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# Mountain Lakes: Eyes on Global Environmental Change

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***Mountain Lakes: Eyes on Global Environmental Change***
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***Abstract***

Mountain lakes are often situated in protected natural areas, a feature that leads to their role as sentinels of global environmental change. Despite variations in latitude, mountain lakes share many features, including their location in catchments with steep topographic gradients, cold temperatures, high incident solar and ultraviolet radiation (UVR), and prolonged ice and snow cover. These characteristics, in turn, affect mountain lake ecosystem structure, diversity, and productivity. The lakes themselves are mostly small and shallow, and up until recently, have been characterized as oligotrophic. This paper provides a review and update of the growing body of research that shows that sediments in remote mountain lakes archive regional and global environmental changes, including those linked to climate change, altered biogeochemical cycles, and changes in dust composition and deposition, atmospheric fertilization, and biological manipulations. These archives provide an important record of global environmental change that pre-dates typical monitoring windows. Paleolimnological research at strategically selected lakes has increased our knowledge of interactions among multiple stressors and their synergistic effects on lake systems. Lakes from transects across steep climate (i.e., temperature and effective moisture) gradients in mountain regions show how environmental change alters lakes in close proximity, but at differing climate starting points. Such research in particular highlights the impacts of melting glaciers on mountain lakes. The addition of new proxies, including DNA-based techniques and novel stable isotopic analyses, provides a gateway to addressing novel research questions about global environmental change. Recent advances in remote sensing and continuous, high-frequency, limnological measurements will improve spatial and temporal resolution and help to add records to spatial gaps including tropical and southern latitudes.

Mountain lake records provide a unique opportunity for global scale assessments that provide knowledge necessary to protect the Earth system.

Key Words: Mountain lakes, paleolimnology, climate change, atmospheric deposition, dust, carbon cycle, species invasions

## 1. Introduction

*"A lake is the landscape's most beautiful and expressive feature. It is the earth's eye, looking into which the beholder measures the depth of his own nature." Henry David Thoreau, Walden, Chapter 9, pg. 121.*

*"We touch the ancient mysteries of life in the wild. We may even learn to see in new ways — more closely, perhaps, and deeper into geologic time. If we're lucky we get close to learning how to 'think like a mountain,' in Aldo Leopold's great phrase." Philip Connors, author of Fire Season, 1992, in interview with Marianne Moore March 2011 for Zyzzyva*
https://www.zyzzyva.org/2011/03/

Mountain ranges are found across the world and, owing to the glacial history of many mountain regions, alpine lakes are important features of these landscapes (Figure 1). Regardless of location, mountain lakes are often remote, located in environments characterized by cold temperatures, high incident solar and ultraviolet radiation (UVR), experience prolonged ice and snow cover, and are frequently dilute and oligotrophic. These characteristics, in turn, affect mountain lake ecosystem structure, diversity, and productivity (Wolfe et al., 2003; Catalan et al., 2006; Hobbs et al., 2010).

Important information on long-term environmental change is archived in lake sediments (Catalan et al., 2013a). Using a comparative approach across different mountain regions, lake sediments can provide insights about global change (e.g., climate change, acidification, reactive nitrogen loading, dust and species introductions) (Catalan et al., 2006; Williamson et al., 2009; Catalan and Donato Rondón, 2016). At present, this knowledge is especially important given that humans are forcing environmental change at unprecedented spatial and temporal scales (Steffen et al., 2015). Of particular significance is the effect that humans are having on the Earth's climate system. Fossil fuel use and deforestation have changed the composition of the atmosphere, and resulted in rapid warming of the Earth (IPCC, 2013).

Although mountain regions have been defined many ways, we follow Körner et al. (2011; 2017) who ascribed mountains to areas with >200 m difference in elevation within a 2.5'grid cell (corresponds to 4.6 km × 4.6 km area near the equator) and 0.5' resolution irrespective of elevation. Based on this definition ~20% of all terrestrial land area outside of Antarctica is mountainous (Figure 1; Körner et al., 2017). Certain high elevation, level areas are excluded from this definition, such as plateaus. Despite the large proportion of mountainous landscapes across the globe, paleolimnological studies have been focused in the Northern Hemisphere and particularly in temperate regions (Figure 1), thus our review is also focused on northern systems, although, where possible, we include Southern Hemisphere and tropical mountain lakes. We also concentrate on small mountain lakes (<20 ha).

Mountain lakes are sensitive recorders of global change owing in part to their remoteness (Catalan et al., 2013b). In addition, steep climatic and environmental gradients that characterize mountain regions affect how lakes respond to various stressors, including atmospheric deposition, dust and biological manipulations. For example, low elevation lakes are generally characterized by higher concentrations of dissolved organic carbon (DOC) and lower levels of nitrogen than high elevation sites, which is related to greater soil and vegetation coverage at lower sites and greater precipitation at higher elevations (Figure 2 and 3). Owing to these steep gradients, lakes in mountain regions may all respond to an environmental stressor in a spatially coherent manner, but the direction of change may vary from lake to lake dependent on starting points and catchment characteristics (Soranno et al., 1999). Such steep gradients compress environmental differences normally recorded at the scale of 1000s of km across continents to scales of 10s of km in mountain regions. This compression provides the opportunity for future research efforts to use mountain lakes to test the response and resiliency of lakes with different catchment characteristics, but still in close proximity, to environmental change.

Regardless of a lake's position on the landscape, individual lakes are connected by climate (Livingstone, 2008). Using climate change as the overarching theme of this review, we highlight some of the exciting opportunities available through technological and methodological advances to show how paleolimnology assessments of mountain lakes are providing insights into global environmental change, including climate change, the carbon cycle, atmospheric deposition, dust, and biological manipulations (Figure 4). We then look ahead to future research directions. This paper builds on previous reviews of remote lakes and the records of environmental change that they store (e.g., Catalan et al., 2013a) by highlighting advances from recent research.

Although our focus is on paleolimnological research that has provided insights into regional and global change, we also include contemporary limnological studies, which are frequently done in tandem to inform paleolimnological interpretations in mountain regions. We review recent technological advances that have contributed to advances in paleolimnology in general, but highlight those that are pushing the frontiers of mountain paleolimnology specifically. In this review, we highlight how mountain lakes act as bellwethers and are the "eyes" on environmental change, allowing us to see better the interconnectedness of aspects of global change and to hopefully use this information to think deeper and with greater perspective "like a mountain" about the future.

We frame our review in the context that climate connects lakes to atmospheric, landscape, and in-lake processes (Leavitt et al. 2009; Figure 4). Lakes were once considered to be individual and stationary, responding to local changes in weather, but these concepts have evolved to consider lakes as being connected by atmospheric processes (Livingstone, 2008). For example, warming conditions may promote algal production, and at the same time increased summer precipitation and reduced snow may lead to a change in timing of the delivery of nutrients from atmospheric deposition that could further promote or mitigate algal production. Not all mountain lakes will respond in the same way or at the same time because climate signals will be modified through internal lake processes (Baron and Caine, 2000). The sum of these processes and interactions are integrated in lakes and preserved in lake sediments, as described by the airshed-to-sediment continuum (Catalan and Donato Rondón, 2016). Lakes can also affect climate through their role in the carbon cycle, so that the continuum flows in both directions (Tranvik et al., 2009).

## 2. Paleolimnological advances provide opportunities for studying global change in mountain lakes

Paleolimnology continues to benefit from rapid technological advances and the effective linkage of process-oriented limnological studies with paleolimnology (Smol, 2008). Paleolimnologists have used a number of well-established proxies to contribute to our understanding of environmental change from local to global scales. These proxies include geological and geochemical (e.g., grain size and composition, organic matter, stable isotopes, heavy metals), biological (e.g., diatoms, cladocerans, chironomids, pollen, pigments), biogeochemical (e.g., biogenic silica, stable isotopes), and environmental (spheroidal carbonaceous particles, xenobiotics) archives, which integrate environmental changes from the surrounding catchment, from the atmosphere, and from within the lake itself (Last and Smol 2001a, b; Smol et al., 2001a, b). The expanding list of proxies available to paleolimnologists adds new opportunities to further our understanding of global environmental change in mountainous systems.

In sediment cores from mountain lakes, stable isotope analysis (SIA) of carbon and nitrogen can provide a wealth of information about sources of organic matter and shifts in nutrient cycling, while isotopic analysis of oxygen from cellulose and carbonates can provide information on synoptic-scale climate change and hydrology (Anderson et al., 2005; Bartrons et al., 2010; Brahney et al., 2010; Hundey et al., 2014). Interpretations are being improved by recent advances including SIA of particular organisms and compound-specific stable isotope analyses (CS-SIA). For example, in lakes from the French Alps, investigators characterized energy movement through the food web using SIA of invertebrate remains (Frossard et al., 2014). In a subalpine lake in the Alps, researchers used CS-SIA to track the carbon sources that sustain benthic consumers and found that carbon cycling in shallow lake food webs is sensitive to temperature change (Belle et al., 2018).

New techniques for analyzing plant biomarkers provide investigators with further insight into carbon cycling, although these techniques are only beginning to be used in mountain environments. For example, n-alkyl plant wax compounds from lake sediment records can be used to reconstruct paleoclimate, paleovegetation and carbon cycling (Diefendorf and Freimuth, 2017). Carbon isotopic n-alkane analyses have been applied in the Colorado Rockies to track sources of organic matter (Enders et al., 2008). Wider application of dual isotope (carbon and hydrogen) n-alkane analyses in other mountain systems could enable us to examine the degree to which climatic changes have altered C inputs and energy flows.

Advances in methodologies for characterizing shifts in algal functional groups in lake sediment cores complement more established methods, such as diatom assemblages and pigment analyses. DNA-based techniques have enabled biodiversity research at unparalleled levels of detail (Domaizon et al., 2017). Sedimentary algal DNA has been successfully extracted and sequenced to reveal distinct community shifts in relation to variable climatic and environmental regimes (Capo et al., 2016, Monchamp et al., 2018) even from sediments ~270,000 years old (Randlett et al., 2014). DNA-based techniques are expanding our understanding of aquatic microbial community composition and distribution in remote areas of the world (e.g., Hayden and Beman, 2016; Peter and Sommaruga, 2016; Aguilar et al., 2018). Although analysis of genomic DNA from mountain lake sediments is not yet widespread, it offers novel ways to gain insights into past biota that do not leave reliable morphological or biogeochemical proxies. For example, some key invertebrate groups, such as copepods, are often lacking in paleoenvironmental assessment, yet these organisms play key roles in lake ecosystems.

Recent advances in interpreting contemporary data can also be leveraged to aid interpretation of paleolimnological data. Bracht-Flyr and Fritz (2016) used contemporary mountain lake weather data, surface and groundwater fluxes, lake bathymetry, and initial lake conditions in a thermodynamic-ecological coupled model to better interpret changes in fossil diatoms and understand the linkages among climate forcings, lake thermodynamics, and species assemblages. This paired approach constrained the range of conditions that can affect lake thermal structure and biological communities during the last 1000 years.

Advances in high-frequency sensors that allow for continuous, high-resolution measurements of physical variables, including temperature, chlorophyll *a* and dissolved oxygen (e.g., Jacquet et al., 2014) and monitoring using remote sensing (Riffler et al., 2015, Huang et al., 2017), hold potential for water monitoring in remote regions where access can be challenging. In their bibliometric analysis, Zhang et al. (2017) suggest that remote sensing research should focus on water quality monitoring, phenology, and climate change impacts, but complications like cloud cover, edge effects, adjacency effect, and turbidity have limited research to relatively large lakes. However, the potential for using remote sensing to test hypotheses in mountain regions is improving as satellite records with finer spatial resolutions and more frequent observations (e.g., WorldView, Sentinel 2) become available. For example, remote sensing can be used to infer phytoplankton blooms in mountain lakes (Bresciani et al. 2018). Advances in hyperspectral imaging and aerial drones will provide further opportunities to access and study remote sites. The development of high frequency, in-situ sensors have been used extensively in recent years to document temporal variability in, for example, temperature, dissolved oxygen, and nutrients, which are critical to understanding species biology and distribution (Rundel et al., 2009).

The expanding list of paleolimnological tools, in tandem with other technical advances, provides both challenges and opportunities. In order to use mountain lake data sets from across the globe to study environmental change, it will be necessary to synthesize diverse regional mountain data sets to create a global database. Regional efforts have highlighted some of the challenges involved, but also show the potential of these data sets to address global change issues (Williams and Labou, 2017; Williams et al., 2017). Below, we present examples of environmental changes that affect mountain lakes, starting first with contemporary descriptions of the drivers and responses, and following with contributions to understanding these changes over time from paleolimnological literature.

# 3. Global change archived in mountain lakes

## 3.1 Climate change

### 3.1.1 Mountain lake sensitivity to global climate change

Climate warming is rapidly occurring as a result of human activities, and there is an urgency to determine how atmospheric circulation, precipitation patterns and extreme events will affect water resources, which are often concentrated in mountain regions. Mountain regions play an essential or supportive role in downstream water supplies (Viviroli et al., 2007), and it has been purported that half of the world's population is dependent on water originating in mountains (Woodwell, 2004). Owing to steep elevational and climate gradients, mountain lake ecosystems are particularly sensitive to climate change (Sommaruga, 2001; Williamson et al., 2009). Temperatures are increasing faster in mountain regions than in adjacent lowland sites (Mountain Research Initiative EDW Working Group, 2015), and these differences are greatest in winter (Qixiang et al., 2018). This elevation-dependent warming can accelerate the rate of change in mountain lake ecosystems, although the full spectrum of these effects is still being determined.

Climate influences mountain lake structure and function directly by exerting controls on water temperature, hydrology, solute concentrations and aquatic biota (Beniston et al., 2003; Adrian et al., 2009). Inputs and losses of energy affect the formation and loss of lake ice (Kainz et al., 2017), and the accumulation and persistence of snow (Duguay et al., 2003; Sadro et al., 2018). Generally, a warming climate shortens ice cover duration (Livingstone, 1997; Thompson et al., 2005; Preston et al., 2016; Roberts et al., 2017), which results in longer ice-free seasons and warmer surface temperatures (Butcher et al., 2015; Preston et al., 2016) and strengthens connectivity of the lake to the air and watershed (Sommaruga-Wögrath et al., 1997; Koinig et al., 1998). As surface waters warm, the duration and intensity of thermal stratification generally increases. This may reduce deep water oxygen concentrations (Missaghi et al., 2017), which in turn affects carbon and nutrient cycling. Warmer winter temperatures were shown to affect the depth of vertical mixing during spring turnover and limit replenishment of epilimnetic phosphorus, which had cascading effects on seasonal plankton succession (Lepori et al., 2018). Changes in thermal stratification, however, will also be influenced by local variations in microclimate, surrounding catchment slope and aspect and lake morphology (Kraemer et al., 2015). Glacier-fed, cold, discontinuous polymictic lakes can become dimictic when the hydrological connectivity to the glacier is lost (Peter and Sommaruga, 2017).

Climate also influences mountain lake structure and function indirectly through landscape changes, including loss of upstream glaciers and snow pack (Beniston et al., 2003; Adrian et al., 2009) and shifts in vegetation type and cover. An upward shift of treeline (Grace et al., 2002; Harsch et al., 2009) and ranges of mountain plant species (Gottfried et al., 2012), collectively, can alter carbon cycling and alpine biodiversity (Grace et al., 2002; Harsch et al., 2009). Changes in vegetation, however, will likely be slower compared to recent observations of cryosphere response.

Between 2001 and 2010, 53% and 39% of glacial area has been lost in central Europe and western North America, respectively (Zemp et al., 2015). In the tropical Andes, some glaciers have already disappeared (Rabatel et al., 2013). Climate warming has additionally affected mountain permafrost, with clear signs of degradation of rock glaciers and mountain slopes

(Haeberli, 2013). Changes in the frequency and severity of drought and increasing air temperatures have caused snowpack in mid-latitude mountains to decrease in extent and duration, particularly in spring, although with large spatial variability (Beniston, 2003; Brown, 2018). Earlier melting of snow causes earlier seasonal runoff, which influences lake hydrology (Huss et al., 2017). In the Colorado Rockies, for instance, peak snowmelt and streamflow has shifted over 29 years occurring now two to three weeks earlier (Clow, 2010). Snowmelt influences a large number of key physical and chemical variables in mountain lakes including summer temperature, timing of ice-out, onset of thermal stratification, the magnitude of the delivery of acids, nutrients and DOC, and algal biomass (Parker et al., 2008; Miller and McKnight, 2015; Sadro et al., 2018; 2019). Smaller snowpack size can lead to warmer summer epilimnetic temperatures as a result of links among snowpack, the duration of ice cover, and the volume of inflowing spring snowmelt (Sadro et al., 2019). Snowmelt is also a major mediator of the transfer of allochthonous material through the air-to-sediment continuum, which, along with the physical changes to lakes, can affect algal production through variable and complex pathways (McKnight and Miller, 2015; Sadro et al., 2019).

Because glaciers have a pronounced influence on lakes, glacial loss can result in complete reorganization of the ecosystem. Vinebrooke et al. (2010) examined the biotic shifts in the sediments of mountain lakes following loss of glaciers from the lake catchment. They found striking shifts in sediment type and organic carbon content, as might be expected with the cessation of input of glacial flour. Further, these changes altered underwater light regimes influenced both primary productivity and community composition. Such changes have also been studied using paleolimnological records (Russell et al., 2009).

3.1.2 Paleolimnological records provide insight into global climate change

Paleolimnological records capture hundreds to thousands of years of lake responses to earlier periods of climate change, including the warm mid-Holocene (Reinemann et al., 2009) and the cooler, wetter Neoglacial (Stone and Fritz, 2006; Shuman et al., 2009; Menounos and Reasoner, 1997), the spatially variable conditions of the Medieval Climate Anomaly and Little Ice Age (Anderson et al., 2016; Bracht-Flyr and Fritz, 2012; Stone et al., 2016), and the initiation of recent warming at the end of the $19^{th}$ century (Anderson et al., 2016). These records also capture lake response to dry conditions and varying climate modes and shifting storm tracks, with careful selection of sites along climate gradients yielding insight into drivers of spatial variability (Anderson et al., 2016). Paleolimnological studies from mountain regions are particularly useful for understanding global change owing to the sensitivity of mountain landscapes and lakes. However, many mountain regions, particularly at lower and southern latitudes, are under-represented (Figure 1), leaving critical gaps in our understanding of global climate change.

Paleolimnological records have been used to determine large-scale climate reorganizations, such as changes in atmospheric circulation and changes in atmospheric-oceanic links that have driven past shifts in climate, which in turn provide critical information for better predictions of future climate change (MacDonald et al., 2008; MacDonald et al., 2016). For example, diatom-inferred lake level and salinity were used to reconstruct Holocene drought in the Sierra Nevada, California (MacDonald et al., 2016). These records, along with others, collectively demonstrated variation in Pacific Ocean-atmosphere modes over the Holocene, which were used to project a possible drier future for California (MacDonald et al., 2016). Across three lakes in the central Rocky Mountains of North America, diatom-inferred lake mixing depths revealed coherent shifts in lake thermal structure over the last 4,000 years (Stone et al., 2016). These shifts in thermal regimes coincided with oxygen-isotope inferred location and intensity of the Aleutian Low, revealing how high elevation lakes responded to changes in atmospheric circulation across the region.

Oxygen isotopes in opaline silica were also used to track variations in lake level related to changes in moisture balance and glacier meltwater in tropical lakes on Mount Kenya (Rierrt-Shati et al., 1998; Barker et al., 2001). These records provided important insights into Earth's climate system, particularly changes in the strength of the African and Asian monsoons related to changing sea surface temperatures (Barker et al., 2002). Paleolimnological records from West African Lakes also revealed regional hydroclimatic changes (Stager and Anfang-Sutter, 1999). Based on this research, enhanced upwelling and cooling sea surface temperatures could increase stratiform clouds delivering moisture to high elevation sites, whereas warming sea surface temperatures would result in more cumuliform clouds and reduced mountain moisture.

Lake sediment records also archive information about long-term variations in water availability and drought, which can help water managers plan for the future. Warmer temperatures can increase evaporation, which, depending on precipitation timing, can result in lower lake levels and increased solute concentrations. Such hydroclimatic changes can be both frequent and rapid, as was shown in the tropical Andes, leading to changes in aquatic biodiversity (Hillyer et al., 2009). In some estimates, Lake Titicaca was as much as 100 m below current levels in the early Holocene (Cross et al. 2001). In the western USA, reconstructed lake levels and oxygen isotope ratios reveal that small, high elevation lakes fluctuated by as much at 10 m, roughly 25% of their current depth, during the mid-Holocene, coincident with many other markers of strong regional aridity 3000 to 2000 years ago (Shuman et al., 2009; Anderson et al., 2016; Shuman and Serravezza 2017).

Paleolimnological records also track recent temperature changes, providing longer records than historical measurements (Reinemann et al., 2014a). Such records are particularly important for remote mountain regions where long-term records are otherwise unavailable and provide insights into regional variations of global warming. Sub-fossils of chironomids, which are particularly sensitive to temperature changes, have been used to infer past air temperatures and show that in many mountain regions temperatures have increased rapidly over the last century (Battarbee et al., 2002; Solovieva et al., 2005; Reinemann et al., 2014b; Williams et al., 2016; Porinchu et al., 2017). In the southern mountains of Costa Rica, sub-fossil chironomids quantified late-Holocene thermal variability including evidence for the Little Ice Age as well as changes in lake level caused by drought (Wu et al., 2017).

As well as quantifying mountain warming, paleolimnology has recorded mountain lake response to that warming. Shifts in diatom assemblages, particularly increases in small *Cyclotella* species, have been shown to track changes in lake conditions related to warming, including ice cover and duration and strength of thermal stratification (Catalan et al., 2013a; Rühland et al., 2008; 2015). Most of these studies have been made at northern latitudes; however, recent research from tropical, mountain lakes indicate that similar changes may be occurring globally. Michelutti et al. (2015a, b; 2016) and Labaj et al. (2018) showed that warming temperatures and reduced winds in the tropical Andes have led to increased thermal stability in deep lakes, with concurrent striking alteration of diatom assemblages, including reductions in production. From the same region, shallow lakes and ponds (<0.5 – 4 m) that do not thermally stratify have remained relatively unchanged in diatom assemblages, as predicted (Giles et al., 2018).

Warming temperatures are also resulting in a loss of glaciers and rock glaciers, which reduces water resources, but also can degrade water quality with potential toxic effects to aquatic organisms (Bain, 2017). A limnological survey in the Cordillera Vilcanota of Peru showed that much of the variability in nutrient and metal concentrations among sites could be linked to whether or not the lake was connected to a glacial watershed, with lakes in glacial catchments having elevated metals and nutrients due to glacial runoff over freshly comminuted bedrock (Michelutti et al., 2019). In some mountain regions changes in ice coverage has exposed sulfide-bearing bedrock, leading to oxidation of sulfide minerals and acid rock drainage (Fortner et al., 2011; Ilyashuk et al., 2017). Acid rock drainage leads to reduced pH and increased concentrations of certain metals in lakes. Furthermore, warming temperatures increase the rate of oxidation of sulfide minerals (Ahonen and Tuovinen, 1991), which should exacerbate water degradation. A paleolimnological study, however, showed that morphological deformities of chironomid head capsules caused by elevated metal concentrations were greater during the cold Little Ice Age compared to warmer conditions today (Ilyashuk et al., 2017). This research suggests that at higher temperatures the effects related to a lower metal toxicity to invertebrates outweighed the effects related to enhanced oxidation of sulfide minerals and acid rock drainage. These findings indicate the complexities and challenges of predicting the effects of warming temperatures on mountain lake ecosystems.

## 3.2 Carbon in mountain lakes

### 3.2.1 Carbon cycling and mountain lakes

Lake ecosystems play a key role in the carbon (C) cycle, where C is either retained in the biota, sequestered in sediments, transformed and respired, or exported downstream (Tranvik et al., 2009; Ejarque et al., 2018). Lakes are important conduits of carbon from the terrestrial system to the atmosphere (Cole et al., 1994; 2007), so understanding factors that affect $CO_2$ saturation, and therefore fluxes from lakes to the atmosphere, is an important contribution to our understanding of the global carbon cycle. A primary control on C cycling is climate (Gudasz et al., 2010). Ongoing changes in climate (section 3.1) have the potential to alter lake C dynamics through changes in weathering, terrestrial fluxes, productivity, and respiration (e.g., Parker et al., 2008; Gudasz et al., 2010; Sadro et al., 2012; Williamson et al., 2016).

Organic carbon originates from a complex mixture of lipids, carbohydrates, proteins, and other biochemical components produced by various organisms that have lived in and around the lake. Assessments of C pools and fluxes in mountain lakes are important owing to their large numbers and the sensitivity of both mountain lakes and the carbon cycle to climate change, yet such studies are limited. In temperate lakes, the DOC fraction is often larger than the particulate C fraction (Prairie, 2008). The largest reservoir of C, however, is found in lake sediments (Kortelainen and Pajunen, 2000). Although C in mountain lakes may be similarly subdivided among lake water, biota, and sediments, the relative proportions often depend on the landscape setting. Lakes in steep basins with harsh climates and little surrounding soil and vegetation will receive less C from both in-situ production and their catchments than lakes in less topographically extreme catchments that often provide C and nutrient-rich soil water (Müller et al., 1998). Müller et al. (1998) showed that total C contents in surface sediments are about twice as high in Swiss lakes above 700 m.a.s.l. (i.e., <100 mg C/g) compared to lakes at higher elevations (i.e., >100mg C/g),.

An elevational gradient of DOC concentrations is evident from North American mountain lakes, ranging from <1 mg C $L^{-1}$ to >20 mg C $L^{-1}$, with higher values at the lower elevation sites (Figure 2 and 3). Higher DOC concentrations are related to greater soil and vegetation cover but can also be influenced by peatlands, which can export up to 10× more DOC than forest soils (Sadro et al., 2012). DOC concentrations in 57 mountain lakes of the Austrian Alps also decreased with increasing elevation, particularly in lakes that were glacier-fed (~0.4 mg C $L^{-1}$) (Sommaruga et al., 1999).

Owing to complex interactions among climatic and non-climatic factors, the consequences of climate warming on alpine treeline is unclear (Davis and Gedalof, 2018); however, evidence indicates that afforestation is occurring at some alpine sites (Daniels and Veblen, 2004; Elliott and Kipfmueller, 2011). Afforestation and the predicted increase of unusually high precipitation events (IPCC, 2013) are likely to increase particulate and dissolved C fluxes to mountain lakes. In a recent multi-annual study of subalpine Lake Lunz (600 m.a.s.l.), Austria, Ejarque et al. (2018) found that DOC concentrations varied from 1 and 2.5 mg $L^{-1}$ between 2015 to 2017, with higher values occurring during wetter periods. These values were similar to the variation in DOC in several mountain lakes in Utah and Colorado, USA (Figure 2, 3), which ranged from 0.5 and 3.5 mg $L^{-1}$. In these studies, the DOC delivery to the lakes was sensitive to stream discharge; higher DOC concentrations corresponded to higher discharge. Data from Colorado show temporal variation with higher DOC values most likely occurring with peak flows during spring melt (Figure 3). Carbon loading from extreme rain events can simultaneously flush phytoplankton from lakes and increase allochthonous carbon loads, causing dramatic changes in lake metabolic balance (Sadro and Melack, 2012).

Variations in DOC source and supply may have a direct bearing on microbial C utilization and respiration dynamics (Sadro et al., 2011). To date, our understanding of C respiration in mountain lakes is limited. It is, however, plausible that C respiration will increase with higher water temperatures and shorter periods of full ice-cover (Gudasz et al., 2010; Hampton et al., 2017; Kainz et al., 2017). Warmer temperatures and longer growing season will increase the flux of particulate carbon to the sediments (Hanson et al., 2004; Downing et al., 2008). Phenological changes in snowmelt timing, flushing, nutrient delivery, and warming associated with dry years in a high elevation lake in the Sierra Nevada of California resulted in increased phytoplankton biomass (Sadro et al., 2018). As is the case for lakes worldwide, such complexities make it difficult to predict whether mountain lakes will become net sources or storage for C in the future.

#### 3.2.2 Historical perspectives elucidate the role of lakes for carbon storage

Paleolimnological studies that examine $CO_2$ limitation and saturation, C sources and burial, and DOC through the Holocene and Anthropocene may help define limits for future predicted change (Meyers & Lallier-Vergès, 1999; Catalan et al., 2009; Kastowski et al., 2011; Rouillard et al., 2011). Research using compound-specific stable isotope analyses of leaf waxes and algal biomarkers from tropical mountain lakes in Africa revealed that lower partial pressure of $CO_2$ during glacial periods caused severe carbon limitation in alpine lakes that favoured organisms possessing $CO_2$-concentrating mechanisms (Street-Perrott et al., 1997). It is also possible to derive estimates of $CO_2$ supersaturation from diatoms in lake sediments (Catalan et al., 2009). Diatom-inference models were used to determine estimates of past lake water alkalinity and pH, from which $CO_2$ concentrations were estimated in Pyrenean lakes during the Holocene. These reconstructions were used to explore climate-carbon cycle relationships, including that $CO_2$ supersaturation increased with increasing temperatures and alkalinity (Catalan et al., 2009).

Even though most lakes are supersaturated with respect to $CO_2$ and thus outgas $CO_2$ (Cole et al., 1994), the rate of carbon burial in lake sediments is similar to that in marine sediments and important to the global carbon cycle (Dean and Gorham, 1998; Cole et al., 2007; Mendonça et al., 2017). Several studies have determined records of organic C burial rates using loss-on-ignition (Dean, 1974) of sediments in dated cores to examine spatial and temporal variations of C burial in lakes at regional to global scales (Kastowski et al., 2011; Heathcote et al., 2015; Mendonça et al., 2017). Recent research has coupled measurements of organic C from sediment cores with predictive models to upscale to regional and global estimates of organic C burial in lakes and reservoirs (Heathcote et al., 2015; Mendonça et al., 2017). These studies suggest that lakes and reservoirs are globally important storages of C, with organic carbon burial in lakes ranging from 0.06 to 0.25 Pg C $yr^{-1}$. Regional studies of changes in sequestration of C in mountain lakes are lacking; however, many studies have shown that temperatures are rising rapidly in mountain regions (Kainz et al., 2017; Niedrist et al. 2018) and that lakes in these regions have become more productive because of atmospheric nitrogen deposition (section 3.3), dust deposition (section 3.4), and glacier recession (section 3.1). As the climate continues to change mountain lakes may have an increasingly important role for carbon storage. Important to understanding the role of lakes and refining carbon budgets is knowledge of the relative contribution of terrestrial and aquatic organic C to sediment organic C (Mendonça et al., 2017). New research using the $\delta^{13}C$ of specific biomarkers (e.g., n-alkanes, fatty acids) and mixing models may help to improve our ability to fingerprint OC sources and in-lake carbon processes.

### 3.3 Atmospheric deposition

#### 3.3.1 Sensitivity and susceptibility of mountain lakes to atmospheric deposition

The high elevations of mountain lakes make them particularly vulnerable to atmospheric deposition of pollutants and nutrients because they tend to receive more precipitation than other regional landscapes, and because deposition of certain contaminants, such as organochlorines, are enhanced at cold temperatures associated with higher altitudes (Wania and MacKay, 1993; Blais et al., 1998; Grimalt et al., 2001). Pollutants and nutrients can come from direct atmospheric deposition of gases, aerosols, and particulates, and from the release of materials stored in upstream cryogenic features including glaciers, rock glaciers, and permafrost (Figure 5). Delivery of atmospheric deposition to lakes is influenced by climate and catchment characteristics, and the resulting inputs to lakes can affect both in-lake processes and biota (Nanus et al., 2012).

Dust and particulate aerosols are generated from a number of natural and anthropogenic sources not limited to soil erosion, and include industrial emissions (e.g., mining, fossil fuel burning, cement production), transportation, civil engineering, biomass burning and residential heating sources, plant products (e.g., pollen), and volcanic emissions (Mahowald et al., 2008). Because all the above have the capacity to influence mountain lakes, for the purpose of this review, all particulates including particulate aerosols will be considered as atmospheric dust and discussed separately in section 3.4.

The suite of characteristics that render mountain lakes sensitive to atmospheric deposition include cold temperatures, snowmelt-dominated hydrology, relatively insoluble bedrock, poorly buffered waters, shallow soils, short water residence time in catchments, and sparse vegetation (Glass et al., 1982; Psenner, 1989; Baron, 1991; Sommaruga-Wögrath et al., 1997). These characteristics limit a lake's ability to neutralize acid rain and a watershed's ability to sequester nutrients or contaminants. Metals, organochlorines, and other persistent organic pollutants recorded in mountain lake sediment cores chronicle the increase, and subsequent, regulatory decrease, of these substances in society (Fernandez et al., 2000; Camarero et al., 2009; Usenko et al., 2010; Heard et al., 2014). Some of these compounds can be more abundant in mountain lakes than at lower elevations due to cold condensation, a phenomenon where organochlorines that volatilize in warm environments move into mountain areas with air currents and condense at colder temperatures (Blais et al. 1998). Sediment records of remote alpine lakes reflect accumulation from cold condensation in addition to melting of glaciers and other ice bodies where organochlorines and other organic pollutants have accumulated over time (Blais et al. 1998, Bogdal et al. 2009).

Atmospheric deposition of pollutants is indicative of regional to global changes, as is climate change, and there are interactions among these potential stressors. Atmospherically deposited materials can be stored in either short- or long-term reservoirs within the catchment before entering surface waters (Figure 5). Reservoirs with short residence times include the lake surface itself and seasonal snow. Time scales of nutrient or contaminant delivery depend on the hydrology of the system and can range from instantaneous to annual. Annual snowmelt plays a major role in delivering both wet and dry deposition stored in the snowpack over the winter months. Catchment soils and cryogenic features (permafrost, glaciers, and rock glaciers) accumulate nutrients and contaminants deposited over decades to centuries (Blais et al., 2001; Bacardit et al., 2012; Homyak et al., 2014). The mass of materials stored in these longer-term reservoirs can dwarf annual deposition (Bacardit et al., 2012; Catalan et al., 2013a; Homyak et al., 2014). Release from soils involves complex interactions among warming, precipitation patterns, soil erosion, soil chemistry (i.e., pH and organic C) and soil-water interactions (Catalan et al., 2013a). Glacial meltwater can directly discharge stored trace metals (Thies et al., 2007; Colombo et al., 2018), nitrogen, phosphorus, and dissolved organic carbon (Baron et al., 2009, Saros et al., 2010; Peter and Sommaruga, 2016; Fegel et al., 2016) and organic contaminants (Blais et al., 2001) to surface waters.

### 3.3.2 Insights from paleolimnology on the effects of atmospheric deposition

Atmospherically deposited sulfur (S) and nitrogen (N) compounds caused widespread acidification of geologically sensitive regions over the Northern Hemisphere during the last century (e.g., Schindler et al., 1985; Battarbee, 1990; Psenner and Catalan, 1994). In some cases, acidic deposition altered the biota of mountain lakes, reducing overall biodiversity and primary productivity, extirpating acid-sensitive fauna, and causing fish mortality (Nilssen and Sandoy, 1990). Termed acid rain (Likens et al., 1979), acidic deposition became a widely reported environmental issue beginning in the 1960s, but some ecosystems had begun to respond to deposition of strong acid anions as early as ca.1900 (Likens, 2010; Catalan et al., 2013a;

Sickman et al., 2013). Strong scientific evidence in Europe and North America contributed to air pollution control regulations.

Intensive research into the effects of acidic deposition on mountain lakes, including paleolimnological reconstructions, used proxies of acidification and its sources. These research efforts led to significant advances in paleolimnology, including improved sampling as well as chronological control and quantitative approaches. These advances, in turn fueled a rapid expansion of paleoecological research (Battarbee et al. 2010). Successful indices of change in lake sediment cores were developed. These took advantage of the sensitivity of diatom, chrysophyte, and some invertebrate species assemblages to lake pH, and synchronous changes in heavy metal concentrations that were indicative of industrial emission sources and biogeochemical/biological responses (Charles et al., 1989; Cumming et al., 1992; 1994; Evans et al., 2001; Kopáček et al., 2015a). Since 1980 and with the advent of controls on industrial emissions and socio-economic changes in industrial and agricultural production, there has been some recovery from acidification in certain lakes. Chemical recovery precedes biological recovery, but there is evidence of both (Evans et al., 2001). Although there has been recovery from acidification in some lakes, in some cases it has taken longer than expected with the potential to exacerbate other global change issues, such as increasing nutrients from atmospheric deposition (Figure 6).

Sediment cores from the Tatra Mountains of Slovakia and Poland demonstrate the ecological response to increasing and then decreasing acidic deposition (Figure 6; Kopáček et al., 2015b). Lakes became progressively more oligotrophic during acidification beginning in the 1940s. During the following recovery and eutrophication phase, beginning in the late-1980s, phytoplankton biomass increased and some of extirpated zooplankton species reappeared in the lake in increasing numbers. One causal factor of increased productivity is increased concentrations of phosphorus in lake water, even in areas that do not receive important atmospheric P inputs from dust. As soils become less acidic, their ability to adsorb P is reduced, and P is exported to lakes. In addition, soils leach less aluminum, which means that the in-lake P immobilization by aluminum is reduced (Kopáček et al., 2015b).

The increased availability of reactive nitrogen over the past century as a product of industrialization, transportation, and agricultural intensification has increased primary production in some mountain lakes (Bergström and Jansson, 2006; Battye et al., 2017). Mountain lakes are naturally oligotrophic, and by virtue of their location high in catchments, are especially sensitive to atmospheric nutrient inputs. Effects of N enrichment on remote mountain lakes have been reported from Europe, eastern and western North America, and Japan (Lepori and Keck, 2012). Some headwater mountain catchments, with sparse vegetation and poor soil development, have become saturated with N, allowing excess nitrate to leach to mountain lakes (Baron et al., 2000). While inputs of nitrate and ammonium to mountain catchments contribute to acidification, another effect is stimulation of primary productivity. N fertilization alters lake water N:P ratios, and species composition, since N is a limiting nutrient in many mountain lakes without prior history of disturbance (Saros et al., 2003; Sickman et al., 2003; Bergström and Jansson, 2006; Elser et al., 2009).

Using stable N isotopic ratios from dated sediments of remote Northern Hemisphere lakes, Holtgrieve et al. (2011) found a coherent signal of an isotopically distinct N source beginning around the year 1895 and coincident with widespread industrial activity and increased $CO_2$ emissions. The rate of change accelerated in the mid-20$^{th}$ century in conjunction with commercial production of synthetic nitrogen fertilizers through the Haber-Bosch process (Battye et al., 2017). Isotopic concentrations ($\Delta^{17}O$, $\delta^{18}O$ and $\delta^{15}N$) from Uinta Mountain (Utah, USA) snow, inflow and lake nitrate, in combination with a Bayesian-based stable isotope mixing model, showed that at least 60% of the nitrate in these aquatic systems was anthropogenic and from synthetic fertilizers arriving to the lakes through atmospheric deposition (Hundey et al., 2016). Increased atmospheric N deposition has been paralleled by substantial changes in algal communities. These include accelerated turnover in species composition, increased planktonic species, and greater abundance of nitrophilous taxa (Wolfe et al., 2001; Hobbs et al., 2010; Saros et al., 2011; Hundey et al., 2014). Specifically, these studies show an abrupt shift from typical flora of dilute nutrient-poor alpine waters, such as small Fragilariaceae and *Achnanthes* spp., to domination by *Asterionella formosa* and *Fragilaria crotonensis*. The effects of altered phytoplankton assemblages extend to higher trophic levels. Elser et al. (2010) found experimental evidence that consumption of N-rich algae may cause P-limitation in some cladocera taxa that are key herbivores in pelagic food webs. Nitrogen deposition to mountain lakes may therefore impair the efficiency of trophic transfer by accentuating nutrient imbalances in lake food webs (Lepori and Keck, 2012). Changes in climate can influence the response of lake algal assemblages to atmospheric N deposition through changes in thermal stratification (Saros et al., 2012).

Lake sediment records have revealed that nutrient subsidies from glacial meltwaters began altering the chemistry and algal community structure of alpine lakes 100 to 1000 years ago across the US Rocky Mountains (Slemmons et al., 2017). This research showed that glacier-fed lakes in the northern Rocky Mountains contain 40× more nitrogen than snow-fed lakes. Increased N inputs have altered diatom species assemblages and reduced diversity. Although multiple mechanisms, including flushing and increased mineralization, may contribute to N-enrichment, the response of glaciers to warming seems to alter lake biodiversity through release of nutrients (Slemmons et al., 2017). The examples above suggest a growing role of interactive effects of climate change with the cryosphere and its store of atmospherically deposited materials (Saros et al., 2012; Catalan et al., 2013a).

Schmid et al. (2011) demonstrated how the reservoir of persistent organic pollutants (POPs) in glaciers fueled multiple peaks in the influx of POPs into a Swiss alpine lake over the 20$^{th}$ century, in contrast to a single peak in the sediments of a lake situated in a nearby non-glaciated watershed. The release of nutrients, metals, and legacy contaminants from glaciers can increase chemical loading to headwater alpine lakes, which has implications for freshwater systems further downstream.

## 3.4 Dust

### 3.4.1 Dust to mountain lakes

Mountain ranges are natural barriers to atmospherically transported particulates that are derived from lowland areas, and thus mountain lakes are excellent recorders of dust emissions due to climate, drought, and upwind land-use change. Under natural circumstances, dust generation from soils is controlled by factors that 1) expose soil surfaces to the atmosphere and 2) provide the energy for erosion and entrainment. The former is related to drought, which is largely a function of storm patterns and wind speeds, and the presence of vegetation or other surface protectors (Field, 2009). These biogeoclimatic factors may interact to produce natural fluctuations in dust generation across space and from year to year.

Human activity on the Earth's surface, combined with persistent and intensified droughts, has led to an increase in atmospheric dust generation in the 20$^{th}$ century (Mahowald et al., 2010), which can significantly alter the natural biogeochemistry of mountain lakes. Anthropogenic factors may exacerbate dust generation in regions that already produce dust (Neff et al., 2008, Mulitza et al., 2010), as well as expose land surfaces that may generate new sources of dust emissions (Lee et al., 2012, Brahney et al., 2015a). Water diversions can lead to desertification and sometimes the complete loss of lake ecosystems, exposing lakebeds to wind erosion (Reheis, 1997, Larsen, 2014). Agricultural activities and pastoralism can exacerbate soil erosion by reducing the threshold wind velocity required for soil entrainment (Leys and Eldridge, 1998, Neff et al., 2005). Other types of land-use including, construction, oil and gas operations, biomass burning, and recreational off-road vehicle use have led to increases in local to regional scale particulate emissions (Andreae et al., 1988, Goossens and Buck, 2009). Effects of dust on aquatic systems will differ due to variation in dust fluxes and composition, and pre-existing conditions in depositional regions. For example, the addition of acid-neutralizing capacity will have greater implications for lakes situated in granitic than in limestone basins, and the addition of nutrients will have greater impacts on steep, poorly vegetated catchments than in mountain catchments with well-developed or even legacies of grazing.

The composition of dust varies with source region and factors that alter composition during transport. The primary control on dust composition is the parent geology and degree of soil development and/or land use. For example, dusts from the Sahara tend to be minerogenic, with only a few percent of organic matter composition (Eglinton et al., 2002). In contrast, dusts generated from semi-arid and agricultural regions tend to contain the fine organic and nutrient-rich fraction, leading to dust material that may have >60% organic material (Malm et al., 2004). As a result, dusts from these regions may be enriched in rock-derived nutrients, such as phosphorus and calcium, as well as plant fixed nutrients, such as nitrogen. Dusts eroding from agricultural fields may contain traces of pesticides and fertilizers.

Understanding the bioavailability of nutrients from dust is an active area of research (e.g., Zhang et al., 2018), and there is growing circumstantial evidence to suggest that dust may transport significant quantities of nutrients to mountain lake ecosystems (Morales-Baquero et al., 2006, Brahney et al., 2014). In general, alpine aquatic systems respond rapidly to nutrient additions where a small change in absolute concentration may translate into a large change in relative availability. Elevated deposition of nutrients may not only increase primary productivity in alpine lakes, but also lead to shifts in the relative availability of N and P, which has the potential to alter algal community structure (Tilman et al., 1982). A meta-analysis of atmospheric and lake-water chemistry data from around the world showed a strong correlation of N:P ratios. Mountain lakes with low N:P ratios were found proximal to areas of moderate to high dust and ash deposition (Brahney et al., 2015b).

Nitrogen contributions from dry deposition are rarely analyzed and potentially an underappreciated component of the atmospheric nitrogen contribution to mountain lakes (Sickman et al., 2001; Neff et al., 2002, Cornell, 2011). The form and bioavailability of nitrogen associated with particulates will likely vary by biogeoclimate and land-use. In the Mediterranean region, the organic fraction has been associated with calcium deposition, indicating a dust source of organic N (Mace et al., 2003b); however, agriculture and biomass burning may also significantly contribute to the particulate N flux in other areas (Mace et al., 2003a). In contrast to atmospheric nitrogen, phosphorus has no stable gaseous form and thus atmospheric transport largely occurs as particulates. The most important sources of phosphorus containing dusts are from wind-generated soil emissions, biomass burning, and to some extent industrial and mining emissions (Mahowald et al., 2008; Vicars et al., 2010). Because soil erosion tends to remove the fine-grained, nutrient-rich fraction, the dusts generated tend to have relatively enriched concentrations of phosphorus. On average, dusts are enriched by a factor of 1.6 over soils (Lawrence and Neff, 2009) and therefore have the capacity to fertilize mountain aquatic environments.

The water-soluble organic carbon fraction of dusts has been correlated to DOC concentrations in lakes over large-spatial scales and across time (Reche et al., 2009, Mladenov et al., 2011). The dust-mediated transport of water-soluble organic carbon to lakes above elevational treeline may have both physical and biotic implications because these lakes are typically characterized by much lower levels of DOC than subalpine lakes (Figure 2 and 3). For example, a study in the Sierra Nevada of Spain demonstrated that dust-associated additions of DOC reduced transparency and penetration of UVR, and was associated with shallower mixing depth (Vicente et al., 2012). Several authors have suggested that DOC inputs in conjunction with elevated nutrient deposition from dust may further support microbial growth in alpine lake systems (Pulido-Villena et al., 2008, Reche et al., 2009, Vicente et al., 2012).

The above research exemplifies the unique role that mountain lakes play in understanding complex phenomena such as dust origin and transport. Because of the distinct geochemical signatures found in most mountain bedrock, it is possible to determine the historical variation in dust generation and deposition that would not be possible from valley bottom lakes. Similarly, because of the larger airshed influence on mountain lakes, the signature of atmospheric deposition and explicit impact on bottom-up processes is discernable, which would not be possible with the confounding factors of land-use, climate, vegetation, and catchment areas for lower elevation lakes.

3.4.2 Paleolimnological analyses show the importance of dust deposition in lakes

Paleolimnological analyses in mountain lakes worldwide has shed light on long- and short-term dust histories as well as the effects of dust on aquatic chemistry and ecosystems through the addition of alkalinity, nutrients, trace elements, contaminants, and organisms. The addition of alkalinity from dust may offer mountain lakes protection from acidification (Psenner, 1999). Dust can increase the pH and alkalinity of precipitation received at mountain lakes, even completely neutralizing air-borne acids in dusty years (Rogora et al., 2004).

The dissolution of calcium carbonate and other dust minerals either in precipitation or in depositional water bodies can provide readily available $Ca^{2+}$ to remote mountain lakes (Pulido-Villena et al., 2006). For regions with catchments having naturally low calcium abundances, this contribution may be a critical source of calcium to aquatic organisms with relatively high calcium requirements. For example, in the Sierra Nevada of Spain, paleolimnological research showed that in the last ~50 years there has been an intensification of dust and $Ca^{2+}$ inputs from the Sahara (Jiménez et al., 2018). This, combined with the effects of climate change, including increased evapoconcentration and greater dust exposure due to a longer ice-free season, resulted in increased $Ca^{2+}$ concentrations. This, in turn, led to an increase in *Daphnia* (Jiménez et al., 2018), a cladoceran taxon whose growth and reproduction can be limited by $Ca^{2+}$ availability (Jeziorski et al., 2008; Jeziorski and Smol, 2017). *Daphnia* is a keystone genus, and expansion of their populations is an indication of significant environmental changes in this region.

The capacity for dust to affect phosphorus subsidies in mountain lakes systems was first identified in the Austrian Alps (Psenner, 1999). Since then, other studies elsewhere in mountain regions of Europe, Asia, and the USA have shown the effects of dust associated P deposition on influencing lake water nutrient chemistry, productivity, and species composition. For example, a paleolimnological study in the Wind River Range, Wyoming, used isotopic tracers of dust ($^{143}Nd/^{144}Nd$, $^{87}Sr/^{86}Sr$) that indicated an abrupt increase in dust deposition around 1950 AD (Brahney et al., 2015a). These data, combined with parallel shifts in sedimentary pigments, diatom productivity, and diatom-inferred increases in total P indicated that even modest dust deposition rates can alter nutrient and plankton communities in mountain lakes (Brahney et al., 2015a). In the Sierra Nevada of Spain, dust-associated P deposition ranged from 24-38 µg P $m^{-2}$ $d^{-1}$, a seemingly small contribution, yet this deposition rate had measurable effects on productivity, inferred from chlorophyll-a, bacterial abundance, and plankton diversity (Morales-Baquero et al., 2006, Pulido-Villena et al., 2008, Reche et al., 2009). In several mountain regions around the world, the atmospheric deposition of P has surpassed the effects of N deposition, leading to N-limited phytoplankton growth (Vicars et al., 2010, Camarero and Catalán, 2012).

## 3.5. Mountain lake biota and environmental change

### 3.5.1 Mountain lake biota with emphasis on fish introductions

Mountain areas are rich in biodiversity (Körner et al., 2017); about one third of terrestrial species diversity and half of all 34 global hotspots are situated in mountains (Körner et al., 2004; Chape et al., 2008). Although these figures are for the terrestrial ecosystem, diversity of mountain lakes is expected to be equally high. Kammerlander et al. (2015) showed that genetic diversity of the planktonic protist community was high in glacial lakes of the European Alps and the Himalayas. High diversity in this microbial community was tied to rapidly changing physicochemical conditions resulting from changing connectedness with glaciers. Endemic and native species may be increasingly sensitive to extinctions and extirpations since there is limited ability for re-establishment (e.g., limited dispersal in mountain environments) and escalating stress from introduced species, pollution, climate change and interactions among the three. In the context of climate warming and refugia, such knowledge is critical for conservation, yet such issues remain understudied (Catalan and Donato Rondón, 2016).

High mountain lakes are generally fishless because they are often isolated from lower elevation streams by physical barriers (e.g., waterfalls) that prevent natural colonization by fish. In western North America, it is estimated that ~95% of mountain lakes were historically fishless. Over time, 60% have been stocked with non-native fishes (Bahls, 1992). The creation of angling opportunities drove much of the early stocking practices in North American and European mountain lakes (Pister, 2001; Ventura et al., 2017). Stocking, however, was also motivated by a perception that mountain systems were unproductive and would benefit from the addition of organisms, such as fish and invertebrates (e.g., opossum shrimp, *Mysis relicta*: Spencer et al., 1991). The establishment of introduced fish caused the decline or elimination of native zooplankton, macroinvertebrates, and amphibians, which altered food web structure and resulted in a loss of ecological integrity (Eby et al., 2006). These top-down effects can be complex. For example, the recent introduction of a non-native minnow (*Phoxinus* sp.) in the Pyrenean high mountain range increased sediment resuspension and nutrient release, as well as exerting strong predation on zooplankton and zoobenthos (Gacia et al., 2018). These factors shifted epiphytic communities from low to high biomass, and chlorophytes and diatoms to cyanobacteria. Epiphytic cyanobacteria blooms reduced light leading to increased aboveground biomass of quillwort (*Isoetes lacustris*), which eventually led to reduced root mass and uprooting. The loss of aquatic plants in mountain lakes and ponds can lead to profound ecological effects because aquatic plants provide shelter for associated fauna and modulate trophic status (Gacia et al., 2018).

The addition of fish can also alter the distribution of contaminants (Walters, 2008). Fish exert strong, top-down controls on insect emergence and contaminant flux to riparian habitats. Insect emergence was 20-fold higher in naturally fishless lakes than lakes with fish in alpine lakes of the Sierra Madre in California (Finlay and Vredenburg, 2007). Because larval aquatic insects accumulate contaminants in their tissues, fish can be an important vector of contaminants to riparian insectivores (Walters et al., 2008).

In addition to the effects of introductions and establishments of non-native species, other regional and global disturbances are having consequences on mountain lake biota. For example, the increased nitrogen deposition alters algal (Wolfe et al., 2001) and zooplankton (Brittain and Strecker, 2018) communities, potentially influencing rates of primary production and the transfer of energy through the food web. The cascading effects of climate change on physical variables in mountain lakes may have significant consequences on biological communities. Ice phenology plays a fundamental role in governing autochthonous and microbial production and therefore budgets of lake productivity (Preston et al., 2016). Hampton et al. (2017) compared physical, chemical, and biological characteristics of lakes during winter (under ice) and summer, and found that algal biomass can be substantial during winter. Dissolved nitrogen concentrations in mountain lakes are consistently higher under ice compared to summer. Extremes in climate variables, such as warm temperatures and reduced precipitation, limit biodiversity of macroinvertebrate community composition in mountain lakes (Boersma et al., 2016). Thermal regimes in mountain lakes may shift in the future to be optimal for native fishes, like cutthroat trout (*Oncorhynchus clarkii*), in some lakes, but not all, as other lakes may become too warm for native fishes (Roberts et al., 2017). Rising temperatures will lead to declining abundances of cold-water obligate insects, which has been shown in alpine lakes where reductions in glacial and snowmelt inputs led to higher water temperatures (Brown et al., 2007; Giersch et al., 2017). Estimating the cumulative effects of these multiple stressors on mountain lake ecosystems is difficult.

Multiple environmental stressors can also affect the adaptive strategy of organisms in mountain lakes. For example, the introduction of fish combined with the complex interactions between warming temperatures and UVR can affect the selected behavioral and physiological strategy of copepods (Sommaruga, 2010; Tartarotti et al., 2017). UVR generally increases with elevation, however the amount of UVR that an organism is exposed to is also dependent on turbidity, which is largely controlled by proximity to glaciers and climate (Vinebrooke et al., 2010), as well as dissolved organic carbon (DOC), which is influenced by the cover and type of catchment vegetation, wetlands and climate (Schindler et al., 1996).

Zooplankton may follow various strategies to reduce the harmful effects of UVR, including vertical downward migration during daytime (Alonso et al., 2004; Fisher et al., 2015) or accumulation of photo-protective compounds such as carotenoids (Hairston, 1976) or mycosporine-like amino acids (MAAs) (Sommaruga and Garcia-Pichel, 1999). Owing to their red colour, carotenoids can increase a copepod's visibility to predatory fish, and therefore when exposed to both UVR and fish predation carotenoids offer protection, but increase vulnerability (Hansson, 2000). This makes predicting a copepod's adaptive strategy to high UVR exposure difficult, particularly in the light of environmental change (Sommaruga, 2010; Tartarotti et al., 2017).

3.5.2. Paleolimnology identifies effects of environmental change on mountain lake biota

Lake sediment records have provided a means to determine when lakes were stocked and a long-term perspective on the effects of fish stocking. For instance, Schilling et al. (2008) used the presence of *Chaoborus americanus* mandibles (a taxon that rarely co-exist with fish; Sweetman and Smol, 2006) in the sediment record to infer fish presence or absence in mountain and lowland lakes. Nevalainen et al. (2011) showed that reductions in *Daphnia longispina* and extirpation of *Eurycercus lamellatus* in the sediment record were likely the result of fish introductions. Additionally, increased algal fossil pigment concentrations were observed in mountain lakes corresponding with fish introductions (Leavitt et al., 1994; Schindler et al., 2001). Paleolimnology has also provided critical information about how systems recover after fish are removed or are no longer present. Knapp and Sarnelle (2008) used the historical presence of dormant zooplankton eggs in the sediment record to infer that the taxa *Daphnia melanica* and *Hesperodiaptomus shoshone* were not recovering following non-native fish removal. Additionally, diatom communities shifted with the introduction of non-native fish in mountain lakes, but did not respond to fish removal, indicating that lakes have not recovered (Drake and Naiman, 2000).

Lake sediments provide an archive of the effects of global change on the biota of mountain lakes. For example, climate change affects both the physical and chemical characteristics of lakes (section 3.1). In the tropical Andes, rapid climatic changes have increased the thermal stability in some lakes, and this has restructured lake algal and cladoceran assemblages, changing lake trophic structure (Figure 7; Michelutti et al., 2015a; b; Labaj et al., 2017). With continued warming, it is anticipated that similar changes of equal or greater magnitude will be reported from alpine lakes worldwide (Labaj et al., 2017). Such altered states may be contemporaneously impacted by other stressors.

Lake sediment records from three lakes in the Swiss Alps were used to determine the effects of multiple stressors (increased nutrients, fish predation and climate) and their interactions on lake ecosystems over time (Perga et al., 2015). Results showed an increasing influence of warming temperatures towards the present day, but also showed differences in response between lakes and taxonomic groups. This research found that the effects of climate on phytoplankton were strongest in mesotrophic lakes (where phytoplankton were not limited by nutrients) as compared to oligotrophic lakes (van de Waal et al., 2010; Perga et al., 2015). Whereas climate warming favored *Bosmina* in all three lakes, in two lakes the response of *Bosmina* was linked to climate warming re-enforcing top-down controls by increasing the growing season, per-capita feeding rates, and recruitment of zooplankton larval stages (Kratina et al., 2012; Perga et al., 2015). This study highlights the complexity possible in the interplay of fish predation, nutritional constraints and climate change to create multiple, indirect community response pathways (Perga et al., 2015).

## 4. Conclusions, research perspectives and future directions for mountain limnology and paleolimnology

Mountain lakes provide us with 'eyes' to see environmental change at a variety of spatial and temporal scales. Paleolimnology provides a historical perspective not otherwise possible that provides important insights into lake ecosystem responses to regional and global change. Mountain lakes are subjected to multiple and integrated disturbances that change in magnitude over time, and our review highlights the complexities of the interactions among stressors and the ultimate organism to lake ecosystem response. Paleolimnological studies have contributed significantly to our understanding of the interaction of multiple stressors on lake ecosystems because lake sediments integrate and preserve a record of environmental changes originating from the atmosphere, catchment, and lake (Catalan et al., 2013a).

Our review indicates some additions to existing approaches that would increase insights and target key areas for future research on global change. Increased spatial and temporal resolution will benefit this research. The remoteness of many sites has made access and logistics difficult, meaning spatial coverage is low and high-resolution measurements have been relatively rare. A variety of technical advances in the field of remote sensing will provide the means to overcome this issue, providing knowledge about the effects of climate change on limnological processes and the air-to-sediment continuum. These advances should also improve spatial coverage to include all mountain regions of the world, reducing the bias towards Northern Hemisphere mountain lakes (Figure 1).

The high degree of spatial and temporal heterogeneity found in mountain regions means large-scale climate processes are mediated at local scales, creating a mosaic of possible lake responses at the landscape scale. To make valuable predictions on the ecological stability of alpine lakes, understanding the impacts of directional multifaceted disturbances will be crucial. Our ability to predict how high-elevation lakes will respond to ongoing changes in climate will be strengthened by approaches that integrate an understanding of responses at long time scales (i.e., centuries to millennia) with an emerging understanding from contemporary studies of effects on lake temperatures, thermal structure, lake chemistry and biota. For example, combining high-frequency, limnological monitoring data with long-term paleo data could lead to more accurate estimates of the overall effect of climate change on mountain lake ecosystems. One area this could be applied is in determining the effects of extreme events.

Our review suggests several key research targets for the better understanding of global environmental change. As shown in section 3.1, mountain regions and lakes are particularly sensitive to warming temperatures, but intense episodic weather events may be as important as gradual warming in driving the long-term trajectories of ecosystems (Perga et al., 2018). Climate change is expected to manifest itself in increased frequency and magnitude extreme weather events, including heatwaves, droughts, heavy rainfalls, floods and windstorms (IPCC, 2013), and extreme weather events are typical climate features of mountain lacustrine ecosystems (Wilhelm et al., 2012; Fouinat et al., 2017). However, the effects of high frequency events are poorly understood for lake ecosystems (Woodward et al., 2016), and are not yet incorporated into estimates of lake ecosystem response to climate.

Lakes play an important role in the global carbon cycle (section 3.2), but many questions about carbon and lakes remain unanswered. Mountain regions are an excellent place to tackle questions about the carbon cycle owing to steep elevational gradients, which result in variations in carbon fluxes and storage capacity of lakes. This variation results in a natural experimental area to determine the role of lakes in close proximity that cover a wide range of C-related conditions. This is illustrated by changes in DOC concentrations of lakes across elevational gradients (Figure 2 and 3). An opportunity for better understanding the role of lakes in the carbon cycle, but also the effects of changes in inputs and composition of carbon on lake ecosystems is in tracking long-term variations in DOC in lake sediments. DOC can originate in lakes or be exported from the terrestrial system to lakes and is a fundamental control on lake ecosystem structure and function (Williamson et al., 1999; Prairie, 2008; Solomon et al., 2015).

Organic C burial is also related to DOC, which can be sequestered in sediments by a process that increases C burial (Tranvik et al. 2009). Contemporary measurements of DOC show that in many northern temperate and boreal lakes DOC is increasing, a phenomenon referred to as browning (Skjelkvale et al., 2005; Roulet and Moore, 2006). However, in other regions, DOC has been shown to be decreasing (Schindler et al., 1996). A number of different mechanisms have been suggested, including climate change, atmospheric deposition and hydrology (Solomon et al., 2015). Neither baseline DOC concentrations nor the reasons for changing DOC are clear, however, answering these questions is critical to better predict future levels of DOC. Recent advances in paleolimnological methods to measure DOC and TOC using visible-near-infrared spectroscopy (VNIRS) (Rouillard et al., 2011; Valina et al., 2015; Meyer-Jacob et al., 2017) should help address these questions (Valina et al., 2015).

Based on research completed, we predict that future change in mountain lake catchments will result in both higher allochthonous and autochthonous C contribution to lakes. By designing research programs across the treeline ecotone of mountain regions, paleolimnology and limnological research could investigate a variety of questions regarding C sources, controls on those sources, and the fate of additional C to lakes. Future work should focus on understanding how environmental change affects the relative roles of autochthonous versus allochthonous C sources, its transport within lakes and into downstream waterbodies, and the consequences of altered C dynamics for lake food webs and productivity.

Methodological advances may provide the opportunity for paleolimnology to contribute to these questions. For example, advances in determining n-alkane relative abundances and their C and N isotopic values can help elucidate C sources for organics in sediment records. Addressing these questions to eventually predict C dynamics in lakes, however, is not possible based solely on sediment records. Rather, this will require estimating how much lakes will warm and how snowmelt hydrodynamics will change, coupled with analysis of concurrent C inflow, metabolism, sedimentation, and outflow, along with the interactions of the C, N and P cycles. This calls for a concerted sampling strategy among mountain lake investigators. Objectives of such a common strategy may include sampling of: a) DOC as an energy-yielding substrate for bacteria, whose response to different DOC composition will affect their biomass and respiration; b) particulate C as equally energy-yielding substance for aquatic consumers; and c) $CO_2$ and $CH_4$, as a measure of C release to the atmosphere. All such forms of C are measured in various aquatic systems worldwide, yet mountain lakes are thus far underrepresented (Pighini et al., 2018). Furthermore, innovative paleolimnological research using $\delta^{13}C$ of biomarkers and ancient DNA is being used to constrain how lacustrine methane production, oxidation, and emissions respond to global change drivers (Stötter et al., 2018); however, such research has yet to take full advantage of the steep C gradients observed in mountain lakes.

Dust particles can transport significant amounts of nutrients, pesticides, harmful pathogens, and heavy metals (Zabik and Seiber 1993; Tamatamah et al., 2005; Reynolds et al., 2010). Importantly for mountain lakes, these pollutants have been stored in the cryosphere, and are now being released rapidly with climate warming (section 3.3). Probably the most studied of the constituents of dust is phosphorus, which can be the limiting nutrient in many terrestrial and freshwater ecosystems (Elser et al., 2009). Yet, owing in part to relatively low spatial resolution of atmospheric monitoring networks, we lack a clear understanding of the total dust and P deposition load in both space and time. Many other questions remain unanswered regarding the importance of dust as a transport vector of phosphorus and other contaminants, the specific sources of phosphorus and other contaminants, and the effects of dust on mountain lake ecosystems. Improved spatial resolution and more inclusive measurements of contaminants in atmospheric monitoring networks, advanced geospatial modelling (Nanus et al., 2012), innovations in SIA, particularly of the oxygen isotope ratio of dissolved inorganic phosphate ($\delta^{18}$Op) (Davies et al., 2014; Xu et al., 2018), and new methods to track contaminants and their effects (ecotoxicology) using the paleolimnological record (Korosoi et al., 2017) should provide future insights on the effects of dust on lake ecosystems.

There are ample opportunities to use paleolimnology to better understand biodiversity and evolutionary and ecological processes in mountain lakes. Combining new genetic techniques in lakes (e.g., Kammerlander et al., 2015) can provide insights into the effects of global change on biodiversity and evolutionary processes. Research on mountain lake biota has tended to focus on the pelagic zone, but the littoral and deep zones may be very important for different processes including production. Recent findings suggest that the littoral zone of these lakes is more productive and diverse than the pelagic zone (Zaharescu et al., 2016). Paleolimnological research in littoral zones can provide insights into changes in these habitats are often overlooked and may be particularly important in mountain lakes.

Mountain lake biodiversity can also be divided into micro- and macro-scales, and advances in molecular techniques are providing a new view of mountain lake ecosystems (Auguet and Casamayor, 2013; Vila-Costa et al., 2013). In particular, these methods may provide a lens to habitats difficult to sample and observe, such as biofilms (Bartrons et al., 2012) and slush layers in ice and snow cover (Llorens-Mares et al., 2012). Although presently restricted to contemporary studies, in time it may be possible to "see" these communities in the paleolimnological record. The coupling of molecular biodiversity studies with biogeochemistry studies provides new opportunities to explore the role of microorganisms in the biogeochemical cycles of mountain ecosystems (Vila-Costa et al., 2013; Rofner et al., 2017).

Another exciting opportunity is the field of resurrection ecology, in which dormant propagules (e.g., ephippia, cysts) that accumulate in the sediment over time are obtained from a sediment core and revived (Hairston et al., 1999; Kerfoot and Weider, 2004). These organisms can then be studied in the light of ecology and evolution, which has led to some novel discoveries. For instance, diapausing eggs of *Daphnia retrocurva* were hatched and grown in a common garden experiment where evolutionary changes in morphology over time were exhibited (Kerfoot and Weider, 2004). More recently, these propagules have been used in genetic and genomic studies to examine changes in species evolutionary dynamics through time (Orsini et al., 2013). Additionally, there is the potential to use viable propagules of organisms to restore lake ecosystems (Burge et al., 2018), which presents a new frontier in our understanding of ecological restoration.

Recent advances are providing us with new lenses to view the archives preserved in lake sediments and incredible opportunities to address a wide range of questions about global change that contribute to our knowledge of climate change, biogeochemical cycles, atmospheric pollution, dust, and species invasions and biodiversity. By combining paleolimnology with other approaches, particularly remote sensing, we are able to better access these remote sites and expand the range of our observations both spatially and temporally. Paleolimnology of mountain lakes documents the spatial and temporal dimensions of environmental change, which contributes to our understanding of global change. Mountain lake research has shown that these ecosystems are crossing ecological thresholds with establishment of new physical, chemical and ecological states not previously observed. Knowledge from mountain lakes can provide the impetus for humans to slow the unprecedented and rapid changes that we have initiated and provide us with time to ensure a complete knowledge of the trajectories we are following in order to make better decisions about our future.

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Figure captions

Figure 1. Map showing spatial gaps in mountain lake research. Map shows mountain regions of the world in grey based on Körner et al. (2017). Data retrieved from https://ilias.unibe.ch/goto_ilias3_unibe_cat_1000515.html. Superimposed are locations of limnological and palelimnological studies, shown by blue circles with the size of the circle representing the number of lakes included in a given study. To determine mountain lake study sites, we conducted a review of peer-reviewed literature beginning in 2018 and going back in time, focusing our search on paleolimnological studies, but including limnological studies particularly when they were used to inform paleolimnological research. While some mountain sites have been studied for many years, generally long-term records are only available through paleolimnology.

Figure 2. A set of 56 lakes from the Sierra Nevada (SN), California (Porinchu et al., 2002; Bloom et al., 2003) and 61 lakes from the Uinta Mountains (UM) shows how nutrients and carbon vary with elevation in summer. A) Total phosphorus (TP) in the SN shows little relationship with elevation. B) Nitrate ($NO_3^-$) in the SN increases beginning below treeline, but a relationship with elevation is weak. C) Dissolved organic carbon (DOC) decreases with increased elevation both in the SN and the UM. This is likely related to vegetation cover, which is greater below treeline.

Figure 3. Two lakes in Colorado, a subalpine (The Loch) and an alpine lake (Sky Pond), display differences in nutrient concentrations over time between high and low elevation sites. Nutrients are in higher and dissolved organic carbon (DOC) is in lower concentrations in high elevation

sites compared to low elevation sites. These plots also show temporal variations and the importance of snowmelt in delivering nutrients and DOC to mountain lakes.

Figure 4. Conceptual framework for this review. Mountain lakes are connected broadly across landscapes atmospherically, and the main control on mountain lake ecosystems is climate, and in particular energy, which determines physical, chemical and biological properties of lakes (Leavitt et al., 2009). Natural processes, including climate and human activities alter biogeochemical cycles, shown by grey arrows. Lakes integrate climate and biogeochemical signals in lake sediments providing archives of environmental change. These ideas together form what has been called the air-sediment continuum concept (Catalan and Donato Rondón, 2016).

Figure 5: Atmospheric deposition to lakes. Many chemical constituents are delivered to mountain regions atmospherically (Figure 4). These can be stored for short or long periods before following a variety of pathways to lakes where they can be transformed or stored by in lake and biological processes.

Figure 6: Effect of atmospheric acidification and recovery on water chemistry (a) Cladocera (b) and Chironomidae (c) in Starolesnianske Lake (Tatra Mountains, Slovakia). Water chemistry: solid lines represent model hindcasts (MAGIC, Stuchlík et al. 2002), points are measured data. Cladocera: CS, *Chydorus sphaericus* (head shields); AQ, *Alona quadrangularis* (head shields); AE, *Alonella excisa* (shells); and CQ, *Ceriodaphnia quadrangula* (ephippia); data are based on two dated cores (1820–1992, Stuchlík et al. 2002; and 1897–2010, D. Vondrák et Z. Hořická, pers. commun.). Chironomidae: TL, *Tanytarsus lugens*; and TG, *Tanytarsus gregarius*; data are

based on dated core (1820–1992, Stuchlík et al. 2002) and uppermost sediment layer, re-sampled in 2013 (open points, P. Bitušík, pers. commun.). Gray area represents period of permanently depleted carbonate buffering system in lake water (1951–2000). Some of the data presented here were also presented in Catalan et al. (2013).

Figure 7: Abrupt changes in diatom community composition in the Ecuadorian Andes are linked to changing climate of the last ~50 years. A) The early diatom community composition was characterized by diatoms living in the littoral zone, including large pennates shown here. B) Warming temperatures and reduced winds have led to increases in *Discostella stelligera* (basionym: *Cyclotella stelligera*), which tends to appear with intensified thermal stratification (Rühland et al., 2008; 2015). The rapidity of these climatic changes has led to ecological restructuring of phytoplankton assemblages and the crossing of ecological thresholds (Michelutti et al., 2015b; 2016; Labaj et al., 2018) here and around the world (Rühland et al., 2015).

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Highlights

1. Mountain lakes are sensitive recorders of global environmental change, partly due to their remoteness, but also because mountain regions are characterized by steep environmental gradients. Lake sediments archive important environmental information on temporal scales not typically available with direct monitoring.
2. Paleolimnology continues to benefit from technological and methodological advances, which have allowed for exciting discoveries including information on global atmospheric circulation, the effects of a changing cryosphere and extreme climate events on lake ecosystems, the role of lakes in the global carbon cycle, the results of atmospheric deposition and dust on lake nutrient budgets and contaminant loads, and the multifaceted consequences of introduced species.
3. Paleolimnology can be used to identify threats to the quantity and quality of mountain reservoirs. However, gaps in spatial coverage are particularly evident in the tropics and many regions in the Southern Hemisphere, where these issues are of great concern.
4. Our review highlights the complexities of ecosystem responses to the multiple and interconnected stressors that comprise global environmental change.

ACCEPTED MANUSCRIPT

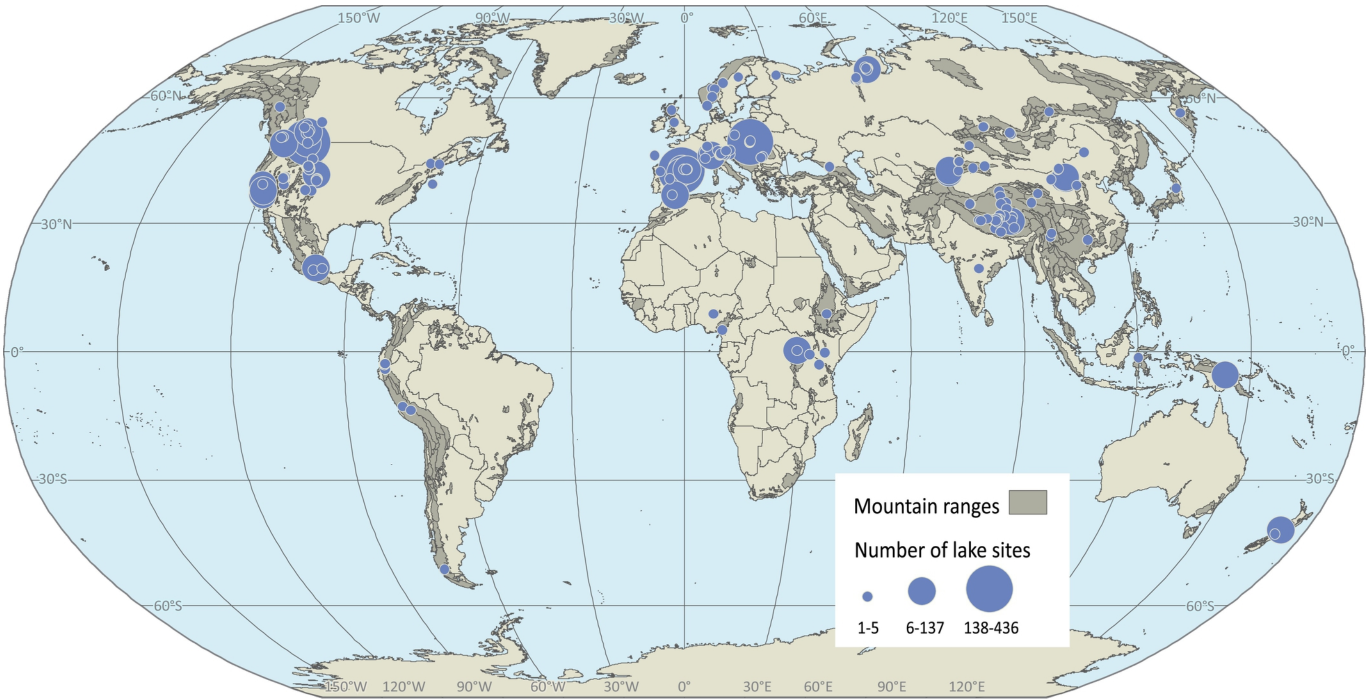

150°W
90°W
30°W
0°
60°E
120°E
150°E
60°N
30°N
0°
30°S
60°S
150°W
120°W
90°W
60°W
30°W
0°
30°E
60°E
90°E
120°E
Mountain ranges
Number of lake sites
1-5
6-137
138-436

Figure 1

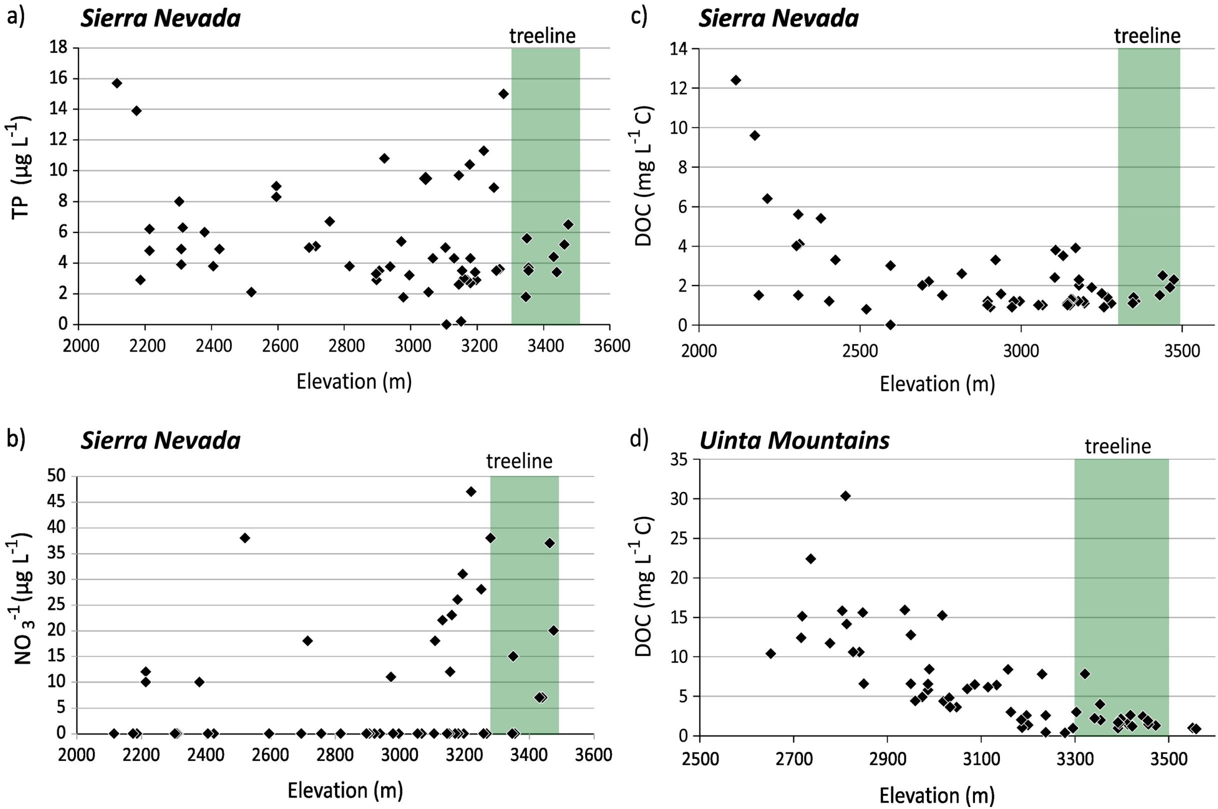

a)
Sierra Nevada
treeline
TP (µg L-1)
Elevation (m)
b)
Sierra Nevada
treeline
NO3 -1(µg L-1)
Elevation (m)
c)
Sierra Nevada
treeline
DOC (mg L-1 C)
Elevation (m)
d)
Uinta Mountains
treeline
DOC (mg L-1 C)
Elevation (m)

Figure 2

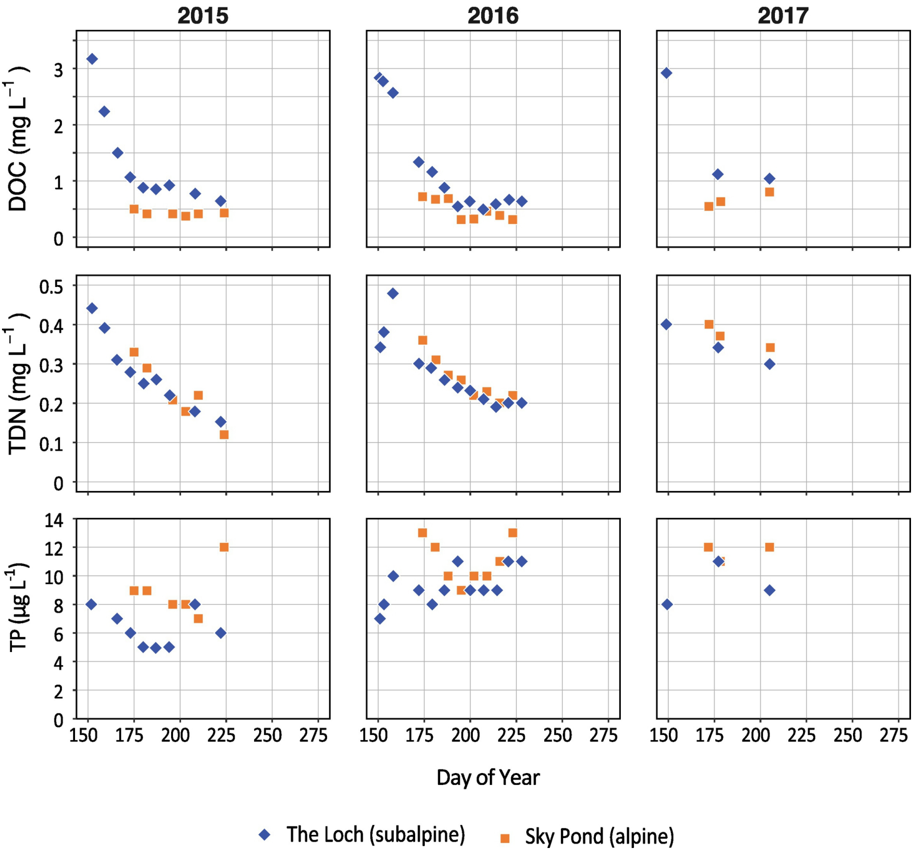
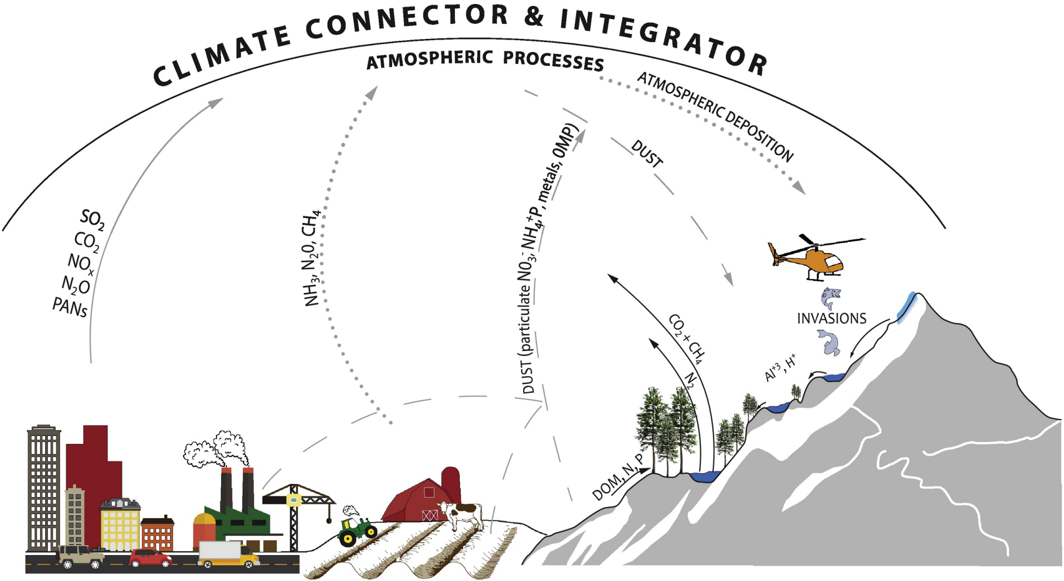

2015
2016
2017
DOC (mg L⁻¹)
TDN (mg L⁻¹)
TP (µg L⁻¹)
0
1
2
3
0.5
0.4
0.3
0.2
0.1
14
12
10
8
6
4
2
150
175
200
225
250
275
Day of Year
The Loch (subalpine)
Sky Pond (alpine)

Figure 3



CLIMATE CONNECTOR & INTEGRATOR
ATMOSPHERIC PROCESSES
$SO_2$
$CO_2$
$NO_x$
$N_2O$
PANs
$NH_3$, $N_2O$, $CH_4$
DUST (particulate $NO_3^-$ $NH_4^+$ P, metals, OMP)
DUST
ATMOSPHERIC DEPOSITION
INVASIONS
$CO_2 + CH_4$
$N_2$
$Al^{+3}$, $H^+$
DOM, N, P


Figure 4

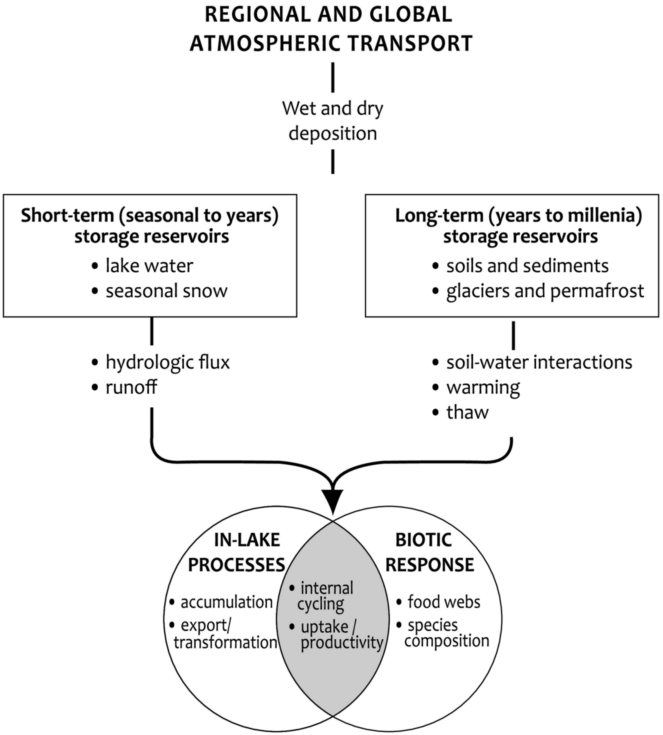
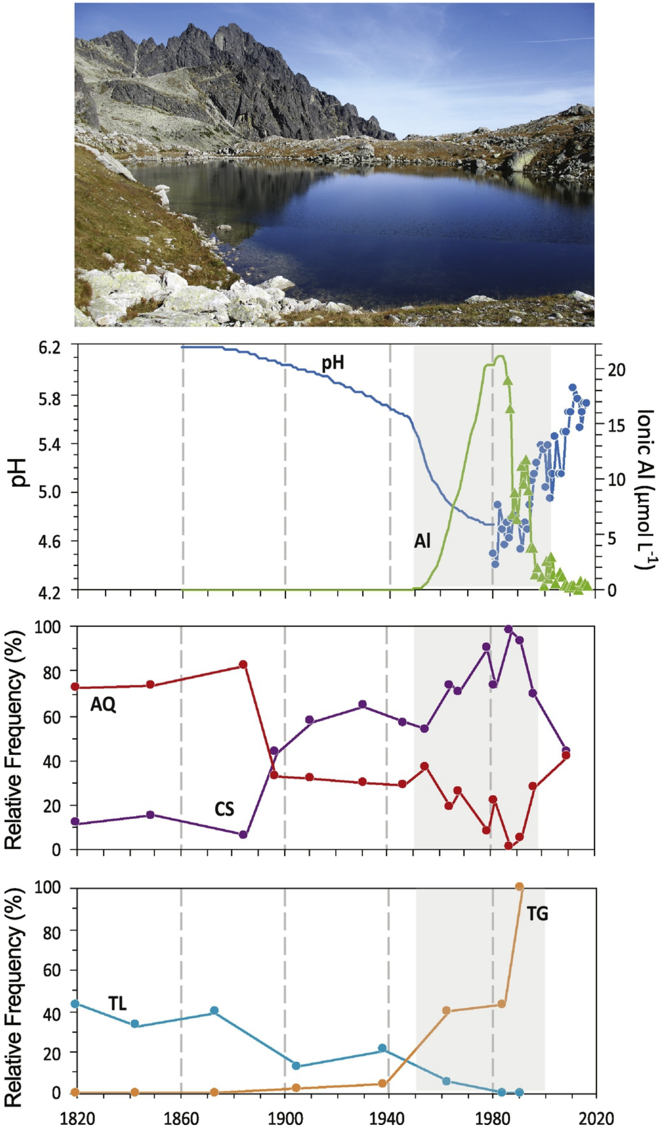
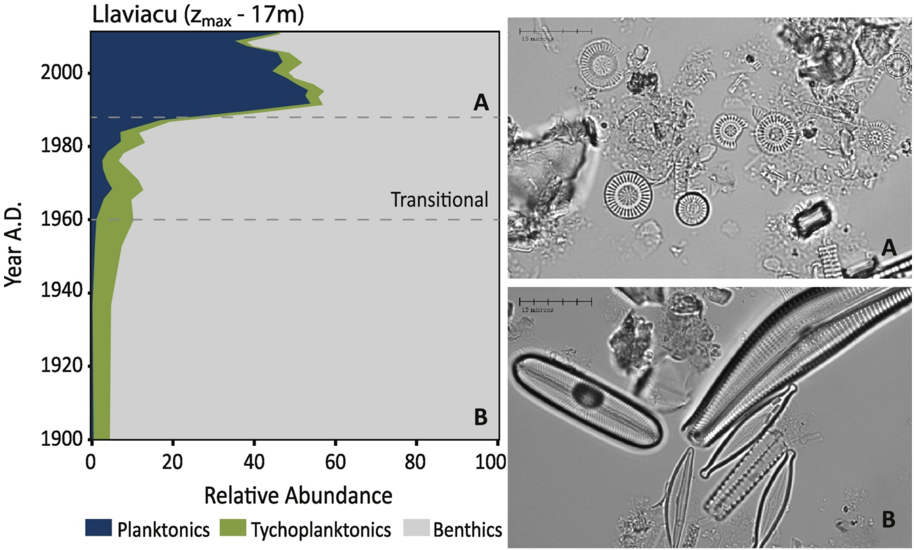

REGIONAL AND GLOBAL ATMOSPHERIC TRANSPORT
Wet and dry deposition
Short-term (seasonal to years) storage reservoirs
• lake water
• seasonal snow
Long-term (years to millenia) storage reservoirs
• soils and sediments
• glaciers and permafrost
• hydrologic flux
• runoff
• soil-water interactions
• warming
• thaw
IN-LAKE PROCESSES
• accumulation
• export/ transformation
• internal cycling
• uptake / productivity
BIOTIC RESPONSE
• food webs
• species composition

Figure 5



6.2
5.8
5.4
5.0
4.6
4.2
pH
pH
Al
20
15
10
5
0
Ionic Al (μmol L-1)
100
80
60
40
20
0
Relative Frequency (%)
AQ
CS
100
80
60
40
20
0
Relative Frequency (%)
TL
TG
1820
1860
1900
1940
1980
2020


Figure 6



Llaviacu ($z_{max}$ - 17m)
A
Transitional
B
Year A.D.
2000
1980
1960
1940
1920
1900
0
20
40
60
80
100
Relative Abundance
Planktonics
Tychoplanktonics
Benthics
15 microns
A
15 microns
B


Figure 7