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1	Terrestrial and aquatic responses to climate change and human impact on the
2	southeastern Tibetan Plateau during the past two centuries
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21	turnover, Procrustes rotation, Pollen, Diatoms
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24	Running title: Recent pollen and diatom response in SE Tibet

Rapid population growth and economic development have lead to increased anthropogenic pressures on the Tibetan Plateau, potentially causing significant land cover changes with partly severe ecological consequences. To assess whether these pressures are also affecting the remote montane-boreal lakes on the SE Tibetan Plateau, fossil pollen and diatom data from two lakes were synthesised to explore the interplay of aquatic and terrestrial ecosystem response, in respect to climate variability and human activity over the past 200 years. Non-metric multidimensional scaling and procrustes rotation analysis were applied to assess the similarity and synchronicity of response to environmental change between the corresponding pollen and diatom assemblages of each lake. 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 reorganisations 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, 20<sup>th</sup> century climate warming and extensive reforestations since the 19<sup>th</sup> century have initiated a change from natural oak-pine forests to semi-natural, likely less resilient pine-oak forests. Further warming and anthropogenic disturbances would

- 50 possibly exceed the ecological threshold of these ecosystems and lead to severe
- 51 ecological consequences.

## 52 Introduction

Due to its potential to influence regional and global climate patterns, the Tibetan Plateau has become a focus study area of 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 particularly the southeastern Tibetan Plateau, is very sensitive to global warming. Additionally, the Plateau has been under the pressure of rapid population growth and economic development. The population of China has increased 2.5 times in the past 50 years (Zhang et al. 2000), and also the population of the Tibet Autonomous Region has grown from 1.2 million 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 in timber has resulted in extensive forest clearances since the 1950s (Zhang *et al.* 2000), particularly at the steep forested slopes of the southeastern Tibetan Plateau (Studley 1999). Overgrazing, grassland degradation 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 partly severe and irreversible consequences for ecosystems and mankind. 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). Additionally, anthropo-zoogenic pressures are

77	not evenly spread and lead to regions on the Plateau that are more affected by land
78	cover changes than others (Cui & Graf 2009). Therefore, global climate models are
79	still imprecise in estimating possible future land cover changes on the Tibetan Plateau
80	as they lack the spatial and temporal resolution of climatic, ecosystem and
81	anthropogenic parameters in that topographically challenging landscape (Cui & Graf
82	2009). Therefore, it is necessary to establish a dense and integrated network of
83	instrumental, palaeoecological and archaeological studies, to help to reduce the
84	uncertainties of climate variability and anthropo-zoogenic activities and associated
85	land cover changes in the past and present, and to assess their future impact on
86	ecosystems on the Tibetan Plateau.
87	To date, only a few and spatially widespread proxy studies have investigated
88	environmental changes on the Tibetan Plateau focusing on the last few centuries
89	(Henderson et al. 2003; Bräuning & Mantwill 2004; Bräuning 2006; Liang et al.
90	2009; Fan et al. 2010; Henderson et al. 2010; Lami et al. 2010; Wrozyna et al. 2010;
91	Yang et al. 2010; Wang et al. 2011; Wischnewski et al. in revision) – a time period
92	strongly affected by increasing land use activity. Pollen and diatoms in particular,
93	have not received much attention on centennial and decadal time scales, despite their
94	potential to reflect vegetation, land use and climate change reliably (Douglas & Smol
95	2001; Lotter et al. 2001; Zhao et al. 2008; Schlütz & Lehmkuhl 2009; Herzschuh et
96	<i>al.</i> 2010).
97	Here we present the results of fossil pollen and diatom records from two
98	montane-boreal lakes (LC6 Lake and Wuxu Lake) on the southeastern Tibetan

99 Plateau. Our aim is to evaluate the comparability of aquatic and terrestrial proxy

- 100 responses in respect to climate variability and human activity, using rigorous
- 101 statistical methods. We focus on the following questions: (a) Do pollen and diatom

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records reflect similar and synchronous species shifts in response to environmental changes on the southeastern Tibetan Plateau? (b) 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? (c) What are the potential causes of ecosystem change on the southeastern Tibetan Plateau? As such, this paper 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.

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## 111 Regional setting and study sites

112 Wuxu Lake and LC6 Lake (working name) are located on the southeastern Tibetan 113 Plateau. This part of the Plateau is characterised by the strong and varied relief of the 114 Hengduan Mountains, which stretch across western Sichuan, northwestern Yunnan 115 and the easternmost part of the Tibet Autonomous Region. Altitudes of over 5000 m 116 above sea level (asl) in the northern parts of the southeastern Tibetan Plateau drop to 117 less pronounced features of ~ 1500 m asl towards the southern limit of the Tibetan 118 Plateau (northwestern Yunnan) causing steep environmental gradients in the region. 119 Mean annual summer temperatures range from 8°C to 20°C, and mean annual 120 precipitation varies from 400 mm to 1400 mm (Sun 1999; Yu et al. 2001). The 121 southeastern Tibetan Plateau is affected by two major circulation systems. The mid-122 altitude westerly circulation brings limited moisture to the region from November to 123 March, while the Asian summer monsoon circulation, particularly the Indian monsoon 124 system, is responsible for the majority of precipitation from May to September 125 (Domrös & Peng 1988; Su & Shi 2002). This results in abundant rainfall and high 126 temperatures in summer, which contrast to cool and relatively dry winters. 127 The LC6 Lake is located in the Nyaintêntanglha Mountain range, a western 128 branch of the Hengduan Mountains (Fig. 1). The LC6 Lake lies at 4230 m asl. The 129 closest weather station is in Nyingchi at 3000 m asl, 26 km to the south of the lake, 130 which records mean T<sub>July</sub> 15.6°C, mean T<sub>Jan</sub> 0.2°C, and mean P<sub>ann</sub> 657mm (85% of 131  $P_{ann}$  falling between May and September). Based on a lapse rate of - 0.5°C/100 m 132 (Böhner 2006), estimated mean temperatures for July are ~ 9.6°C and for January ~ -133 5.5°C at the LC6 Lake. According to climate station-based calculations from Böhner 134 (2006) annual precipitation is 1450 mm, and the evaporations rate 800 mm at the lake site. The LC6 Lake has a small lake area of  $0.6 \text{ km}^2$  and is mainly fed by runoff from 135

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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*), and patches of *Kobresia pygmaea* meadow characterise
the vegetation in the catchment. 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 ~ 680 km to the west of LC6 Lake in an eastern branch of the Hengduan Mountains (Fig. 1). Wuxu Lake lies on 3705 m asl. The closest weather station is Litang at 3948 m asl, 140 km northwest of the lake, which records mean T<sub>July</sub> 10.5°C, mean T<sub>Jan</sub> -6°C, and mean P<sub>ann</sub> 720 mm (90% falling between May and September). The lake area  $(0.5 \text{ km}^2)$  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 characterised by coniferous (Picea likiangensis, Abies squamata) and sclerophyllous trees (Quercus aquifoliodes, Q. pamosa), intermixed with Rhododendron sp. and Salix sp. shrubs. A day trip away from Jiulong Town, Wuxu Lake is destination of minor tourism. 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 summarised in Table 1.

157	Material	and	methods
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158 Field sampling and dating of lake sediment cores

159 LC6 Lake and Wuxu Lake were sampled in summer 2005 and winter 2007,

160 respectively. A 45-cm sediment core was taken at the deepest part (23 m) of LC6

161 Lake; at Wuxu Lake a 40-cm sediment core was taken at 30 m water depth. Both

162 cores were taken using a UWITEC gravity corer and were sectioned at site in 0.5-cm

163 intervals directly after coring.

Both cores were dated using <sup>210</sup>Pb, <sup>226</sup>Ra, and <sup>137</sup>Cs analyses by direct gamma
assay in the Liverpool University Environmental Radioactivity Laboratory.

166 Radiometric dates were calculated using both the constant rate of supply (CRS) and

167 constant initial concentration (CIC)<sup>210</sup>Pb dating models (Appleby & Oldfield 1978).

168 The 1963 depth was determined from the <sup>137</sup>Cs stratigraphic record. Discrepancies

169 between the <sup>210</sup>Pb models were resolved using the methods described in Appleby

170 (2001). Dates of points below the base of the unsupported <sup>210</sup>Pb record were

171 calculated by extrapolation of the <sup>210</sup>Pb depth/age curve using a best estimate of the

172 sedimentation rate for this part of the core. For Wuxu Lake, two additional

173 radiocarbon dates from bulk sediments were obtained by the AMS (accelerated mass

174 spectrometry) method at the Leibnitz-Laboratory for Radiocarbon Dating and Isotope

175 Research, Kiel to support the extrapolated age.

176 Pollen Analysis

177 Sediments for pollen analyses for both lakes were treated using standard laboratory

178 methods (Fægri & Iversen 1989), including treatment with HCl (10%), KOH (10%),

and HF (50%, 2 h boiling), followed by acetolysis, sieving (7  $\mu$ m) in an ultrasound

180 bath, and mounting in glycerine. Two tablets of *Lycopodium* spores (10 979

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181	spores/tablet) were added to calculate the pollen concentrations. At LC6 Lake, 30
182	horizons (5 to 12-year intervals) were analysed and at least 600 (mean 1070)
183	terrestrial pollen were counted for each level. For Wuxu Lake, 26 horizons (7 to 20-
184	year intervals) were analysed with counts between 360 and 650 (mean 470) terrestrial
185	pollen for each level. Pollen identifications followed relevant literature (Moore et al.
186	1991; Wang et al. 1997; Beug 2004; Fujiki et al. 2005). Pollen taxa, occurring in at
187	least one sample at >1% were used to develop pollen diagrams and implement
188	numerical methods.
189	Diatom Analysis
190	Diatom analysis followed standard procedures using the water bath technique
191	(Renberg 1990; Battarbee <i>et al.</i> 2001). Slides were mounted using Naphrax®. Diatom
192	concentration was estimated using divinylbenzene microspheres (Battarbee & Kneen
193	1982). At LC6 Lake 400 to 500 valves were counted for 45 horizons (2 to 11-year
194	intervals). At Wuxu Lake 630 to 1200 valves were counted for 27 horizons (7 to 20-
195	year intervals), using phase contrast at x1000 magnification. Taxonomic
196	identifications primarily followed Krammer & Lange-Bertalot (1986-1991), Lange-
197	Bertalot & Metzeltin (1996), Zhu & Chen (2000) and Camburn & Charles (2002).
198	Diatom taxa with percentages of $>1\%$ in at least one sample were used for the
199	illustrations and all statistical analyses.
200	Data treatment and statistical analyses
201	The significance of pollen- and diatom-based biostratigraphic zones was calculated by
201	aluster analysis using constrained incremental sum of squares (CONISS) (Crimm
202	cruster analysis using constrained incremental sum of squares (COM55) (Offmm
203	1991) and the Edwards and Cavalli-Sforza's chord distance as the dissimilarity
204	coefficient.

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The ordination technique non-metric multidimensional scaling (nMDS) was used to explore patterns of variation in the pollen and diatom data sets (Minchin 1987). 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 standard deviation (SD) units (as beta diversity), which provides an estimate of compositional change along an environmental or temporal gradient (ter Braak & Verdonschot 1995). To estimate the amount of compositional change of the LC6 Lake and Wuxu Lake records over the last ~200 years, <sup>210</sup>Pb derived sample ages were used as the only constraining variable in DCCA. In DCCA, species data were square-root transformed, no rare species down-weighting was applied, and non-linear rescaling and detrending by segments was used. To place the degree of compositional species turnover into relation, SD units were compared to studies from Smol et al. (2005), Birks (2007) and Hobbs et al. (2010) that used DCCA as a tool to estimate compositional species turnover and established that changes greater than 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). As Procrustes and PROTEST require ordination (e.g. nMDS) scores of like-for-like data, the four data sets (1) LC6 diatom, (2) LC6 pollen, (3) Wuxu diatom, and (4) Wuxu

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230 *pollen* had to be harmonised and adapted to a common time scale before applying 231 nMDS. Therefore, all diatom and pollen samples in taxa percentages from the original 232 data sets were interpolated (by simple linear interpolation) and then re-sampled in 233 five-year intervals from 2000 to 1810 A.D.. 234 All nMDS, Procrustes analysis and PROTEST were performed in R (The R 235 Development Core Team 2008) using the vegan package (Oksanen et al. 2008). The 236 PROTEST function in R, which performs a random permutation test, was modified to 237 allow restricted permutations for time series data (Besag & Clifford 1989). DCCA 238 was implemented using the program CANOCO 4.5 for Windows (ter Braak & 239 Šmilauer 2002) and the interpolation and re-sampling was carried out in AnalySeries

240 2.0.4.2. (Paillard *et al.* 1996).

## **Results**

## 242 Dating

243	A detailed description and interpretation of the LC6 Lake age-depth model is given in
244	Wischnewski et al. (in revision). Therefore, only major features of the model are
245	outlined here. Results of the radiometric dating are summarised in Figure 2. Dry mass
246	sedimentation rates at the core site have been relatively uniform during much of the
247	past 100 years (0.15 cm yr <sup>-1</sup> ), apart from a period of rapid sedimentation rates
248	between 8 and 27 cm core depth. The discrepancy between raw <sup>210</sup> Pb dates calculated
249	using the CRS dating model and a well-defined 1963 <sup>137</sup> Cs date (Appleby 2001)
250	suggest that an extreme event, possibly a landslide or sub-surface sediment slump
251	caused these anomalous sedimentation rates, occurring in the late 1940s or early
252	1950s. This is coincident with the Assam-Tibet earthquake, recorded in August 1950
253	in North India, just ~ 280 km southeast to the site. Therefore, samples from 8-27 cm
254	core depth were excluded from further analyses. Dates below the base of the
255	unsupported <sup>210</sup> Pb record were extrapolated back to ca. 1800 A.D
256	The age chronology for Wuxu Lake is outlined in Figure 3. Unsupported <sup>210</sup> Pb
257	activity declines more or less exponentially with depth, suggesting relatively uniform
258	sedimentation rates (0.10 cm yr <sup>-1</sup> ) during the past 100 years. Small irregularities
259	appear between 4-6 cm depth, corresponding to the early 1960s, but differences
260	between the CRS model and the alternative CIC model were relatively small. <sup>137</sup> Cs
261	activity has a well-defined peak in the 5-5.25 cm section, which almost certainly
262	marks 1963. The <sup>210</sup> Pb dates place 1963 slightly below the depth suggested by the
263	<sup>137</sup> Cs record, possibly caused by the short-term fluctuations in the sedimentation rate
264	mentioned above. The equilibrium between total <sup>210</sup> Pb activity and supporting <sup>226</sup> Ra

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265	was reached at 12 cm depth. Dates below this point were extrapolated back to ca.
266	1652 A.D Two additional <sup>14</sup> C AMS dates, using the leaching residue, support the
267	extrapolated <sup>210</sup> Pb/ <sup>137</sup> Cs chronology. The reservoir-effect was calculated by
268	subtracting the last reliable $^{210}$ Pb/ $^{137}$ Cs age (WX 23) from the non-calibrated
269	radiocarbon age of the same horizon (see Table 2). After reservoir-effect correction
270	(1337±30 years) and age calibration using Calib Rev. 6.0 (Stuiver & Reimer 1993)
271	the base of the core (WX 51) dates back to 1433 A.D 1645 A.D. (2 $\sigma$ -range), which
272	moderately agrees with the <sup>210</sup> Pb-extrapolated date. As high radiocarbon dating
273	residuals and a radiocarbon plateau between ~ A.D. 1780 - 1600 contribute to high
274	uncertainty, radiocarbon ages are regarded as supporting material only. Therefore, the
275	<sup>210</sup> Pb/ <sup>137</sup> Cs chronology is primarily used for the Wuxu Lake age model. The results of
276	the <sup>14</sup> C AMS dates and calculated reservoir effect are summarised in Table 2.
277	Pollen Analysis
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277 278 279 280 281 282 283 284 285 286 287 288	<ul> <li>Pollen Analysis</li> <li>The results of the pollen analysis for LC6 Lake are summarised in Figure 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</li> <li>spectrum is dominated by arboreal and shrub taxa, amongst which <i>Pinus</i> (~ 19%),</li> <li><i>Quercus</i> (~ 19%), <i>Betula</i> (~ 11%), <i>Picea</i> (~ 4%), and <i>Rhododendron</i> (~ 3%) are the most abundant pollen taxa. Herbaceous taxa contribute with mainly <i>Artemisia</i> (~ 12%), Cyperaceae (~ 7%) and <i>Polygonum</i> (~ 4%) to the spectra in moderate amounts.</li> <li>In general, arboreal taxa show a slight increase since the late 1890s, mostly linked to the increase of <i>Pinus</i>, <i>Betula</i>, <i>Abies</i> and <i>Salix</i>, whereas herbaceous taxa decline on the expense of <i>Polygonum</i>, <i>Artemisia</i>, Poaceae and <i>Gentiana</i>. Grazing-taxa (i.e.,</li> <li>Apiaceae, Liliaceae) show slight increases in the 1870s to 1940s and taxa most likely</li> </ul>

289 introduced through human cultivation (i.e., Humulus, Fabaceae) increased in the

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1870s to 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 summarises the results from the Wuxu Lake pollen record. Similar to
the LC6 Lake, no distinct first-order biostratigraphic zone 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 (~ 37%), Pinus (~ 23%),
Betula (~ 6%) and Abies (~ 5%). Herbaceous taxa, mainly comprised of Artemisia,
Cyperaceae and Poaceae contribute with abundances between 2-4%. As at LC6 Lake,
herbaceous taxa decrease since the 1870s in favour for arboreal taxa (mainly Pinus.
and Quercus). Cultivated plants contribute with insignificant amounts to the pollen
spectra and do not show distinct appearances, however, grazing-indicating-taxa (e.g.,
<i>Rumex, Sanguisorba</i> ) are present throughout the core with abundances of ~ $1-2\%$ . 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).

304 Diatom Analysis

305 The diatom stratigraphies of LC6 Lake and Wuxu Lake are illustrated in 306 Figures 6 and 7, respectively. The common feature of both diatom data sets is the 307 small degree of compositional species turnover throughout both cores. In both cases 308 CONISS revealed a low total sum of square (1.0 at Wuxu Lake, 1.7 at LC6 Lake), 309 indicating the absence of first-order biostratigraphic zones. The DCCA yielded a beta-310 diversity of 0.55 SD (p= 0.03) for Wuxu Lake and 0.94 SD (p= 0.59) for LC6 Lake 311 over the last 200 years (Table 3). The diatom taxa of LC6 Lake and Wuxu Lake are 312 plankton-dominated taxa and common in slightly acidic to circumneutral habitats. 313 Many are cosmopolitan species that are commonly found in freshwaters of high-

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314 latitude and alpine regions (Lotter & Bigler 2000; Sorvari *et al.* 2002; Rühland &
315 Smol 2005).

316 The LC6 Lake diatom record revealed 158 species from 39 genera, dominated 317 by monoraphid taxa (Achnanthidium sp., Achnanthes sp. and Psammothidium sp.), 318 Cyclotella sp. and fragilarioid taxa, which contribute with up to 40%, 35% and 20% 319 relative abundance. The most common species is the planktonic diatom Cyclotella 320 ocellata (up to 35%). A subtle but consistent decline of Cyclotella ocellata is apparent 321 throughout the core, accompanied with small increases of Achnanthidium 322 minutissimum, tychoplanktonic Aulacoseira lirata var. lirata and benthic Fragilaria 323 capucina and Cymbella species (Fig. 6). 324 At Wuxu Lake, 120 taxa from 38 genera were identified. The species 325 assemblage was dominated by the planktonic taxa *Cyclotella cyclopunctata* (~ 63%) 326 and Aulacoseira distans (~ 15%). Achnanthidium minutissimum and varieties (~ 5%) 327 and fragilarioid taxa such as *Fragilaria construens* f. venter ( $\sim 3\%$ ) and *Staurosirella* 328 *pinnata* (2%) contribute with small percentage abundances to the benthic component 329 of the diatom assemblage. However, no significant species shifts were detected 330 throughout the record, only subtle changes appear from the 1840s onwards, linked to 331 the appearance of some fragilarioid taxa (Fig. 7). 332 **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
All nMDS biplots are provided as supplementary material online.

Procrustes rotation and the associated PROTEST function were performed on
(a) both pollen data sets, (b) both diatom data sets, (c) pollen and diatom data sets of

the LC6 Lake, and (d) on the pollen and diatom data sets of Wuxu Lake. Table 5

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339	summarises the diagnostics of Procrustes rotation and PROTEST and Figure 8
340	illustrates the goodness of fit between all data sets compared. The size of residuals for
341	each time slice between 1810 A.D. and 2000 A.D. is shown. Low residuals indicate a
342	good agreement between data sets, high residuals indicate a weak agreement. The best
343	fit was produced for the within-lake comparison at LC6 Lake (Fig. 8c). The pollen
344	and diatom record produced a significant and well-correlated fit ( $p=0.02$ , r=0.70). A
345	good fit was also produced between the corresponding pollen records from LC6 Lake
346	and Wuxu Lake ( $p=0.02$ , $r=0.53$ ) (Fig. 8a). However, several time slices display a
347	lower degree of similarity as indicated by higher residuals. The poorest fit was
348	produced between the corresponding diatom records from both lakes, as suggested by
349	a relatively high p value and low PROTEST score ( $p=0.13$ , r=0.43)(Fig. 8b).

#### **Global Change Biology**

## 350 Discussion

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

352 Plateau

353 Regional vs. local response

The pollen records from the LC6 Lake and Wuxu Lake have a very similar species composition and changes in the species composition 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 occur in response to regional, as opposed to local environmental changes. The vegetation pollen assemblages in both records are characteristic for 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 3000-4000 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 as at Wuxu Lake. This most likely represents the more widespread distribution of alpine meadows, as LC6 Lake is located ~ 400 m higher than Wuxu Lake and therefore closer to the sub-alpine shrubland and alpine meadows, typically covering the slopes above 4000 m asl on the southeastern Tibetan Plateau (Chang 1981; Yu et al. 2001).

371 Comparing the diatom records of both lakes with each other, the picture is
372 different. The Procrustean rotation produced an insignificant and poorly correlated fit
373 (Fig. 8b), indicating that the timing, duration or magnitude of change of the diatom

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374	assemblage in response to environmental changes varies between both lakes and that
375	care needs to be taken when making regional climate inferences from the aquatic
376	record alone. Lakes can have fundamentally different properties and therefore
377	different climate sensitive thresholds (Battarbee 2000). Procrustean residuals (Fig. 8b)
378	indicate that mismatches between both aquatic data sets were greatest between 1810-
379	1840 A.D. and between 1940-1975 A.D., which correspond with time periods when
380	compositional turnover is highest in both lake systems (compare DCCA scores in
381	Figures 4 and 5).

382 Compositional species turnover

383 The overall characteristic of both pollen records, is the very stable species 384 composition throughout the entire profile. Species shifts are very subtle over the last 385 200 years (at LC6 Lake) and 350 years (at Wuxu Lake). The low total sum of squares 386 indicated by CONISS and a low compositional species turnover (0.36-0.81 SD) 387 confirm this. For comparison, Birks (2007) investigated compositional species 388 turnover on Holocene pollen-stratigraphical sequences from southern Norway and 389 associated DCCA scores above 1.0 SD units with high compositional turnover and 390 ecologically substantial changes. Compared to the dramatic vegetation shifts on the 391 Tibetan Plateau at the transition from the Lateglacial to the early Holocene or during 392 the mid-Holocene (Jarvis 1993; Demske et al. 2009; Wischnewski et al. 2011), the 393 degree of vegetation change over the last two to four centuries is less significant. 394 Kramer et al. (2010) reconstructed a 2-3°C temperature rise at the 395 Pleistocene/Holocene boundary (using a pollen record from Naleng Lake, southeast 396 Tibet) which triggered the spreading of forest on the expense of the steppe and 397 meadow ecotone. The same record shows a considerable reorganisation of the 398 vegetation during the shorter lived cold event around 8.1 cal. kyr BP, when

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399	temperatures dropped by 1-2 °C (Kramer et al. 2010). DCCA scores for these two
400	time periods (0.64-1.61 SD) indicate substantial ecological changes (unpublished
401	data) (Table 3). You <i>et al.</i> (2007) found a ~ $1.4^{\circ}$ C warming over the last 40 years for
402	the southeastern Tibetan Plateau, but changes in the vegetation structure did not show
403	a similar strong compositional turnover as over the Holocene time scale, suggesting
404	that the length and magnitude of the recent warming period at our sites has not yet led
405	to the crossing of climatically-induced ecological thresholds. However, a further
406	increase in temperature under current warming rates could cause a ecological
407	threshold crossing, similar to that during the Holocene. A direct comparison of the
408	Holocene with the recent past is, however, difficult as previous environmental
409	conditions, e.g. at the Pleistocene/Holocene boundary, were different and trees were
410	not the dominant vegetation type and the vegetation density was generally low
411	(Kramer et al. 2010). With the onset of warmer and moister conditions in the early
412	Holocene, trees could migrate into new niches as climate became more favourable to
413	their growth. During the late Holocene and the recent past these niches were already
414	occupied, so a temperature increase alone would not necessarily cause similar results.
415	Similar to the pollen records, the overall compositional change in both diatom
416	records is very low as well, which is confirmed by low total sum of square scores
417	indicated by CONISS and by a low compositional species turnover (0.55 SD $-$ 0.94
418	SD). For comparison, similar low SD values (0.84 SD) were calculated for diatom
419	records from northern Quebec, where diatom compositional change in agreement with
420	instrumental data suggest no significant warming over the past 150 years (Smol et al.
421	2005). In contrast, lots of other palaeoecological records in the circum arctic show
422	significant shifts in the diatom assemblage, starting in the mid-19 <sup>th</sup> century, with a
423	compositional species turnover of ~ 1 SD - 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 resulting 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 temperature and precipitation increase (You et al. 2007). So far no diatom records exist in the region for comparison of compositional turnover rates. At both sites, diatom evidence suggests that aquatic ecosystems have been relatively stable during the recent centuries, through periods of distinct climate variability. Unlike other regions, these sites have not yet cross climatically-induced ecological thresholds, although we acknowledge that confounding processes, such as increasing precipitation and persistent cloud cover, may act to subdue the impact of increasing temperatures (Wischnewski et al. in revision).

437 Causes of terrestrial and aquatic ecosystem change

438 The terrestrial system

Apart from the low overall compositional change, minor species shifts could be identified in both pollen records. After ~ 1880, both pollen records reveal an increase of arboreal taxa, with an increasing trend lasting until present. 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 defragmentation since the 1950s (Studley 1999). Whilst there is still an ongoing discussion whether forest decline since the mid-Holocene was primarily caused by climatic conditions, human impact, or a combination of both (Yang et al. 2005; Schlütz & Lehmkuhl 2009; Herzschuh et al. 2010; Kramer et al. 2010), the

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448	severe loss of natural forest in the recent past (last 2000 years), and particularly in the
449	past decades (since the 1950s) is attributed to anthropogenic forest clearances as a
450	consequence of the high timber, grazing and agricultural ground demand of a
451	constantly growing population of China(Studley 1999; Zhang et al. 2000; Elvin et al.
452	2002; Dearing et al. 2008). The forest increase since ~ 1880 in the LC6 Lake and
453	Wuxu Lake catchments is mainly linked to species of Quercus, Pinus, Cupressaceae,
454	Abies and Larix. Pinus, Larix and genera of the Cupressaceae family are fast growing
455	tree species that are used for reforestation purposes within governmental programs
456	(Bao & Jiang 1998; Zhang et al. 2000). Furthermore, Quercus-Pinus forests are often
457	described as secondary forests, developing after human disturbance. Their growth is
458	promoted by human-induced fires for the purpose of forest clearance (Winkler 1996;
459	Yan et al. 2005; Shen et al. 2006), suggesting that at least a part of the forest increase
460	results from reforestation, rather than natural forest growth. A historical study of Lake
461	Erhai (SW China) provides evidence that reforestation started as early as the A.D.
462	1780s in some parts on the SE Tibetan Plateau (Elvin et al. 2002). Also, the Wuxu
463	Lake pollen record shows high abundances of grazing indicators (Apiaceae, Rumex,
464	Sanguisorba) from the ~ A.D. 1760s – 1800, indicating anthropo-zoogenic pressures
465	in the study region. The increase of <i>Pinus</i> , Cupressaceae (at LC6 Lake), <i>Larix</i> and
466	Abies (at Wuxu Lake) since the mid-1990s can be linked to China's latest attempts to
467	reforest wide parts of the degraded landscapes in the North, Northwest and Southwest
468	(Three-North Protective Forest Program, start 1978; Natural Forest Conservation
469	Program, start 1998) (Zhang et al. 2000; Fang et al. 2001). Other studies on the
470	southeastern Tibetan Plateau confirm this trend. Shen et al. (2006) identified a sharp
471	increase in Pinus over the past 25 years, and Fang et al. (2001) shows evidence of

472 significant increase in total forest biomass carbon storage since the 1970s, indicating473 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 slight 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 ~ 200 years (Thompson et al. 2000; Thompson et al. 2006; Hou et al. 2007). Furthermore, instrumental data suggest that annual temperatures, and particularly winter and autumn temperatures, increased by 0.30 °C, 0.37°C 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 ~1880, observed at the Wuxu Lake pollen record, could be the response to these climatic trends. 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 20<sup>th</sup> century in both pollen records, may be linked to increasing precipitation rates as reported by You et al. (2007). Hence, the synergistic processes of post Little Ice Age warming, 20<sup>th</sup> century climate warming and extensive reforestations since the 19<sup>th</sup> century have promoted the growth of semi-natural pine-oak forests, intermixed with fir and larch.

#### **Global Change Biology**

496 The aquatic system

Changes in both diatom records after 1880 A.D. are less pronounced than changes in the pollen spectra, but a slight increase in tychoplanktonic and small fragilarioid taxa after the 1930s/50s can be observed in both records. Tychoplanktonic and fragilarioid taxa, which are known to be *R*-strategists, are better adapted to rapidly changing environments (Lotter & Bigler 2000) and therefore indicative for higher ecosystem variability. Furthermore, Kinzie et al. (1998), argue that R-strategist taxa are better adopted to increasing ultraviolet radiation (UVR), possibly indicating changing UVR at the lake site. 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 ~200 years. Even though LC6 Lake and Wuxu Lake are located above 3700 m asl, they closer compare to the temperate montane-boreal lake systems in e.g. North America than to the treeless 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 imagines from the Landsat archive (USGS earth explorer 2010), LC6 Lake and Wuxu Lake are currently eight to ten 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. Additionally, 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

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521 (Heegaard et al. 2006). Furthermore, several studies have shown that the composition 522 and distribution of aquatic organisms is often correlated to changes in the terrestrial 523 environment of the lake (Heegaard et al. 2006). The relative stable vegetation 524 composition in the LC6 Lake and Wuxu Lake catchment over the past two decades, 525 could have contributed to the limited aquatic response. Other factors, such as local 526 temperature peculiarities, increasing precipitation and cloud cover (Wischnewski et 527 *al.* in revision), or negative climate feedbacks due to a constant supply of cold glacier 528 meltwaters (Rühland et al. 2006) introduced to the lakes, could further explain the 3 529 limited diatom response despite the well-established climate warming on the 530 southeastern Tibetan Plateau.

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## 531 Conclusions

532 Despite instrumental and palaeo-climatological evidence of recent climate warming 533 on the southeastern Tibetan Plateau, diatom and pollen records from two montane-534 boreal lakes show only very subtle species compositional changes over the past two to 535 four centuries. The subtle species changes observed, are similar and synchronous in 536 both pollen records, but less similar in the corresponding diatom records, suggesting 537 that the terrestrial records summarise primarily regional environmental changes, 538 whereas the aquatic records possibly capture rather local environmental changes. The 539 combination of aquatic and terrestrial proxies is therefore valuable, to move from a 540 local to a regional scale, but also to understand the many facets of the 541 microenvironments in that complex mountain landscape of the Tibetan Plateau. 542 The overall limited response of the pollen and diatom assemblages from LC6 543 Lake and Wuxu Lake over the last 200 to 350 years suggest that both lakes and their 544 catchments seem to be resilient against the current rate and magnitude of climate 545 warming and that climatically-induced ecological thresholds are not yet crossed. In 546 comparison to the extensive reorganisations of the vegetation in the Holocene that 547 underwent temperature changes of 1-3°C, or to the significant recent shift in diatom 548 communities in many circum-arctic lakes, the current shifts in species and species 549 abundance on the SE Tibetan Plateau are insignificant. 550 More influential and alarming than the current rate of climate warming are the

consequences of human-caused land cover change, that have already caused forest degradation and habitat defragmentation 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

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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, i.e. a trend to less resilient, secondary pine-oak forests, whilst post-Little Ice Age and 20<sup>th</sup> century warming have contributed to their growth, promoting the regeneration of these semi-natural forests on the southeastern Tibetan Plateau. To disentangle to 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), and any further anthropogenic disturbance, will surpass the ecological threshold of these vulnerable secondary forests and cause the further degeneration of the vegetation structure and defragmentation with severe ecological consequences, like reduced water retention capacity, biodiversity reduction and increasing natural disasters (Yan et al. 2005; Cui et al. 2007).

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**Table 1**Selected physical and chemical characteristics of LC6 Lake and Wuxu825Lake

	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 x 300 m, 0.6 km <sup>2</sup>	$1000 \text{ x } 500 \text{ m}, 0.5 \text{ km}^2$
Catchment area	$\sim 7.2 \text{ km}^2$	$\sim 6.5 \text{ km}^2$
Max. water depth	23.0 m	30.8 m
Secchi depth	6.9 m	5.3 m
Conductivity	0.013 mS/cm	0.033 mS/cm
рН	7.00	7.67
Alkalinity	0.4 mmol/l	0.4 mmol/l
Inflow	Mountain runoff	Mountain runoff
Outflow	One outlet	One outlet

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Calibrated

reservoir

corrected

age (a BP)

1718-1827

and

effect

-	Sample	Depth (cm)	Material	<sup>14</sup> C age Leaching residue (a BP)	Calculated reservoir effect (yrs) ( <sup>14</sup> C age – Pb/Cs dated WX 23 age)	Calibrated and reservoir effect corrected age (a A.D.)	<sup>14</sup> C age Humic acid (aBP)	Calculated reservoir effect (yrs) ( <sup>14</sup> C age – Pb/Cs dated WX 23 age)
-	WX 23 WX 51	11.5 35.5	Bulk sed. Bulk sed.	1430±30 1755±35	1377±30 1377±30	1433-1645	1490±25 1655±30	1437±25 1437±25

Wuxu       Pollen       Last 200 yrs       0.3         Diatoms       Last 200 yrs       0.5         LC6       Pollen       Last 200 yrs       0.9         Naleng       Pollen       Last 200 yrs       0.9         Naleng       Pollen       Last 200 yrs       0.9         Pollen       Last 200 yrs       0.9         Naleng       Pollen       Lateglacial/Holocene       1.5         Pollen       Pleistocene/Holocene boundary       1.6         Pollen       "8.2 event"       0.6	Wuxu Pollen Last 200 yrs 0.36 Diatoms Last 200 yrs 0.55 LC6 Pollen Last 200 yrs 0.94 Naleng Pollen Lateglacial/Holocene 1.51 Pollen Pleistocene/Holocene boundary 1.61 Pollen "8.2 event" 0.64		Proxv	Time period	SD u
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Diatoms Last 200 yrs 0.9 Naleng Pollen Lateglacial/Holocene 1.5 Pollen Pleistocene/Holocene boundary 1.6 Pollen "8.2 event" 0.6	Naleng Pollen Lateglacial/Holocene 1.51 Pollen Pleistocene/Holocene boundary 1.61 Pollen "8.2 event" 0.64	LC6	Pollen	Last 200 yrs	0.81
Naleng Pollen Lateglacial/Holocene boundary 1.5 Pollen "8.2 event" 0.6	Naleng Pollen Pleistocene/Holocene boundary 1.51 Pollen "8.2 event" 0.64		Diatoms	Last 200 yrs	0.94
Pollen Pleistocene/Holocene boundary 1.6 Pollen "8.2 event" 0.6	Pollen Pleistocene/Holocene boundary 1.61 Pollen "8.2 event" 0.64	Naleng	Pollen	Lateglacial/Holocene	1.51
Pollen "8.2 event" 0.6	Pollen "8.2 event" 0.64	8	Pollen	Pleistocene/Holocene boundary	1.61
	FOR RELIEN ONLY		Pollen	"8.2 event"	0.64

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835	Table 4	NMDS stress scores and applied distance measure. Data sets 1 - 4 refer
836	to analyses of	n harmonised (interpolated and resampled in 5 year intervals between
837	1810 and 200	0 AD) pollen and diatom counts.

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

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	and the associate	mmetric Procrustes d p value (based c cant fit between data	rotation u n 39 per sets.	using nMD rmutations	S axis scores). Bold print
Comparisons		Procrustes rotation sum of squares	RMSE	PROTES	T (r) P value
(a) LC6 Poll	en vs. Wuxu Pollen	0.72	0.13	0.53	0.02
(b) LC6 Diat	toms vs. Wuxu Diatoms	0.82	0.14	0.43	0.13
(c) LC6 Pollen vs LC6 Diatoms		0.51	0.11	0.70	0.02
(d) Wuxu Po	llen vs Wuxu Diatoms	0.75	0.14	0.49	0.025

 

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# 844 Figure Legend

Figure 1 Location of LC6 Lake and Wuxu Lake and corresponding coring
locations. Nyingchi and Litang are the closest climate stations. Figure adapted from
Google Earth, Landsat, and the Online Map Creation Tool.

Figure 2 Radiometric chronology for LC6 Lake showing the 1963 depth
determined from the <sup>137</sup>Cs, the piecewise CRS model <sup>210</sup>Pb dates and sedimentation
rates, and the CIC model <sup>210</sup>Pb dates calculated for sections above 7.5 cm and below
30 cm

853854Figure 3Age chronology of the Wuxu Lake sediment core showing the CRS855model  $^{210}$ Pb dates, the approximate 1963 depth determined from the  $^{137}$ Cs856stratigraphy, the extrapolated  $^{210}$ Pb/ $^{137}$ Cs age and the (calibrated and reservoir-effect857corrected) radiocarbon age (2σ-range) of the core basis.

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

Figure 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 4 to ease visibility. Italic ages indicate extrapolated ages.

Figure 6 Diatom stratigraphy of LC6 Lake. Selected taxa are shown in relative
abundance. The gap captures the sediment slump between 8 – 27 cm. Italic ages
indicate extrapolated ages.

Figure 7 Diatom stratigraphy of Wuxu Lake. Selected taxa are shown in relative
abundance. Italic ages indicate extrapolated ages.

Figure 8 Within-lake and between-lake comparisons. Results from 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.

883 Supplementary figure nMDS ordination biplots (2D) on interpolated and
884 resampled data sets. Dashed line indicates division between samples older 1880 AD
885 and sample younger 1880 AD.



Location of LC6 Lake and Wuxu Lake and corresponding coring locations. Nyingchi and Litang are the closest climate stations. Figure adapted from Google Earth, Landsat, and the Online Map Creation Tool. 182x60mm (300 x 300 DPI)



Radiometric chronology for LC6 Lake showing the 1963 depth determined from the 137Cs, the piecewise CRS model 210Pb dates and sedimentation rates, and the CIC model 210Pb dates calculated for sections above 7.5 cm and below 30 cm 123x73mm (500 x 500 DPI)



Age chronology of the Wuxu Lake sediment core showing the CRS model 210Pb dates, the approximate 1963 depth determined from the 137Cs stratigraphy, the extrapolated 210Pb/137Cs age and the (calibrated and reservoir-effect corrected) radiocarbon age ( $2\sigma$ -range) of the core basis.

244x116mm (300 x 300 DPI)

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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 abu. Jeen 8 -Ix80mm (J the background exaggerate the original abundance of rare species by 4 to ease visibility. The gap captures the sediment slump between 8 – 27 cm. Italic ages indicate extrapolated ages.

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Within-lake and between-lake comparisons. Results from 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. 188x258mm (300 x 300 DPI)



nMDS ordination biplots (2D) on interpolated and resampled data sets. Dashed line indicates division between samples older 1880 AD and sample younger 1880 AD. 175x172mm (300 x 300 DPI)