Reviews and syntheses: How do abiotic and biotic processes respond to climatic variations at the Nam Co catchment (Tibetan Plateau)?

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Abstract. The Tibetan Plateau (TP) is the largest alpine plateau on Earth and plays an important role in global climate dynamics. On the TP, climate change is happening particularly fast, with an increase in air temperature twice the global average. The particular sensitivity of this high mountainous environment allows the observation and tracking of abiotic and biotic feedback mechanisms. Closed lake systems, such as the Nam Co on the central TP represent important natural laboratories for tracking past and recent climatic oscillations, as well as geobiological processes and interactions within their respective catchments. This review gives an interdisciplinary overview of modern and paleoenvironmental changes, focusing on Nam Co as model system. In the catchment area, the steep rise in air temperature forced glaciers to melt, leading to a rise in lake levels and changes in water chemistry. Some studies base their conclusions on inconsistent glacier inventories but an ever-increasing deglaciation and thus higher water availability have persisted over the last decades. The enhanced water availability causes translocation of sediments, nutrients and dissolved organic matter to the lake, as well as higher carbon emissions to the atmosphere. The intensity of grazing has a significant effect on CO_2 fluxes, with moderate grazing enhancing belowground allocation of carbon while adversely affecting the C-sink potential through reduction of above- and subsurface biomass at higher grazing intensities. Furthermore, increasing pressure from human activities and livestock grazing are enhancing grassland degradation processes, thus shaping biodiversity patterns in the lake and catchment. The environmental signal provided by taxon-specific analysis (e.g. diatoms and ostracods) in Nam Co have revealed profound climatic fluctuations between warmer/cooler and wetter/drier periods since the late Pleistocene and an increasing input of freshwater and nutrients from the catchment in recent years. Based on the reviewed literature, we outline perspectives to further understand the effects of global warming on geo- and biodiversity and their interplay in the Lake Nam Co, which acts as a case study for potentially TP-wide processes that are currently shaping the earth's future.

Key words: bioindicators, carbon cycle, climate change, climate reconstruction, deglaciation, geobiodiversity, lake level change, lake Nam Co, paleo-environmental proxies, pasture degradation

1 Introduction

The Tibetan Plateau (TP), often referred to as "The Third Pole" and "The Water Tower of East Asia", is the highest and largest alpine plateau on earth. With an area of about 2.5 million km² at an average altitude of > 4000 m above sea level (a.s.l.), it includes the entire southwestern Chinese provinces of Tibet and Qinghai, parts of Gansu, Yunnan, Sichuan and neighboring countries (Fig. 1). The basins on the TP are forming the headwaters of several major rivers (i.e., Amu Darya, Brahmaputra, Ganges, Hexi, Indus, Mekong, Salween, Yangtze, and Yellow) providing fresh water for ~1.65 billion people and to many ecosystems in greater Asia (Cuo and Zhang, 2017). On the TP, the effects of climate change are expressed stronger than the global average, showing a steep rise in air temperature of about 0.3°C per decade since 1960 (Yao et al., 2007) and a moderate rise in precipitation during the last decades (Dong et al., 2018). The warming rate increases with altitude (Pepin et al., 2015) which is why the air temperature on the TP is soaring roughly twice the global average, thus substantially affecting the geo-

and biodiversity. Glaciers and lakes are the dominant components for the Tibetan water sources, and their actual status and future development are strongly impacted by global warming. Since the 1990's, nearly all glaciers on the TP have exhibited retreat, causing a 5.5 % increase in river runoff from the Plateau (Yao et al., 2007). The consequences of deglaciation and permafrost degradation (Wu et al., 2010) are observable in higher water and sediment fluxes, relief changes and arising natural

5   hazards (floods, rock falls, landslides, desertification, ecosystem degradation). Consequently, landscapes are continuously being rearranged which alters the spatial distribution and composition of the inhabiting species, many of which are endemic to the TP (Walther et al., 2002). Even conservative estimates predict substantial species extinction and considerable changes to the ecosystems (Chen et al., 2011; Bellard et al., 2012). The future trajectory of such complex processes is difficult to map accurately, thus it is important to monitor the current state as well as the evolution of this highly sensitive region. The large

10   number of water bodies on the TP, its geological diversity, climatic setting as well as sensitivity to climate change, and still relatively little human impact make it a unique natural laboratory, which could be used as an early warning system for other alpine environments. Many lakes on the TP are superficially closed systems, which is why they are particularly suitable as "thermometers" and "rain gauges" to measure the climatic, hydrological, geomorphological, pedological and ecological changes in their respective catchments. With an area of 2018 km², Nam Co is the second largest lake on the central TP. As an

15   endorheic system, it acts as a sink for water, sediment and carbon fluxes, making it an excellent model ecosystem. With good accessibility and infrastructure such as the Nam Co Monitoring and Research Station for Multisphere Interactions (NAMORS), the Nam Co catchment has become a frequent study location for monitoring and tracking of environmental changes over various timescales.

Here we present an interdisciplinary overview of how earth-surface fluxes have developed with changing environmental

20   conditions and which consequences are to be expected for biodiversity as well as for water, sediment and carbon fluxes within the model ecosystem of the Nam Co catchment on the central TP. In particular, this review considers past and modern geobiodiversity changes with focus on glacier retreat in relation to hydrological patterns and changes in lake water chemistry. The corresponding changes in terrestrial ecosystems concerning carbon cycle, greenhouse gas releases as well as pasture degradation are discussed. We provide an overview of how the paleoenvironment on the Tibetan Plateau with respect to

25   landscape evolution around Nam Co was shaped by geodiversity, lake level changes and Holocene vegetation cover. Lastly, based on the available studies, this review identifies the major research gaps that are awaiting further exploration and comparison with other high-altitude environments.
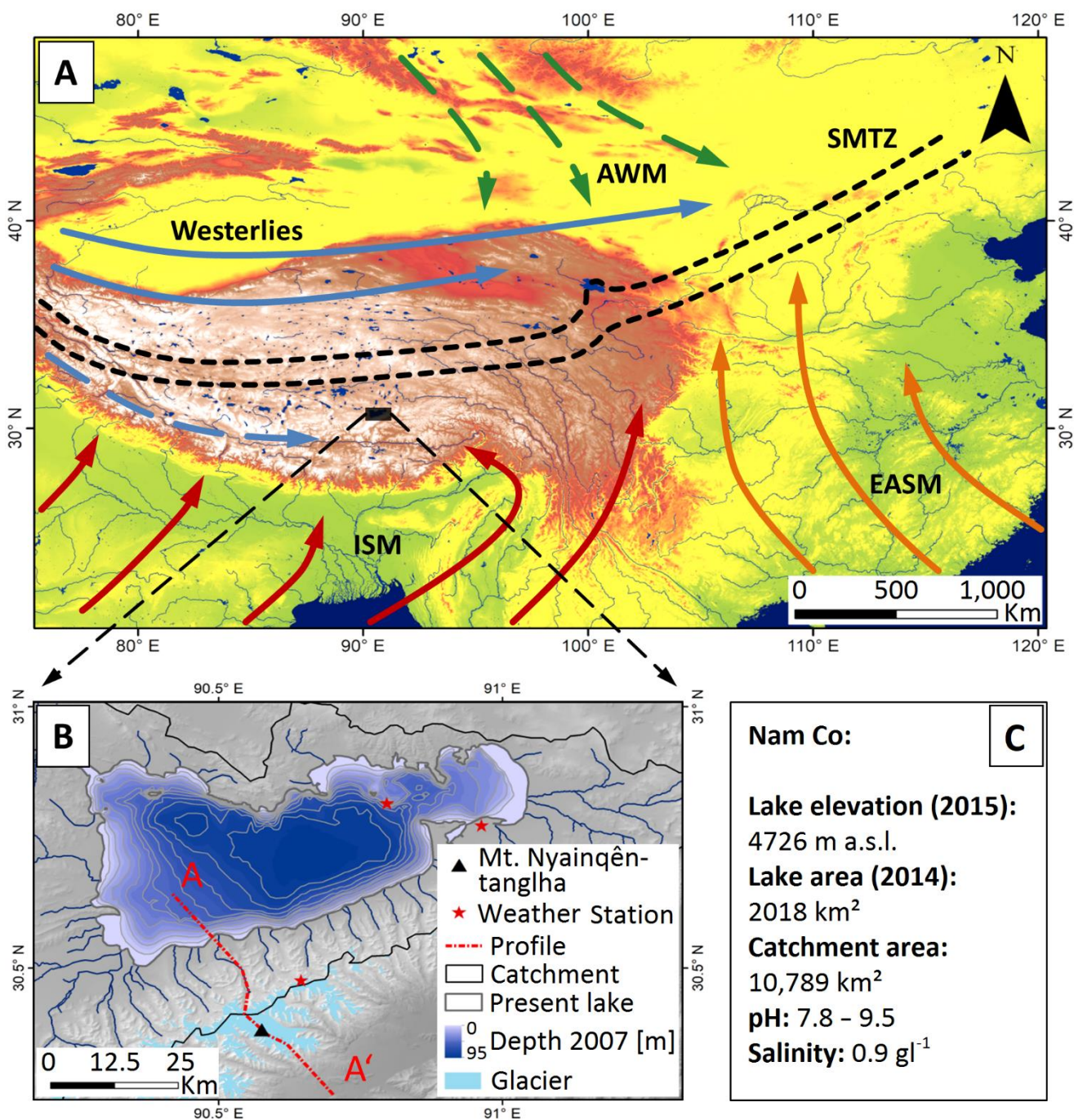
Figure 1. Major atmospheric systems governing the climate in China (A); Nam Co study site (B); and characteristics of Nam Co's catchment (C). A: Continuous arrows indicate systems active in summer. These are the Indian Summer Monsoon (ISM) in red, the East Asian Summer Monsoon (EASM) in orange and the Westerlies in blue. Dashed arrows represent systems active in winter. These

5 **are the Asian Winter Monsoon (AWM) in green and southern parts of the Westerlies in blue. The black dotted lines denote the**

2 Environmental changes in lake Nam Co and its catchment

2.1 Climatic characteristics of the Nam Co basin

The prevailing climate at Nam Co is characterized by strong seasonality, with long, cold winters and short but moist summers. During winter, the Westerlies control the general circulation and lead to cold and dry weather, with temperature minima below -20 °C. In springtime, the TP heats up and allows the melt water to percolate to deeper soil layers. The drought situation increases gradually until the monsoon rains arrive, typically between May and June. During autumn, weather shifts again to clear, cold and dry conditions (Yao et al., 2013). The mean annual temperature measured at the NAMORS research station (Fig. 1) between 2006 and 2017 was -0.6 °C and the annual precipitation was between 291-569 mm (mean = 405 mm), with the majority occurring during the monsoon season from May to September (Wei et al., 2012). However, the precipitation rates are subject to spatial variations due to the > 7000 m high Nyainqêntanglha mountain range which represents the southern border of the lake catchment. This leads to considerably larger glacial areas in the southwestern part (~700 km^2) than in the northeastern part of the mountain range (~100 km²) (Bolch et al., 2010).

2.2 Glacier retreat and hydrological patterns of Nam Co

The rise of satellites such as Envisat, CryoSat and ICESat and the increasingly wide-spread availability of their data, have enabled the accurate study of lake and glacier parameters as far back as the early 1970's (Wu and Zhu, 2008; Zhu et al., 2010b; Liao et al., 2013). The size of Nam Co as well as the extent and distribution of glaciers in the Nyainqêntanglha mountain range have been the subject of many publications over the recent years (Yao et al., 2007; Frauenfelder and Kääb, 2009; Bolch et al., 2010; Wang et al., 2013; Fig. 2; Table 1). Due to different data sources with varying resolutions as well as different mapping procedures, the estimated glacier area varies between different studies (Fig. 2; Table 1), as the delineation of debris- and snow-covered glaciers is rather subjective (Wu et al., 2016). This is especially true for the first glacier inventory (Li et al. 2003), which has been discussed in various studies due to inaccuracies and the quality of its base data (Frauenfelder and Kääb, 2009; Bolch et al., 2010). Nevertheless, recent studies show glacier shrinkage in the Nyainqêntanglha mountain range at a rate of 0.3–0.5 % yr^{-1} as measured since 1970 when the first satellite images were acquired (Fig. 2; Table 1). As a result of this glacier melting, the lake surface area has expanded from ca. 1930 km² to ca. 2018 km² at a rate of 2.1 km² yr^{-1} (Fig. 3A), and the lake level has risen at a rate of 0.3 m yr^{-1} until approximately 2009, and at lower rates since then (Fig. 3B). The initial rising trends

of both lake level and surface area are mirrored by most lakes in the southern part of the TP, but the slowdown of this trend observed at lake Nam Co around 2009 seems unique (Jiang et al., 2017). This suggests that the lakes on the TP react to changing environmental parameters in a variety of different ways, and that geographical proximity among lakes does not necessarily produce similar reactions to change. The effects on freshwater input to the lake are discussed in the following section (2.3).

5 Although changes in monsoonal precipitation and wind direction may influence glacial retreat rates (Wang et al., 2013), rising temperatures remain their primary cause (Ji et al., 2018). The total contribution of glacial melt water as surface runoff to this lake level increase has been estimated ranging from 10 % to 53 % (Zhu et al., 2010b; Lei et al., 2013; Wu et al., 2014; Li and Lin, 2017), with recent studies at the lower end of this spectrum. Increased precipitation is estimated to be responsible for 50–70 % of lake growth (Zhu et al., 2010b; Lei et al., 2013). Whether there is a change in evaporation remains unclear as studies

10 for approximately the same time period have suggested both a slightly increasing and a slightly decreasing evaporation rate since the late 1970´s (Lazhu et al., 2016; Ma et al., 2016).

Table 1. Overview of glacier area changes (%) in the western Nyainqêntanglha range (changed after Wu et al., 2016).

Period	Region of the Nyainqêntanglha range	Glacier shrinkage (%)	Reference
1970–2000	Southeastern slope	-5.2	Shangguan et al. (2008)
1970–2000	Northwestern slope	-6.9	Shangguan et al. (2008)
1970–2000	Western	-5.7	Shangguan et al. (2008)
1977–2010	Western	-22.4 ± 2.9	Wang et al. (2013)
1970–2009	Western	-21.7 ± 3.4	Wu et al. (2016)
1970/80–2000	Southwestern	-19.8	Frauenfelder and Kääb (2009)
1970–2000	Nam Co Basin	-15.4	Wu & Zhu (2008)
1976–2001	Nam Co Basin	-6.8 ± 3.1	Bolch et al. (2010)
1976–2001	Southeastern slope	-5.8 ± 2.6	Bolch et al. (2010)
1976–2009	Detailed glaciers (Zhadang, Tangse No.2, Lalong, Xibu, Panu)	-9.9 ± 3.1	Bolch et al. (2010)

The rises in temperature and precipitation are also affecting permafrost soils that are extending over an area of ca. 1.4 million km^2 (Yang et al., 2004) on the TP. The permafrost layers can be described as relatively warm and thin, with temperatures

15 mostly > -1.5 °C and < 100 m thickness (Wu et al., 2010). The mean annual soil temperature of permafrost in particular areas of the TP has increased by 0.1–0.3 ˚C between 1970–1990 (Cheng and Wu, 2007). Simulation studies have shown that along with climate warming, the permafrost extent may decrease by 9–19 % by 2049 and by 13–58 % by 2099 (Li and Cheng, 1999; Nan, 2005). Although there is no clear estimate of permafrost extent in the Nam Co basin, Tian et al. (2009) reports a lower limit of permafrost at an elevation around 5300 m a.s.l. along the northern slopes of Mt. Nyainqêntanglha (7162 m). A frost

20 lens was also encountered 9 m below surface (4738 m a.s.l.) while sampling an outcrop along the right bank of the Gangyasang Qu close to the northwestern lake shore in 2005 (Schütt et al., 2010). Thus, due to increasing temperatures, permafrost degradation may serve as an additional recharge factor to groundwater, resulting in increased subsurface inflow into the lakes.

Focusing on lake Nam Co, the hydraulic interaction between lake and groundwater is still uncertain, as previous studies either neglected or ignored the influence of groundwater due to a lack of reliable data (Zhang et al., 2011). However, recent studies revealed a water imbalance, which was explained by lake water seepage with an estimated outflow of 1.9×10^9 m^3 and 1.5×10^9 m^3 during 1980–1984 and 1995–2009, respectively (Zhou et al., 2013; Du et al., 2018).
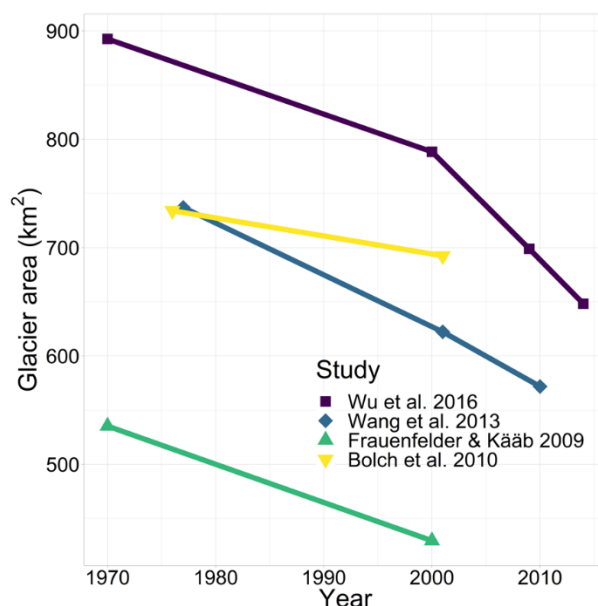
Figure 2. Glacier area reduction at south-western Nyainqêntanglha range since 1970 as evaluated in various studies.

2.3 Enhanced water availability controls changes in lake water chemistry

The maximum recorded depth of lake Nam Co is 122 m (Li et al., 2008a), with brackish water characterized by an alkaline pH of 7.8–9.5 and a conductivity of 1920 µS mm^{-1} (Keil et al., 2010). The chemical composition of a lake is essentially a function

10   of its climate (which affects its hydrology) and the basin geology. Increased freshwater input from precipitation, melting glaciers and thawing permafrost alters the chemical composition of the lake water and enhances surface runoff, infiltration rates as well as subsurface flow. Together with the input of freshwater, streams transport dissolved organic matter (DOM) which is composed of a wide range of dissolved components and particles (≤ 0.45 µm), thus affecting the water chemistry in the lake (Spencer et al., 2014). Excessive landscape disturbance through removing vegetative cover causes higher rates of

15   DOM leaching, more erosion and increasing water runoff velocity, resulting in additional input of minerals and nutrients into the lake. Since the process of DOM leaching and translocation itself is largely dependent on water and sediment cycles (Kaiser and Kalbitz, 2012), it represents both the seasonal and inter-annual variation in an ecosystem as well as its long-term trend. As the glaciers on the TP retreat, highly bioavailable DOM may provide additional nutrients to downstream environments and amplify the trend of eutrophication of lotic and lacustrine ecosystems. Furthermore, the rivers on the TP have been shown to

20   transport dissolved organic carbon from thawing permafrost areas (Qu et al., 2017), which is likely rapidly degraded via

microbial activity, resulting in CO_2 emissions, thus potentially producing a positive feedback on global warming. However, the research of DOM as an important allochthonous source of nutrients, and as a capture of bio- and geodiversity of its respective catchment area is largely lacking for High Asia. The concentration and ratios of different ions in the water have a regulatory impact on the structure of biotic communities (microbes, invertebrates and fish), that can best tolerate abiotic

5   conditions (Wrozyna et al., 2012). In Nam Co, water conductivity has been regarded as the most important environmental factor for shaping communities such as ammonia-oxidizing archaea, as well as phytoplankton (Hu et al., 2010; Wang et al., 2011). These organisms play essential roles in nitrogen cycling processes and the aquatic food-chain, respectively. Ultimately, the changes in the communities of primary producers could alter the lake's trophic structure, which affects also the top predators of the ecosystem. The primary productivity, as an indicator of nutrient supply and a longer growing period associated

10   with a shorter ice-cover duration, has increased markedly at Nam Co within the last 100 years (Lami et al., 2010). Wang et al. (2011) reported the increasing abundance of the diatom species *Stephanodiscus minutulus* during the last decades (ca. 1970–2001). This species is generally viewed as an indicator of water phosphorus enrichment, suggesting increasing inputs from the lake's catchment and stronger mixing in spring season. To predict future consequences of ongoing climate change, it is essential to understand the responses of biotic communities to hydrological variations. Thus, long-term monitoring is needed

15   to adequately address the feedbacks of recent environmental changes, while climatic conditions of the past can be reconstructed through the study of organisms such as diatoms and ostracods that are sensitive to hydrologic and chemical variations (see section 3.2).
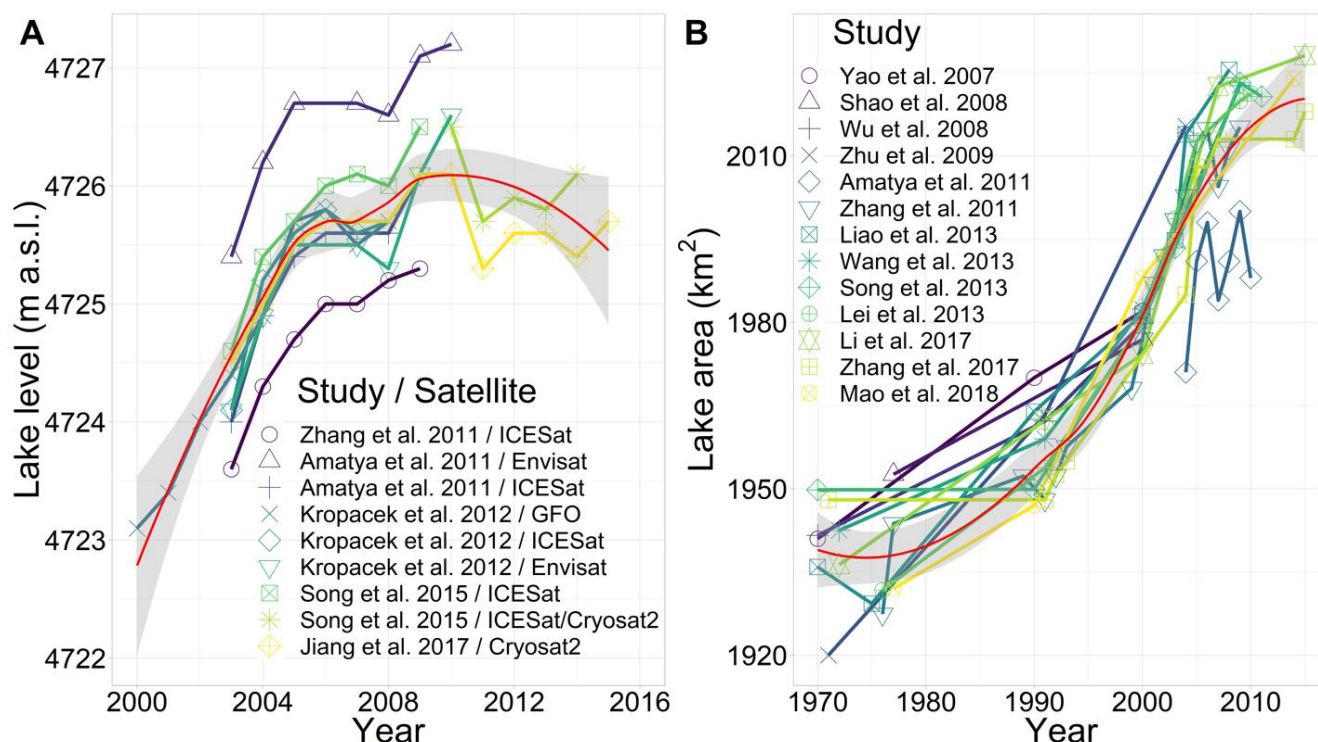
Figure 3. A) Lake level changes of Nam Co since 2000 (notable shift in the water balance in 2009); and B) changes of the lake surface area since 1970, as evaluated in previous studies. Overall increase rate of lake area is 2.1 km² yr⁻¹. Red lines denote LOESS curves with the 95 % confidence interval in gray.

2.4 Vegetation, soils and pasture degradation in the catchment

5   Lake Nam Co is located in the transition zone between the central Tibetan *Kobresia pygmaea* meadows and the north western alpine steppe ecosystem (Fig. 4). Situated on the northern slope of the Nyainqêntanglha mountain range, the vegetation pattern changes according to elevation, moisture availability and temperature. Grazing intensity and abundance of small rodents, such as the plateau pika (*Ochotona curzoniae*), may contribute to the shaping of the vegetation cover (Dorji et al., 2014; Miehe et al., 2014). The area close to the lake (< 4800 m) is covered mainly with alpine steppe vegetation consisting of *Artemisia, Stipa,*

10 *Poa, Festuca* and *Carex* (Li, 2018). Soils developed in the drier steppe areas consequentially tend to show lower organic carbon contents, naturally lowering their total C sink or source potential, as indicated by a study from Ohtsuka et al. (2008). Only one evaluable soil investigation exists from the area of Nam Co. Wang et al. (2009b) investigated two lake terrace sites, situated in the alpine steppe biome. According to their findings, the soils reflect the cold semiarid climate of the area, by showing low biologic activity, while the influence of physical weathering is dominant. The soils showed several decimeter

15 thick layers of loess in which mainly the A-horizons were developed. Although only very sparse to moderate vegetation cover occurs, an almost 30 cm thick organic rich topsoil with granular structure was developed there (Wang et al., 2009b). Further organic-rich buried horizons were found and dated in both profiles, showing phases of climatic conditions enabling the buildup of organic material related to warm-wet periods in the past (before 2.4 and 1.6 cal ka BP) and interchanging with phases of erosion, leading to e.g.: sheet erosion, the formation of gullies and alluvial fans, supposedly during colder periods. These

20 results fit well to climate reconstructions presented in part 3.3 of our review. In accordance with the World Reference Base for Soil Resources (WRB) classification, we propose that the soils described by Wang et al. (2009b) can be classified as Calcisols as there is evidence of carbonate translocation. Higher up the slope (4800–5200 m), the alpine steppe is replaced by *Kobresia pygmaea* meadow. Wang et al. (2007) and Kaiser et al. (2008) investigated the relationship between plant communities and development of soil types on the High Asian Plateau and for meadow soils in the wider area. Vegetation strongly controls the

25 input of organic material into the soil, but beyond that also stabilizes fine materials (< 0.1 mm) and governs the degree of chemical weathering. The authors found soils with stronger signs of biologic activity and chemical weathering (e.g. Cambisols) associated with alpine meadow sites. *Kobresia* root mats are usually developed in up to 40 cm thick loess layers and form a distinctive felty horizon which protects against erosion. At higher elevation (5200–5900 m), only alpine sparse vegetation associated with initial soil processes occurs (Ohtsuka et al., 2008). Where water availability is abundant, alpine meadow

30 swamps with *Carex sagensis and Kobresia schoenoides* are formed, especially at source areas, along river banks and in waterlogged depressions, some of which can cover large areas (Li et al., 2011). Concerning soil development in alpine wetlands, the data base is sparse compared to the meadow and steppe biome. However, it was pointed out for alpine meadows, that a strong relationship exists between plant communities and (top)soil genesis. This relationship probably also holds true

for alpine wetlands, with the exception, that the influences of water logging and seasonal fluctuations and frost-melt cycles in the water table are likely to have an effect on soils. This can be expressed in terms of formation of gleyic features, frost turbations, heaves or other azonal features related to the soil forming effects of water (Chesworth et al., 2008). It still needs to be clarified, how these water-logged areas effect the cycling and processing of organic matter and nutrients. The only tree-like

5   plants in the area are the evergreen shrubs of *Juniperus* spp., which are found on the south-facing slopes of the northern Nam Co catchment, and shrubs of *Salix* spp. in the Niyaqu Valley in the eastern lake catchment (Li, 2018). The diversity of terrestrial flora varies within the vegetation zones and is reflected by their spatial distribution throughout the catchment, with higher diversity in the south-east of the Nam Co catchment (Li, 2018). Alpine steppe comprises more plant species compared to meadow and marsh ecosystems, which are predominantly covered with *Carex* spp. and *Kobresia spp.* (Miehe et al., 2011).

10   The occurrence of different vegetation types in the form of a steppe-meadow ecotone along the high mountain slopes of the Nyainqêntanglha range further amplifies species diversity.

Alpine meadows are often described as "golf-course-like" (Miehe et al., 2014) with the intention of illustrating their unique plane surface. However, small scale structures such as thufa or hummocks are also present. The origin of these structures around Nam Co remains unclear; however, frost heave and permafrost degradation processes are considered to play a major

15   role (Adamczyk, 2010). The landscape, generally dominated by endemic *Kobresia pygmea* sedges, harbors only a few other species (Miehe et al., 2019), but the additional microhabitats provided by thufa and hummocks enable rarer and low-competitive species to settle in niches in these heterogeneous structures (Vivian-Smith, 1997). Compared to the surroundings, the microtopography of thufa possesses different degrees of wetness, exposition and insulation, depth of soil material and type of topsoil. Local studies of the Nam Co area state that slightly degraded bare soil patches and gullies are often areas where

20   plants have the chance to evade the suppression of the closed *Kobresia pygmea* root mat (Schlütz et al., 2007; Dorji et al., 2014). Thus, the genesis of thufa and mild, limited degradation processes are likely to increase species richness and diversity by cracking open the closed root mat of alpine meadows. These structures can also be formed by grass species that grown in tussocks (i.e. clumps, bunches or tufts), such as the endemic species *Stipa purpurea* (Liu et al., 2009) or *Kobresia tibetica* (Yu et al., 2010). The degradation processes in the *Kobresia* meadows are initiated by natural polygonal cracking (Miehe et al.,

25   2019), which can occur through drying (Velde, 1999), and then tend to be amplified by livestock trampling and plateau pikas using the cracks as highways (Liu et al., 2017b; Hopping et al., 2016). Overgrazing in alpine meadows is one of the most frequently mentioned causes of pasture degradation (Unteregelsbacher et al., 2012; Harris, 2010; Miehe et al., 2008) as excessive trampling by livestock might aggravate the initial conditions of polygonal cracking (Miehe et al., 2019). Some researchers argue that climate change is the dominant or even sole driver of degradation (Wang et al., 2007), though the effects

30   of rising temperatures and increasing precipitation appear to be an intensifier rather than the cause of degradation (Zhou et al., 2005; Harris, 2010). In turn, the degradation of wide areas of alpine meadows is not without effect to pastoralists as severe degradation and sloughing off of the whole topsoil removes the basis for business and might lead to unknown consequences for the lake ecosystem. The economic rationale of herders might be to increase the numbers of livestock as this represents a

form of social security (Simpson et al., 1994). The bottom line is that conflicts arise as less land is available for grazing (Hopping et al., 2016).

To reduce the ecological impact of poorly managed pastoralism, the Chinese government has favored policies such as sedentariness and fostered the construction of stationary settlements, which have, in turn, created hotspots of overgrazing

5   (Miehe et al., 2008). In these hotspots, large portions of the topsoil are lost by erosion and denudation, leaving only an area of humic material or subsoil, thus being called "black beach" (Miehe et al., 2008) or "black-soil patch" (Liu et al., 2017a). The remaining landscapes are usually dry, poor in plant cover and prone to further degradation. Increasing areas of bare soil patches enhance evapotranspiration, causing earlier cloud cover formation especially before noon. This may, in turn, lead to reduced radiation and temperature at the surface, thus hampering photosynthesis and consequently overall carbon sequestration (Babel

10   et al., 2014). However, the evolution of grasslands on the TP has been accompanied by herbivore communities, thus, the plants have developed coping mechanisms to persist under continuous grazing pressure. According to the intermediate disturbance hypothesis, species diversity is higher under moderate disturbances, which suggests the positive effect of intermediate level of grazing pressure. Indeed, a plant clipping experiment to simulate grazing demonstrated that under the effect of climate warming, the grazing activities mitigated the negative effects of rising temperature by maintaining a higher number of plants

15   (Klein et al., 2008). Many studies hold the traditional nomadic practice to be a sustainable one (Miehe et al., 2008; Babel et al., 2014; Hafner et al., 2012), but the current policy of removing pastoralist lifestyles from certain regions could potentially reduce overall species richness.
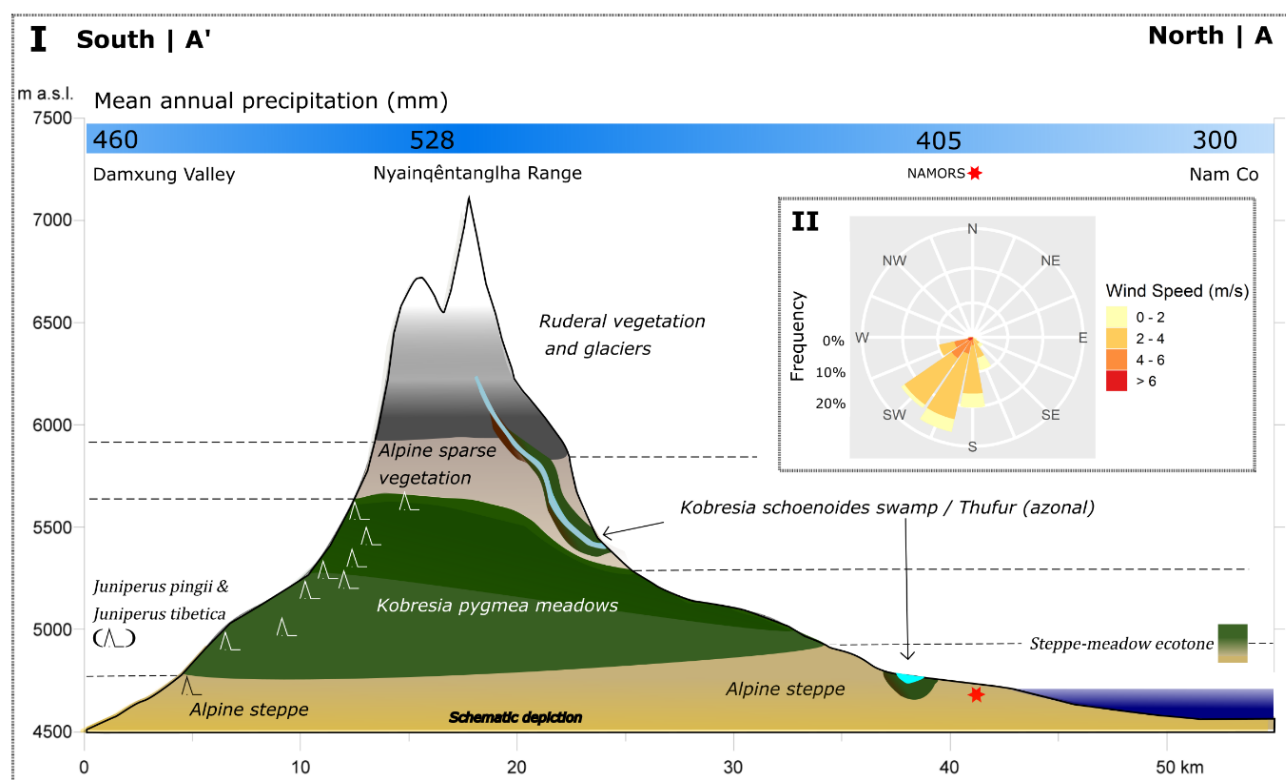
Figure 4. I: Cross-section from Damxung valley to lake Nam Co study area (A'-A) as shown in Fig. 1 (B). Depiction of altitudinal dependent biomes and azonal landforms, changes in chroma denote height-dependent biome shifts. II: Frequency, direction and velocity of mean daily wind measurements at the NAMORS (30°46'22" N, 90°57'47" E) between 2005–2015

2.5 Effects on carbon cycling in alpine ecosystems

Changes in temperature and moisture have a significant effect on the biotic community structure with feedbacks on ecosystem productivity. Alpine meadows respond with increased plant productivity to warming, while productivity may be hampered in alpine steppe ecosystems (Ganjurjav et al., 2016). As soil moisture governs the community response to warming, negative effects of warming on the plant productivity likely occur due to limited water availability (Ganjurjav et al., 2016). Warming was also reported to have a negative effect on plant species diversity in both alpine meadow and steppe ecosystems(Klein et al., 2008; Ganjurjav et al., 2016). Possible explanations for a decline in plant species diversity include changes in small mammal activity, storage of belowground nutrient resources as well as water stress and microclimate in general (soil temperature and moisture) (Ganjurjav et al., 2016; Klein et al., 2008, 2004). Thus, climate change may reduce the habitat quality for the local populations of grazers and reduce well-being of the pastoralists by diminishing abundance of palatable and medicinal plant groups. The changes in the plant productivity levels as well as community changes affect the local carbon cycle. Alpine grassland root mats on the TP are estimated to store up to 10 kg of carbon (C) per square-meter (Li et al., 2008b),

summing up to roughly 2.5 % of the global terrestrial carbon stocks (Wang et al., 2002). At Nam Co, the top soils contain an almost 30 cm thick organic rich layer (Wang et al., 2009b), thus representing considerable soil organic carbon (SOC) stocks. Due to higher plant productivity, alpine meadows in general represent a CO_2 sink, however, the interannual and seasonal uptake is highly variable (Kato et al., 2004; Kato et al., 2006; Gu et al., 2003). Like plant productivity, the CO_2 uptake depends

5 on water availability and temperature which exhibit a diurnal, seasonal, and annual fluctuation. The overall great importance of water availability and temperature on ecosystem-atmosphere CO_2 exchange in the central Tibetan alpine *Kobresia* meadows was demonstrated in several studies through Eddy Covariance measurements (Zhang et al., 2018), chamber measurements (Zhang et al., 2018; Zhao et al., 2017), decomposition of cellulose cotton strips (Ohtsuka et al., 2008) and altitudinal transplantation experiments (Zhao et al., 2018). Similarly, carbon fluxes in alpine steppe are driven by precipitation and

10 temperature on a daily to seasonal and annual time scale. The inter-annual flux variability follows the varying monsoonal precipitation, showing stronger tendencies to function as a C sink in wetter years and as a source in drier years (Wang et al., 2018; Zhu et al., 2015b). Soils that develop in the drier steppe areas tend to show lower organic carbon contents, therefore lowering the total C sink and source potential (Ohtsuka et al., 2008). Although the production of plant biomass may be hampered in steppes, the ecosystem may still act as a carbon sink through microbial CO_2 fixing activities as shown by a recent

15 study on the TP that reported relatively high CO_2 fixation capacity (29 mg kg^{-1} soil d^{-1}; Zhao et al., 2018). Interestingly, this study also found that alpine steppe soils demonstrated significantly higher microbial CO_2 fixation capacity compared to meadow soils (29 *vs.* 18 mg kg^{-1} soil d^{-1}, respectively).

As a result of increasing precipitation and glacier runoff, wetlands in the Nam Co area are expanding, thus increasing emissions of CH_4, which is 28 times more climate active than CO_2 (Intergovernmental Panel on Climate Change, 2014). A study

20 conducted in the alpine wetlands around Nam Co reported, that CH_4 emissions have increased exponentially with increasing precipitation, especially when soil moisture exceeded 80 % (Wei et al., 2015). However, there was a large difference between swamp meadows and swamps (67 and 1444 µg CH_4 m^{-2} h^{-1}, respectively). Swamps are permanently inundated, while swamp meadows are usually seasonally inundated. Furthermore, SOC stocks are higher in swamps compared to swamp meadows (Wei et al., 2015). The large amounts of SOC in combination with anaerobic conditions are the main precursors for

25 methanogens activity that stimulate CH_4 emissions to the atmosphere (Kato et al., 2013). Thus, the saturated soils with high SOC content produce higher CH_4 emissions (Deng et al., 2013). Observations from 2008 to 2013 at Nam Co have shown, that alpine steppe and alpine meadows show annual uptake rates of 72 and 59 µg CH_4 m^{-2} h^{-1}, respectively (Wei et al., 2015); however, the corresponding emission rates are much higher. Generally, it is expected that the alpine wetland acts as a CH_4 source while the aerated soils of alpine steppe and alpine meadow act mainly as a CH_4 sink.

30 As the grasslands on the TP are widely used for yak and sheep grazing, carbon cycling is influenced particularly through human activities and the degree of degradation. The intensity of grazing has a significant effect on CO_2 fluxes, with moderate grazing enhancing belowground allocation of carbon (Hafner et al., 2012), while adversely affecting the C-sink potential through reduction of above- and belowground biomass at higher grazing intensities (Babel et al., 2014). Expanding wetland areas provide anoxic conditions for the release of methane and, due to the greater temperature sensitivity of permafrost areas,

subsurface SOC is at high risk of loss, which may decrease the carbon sequestration potential in the region (Li et al., 2018). Besides carbon cycling through decomposition processes, responses to changing temperature and precipitation depend on the composition of decomposer communities (Glassman et al., 2018). Thus, the conclusive effects and feedback mechanisms (i.e. positive *vs.* negative loop) on warming are complex and not always clear.

5   ## 3 Paleoenvironments on the Tibetan Plateau and landscape evolution at Nam Co

3.1 Geodiversity and evolution of biodiversity

Topography, geological context, climate and their complex interplay are key determinants for the distribution of organisms. In general, the ecoregion can serve as a proxy for community- and species-level biodiversity, which best describe communities of mammals, birds and plants (Smith et al., 2018). The TP forms a distinctive zoographical region, characterized by fauna that

10   is adapted to high altitudes, drought, low temperatures and low oxygen levels (He et al., 2018). Certainly, the TP harbors also many unique lineages of other organisms, with higher endemism of low dispersal species (Yang et al., 2009; Clewing et al., 2016). The TP, including Himalayas and Hengduan Mountains, harbor more than 12000 species of seed plants, 1000 species of terrestrial vertebrates and 800 species of birds (Zhang et al., 2016; Zheng and Zhao, 2017). The proportion of endemism among these plants and vertebrates is relatively high, about 38% and 20%, respectively, but only about 4% among breeding

15   birds (Yang et al., 2009). The recorded species richness of fish exceeds the count of 150, with most common and abundant group being endemic schizothoracine (Zheng and Zhao, 2017). As the structure of soil microbial (including fungal) communities are affected by vegetation, climatic and soil parameters, the unique habitats of the TP potentially harbor many unique microbial lineages that are adapted to high altitude and cold environments (Huang et al., 2014). Mountain building has been directly associated with the development of biodiversity (Hoorn et al., 2013; Antonelli et al., 2018), and the biodiversity

20   hotspots are located especially in the south and south-east of the TP. One of the driving factors is the strong altitudinal zonation, which creates habitat diversity and forms various ecosystems. On the TP, ecosystems are ranging from tropical rain forest over coniferous forest, shrubland, alpine meadows and alpine steppe to dry and desert steppe. There is also a pattern of increasing biodiversity from west to east, which correlates positively with increasing precipitation. In contrast, the harsh central areas of the TP show much lower richness, but nevertheless harbor various endemics (Päckert et al., 2015). Throughout the geological

25   formation of the TP, the mountainous south-eastern parts have been hypothesized to serve as center of species diversification (Mosbrugger et al., 2018), although the core TP region is also suggested to represent a center of origin (Deng et al., 2011). The TP has been a source area for several mammalian lineages (Out-of-Tibet hypothesis; Deng et al., 2011), including the snow leopard and the arctic fox (Wang et al., 2015), as well as birds, such as redstarts (Voelker et al., 2015), and plants, such as *Gentiana* (Favre et al., 2015). These mountainous areas may also have acted as refugia, which preserved unique lineages over

30   long periods (López-Pujol et al., 2011; Lei et al., 2014). Whether some endemic taxa represent relics of a formerly more diverse clade or have never extensively diversified, remains unclear (Päckert et al., 2015). Besides being a center of origin, the TP

may represent a center of accumulation as proposed by the examples of *Saxifraga* (Ebersbach et al., 2017), warblers (Johansson et al., 2007) and hynobiid salamander (Zhang et al., 2006). Overall, the regional biota of the TP is comprised mainly of Palearctic and Oriental species, Nearctic species from the Bering land bridge, as well as species from speciation *in situ*, and postglacial recolonization from adjacent areas. The evolution of biodiversity on the TP has been affected by the combination

5 of geological and climatic changes over the time of the uplift phases (started ca. 55–50 Ma ago; Mosbrugger et al., 2018). High mountain ranges, such as the Himalayas, represent a great distribution barrier for biota (Oheimb et al., 2013). Although many studies have associated recent *in situ* radiations to different uplift phases of the TP, Renner (2016) pointed out that the evidence for recent rapid uplift (9–8 or 3.6–2.6 Ma) remains doubtful and controversial. As proposed by the "mountain-geobiodiversity" hypothesis, the evolution of biodiversity on the TP is a result of an increasing local geodiversity in combination with rapid

10 climatic oscillations and steep ecological gradients (Mosbrugger et al., 2018).

The combination of geological, climatic and ecological changes has left its footprint in the history of Nam Co. It has been inferred that during some phases of the Mid-Late Pleistocene, Nam Co was connected to several other neighboring lakes and covered an area of about 30,000–50,000 km^2 or more (Zhu et al., 2002). The connections allowed the gene flow between drainages, which is reflected, for example, by the closely related clades of schizothoracine fish (Cyprinidae, Osteichthyes)

15 from Nam Co and the surrounding lakes, compared with more distant parts of the TP (He et al., 2016). In contrast, due to a vector-mediated passive dispersal across large areas, other aquatic taxa such as freshwater snails seem to be less influenced by drainage histories (Oheimb et al., 2011). Findings from lake terraces suggest lake shrinkage starting during the Late Pleistocene (Zhu et al., 2002). There are at least seven different levels of continuous terraces around Nam Co, with the highest being over 30 meters above current lake level. Higher terraces are older, suggesting a long-term reduction in lake level, with the last large

20 lake phase likely taking place during ca. 40–25 cal ka BP (Lehmkuhl et al., 2002; Zhu et al., 2002). With the generally drying climate since the onset of the Holocene, Nam Co gradually shrank and evolved into the present state (Fig. 5; modern lake area is 2018 km^2).

3.2 Paleo-lake level changes and climate reconstruction based on aquatic bioindicators

Lake sediments contain important indicators, or proxies, that can be used to reconstruct limnological and (hydro-) climatic
25 conditions over long time periods (Zhu et al., 2010a; Wrozyna et al., 2010). Widely used environmental indicators include communities of diatoms (Bacillariophyceae) and ostracods (Crustacea: Ostracoda) as they are abundant and usually preserve well in sediments (Kasper et al., 2013). For example, the investigations of Quaternary ostracods, modern assemblages, and stable isotopes from Nam Co and nearby water bodies represent the most detailed application of ostracod analysis in the south-central region of the TP (Mischke, 2012). Different approaches (stratigraphy, paleoecology, etc.) detected several climatic

30 fluctuations between warmer/cooler and wetter/drier periods (Fig. 5). In general, higher lake levels based on aquatic fauna suggest a more humid environment during the early and middle Holocene, which displayed a shift pattern compared to the northern TP (Wünnemann et al., 2018). Together with the indicator species approach, and the application of transfer functions

for Nam Co sediments different stages can be recognized. Stage I (8.4–6.8 cal ka BP): climate changed from warm-humid to cold-arid with water depth being much lower than today (Zhu et al., 2010a). Stage II (6.8–2.9 cal ka BP): environmental conditions returned to warm and humid (Zhu et al., 2010a). During 4–2 cal ka BP, lake water depth initially remained much shallower than today but then gradually increased due to high rates of precipitation (Frenzel et al., 2010). The presence of the

5   diatom taxa *Stephanodiscus* in this stage indicated stronger monsoon activity and higher availability of nutrients (Kasper et al., 2013). Finally, stage III (2.9 cal ka BP to present): the climate again became warm-humid, with a cold-dry event between 1.7 and 1.5 cal ka BP (Zhu et al., 2010a). Between 2 and 1.2 cal ka BP, benthic diatoms, inferred a lower water level and drier climate (Kasper et al., 2013). Subsequently, wetter conditions and an increase in lake level was detected (1.2 cal ka BP until 250 cal BP), possibly corresponding to the Medieval Warm Period (MWP), with high planktonic diatom species and high

10   ostracods diversity (Kasper et al., 2013). During the late Holocene, the minimum water level occurred throughout the Little Ice Age (LIA) (~1490 and 1760 AD) (Frenzel et al., 2010). However, the lake level increased towards the present, which is plausibly linked to the melting of the glacier due to the current warming.

Although a large number of studies describe profound hydrological changes and general climate fluctuations, there are several uncertainties regarding taxonomy, resolution and proxy sensitivities. For example, modern ostracod data detects several

15   morphological variations, characterized by different nodding or shell sizes, which could lead to an erroneous ecological interpretation and later, vague paleoenvironmental conclusions in relation to salinity changes (Fürstenberg et al., 2015). In paleo-studies, different sedimentation rates and uncertainties in the core chronologies also cause a lack of correspondence between signals detected by different proxies (Wang et al., 2012). For this reason, it is surrogate to understand the precise causal relationships between a complex environmental gradient (e.g. water depth, water chemistry, temperature, etc.) and the

20   response of bioindicators. Although ecological information is still poorly known for many species, ostracod and diatom assemblages represent reliable proxies to trace the climatic history of Nam Co.

Further emphasis should be placed on combining morphology and DNA analysis to corroborate the classification of the species already described. Furthermore, experiments with living individuals should be performed under controlled environmental variables to allow the setup of a transfer function that could be used to evaluate quantitative data for

25   paleoreconstructions.
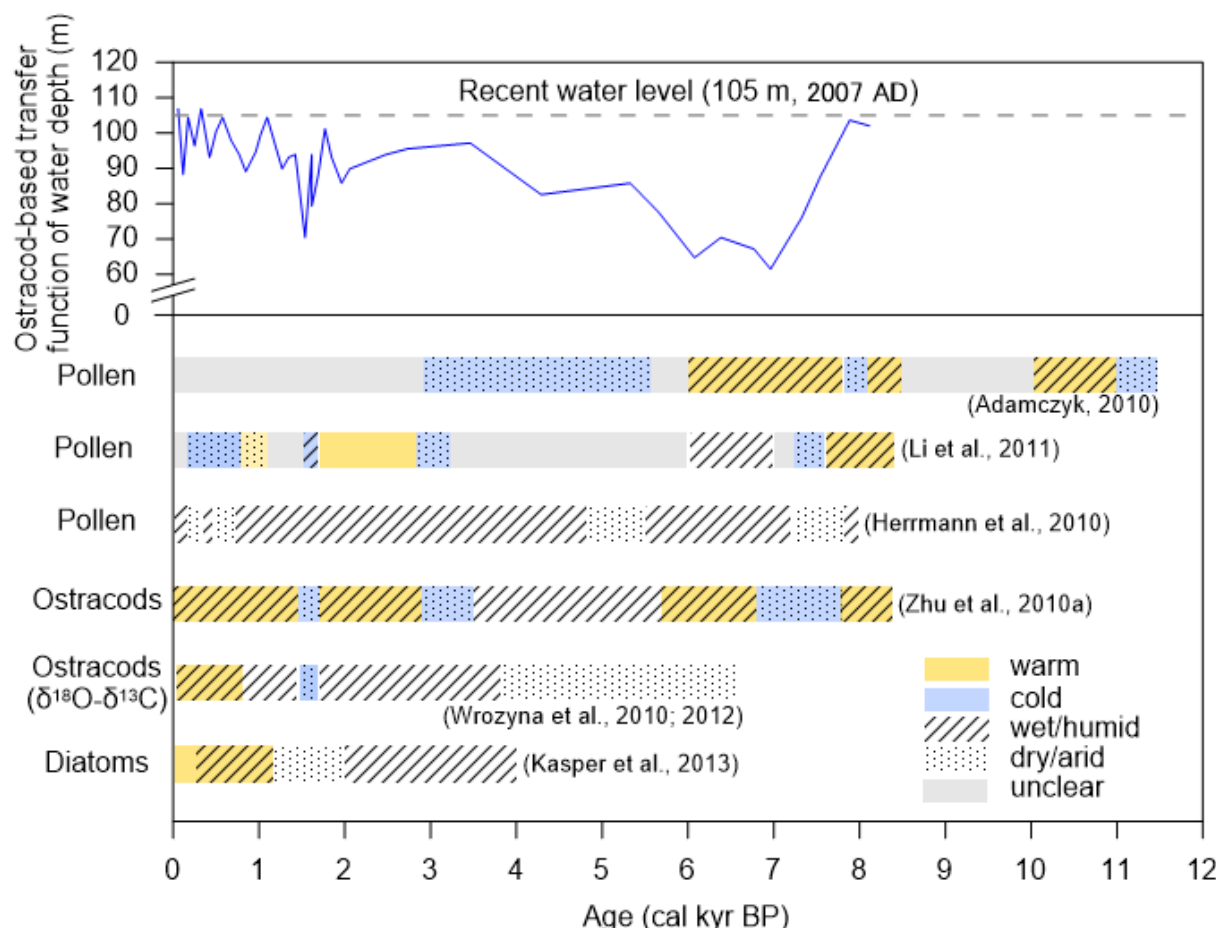
Figure 5. Comparisons of the reconstructed climate conditions based on fossils of pollen (Li et al., 2011; Adamczyk, 2010; Herrmann et al., 2010), Ostracods (Zhu et al., 2010a), Ostracod δ18O (Wrozyna et al., 2012; Wrozyna et al., 2010) and diatoms (Kasper et al., 2013) from sediment cores in, and at the shoreline of lake Nam Co. Ostracod-based water-depth transfer function (Zhu et al., 2010a); blue line) was used to indicate long-term hydrological changes and all reconstructed water-depth values were adjusted to the maximum water level of the lake according to the 45 m difference between this study site (60 m) and deepest site (105 m) of lake Nam Co. Main species also shown in different periods.

3.3 Holocene vegetation cover and climate reconstruction based on pollen records

The comparison of modern pollen assemblages with those from sediment cores allows the reconstruction of floristic diversity and distribution across various time scales. Vegetation patterns contribute to reconstruct past climate and also with assessing the degree of local human influence. Modern vegetation belts around Nam Co reveal that alpine steppe is containing mostly species of *Artemisia* (*Asteraceae*) and *Poaceae*, while alpine meadows and swamps are dominated by *Cyperaceae* (Li et al., 2011). The sedimentary pollen ratio of *Artemisia* to *Cyperaceae* (A/Cy) can, within certain limitations, be used to reconstruct past climates (Li et al., 2011; Li, 2018; Zhu et al., 2015a) provided that vegetation belts move with altitude during climate

change. For example, when the climate is warmer and drier, alpine steppe reaches higher up the mountain, displacing alpine meadow into areas further away from the lake, leading to a higher input of *Artemisia* pollen into the nearby lake and consequently a higher A/Cy pollen ratio in the sediments. However, the A/Cy pollen ratio and abundance of tree-pollen originating from a short distance can be altered by human-driven change of plant composition, hence the beginning of pastoral

5 economy might limit the explanatory power of pollen records (Adamczyk, 2010; Miehe et al., 2014). Pollen composition inferred from sediment cores reveals a downward shift of the altitudinal vegetation belts since 8.4 ka BP (Li et al., 2011). A major extension of alpine meadow and alpine sparse vegetation closer to the lake shore during the late Holocene is corroborated by a pollen-based climate reconstruction from a peat core near Nam Co (Herrmann et al., 2010) and two other pollen records from the eastern lake shore (Adamczyk, 2010). They found a trend of increasing temperatures from the late glacial until the

10 early Holocene, accompanied by an extension of alpine steppe, tree and shrub vegetation. Climate fluctuated between dry and humid from 8.5 to 4.8 ka BP, with an intense cold regression between 8.1to 7.8 ka BP. The onset of human activity at Lake Nam Co is dated to 5.6 ka BP. Between 4.8 and 0.7 ka BP, a relatively stable climate with predominantly humid conditions developed (Fig. 5), the vegetation pattern already showed trends of a human-made steppe biome, potentially a plagioclimax (Adamczyk, 2010). Since 0.7 ka BP, drier conditions prevailed.

15 Whether and to what extent the central Tibetan Plateau was forested, and what caused the forest decline is the subject of ongoing discussion (e.g. Miehe et al., 2006; Miehe et al., 2019). Besides some *Juniperus pingii* and *Salix* occurrences (Nölling, 2006) there are no remains of this once potentially tree-rich vegetation in the Nam Co catchment. Charred micro remains, however, can be found throughout the Holocene until 1 cal ka BP (Herrmann et al., 2010). The authors attribute the size and shape of the charcoal remains to local, small-scale burning of wood and leaves. In addition to the burning of *Juniperus* trees

20 for religious reasons (Miehe et al., 2006), trees and shrubs may have been burned for heating or clearing of pastures by nomads. The trees were previously able to spread again due to sufficient precipitation provided by the summer monsoon. Furthermore, the occurrence of synanthropic taxa has been observed in the nearby Damxung valley since 8.5 cal ka BP, corroborating the strong anthropogenic influence on the formation and restructuring of the vegetation patterns in the area (Schlütz et al., 2007). The decrease of summer precipitation and temperature, very likely in conjunction with ongoing human activity ultimately led

25 to the total disappearance of trees and the formation of the alpine grasslands and steppe as we know them today (see section 2.4).

4. Conclusions and perspectives

The Ecosystems of the Tibetan Plateau experience an increase in air temperature roughly twice the global average. Based on the model system of the Nam Co catchment in central Tibet, this literature review describes the manifold environmental

30 changes affecting abiotic and biotic processes in the area. The air temperature increase has accelerated deglaciation of the Nyainqêntanglha mountain range during the last decades, leading to substantial inflow of freshwater and various solutes resulting from weathering to the lake. The combined effects of overgrazing by livestock and warming accelerated degradation

processes of the alpine grasslands further increase surface runoff in the catchment. Further down the slope, increasing glacier runoff leads to an enlargement of the wetland extent, thus augmenting anaerobic conditions leading to enhanced release of methane. Moreover, warmer and wetter climate as well as pasture degradation may turn alpine grassland and steppe ecosystems into an overall source of carbon dioxide. Based on the reviewed literature focusing on the model catchment of Nam Co, we

5   outline future perspectives to further improve the understanding about the close connections between geo- and biodiversity. (1) Permafrost areas act as buffers of the water budget, and influence the behavior of geomorphological processes and periglacial landforms. Although a significant warming and consequent decay of permafrost have been reported throughout the TP in recent decades, studies on permafrost in the Nam Co catchment and in the immediate Nyainqêntanglha range are missing. (2) The rising lake level trend, starting in late 1970, had a point of reflection around 2009, which indicates changes of variable

10   precipitation and evaporation trends, reduced water inflow from already melted glaciers and additional ground water seepage out of the lake. Therefore, long term monitoring is necessary to calibrate and validate models properly, focusing on a more accurate climate prognosis. (3) To improve climate modelling approaches, the dynamics of DOM, CO_2 and CH_4 fluxes need further clarification. (4) The development of molecular methods for biomonitoring and water quality assessment has improved greatly during last decade with the aim to provide clear monitoring standards. These offer time- and cost-effective approaches

15   for complementary studies to tackle community shifts of various water quality indicator organisms. (5) Alongside the 'traditional' paleobioindicator analysis, DNA based taxa identification methods hold also a great potential to be used in paleoecological studies to provide improved taxa differentiating accuracy. Various biological and geochemical proxies in Nam Co sediments have enabled the tracking of historical events and the reconstruction of past environments, which provide information about the magnitudes and directions of past climate change and thus a key to assess future changes. Both the

20   formation of high elevation environments and pronounced past climate oscillations have contributed to the development of biota on the TP. Interdisciplinary research of the catchment of Nam Co has provided vast insights into how warming trends may affect ecosystems from microbes to the top of the food chain. Recognizing the impacts of a warming climate is the base for establishing effective climate change adaptation strategies and actions in the TP region and in alpine regions in general.

Team list:

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Author contributions:

SA, MAR, JB, PEG, JK, WK, LK, PM, FN, ER, HT, TVT, YW contributed equally to the content of the Manuscript. SA conceived the idea and was responsible for funding acquisition. SA, JB, PM, FN structured the main text body; The following authors were in charge of the corresponding sections: JB, ER, TVT: *Glacier retreat and hydrological patterns of Nam Co*;

5   PEG, LK: *Enhanced water availability controls changes in lake water chemistry*; PM, FN: *Vegetation, soils and pasture degradation in the catchment & Effects on carbon cycling in alpine ecosystems & Holocene vegetation cover and climate reconstruction based on pollen records*; SA, PEG, WK: *Geodiversity and evolution of biodiversity & Paleo-lake level changes and climate reconstruction*; The figures were prepared as follows: ER: fig. 1, JB and FN: fig. 2 and fig. 3, PM: fig. 4, WK: fig. 5.

10   **Competing interests:**

The authors declare that they have no conflict of interest.

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