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

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Abstract

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

Introduction

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

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

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

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

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

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

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

Study sites

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

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

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

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

Method

Materials

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

Numerical analyses

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

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

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

Results

Diatom assemblage change

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

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

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

Statistical analyses

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

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

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

Discussion

Diatom assemblage changes

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

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

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

Diatom turnover rates variation with lake characteristics

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

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

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

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

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

Drivers of diatom assemblage change

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

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

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

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

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

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

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

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

Conclusion

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

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Figures:

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

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

Figure 4. Comparison of Z-scores of PCA sample scores from 7 lakes (excluding Heihai and Wuxu Lake): PCA 1 scores from 5 lakes and PCA 2 scores from Moon Lake and LC 6; reconstructed summer temperature from tree rings on the Southeast Tibet Plateau (Liang et 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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