

1 **The landscape-atmosphere continuum determines ecological change in alpine lakes of**

2 **SE Tibet**

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12

13 **Abstract**

14 Remote alpine regions were considered to be largely unimpacted by anthropogenic
15 disturbance but it is now clear these areas are changing rapidly. It is often difficult to identify
16 the causal processes underpinning ecological change because the main drivers (direct and
17 indirect climate forcing, land use change and atmospheric deposition) are acting
18 simultaneously. In addition, alpine landscapes are morphometrically complex with strong
19 local environmental gradients creating natural heterogeneity which acts as a variable filter to
20 climate and anthropogenic forcing, emphasizing the need for analyzing responses at multiple
21 sites. The eastern margin of Tibet is a hotspot of global biodiversity, and is affected by both
22 atmospheric N and dust deposition while regional climate warming is comparatively recent.
23 Here we use ^{210}Pb and ^{137}Cs dated sediment records from 9 alpine lakes, and statistical
24 measures of diatom ecological change (turnover and PCA axis 1 scores) to determine
25 regional scale patterns in community response to global environmental change forcing over
26 the last ~150 years. The study lakes showed contrasting ecological responses with increased
27 nutrient input as the primary driver of change, mediated by lake morphology and catchment
28 characteristics. Turnover rates of diatom composition, although low, are significantly
29 associated with lake volume, lake area, altitude and DOC.

30

31 **Introduction**

32 Global scale anthropogenic impacts are so pervasive that there are few ecosystems, however
33 remote, that have not been affected (Battarbee et al., 2002; Wolfe et al., 2013). Alpine
34 landscapes are morphometrically and environmentally complex (Barnard et al., 2006; Larsen
35 et al., 2014): variable relief, geology, soil development, weathering and vegetation patchiness
36 are coupled with multifaceted hydrological pathways to create hydrochemistry that varies at a
37 range of spatial scales (valley, catchment to sub-catchment) (Larsen et al., 2014). This
38 landscape complexity creates a naturally heterogeneous template which acts as a variable
39 filter to climate and anthropogenic disturbance (Seastedt et al., 2004) with the result that it
40 can be difficult to identify representative sites, in terms of their response to forcing, within a
41 given area (Hood et al., 2003).

42 Determining ecological change over decadal to centennial timescales in alpine
43 environments is largely derived from lake sediment records (Catalan et al., 2002) which has
44 provided unambiguous evidence for substantial change in alpine lakes in the European Alps
45 and North American Rocky Mountains (Psenner and Schmidt, 1992; Baron et al., 2000).
46 Although there are numerous individual lake studies, there is growing evidence for local scale
47 variability in how lakes respond to regional drivers, such as climate and/or atmospheric
48 pollution. Lake position in the landscape can determine how it responds to environmental
49 forcing (Webster et al., 2000), emphasizing the need for multiple site studies. Recent
50 developments in landscape limnology have not fully translated to palaeolimnological studies
51 (Anderson, 2014).

52 The influence of climate on alpine lakes has been emphasized (Smol et al., 2005),
53 however, the direct and indirect effect of climate interactions with atmospheric deposition
54 make it difficult to identify drivers. Moreover, reactive nitrogen (Nr) may play an important
55 role in increasing lake production (Bergström and Jansson, 2006). Besides Nr and SO₄

56 deposition associated with industrial emission, atmospheric pollutants also include
57 agriculturally-derived dusts, in which phosphorus is a crucial component/element (Neff et al.,
58 2008). Indirect effects of climate on alpine lakes occur as a result of catchment ontogeny, soil
59 and vegetation development (such as treeline changes) and influence dissolved organic
60 carbon (DOC), pH and nutrient loadings (Anderson, 2000). Changes in glacial runoff can
61 influence terrestrial matter input (Saros et al., 2010), and even reduce lake water temperature
62 (Thies et al., 2007; Slemmons et al., 2013).

63 As well as the effects of long-range trans-boundary pollution and climate changes,
64 local/regional and catchment specific cultural impacts can occur even at high altitudes.
65 Cultural impacts such as transhumance and upland grazing have occurred over millennia in
66 the European Alps (Koinig et al., 2003). More recently, land-cover change (forest
67 exploitation) and land-use intensification have occurred (Tasser et al., 2007). Regional trans-
68 boundary forcing (i.e. N deposition) can be super-imposed on local scale processes (i.e.
69 grazing), while the physical nature of the catchment itself also influences the response of a
70 lake to disturbance (Seastedt et al., 2004; Anderson, 2014).

71 South-west China, which includes the eastern margin of Tibet (Figure 1), is a hotspot of
72 global biodiversity (Myers et al., 2000). It is, however, undergoing rapid ecological change
73 due to global environmental forcing, most notably land-cover change and Nr deposition. In
74 some areas Nr deposition is in excess of 50 kg ha yr^{-1} , grazing stock densities have increased
75 substantially and deforestation and clearance have occurred extensively (Cui and Graf, 2009;
76 Liu et al., 2011); there has also been limited regional warming over the last 100 years (Liang
77 et al., 2009). The interactions of climate, atmospheric deposition and land use as drivers of
78 recent ecological change across SE Tibet are unclear. There is a need to assess the regional
79 synchrony of lake response to anthropogenic drivers in this diverse, high elevation landscape
80 (Chen et al., 2013). We used ^{210}Pb -sediment records from 9 alpine lakes on the eastern

81 margin of Tibet (Sichuan, Yunnan, Qinghai and Tibet, China) combined with statistical
82 measures of ecological change (turnover in diatom assemblages) to determine regional scale
83 patterns in lake response to global environmental change (GEC) forcing over the last ~150
84 years. We explicitly test the hypothesis that there has been minimal ecological change across
85 the region as it has not warmed significantly until very recently.

86

87 **Study sites**

88 The study area lies on the southeast margin of the Tibetan Plateau, stretching across the
89 western section of the Hengduan Mountain range. The topography of this area is
90 characterized by strong and varied vertical relief, resulting from historical tectonic
91 movements. A monsoon climate characterizes this region; a warm and moist summer (May to
92 October) is dominated by the southwest monsoon (Duan and Wu, 2005), with around 77-90%
93 of the annual precipitation falling during summer (details of the regional climate are given in
94 the Supplementary Information).

95 Monitoring of nitrogen deposition in this area indicates a wet deposition rate at Gongga
96 Mountain of $\sim 34 \text{ kg ha}^{-1} \text{ yr}^{-1}$ between 2005 and 2006 (Zhang et al., 2008), while the total N
97 deposition across the SE Tibet Plateau was estimated to be around $20 \text{ kg ha}^{-1} \text{ yr}^{-1}$ in 2013
98 (Zhu et al., 2015). Reactive nitrogen deposition is also accompanied by increased dust
99 deposition (Xu et al., 2009). With increasing human population pressure, transhumance on
100 the rangelands above 3500m on the Tibet Plateau has increased (Miller, 1999).

101 Nine lakes from the SE margin of Tibet Plateau were used in this analysis (Table 1,
102 Figure 1). The study sites are all small fresh water glacial lakes, characterized by low water
103 temperatures, extended periods of ice-cover, low nutrient concentrations and are all fishless.
104 Cuoqia, LC6, Tiancai and Wuxu Lake are forest lakes, while the other lakes are located
105 above the local tree line (3800–4200 m) (Table 1). Except for the catchment of Heihai, the

106 lower levels of which are heavily grazed, none of the sites have direct cultural impacts in
107 their catchments. The inflows at most sites are fed by mountain runoff, but Heihai, Jiren, LC
108 6 and Wuxu also have glaciers in their catchments. The catchment vegetation of lakes below
109 treeline is dominated by *Picea* and *Abies* forest, while the higher altitude lakes are
110 surrounded by *Rhododendron* shrubs and *Kobresia* meadows. Water chemistry data are only
111 available for the lakes from which we took sediment cores.

112

113 **Method**

114 **Materials**

115 The sediment cores from the four new sites used in this study were taken from Cuoqia
116 Lake, Heihai, Jiren and Tiancai Lake in 2012, 2011, 2014 and 2008 respectively. The short
117 cores from Shade Co and Moon Lake were taken in 2011 (Hu et al., 2014). Sediment cores
118 were taken using a Kajak gravity corer, and extruded at 0.5 cm intervals in the field. Cores
119 were dated using ^{210}Pb and ^{137}Cs analyses by direct gamma assay at the Nanjing Institute of
120 Geography and Limnology (see detail in supplementary file). Radiometric dates were
121 calculated using a compound CRS and CIC model (Appleby, 2002) (see Figure S1). Diatom
122 slides were prepared using standard methods and were identified and counted under oil
123 immersion at 1000x using an OLYMPUS BX-51 microscope. A minimum of 500 valves
124 were counted per sample and taxonomy mainly followed (Krammer and Lange-Bertalot,
125 1986-1991). pH and SD was measured in the central part of each lake, and water samples
126 taken for DOC and nutrient analyses. The data from LC 6 and Wuxu Lake are taken from
127 Wischnewski et al. (2011b), while the Dongerwuka data are from Wischnewski et al. (2014),
128 and were extracted using Get Data version 2.20.

129

130 **Numerical analyses**

131 Statistical analyses were undertaken on diatom taxa occurring in at least one sample at
132 1% abundance since ~1860. Diatom data were square root transformed. As an exploratory
133 Detrended Correspondence Analysis (DCA) showed that the gradient lengths of the diatom
134 data from all lakes were short (< 2 SD), the linear ordination model of principal component
135 analysis (PCA) was chosen to summarize the major ecological changes. DCA and PCA
136 analysis was done using CANOCO 4.5. The PCA scores versus age from each lake were
137 tested for temporal autocorrelation before the application of linear regression. For those data
138 without temporal autocorrelation, linear regression was carried out, otherwise, generalised
139 least squares (GLS) models were used. GLS models extend the linear regression by
140 modelling the heterogeneity with covariates. As the data in this study represent time series,
141 allowance for autocorrelation in the residuals was made by introducing an autoregressive
142 moving average process (ARMA) to the model (Zuur et al., 2009). Piece wise regression
143 analysis was also applied to the PCA scores at all the sites. This is a form of regression that
144 allows multiple segment linear models to be fitted to the data for different ranges of X. The
145 boundaries between the segments are breakpoints. (Toms and Lesperance, 2003). Break
146 point analysis can determine the timing of changes in the PCA scores, and the significance of
147 the slope of the piecewise linear regression is tested by the “Davies test”. The slope of
148 segments was not estimated when they represented intervals of less than 5 samples. The use
149 of PCA axis 1 or axis 2 sample scores was determined by the significance (p value) of the
150 linear or GLS model and piecewise regressions and then the R-squared value if they had the
151 same level of significance (see Supplementary Table 1). The auto-correlation test, linear
152 regression, GLS model, piecewise regression and the Davies test were carried out by using
153 ‘nlme’ package (Pinheiro et al., 2014), ‘mgcv’ package (Wood and Wood, 2017) and
154 ‘segmented’ package (Muggeo, 2008) with the R statistical software.

155 With regard to the PCA scores from different lakes, Z-scores were calculated through
156 axis scores centred (minus the mean) and standardized (divided by the standard deviation) for
157 each core respectively to allow direct comparison across cores from different lakes and to
158 derive a regional trend. GAM smoothing of Z-scores was used to summarize the major trends
159 of regional change of diatom assemblage, with the consideration of temporal auto-correlation.
160 The diatom turnover rate (squared root chord distance) of all the lakes was calculated
161 between the core base (average of the samples before 1860 AD) and the surface sediment
162 samples from each core. The correlation between the diatom turnover rate and the
163 environmental characters of the study sites (i.e. altitude, water depth, lake area, DOC,
164 catchment area, lake water pH and secchi disk depth (SD)) was calculated. Squared chord
165 distance values range from 0 to 2 (Williams, 2007).

166 Nitrate and dust concentration in an ice core from the Dasuopu glacier in the Himalaya
167 (Thompson et al., 2000) were used in this study as indicators of atmospheric deposition.
168 Reconstructed summer temperature from tree rings on the Southeast Tibet Plateau (Liang et
169 al., 2009) was also used as a climate record, and this record was significantly correlated with
170 the instrumental Kangding summer temperature since 1951 ($r=0.58$, $p<0.001$). Kangding
171 summer temperature was accessed at the National Climate Center (<http://ncc.cma.gov.cn/cn>).
172 The smoothed trend of the diatom Z-scores was statistically compared with nitrate
173 concentration and temperature data by interpolating of Z-scores according to the nitrate or
174 temperature data.

175

176 **Results**

177 Diatom assemblage change

178 Summary diatom diagrams of 9 lakes are given in Figure 2. The diatom assemblages
179 were divided into two functional groups: planktonic taxa (including *Cyclotella* spp. and
180 *Aulacoseria* spp.) and benthic taxa (including small *Fragilaria* and other benthic species).

181 The diatom assemblages at Shade Co and LC 6 were dominated by benthic taxa
182 (excluding small *Fragilaria*), while *Cyclotella* spp. *sensu lato* dominated at Moon, Wuxu and
183 Dongerwuka Lakes. The dominant species at Heihai and Jiren Lakes were small *Fragilaria*
184 and *Cyclotella*. *Aulacoseira* spp. and benthic species were dominant at Tiancai and Cuoqia
185 Lakes. The diatom assemblage composition change during the last 160 years is mainly
186 reflected in changes in benthic taxa, with only Heihai, Cuoqia and Dongerwuka Lake
187 showing an increase in *Cyclotella* species. Of those lakes located above the treeline, Shade
188 Co was characterized by the increase of *Denticula elegans* since ~1950 and *Cyclotella* spp.
189 exhibited a steady increase since the 1860s. At Moon Lake, diatoms indicative of higher
190 nutrient levels (*Navicula pupula*, *Navicula moskalii* and *Navicula seminulum*) began to
191 increase after ca. 1940. At Jiren Lake small *Fragilaria* began to increase in the 1930s and at
192 Dongerwuka, an increasing trend in *Staurosirella lapponica* at the expense of *Fragilaria*.
193 *construens* f. *venter* from the 1960s, was accompanied by a subtle increase in *Cyclotella*
194 species from ~1970. The changes at Heihai are characterized by the increase in *Cyclotella*
195 *distinguenda* var. *unipunctata* during the 1960s, which was only present at trace level in the
196 lower part of the sediment core.

197 For the four forest lakes, small *Fragilaria*, *Achnanthes* and *Aulacoseira* species
198 increased from the 1950s at LC 6 while at Tiancai Lake showed an increase of small
199 *Fragilaria*, *Pinnularia interrupta*, *Tabellaria fenestrata* and *Tabellaria flocculosa* increased
200 during the 1990s. However, Cuoqia and Wuxu Lakes diatom assemblages are relatively
201 stable, the diatom composition changes are muted, except for the arrival and increase of
202 *Cyclotella schumannii* in the 1990s at Cuoqia Lake.

203 Statistical analyses

204 With the exception of Shade Co, Heihai and LC6 Lake, the temporal autocorrelation of
205 the other 6 lakes can be ignored. A GLS model was used to fit the PCA scores of these three
206 lakes. The results of the linear regression, GLS model and two segment piecewise regression
207 for all the lakes are given in Table S1. Four lakes exhibited significant linear change (as PCA
208 axis 1 scores versus sample age) over the last 160 years: Shade Co, Jiren, Cuoqia, Tianca and
209 Dongewuka Lake; PCA 1 scores of Moon and LC6 Lake are not significant in both linear
210 change and piecewise regression (breakpoint analysis), but significant linear change in PCA
211 axis 2 was observed at both lakes (see Table S1 and Figure S3). The low amount of variance
212 captured by PCA 2 is discussed below. For Moon Lake, PCA 2 scores capture 9% of the
213 diatom variance, while PCA 2 of LC6 capture 21% variance. These secondary gradients were
214 used in subsequent analyses. The two segment piecewise regression on PCA 1 scores was
215 significant at Heihai and Tiancai Lake. The break point dates of the lake located above
216 treeline is 1958 (Heihai Lake); the break points dates of the forest lake is also relatively
217 recent: 1983 (Tiancai) (Table 1). Neither forms of regression analysis (on both PCA-1 and 2
218 scores) at Wuxu Lake (data from Wischnewski et al. (2011a)) were significant (Table S1).

219 The highest diatom turnover rate was observed at Heihai, while the lowest rate was
220 observed at Wuxu Lake (Table 1). As Heihai is the only lake directly affected by cultural
221 impact, this site was excluded from the analysis of the relationship between turnover rate and
222 environmental variables. In the eight remaining lakes, turnover rate is correlated with lake
223 area ($r=0.60$, $p<0.5$), lake volume ($r=0.69$, $p<0.1$), DOC ($r=0.7$, $p<0.5$), and is significantly
224 correlated with log (altitude) ($r=0.81$, $p<0.05$) (Figure 3) (if Heihai is included, the
225 relationships are weaker: lake area ($r=0.53$, $p<0.5$), lake volume ($r=0.51$, $p<0.5$), DOC ($r=0.6$,
226 $p<0.5$) and log (altitude) ($r=0.44$, $p<0.5$)). The Z-scores of PCA scores from 7 lakes (Heihai
227 Lake, which is cultural impacted, and Wuxu Lake where there was no significant regression

228 fit, were excluded), showed an increasing trend overall, especially after ca. 1950. PCA scores
229 include PCA-1 scores from 5 lakes (i.e. excluding Heihai, Moon, LC6 and Wuxu Lakes) and
230 the PCA-2 scores from Moon Lake and LC6. The loess smoother fitted to the diatom Z-
231 scores and nitrate from an Himalayan ice core are significantly correlated ($r=0.89$, $p<0.001$,
232 $n=36$) (Figure 4). The linear change of Z scores is not correlated with the temperature record,
233 which only showed unambiguous change from the 1980s in most areas (Figure 4). The nitrate
234 concentration in an Himalayan ice core exhibits a linear change since the 1860s (Thompson
235 et al., 2000), which implies an important role for in-lake nutrient increases associated with
236 regional N deposition (Figure 4).

237

238 **Discussion**

239 Diatom assemblage changes

240 The diatom assemblages in the nine lakes exhibit spatial and temporally variable responses
241 within an alpine landscape over the last 160 years. Most interesting, perhaps, are the variable
242 responses of the functional groups among the different lakes. There are lakes that are today
243 dominated by planktonic taxa (e.g. Moon, Heihai, Tiancai, Wuxu and Dongerwuka Lake) and
244 benthic diatoms (e.g. Shade Co, Jiren, Cuoqia and LC6 Lake). The differences between
245 benthic and planktonic forms reflect ecological responses to the external forcing mediated by
246 morphometric differences among the different lakes as well as contrasting changing light and
247 stratification patterns (Saros et al., 2012). The change of *Cyclotella* [*sensu lato*] species was
248 not unidirectional within the region and importantly this genus has been abundant in Tibetan
249 lakes for millennia (Hu et al., 2015). In contrast, noticeable changes in benthic taxa have been
250 observed in the SE Tibetan lakes over the last 160 yrs (Hu et al., 2014). There are some
251 alpine lakes that show long-term (10^3 yr) stability in their diatom assemblages, such as

252 Tiancai Lake (included in this study) during the Holocene (Chen et al., 2014), although the
253 climate change was inferred from the pollen record at this site (Xiao et al., 2014).

254 Benthic and epiphytic diatom communities growing in the littoral zone are closer to
255 catchment-derived nutrient sources and also experience different light climates compared
256 with planktonic taxa. The littoral zone often acts as a filter of catchment inputs, such as DOC
257 and nutrients which can be preferentially retained thereby enhancing benthic production
258 (Reynolds, 2008). Therefore, the benthic communities have a competitive advantage due to
259 their proximity to catchment inputs when compared with pelagic assemblages. At Moon
260 Lake, Heihai and LC 6, the relative abundance of benthic species all showed subtle increases
261 after ~1947, 1963 and 1953, respectively (Figure 2). It has been hypothesized that the
262 increased abundance and diversity of benthic species may reflect increased habitat
263 availability associated with regional warming (Smol et al., 2005), but increased benthic
264 diversity is also observed at sites undergoing cooling (Lotter and Bigler, 2000). Benthic algae
265 in the littoral zone are also directly affected by dust deposition. Consequently, the increased
266 abundance of benthic communities may be associated with enrichment by atmosphere
267 deposition.

268

269 Diatom turnover rates variation with lake characteristics

270 Four lakes had significant changes in ecological trajectory as identified by piecewise
271 regression (Figure S3). At Heihai Lake, which also has the highest turnover rate, the change
272 occurred around 1958, which predates the increase in air temperature observed at a nearby
273 meteorological site from 1965; the change is more likely associated with the start of grazing
274 of the lake catchment (personal communication with local citizens). At the forest lake Tiancai
275 change occurred post-1980 and was mainly associated with benthic taxa. The later response
276 of the lake located below the tree-line may be due to the buffering effect of DOC (De

277 Laurentiis et al., 2012) (Figure 3c, d). DOC is a primary regulator of many physical, chemical
278 and biological characters of lakes, and is particularly associated with water transparency,
279 mixing depth etc. (Read and Rose, 2013) which directly impact algae (Fee et al. 1996).

280 The turnover rate of the diatom assemblages decreased with increasing lake area and
281 volume and decreased with increasing elevation (Figure 3a, b, d), suggesting that the smaller
282 lakes located at higher elevation are more sensitive to environmental change. When
283 comparing lakes at similar altitude, larger lakes have stronger resistance to fluctuations in
284 regional air temperatures and their greater volume can dilute increased nutrient input more
285 than in smaller lakes. These effects are illustrated by the limited diatom assemblage changes
286 at Wuxu Lake, which is located below the tree line and at a lower elevation than LC 6 Lake
287 but has a similar lake area; this lake is large relative to the other forest lakes (Cuoqia and
288 Tiancai Lake) (Table 1). The smaller lakes showed greater variation than larger lakes in terms
289 of limnology, water clarity and DOC concentration in an investigation of Canadian Shield
290 lakes (Fee, 1996). In the Austrian Niedere Tauern, excluding lakes located above the snow
291 line, higher altitude lakes presented more sensitivity to climate change than lower altitude
292 lakes (Thompson et al., 2005).

293 The contrasting patterns and non-synchronous response of the nine study lakes reflect
294 the interplay of a range of environmental drivers. The effect of multiple drivers was evident
295 at the regional as well as the site-specific scale. Although the PCA axes from all lakes do not
296 track the regional climate (temperature) change trend (Figure 4), the indirect influence of
297 climate through lake thermal regimes and/or catchment processes cannot be excluded. The
298 limited diatom response at LC 6 may reflect the weak thermal stratification at this site
299 (Wischnewski et al., 2011b). Lake catchment can act as a site-specific filter of both climate
300 and atmospheric deposition effects of ecological change in lakes (Anderson, 2014). The
301 delayed and muted response of lakes below the treeline may be related to terrestrial

302 vegetation and DOC export, the latter is an important factor determining the sensitivity of
303 lakes due to its buffering of water temperature (DOC alters heat absorbance (Leavitt et al.,
304 1997)). The lakes located above the treeline are surrounded by sparsely vegetated fell field,
305 and have lower DOC concentration than the forest lakes (De Laurentiis et al., 2012).
306 Catchment influence on biological change may be particularly pronounced in high alpine
307 lakes with low DOC, as even slight reductions in DOC following droughts or acidification
308 can substantially increase penetration of UV radiation (Leavitt et al., 1997). This inference is
309 supported by the significant relationship between the diatom turnover rate with decreased
310 DOC and increased lake elevation (Figure 3c, d).

311

312 Drivers of diatom assemblage change

313 Direct cultural influence on landscape-lake interactions is mainly through grazing and
314 deforestation in alpine regions (Kreutzweiser et al., 2008; Anderson, 2014) (see below).
315 Nutrient sources for these alpine lakes in SE Tibet include atmospheric deposition (both Nr
316 and dust), yak faeces and enhanced input of soil nutrients associated with erosion resulting
317 from overgrazing grazing in the catchment. At some sites, glacier melt water can be an added
318 nutrient source (Saros et al., 2010).

319 The current N deposition rate in the mountains of SE Tibet is high (around 40 kg N ha^{-1}
320 yr^{-1}) (Zhang et al., 2012), and close to or above the estimated critical load of N deposition for
321 this region (Liu et al., 2011). In this area atmospheric N deposition has a distinct seasonal
322 signal, due to its relationship with precipitation (Jia et al., 2014). In southeast Tibet, the Nr
323 deposition is mainly derived from anthropogenic sources in south Asia, and transported by
324 the Indian monsoon during the summer (Liu et al., 2015). The diatom assemblage Z-scores
325 for all lakes (excluding Wuxu Lake, which is more resistant to change than other lakes due to
326 its relative large lake area combined with lower altitude) exhibit a significant relationship

327 with the trend in NO₃ concentration in a Himalayan Ice core, which increased linearly from
328 ~1850 (Thompson et al., 2000) (Figure 4). Besides N, however, P is also an important
329 nutrient control on lake productivity. With N saturation Bergström and Jansson (2006) found
330 evidence that P had begun limiting productivity in oligotrophic lakes previously limited by N.
331 Increased atmospheric phosphorus load in the Pyrenees caused lakes to revert from
332 phosphorus to nitrogen limitation (Camarero and Catalan, 2012). A global investigation
333 revealed that dust is enriched in nutrients, especially P (Lawrence and Neff, 2009). In the
334 Mediterranean region, the atmospheric deposition of dust is an important source of
335 phosphorus affecting biogeochemistry of oligotrophic high mountain lakes, which is
336 associated with dryfall mainly during spring and summer, similar to the regime of Saharan
337 dust export to this area (Morales-Baquero et al., 2006). It has been suggested that over 80%
338 of total P deposition in SE Tibet can be attributed to dust, with the total phosphorus
339 deposition rate at around 50-100 g ha⁻¹ yr⁻¹ (Mahowald et al., 2008). Glaciers in the south
340 eastern Tibetan Plateau record the influx of dust generated in the arid and semi-arid regions
341 to the west (Wake et al., 1994).

342 Land-cover change at lower altitude will also contribute to the regional dust load.
343 Grazing, deforestation and burning are important cultural factors in Southeast Tibet
344 (Herzschuh et al., 2009) that increase erosion rates and deflation from soils. In addition,
345 recent changes to the soil microbial community, soil properties and plant community near the
346 tree line zone have been observed in eastern Tibet (Xiong et al., 2016). Remote sensing data
347 indicate that the vegetation changed from mixed forests into cropland and built-up areas
348 between 1950 and 2000 at this region (Cui and Graf, 2009). Deforestation has increased
349 surface runoff (Cui et al., 2007), while the expanded area of cropland has also increased the
350 use of fertilizer. Transhumance is an important cause of alpine meadow degeneration on the
351 Tibetan Plateau (Harris, 2010). In this study, the alpine meadow of the Heihai Lake

352 catchment is overgrazed, and is probably the main reason for the sudden increase of small
353 *Cyclotella* species around 1963.

354 Glaciers are also an important landscape feature of a number of the study sites (Table
355 1), and glacial runoff may affect algal communities through hydrology (flushing rates),
356 physical characteristics (light) and biogeochemistry (nutrients) (Slemmons et al., 2015). The
357 effect of alpine glacial meltwater on algal composition in lakes has been reported in the
358 central Rocky Mountains (USA), with greater diatom assemblage turnover in a glacially-fed
359 lake than in a neighbouring snow-fed lake during the late Holocene, most likely through
360 enhanced nitrogen delivery (Slemmons et al., 2015). Enhanced input of cold glacial
361 meltwater may also lower lake water temperatures, which would offset the effects of regional
362 warming. Integrating the results of the statistical analyses, it appears that the lakes above the
363 treeline are more responsive to regional environmental forcing than forest lakes. In contrast to
364 lakes located above tree line, the change in the forest lakes was muted (the average turnover
365 rate of forest lakes is 0.51, 0.80 for lakes above treeline) Moreover, sensitivity also
366 decreased with increasing lake size, e.g. Dongerwuka Lake (see above); and at most of the 9
367 study lakes benthic diatoms showed an earlier response to the environmental change rather
368 than planktonic diatoms, including *Cyclotella sensu lato* as has been observed in alpine
369 regions in North American and Europe (Saros and Anderson, 2015).

370 Although the relatively higher rates of change are observed in lakes located above
371 treeline, the overall composition change is low (0.07–1.0 SD). Given the high N deposition
372 rate, the subtle change in the diatom assemblage contrasts with the biological change in
373 alpine lakes in the Rocky Mountains which occurred at a N deposition rate of 1.5–3 kg N ha⁻¹
374 yr⁻¹ (Bowman et al., 2012). This difference, while counter-intuitive, may result from the very
375 different nutrient delivery regimes. Spring snow meltwater is the main mechanism for N_r
376 delivery in alpine lakes in the Rocky Mountains (Bowman, 1992). In SE Tibet, the surface

377 runoff to the lakes, increased flushing rate, and the wet N deposition all reach their maximum
378 during the summer monsoon season when substantial precipitation events contribute up to 70-
379 80% of total precipitation (Bräuning and Mantwill, 2004). In contrast, the growing season for
380 diatoms is in the spring and autumn primarily. Therefore, wet deposition is limited during the
381 main diatom growing season. Moreover, the regional summer monsoon climate results in
382 different nutrient seasonality, light availability and thermal regimes (Wang et al., 2015),
383 when compared with lakes in Europe and North America. The factors above may contribute
384 to the relatively subtle changes in the diatom assemblage in alpine lakes in SE Tibet.

385

386 **Conclusion**

387 The nine study lakes showed contrasting ecological responses reflecting the interplay of a
388 range of environmental drivers, landscape and morphometric factors. The significant
389 correlation between regional diatom change and the ice core record of nitrate deposition
390 (Figure 4), suggests that increased nutrient input is the primary driver of change in these
391 lakes. As well as atmospheric deposition, nutrient sources may include grazing and glacier
392 meltwater. The turnover rates of diatom composition are correlated with lake volume, lake
393 area, DOC and altitude, which indicate the importance of lake morphology and catchment
394 characteristics.

395

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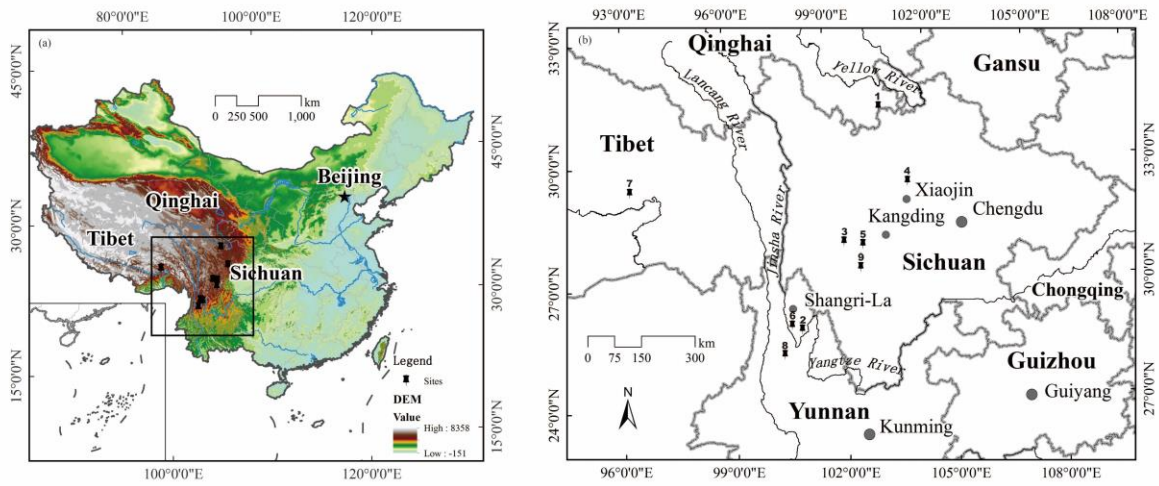
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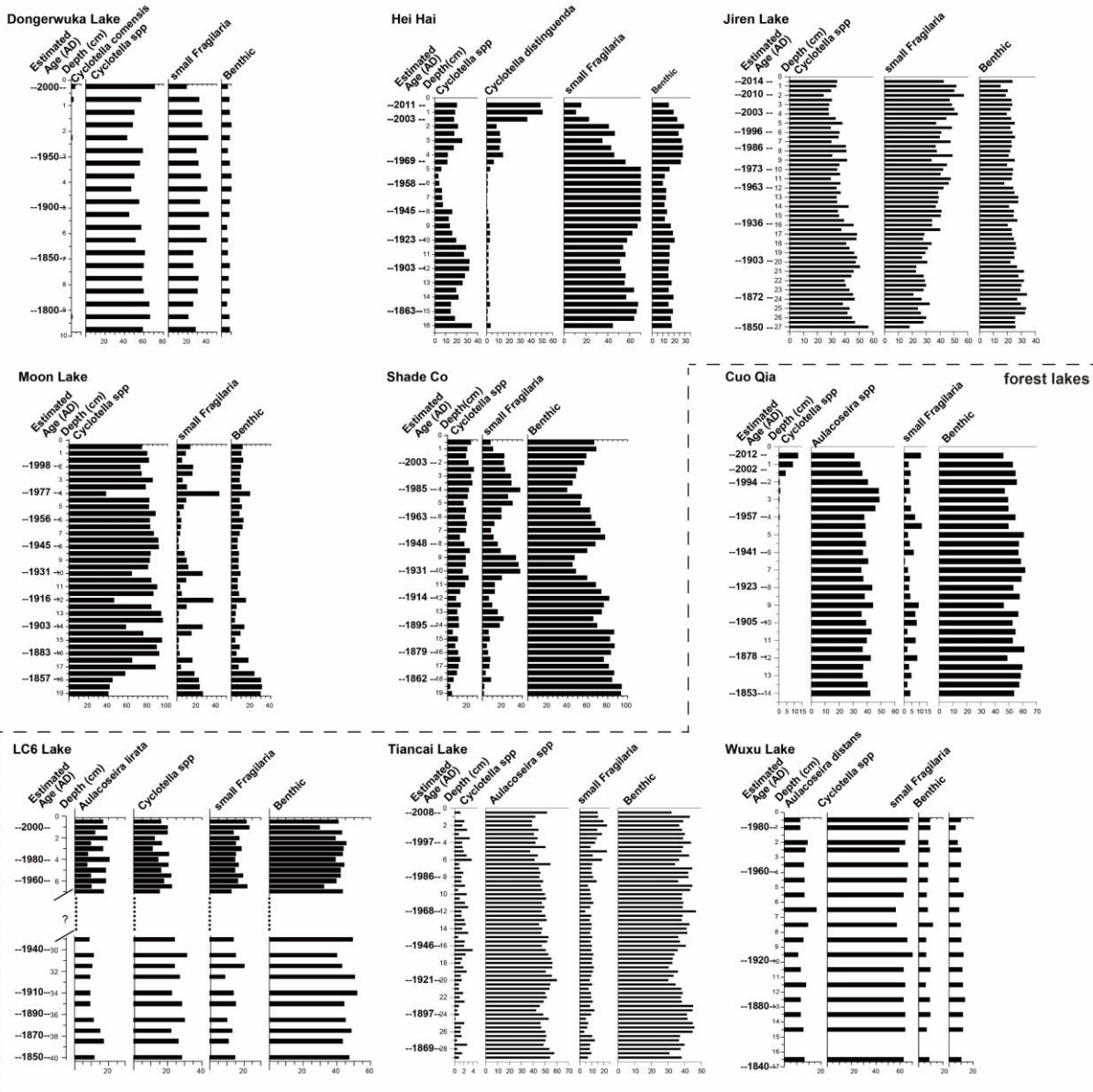
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643 **Figures:**



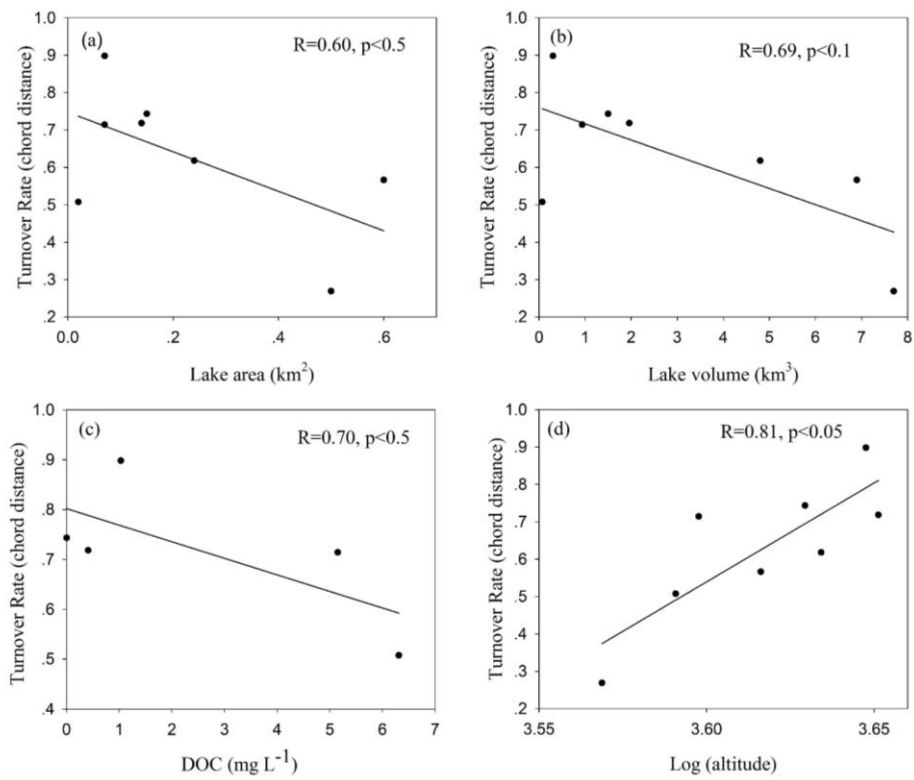
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645 Figure 1 Location of SE Tibet (a), location of the 9 alpine lakes in SE Tibet (b): including
646 above treeline lakes: 1, Dongewuka Lake; 2, Hei Hai; 3, Jiren Lake; 4, Moon Lake; 5, Shade
647 Co; and forest lakes: 6, Cuo Qia; 7, LC6; 8, Tiancai Lake; 9, Wuxu Lake.



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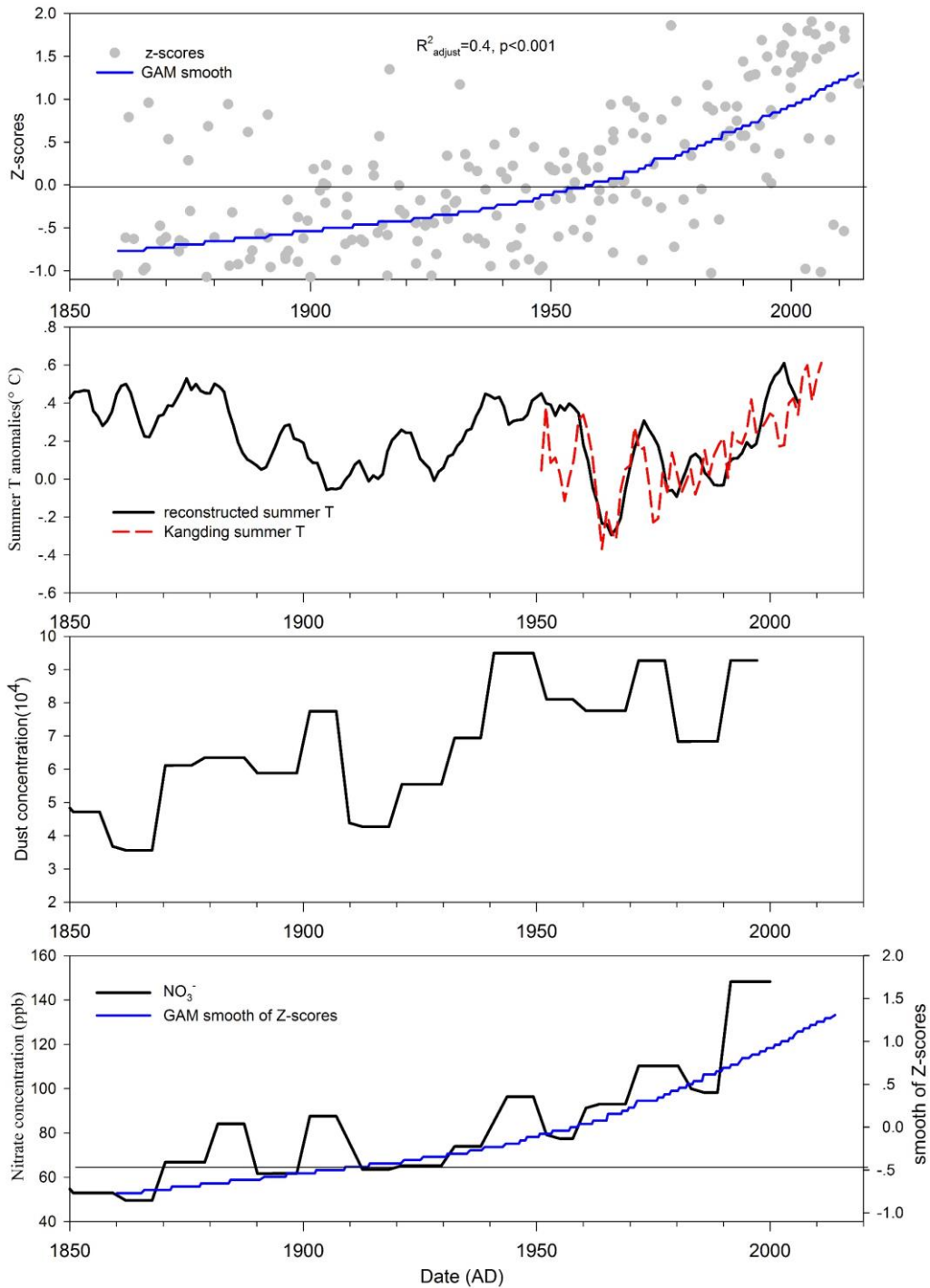
649 Figure 2 Summary diatom profiles for the study lakes: lakes above the treeline: Dongerwuka
 650 Lake; Hei Hai; Jiren Lake; Moon Lake; Shade Co; and forest lakes: Cuo Qia; LC6; Tiancai
 651 Lake; Wuxu Lake.



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653 Figure 3. Diatom turnover rate versus (a) lake area, (b) volume, (c) DOC (for only 5 lakes)

654 and (d) altitude.



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656 Figure 4. Comparison of Z-scores of PCA sample scores from 7 lakes (excluding Heihai and

657 Wuxu Lake): PCA 1 scores from 5 lakes and PCA 2 scores from Moon Lake and LC 6;

658 reconstructed summer temperature from tree rings on the Southeast Tibet Plateau (Liang et

659 al., 2009), dust and nitrate concentration from Himalayan Ice Core (Thompson et al., 2000).

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Table 1 location, characteristics, significant breakpoints of two segment piecewise regression and turnover rate of 9 alpine lakes (divided into above treeline lakes and forest lakes according to lake altitude)

Lake names	Above treeline lakes					Forest lakes			
	Dongerwuka Lake	Heihai Lake	Jiren Lake	Moon Lake	Shade Co	Cuoqia Lake	LC6 Lake	Tiancai Lake	Wuxu Lake
Latitude(°N)	33°13.2'	27°21'	29°43'	31°29'	29°44'	27°24'	29°49'	26°38'	29°9'
Longitude(°E)	101°7'	100°04'	100°48'	102°20'	101°21'	99°46'	94°27'	99°43'	101°24'
Altitude(m)	4307	4118	4480	4260	4442	3960	4132	3898	3705
Lake area (km ²)	0.24	0.18	0.14	0.15	0.07	0.07	0.6	0.02	0.5
Catchment area (km ²)	1.7	1.69	5.29	1.54	2.73	0.44	7.2	0.55	6.5
Catchment: lake area	7.1	9.4	37.7	10.3	39	6.3	12	27.5	13
Maximum depth (m)	40	42.2	28	20	8.7	26.8	23	7	30.8
pH	8	7.9	7.39	7.42	7.79	6.67	7	7.45	7.67
SD	6.8	4.5	8.5	6	8	3.7	6.9	3	5.3
TN (mg L ⁻¹)		0.26	0.61	0.25	0.26	0.08		0.33	0.19
TP (mg L ⁻¹)		0.013	0.083	<0.001	0.004	0.01		0.048	0.025
DOC (mg L ⁻¹)		1.42	0.41	0.001	1.03	5.15		6.31	
Significant breakpoint	-	1958	-	-	-	-	-	1983	-
Diatom Turnover rate	0.62	1.00	0.72	0.74	0.90	0.71	0.57	0.51	0.27
Reference	Wischnewski et al., 2014	this study	this study	Hu et al., 2014	Hu et al., 2014	this study	Wischnewski et al., 2011	this study	Wischnewski et al., 2011

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