may have led to the relatively low resilience of the vegetation to anthropogenic disturbance. Even relatively low-intensity trampling by humans can be as damaging as high-intensity trampling in certain plant communities (Pescott and Stewart, 2014). For example, a previous study showed that the chamaephyte subgroup had a very limited ability to recover after die-back, even after a period free from further disturbance (Pescott and Stewart, 2014).

However, during 9.0–6.4 kyr BP, human activities at the YWY site can be seen to have had a pronounced impact on the vegetation, as indicated by the high values of Chenopodiaceae and Rosaceae at this time (Fig. 5b). Based on previous studies of surface pollen spectra in the Qinghai Lake area, Chenopodiaceae and *Potentilla*-type are indicative of vegetation degradation caused by human activity (Wei et al., 2018). Moreover, Liu et al. (2006) concluded that Chenopodiaceae pollen, as well as being an indicator of aridity, was also indicative of human activity, and Hicks and Birks (1996) also found that Chenopodiaceae was related to human settlement. Chenopodiaceae is the most important taxon in the pollen spectra of desert steppe vegetation. High Chenopodiaceae frequencies in the pollen spectra of meadow or steppe are potentially indicative of vegetation degradation caused by human activity. A recent modern pollen study (Wei et al., 2018) found that *Potentilla*-type was relatively well-represented in overgrazed alpine meadow, indicating that *Potentilla* is an indicator of anthropogenic disturbance. These various lines of evidence indicate the possibility of a significant human influence on the environment of the YWY area at this time.

After 4.6 kyr BP, animal herding by humans began to have a pronounced impact on the vegetation of the entire Qinghai Lake area, evidenced by the increased coverage of Chenopodiaceae and Asteraceae (Fig. 4b), which are regarded as grazing indicators (Wei et al., 2018). An early pastoral economy appeared in the Qinghai Lake area ~ 6.0–5.5 kyr BP and then intensified (Wei et al., 2020b), which supports our inference. Subsequently, as well as up to the present day, the Qinghai Lake area was used as summer pasture for sheep and cattle grazing by herdsmen who transported their livestock several hundreds of kilometers to the area.

6. Conclusions

A quantitative vegetation reconstruction for the YWY archaeological site and Qinghai Lake provides a continuous picture of local and regional vegetation evolution from the lateglacial until the present. During the lateglacial, coniferous forest developed at high altitudes on the surrounding mountains. From the lateglacial until the middle Holocene, spruce woodland expanded downslope and eventually reached the YWY site. During this interval, the living environment of the small group of Paleolithic hunter-gatherers occupying the site changed from shrub-steppe to coniferous forest-steppe. The activities of these hunter-gatherers may have affected the vegetation at the local scale, as indicated by a reduction in biodiversity and the occurrence of pollen indicators of vegetation degradation. Overall, our results contribute to an improved understanding of Paleolithic human-environment interactions in the Tibetan Plateau and are a basis for subsequent research in the region.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2021.105892.

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