Terrestrial and aquatic responses to climate change and human impact on the southeastern Tibetan Plateau during the past two centuries

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Abstract

Rapid population growth and economic development have led to increased anthropogenic pressures on the Tibetan Plateau, causing significant land cover changes with potentially severe ecological consequences. To assess whether or not these pressures are also affecting the remote montane-boreal lakes on the SE Tibetan Plateau, fossil pollen and diatom data from two lakes were synthesized. The interplay of aquatic and terrestrial ecosystem response was explored in respect to climate variability and human activity over the past 200 years. Nonmetric multidimensional scaling and Procrustes rotation analysis were undertaken to determine whether pollen and diatom responses in each lake were similar and synchronous. Detrended canonical correspondence analysis was used to develop quantitative estimates of compositional species turnover. Despite instrumental evidence of significant climatic warming on the southeastern Plateau, the pollen and diatom records indicate very stable species composition throughout their profiles and show only very subtle responses to environmental changes over the past 200 years. The compositional species turnover (0.36–0.94 SD) is relatively low in comparison to the species reorganizations known from the periods during the mid- and early-Holocene (0.64–1.61 SD) on the SE Plateau, and also in comparison to turnover rates of sediment records from climate-sensitive regions in the circum arctic. Our results indicate that climatically induced ecological thresholds are not yet crossed, but that human activity has an increasing influence, particularly on the terrestrial ecosystem in our study area. Synergistic processes of post-Little Ice Age warming, 20th century climate warming and extensive reforestations since the 19th century have initiated a change from natural oak-pine forests to seminatural, likely less resilient pine-oak forests. Further warming and anthropogenic disturbances would possibly exceed the ecological threshold of these ecosystems and lead to severe ecological consequences.

Keywords: climate change, compositional species turnover, diatoms, human impact, pollen, Procrustes rotation, Tibetan Plateau

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Introduction

Due to its potential to influence regional and global climate patterns, the Tibetan Plateau has become a focus study area for past and recent climate and ecosystem change. Studies focusing on the past 200 years report a significant mean annual and winter temperature increase (Liu & Chen, 2000; You *et al.*, 2007), permafrost degradation (Wu & Zhang, 2008) and significant glacial retreat (Su & Shi, 2002; Berthier *et al.*, 2007), suggesting that the Tibetan Plateau, and particu-

larly the southeastern Tibetan Plateau, is very sensitive to global warming. In addition, the Plateau has been under pressure from rapid population growth and economic development. The population of China has increased by 2.5 times in the past 50 years (Zhang *et al.*, 2000), whilst the population of the Tibet Autonomous Region has grown from 1.2 to 2.2 million since 1960 (Cui & Graf, 2009). Livestock and meat production on the Tibetan Plateau has increased by up to three times since 1978 (Du *et al.*, 2004) and the demand for timber has resulted in extensive forest clearances since the 1950s (Zhang *et al.*, 2000), particularly on the steep, forested slopes of the southeastern Tibetan Plateau (Studley, 1999). Overgrazing, grassland degradation

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and desertification (Cui & Graf, 2009), decline in natural woodlands, fragmentation of natural habitats and an alarming loss in plant and wildlife species are problems in wide parts of the Plateau (Studley, 1999; Zhang *et al.*, 2000). In summary, the pressures on the Tibetan Plateau are manifold and whether these are caused by climate change or human activity, they result in significant land cover changes with severe and possibly irreversible consequences for ecosystems and the populations they support.

At the same time, the Tibetan Plateau is known for its heterogeneous mountain landscape and therefore highly complex temperature and moisture patterns (An *et al.*, 2000; Niu *et al.*, 2004; You *et al.*, 2010). In addition, anthropo-zoogenic pressures are not evenly spread and lead to regions on the Plateau that are more affected by land cover changes than others (Cui & Graf, 2009). Global climate models are therefore still imprecise in estimating possible future land cover changes on the Tibetan Plateau. This is because they lack the spatial and temporal resolution of climatic, ecosystem and anthropogenic parameters in the topographically challenging landscape of the Tibetan Plateau (Cui & Graf, 2009). Therefore, it is necessary to establish a dense and integrated network of instrumental, palaeoecological and archaeological studies, to help reduce the uncertainties of climate variability and anthropo-zoogenic activities and associated land cover changes in the past and present, and to assess their future impact on ecosystems on the Tibetan Plateau.

To date, only a few and spatially widespread proxy studies have investigated environmental changes on the Tibetan Plateau focusing on the last few centuries (Henderson *et al.*, 2003; Bräuning & Mantwill, 2004; Bräuning, 2006; Liang *et al.*, 2009; Fan *et al.*, 2010; Henderson *et al.*, 2010; Lami *et al.*, 2010; Wrozyna *et al.*, 2010; Yang *et al.*, 2010; Wang *et al.*, 2011; Wischnewski *et al.*, in press) – a time period strongly affected by increasing land use activity. Pollen and diatoms in particular, have not received much attention, despite their potential to reflect vegetation, land use and climate change reliably (Douglas & Smol, 2001; Lotter *et al.*, 2001; Zhao *et al.*, 2008; Schlütz & Lehmkuhl, 2009; Herzschuh *et al.*, 2010).

Herein we present the results of fossil pollen and diatom records from two montane-boreal lakes (LC6 Lake and Wuxu Lake) on the southeastern Tibetan Plateau. Our aim is to evaluate the comparability of aquatic and terrestrial proxy responses with respect to climate variability and human activity, using rigorous statistical methods. We focus on the following questions: (i) Do pollen and diatom records reflect similar and synchronous species shifts in response to environmental changes on the southeastern Tibetan Plateau? (ii) How sensitive are the pollen and diatom assemblages to

environmental change in the past 200 years, and is the magnitude of compositional species turnover comparable to the magnitude of change at other sites on similar and longer time scales? (ii) What are the potential causes of ecosystem change on the southeastern Tibetan Plateau? As such, this article exhibits one of the very few studies in the region that directly compares aquatic and terrestrial proxy response within and between two different lake sites and provides insights to recent environmental change on the southeastern Plateau.

Regional setting and study sites

Wuxu Lake and LC6 Lake (informal name) are located on the southeastern Tibetan Plateau. This part of the Plateau is characterized by the strong and varied relief of the Hengduan Mountains, which stretch across western Sichuan, northwestern Yunnan and the easternmost part of the Tibet Autonomous Region. Altitudes of over 5000 m above sea level (asl) in the northern parts of the southeastern Tibetan Plateau drop to less pronounced features of ca. 1500 m asl towards the southern limit of the Tibetan Plateau (northwestern Yunnan) causing steep environmental gradients in the region. Mean summer temperatures range from 8 to 20 °C, and mean annual precipitation varies from 400 to 1400 mm (Sun, 1999; Yu *et al.*, 2001). The southeastern Tibetan Plateau is affected by two major circulation systems. The mid-latitude westerly circulation brings limited moisture to the region from November to March, whilst the Asian summer monsoon circulation, particularly the Indian monsoon system, is responsible for the majority of precipitation from May to September (Domrös & Peng, 1988; Su & Shi, 2002). This results in abundant rainfall and high temperatures in summer, which contrast to cool and relatively dry winters.

The LC6 Lake is located in the Nyaintêntanglha Mountain range, a western branch of the Hengduan Mountains (Fig. 1). LC6 Lake lies at 4230 m asl. The closest weather station is in Nyingchi at 3000 m asl, 26 km to the south of the lake, which records mean T_{July} 15.6 °C, mean T_{Jan} 0.2 °C and mean P_{ann} 657 mm (85% of P_{ann} falling between May and September). Based on a lapse rate of -0.5 °C/100 m (Böhner, 2006), estimated mean temperatures for July are ca. 9.6 °C and for January ca. -5.5 °C at the LC6 Lake. According to climate station-based calculations from Böhner (2006) annual precipitation is 1450 mm, and the potential evapotranspiration is 800 mm at the lake site. LC6 Lake is a small lake with an area of 0.6 km^2 and is mainly fed by runoff from surrounding, moderately steep sloping mountains which generally peak around 4700 m asl. The lake's outflow cascades into another lake to the southwest. Dense *Rhododendron* shrubs and coniferous forests

(*Picea likiangensis* var. *balfouriana*, *Abies georgii* var. *smithii*, sclerophyllous *Quercus*), and patches of *Kobresia pygmaea* meadow characterize the vegetation in the catchment. A stronger sclerophyllous *Quercus* component is apparent in the lower regions to the LC6 Lake. Lichens are typical epiphytes on surrounding shrubs and trees. No signs of immediate, catchment-scale human impact were observed during fieldwork.

Wuxu Lake is located ca. 680 km to the west of LC6 Lake in an eastern branch of the Hengduan Mountains (Fig. 1). Wuxu Lake lies at 3705 m asl. The closest weather station is Litang at 3948 m asl, 140 km northwest of the lake, which records mean T_{July} 10.5 °C, mean T_{Jan} −6 °C and mean P_{ann} 720 mm (90% falling between May and September). The lake area (0.5 km^2) is comparable with that of LC6 Lake, with a small catchment area comprised of steep sloping mountains to the sides. A tributary feeding from perennial snow covered peaks and glaciers to the northwest, feeds into the lake. Wuxu Lake has one outflow to the southeast. The vegetation in the catchment is characterized by coniferous (*P. likiangensis*, *Abies squamata*) and sclerophyllous trees (*Quercus aquifoliodes*, *Quercus pamosa*), intermixed with *Rhododendron* sp. and *Salix* sp. shrubs. A day trip away from Jiulong Town, Wuxu Lake is a minor tourism destination. Some Tibetan summer tents are pitched along the shorelines and yaks graze in the area during summer. General information about both lakes and their catchment are summarized in Table 1.

Material and methods

Field sampling and dating of lake sediment cores

The LC6 Lake and Wuxu Lake were sampled in summer 2005 and winter 2007, respectively. A 45-cm sediment core was taken from the deepest part (23 m) of LC6 Lake; at Wuxu Lake a 40-cm sediment core was taken at 30 m water depth. Both cores were taken using a UWITEC (Niederreiter Richard, UWITEC, Mondsee, Austria) gravity corer and were sectioned in 0.5 cm intervals directly after coring.

Both cores were dated using ^{210}Pb, ^{226}Ra and ^{137}Cs analyses by direct gamma assay in the Liverpool University Environmental Radioactivity Laboratory. Radiometric dates were calculated using both the constant rate of supply (CRS) and constant initial concentration (CIC) ^{210}Pb dating models (Appleby & Oldfield, 1978). The 1963 depth was determined from the ^{137}Cs stratigraphic record. Discrepancies between the ^{210}Pb models were resolved using the methods described in Appleby (2001). Dates of points below the base of the unsupported ^{210}Pb record were calculated by extrapolation of the ^{210}Pb depth/age curve using a best estimate of the sedimentation rate for this part of the core. For Wuxu Lake, two additional radiocarbon dates from bulk sediments were

Table 1 Selected physical and chemical characteristics of LC6 Lake and Wuxu Lake

	LC6 Lake	Wuxu Lake
Latitude	29.82515	29.15319
Longitude	94.45615	101.406
Elevation	4132 m asl	3705 m asl
Genesis	Glacial lake	Glacial lake
Lake area	2000 × 300 m, 0.6 km^2	1000 × 500 m, 0.5 km^2
Catchment area	ca. 7.2 km^2	ca. 6.5 km^2
Maximum water depth	23.0 m	30.8 m
Secchi depth	6.9 m	5.3 m
Conductivity	0.013 mS cm^{-1}	0.033 mS cm^{-1}
pH	7.00	7.67
Alkalinity	0.4 mmol L^{-1}	0.4 mmol L^{-1}
Inflow	Mountain runoff	Mountain runoff
Outflow	One outlet	One outlet
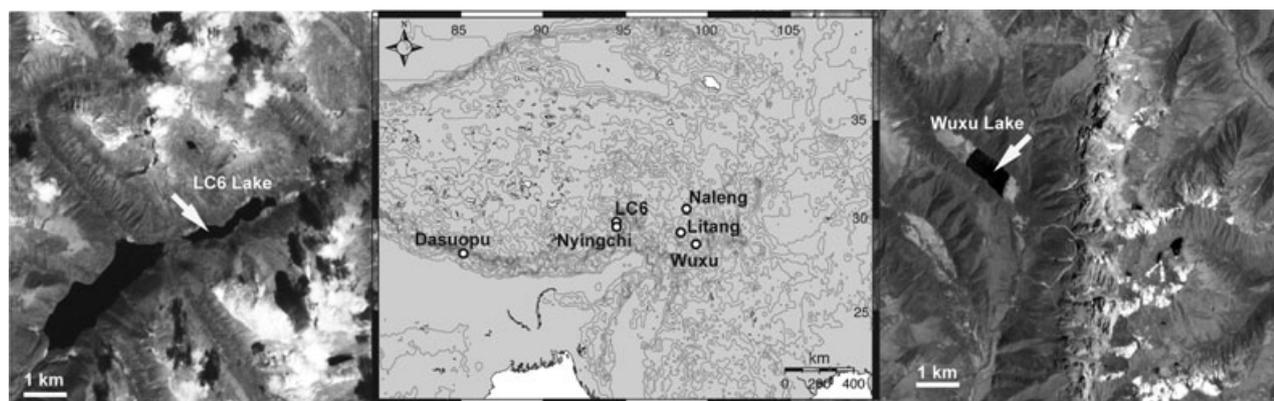
Fig. 1 Location of LC6 Lake and Wuxu Lake and corresponding coring locations. Nyingchi and Litang are the closest climate stations; Dasuopu Glacier holds the closest δ^{18}O record; Lake aleng is a study site used for comparison. Figure adapted from Google Earth, Landsat and the Online Map Creation Tool.

obtained by accelerated mass spectrometry (AMS) at the Leibnitz-Laboratory for Radiocarbon Dating and Isotope Research, Kiel to support the extrapolated age.

Pollen analysis

Sediments for pollen analyses for both lakes were treated using standard laboratory methods (Fægri & Iversen, 1989), including treatment with HCl (10%), KOH (10%) and HF (50%, 2 h boiling), followed by acetolysis, sieving (7 μm) in an ultrasound bath, and mounting in glycerine. Two tablets of *Lycopodium* spores (10 979 spores per tablet) were added to calculate the pollen concentrations. At LC6 Lake, 30 horizons (5–12 year resolution) were analysed and at least 600 (mean 1070) terrestrial pollen were counted for each level. For Wuxu Lake, 26 horizons (7–20 year resolution) were analysed with counts between 360 and 650 (mean 470) terrestrial pollen for each level. Pollen identifications followed relevant literature (Moore *et al.*, 1991; Wang *et al.*, 1997; Beug, 2004; Fujiki *et al.*, 2005).

Diatom analysis

Diatom analysis followed standard procedures using the water bath technique (Renberg, 1990; Battarbee *et al.*, 2001). Slides were mounted using Naphrax®(Brunel Microscopes Ltd, Chippenham, UK). Diatom concentrations were estimated using divinylbenzene microspheres (Battarbee & Kneen, 1982). At LC6 Lake 400–500 valves were counted for 45 horizons (2–11 year resolution). At Wuxu Lake 630–1200 valves were counted for 27 horizons (7–20 year resolution), using phase contrast at ×1000 magnification. Taxonomic identifications primarily followed Krammer & Lange-Bertalot (1986–1991), Lange-Bertalot & Metzeltin (1996), Zhu & Chen (2000) and Camburn & Charles (2000).

Data treatment and statistical analyses

Multivariate analyses were undertaken on pollen and diatom taxa occurring in at least one sample at >1%. The significance of pollen- and diatom-based biostratigraphic zones was calculated by cluster analysis using constrained incremental sum of squares (CONISS) (Grimm, 1991) and the Edwards and Cavalli-Sforza's chord distance as the dissimilarity coefficient.

The ordination technique nonmetric multidimensional scaling (nMDS) was used to explore patterns of variation in the pollen and diatom data sets (Minchin, 1987) (see Supporting Information). The dissimilarity matrix, needed for nMDS, was calculated using the Bray Curtis coefficient (Faith *et al.*, 1987). nMDS was run on a two-dimensional model, being the most parsimonious model compared to higher dimensional models, which did not produce significantly lower stress values (a measure of the variation explained).

Detrended canonical correspondence analysis (DCCA) was applied to estimate the overall compositional species turnover measured in SD units (as beta diversity), which provides an estimate of compositional change along an environmental or temporal gradient (ter Braak & Verdonschot, 1995). To esti-

mate the amount of compositional change of the LC6 Lake and Wuxu Lake records over the last ca. 200 years, ^{210}Pb-derived sample ages were used as the only constraining variable in DCCA. In DCCA, species data were square-root transformed and nonlinear rescaling and detrending by segments was applied. To place the degree of compositional species turnover into wider context, SD units were compared to studies from Smol *et al.* (2005) and Hobbs *et al.* (2010), who established that changes >1 SD units were deemed ecologically substantial.

To assess whether the corresponding pollen and diatom data sets of the LC6 Lake and Wuxu Lake show significant similarities and synchronicity in their variability over time, Procrustes rotation and the associated PROTEST permutation test were implemented (Gower, 1971; Jackson, 1995; Peres-Neto & Jackson, 2001) (see Supporting Information). As Procrustes and PROTEST require ordination (e.g. nMDS) scores of like-for-like data, the four data sets (i) *LC6 diatom*, (ii) *LC6 pollen*, (ii) *Wuxu diatom* and (iv) *Wuxu pollen* had to be harmonized and adapted to a common time scale before applying nMDS. Therefore, all diatom and pollen samples in taxa percentages from the original data sets were interpolated (by simple linear interpolation) and then re-sampled in 5 year intervals from 2000 to 1810 AD.

All nMDS, Procrustes analysis and PROTEST were performed in R (The R Development Core Team 2008) using the vegan package (Oksanen *et al.*, 2008). The PROTEST function in R, which performs a random permutation test, was modified to allow restricted permutations for time series data (Besag & Clifford, 1989). DCCA was implemented using the program CANOCO 4.5 for Windows (ter Braak & Šmilauer, 2002) and the interpolation and re-sampling was carried out in AnalySeries 2.0.4.2. (Paillard *et al.*, 1996).

Results

Dating

A detailed description and interpretation of the LC6 Lake age-depth model is given in Wischnewski *et al.* (in press). Therefore, only major features of the model are outlined here. Results of the radiometric dating are summarized in Fig. 2. Dry mass sedimentation rates at the core site have been relatively uniform during the past 100 years (0.15 cm yr^{-1}), apart from a period of rapid sedimentation rates between 8 and 27 cm core depth. The discrepancy between raw ^{210}Pb dates calculated using the CRS dating model and a well-defined 1963 ^{137}Cs date (Appleby, 2001) suggest that an extreme event, possibly a landslide or sub-surface sediment slump caused these anomalous sedimentation rates, occurring in the late 1940s or early 1950s. This is coincident with the Assam-Tibet earthquake, recorded in August 1950 in North India, just ca. 280 km southeast to the site. Therefore, samples from 8 to 27 cm core depth were excluded from further analyses. Dates
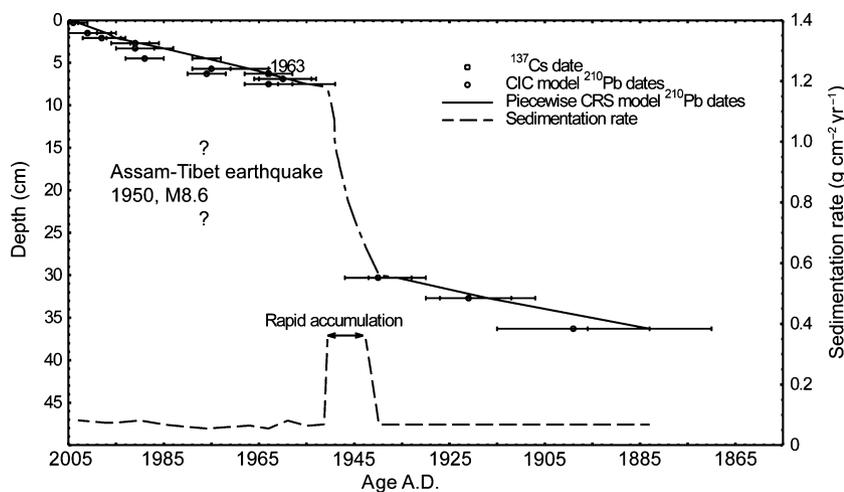
Fig. 2 Radiometric chronology for LC6 Lake showing the 1963 depth determined from the ^{137}Cs, the piecewise constant rate of supply (CRS) model ^{210}Pb dates and sedimentation rates, and the constant initial concentration (CIC) model ^{210}Pb dates calculated for sections above 7.5 cm and below 30 cm.

below the base of the unsupported ^{210}Pb record were extrapolated back to ca. 1800 AD.

The age chronology for Wuxu Lake is outlined in Fig. 3. Unsupported ^{210}Pb activity declines more or less exponentially with depth, suggesting relatively uniform sedimentation rates (0.10 cm yr^{−1}) during the past 100 years. Small irregularities appear between 4 and 6 cm depth, corresponding to the early 1960s, but differences between the CRS model and the alternative CIC model were relatively small. [137]Cs activity has a well-defined peak in the 5–5.25 cm section, which almost certainly marks 1963. The ^{210}Pb dates place 1963 slightly below the depth suggested by the ^{137}Cs record, possibly caused by the short-term fluctuations in the sedimentation rate mentioned above. The equilibrium between total ^{210}Pb activity and supporting [226]Ra was reached at 12 cm depth. Dates below this point were extrapolated back to ca. 1650 AD. Two additional ^{14}C AMS dates, using the leaching residue, support the extrapolated ^{210}Pb/^{137}Cs chronology. The reservoir effect was calculated by subtracting the last reliable ^{210}Pb/^{137}Cs age (WX 23) from the non-calibrated radiocarbon age of the same horizon (see Table 2). After reservoir-effect correction (1337 ± 30 years) and age calibration using Calib Rev. 6.0 (Stuiver & Reimer, 1993) the base of the core (WX 51) dates back to 1433–1645 AD (2σ-range), which broadly agrees with the ^{210}Pb-extrapolated date. As a plateau in the radiocarbon calibration curve between ca. AD 1450–1650 inhibits a precise radiocarbon dating of the core base (Fig. S1), the obtained radiocarbon ages can only be regarded as supporting data. Therefore, the ^{210}Pb/^{137}Cs chronology is primarily used for the Wuxu Lake age model. The

results of the ^{14}C AMS dates and calculated reservoir effect are summarized in Table 2.

Pollen analysis

The results of the pollen analysis for LC6 Lake are summarized in Fig. 4. The cluster analysis CONISS calculated a total sum of squares of 1.3. Therefore, no distinct first-order pollen biostratigraphic zones were established. The pollen spectrum is dominated by arboreal and shrub taxa, amongst which *Pinus* (ca. 19%), sclerophyllous *Quercus* (ca. 19%), *Betula* (ca. 11%), *Picea* (ca. 4%) and *Rhododendron* (ca. 3%) are the most abundant pollen taxa. Notable herbaceous taxa include *Artemisia* (ca. 12%), Cyperaceae (ca. 7%) and *Polygonum* (ca. 4%). In general, arboreal taxa show a slight increase since the late 1890s, mostly linked to the increase of *Pinus*, *Betula*, *Abies* and *Salix*, whereas herbaceous taxa decline on the expense of *Polygonum*, *Artemisia*, Poaceae and *Gentiana*. Grazing-taxa (i.e. Apiaceae, Liliaceae) show slight increases in the 1870s to 1940s and taxa most likely introduced through human cultivation (i.e. *Humulus*, Fabaceae) increased in the 1870–1940s and in the 1970s. The DCCA revealed a low and non-significant compositional species turnover of 0.81 SD (*P* = 0.25) for the last 200 years (Table 3).

Figure 5 summarizes the results from the Wuxu Lake pollen record. Similar to the LC6 Lake, no distinct first-order biostratigraphic zones were calculated by the cluster analysis CONISS (total sum of squares of 1.3). The pollen spectra are dominated by arboreal taxa, such as sclerophyllous *Quercus* (ca. 37%), *Pinus* (ca. 23%), *Betula* (ca. 6%) and *Abies* (ca. 5%). Herbaceous
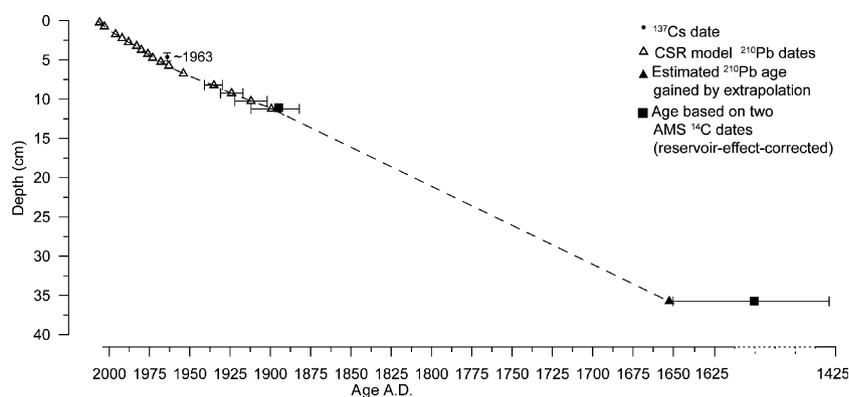
Fig. 3 Age chronology of the Wuxu Lake sediment core showing the constant rate of supply (CRS) model ^{210}Pb dates, the approximate 1963 depth determined from the ^{137}Cs stratigraphy, the extrapolated ^{210}Pb/^{137}Cs age and the (calibrated and reservoir effect corrected) radiocarbon age (2σ-range) of the core basis.

taxa, mainly comprised of *Artemisia*, Cyperaceae and Poaceae contribute with abundances between 2% and 4%. As at LC6 Lake, herbaceous taxa decrease since the 1870s whilst arboreal taxa (mainly *Pinus* and *Quercus*) increase. Pollen from cultivated plants are present in only insignificant amounts, although taxa indicative of grazing (e.g. *Rumex*, *Sanguisorba*) are present throughout the core with abundances of ca. 1–2%. The DCCA yielded a low and non-significant compositional species turnover of 0.36 SD (*P* = 0.09) over the last 200 years (Table 3).

Diatom analysis

The diatom stratigraphies of LC6 Lake and Wuxu Lake are illustrated in Figs 6 and 7, respectively. The common feature of both diatom data sets is the small degree of compositional species turnover throughout both cores. In both cases CONISS revealed a low total sum of squares (1.0 at Wuxu Lake, 1.7 at LC6 Lake), indicating the absence of first-order biostratigraphic zones. The DCCA yielded a beta diversity of 0.55 SD (*P* = 0.03) for Wuxu Lake and 0.94 SD (*P* = 0.59) for LC6 Lake over the last 200 years (Table 3). The diatom taxa of LC6 Lake and Wuxu Lake are plankton-dominated taxa and common in slightly acidic to circum-

neutral habitats. Many are cosmopolitan species that are commonly found in freshwaters of high-latitude and alpine regions (Lotter & Bigler, 2000; Sorvari *et al.*, 2002; Rühland & Smol, 2005).

The LC6 Lake diatom record revealed 158 species from 39 genera, dominated by monoraphid taxa (*Achnanthidium* sp., *Achnanthes* sp. and *Psammothidium* sp.), *Cyclotella* sp. and fragilarioid taxa, with contributions up to 40%, 35% and 20% relative abundance, respectively. The most common species is the planktonic diatom *Cyclotella ocellata* (up to 35%). A subtle but consistent decline of *C. ocellata* is apparent throughout the core, alongside small increases of *Achnanthidium minutissimum*, tychoplanktonic *Aulacoseira lirata* var. *lirata* and benthic *Fragilaria capucina* and *Cymbella* species (Fig. 6).

At Wuxu Lake, 120 taxa from 38 genera were identified. The species assemblage was dominated by the planktonic taxa *Cyclotella cyclopunctata* (ca. 63%) and *Aulacoseira distans* (ca. 15%). *Achnanthidium minutissimum* and varieties (ca. 5%) and fragilarioid taxa such as *Staurosira construens* f. *venter* (ca. 3%) and *Staurosirella pinnata* (2%) contribute with small percentage abundances to the benthic component of the diatom assemblage. However, no significant species shifts were detected throughout the record with only subtle

Table 2 Accelerator mass spectrometry radiometric data for Wuxu Lake

Sample	Depth (cm)	Material	[14]C age leaching residue (a BP)	Reservoir effect (years)	Calender age (a AD)	[14]C age humic acid (a BP)	Reservoir effect (years)	Calender age (a AD)
WX 23	11.5	Bulk sediments	1430 ± 30	1377 ± 30	–	1490 ± 25	1437 ± 25	–
WX 51	35.5	Bulk sediments	1755 ± 35	1377 ± 30	1433–1645	1655 ± 30	1437 ± 25	1718–1827

Calibration was performed using CALIB Rev. 6.0 (Stuiver & Reimer, 1993). Reservoir effect was calculated by subtracting the ^{210}Pb/^{137}Cs dated WX23 age from the original ^{14}C age. Calibrated ages lie within the 2σ-range.

Fig. 4 Pollenstratigraphy of LC6 Lake. Only taxa with an abundance of >1% in at least one sample are shown. The black filled silhouettes represent original pollen abundance; transparent silhouettes in the background exaggerate the original abundance of rare species by four to ease visibility. The gap captures the sediment slump between 8 and 27 cm. Italic ages indicate extrapolated ages.

Fig. 5 Pollenstratigraphy of Wuxu Lake. Only taxa with an abundance of >1% in at least one sample are shown. Black filled silhouettes represent actual abundance, white silhouettes in background illustrates abundance exaggerated by factor four to ease visibility. Italic ages indicate extrapolated ages.

Table 3 DCCA axes 1 scores (in SD units) estimating compositional species turnover

Lake	Proxy	Time period	SD units
Wuxu	Pollen	Last 200 years	0.36
	Diatoms	Last 200 years	0.55
LC6	Pollen	Last 200 years	0.81
	Diatoms	Last 200 years	0.94
Naleng	Pollen	Late glacial/Holocene	1.51
	Pollen	Pleistocene/Holocene boundary	1.61
	Pollen	'8.2 event'	0.64

DCCA, Detrended canonical correspondence analysis.

changes apparent from the 1840s onwards, linked to the appearance of some fragilarioid taxa (Fig. 7).

Procrustes rotation and PROTEST

All four nMDS produced stress values between 17% and 20% (Table 4) suggesting a good fit between fitted values and the original distance (Kruskal & Wish, 1978; Clarke, 1993). All nMDS biplots are provided as Supporting Information.

Procrustes rotation and the associated PROTEST function were performed on (i) both pollen data sets, (ii) both diatom data sets, (iii) pollen and diatom data sets of the LC6 Lake and (iv) on the pollen and diatom data sets of Wuxu Lake. Table 5 summarizes the diagnostics of Procrustes rotation and PROTEST and Fig. 8 illustrates the goodness of fit between all data sets compared. The size of residuals for each time slice between 1810 and 2000 AD is shown. Low residuals indicate a good agreement between data sets, and high residuals indicate a weak agreement. The best fit was produced for the within lake comparison at LC6 Lake (Fig. 8c). The pollen and diatom record produced a significant and well-correlated fit ($P = 0.02$, $r = 0.70$). A good fit was also produced between the corresponding pollen records from LC6 Lake and Wuxu Lake ($P = 0.02$, $r = 0.53$) (Fig. 8a). However, several time slices display a lower degree of similarity as indicated by higher residuals. The poorest fit was produced between the corresponding diatom records from both lakes, as suggested by a relatively high p value and low PROTEST score ($P = 0.13$, $r = 0.43$) (Fig. 8b).

Discussion

Biological response to climate and human-induced changes on the SE Tibetan Plateau

Regional vs. local response. The pollen records from the LC6 Lake and Wuxu Lake have very similar species

compositions that are temporally consistent. This concordance between both data sets is also shown by the significant and well-correlated procrustean fit (Fig. 8a), suggesting that the timing, magnitude and direction of change in both pollen records is very similar over the last 200 years and that changes are likely to have occurred in response to regional, as opposed to local drivers. The pollen assemblages in both records are characteristic of the montane forest belt on the southeastern Tibetan Plateau, dominated by evergreen oak-pine forests (sclerophyllous *Quercus*, *Pinus*) intermixed with *Abies*, *Picea* and *Betula*, typically found between 3000 and 4000 m asl (Chang, 1981; Winkler, 1996; Hou, 2001; Yu *et al.*, 2001). In the LC6 Lake pollen spectra, herbaceous taxa, mainly comprised of *Polygonum*, *Artemisia* and Cyperaceae, are a stronger component than those at Wuxu Lake. This most likely represents the closer proximity of LC6 Lake to alpine meadows, which on the southeastern Tibetan Plateau typically cover the slopes above 4000 m asl (Chang, 1981; Yu *et al.*, 2001).

Comparing the diatom records of both lakes with each other, the picture is different. The Procrustean rotation produced an insignificant and poorly correlated fit (Fig. 8b), indicating that the timing, duration or magnitude of change of the diatom assemblage in response to environmental drivers varies between both lakes and that care needs to be taken when making regional climate inferences from the aquatic record alone. Lakes can have fundamentally different properties and therefore different climate sensitivity thresholds (Battarbee, 2000). Procrustean residuals (Fig. 8b) indicate that mismatches between both aquatic data sets were greatest between 1810 and 1840 AD and between 1940 and 1975 AD, which correspond with time periods when compositional turnover is highest in both lake systems (compare DCCA scores in Figs 4 and 5).

Compositional species turnover. The overall characteristic of both pollen records is the very stable species composition throughout the entire profile. Species shifts are very subtle over the last 200 years (at LC6 Lake) and 350 years (at Wuxu Lake). The low total sum of squares indicated by CONISS and low compositional species turnover (0.36–0.81 SD) confirm this and likely indicate insignificant ecological changes throughout both records. Compared to the dramatic vegetation shifts on the Tibetan Plateau at the transition from the Lateglacial to the early Holocene or during the mid-Holocene (Jarvis, 1993; Demske *et al.*, 2009; Kramer *et al.*, 2010; Wischnewski *et al.*, 2011), the degree of vegetation change over the last two to four centuries is less significant. Kramer *et al.* (2010) reconstructed a 2–3 °C temperature rise at the Pleistocene/Holocene boundary (using a pollen record from Naleng Lake, southeast
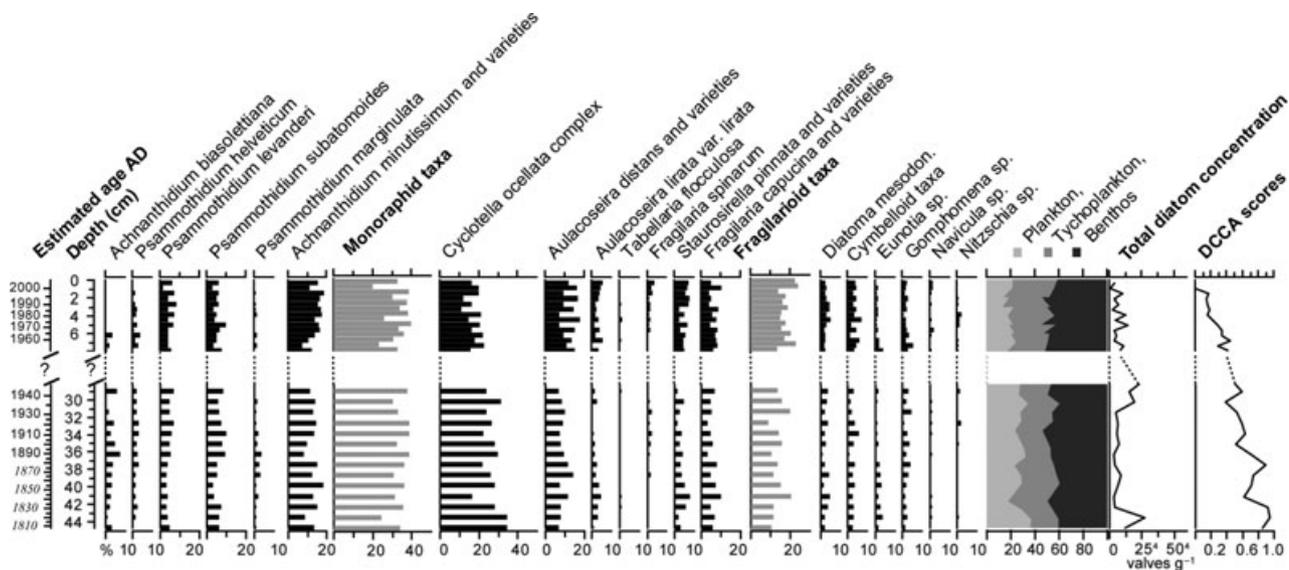
Fig. 6 Diatom stratigraphy of LC6 Lake. Selected taxa are shown in relative abundance. The gap captures the period of rapid accumulation between 8 and 27 cm. Italic ages indicate extrapolated ages.
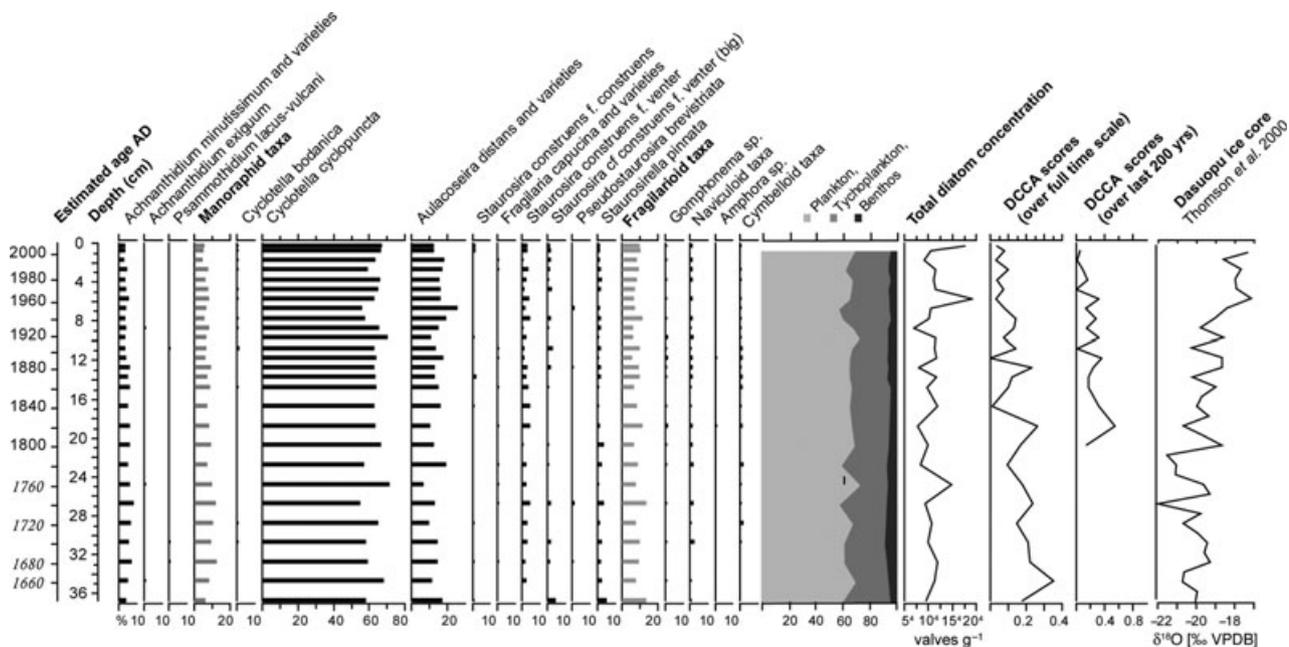
Fig. 7 Diatom stratigraphy of Wuxu Lake. Selected taxa are shown in relative abundance. Italic ages indicate extrapolated ages.

Tibet) which triggered the spreading of forest at the expense of the steppe and meadow ecotone. The same record shows a considerable reorganization of the vegetation during the shorter lived cold event around 8.1 calender kyr BP, when temperatures dropped by 1–2 °C (Kramer *et al.*, 2010). DCCA scores for these two time periods (0.64–1.61 SD) indicate substantial ecological changes (A. Kramer and J. Wischnewski, unpublished data) (Table 3). You *et al.* (2007) found a similar rate warming of ca. 1.4 °C (based on instrumental air temperature data) over the last 40 years for the southeastern Tibetan Plateau, but changes in the vegetation structure did not show a similar strong compositional turnover as at times during the Holocene. This suggests that the length and magnitude of the recent warming period at our sites has not yet led to the crossing of climatically induced ecological thresholds. A direct comparison of the Holocene with the recent past is,

Table 4 nMDS stress scores and applied distance measure

Data set	Distance measure	nMDS stress score (%) for 2D model
1. LC6 Lake diatoms (resampled between 1810 and 2000)	Bray Curtis	19.33
2. LC6 Lake pollen (resampled between 1810 and 2000)	Bray Curtis	17.31
3. Wuxu Lake diatoms (resampled between 1810 and 2000)	Bray Curtis	19.62
4. Wuxu Lake pollen (resampled between 1810 and 2000)	Bray Curtis	20.77

nMDS, nonmetric multidimensional scaling.
Data sets 1–4 refer to analyses on harmonized (interpolated and resampled in 5 year intervals between 1810 and 2000 AD) pollen and diatom counts.

however, difficult as earlier boundary conditions, for example, at the Pleistocene/Holocene transition, were different, trees were not the dominant vegetation type and the vegetation density overall was low (Kramer *et al.*, 2010). With the onset of warmer and moister conditions in the early Holocene, trees could migrate into new niches as climate became more favourable to their growth. During the late Holocene and the recent past these niches were already occupied, so a temperature increase alone would not necessarily cause similar results. Furthermore other aspects, such as different solar insolation, varying atmospheric CO_2 levels (Herzschuh *et al.*, in press) or different degrees of soil development (Fang *et al.*, 2003; He & Tang, 2008) set different boundary conditions for plant development for the early and late Holocene, suggesting that temperature is not necessarily the sole driver for recent terrestrial ecosystem change. However, a further increase in temperature under current warming rates, could lead to an ecological threshold being crossed, and for example, cause forest expansion upslope into the alpine meadows. Such an impact would result in the LC6 Lake pollen assemblage becoming more similar to today's Wuxu Lake pollen assemblage (higher arboreal and lower herbaceous component). Vegetation-climate models support this hypothesis, as they predict an increase in cold-temperate conifer forest and a general north-westward shift of all vegetation zones for the Tibetan Plateau under a doubling CO_2 scenario until 2100 (Ni, 2000; Song *et al.*, 2004).

Similar to the pollen records, the overall compositional change in both diatom records is very low as well, which is confirmed by low total sum of square scores indicated by CONISS and by a low compositional species turnover (0.55–0.94 SD). So far no diatom records exist in the region for comparison of compositional turnover rates, and so herein we compare our Tibetan records to diatom records from the arctic, a region that is also significantly impacted by recent climatic warming. Many of the palaeoecological records

in the circum arctic show significant diatom assemblage shifts, starting in the mid-19th century, with a compositional species turnover of ca. 1–2.8 SD units (Smol *et al.*, 2005; Hobbs *et al.*, 2010). Smol *et al.* (2005) and Rühland *et al.* (2008) link these changes primarily to climate and associated limnological changes (longer growing season, changes in the light and mixing regime, increased nutrient cycling), which promote a shift from benthic (e.g. small fragilarioid species) to planktonic taxa (e.g. small *Cyclotella* species). These taxa shifts could not be detected at LC6 Lake or Wuxu Lake despite evidence of significant instrumental temperature and precipitation increase in the region (You *et al.*, 2007). At both sites, diatom evidence suggests that aquatic ecosystems have been relatively stable during the recent centuries, through periods of distinct climate variability, such as the post-Little Ice Age warming (Thompson *et al.*, 2000) and the significant temperature increase since the 1960s (You *et al.*, 2007). Unlike other regions, these sites have not yet crossed climatically induced ecological thresholds, although we acknowledge that confounding processes, such as increasing precipitation and persistent cloud cover, densely vegetated catchments and different edaphic boundary conditions may act to subdue the impact of increasing temperatures (Wischnewski *et al.*, in press).

Causes of terrestrial and aquatic ecosystem change

The terrestrial system. Apart from the low overall change, minor compositional shifts could be identified in both pollen records. After ca. 1880 to the present, both pollen records reveal an increase in arboreal taxa. This is contradictory to studies that show evidence of forest decline on the Plateau since the mid-Holocene (Shen *et al.*, 2005; Kramer *et al.*, 2010) and other studies that report on alarming forest loss and habitat fragmentation since the 1950s (Studley, 1999). There is still debate as to whether forest decline since the mid-Holocene was primarily caused by climatic conditions, human impact or a combi-
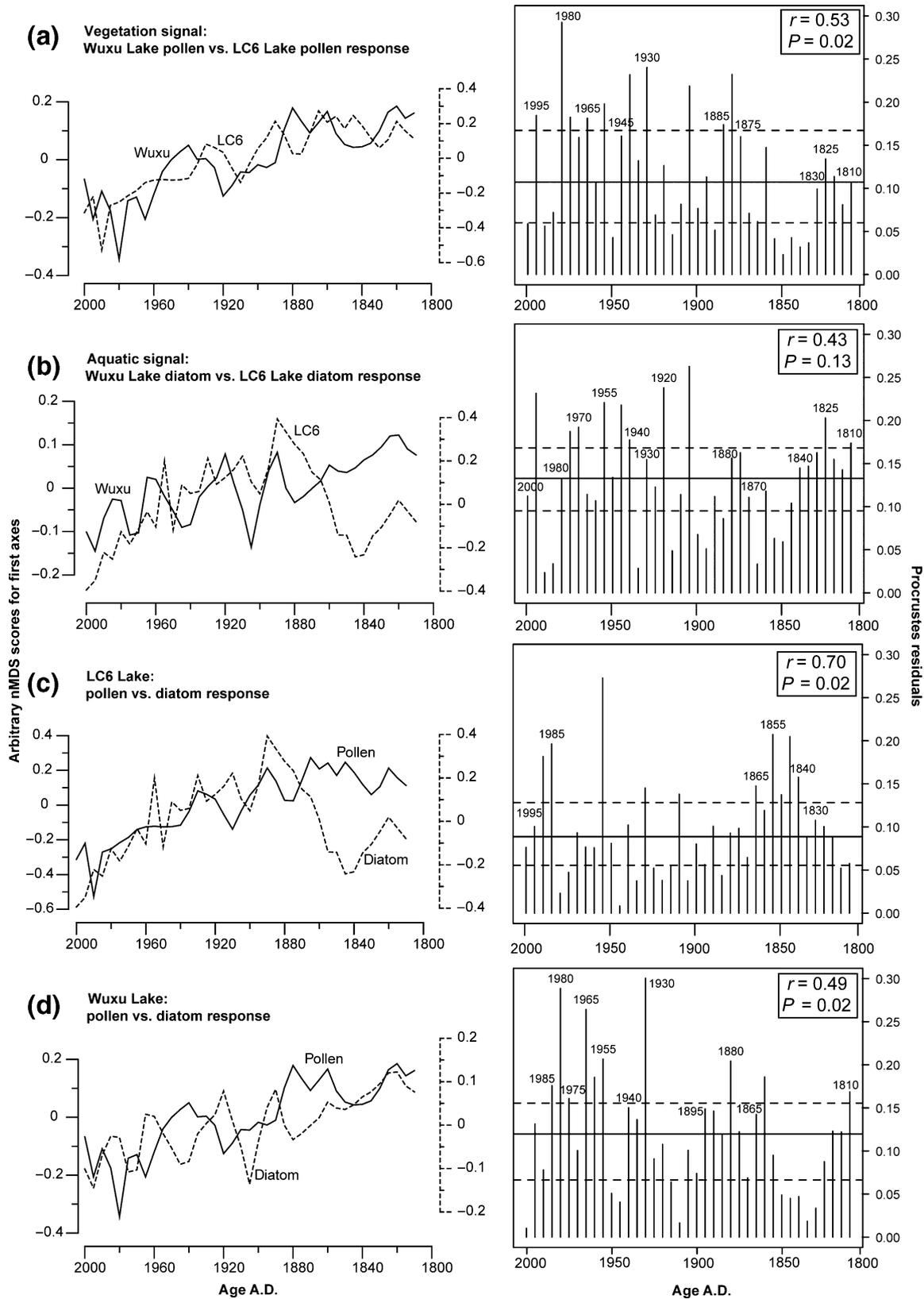
Fig. 8 Within-lake and between-lake comparisons. Results from nonmetric multidimensional scaling (nMDS) axis 1 scores and impulse diagram of Procrustes rotation residuals. Height and occurrence of peaks in impulse diagram indicate the degree of dissimilarity between two data sets compared. Dashed and solid lines across indicate the first, second and third quartile, respectively.

Table 5 Procrustes rotation and PROTEST diagnostics

Comparisons	Procrustes rotation sum of squares	RMSE	PROTEST (*r*)	*P* value
LC6 pollen vs. Wuxu pollen	0.72	0.13	0.53	**0.02**
LC6 diatoms vs. Wuxu diatoms	0.82	0.14	0.43	0.13
LC6 pollen vs. LC6 diatoms	0.51	0.11	0.70	**0.02**
Wuxu pollen vs. Wuxu diatoms	0.75	0.14	0.49	**0.025**

RMSE, root mean square error; nMDS, nonmetric multidimensional scaling.
PROTEST is the correlation on a symmetric Procrustes rotation using nMDS axis scores and the associated p value (based on 39 permutations). Bold values indicate a significant fit between data sets.

nation of both (Yang *et al.*, 2005; Schlütz & Lehmkuhl, 2009; Herzschuh *et al.*, 2010; Kramer *et al.*, 2010). However, the severe loss of natural forest during the past 2000 years and since the 1950s is attributed to anthropogenic forest clearance as a consequence of the high timber, grazing and agricultural ground demand of a constantly growing Chinese population (Studley, 1999; Zhang *et al.*, 2000; Elvin *et al.*, 2002; Dearing *et al.*, 2008). The forest increase since ca. 1880 in the LC6 Lake and Wuxu Lake catchments is mainly linked to species of *Quercus*, *Pinus*, Cupressaceae, *Abies* and *Larix*. *Pinus*, *Larix* and genera of the Cupressaceae family are fast growing tree species that are used for reforestation purposes within governmental programmes (Bao & Jiang, 1998; Zhang *et al.*, 2000). Furthermore, *Quercus–Pinus* forests are often described as secondary forests, developing after human disturbance. Their growth is promoted by human-induced fires for the purpose of forest clearance (Winkler, 1996; Yan *et al.*, 2005; Shen *et al.*, 2006), suggesting that at least a part of the forest increase results from reforestation, rather than natural forest growth. Also, the Wuxu Lake pollen record shows high abundances of grazing indicators (Apiaceae, *Rumex*, *Sanguisorba*) from the ca. AD 1760–1800, indicating anthropozoogenic pressures in the study region. A historical study of Lake Erhai (SW China) provides evidence that reforestation started as early as the AD 1780s in some parts on the SE Tibetan Plateau (Elvin *et al.*, 2002). However, the high abundance of *Quercus* in both pollen records is most likely an overrepresentation of the real distribution, as *Quercus* is known as a strong pollen producer and prone to long distance transport (Jarvis & Clay-Poole, 1992). The dominance of oak-pine forest in both pollen records may therefore partly reflect elements of the evergreen needle-leaved and deciduous broad-leaved mixed forests from the adjacent but lower elevated hills (2000–3000 m) (Yu *et al.*, 2004). The increase of *Pinus*, Cupressaceae (at LC6 Lake), *Larix* and *Abies* (at Wuxu Lake) since the mid-1990s can be linked to China's latest attempts to reforest wide parts of the degraded landscapes in the North, Northwest and Southwest

(Three-North Protective Forest Programme, start 1978; Natural Forest Conservation Programme, start 1998) (Zhang *et al.*, 2000; Fang *et al.*, 2001). Other studies on the southeastern Tibetan Plateau confirm this trend. Shen *et al.* (2006) identified a sharp increase in *Pinus* over the past 25 years, and Fang *et al.* (2001) shows evidence of significant increase in total forest biomass carbon storage since the 1970s, indicating secondary forest growth.

Apart from direct anthropogenic pressures, changing climate in combination with a national fire ban that was set to prevent burning practices by herders (Baker & Moseley, 2007) might have also had influence on the subtle forest increase in the LC6 Lake and Wuxu Lake catchment. Ice core records indicate warmer and moister conditions, associated with post-Little Ice Age warming, over the past ca. 200 years (Thompson *et al.*, 2000, 2006; Hou *et al.*, 2007). Furthermore, instrumental data suggest that spring/summer temperatures, and particularly winter and autumn temperatures, increased by 0.17, 0.37 and 0.35 °C/decade, respectively, since 1961 on the SE Tibetan Plateau (You *et al.*, 2007). The most recent global warming trend is therefore also detectable in regions of the Tibetan Plateau. You *et al.* (2007) also identified rising precipitation trends for the SE Tibetan Plateau since the 1980s, which are most obvious in the autumn and spring season. The increase in sclerophyllous *Quercus* sp. since ca. 1880, observed at Wuxu Lake and a little later at LC6 Lake, could be the response to these climatic trends, indicating an upslope expansion of the cold-temperate conifer forests into the alpine meadows. A dry early spring (temperatures rise before the onset of the monsoon) and milder winters would promote predominantly sclerophyllous taxa (Jarvis, 1993). *Abies*, on the other hand, has often been associated with increasing effective moisture (Yan *et al.*, 1999; Kramer *et al.*, 2010), hence the increase of *Abies* in the second half of the 20th century in both pollen records may be linked to increasing precipitation rates (You *et al.*, 2007). Hence, the synergistic processes of post-Little Ice Age warming, 20th century climate warming and extensive reforestations since the 19th century have promoted the

growth of seminatural pine-oak forests, intermixed with fir and larch.

The aquatic system. Changes in both diatom records after 1880 AD are less pronounced than changes in the pollen spectra, but minor increases in tychoplanktonic and small fragilarioid taxa after the 1930/1950s can be observed in both records. Tychoplanktonic and fragilarioid taxa, which are known to be *r*-strategists (organisms with high and quick reproduction and dispersal rates, and short generation times), are better adapted to rapidly changing environments (Lotter & Bigler, 2000) and therefore indicative for higher ecosystem variability. Higher ecosystem variability during this time was also recorded in other palaeo-climate records across the Tibetan Plateau (Yang *et al.*, 2004; Lami *et al.*, 2010; Wrozyna *et al.*, 2010). Nevertheless, the stability of both diatom assemblages throughout the cores is indicative of no significant change within the lake systems over the past ca. 200 years. Even though LC6 Lake and Wuxu Lake are located above 3700 m asl, they are more comparable to the temperate montane-boreal lake systems in, for example, North America than to the tree-less alpine and arctic lake systems, as they are free from ice cover for most of the year and surrounded by dense forests. At temperate montane-boreal lakes with a longer open water season, thresholds for diatom taxonomic shifts are more gradually met (Hobbs *et al.*, 2010). According to recorded mean monthly temperatures and monthly satellite images from the Landsat archive (USGS earth explorer 2010), LC6 Lake and Wuxu Lake are currently 8–10 months of the year ice-free, suggesting that much higher magnitudes of temperature change would be necessary to significantly shorten/lengthen the growing season or alter the mixing regime to effect the diatom composition. In addition, temperate lakes are potentially not so sensitive to small changes in climate or nutrient input (Rühland *et al.*, 2008), in part due to the edaphic stability of their catchments (Heegaard *et al.*, 2006), which in turn may lead to a more resilient vegetation towards a changing climate (Theurillat & Guisan, 2001). Furthermore, several studies have shown that the composition and distribution of aquatic organisms is often correlated to changes in the terrestrial environment of the lake (Heegaard *et al.*, 2006). The edaphic stability and the relatively stable vegetation composition in the LC6 Lake and Wuxu Lake catchment over the past two decades, could have contributed to the limited aquatic response. Other factors, such as local temperature peculiarities, increasing precipitation and cloud cover (Wischnewski *et al.*, in press), or negative climate feedbacks due to a constant supply of cold glacier melt-waters (Rühland *et al.*, 2006) introduced to the lakes,

could further explain the limited diatom response despite the well-established climate warming on the southeastern Tibetan Plateau.

Conclusions

Despite instrumental and palaeo-climatological evidence of recent climate warming on the southeastern Tibetan Plateau, diatom and pollen records from two montane-boreal lakes show only very subtle species compositional changes over the past two to four centuries. The subtle species changes observed are similar and synchronous in both pollen records, but less similar in the corresponding diatom records. This suggests that the terrestrial records summarize primarily regional environmental changes, whereas the aquatic records possibly capture rather local environmental changes. The combination of aquatic and terrestrial proxies is therefore valuable, to move from a local to a regional scale, but also to understand the many facets of the microenvironments in that complex mountain landscape of the Tibetan Plateau.

The overall limited response of the pollen and diatom assemblages from LC6 Lake and Wuxu Lake over the last 200–350 years suggest that both lakes and their catchments seem to be resilient against the current rate and magnitude of climate warming, and that climatically induced ecological thresholds are not yet crossed. In comparison to the extensive reorganizations of the vegetation in the Holocene that underwent temperature changes of 1–3 °C, or to the significant recent shift in diatom communities in many circum-arctic lakes, the current shifts in species and species abundance on the SE Tibetan Plateau are insignificant suggesting that the impacts of and sensitivity to climate change vary amongst ecosystems.

More influential and alarming than the current rate of climate warming are the consequences of anthropogenic land cover change, that have already caused forest degradation and habitat fragmentation in wide parts of China. Even though our remote montane-boreal sites are not severely affected yet, anthropogenic signs are clearly visible. Humans have been shaping the landscapes of the southeastern Tibetan Plateau for several thousands of years by extensive forest clearances and reforestations as a consequence of rapid population and economic growth, making it difficult to establish how the natural forest in these regions originally looked like. Our records indicate that over the past two centuries, human activities have initiated a conversion of the forest structure, that is, a trend to less resilient, secondary pine-oak forests, whilst post-Little Ice Age and 20th century warming have contributed to their growth, promoting the regeneration of these semi-

natural forests on the southeastern Tibetan Plateau. To disentangle the effects and causes of natural climate variability and anthropogenic impact are therefore difficult, in fact synergistic processes are more likely. A further temperature increase of 3.7 °C on the Tibetan Plateau, as predicted in a coupled atmosphere-ocean global climate model (Lal & Harasawa, 2001), will lead to an upslope expansion of the tree-line. In combination with further anthropogenic disturbances, ecological thresholds could be surpassed and cause further degeneration of the vegetation structure and fragmentation with possibly severe ecological consequences, such as reduced water retention capacity, biodiversity reduction and increasing natural disasters (Yan *et al.*, 2005; Cui *et al.*, 2007).

Acknowledgements

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Supporting Information

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

Figure S1. Radiocarbon age (reservoir effect corrected, in BP) against calibrated ages (AD). Illustrated is the sigma 2 range.

Figure S2. nMDS ordination biplots (2D) on interpolated and resampled data sets. Dashed line indicates division between samples older 1880 AD and sample younger 1880 AD.

Data S1. Material and Methods: Non-metric multidimensional scaling (nMDS) is an ordination technique which is particularly useful for the exploration of patterns of variation in multivariate species data sets. The main advantage over other ordination techniques [e.g. principal components analysis (PCA) or correspondence analysis (CA)] is that it does not impose an underlying response model for the species as nMDS can use any dissimilarity matrix as input. nMDS aims to preserve the rank ordering of the original pair-wise distances rather than the distances themselves. It was preferred over other ordination techniques as it has been shown to be a more robust technique for indirect gradient analysis and is generally a very effective method for ordinating ecological community data (Minchin, 1987; McCune & Grace, 2002). The Bray Curtis distance coefficient was used to calculate the dissimilarity matrix, as it has been demonstrated to provide a robust monotonic relationship with ecological distances as well as a robust, linear relationship over a wide range of distances (Faith *et al.*, 1987). The stress value produced by nMDS is an evaluation on how well the computed data matrix is representing the original data set in *n*-dimensional space and can therefore be understood as a measure of the variation explained. According to Clarke (1993) and McCune & Grace (2002), stress values in the range of 10–20% are common in most ecological community data and indicate a decent fit between the original distance of objects and the fitted values. Procrustes rotation analysis and the associated PROTEST permutation test were used to explore the similarity/dissimilarity between different data sets and to test the significance of any relationship found. Procrustes rotation assesses the overall degree of correlation between two data sets on the basis of their ordination (nMDS) scores through a Procrustean superimposition approach (Gower, 1971; Peres-Neto & Jackson, 2001). Geometrically, Procrustes rotation can be viewed as if one ordination configuration remains fixed in space, whilst the other configuration is rotated, flipped and scaled in a series of translations relative to the fixed configuration. The degree of similarity between the configurations is then computed between the fixed and translated configuration. The justification for Procrustes rotation is that an nMDS ordination may be rotated arbitrarily without loss of information and that the absolute spacing of the samples in nMDS space is a function of the scale of the data and the dissimilarity used. As such the ordination configuration provided by nMDS is data set specific and a means is needed by which to such-derived configurations may be compared. Diagnostics such as Procrustes rotation sum of squares and the root mean square error (RMSE) indicate the performance of the model; the correlation-like statistic PROTEST (*r*) and the associated *P* value indicate the quality and likelihood of the fit.

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