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ORIGINAL PAPER

Persistence of *Artemisia* steppe in the Tangra Yumco Basin, west-central Tibet, China: despite or in consequence of Holocene lake-level changes?

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Abstract The closed Tangra Yumco Basin underwent the strongest Quaternary lake-level changes so far recorded on the Tibetan Plateau. It was hitherto unknown what effect this had on local Holocene vegetation development. A 3.6-m sediment core from a recessional lake terrace at 4,700 m a.s.l., 160 m above the present lake level of Tangra Yumco, was studied to reconstruct Holocene flooding phases (sedimentology and ostracod analyses), vegetation dynamics and human influence (palynology, charcoal and coprophilous fungi analyses). Peat at the base of the profile proves lake level was below 4,700 m a.s.l. during the Pleistocene/Holocene transition. A deep-lake phase started after 11 cal ka BP, but the ostracod record indicates the level was not higher than ~4,720 m a.s.l. (180 m above present) and decreased gradually after the early Holocene maximum. Additional sediment ages from the basin suggest recession of Tangra Yumco from the coring site after 2.6 cal ka BP, with a shallow local lake persisting at the site until ~1 cal ka BP. The final peat formation indicates drier conditions thereafter. Persistence of *Artemisia* steppe during the Holocene lake high-stand resembles palynological records from west Tibet that indicate early Holocene aridity, in spite of high lake levels that may have resulted from meltwater input. Yet pollen assemblages indicate humidity closer to that of present potential forest areas near Lhasa, with 500–600 mm annual precipitation. Thus, the early mid-Holocene humidity was sufficient to sustain at least juniper

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In memoriam: Burkhard Frenzel (2010).

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forest, but *Artemisia* dominance persisted as a consequence of a combination of environmental disturbances such as (1) strong early Holocene climate fluctuations, (2) inundation of habitats suitable for forest, (3) extensive water surfaces that served as barriers to terrestrial diaspore transport from refuge areas, (4) strong erosion that denuded the non-flooded upper slopes and (5) increasing human influence since the late glacial.

Keywords Tibetan Plateau · Pollen · Spores · Ostracods · Charcoal · Human impact · Vegetation ecology · Asian monsoon

Introduction

Sediments in lake basins of the northern hemisphere desert belt indicate extremely unstable environments since the late Pleistocene (Patrickson et al. 2010). Ancient shorelines (Fang 1991; Kong et al. 2011), geochemical variables (Fontes et al. 1996; Wei and Gasse 1999; Doberschütz et al. this issue) and aquatic organisms (Van Campo and Gasse 1993; Fan et al. 1996) indicate a dramatic rise in humidity on the Tibetan Plateau after the Last Glacial Maximum (LGM). Regional differences in timing and strength of the wet phases, however, are not yet clearly understood (Fang 1991; Wei and Gasse 1999; Morrill et al. 2003; Mischke et al. 2008; Kong et al. 2011). Lake basins west of 90° E have conspicuously larger lake-level fluctuations than those farther east (Fang 1991; Kong et al. 2011; Miehe et al. 2011a). Consequently, one would expect stronger vegetation changes in west Tibet than in the east. Previous studies, however, indicate persistence of *Artemisia* steppe in the west throughout the Holocene (Van Campo et al. 1996; Wu and Xiao 1996), whereas Cyperaceae mats or forests spread in the east (Frenzel et al. 1995; Frenzel 2001; La Duo 2008; Shen et al. 2008; Schlütz and Lehmkuhl 2009). Likewise, high proportions of endemic plants suggest high ecological stability in the western Tibetan highlands. Little attention has been paid to the discrepancy between this apparent ecological stability and pronounced climate changes (Ni et al. 2010; Miehe et al. 2011a).

In this paper we hypothesize that environmental instability, especially lake-level changes, contributed to the apparent vegetational stability in endorheic Tibetan drainage systems. Furthermore, we consider early herbivore and human influence on the vegetation as additional environmental disturbance factors. Genetic studies revealed that early humans occupied the Plateau during the LGM (Zhao et al. 2009). The Tibetan highlands are littered with artefacts from Palaeolithic to Neolithic times (Frenzel et al. 2001). Burkhard Frenzel (Frenzel 2001; Frenzel et al. 1995, 2003) was the first palaeobotanist to point out the early human influence on vegetation in Tibet. Palynological studies in south-central Tibet have elucidated a non-negligible human influence on the vegetation, at least since the middle Holocene (La Duo 2008; Miehe et al. 2009; Schlütz and Lehmkuhl 2009). Comparable studies from more western areas in Tibet are still lacking.

The Tangra Yumco Basin, in the climatic transition between central and west Tibet (Fig. 1), is ideally suited to investigate complex relations among climate, environment and humans. This interior basin experienced the greatest Quaternary lake-level changes found on the plateau (370 m; Kong et al. 2011). Furthermore, it was a centre of ancient civilizations (Bellezza 2008) and harbours the world's highest-altitude agriculture, at the hygric and altitudinal borderline for tree growth (Miehe et al. 2008). Consequently this environment should react most sensitively to climatic changes and human impact.

We studied a lacustrine and peat sediment core from an ancient lake terrace 160 m above present Tangra Yumco. Palynological results were evaluated using the indicator species approach, based on vegetation ecology. Stratigraphy and ostracod assemblages provided information about lake-level changes and water properties. Charcoal particles and dung-indicating fungal spores gave further information on human activities.

With this approach, we addressed the following questions:

(1) Do Holocene vegetation dynamics at Tangra Yumco follow the pattern known from western Tibet, i.e. persistence of *Artemisia* steppes despite dramatic lake-level changes? If this is confirmed, (2) what are the reasons for the apparent vegetational stability? Is

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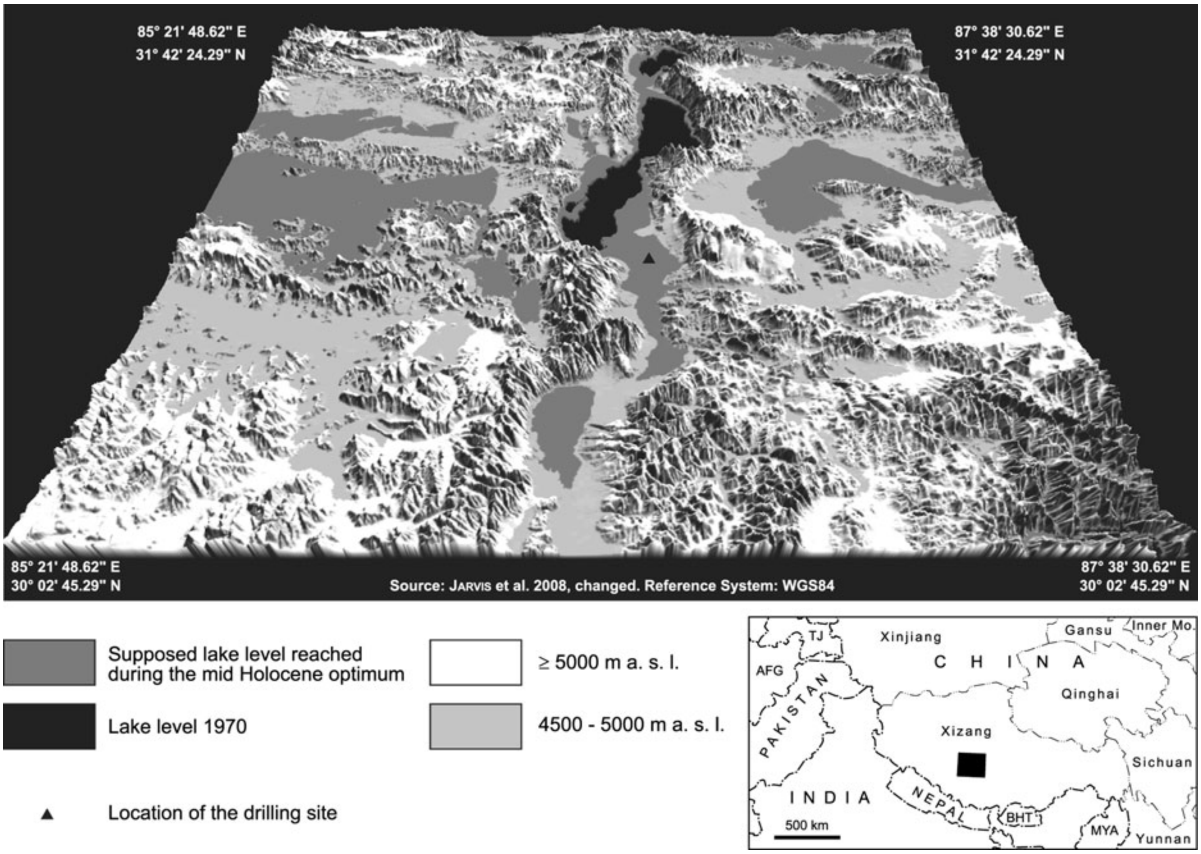

Source: Jarvis et al. 2008, changed. Reference System: WGS84

Fig. 1 The Tangra Yumco Basin and supposed Holocene lake high-stands. Lake level of Tangra Yumco in 1970 (*black*, 4,530 m a.s.l.) after Institute of Geography Beijing (1990), and high stand at 4,720 m a.s.l. Highest lake-marl terraces visible on satellite images (Google Earth) were depicted for former adjacent lakes. Cartography by C. Enderle, Marburg

it, counter-intuitively, a consequence of prolonged environmental instability, including large lake-level fluctuations?

Study site

The interior basin of Tangra Yumco belongs to a south–north-extending graben on the northern slope of the Transhimalaya (29°55′–31°40′N). Tangra Yumco Lake (4,540 m a.s.l.) covers an area of 818 km^2 (T. Wiatr pers. commun. 2011). The western mountain range has glaciated massifs with peaks up to 6,132 m a.s.l. (Institute of Geography Beijing 1990). The upper mountain slopes are covered with frost debris, the lower slopes pass into loess-covered pediments with open deflation pavements (Miehe et al. 2011b). The highest ancient lake terraces (4,900–4,825 m a.s.l.) have mid-Pleistocene ages, whereas well-preserved Holocene lake-marl terraces are found up to 4,740 m a.s.l. (Kong et al. 2011; Long et al. 2011).

The Tangra Yumco region belongs to the Indian Summer Monsoon domain. The mean annual precipitation extrapolated from the nearest meteorological stations, is 200–250 mm (Institute of Geography Beijing 1990). Convective summer rainfall prevails. The extrapolated mean January and July temperatures are −11.4° and 10.9 °C (J. Böhner, pers. commun. 2010).

Plant cover in the basin can be assigned to the following Tibetan highland biomes:

1. Above 5,400 m a.s.l., gelifluction-adapted cushion communities attain coverage of 30 %. Small grass tufts and rosette plants (Brassicaceae, *Saussurea, Soroseris, Gentiana*) grow together with mat-forming Cyperaceae (*Kobresia pygmaea* C.B. Clarke) and cushion plants.

2. Between 5,400 and 4,900 m a.s.l., mosaics of Cyperaceae mats and alpine steppe prevail. These are the altitudinal equivalents of an ecotone between the humid *Kobresia pygmaea* mats (commonly ‘meadows’) of the eastern highlands and the arid alpine steppe of the west (Miehe et al. 2011b). The plant cover ranges between 30 and 50 % (Electronic Supplementary Material S1).
3. The alpine steppes surrounding the core locality are Central Asian short-grass steppes with cushions and *Artemisia* dwarf-shrubs. The mean plant cover is 24 % (Electronic Supplementary Material S2). Cyperaceae constitute 14 % of the total vegetation cover. Communities in the Tangra Yumco area differ from typical *Stipa purpurea* grasslands (Miehe et al. 2011b) in possessing a conspicuous proportion of pasture plants typical of juniper-forest replacement communities at their upper limit. Reports of relict junipers (Miehe et al. 2008) require confirmation.
4. Cyperaceae swamps are strictly limited to water-surplus sites (Electronic Supplementary Material S3). Little-disturbed sites have durable hummocks of *Kobresia schoenoides* (C.A. Mey.) Steud., covering more than 75 %. With increasing grazing influence, matted Cyperaceae and rosette plants (*Thalictrum alpinum* L., *Parnassia, Pedicularis, Primula* spp. and Gentianaceae) replace *Kobresia schoenoides.* Widespread salt-indicator plants are present (*Glaux, Triglochin* spp.).

Despite the remoteness of the Tangra Yumco Basin, numerous undated stone tools, a megalith assemblage, the density of ruined buildings, abandoned fields and irrigation channels provide evidence for former local economies. The Tangra Yumco area was a centre of the ancient Zhang Zhung kingdom (Bellezza 2008). Today, irrigated cultivation of barley, peas and turnips is very limited. Pastoralism is the main occupation of the sparse population.

Materials and methods

Core location

A 360-cm sediment core was recovered by Frank Schlütz and La Duo in 2003, using a Nordmeyer Rammkernsonde. The core was taken from an extensive Cyperaceae swamp with numerous small ponds, on the 4,700-m a.s.l. lake terrace near the Targo Xian settlement (30°46′N/86°40′E, Electronic Supplementary Material S4). The site is 160 m above and 16 km east of the present southeastern shoreline of Tangra Yumco. The wetland receives hydrologic input from a stream that originates 0.5 km away. The upslope margin of the swamp is about 130 m from and 5 m above the coring site. Ancient shorelines are discernible on satellite images at altitudinal intervals of 1–2 m, up to 4,742 m a.s.l., to a maximum distance of ~1 km from the coring site.

Stratigraphic analyses and radiocarbon dating

Cores were opened, photographed and described lithologically. Carbonate presence was checked with HCl. Ten radiocarbon (AMS) ages were determined from both bulk and pollen samples (Electronic Supplementary Material S5). Ages were calibrated with the software Calib® (Version 6.0) using the INTCAL 09 dataset (Stuiver and Reimer 1993; Reimer et al. 2009). Calibrated ages are given as median ages with the respective 2σ ranges (Electronic Supplementary Material S5).

Ostracod analysis

Samples for ostracod analysis were taken wherever a change in core lithology was observed. In sections where no change was seen over a considerable depth, several levels from the unit were sampled to provide nearly equal sampling intervals. This approach resulted in 86 subsamples. Prior to extraction of the ostracod valves, samples were processed with 3 % H_2O_2 for 24 h, washed through 1-mm, 200-µm, 125-µm and 63-µm sieves and dried at 50 °C. Ostracods were counted in the >200-µm size fraction. Ostracods were picked from dry residues using a fine paint brush, until at least 300 valves, if present, were collected. Counting of splits (partial samples) served as a basis for determining total ostracod numbers and calculating relative abundances of taxa. Additionally, we determined the number of carapaces (both valves articulated), adult/juvenile ratios, broken valves and the percentage of black- or grey-coated and abraded valves, which serve as an indicator for post-mortem transport and sedimentation conditions (De Deckker and Forester 1988). The material is stored in the collection of Claudia Wrozyna at the Institute of Earth

Sciences, University of Graz, Austria. Diversity was determined using the Shannon–Wiener diversity index (Spellerberg and Fedor 2003) and evenness was calculated according to DeJong (1975).

Pollen analysis

Forty subsamples of 1 cm^3 each were used for pollen analysis. Sampling intervals were generally 10 cm, smaller (to 1 cm) in peat and larger (to 50 cm) in pollen-poor, silty sediment. Additionally, a turf sod of the present Cyperaceae-covered bog surface at the approximate coring site was analyzed in 2-cm intervals. This replicate of the top 25 cm of the core was analyzed because the top 15 cm of the core was compressed and sedge-free. Samples were prepared according to standard protocols using hydrofluoric acid (Moore et al. 1999). A known number of *Lycopodium* spores was added to enable calculation of concentrations of palynomorphs (Stockmarr 1971). Percentages of all taxa were calculated using a terrestrial pollen sum that excluded aquatic and wetland taxa such as Cyperaceae. Zonation of the pollen diagram was achieved using the optimal sum-of-squares partitioning method (Birks and Gordon 1985), as implemented in the program ZONE (Lotter and Juggins 1991), and the broken-stick model (Bennett 1996). Non-pollen palynomorphs included coprophilous fungi (Van Geel and Aptroot 2006).

Modern vegetation

The modern vegetation in the study area was described from analysis of 10 × 10 m sampling plots according to a modified Zürich–Montpellier approach (Mueller-Dombois and Ellenberg 1974), recording the absolute percentage cover of all species. Plant names mainly follow Wu (1983–1986) and Wu and Raven (1994–). Full records are given in Electronic Supplementary Materials S1–S3. Surface pollen assemblages of different biomes in central Tibet (Shen 2003; Herzschuh et al. 2009a) were further used to assess the palaeo-vegetation.

The indicator species approach for interpreting palynomorph spectra

Two approaches to infer environmental changes from pollen records have been applied in Tibet. In the first method, calibrations of palaeo-vegetation, using modern pollen spectra allocated to biomes (Chen et al. 2010), have been applied to local studies and compilations of inferred regional biome shifts (Herzschuh et al. 2009b; Herzschuh and Birks 2010). Human impact, however, is not considered in this approach. In the second approach, the ‘indicator species’ concept (Behre 1981; Gaillard 2007), derived from Ellenberg (1974), is used. This approach aims to identify species groups that are unequivocally linked with either environmental change or human influence. It requires higher-resolution pollen identification than usually employed in studies from the Tibetan highlands. We refrained from placing all human-indicator taxa into one group of synanthropic plants (Frenzel and Adamczyk 2004), as it masks the proportion of the constituent taxa in different pollen zones and makes it impossible to distinguish between their grazing- or climatically-induced presence. The Electronic Supplementary Material S6 compiles recorded pollen taxa, corresponding local plant species, indicator values and pollen dispersal.

Charcoal analysis

Charred particles exceeding 10 µm were counted in each pollen sample. Charcoal values were calculated in relation to the pollen sum (100 % by definition), so values can exceed 100 %. Values of 100–200 % and above likely indicate local fires in pollen diagrams from southern Tibet, as also suggested by charcoal fragments >125 µm found in parallel analyses of macro-remains (La Duo 2008). Local fires indicate human presence in the catchment, as none of the Tibetan highland biomes is naturally fire-shaped (Miehe et al. 2009).

Results

Lithology

The core base (unit I, 360–347 cm, Fig. 2) consists of black-brown peat. The heterogeneous unit II (347–332 cm) has humic, brown-grey silt and clay with sandy concretions, snail fragments and Cyperaceae rhizomes. Unit III (332–305 cm) forms a transition from brown humic silt to grey clayey lake sediment. The upper 7 cm consist of fine humic sand, with roots and rhizomes near the top. Unit IV (305–222 cm) includes a thin layer of snail debris at the base and rootless grey clay sediments in the lower 10 cm overlain by a thin deposit of yellow–brown sand (294 cm) and a thick homogenous stratum of grey clayey calcareous silt (lake marl consisting of almost pure carbonates). Roots and rhizomes are present between 285 and 277 cm, but become rare above. Above 242 cm there are admixtures of yellow sand with thin roots, forming the transition to unit V (222–180 cm). This unit is dominated by yellowish-brown fine sand, below 212 cm partly mixed with gravel. Between 206 and 190 cm there is a laminated horizon of yellowish, carbonate-free silty sand with few pebbles, alternating with grey calcareous silty sand. Increasing proportions of calcareous silty sand in the upper part of the unit and gravel up to 4 cm diameter form the transition to unit VI (180–140 cm). The lake marl of unit VI is sandier than that of unit IV and contains rare plant remains and numerous snail fragments. The transition to unit VII contains gravel up to 4 cm diameter. Unit VII (140–80 cm) includes an increasingly humic layer (140–135 cm) with Cyperaceae remains and fine to coarse sand, gravel and stones to 2 cm. Most of unit VII consists of heterogeneous sandy Cyperaceae peat that lacks stones, but between 101 and 97 cm there is a humic sand and gravel layer. Unit VIII consists of Cyperaceae peat. A zone of purest peat occurs between 69 and 55 cm. The upper 15 cm consist of clayey mud with Cyperaceae remains.

Chronology

Radiocarbon dates are shown in Fig. 2 and in Electronic Supplementary Material S5. Pollen of the basal peat (unit I, 354 cm) provided an age of 11.1 cal ka BP. Plant remains in the lower lacustrine sediments (unit IV, 262 cm) yielded an age of 9.6 cal ka BP, whereas bulk sediment samples of humic sand in the unit IV/V transition (233 and 215 cm) had ages between 2.6 and 2.2 cal ka BP. Pollen samples of the upper lake-marl zone (unit V/VI transition: 183 cm and unit VI: 154 cm) showed ages of 5.4 and 4.6 cal ka BP. Ages of pollen and bulk samples from the transition zone to the top peat (unit VII, 134–81 cm) range between 1.3 and 0.9 cal ka BP. Peat from the top section (unit VIII, 47 cm) provided an age of 0.5 cal ka BP.

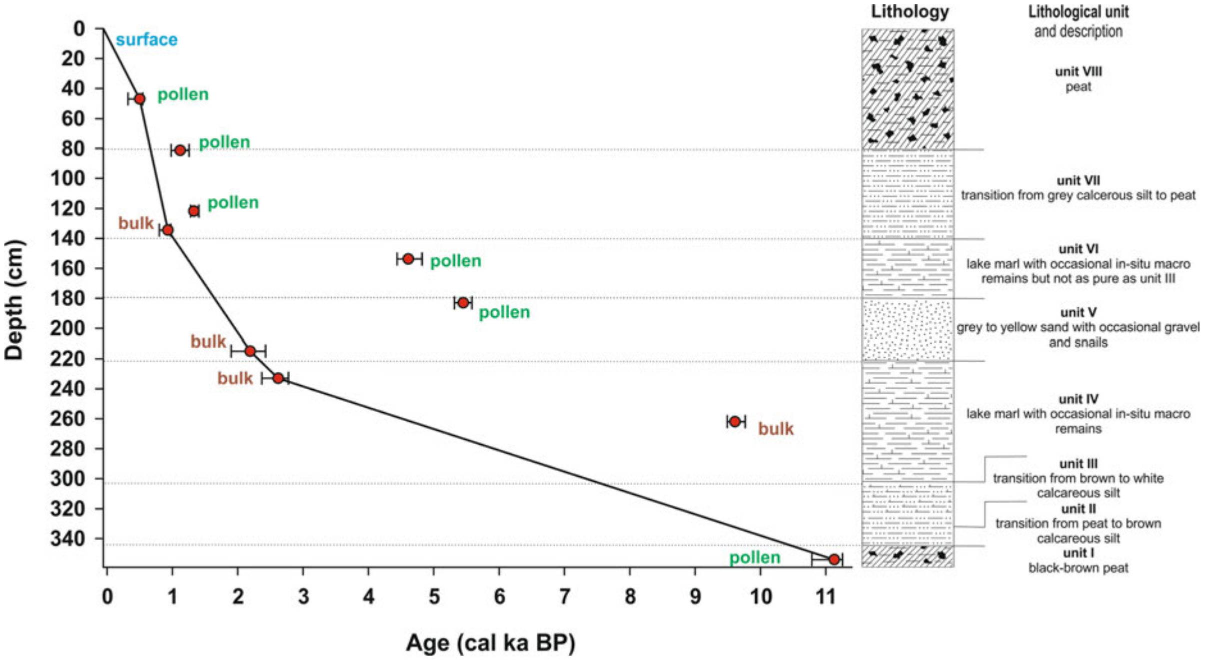

Fig. 2 Lithology and tentative chronology showing median values (*points*) and ranges (*error bars*) of calibrated radiocarbon ages of the Targo Xian sediment record (Electronic Supplementary Material S5). The top of the sequence represents the year of coring. The age–depth relation (*solid line*) is established using youngest ages for samples from similar stratigraphic levels because older ages are regarded as biased by reservoir effects

Ostracods

Ostracods were present between 339 and 142 cm core depth, with abundances between 0.5 and >10,000 valves g^{-1} (Fig. 3). The highly variable abundance shows a broad maximum between 306 and 219 cm and a decrease towards the core top. Eight ostracod species were recorded. *Leucocytherella sinensis* Huang represents more than 90 % of the total valves. ?*Leucocythere dorsotuberosa* Huang and *Ilyocypris* cf. *mongolica* Martens occur continuously above 300 cm, the former with maximum abundances in the lower part (300–278 cm), the latter with increasing amounts in the upper part, above 190 cm. The rare taxa (<2 %) *Fabaeformiscandona gyirongensis* Huang, *Eucypris gyirongensis* Yang, *Candona xizangensis* Huang, *Limnocythere inopinata* Baird and *Candona* sp. reach their highest abundance between 300 and 225 cm. Within this zone there is also a broad maximum of juvenile candonids. In general, ostracod diversity and evenness are low (mean E: 0.5).

Carapaces and broken valves are frequent below 300 cm and above 240 cm. The number of carapaces displays a weak negative correlation with species abundance (r: −0.43). Black- or grey-coated valves are rare except for two peaks (242–229 and 190–180 cm). Overall, adult/juvenile ratios are relatively low (mean 0.5) because of the high number of juvenile *L. sinensis* valves.

Palynomorphs and charcoal

Palynological analysis revealed 132 palynomorphs (Fig. 4). Pollen of Cyperaceae and *Artemisia* are dominant in major sections of the profile. *Botryococcus* dominates the remnants of aquatic microorganisms, whereas *Glomus* dominates those of terrestrial ones, reaching a maximum that is nine times the pollen sum. The amount of charred particles exceeding 10 µm ranges between 0 and 11,000 % of the pollen sum.

Figure 4 shows five pollen zones (PZ). Below, numbers of indicator species groups are given in brackets.

PZ-1 (360–347 cm) has highly variable palynomorph spectra, rich in aquatic (2) as well in terrestrial taxa (3–9). Among the latter, Cyperaceae (3), *Artemisia* (6) and Gramineae (7) are dominant.

PZ-2 (347–235 cm) shows a distinct succession of dominant water plants (2), combined with a stepwise reduction in terrestrial plant taxa. Cyperaceae (3) is almost absent, whereas *Artemisia* and Poaceae dominate in sub-zone PZ-2A (347–310 cm). *Botryococcus* (2) dominates the aquatic palynomorphs in sub-zone

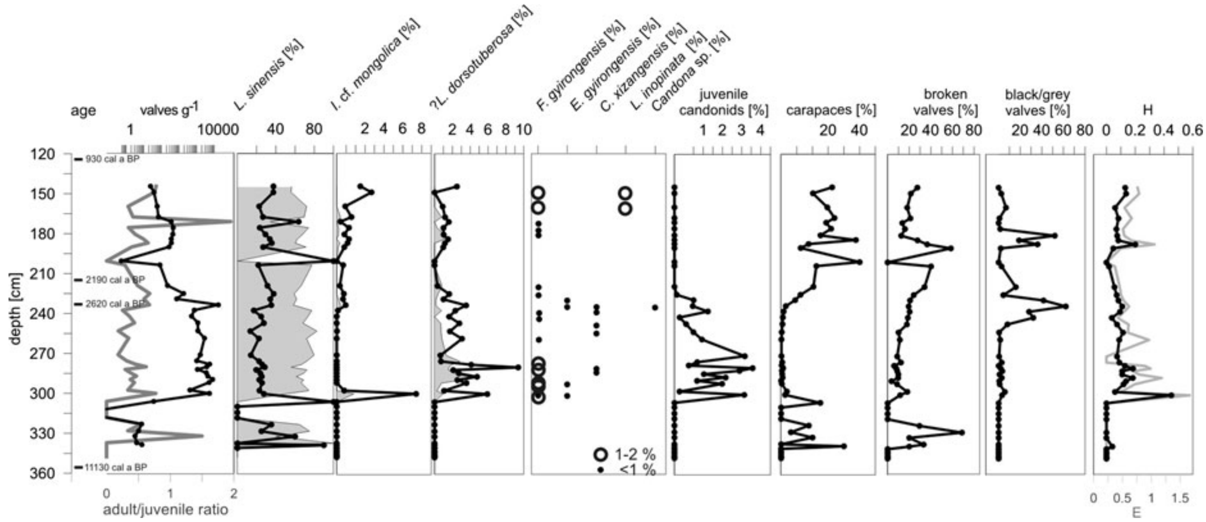

Fig. 3 Lacustrine ostracod valves from Targo Xian/Tangra Yumco Basin: abundance, species percentage, Shannon–Wiener diversity (H) and evenness (E). *Grey areas* refer to juvenile percentages of the species. Apart from the cosmopolitan *Limnocythere inopinata* Baird, all species are described from the Tibetan Plateau and seem to be endemic to regions of central Asia and Tibet. All species except one (*Candona* sp.) are known from recent and Pleistocene/Holocene sediments of Lake Nam Co (Wrozyna et al. 2009, 2010, 2012). No ostracod valves were found below 339 cm or above 142 cm core depth

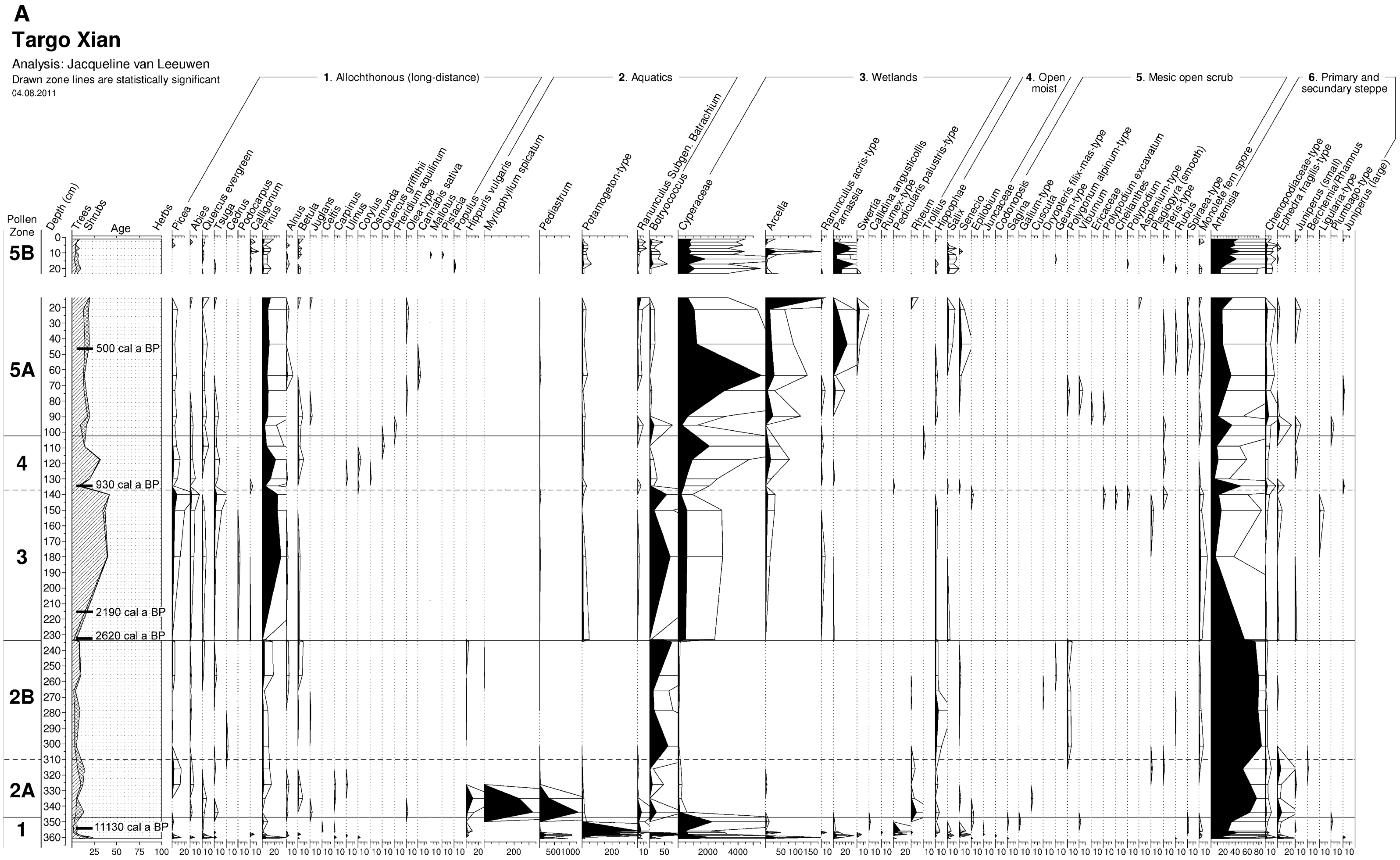

Fig. 4 Pollen percentage diagram of the Targo Xian record. Percentage data are based on a pollen sum without Cyperaceae. For *Artemisia* and Cyperaceae proportions, with inclusion of Cyperaceae in the pollen sum, see Electronic Supplementary Material S10. *White areas* represent ×10 exaggeration. Exotic *Lycopodium* spores were added for determination of concentrations (see text). Palynomorphs are grouped according to habitat/ecological indicator value regardless of life form; for details see Electronic Supplementary Material S6. *Solid lines* separating pollen zones are statistically significant. Palynomorph concentrations are given in Electronic Supplementary Material S7. The most reliable ages are indicated and come from Fig. 2

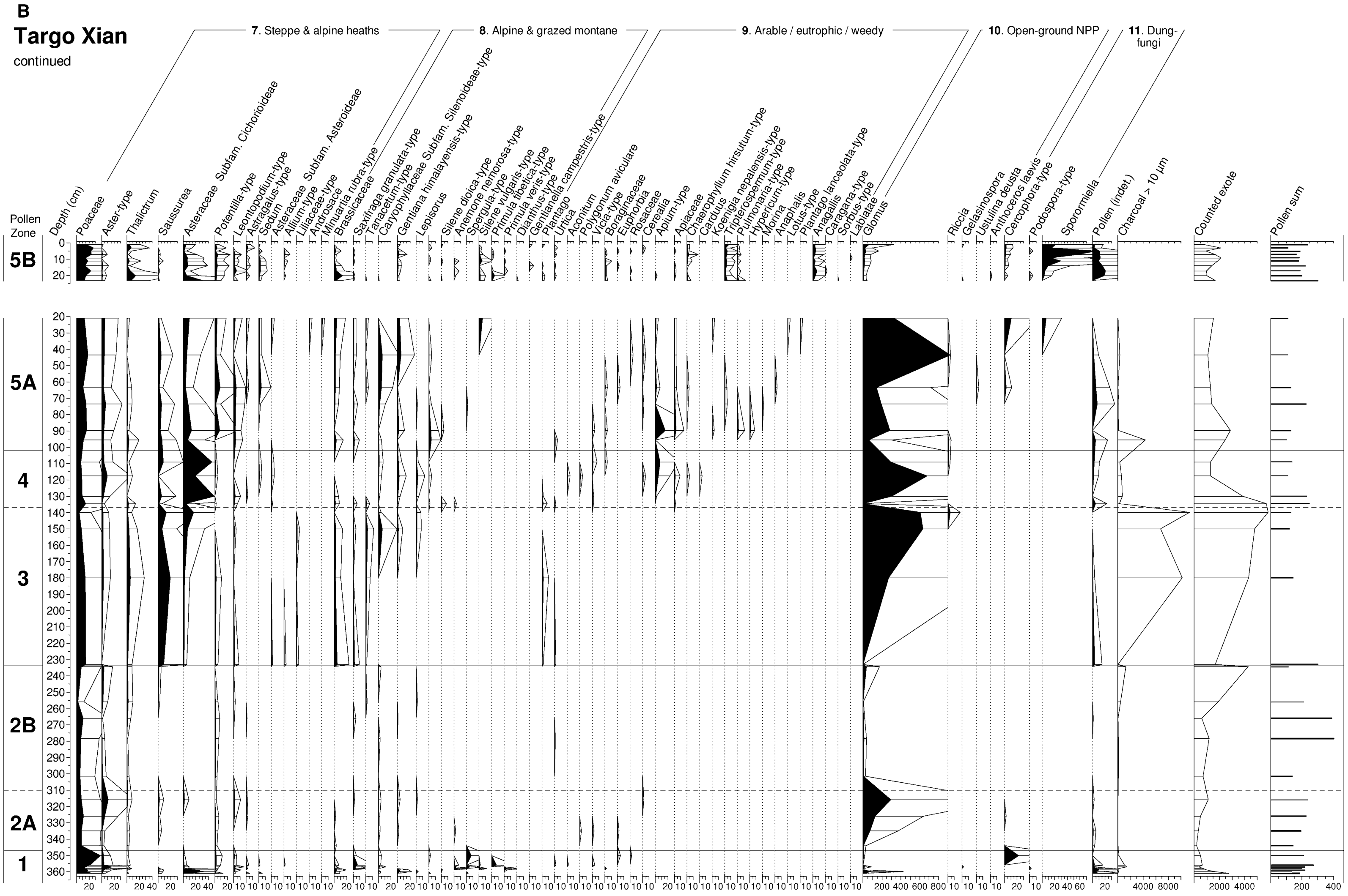

Fig. 4 continued

PZ-2B (310–235 cm). The number and share of taxa are strongly reduced, which also applies to concentrations (Electronic Supplementary Material S7). This impoverishment cannot be explained by pollen preservation conditions, which were good.

PZ-3 (235–135 cm) has continued dominance of *Botryococcus*, whereas Cyperaceae (3), Poaceae (7) and various herbs (7, 8) increase at the expense of *Artemisia* (6). *PZ-3* is further characterized by rising values of *Glomus* (10) and charcoal, and by the appearance of *Plantago* (9).

Cyperaceae and *Artemisia* are abundant in zones *PZ-4* (135–102 cm) and *PZ-5* (above 102 cm) and herbaceous plant taxa and *Glomus* reach relatively high values. Herb pollen and *Glomus* values (10) are mostly higher than in PZ-1, at the expense of Poaceae (7). PZ-4 is dominated by various Asteraceae (7); in contrast, PZ-5 has more Cyperaceae (3), *Artemisia* (6) and Poaceae (7), and new weedy taxa (9) appear and dung-colonizing fungi (11) become prominent in the upper part. Sub-zone PZ-5B replicates the upper 25 cm of the core, based on more peaty substrate and higher time resolution. Percentages and concentrations (Electronic Supplementary Material S7) both show higher values for most palynomorphs. *Glomus* (10), *Cercophora*-type (11) and *Sporormiella* (11) show strong increases within the zone, *Artemisia* (6) and Poaceae (7) to a lesser extent. Most herbs have constant or decreasing values.

Discussion

The lithology, ostracods and palynomorphs in a Holocene sediment core from the Targo Xian site, 160 m above the present level of Tangra Yumco, display partly congruent and partly incongruent zones. Out of the seven zones, four display congruence among all investigated variables, more or less. The basal and top zones consist of pure Cyperaceae peat, with a maximum diversity of terrestrial pollen taxa and absence of ostracods. The two central zones consist of lake marl, the lower being less sandy, richer in ostracods and poorer in palynomorphs than the upper. These four zones are linked by transitional, sandier horizons. This sequence indicates large environmental changes at the coring site since the onset of the Holocene.

Holocene environmental changes recorded at Targo Xian

360–347 cm/ca.11 cal ka BP

Peat at the core base indicates that the level of Tangra Yumco was below the coring site. High Cyperaceae values, in combination with wetland plants, suggest a sedge swamp similar to the present one. The lowermost palynomorph samples are dominated by terrestrial plants (*Artemisia*, Poaceae; Fig. 4) similar to today's pollen assemblage, but higher *Ephedra* values point to conditions drier than present, and the abundance of Asteraceae Subfam. Cichorioideae and Brassicaceae indicate open pioneer vegetation. This may represent the end of the cold–dry period recognized around 11.5 cal ka BP in west and central Tibet, which was associated with the Younger Dryas (Wei and Gasse 1999).

A rapid change to wetter conditions followed shortly afterwards, with more ponds in the bog. *Potamogeton* indicates a maximum water depth of 1.1 m, if conditions of the present Ahung Co (Morrill et al. 2006) are comparable to those at our coring site. The lack of ostracod valves supports the inference of shallow and possibly unstable water levels. Wetter conditions are suggested by decreasing *Ephedra* and Cyperaceae pollen (Cyperaceae vanishing in drowned swamps), the appearance of *Hippophaë* and *Spiraea*-type, and increasing *Salix*, *Artemisia* and many herbs. High charcoal values, with two maxima representing local fires, indicate that vegetation cover and productivity were higher than at present. Today's zonal steppe (Electronic Supplementary Material S2) is too open for the occurrence of fires. This wetter period is probably coeval with the first region-wide Holocene monsoon strengthening recorded after 11 cal ka BP (Wei and Gasse 1999; Doberschütz et al. this issue).

The lack of water plants, dominance of Cyperaceae and presence of *Callidina angusticollis* Murray at 350 cm suggest periodically desiccating swamps and a dry climate pulse.

347–305 cm/after 11 cal ka BP

The transition from peat to lacustrine sediments indicates a renewed rise in the water table. The water depth did not exceed ~0.5 m in the initial phase

(345–330 cm), because both *Myriophyllum* and *Hippuris* grow only in shallow water. In contrast, the only ostracod species found, *L. sinensis*, is known only from large, deep lakes on the southern Tibetan Plateau (Wrozyna et al. 2009). Low ostracod abundance and diversity, however, combined with high abundance of broken valves, indicate reworked older material from rising lake level, rather than an autochthonous assemblage. This interpretation supports the view that the flooding was a consequence of the rising level of Tangra Yumco Lake, rather than an expanding local pond. Higher precipitation and warmth is indicated by an increase in *Artemisia* at the expense of Poaceae. Peaks of evergreen oaks and *Tsuga*, coincident with a minimum of *Pinus*, point to a generally humid period. This phase probably coincides with the first monsoon maximum in west to central Tibet, 10.8/10.5–9.5 cal ka BP (Wei and Gasse 1999; Doberschütz et al. this issue).

The younger part of this period (323–305 cm) is characterized by pronounced instability and erosion. A drop in lake level is inferred from the retreat of all water plants and lack of ostracods above 320 cm. Humic sand layers between 313 and 305 cm point to terrestrial influx associated with strong slope wash or shoreline erosion. Lake level may have oscillated around the coring site, but there was no new swamp formation. We infer cool–dry and unstable conditions from the decrease in *Artemisia* pollen to a minimum at 315 cm, combined with a pollen assemblage of pioneer plants, including many Asteraceae of group 7 (Fig. 4), reappearance of many alpine taxa already present at the core base and another peak in Chenopodiaceae, *Ephedra* and *Glomus*. Similar indications of strong erosion combined with low water levels were found by Mischke et al. (2008) in northeast Tibet and explained by the 8.2 ka BP event, noticed across the Tibetan Plateau between 7.9 and 7.4 cal ka BP (Mischke and Zhang 2010). At west Tibetan Bangong Co, a dry period occurred between 9.6 and 8.0 cal ka BP (Gasse et al. 1996). The record of *Berchemia/Rhamnus* indicates minimal summer temperatures at Targo Xian around that time. Today, both genera have their nearest occurrences in the Tibetan Himalaya. The highest-elevation species, *Berchemia edgeworthii* Lawson, found at a maximum of 4,500 m a.s.l. (Wu 1983–1986), suggests that temperatures were at least 1.1 °C higher than at present, given a lapse rate of 0.55 °C per 100 m.

305–222 cm/before 2.2 cal ka BP

Lake marl, maximum ostracod diversity and autochthonous sedimentation indicated by a high proportion of juvenile ostracods, low adult/juvenile valve ratios and low numbers of carapaces and broken valves (Fig. 3) suggest stable lacustrine conditions with low-energy deposition. The lake was consistently several metres deeper at the coring site during the earlier part of this period (305–270 cm). Relatively high abundances of the ostracods *L. dorsotuberosa* and *F. gyirongensis* suggest a maximum water depth of 20–30 m, because these taxa prefer water depths near and below the thermocline (Frenzel et al. 2010). A maximum Holocene lake level is supported by the lack of rooted water plants, minima in Cyperaceae and the low number and concentration of palynomorph taxa, despite good pollen preservation (Fig. 4, Electronic Supplementary Material S7). Maximum values of *Hippophaë* pollen indicate widespread, high groundwater tables. Highest proportions of *Artemisia* and the appearance and continuous presence of *Polygonum alpinum*-type (*Polygonum tortuosum* D. Don), combined with minimum proportions of *Ephedra* and Poaceae, provide evidence for a mesic shrub-steppe. Local arboreal pollen is, however, completely missing. Also, allochthonous tree pollen shows minimum values. The low tree pollen values are surprising in light of the inferred favourable growing conditions. The section from 305 to 270 cm probably represents the mid-Holocene moisture optimum, recognized for west Tibet at 8.3–7.2 cal ka BP (Gasse et al. 1996), but much later for central Tibet, at 6.6–4.8 cal ka BP (Doberschütz et al. this issue).

Above 270 cm, the lake became shallower, suggested by the reappearance of rooted water plants and lower abundances of *L. dorsotuberosa* and *F. gyirongensis*. Allochthonous, partly humified sediments and a gradual increase in ostracod carapaces and broken valves after 2.6 cal ka BP (234 cm), indicate falling lake level. This is corroborated by a rise in wetland and terrestrial palynomorph abundances. Drier climate conditions are indicated by decreases in *Artemisia* and *Hippophaë*. The humic sand influx after 2.6 cal ka BP may mark a drought, starting around 2.5 cal ka BP at Bangong Co (Wei and Gasse 1999). Shen et al. (2008) postulated a phase of monsoon weakening in central Tibet between 3 and 2 cal ka BP.

222–180 cm/~2.2–1.8 cal ka BP

This zone represents a period of instability. Highest proportions of gravel, sand and humus point to pronounced sediment movement at the coring site, probably as a consequence of shoreline erosion. Decreasing ostracod abundance, higher amounts of carapaces and broken valves and lower ostracod diversity, combined with rising proportions of *Potamogeton*, point to lower lake levels than in the underlying zone, and fluctuating depositional conditions. This is also inferred from exclusively adult valves of *L. sinensis* between 202 and 199 cm, probably representing reworked material. The maximum proportion of black and grey ostracod valves between 190 and 180 cm supports increased re-mobilization of older material under shallow-water conditions. The proximity of the shoreline is also indicated by the augmentation of terrestrial plant pollen. Percentages of *Glomus* increase, and charcoal and *Plantago* reach first maxima at 180 cm, indicating the presence of humans. A lack of *Ephedra* pollen and maxima of herbaceous pioneers suggest that the *Artemisia* minimum was caused by human disturbance rather than drought. Between 2.8 and 1.3 cal ka BP, dry periods occurred in many areas of Tibet (Morrill et al. 2003; Shen et al. 2008; Kasper et al. 2012; Doberschütz et al. this issue).

180–140 cm/~1.8–1.0 cal ka BP

Lake marl, ostracods and a *Botryococcus* maximum indicate moister conditions again and another lake phase. This lake was unstable and shallower than the earlier one (305–222 cm), indicated by increased proportions of *Ilyocypris* cf. *mongolica* (Wrozyna et al. 2009). Valves of *Ilyocypris* spp. were abundant in recent samples from a tributary to Tangra Yumco (P. Frenzel pers. commun. 2011), thus indicating its preference for or tolerance of flowing waters and suggesting that an inflow existed close to Targo Xian. Allochthonous or relocated older material is further indicated at 171 cm by the predominance of adult *L. sinensis*. Continued erosion is inferred from *Glomus* peaks between 150 and 140 cm. Coincidence with high charcoal concentrations suggest anthropogenic disturbance.

140–80 cm/~1.0-0.9 cal ka BP

Sandy peat, alternating with sand layers, decreasing *Botryococcus* proportions, absence of ostracods, together with increasing Cyperaceae and *Arcella* and appearance of other terrestrial plants, mark the transition from lacustrine to swamp conditions. Approximately constant ages between 134 and 47 cm suggest rapid sedimentation or reworking of sediments, both of which would be supported by alternation between sandier and more peaty layers (Fig. 2). Varying Cyperaceae and *Botryococcus* values further show that the lake level oscillated near the core site. Pollen assemblages dominated by herbs, at the expense of *Artemisia* and Poaceae, indicate strongly grazed pioneer communities. The recession of the lake is synchronous with drought pulses at Nam Co (1.2–0.3 cal ka BP, Kasper et al. 2012; 0.9–0.5 cal ka BP, Wrozyna et al. 2012) and Co Ngoin (0.7–0.3 cal ka BP, Shen et al. 2008).

80–0 cm/~0.9 cal ka BP to present

Peat with sand and prominence of sedges represent the formation of the modern Cyperaceae bog. Peat and a Cyperaceae maximum at 65 cm indicate optimum development of the bog. A major disturbance is indicated at 42 cm (after ~0.5 cal ka BP) by the highest proportions of *Glomus* and a sudden decrease in Cyperaceae pollen. *Salix*, *Rubus* and *Spiraea*-type pollen indicate humid conditions if these plants grew outside the swamp. Wrozyna et al. (2010) and Kasper et al. (2012) inferred a rising water table at Nam Co after 0.3 cal ka BP. High *Sporormiella* abundance during recent centuries indicates the strongest grazing influence within the whole study period. The section from 80 to 0 cm is further characterized by the absence of fire probably a consequence of lack of combustible biomass. Differences between the compressed upper part of the main core (uppermost PZ-5A) and the turf sod of the upper 25 cm (PZ-5B), with respect to substrate and pollen assemblages, are attributed to differences in local micro-habitats in relation to livestock trampling.

The final peat development is explained by the regional desiccation phase of the last millennium. Tibet-wide cold events during 1.7–1.3 and 0.6–0.1 (LIA) cal ka BP (Mischke and Zhang 2010) are not clearly evident in our pollen record (Electronic

Supplementary Material S8). The major difficulty is that plants that spread under heavy grazing are in wetlands represented by alpine pollen taxa that suggest climate cooling. This phenomenon strongly limits the use of modern pollen assemblages to interpret palaeovegetation, if the inferred biome shifts are exclusively ascribed to climate change (Herzschuh 2006; Shen et al. 2008; Herzschuh et al. 2009b).

Holocene high stands of Tangra Yumco inferred from the Targo Xian core

The chronology in Fig. 2 is based on few reliable dates (Electronic Supplementary Material S5). Ages of the carbonate-rich lacustrine sediments are probably influenced by reservoir effects, as in all previously recovered sediments from Tibetan Plateau lakes (Hou et al. 2012; Kasper et al. 2012). Quantification of the reservoir effect of the Targo Xian record for the lake phases was not possible because terrestrial plant remains were lacking and charred particles were too small and rare for radiocarbon dating. Because ages of lacustrine deposits dominated by aquatic palynomorphs are regarded as more strongly affected by reservoir effects than those of bulk samples from humic sand and pollen from peat, age data from carbonatic lake marl were excluded from our age–depth relation. Sediments from the lacustrine sediment–peat transition, may however, be biased by reservoir effects as well. Thus, our accepted dating results represent maximum ages, of which the youngest are considered to be less affected by reservoir effects. If we rely on the resulting age–depth relation (Fig. 2), the reservoir effect around 260 cm (within our inferred deep-water phase) would amount to 5.1 ka and between 154 and 183 cm (inferred shallow-water phase) to 3.4–3.7 ka. Our lithological unit IV (305–222 cm) resembles in thickness and appearance the numerous lake-marl banks exposed in canyons all around Tangra Yumco. Comparison of ^{14}C and OSL dates on samples from the lower and upper part of a lake-marl bank, 25 m above the present Tangra Yumco surface and 135 m below our Targo Xian site, revealed reservoir effects of 5.4 and 4.3 ka, respectively (Long et al. 2011). These authors inferred a deep-lake phase of Tangra Yumco between 7.6 and 2.3 ka and a wet middle Holocene. The beginning of the latter phase corresponds to our assumed age for the beginning of lake sediment accumulation at Targo Xian. Lake-marl formation, however, terminated at Targo Xian ~1 cal ka BP, in contrast with the inferred age of 2.3 ka BP based on OSL dating at the much lower study site of Long et al. (2011). Therefore, we conclude that only our lithologic unit IV (Fig. 2), with an extrapolated upper limit of 2.3 cal ka BP, is analogous to the lake-marl bank dated by Long et al. (2011), and that the second lake sediment (unit VI), above the intermediate sandy layers, was deposited by a local shallow lake after the recession of Tangra Yumco. The synchronicity of events inferred for Tangra Yumco at Targo Xian with the ages determined by Long et al. (2011) suggests a rapid rise and fall of lake level. On the other hand, chronological data based on cosmogenic nuclides show that the 4,710 m a.s.l. terrace, 10 m above our coring site, was already exposed between 8.7 and 7.4 ka BP (Kong et al. 2011). This early retreat of Tangra Yumco from the higher basin flanks is supported by Mesolithic stone artefacts on the 4,720 m a.s.l. terrace near Sumbuk (Electronic Supplementary Material S9), with estimated ages of 15–6 cal ka BP (Madsen et al. 2006). Thus, the Targo Xian location is probably close to the highest lake stand for Tangra Yumco during the mid-Holocene recorded. The lake at our coring site was $<$ 20 m deep between these exposure dates and the lake recession ~2.3 cal ka BP, as shown by ostracods. This implies that the higher lake-marl terraces (up to ~4,742 m a.s.l.) represent lake high-stands of unknown age that are not identified in our core.

The homogenous lake marl of lithological unit IV in our core and the assumed analogous bank analysed by Long et al. (2011), suggest a stable lake high-stand. Its persistence until ~2.3 cal ka BP, despite falling lake levels indicated by our ostracod data, is similar to inferences from Nam Co (Kasper et al. 2012). A minor wet phase, at most, is inferred from other Tibetan lake records during the interval 3.5–2.5 cal ka BP, followed by severe drought periods (Wei and Gasse 1999; Zhang and Mischke 2009). Multi-proxy analyses from other Tibetan lakes show that the drought periods 5.6–4.9 and 4.4–3.9 cal ka BP were the most severe of the Holocene, with conditions drier than today leading to the desiccation of present lakes in central Tibet (Morrill et al. 2003; Shen et al. 2008). The two mid-Holocene drought periods, however, were locally weakly expressed (Mischke et al. 2008).

Why did *Artemisia* steppes persist during the mid-Holocene moisture optimum?

Despite the limited pollen evidence in our record during lake high-stands, we conclude that steppe-like vegetation persisted in the Tangra Yumco area throughout the post-glacial period, similar to the pattern reported from lakes farther west (Van Campo and Gasse 1993; Van Campo et al. 1996; Wu and Xiao 1996). This inference is in contrast to high lake levels and optimum growing conditions recorded region-wide during the Holocene Optimum (Shen 2003; Zhang and Mischke 2009). Three main hypotheses for the persistence of steppe vegetation are: (1) Climatic humidity was less pronounced than indicated by the lake high-stands, (2) high lake levels reflect the climatic humidity, but the vegetation did not change significantly because of environmental instability, and (3) human impact reinforced persistence of steppe vegetation.

The first half of the Holocene may have been climatically less humid in western Tibet than suggested by low $\delta^{18}O$ values from Bangong Co (Fontes et al. 1996) and by high shorelines. Both may have resulted from higher meltwater influx during early Holocene warming (Fang 1991; Zhang and Mischke 2009; Kong et al. 2011; Kasper et al. 2012). Stronger insolation effects in the west, from a hypothetically drier climate than in the east, may have reinforced snow melt after the LGM. At the same time, winter snowfall may have been more abundant as a consequence of more frequent westerly winds (Zhang and Mischke 2009), which is possibly indicated by our record of *Cedrus* pollen at 300 cm. The initial Holocene humidity peak was strong in western Tibet (Van Campo and Gasse 1993). The highest preserved shoreline of Sumxi Co was formed ~12.8–11 cal ka BP (Kong et al. 2007). Yet the humidity decreased here earlier than in the south and east (Zhang and Mischke 2009). In contrast, a dry early Holocene was geochemically inferred for Zabuye lake, ~250 km W of Tangra Yumco (Wang et al. 2002), for the Yamdrok Basin (south-central Tibet, Zhu et al. 2009), and locally for the northeastern Tibetan Plateau (Mischke et al. 2008). Higher temperatures may have locally outweighed the precipitation increase (Herzschuh 2006; Mischke et al. 2008). Stronger seasonal contrasts may have enhanced this effect (Wei and Gasse 1999; Ni et al. 2010).

Dry climate conditions during the lake high-stand are consistent with the scarcity of Cyperaceae in our archive. Yet *Artemisia* spp. are not only characteristic of dry steppes, but may also dominate in disturbed forest areas. Terrestrial surface pollen spectra compiled by Shen (2003) show the combination of 60–80 % *Artemisia* with 7–10 % Cyperaceae, as in the present study (Electronic Supplementary Material S10), only in moderately dry montane secondary *Artemisia* steppes. Modern *A. santolinifolia* Turcz. pastures, between 3,700 and 4,460 m in the Lhasa area, are the best analogues. Drier shrub steppes have higher Chenopodiaceae and *Ephedra* proportions than the area around Targo Xian, as shown by Holocene Optimum pollen records from west Tibet (Van Campo et al. 1996).

This comparison suggests that the Holocene Optimum vegetation at Targo Xian can be assigned to mesic montane *Artemisia* dwarf-shrublands with annual precipitation totals between 500 and 600 mm (Miehe et al. 2008). This is twice or three times the precipitation estimated for today, resembling inferences for Holocene Optimum precipitation in east-central Tibet (Shen 2003). Inference from the present vegetation around Lhasa also suggests, at minimum, temperatures at Targo Xian 2 °C higher than today. These differences are, however, inferred from strongly anthropogenic modern vegetation in the Lhasa area, having a much more arid-adapted physiognomy than the potential natural vegetation, which is juniper forests and woodlands on sunny slopes, and *Salix–Rhododendron* scrub and even birches on shady slopes (Miehe et al. 2008).

Consequently, the question of forest indicators must be addressed if we reject the hypothesis of a continuously arid first half of the Holocene at Tangra Yumco. Constituents of a mesic treeline ecotone were recorded in the early Holocene at Targo Xian. *Spiraea, Rubus, Anemone, Cuscuta* and *Vicia*-type may have grown in the wetlands, as did *Salix* and *Hippophaë,* but pollen of certainly local forest-forming trees are absent from our archive. Factors other than humidity must have been decisive.

Environmental instability may have caused the persistence of *Artemisia* pioneer vegetation. High lake levels during the first half of the Holocene precluded colonization of the basin flanks by most forest species. *Betula utilis* D. Don has a present upper limit at 4,200 m a.s.l. and needs at least 400 mm precipitation.

Thus, its growth above the high-stand level of Tangra Yumco (~4,720 m a.s.l.) would have required temperatures at least 3 °C higher. The only other tree/shrub pollen taxon of our core that is possibly of local origin is *Juniperus*. Juniper trees grew in the Tangra Yumco basin until at least 300 years ago (Bellezza 2008). Figure 4 shows juniper pollen in all low-lake-level phases, but only in low abundances. The information about juniper pollen transport is contradictory. Surface samples from central Tibet revealed that juniper pollen is scarce and not transported far from its source (Miehe et al. 2006), but samples from the northern and western Tibetan Plateau (Shen 2003; Herzschuh et al. 2009a) show on the order of 1 % pollen at locations at least 150 km from present pollen sources. This range is comparable to the distance between Tangra Yumco and the northern branch of the upper Yarlung Tsangpo River, where the northernmost junipers grow today. Thus, our pollen record provides no clear proof of local Holocene juniper occurrence in the Tangra Yumco basin. Yet the estimated present precipitation at Tangra Yumco is close to the drought limit of juniper (Miehe et al. 2008), so the higher humidity during the Holocene Optimum was certainly sufficient to sustain junipers, even when temperatures were higher. More critical for tree colonization is the thermal upper limit: juniper trees occur up to ~4,900 m a.s.l. (Miehe et al. 2008). Treelines may have been higher during the early Holocene because of stronger summer insolation (Ni et al. 2010), but, depending on cloudiness and wind conditions, the habitat may have remained marginal when more suitable sites were drowned by Tangra Yumco. Colonization by junipers during periods of lake recession of Tangra Yumco may seem more probable, but the exposed calcareous lake sediments are unfavourable for Cupressaceae (Miehe 1991). In contrast, salt-tolerant *Artemisia* spp. are well adapted to this habitat.

The large flooded areas during the region-wide lake high-stand were not only unavailable for forest occupation, but also formed barriers to plant expansion, together with the local mountain ranges (Miehe et al. 2011a, Fig. 2). Frozen lake surfaces do not favour diaspore wind dispersal from southern refuges, because the winters are governed by western to northern wind directions. The diaspores of all potential forest constituents, except *Betula*, are dispersed locally or by animals. Thus, occupation of isolated closed basins by forest plants takes a long time compared with their spread in valley systems or on the plains of the lower north-eastern Tibetan Plateau, where post-glacial reinvasion of juniper forests has been shown (Zhang et al. 2005). Thus the warm–humid early Holocene may not have persisted long enough for forest expansion into the study area.

Strong morphodynamic processes, along with both high precipitation and droughts, may have contributed to the persistence of pioneer vegetation. The climate was extremely unstable during the first lake-level rise in the early Holocene (Fontes et al. 1996; Wang et al. 2002). Variability of the sediments and peaks of *Glomus* indicate erosion at Targo Xian (Figs. 2, 4). Apparently, the vegetation cover was weak when erosion started. Today, the rocky slopes above the exposed lake-marl deposits are almost devoid of soil and support a poor vegetation cover. The pollen spectra of zone PZ-2B, with continuously high proportions of *Artemisia,* in combination with *Aster*-type (*Aster* or *Heteropappus* spp.), *Polygonum alpinum*-type (*Polygonum tortuosum*) and a minimum in Poaceae, may reflect the sparse pioneer or scree vegetation of such areas. Occurrence of this plant community over a wide humidity range, however, limits the palaeoclimatic significance of this specific pollen assemblage in our record.

Effects of climate instability on regional vegetation were reinforced by grazing and fire. Grazing, indicated by pollen of pasture plants and spores of the dung indicator *Cercophora*-type in our early swamp archive (PZ-1, Fig. 4), was temporarily intensive, even before the introduction of livestock, as was the case in the Rutok and Nienang wetlands in east-central Tibet (La Duo 2008). Increasing herbaceous plant cover at the onset of the Holocene probably caused increases in the number of wild herbivores, which in turn may have attracted early hunters. Hunters' fires are a substantial disturbance factor, through the transformation and reduction of the vegetation cover, even if humans were not abundant and only seasonally present (Miehe et al. 2009). The earliest fire event recorded at our site, about 11 cal ka BP, was certainly local (peak in *Gelasinospora*). Contemporaneous peaks of charred particles have been recorded elsewhere in the southern part of the Tibetan highlands (Miehe et al. 2009), the closest near Ngamring, 180 km to the south (11.9 cal ka BP, J. van Leeuwen unpublished data). Larger early Holocene charcoal pieces from various localities in southern Tibet (11.3 cal ka BP, La Duo 2008; 10.7 cal ka BP, Kaiser et al. 2009) prove their local origin. Near Ngamring, charcoal abundances increased strongly along with grazing indicators after 8.3 cal ka BP (J. van Leeuwen unpublished data). Continuous presence of humans during the lake high-stand at Targo Xian cannot, however, be proven on the basis of our data. Assessment of human impact during the inferred lake phases at Targo Xian is hampered by the lack of locally deposited pollen that characterize most pasture plants, in contrast to the modern swamp phase (Electronic Supplementary Material S8). Pollen records from wetlands in south-central Tibet indicate the earliest intensification of grazing at 8.8 or 7.2 cal ka BP (Miehe et al. 2009; Schlütz and Lehmkuhl 2009). According to Miehe et al. (2009), sheep and goats from the Middle East may have reached Tangra Yumco between 8.8 and 8.6 cal ka BP, i.e. before our inferred humidity optimum. Hence, human-induced fires and grazing may have impeded the regeneration of more mesic montane vegetation. *Artemisia* spp. are typical pioneer taxa after fires in forest-climate areas. Fruticose *Artemisia* species spread under grazing influence, because their main competitors, Poaceae, are preferred by grazing animals. These properties make *Artemisia* species ideally suited to cope with various kinds of disturbance, which probably affected the Tangra Yumco Basin since the Younger Dryas.

Conclusions

The Targo Xian record fills in missing data between lake and wetland records farther west and east on the Tibetan Plateau. With the coring locality at 4,700 m a.s.l., 160 m above the present lake level of Tangra Yumco, our study contributes to knowledge of Holocene lake dynamics. Sedimentological, ostracod and palynological analyses support and clarify earlier dating results for lake recessional terraces at Tangra Yumco. According to our data, the site was flooded after 11.1 cal ka BP and remained under water until at least 2.6 cal ka BP. A local lake persisted at the present boggy coring site up to ~1 cal ka BP, indicating that conditions were still wetter than today. The long duration of the deep-lake phase at Tangra Yumco is unknown from Tibetan lakes farther west, but was reported from Nam Co (Kasper et al. 2012). In contrast, Holocene persistence of *Artemisia* steppes around Tangra Yumco resembles the west Tibetan palaeoenvironmental pattern. Comparison of pollen spectra from this study with surface pollen records from *Artemisia* steppes across the Tibetan Plateau enabled us to infer mesic pioneer or scree vegetation with annual precipitation of 500–600 mm, indicative of a climate capable of supporting forest. Such a climate may have supported juniper trees within a narrow, non-flooded subalpine zone. Other montane woody plants did not invade because lake levels were above the plant altitudinal limits or there was insufficient time for reinvasion. Thus, *Artemisia* steppes persisted as a consequence of basin flooding. Strong erosion, a consequence of heavy precipitation and droughts, probably favoured pioneer vegetation on denuded, stony slopes, which are dominated by *Artemisia* also in forest climates. Hunters' fires likely reinforced the persistence of pioneer vegetation under wetter conditions. *Artemisia* spp. are typical pioneers after fire in forest climates, and fruticose species spread under grazing influence. These factors apparently favoured the persistence of *Artemisia* despite the increased humidity indicated by the Holocene lake high-stand. Thus, we conclude that *Artemisia* steppes persisted in the Tangra Yumco basin despite, but also because of Holocene lake-level changes.

Location of the coring site near the upper Holocene shoreline series enabled documentation of flooding and desiccation. On the other hand, repeated morphodynamic disturbance and flooding of the site constrained interpretation of the mid-Holocene core section. Consequently, the exact timing and magnitude of the Holocene moisture optimum remain uncertain, as is the timing of onset of pastoralism in the region. The study nevertheless confirms our initial hypothesis that environmental instability is a major factor causing continued steppe formation in the western part of the Tibetan Plateau. The Tangra Yumco example indicates that high lake levels during warm–humid "optimum" periods may suppress biome shifts, thus contributing to terrestrial vegetation stability within endorheic drainage basins.

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