Key rules of life and the fading cryosphere: impacts in alpine lakes and streams

Running title: Rules of life and the cryosphere

James J Elser, Flathead Lake Biological Station, University of Montana, Polson, Montana 59860, USA
Chenxi Wu, State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China
Angélica L González, Department of Biology & Center for Computational and Integrative Biology, Rutgers University, Camden, NJ 08102, USA
Daniel H Shain, Department of Biology & Center for Computational and Integrative Biology, Rutgers University, Camden, NJ 08102, USA
Heidi J Smith, Center for Biofilm Engineering, Montana State University, Bozeman, MT 59717, USA
Ruben Sommaruga, Department of Ecology, Lake and Glacier Research Group, University of Innsbruck, Innsbruck, Austria
Craig E Williamson, Department of Biology, Miami University, Oxford, Ohio 45056, USA
Janice Brahney, Department of Watershed Sciences, Utah State University, Logan UT 84322
Scott Hotaling, School of Biological Sciences, Washington State University, Pullman, WA 99164, USA
Joseph Vanderwall, Flathead Lake Biological Station, University of Montana, Polson, MT 59860, USA
Jinlei Yu, State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Science, Nanjing 210008, China
Vladimir Aizen, Department of Geography, University of Idaho, Moscow, ID 83844, USA

Elena Aizen, Department of Geography, University of Idaho, Moscow, ID 83844, USA

Tom J Battin, Stream Biofilm and Ecosystem Research Laboratory, School of Architecture, Civil and Environmental Engineering, Ecole Polytechnique Fédérale Lausanne, Lausanne, Switzerland

Roberto Camassa, Department of Mathematics, Carolina Center for Interdisciplinary Applied Mathematics, University of North Carolina, USA

Xiu Feng, Key Laboratory of Aquatic Biodiversity and Conservation, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China

Hongchen Jiang, State Key Lab of Biogeology and Environmental Geology, China University of Geosciences, Wuhan 430074, China

Lixin Lu, Cooperative Institute for Research in the Atmosphere, Colorado State University, Fort Collins, CO 80526, USA

John J Qu, Global Environment and Natural Resources Institute (GENRI) and Department of Geography and GeoInformation Science (GGS), George Mason University, Fairfax, VA 22030, USA

Ze Ren, Flathead Lake Biological Station, University of Montana, Polson, Montana 59860, USA

Jun Wen, Sichuan Key Laboratory of Plateau Atmosphere and Environment, College of Atmospheric Sciences, Chengdu University of Information Technology, Chendu 610225, China

Lijuan Wen, Key Laboratory of Land Surface Process and Climate Change in Cold and Arid Region, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou 730000, China

H. Arthur Woods, Division of Biological Sciences, University of Montana, Missoula, Montana 59812, USA

Xiong Xiong, State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China

Jun Xu, State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China

Gongliang Yu, Key Laboratory of Algal Biology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China

Joel T Harper, Department of Geosciences, University of Montana, Missoula, Montana 59812, USA

Jasmine E Saros, School of Biology and Ecology, Climate Change Institute, University of Maine, Orono, Maine 04469, USA

Abstract

Alpine regions are changing rapidly due to loss of snow and ice in response to ongoing climate change. While studies have documented ecological responses in alpine lakes and streams to these changes, our ability to predict such outcomes is limited. We propose that the application of fundamental rules of life can help develop necessary predictive frameworks. We focus on four key rules of life and their interactions: the temperature dependence of biotic processes from enzymes to evolution; the wavelength-dependence of the effects of solar radiation on biological and ecological processes; the ramifications of the non-arbitrary elemental stoichiometry of life; and maximization of limiting resource use efficiency across scales. As the cryosphere melts and thaws, alpine lakes and streams will experience major changes in temperature regimes, absolute and relative inputs of solar radiation in ultraviolet and photosynthetically active radiation, and relative supplies of resources (e.g., carbon, nitrogen, and phosphorus), leading to nonlinear and interactive effects on particular biota, as well as on community and ecosystem properties. We propose that applying these key rules of life to cryosphere-influenced ecosystems will reduce uncertainties about the impacts of global change and help develop an integrated global view of rapidly changing alpine environments. However, doing so will require intensive interdisciplinary collaboration and international cooperation. More broadly, the alpine cryosphere is an example of a system where improving our understanding of mechanistic underpinnings of living systems might transform our ability to predict and mitigate the impacts of ongoing global change across the daunting scope of diversity in Earth's biota and environments.

Keywords: rules of life; cryosphere; lakes; streams, glaciers;

1. Introduction

General rules govern life on Earth. At its core, life replicates and evolves, even in challenging, ice- and snow-covered mountain environments that harbor communities uniquely shaped by their extreme nature. However, rapid environmental change is challenging the persistence of these living systems. Among Earth system components, the cryosphere is undergoing some of the most rapid changes, driven largely by anthropogenic impacts (WGMS, 2017). These changes are predicted to be particularly acute in mountain regions (Wang et al., 2016), where permafrost, permanent ice, and snow are rapidly receding, spurring widespread environmental changes (Milner et al., 2017; Shugar et al., 2017; Huss & Hock, 2018). Indeed, this retreat is accelerating commensurate with climate warming during recent decades (WGMS, 2017; Maurer et al., 2019). Crucial changes in snowpack are also occurring, for example, in mountainous areas of the western USA where snowmelt is responsible for 70% of total runoff (Li et al., 2017). Thus, cryosphere-influenced ecosystems and biota are now under threat. Understanding and predicting the impacts of these changes on alpine aquatic ecosystems and their ecological communities poses an urgent challenge for ecologists and environmental scientists (Hotaling et al., 2017*a*; Moser et al., 2019) because alpine aquatic ecosystems provide key services upon which human well-being depends, especially for the inhabitants of mountain regions (Viviroli et al., 2007).

To move beyond merely documenting ecological changes into making predictions requires a grasp of the fundamental mechanisms that drive biological and ecological systems. These mechanisms involve essential "rules of life" that pertain to all or most living things. Here we highlight four potential rules of life that we propose are especially important in understanding how alpine aquatic ecosystems respond to a rapidly changing cryosphere. These key rules are:

temperature dependence of metabolism (Brown et al., 2004); the spectral dependence of biotic responses to solar radiation (Williamson & Rose, 2010); biological stoichiometry (Elser et al., 2000); and resource use efficiency (Hodapp et al., 2019). We describe these key rules and propose them as a framework for understanding and predicting future changes in ecological structure and function in cryosphere-influenced lakes and streams (see Figure 1). Our emphasis will be on the influence of glaciers and snowpack; alpine permafrost is an important component but beyond the scope of this article. Achieving a better grasp on fundamental properties of living systems will greatly enhance our ability not only to understand the impacts of these changes in the cryosphere but also to forecast their consequences.

2. Key rules of life and ongoing shifts in alpine lakes and streams

2.1 What is a "rule of life"? We propose that a rule of life describes a major mechanism, phenomenon, or process that structures most or all of life on Earth. Such rules generally hinge on inescapable aspects of our physicochemical world and can produce emergent structural features of interacting networks of biological units at all levels of biological organization. Here we delineate four such rules that, while relevant in all environments, are especially germane for alpine lakes and streams. We recognize that a variety of other relevant candidate rules could be proposed, including the ubiquity of Darwinian evolution as mentioned above, and may also be of relevance here. However, we contend that the four rules we discuss are especially useful in understanding and predicting the dynamics of alpine lakes and streams in a changing climate given the well-known effects of ice and snow on temperature, light environments, nutrient regimes, and habitat succession.

2.2 Four key rules

We propose four rules of life necessary for obtaining a fundamental and thus predictive understanding of how aquatic biota and ecosystems in alpine environments will respond to a changing cryosphere under ongoing climate change.

Key rule 1: Temperature. Temperature has a fundamental effect on nearly all biological activities due to the underlying physics of biochemical processes (red arrows in Figure 1, center).

Key rule 2: Wavelength dependence. Biological systems are differentially affected by photosynthetically active radiation (PAR) and ultraviolet radiation (UVR) from molecules to ecosystems (Figure 1, top).

Key rule 3: Biological stoichiometry. Earth's species comprise a non-random assemblage of chemical elements that reflects their evolved life histories and shapes their distribution and dynamics (Figure 1, gray bars).

Key rule 4: Efficiency. At different levels of organization, biological systems maximize use efficiency of limiting resources.

2.2.1 Key rule 1: Temperature.

Metabolic theory, based on over a century of theoretical and empirical study, describes rate process kinematics via the Boltzmann relationship:

$$R = B_0 M^{\alpha} e^{(-E/kT)}$$

This function applies to nearly all critical biological functions and represents a rule of life to which all organisms adhere. In this formulation, R is a biological rate process, B_0 is a normalization constant that is independent of body size and temperature, M is body mass, α is an allometric scaling exponent, and $e^{-E/kT}$ is the exponential Arrhenius function, where *E* is the activation energy, *k* is the Boltzmann constant, and T is temperature in Kelvin (Brown et al., 2004; West & Brown, 2005). This relationship implies that, across a moderate range below the point at which temperature becomes stressful, increasing temperature increases enzyme activity, metabolic rate, and all biological rate processes that depend on metabolism, including growth. Via these mechanisms, higher temperatures can drive generation times and even rates of evolution (Allen et al. 2006). However, as discussed below, such general large-scale trends may not apply across narrower ranges of temperature and especially at low temperatures close to the freezing point of water.

At low temperatures, organisms face unique challenges related to molecular flexibility, metabolism, and increased viscosity. To circumvent these bottlenecks, evolutionary trends are observed that increase molecular flexibility (D'Amico et al., 2006) and loosen molecular bonds (Siddiqui & Cavicchioli, 2006), while increasing readily available energy (i.e., ATP supply) (Napolitano & Shain, 2005) to compensate for reduced molecular motion and rates of diffusion. Although these responses are well-suited to low temperatures, as the cryosphere in mountain regions disappears, temperatures will rise and aquatic thermal regimes will increasingly be coupled to air temperature, with reduced buffering from glacier and perennial snowfield melt (Brown et al., 2006). While key habitats for ice-dependent life (Anesio & Laybourn-Parry, 2012) will be lost, downstream aquatic habitats may also undergo dramatic reorganizations leading to changes in temperature as well as the creation or loss of lakes and reorganization of stream channels (Milner & Bailey, 1989; Clague & Evans, 2000; Brahney et al., 2010; Shugar et al., 2017).

Under future temperature regimes, costly adaptations to cold will become useless and could lead to widespread extinction unless evolutionary responses are rapid. Specifically, cold-adapted enzymes, which typically evolve higher flexibility via weaker intramolecular interactions, may denature more readily in novel, warmer environments (Siddiqui & Cavicchioli, 2006).

Likewise, likewise, cold-adapted membranes may fail at modestly high temperatures, with severe disruption to ion and energy homeostasis. The extreme sensitivity of such biota is exemplified by several species of snow algae. These key players in biogeochemical cycling and food webs in snow habitats display narrow optimal growth temperatures ranging between 0°C and 4°C (Hoham et al., 2008). Similarly, freshwater alpine stream invertebrates, including species of Chironomidae, Ephemeroptera, and Trichoptera, have optimal temperatures between 1.2°C and 10.6°C (Niedrist & Füreder, 2020). Taken together, these features of organismal adaptation to low temperature suggest that even subtle increases in temperature above the freezing point of water in cryosphere-influenced aquatic ecosystems will likely lead to an overall decline in diversity of cold-adapted biota as they are thrust into thermal environments for which they are ill-suited. However, recent evidence from studies of glacier-associated insects provides a caveat. Some cold-adapted aquatic taxa can persist despite deglaciation, at least on contemporary time scales (Muhlfeld et al., 2020), with access to persistent low-temperature habitats associated with snowpack or cold seeps and springs. Furthermore, recent studies indicate that some cold-adapted insects have relatively broad temperature performance optima (Pallarés et al., 2020; Treanor et al., 2013). This work highlights the need to examine even basic assumptions about the impacts of cryosphere loss on associated biodiversity and that other key rules beyond temperature dependence may play an important role.

Despite the predicted losses of cold-adapted taxa, a number of biological rates are likely to increase with increasing temperatures as the cryosphere declines, including productivity and evolutionary rate given the fundamental temperature-dependence of rate processes (Rule 1). Furthermore, newly created habitats (e.g., meltwater lakes) as well as formerly ice- and snow-influenced streams and lakes will be invaded by more temperate-adapted species (Shah et al., 2020), dramatically changing community composition (Tiberti et al., 2019) and function.

Ultimately, this will homogenize biodiversity at the level of the alpine landscape (i.e., decrease beta diversity), as has been shown for both insects and microbes in glacier-fed streams (Jacobsen et al., 2012; Wilhelm et al., 2013; Hotaling et al., 2019). Finally, organisms living in the cryosphere itself may themselves contribute to feedbacks that will accelerate the decline of cryosphere environments. One example is decreased albedo triggered by warming-induced increases in biomass of organisms such as snow algae, which populate ice and snow at high altitudes and latitudes (Takeuchi et al., 2006; Lutz et al., 2016).

One challenge for future research is to increase our understanding of thermal performance curves, including lower and upper temperature thresholds, for a variety of cold-adapted taxa. Similarly, data on thermal acclimation responses is lacking for the vast majority of cold-adapted species. However, this information is critical for predicting organismal responses to changes in their climatic niches, via adaptation or through changes in their distributions, in the face of a melting cryosphere. Such efforts would also be greatly advanced by improving our assessments of whole-genomes of cold-adapted biota as well as metagenomic and metatranscriptomic properties of microbial communities in alpine environments across a broad range of temperature regimes.

2.2.2 Key rule 2: Wavelength dependence.

Rule 2 states simply that wavelength matters. At a molecular level, photosynthetically active radiation (PAR; wavelengths from 400 - 700 nm) drives photosynthesis while ultraviolet radiation (UVR; solar wavelengths from 290-400 nm) can damage DNA and other cell constituents. At the ecosystem level, both UVR and PAR underlie basal resource availability. For example, PAR drives primary production whereas UVR can transform refractory organic matter (autochthonous or terrestrially-derived) into energy resources through photodegradation, fueling ecosystem respiration. PAR and UVR also enable many organisms to orient visually to their environments, enabling them to forage, avoid predators, and engage in reproductive behaviors (Williamson & Rose, 2010; Williamson et al., 2014, 2019).

As terrestrial landscapes in mountains transition from predominantly snow and ice cover to vegetation, wavelength-dependent effects of sunlight in lakes and streams also are changing (Cannone et al., 2008; Figure 2). Reductions in the duration of snow and ice cover on lakes and streams (Benson et al., 2012) cause strong increases in exposure to sunlight. The shortest and most damaging wavelengths of UVR increase with elevation much more rapidly than does PAR, increasing by 20% or more per 1,000 m (Blumthaler et al., 1997). In glacierized regions, scouring leads to lakes and streams with high turbidity that greatly reduces PAR as well as UVR (Sommaruga, 2015). Thus, in places where glacial turbidity has subsided, the resulting clear-water lakes and streams at high elevations are among the most UVR-exposed environments in the world (Figure 2) (Sommaruga, 2001; Rose et al., 2009). Extremely high incident UVR:PAR ratios in alpine and subalpine ecosystems lead to photoinhibition of photosynthesis and photodamage of DNA (Cooke et al., 2006; Williamson et al., 2010). Over many decades, UVR penetration in lakes and streams declines due to higher concentrations of DOM from increases in terrestrial vegetation (Figure 2) and lakes shift to low UVR:PAR conditions that favor primary production (Engstrom et al., 2000; Williamson et al., 2001b).

As remote as many high-elevation lakes and streams are, they can be highly susceptible to contamination from the development of more human-dominated lower-elevation landscapes due to a combination of high UVR exposure levels and a phenomenon known as the alpine cold distillery. The mechanism involved here is that precipitation-borne contaminants become increasingly concentrated in high elevation ice and snow due to sublimation and low temperatures that slow contaminant degradation (Daly & Wania, 2005). This concentrating effect can lead to increased levels of contaminants such as polycyclic aromatic hydrocarbons, the toxicity of which is amplified through phototoxicity by exposure to high UVR (Larson & Berenbaum, 1988). As terrestrial vegetation increases over the longer term with climate warming, UVR-absorbing DOM inputs reduce UVR:PAR ratios, photodegradation of organic matter, photoinhibition of photosynthesis, phototoxicity, and photodamage of DNA and other cellular components (Figure 2) (Williamson et al., 2001a, b).

Ultimately, the loss of high UVR:PAR ecosystems as DOM increases with increasing terrestrial vegetation in the catchment (Figure 2b) will likely lead to the loss of unique species that are adapted to these extreme conditions. For example, aquatic invertebrate predators with low UVR tolerance can expand into regions where higher DOM provides a refuge from UVR (Lindholm et al., 2016). In many alpine lakes with high UVR exposure, only one species of highly pigmented crustacean zooplankton species exists (Marinone et al., 2006). Lakes just above treeline are most sensitive to these increases in DOM and reduced UVR (Vinebrooke & Leavitt, 2005).

Several critical knowledge gaps provide a compelling need for further research to understand how changes in the spectral composition of sunlight, and the UVR:PAR ratio in particular will play an important role in a fading cryosphere. Most urgent is the need for more data on the UVR and PAR exposure levels and transparency of high elevation lakes and streams because current UVR transparency data in particular are very sparse. Second is the need for more data on the UVR tolerance levels of both indigenous high elevation as well as potentially invasive lowland species. Third, high elevation ecosystems are nutrient poor and cold at the same time that they are exposed to high levels of UVR, highlighting the need to understand the shifting roles of temperature vs. nutrient vs. light limitation vs. photodamage of aquatic organisms across trophic levels as alpine regions warm. Fundamental shifts in the structure and function of these unique aquatic ecosystems are likely due to differential responses to these drivers across trophic levels in the warming alpine cryosphere.

2.2.3 Key rule 3: Biological stoichiometry.

Due to a shared evolutionary history, organisms have a common biochemistry constructed from a limited suite of chemical elements (Da Silva & Williams, 2001). However, they can differ considerably in the proportion of these elements within and among species (Fagan et al., 2002; Sterner & Elser, 2002; Woods et al., 2003; Gonzalez et al., 2011, 2018). These stoichiometric differences ultimately reflect the evolution of diverse life history strategies and body plans (Elser et al., 2000; Sterner & Elser, 2002; Kay et al., 2005). For example, fast-growing biota tend to have low C:P and N:P ratios due to increased allocation to P-rich ribosomal RNA (Elser et al., 2003). Further, nutrient supplies vary both spatially and temporally, particularly in the mountain cryosphere (Ren et al., 2019), and are often not present in a balanced supply in relation to biotic demands, inducing nutrient limitation that drives local diversity, community assembly, and ecosystem dynamics. Stoichiometric plasticity and stoichiometric adaptations are key mechanisms by which organisms can respond to such challenges in the biogeochemical environment (Quigg et al., 2003, 2011; Litchman et al., 2012). However, evolutionary constraints acting upon the basic biochemical machinery of living organisms may also impose limits on those stoichiometric responses (Zimmerman et al., 2014).

Taking a stoichiometric perspective on the living things that inhabit alpine lakes and streams may be of particular importance in considering the impacts of cryosphere change because glacial meltwaters can be geochemically distinct from other source waters. For example, depending on catchment geology, concentrations of available forms of P can increase, while concentrations of dissolved inorganic and organic nitrogen decrease with increasing catchment glacial coverage (Tockner et al., 2002; Hood et al., 2009). This pattern emerges even when bedrock sources of P are low, potentially owing to the atmospheric deposition of dust (Vandeberg & Vanlooy, 2016). Impacts of glaciers on nitrogen supplies are less clear. In the central Rockies of North America, glacial meltwaters are enriched in nitrate (Wynn et al., 2007; Saros et al., 2010), while studies in other regions have reported variable relationships of N to glacier cover (Tranter et al., 1994; Hood & Scott, 2008). The mechanisms underpinning regional differences are uncertain, but may relate to patterns of atmospheric deposition or microbial activity in glacial sub-habitats (Hamilton et al., 2013; Fegel et al., 2016; Hotaling et al., 2017b).

Less is known about how shifts in snowpack regimes affect nutrient supplies to alpine lakes and streams (Parker et al., 2008; Green, 2012). This is unfortunate as shifts from permanent to seasonal snowpack and from seasonal snow to rain-dominated precipitation are likely to have major effects catchment biogeochemistry. However, we might expect the loss of permanent snowpack as the snowline increases in altitude (Marty et al., 2017) and an increased mobilization of accumulated nutrients in that snow. In addition, weathering of newly exposed bedrock, which releases nutrients, should increase through both biological and physical mechanisms. The relative balance of N and P in that meltwater will likely depend on regional differences in the balance of dust and atmospheric N deposition that has accumulated (Brahney et al., 2015). This requires further research.

Changes in nutrient regimes due to cryosphere loss are expected to affect ecological dynamics in alpine aquatic ecosystems. For example, increases in N:P ratios due to disproportionate runoff of inorganic N from melting glaciers (Saros et al., 2010; Slemmons & Saros, 2012;

Colombo et al., 2019; Figure 3, left), will likely induce P limitation and negatively affect fast-growing, P-rich organisms (Figure 3, right). The effects of nutrient limitation may be particularly severe given the short growing season of alpine environments, which impose strong selection pressures for rapid growth and development. Nevertheless, glacial melting is expected to lengthen the growing season (Fell et al., 2017), which could ultimately benefit slow-growing species and disadvantage fast-growing organisms with high P requirements, especially in low P supply environments (Elser et al., 2000; Kay et al., 2005).

A variety of research opportunities exist to gain a better understanding of stoichiometric dimensions of cryosphere change in mountain regions. For example, as discussed above, some emerging data indicate strong differences in N:P ratios in runoff from glaciers vs snowpack, but regional differences exist. Thus, to develop a clearer picture we need more data about N and P concentrations and ratios from a wider range of glacial environments. We also need more biogeochemical data from other components of the cryosphere, such as rock glaciers and alpine permafrost. Another opportunity would be to investigate nutrients other than N and P, such as changes in the availability of Fe and Ni due to glacial melt. Finally, a key challenge for future research is to understand whether cold-adapted organisms have different stoichiometric niches compared to related species from warmer habitats.

2.2.4 Key rule 4: Resource use efficiency.

Rule 4 states that, at different levels of organization, biological systems maximize the use efficiency of limiting resources. *Resource use efficiency* (RUE) relates to the fraction of supplied or available resources converted into new biomass and thus links potential and real productivity (Hodapp et al., 2019) with major implications for biogeochemical fluxes. Maximizing RUE of a limiting resource is relevant from cells to ecosystems, although it will act at different temporal scales (Hodapp et al., 2019). In resource competition at the community scale (Tilman 1982, Grover 1997), cellular mechanisms contribute to increased RUE via the minimal cell quota of the best competitors, which is the cellular content of a limiting resource required to achieve zero net growth rate. Other examples of mechanisms that maximize use efficiency of limiting nutrients such as phosphorus are known for different levels of organization (Sterner and Elser 2002). For example, at the molecular level, organisms can replace phospholipids with sulfolipids under P limitation (Elser et al., 2010). At the community level, low-P taxa (e.g., *Bosmina*) can replace high-P species (e.g., *Daphnia*) when ecosystem P limitation results in seston with high C:P ratio (Demott and Gulati, 1999).

Resource use efficiency is also strongly linked to that of biodiversity. For example, according to the biodiversity-ecosystem functioning hypothesis (Loreau et al., 2001), higher taxonomic diversity is expected to increase RUE (Hooper et al., 2005). However, considering species functional diversity (i.e., traits) is also important in this relationship because RUE can also *decrease* with increasing taxonomic diversity when functional diversity does not increase concomitantly (Hodapp et al., 2019). Functional redundancy, which describes the ability of several taxa to perform the same function, may provide insurance against alteration in ecosystem functioning upon changes in community composition or loss of species (Miki et al., 2013). Indeed, large changes in biodiversity have been observed in alpine streams and lakes when they shift from their turbid to clear state (Jacobsen et al., 2012; Peter and Sommaruga, 2016; Cauvy-Fraunié & Dangles, 2019) but we do not know how those changes affect ecosystem functioning. In any case, it is expected that the factors discussed above (i.e., temperature, light, and stoichiometry) will predictably influence succession in ecosystem diversity, functionality and productivity within alpine ecosystems as the influence of the cryosphere declines. These changes will reflect broad shifts in limiting resources and thus in RUE across space and time as alpine aquatic ecosystems and especially lakes experience large changes in light/UVR and nutrient conditions (Figure 4). For example, the magnitude and frequency of environmental changes or disturbance caused by the discharge of glacial meltwaters will likely drive RUE as community composition and diversity change during the ecosystem's ontogeny. This contention is based on previous studies showing that relief of P limitation increases the abundance of small-bodied consumers in communities (Mulder & Elser, 2009; Ott et al., 2014; Jochum et al., 2017) and enhances nutrient transfer efficiency from small to larger organisms. Thus, a converse situation in which cryosphere loss enhances P limitation (see discussion of Rule 3) should favor large-bodied organisms and decrease carbon, but increase P transfer efficiencies through food webs.

Considering the four rules of life discussed, Rule 4 is perhaps where we most lack empirical evidence. Thus, future research should include studies on how RUE changes during ecosystem ontogeny as the cryosphere vanishes. Further, we urgently need to understand how changes in biodiversity of alpine aquatic ecosystems affect ecosystem function as this link is intrinsically related to RUE. One of the few assessments of this link in lakes affected by a vanishing glacier showed no evidence for multifunctional redundancy in bacterial communities (Peter & Sommaruga, 2016). However, no information is available for other communities.

2.3 Interactions among the key rules

The rules just described do not operate independently and indeed in alpine ecosystems such interactions may be critical as lakes and streams experience cryosphere change. For example, temperature acclimatization (Rule 1) can affect biomass stoichiometry (Rule 3) (Woods et al., 2003; Cross et al., 2015; Yvon-Durocher et al., 2015; Phillips et al., 2017; Yvon-Durocher et al., 2017). Organismal N and P contents can increase and N:P ratios decrease at lower temperatures due to higher allocation to ribosomes under lower temperatures to compensate for decreased reaction rates (Farewell & Neidhardt, 1998; Woods et al., 2003; Toseland et al., 2013; Daines et al., 2014; Yvon-Durocher et al., 2015, 2017). Stoichiometry (Rule 3) and UVR (Rule 2) also interact. Increased UVR exposure following deglaciation and the loss of ice and snow cover leads to photoinhibition of photosynthesis that may decrease food quantity for grazers, but higher UV may simultaneously lower C:P ratios of primary producers and thus improve food quality (Xenopoulos et al., 2002; Sommaruga, 2015; Stenzel et al., 2017).

Interactions among these key rules extend beyond stoichiometric dimensions. For example, there are also important interactions between temperature (Rule 1) and UVR (Rule 2). Springtime increases in water temperature generally lag increases in UVR exposure (Figure 5). Exposure to high UVR at cold temperatures decreases the potential for molecular repair of DNA damage due to the temperature dependence of repair enzymes (Macfadyen et al., 2004). The combination of higher UVR exposure and earlier ice-out, often timed near summer solstice, the annual peak in sunlight, can lead to very high net UVR damage potential (Figure 3). Note that the patterns we discuss encompass alpine regions in temperate latitudes. Seasonality in alpine temperature and UVR exposure will be dampened in the tropics, but amplified towards the poles. The inhibitory effects of UVR on photosynthetic biota (Rule 2) are moderated at higher temperatures (Rule 1) because DNA repair processes are performed by temperature-dependent enzymes (Beardall et al., 2014). Meanwhile, temperature - PAR interactions may arise in well-illuminated situations because of the well-known temperature dependence of Rubisco activity. Thus, higher temperatures may allow increases in maximum photosynthetic capacity (Davison, 1991; Galmes et al., 2015). An important open question, however, is how these interacting processes ultimately influence emergent resource use efficiency (Rule 4) in communities and ecosystems under cryosphere change.

3. Conclusions: Meeting the scientific challenges of the changing alpine cryosphere

Existing studies have documented the impacts of cryosphere change on the ecology of alpine lakes and streams (see various citations throughout). While important, such efforts do not necessarily provide the ability to forecast future impacts of cryosphere change, especially across diverse environments in the world's mountain regions. Better forecasts across broad spatial scales will require us to understand the fundamental mechanisms that underpin ecological change. These mechanisms likely arise from core biological properties of living things - rules of life. In this paper, we have applied four key rules of life to better understand ongoing ecological changes in cryosphere-influenced aquatic ecosystems in alpine environments (Figure 1) and to predict future transitions.

Achieving better insights is important because ongoing changes in the cryosphere have many impacts on ecosystem services that are valuable in mountain regions (Viviroli et al., 2007; Klein et al., 2019). Mitigating these impacts, or adapting to them if mitigation is impossible, is complicated by considerable regional variability and temporal unpredictability of these impacts. For example, the mechanisms behind variation in the provisioning of nutrients (N, P) from glacial systems are not well understood, but likely involve differences in regional geology and land-use, climate, land-atmosphere interactions, microbial activity, and glacial drainage patterns. Importantly, we need to document not only ongoing ecological responses to such shifts, but also to predict those outcomes based on mechanistic understanding. For example, as delineated earlier, while exposure to DNA-damaging UVR increases with increasing elevation, air and water temperatures decrease, reducing the effectiveness of photoenzymatic repair of DNA damage (as demonstrated in zooplankton; Cooke et al., 2006). The inability to repair UVRinduced DNA damage will in turn require other adaptive responses such as high levels of photoprotective compounds or behavioral avoidance of UVR exposure through diel vertical migration, responses that may vary among taxa of zooplankton (Ekvall et al., 2015; Tartarotti et al., 2017) with important implications for other ecological interactions such as visual predation (Hylander et al., 2009). Likewise, understanding fundamental temperature responses of metabolism and performance, especially at low temperatures as water warms above its freezing point, will permit prediction of biotic responses to forecasted changes in lake and stream temperatures (Jones et al. 2017) as glaciers and snowpack recede in the alpine landscape.

To develop such a predictive, mechanistic understanding and to obtain broadly applicable insights into unfolding global patterns of cryosphere change and impact on alpine lakes and streams, multilateral international cooperation is needed so that studies can be integrated across regions. For example, the vast mountain cryosphere domain of central Asia remains relatively understudied from an ecological perspective and should be a focus of increasing international attention. Furthermore, interdisciplinary integration across atmospheric, earth, and life sciences is essential. Only with such integration can the most ecologically relevant geophysical changes be identified and tracked and their impacts predicted from a foundation of fundamental biological knowledge.

Acknowledgements: None of the authors have any real or perceived conflicts of interest relevant to this article. This paper is a product of a US-China workshop “Rules of Life: A Fading Cryosphere Shifting Temperature and Stoichiometry in Mountain Lakes and Streams” held at the Flathead Lake Biological Station (University of Montana) supported by the US National Science Foundation (DMS-1834494) and the Natural National Science Foundation of China (41981220290). CEW acknowledges support from NSF DEB-1754276 and RS from the Austrian

Science Fund (FWF P24442-B25). SH was supported by NSF OPP-1906015. We thank M. Skidmore (Montana State University), R. McLaughlin (North Carolina State University), and C. Florentine (USGS) for stimulating presentations and discussions during the initial days of the workshop, and Z. Dong (Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences), J. Li (Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences), W. Tan (Central China Normal University), and Z. Song (The National Natural Science Foundation of China) for sharing ideas and findings during the workshop. We are also grateful to the staff of the Flathead Lake Biological Station for their hospitality. C. Muhlfeld and an anonymous reviewer provided useful comments on an earlier draft.

Author Contributions. Contributions are as follows. Workshop conceptualization: JJE, CW, JTH, JES. Funding Acquisition: JJE, CW. Project administration: JJE, CW. Supervision: JJE, CW. Visualization: JJE, CEW, RS, HJS, JB, SH, ALG, JY. Writing – Original Draft: JJE, CW, ALG, DHS, HJS, RS, CEW. Writing – review and editing: JJE, CW, ALG, DHS, HJS, RS, CEW, JB, SH, JV, JY, VA, EA, TJB, RC, XF, HJ, LL, JJQ, ZR, JW, LW, HAW, XX, JX, GY, JTH, JES.

Data Sharing and Data Accessibility. No original data are included in this paper.

References

Allen, A. P., Gillooly, J. F., Savage, V. M. & Brown, J. H. (2006). Kinetic effects of temperature on rates of genetic divergence and speciation. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 9130-9135.

Anesio, A. M. & Laybourn-Parry, J. (2012). Glaciers and ice sheets as a biome. *Trends in Ecology & Evolution*, *27*, 219-225.

Beardall, J., Stojkovic, S. & Gao, K. (2014). Interactive effects of nutrient supply and other environmental factors on the sensitivity of marine primary producers to ultraviolet radiation: implications for the impacts of global change. *Aquatic Biology*, *22*, 5-23.

Benson, B. J., Magnuson, J. J., Jensen, O. P., Card, V. M., Hodgkins, G. & Korhonen, J., et al. (2012). Extreme events, trends, and variability in Northern Hemisphere lake-ice phenology (1855-2005). *Climatic Change*, *112*, 299-323.

Blumthaler, M., Ambach, W. & Ellinger, R. (1997). Increase in solar UV radiation with altitude. *Journal of Photochemistry and Photobiology B-Biology*, *39*, 130-134.

Brahney, J., Clague, J. J., Edwards, T. W. D. & Menounos, B. (2010). Late Holocene paleohydrology of Kluane Lake, Yukon Territory, Canada. *Journal of Paleolimnology*, *44*, 873-885.

Brahney, J., Mahowald, N., Ward, D. S., Ballantyne, A. P. & Neff, J. C. (2015). Is atmospheric phosphorus pollution altering global alpine lake stoichiometry? *Global Biogeochemical Cycles*, *29*, 1369-1383.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*, 1771-1789.

Brown, L. E., Hannah, D. M. & Milner, A. M. (2006). Hydroclimatological influences on water column and streambed thermal dynamics in an alpine river system. *Journal of Hydrology*, *325*, 1-20.

Cannone, N., Diolaiuti, G., Guglielmin, M. & Smiraglia, C. (2008). Accelerating climate change impacts on alpine glacier forefield ecosystems in the European Alps. *Ecological Applications*, *18*, 637-648.

Cauvy-Fraunlé, S. & Dangles, O. (2019). A global synthesis of biodiversity responses to glacier retreat. *Nature Ecology & Evolution* 3, 1675–1685.

Clague, J. J. & Evans, S. G. (2000). A review of catastrophic drainage of moraine-dammed lakes in British Columbia. *Quaternary Science Reviews*, *19*, 1763-1783.

Colombo, N., Bocchiola, D., Martin, M., Confortola, G., Salerno, F., Godone, D., D'Amico, M.E., & Freppaz, M. (2019). High export of nitrogen and dissolved organic carbon from an alpine glacier (Indren Glacier, NW Italian Alps). *Aquatic Sciences* 81:74

Cooke, S. L., Williamson, C. E. & Saros, J. E. (2006). How do temperature, dissolved organic matter and nutrients influence the response of *Leptodiaptomus ashlandi* to UV radiation in a subalpine lake? *Freshwater Biology*, *51*, 1827-1837.

Cross, W. F., Hood, J. M., Benstead, J. P., Huryn, A. D. & Nelson, D. (2015). Interactions between temperature and nutrients across levels of ecological organization. *Global Change Biology*, *21*, 1025-1240.

D'Amico, S., Collins, T., Marx, J. C., Feller, G., and Gerday, C. (2006). Psychrophilic microorganisms: Challenges for life. *EMBO Rep*., *7*, 385–389.

Da Silva, J. F. & Williams, R. J. P. (2001). *The biological chemistry of the elements: the inorganic chemistry of life*. Oxford University Press, Oxford.

Daines, S. J., Clark, J. R. & Lenton, T.M. (2014). Multiple environmental controls on phytoplankton growth strategies determine adaptive responses of the N:P ratio. *Ecology Letters*, *17*, 414-25.

Daly, G. L. & Wania, F. (2005). Organic contaminants in mountains. *Environmental Science & Technology*, *39*, 385-398.

Davison, I. R. (1991). Environmental effects on algal photosynthesis: temperature. *Journal of Phycology*, *27*, 2-8.

DeMott, W. R., & Gulati, R. D. (1999). Phosphorus limitation in *Daphnia*: evidence from a long term study of three hypereutrophic Dutch lakes. *Limnology and Oceanography*, *44*, 1557-1564.

Ekvall, M. T., Hylander, S., Walles, T., Yang, X. & Hansson, L. (2015). Diel vertical migration, size distribution and photoprotection in zooplankton as response to UV-A radiation. *Limnology and Oceanography*, *60*, 2048-2058.

Elser, J. J., Acharya, K., Kyle, M., Cotner, J., Makino, W. & Markow, T., et al. (2003). Growth rate-stoichiometry couplings in diverse biota. *Ecology Letters*, *6*, 936-943.

Elser, J. J., Sterner, R. W., Gorokhova, E., Fagan, W. F., Markow, T. A. & Cotner, J. B., et al. (2000). Biological stoichiometry from genes to ecosystems. *Ecology Letters*, *3*, 540-550.

Elser, J. J., Fagan, W. F., Kerkhoff, A. J., Swenson, N. G., & Enquist, B. J. (2010). Biological stoichiometry of plant production: metabolism, scaling and ecological response to global change. *New Phytologist*, *186*, 593-608.

Engstrom, D. R., Fritz, S. C., Almendinger, J. E. & Juggins, S. (2000). Chemical and biological trends during lake evolution in recently deglaciated terrain. *Nature*, *408*, 161-166.

Fagan, W. F., Siemann, E., Mitter, C., Denno, R. F., Huberty, A. F. & Woods, H. A., et al. (2002). Nitrogen in insects: implications for trophic complexity and species diversification. *American Naturalist*, *160*, 784-802.

Farewell, A. & Neidhardt, F. C. (1998). Effect of temperature on *in vivo* protein synthetic capacity in *Escherichia coli*. *Journal of Bacteriology*, *180*, 4704-4710.

Fegel, T. S., Baron, J. S., Fountain, A. G., Johnson, G. F. & Hall, E. K. (2016). The differing biogeochemical and microbial signatures of glaciers and rock glaciers. *Journal of Geophysical Research-Biogeosciences*, *121*, 919-932.

Fell, S. C., Carrivick, J. L. & Brown, L. E. (2017). The multitrophic effects of climate change and glacier retreat in mountain rivers. *Bioscience*, *67*, 897-911.

Galmes, J., Kapralov, M. V., Copolovici, L. O., Hermida-Carrera, C. & Niinemets, U. (2015). Temperature responses of the Rubisco maximum carboxylase activity across domains of life: phylogenetic signals, trade-offs, and importance for carbon gain. *Photosynthesis Research*, *123*, 183-201.

Gonzalez, A. L., Cereghino, R., Dezerald, O., Farjalla, V. F., Leroy, C. & Richardson, B. A., et al. (2018). Ecological mechanisms and phylogeny shape invertebrate stoichiometry: A test using detritus-based communities across Central and South America. *Functional Ecology*, *32*, 2448-2463.

Gonzalez, A. L., Miguel Farina, J., Kay, A. D., Pinto, R. & Marquet, P. A. (2011). Exploring patterns and mechanisms of interspecific and intraspecific variation in body elemental composition of desert consumers. *Oikos*, *120*, 1247-1255.

Green, K. (2012). Intra- and inter-annual changes in chemistry of Australian glacial lakes. *Marine and Freshwater Research*, *63*, 513-527.

Grover, J. P. 1997. *Resource Competition*, Chapman & Hall.

Hamilton, T. L., Peters, J. W., Skidmore, M. L. & Boyd, E. S. (2013). Molecular evidence for an active endogenous microbiome beneath glacial ice. *The ISME Journal*, *7*, 1402-1412.

Hodapp, D., Hillebrand, H. & Striebel, M. (2019). "Unifying" the concept of resource use efficiency in ecology. *Frontiers in Ecology and Evolution*, *6*, doi: 10.3389/fevo.2018.00233.

Hoham, R. W., Frey, F. M., Mohn, W. W., Felio, J. H., Todd, S., Duncan, J. E., & Banghart, J. B. (2008). Optimum growth temperatures of three species of green *Chloromonas* snow algae from upstate New York and the White Mountains, Arizona. *Arctic, Antarctic, and Alpine Research*, 40, 355–363.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P. & Lavorel, S., et al. (2005).Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, *75*, 3-35.

Hood, E., & Scott, D. (2008). Riverine organic matter and nutrients in southeast Alaska affected by glacial coverage. *Nature Geoscience*, 1, 583–587.

Hood, E., Fellman, J., Spencer, R. G., Hernes, P. J., Edwards, R., D'Amore, D., & Scott, D. (2009). Glaciers as a source of ancient and labile organic matter to the marine environment. *Nature*, *462*, 1044-1047.

Hotaling, S., Finn, D. S., Giersch, J. J., Weisrock, D. W. & Jacobsen, D. (2017a). Climate change and alpine stream biology: progress, challenges, and opportunities for the future. *Biological Reviews*, *92*, 2024-2045.

Hotaling, S., Foley, M. E., Zeglin, L. H., Finn, D. S., Tronstad, L. M., Giersch, J. J., C.C. Muhlfeld, & Weisrock, D. W. (2019). Microbial assemblages reflect environmental heterogeneity in alpine streams. *Global Change Biology*, 25, 2576-2590. https://doi.org/10.1111/gcb.14683

Hotaling, S., Hood, E. & Hamilton, T. L. (2017b). Microbial ecology of mountain glacier ecosystems: biodiversity, ecological connections and implications of a warming climate. *Environmental Microbiology*, *19*, 2935-2948.

Huss, M. & Hock, R. (2018). Global-scale hydrological response to future glacier mass loss. *Nature Climate Change*, *8*, 135-140.

Hylander, S., Larsson, N. & Hansson, L. (2009). Zooplankton vertical migration and plasticity of pigmentation arising from simultaneous UV and predation threats. *Limnology and Oceanography*, *54*, 483-491.

Jacobsen, D., Milner, A. M., Brown, L. E., & Dangles, O. (2012). Biodiversity under threat in glacier-fed river systems. *Nature Climate Change*, *2*, 361-364.

Jochum, M., Barnes, A. D., Weigelt, P., Ott, D., Rembold, K. & Farajallah, A., et al. (2017). Resource stoichiometry and availability modulate species richness and biomass of tropical litter macro-invertebrates. *Journal of Animal Ecology*, *86*, 1114-1123.

Jones, L. A., C. C. Muhlfeld, and L. A. Marshall. 2017. Projected warming portends seasonal shifts of stream temperatures in the Crown of the Continent Ecosystem, USA and Canada. *Climatic Change*, *144*, 641–655.

Kay, A. D., Ashton, I. W., Gorokhova, E., Kerkhoff, A. J., Liess, A. & Litchman, E. (2005). Toward a stoichiometric framework for evolutionary biology. *Oikos*, *109*, 6-17.

Klein, J. A., C. M. Tucker, A. W. Nolin, K. A. Hopping, R. S. Reid, C. Steger, A. Grêt-Regamey, S. Lavorel, B. Müller, E. T. Yeh, R. B. Boone, P. Bourgeron, V. Butsic, E. Castellanos, X. Chen, S. K. Dong, G. Greenwood, M. Keiler, R. Marchant, R. Seidl, T. Spies, J. Thorn, and K. Yager. 2019. Catalyzing transformations to sustainability in the world's mountains. *Earth's Future*, *7*, 2018EF001024.

Larson, R. A. & Berenbaum, M. R. (1988). Environmental phototoxicity. *Environmental Science & Technology*, *22*, 354-360.

Li, D., Wrzesien, M. L., Durand, M., Adam, J. & Lettenmaier, D. P. (2017). How much runoff originates as snow in the western United States, and how will that change in the future? *Geophysical Research Letters*, *44*, 6163-6172.

Lindholm, M., Wolf, R., Finstad, A. & Hessen, D. O. (2016). Water browning mediates predatory decimation of the Arctic fairy shrimp *Branchinecta paludosa*. *Freshwater Biology*, *61*, 340-347.

Litchman, E., Edwards, K. F., Klausmeier, C. A. & Thomas, M. K. (2012). Phytoplankton niches, traits and eco-evolutionary responses to global environmental change. *Marine Ecology Progress Series*, *470*, 235-248.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P. & Hector, A., et al. (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, *294*, 804-808.

Lutz, S., Anesio, A. M., Raiswell, R., Edwards, A., Newton, R. J. & Gill, F., et al. (2016). The biogeography of red snow microbiomes and their role in melting arctic glaciers. *Nature Communications*, *7*, e11968.

Macfadyen, E. J., Williamson, C. E., Grad, G., Lowery, M., Jeffrey, W. H. & Mitchell, D. L. (2004). Molecular response to climate change: temperature dependence of UV-induced DNA damage and repair in the freshwater crustacean *Daphnia pulicaria*. *Global Change Biology*, *10*, 408-416.

Marinone, M. C., Marque, S. M., Suarez, D. A., Dieguez, M. D. C., Perez, P. & Rios, P. D. L., et al. (2006). UV radiation as a potential driving force for zooplankton community structure in Patagonian lakes. *Photochemistry and Photobiology*, *82*, 962-971.

Marty, C., Tilg, A. M. & Jonas, T. (2017). Recent evidence of large-scale receding snow water equivalents in the European Alps. *Journal of Hydrometeorology*, *18*, 1021-1031.

Maurer, J.M., Schaefer, J.M., Rupper, S. and Corley, A., (2019). Acceleration of ice loss across the Himalayas over the past 40 years. *Science advances*, *5*, 6.

Miki T, Yokokawa T, & Matsui K. (2013). Biodiversity and multifunctionality in a microbial community: a novel theoretical approach to quantify functional redundancy. *Proceedings Royal Society B Biology Sciences, 281*, 20132498.

Milner, A. M. & Bailey, R. G. (1989). Salmonid colonization of new streams in Glacier Bay National Park, Alaska. *Aquaculture Research*, *20*, 179-192.

Milner, A. M., Khamis, K., Battin, T. J., Brittain, J. E., Barrand, N. E. & Fuereder, L., et al. (2017). Glacier shrinkage driving global changes in downstream systems. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, 9770-9778.

Moser, K. A., Baron, J. S., Brahney, J., Oleksy, I. A., Saros, J. E. & Hundey, E. J., et al. (2019). Mountain lakes: Eyes on global environmental change. *Global and Planetary Change*, *178*, 77-95.

Muhlfeld CC, Cline TJ, Giersch JJ, Peitzsch E, Florentine C, Jacobsen D, Hotaling S. (2020) Specialized meltwater biodiversity persists despite widespread deglaciation. *PNAS*, 117, 2208-12214.

Mulder, C. & Elser, J. J. (2009). Soil acidity, ecological stoichiometry and allometric scaling in grassland food webs. *Global Change Biology*, *15*, 2730-2738.

Napolitano, M. J. & Shain, D. H. (2005). Distinctions in adenylate metabolism among organisms inhabiting temperature extremes. *Extremophiles*, *9*, 93-98.

Niedrist, G. H., & Füreder, L. (2020). Real-time warming of alpine streams: (re)defining invertebrates' temperature preferences. *River Research and Applications*, https://doi.org/10.1002/rra.3638

Ott, D., Digel, C., Klarner, B., Maraun, M., Pollierer, M. & Rall, B. C., et al. (2014). Litter elemental stoichiometry and biomass densities of forest soil invertebrates. *Oikos*, *123*, 1212-1223.

Pallarés, S., Millán, A., Mirón, J. M., Velasco, J., Sánchez-Fernández, D., Botella-Cruz, M., & Abellán, P. (2020). Assessing the capacity of endemic alpine water beetles to face climate change. *Insect Conservation and Diversity / Royal Entomological Society of London*, *13*, 271–282.

Parker, B. R., Vinebrooke, R. D. & Schindler, D. W. (2008). Recent climate extremes alter alpine lake ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 12927-31.

Peter, H. & Sommaruga, R. (2016). Shifts in diversity and function of lake bacterial communities upon glacier retreat. *The ISME Journal, 10*,1545−1554.

Phillips, K. N., Godwin, C. M. & Cotner, J. B. (2017). The effects of nutrient imbalances and temperature on the biomass stoichiometry of freshwater bacteria. *Frontiers in Microbiology*, *8*, e1692.

Quigg, A., Finkel, Z. V., Irwin, A. J., Rosenthal, Y., Ho, T. Y. & Reinfelder, J. R., et al. (2003). The evolutionary inheritance of elemental stoichiometry in marine phytoplankton. *Nature*, *425*, 291-294.

Quigg, A., Irwin, A. J. & Finkel, Z. V. (2011). Evolutionary inheritance of elemental stoichiometry in phytoplankton. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 526-534.

Ren, Z., Martyniuk, N., Oleksy, I. A., Swain, A., & Hotaling, S. (2019). Ecological stoichiometry of the mountain cryosphere. *Frontiers in Ecology and Evolution*, *7*, 360.

Rose, K. C., Williamson, C. E., Saros, J. E., Sommaruga, R. & Fischer, J. M. (2009). Differences in UV transparency and thermal structure between alpine and subalpine lakes: implications for organisms. *Photochemical & Photobiological Sciences*, *8*, 1244-1256.

Saros, J. E., Rose, K. C., Clow, D. W., Stephens, V. C., Nurse, A. B. & Arnett, H. A., et al. (2010). Melting alpine glaciers enrich high-elevation lakes with reactive nitrogen. *Environmental Science & Technology*, *44*, 4891-4896.

Shah, A.A., Dillon, M.E., Hotaling, S., & Woods, H.A. (2020). High elevation insect communities face shifting ecological and evolutionary landscapes. *Current Opinion in Insect Science, 41*, 10.1016/j.cois.2020.04.002.

Shugar, D. H., Clague, J. J., Best, J. L., Schoof, C., Willis, M. J. & Copland, L., et al. (2017). River piracy and drainage basin reorganization led by climate-driven glacier retreat. *Nature Geoscience*, *10*, 370-375.

Siddiqui, K. S. & Cavicchioli, R. (2006). Cold-adapted enzymes. *Annual Review of Biochemistry*, *75*, 403-433.

Slemmons, K. E. H. & Saros, J. E. (2012). Implications of nitrogen-rich glacial meltwater for phytoplankton diversity and productivity in alpine lakes. *Limnology and Oceanography*, *57*, 1651-1663.

Sommaruga, R. (2001). The role of solar UV radiation in the ecology of alpine lakes. *Journal of Photochemistry and Photobiology B-Biology*, *62*, 35-42.

Sommaruga, R. (2015). When glaciers and ice sheets melt: consequences for planktonic organisms. *Journal of Plankton Research*, *37*, 509-518.

Stenzel, B., Rofner, C., Perez, M. T. & Sommaruga, R. (2017). Stoichiometry of natural bacterial assemblages from lakes located across an elevational gradient. *Scientific Reports*, *7*, e5875.

Sterner, R. W. & Elser, J. J. (2002). *Ecological Stoichiometry*. Princeton University Press, Princeton.

Takeuchi, N., Uetake, J., Fujita, K., Aizen, V. B. & Nikitin, S. D. (2006). A snow algal community on Akkem glacier in the Russian Altai mountains. *Annals of Glaciology*, *43*, 378-384.

Tartarotti, B., Trattner, F., Remias, D., Saul, N., Steinberg, C. E. W. & Sommaruga, R. (2017). Distribution and UV protection strategies of zooplankton in clear and glacier-fed alpine lakes. *Scientific Reports*, *7,* 4487.

Thrane, J., Hessen, D. O. & Andersen, T. (2016). The impact of irradiance on optimal and cellular nitrogen to phosphorus ratios in phytoplankton. *Ecology Letters*, *19*, 880-888.

Tiberti, R., Buscaglia, F., Callieri, C., Rogora, M., Tartari, G., & Sommaruga, R. (2019). Food web complexity of high mountain lakes is largely affected by glacial retreat. *Ecosystems*, https://doi.org/10.1007/s10021-019-00457-8

Tilman, D. 1982. *Resource Competition and Community Structure*, Princeton University Press.

Tockner, K., Malard, F., Uehlinger, U. & Ward, J. V. (2002). Nutrients and organic matter in a glacial river-floodplain system (Val Roseg, Switzerland). *Limnology and Oceanography*, *47*, 266-277.

Toseland, A., Daines, S. J., Clark, J. R., Kirkham, A., Strauss, J. & Uhlig, C., et al. (2013). The impact of temperature on marine phytoplankton resource allocation and metabolism. *Nature Climate Change*, *3*, 979-984.

Tranter, M., Brown, G. H., Hodson, A., Gurnell, A. M. & Sharp, M. J. (1994). Variations in the nitrate concentration of glacial runoff in Alpine and sub-Polar environments. *IAHS Publications-Series of Proceedings and Reports-Intern Assoc Hydrological Sciences*, *223*, 299-312.

Treanor, H. B., Giersch, J. J., Kappenman, K. M., Muhlfeld, C. C., & Webb, M. A. H. (2013). Thermal tolerance of meltwater stonefly *Lednia tumana* nymphs from an alpine stream in Waterton–Glacier International Peace Park, Montana, USA. *Freshwater Science*, *32*, 597–605.

Vandeberg, G. S. & Vanlooy, J. A. (2016). Continental glacier meltwater contributions to late summer stream flow and water quality in the northern Wind River Range, Wyoming, USA. *Environmental Earth Sciences*, *75*, 389. doi.org/10.1007/s1266.

Vinebrooke, R. D. & Leavitt, P. R. (2005). Mountain lakes as indicators of the cumulative impacts of ultraviolet radiation and other global stressors. In: *Global Change and Mountain Regions* (pp. 437-447). Springer, Dordrecht.

Viviroli, D., Durr, H. H., Messerli, B., Meybeck, M. & Weingartner, R. (2007). Mountains of the world, water towers for humanity: Typology, mapping, and global significance. *Water Resources Research*, *43*, W074477.

Wang, Q., Fan, X. & Wang, M. (2016). Evidence of high-elevation amplification versus Arctic amplification. *Scientific Reports*, *6*, e19219.

West, G. B. & Brown, J. H. (2005). The origin of allometric scaling laws in biology from genomes to ecosystems: towards a quantitative unifying theory of biological structure and organization. *Journal of Experimental Biology, 208*, 1575-1592.

WGMS. (2017). Global Glacier Change Bulletin No.2 (2014-2015). Zemp, M., Nussbaumer, S. U., Gärtner, Roer, I., Huber, J., Machguth, H., Paul, F., and Hoelzle, M. (eds.), ICSU(WDS)/IUGG(IACS)/UNEP/UNESCO/WMO, World Glacier Monitoring Service, Zurich, Switzerland, 244 pp., publication based on database version: doi:10.5904/wgms-fog-2017-10.

Wilhelm, L., Singer, G. A., Fasching, C., Battin, T. J., & Besemer, K. (2013). Microbial biodiversity in glacier-fed streams. *The ISME journal*, *7*, 1651.

Williamson, C. E. & Rose, K.C. (2010). When UV meets freshwater. *Science*, *329*, 637-639.

Williamson, C. E., Grad, G., De Lange, H. J., Gilroy, S. & Karapelou, D. M. (2002). Temperature-dependent ultraviolet responses in zooplankton: Implications of climate change. *Limnology and Oceanography*, *47*, 1844-1848.

Williamson, C. E., Neale, P. J., Grad, G., De Lange, H. J. & Hargreaves, B. R. (2001a). Beneficial and detrimental effects of UV on aquatic organisms: Implications of spectral variation. *Ecological Applications*, *11*, 1843-1857.

Williamson, C. E., Neale, P. J., Hylander, S., Rose, K. C., Figueroa, F. L. & Robinson, S. A., et al. (2019). The interactive effects of stratospheric ozone depletion, UV radiation, and climate change on aquatic ecosystems. *Photochemical & Photobiological Sciences*, *18*, 717-746.

Williamson, C. E., Olson, O. G., Lott, S. E., Walker, N. D., Engstrom, D. R. & Hargreaves, B. R. (2001b). Ultraviolet radiation and zooplankton community structure following deglaciation in Glacier Bay, Alaska. *Ecology*, *82*, 1748-1760.

Williamson, C. E., C. Salm, S. L. Cooke, and J. E. Saros. (2010). How do UV radiation, temperature, and zooplankton influence the dynamics of alpine phytoplankton communities? *Hydrobiologia, 648*, 73-81.

Williamson, C. E., Zepp, R. G., Lucas, R. M., Madronich, S., Austin, A. T. & Ballare, C. L., et al. (2014). Solar ultraviolet radiation in a changing climate. *Nature Climate Change*, *4*, 434-441.

Woods, H. A., Makino, W., Cotner, J. B., Hobbie, S. E., Harrison, J. F. & Acharya, K., et al. (2003). Temperature and the chemical composition of poikilothermic organisms. *Functional Ecology*, *17*, 237-245.

Wynn, P. M., Hodson, A. J., Heaton, T. H. E. & Chenery, S. R. (2007). Nitrate production beneath a high Arctic glacier, Svalbard. *Chemical Geology*, *244*, 88-102.

Xenopoulos, M. A., Frost, P. C. & Elser, J. J. (2002). Joint effects of ultraviolet radiation and phosphorus supply on phytoplankton growth rate and elemental composition. *Ecology*, *83*, 423-435.

Yvon-Durocher, G., Dossena, M., Trimmer, M., Woodward, G. & Allen, A. P. (2015). Temperature and the biogeography of algal stoichiometry. *Global Ecology and Biogeography*, *24*, 562-570.

Yvon-Durocher, G., Schaum, C. E. & Trimmer, M. (2017). The temperature dependence of phytoplankton stoichiometry: investigating the roles of species sorting and local adaptation. *Frontiers in Microbiology*, *8*, e2003.

Zimmerman, A. E., Allison, S. D. & Martiny, A. C. (2014). Phylogenetic constraints on elemental stoichiometry and resource allocation in heterotrophic marine bacteria. *Environmental Microbiology*, *16*, 1398-1410.

Figure Legends

Figure 1. A cross section of a lake or a stream channel illustrating major pathways by which four key rules of life mediate the responses of ecological systems to a changing cryosphere in aquatic alpine environments. Temperature modulates molecular processes connected to metabolism and biosynthesis (Rule 1). Solar radiation modulates biotic responses in a wavelength-dependent manner (Rule 2) via effects of photosynthetically active radiation (PAR)

on photosynthesis and consumer behavior while UVR drives photodamage and avoidance responses. Element supplies, temperature, and light affect the variable C:N:P stoichiometry of photoautotroph biomass, which influences the dynamics of food quality for, and nutrient recycling by, stoichiometrically constrained consumers (Rule 3). As a result of interactions among these key rules, resource use efficiency (RUE) emerges at different levels of organization and modulates the efficiency of transformations of energy and materials through the ecological system (Rule 4).

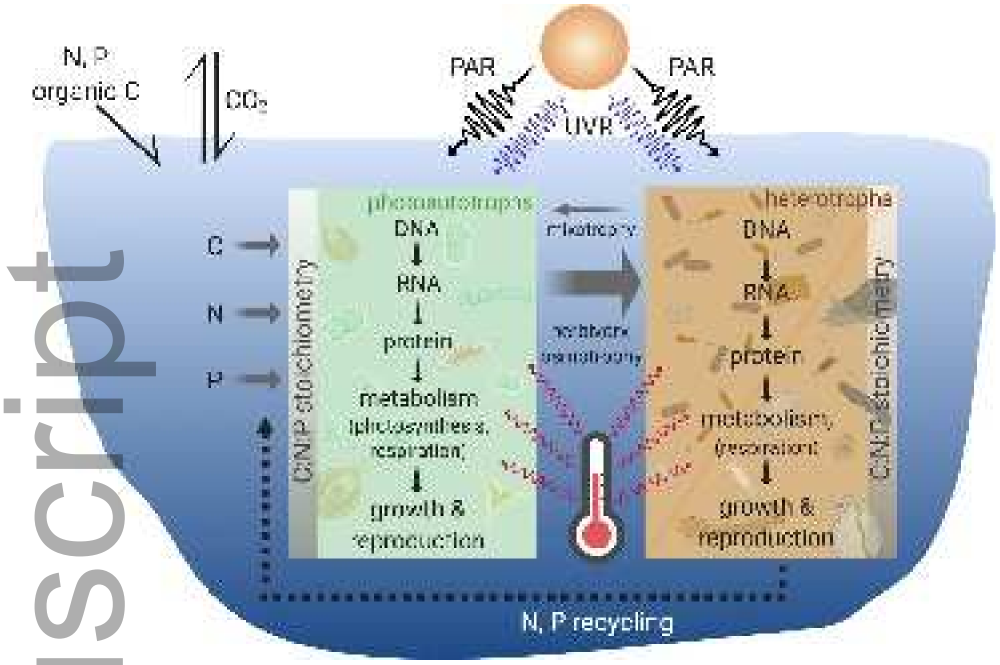
Figure 2. (a) A schematic showing the sequence of expected changes in the light environment and associated light-dependent responses as the alpine cryosphere diminishes in a glaciated catchment. Light attenuation in turbid, young, glacier-fed lakes is dominated by mineral-rich glacial flour particles that attenuate light largely through scattering that is not highly wavelength-selective. After glacial influence subsides, very clear lakes remain in a largely bedrock and till landscape with very little organic matter. In high alpine regions these are the highest ultraviolet radiation (UVR) exposure environments in the world. Incident UVR is high in these environments, and both UVR and photosynthetically active radiation (PAR) show minimal attenuation with depth due to the very high water clarity. As terrestrial vegetation develops in the landscape over time, terrestrially-derived dissolved organic matter (DOM) is leached into the lakes, selectively attenuating UVR relative to PAR. (b) Irradiance (percent of subsurface irradiance) vs. depth profiles for 320 nm UVR (violet line) and (PAR, green line) in three lakes in a glacial chronosequence in Glacier Bay, Alaska. Data from Silty Bruce (a glacier-fed lake still in contact with glacier), Little Esker (~10 years old), and Klotz Hills (~90 years old) lakes (Williamson et al., 2001b).

Figure 3. Predicted shifts in (a) nutrient supply and (b) biological demand of nutrients (i.e., stoichiometric ratios) as glaciers and permanent snowpack in the catchment fade. It is anticipated that SRP will decline as DIN and DOC fluxes increase (Hood et al., 2009; Saros et al., 2010). Cold, turbid systems with increased P availability and short growing seasons are expected to favor fast-growing organisms with greater P requirements (Elser et al., 2000, 2003). These fast-growing biota will be disadvantaged as glacier coverage declines and ecosystem P-limitation emerges.

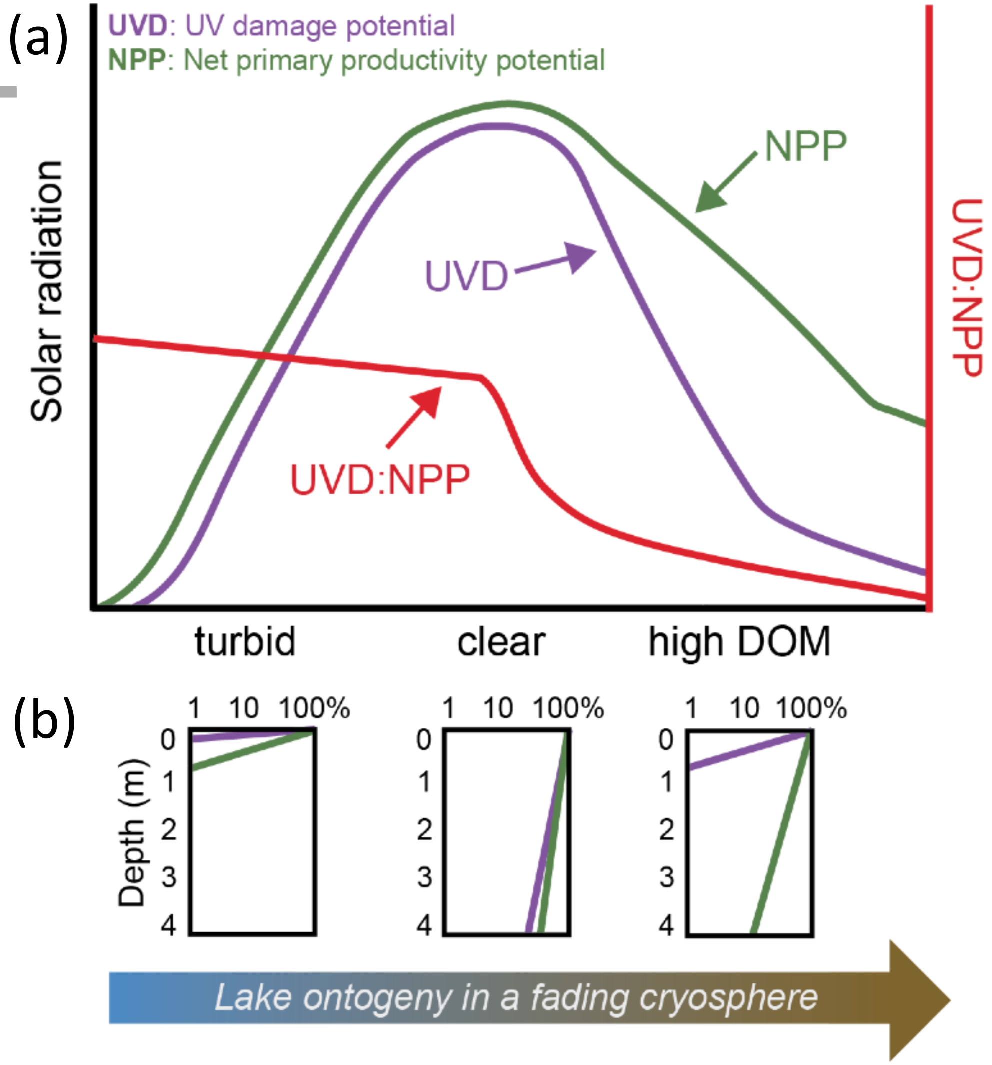
Figure 4. Hypothetical changes in resource use efficiency (RUE) and the factors impacting RUE during lake ontogeny. Initially, with a high degree of glacial connectivity lakes are highly turbid and light limited (Sommaruga, 2015). System turbidity will decrease over time following loss of hydrological connectivity with the glacier. As glacial connectivity recedes, light limitation decreases and in turn RUE increases. We hypothesize a temporary decrease in RUE as the system shifts from a turbid to a clear state largely due to community restructuring. PAR, UVR, and external supplies of nitrogen and organic carbon are all expected to increase over time while phosphorus will decrease (as described in Rule 3). Community assembly will have low functional diversity initially and be dominated by mixotrophic and organisms adapted to low light. Functional diversity will increase over time and be greatest at intermediate levels of disturbance (i.e., the transition between turbid and clear states). Following the loss of turbidity, a major disturbance, functional diversity will decrease and be dominated by fewer and specialized keystone taxa during the highly clear state. A similar trajectory may be followed in glacier-dominated streams as turbidity conditions change.

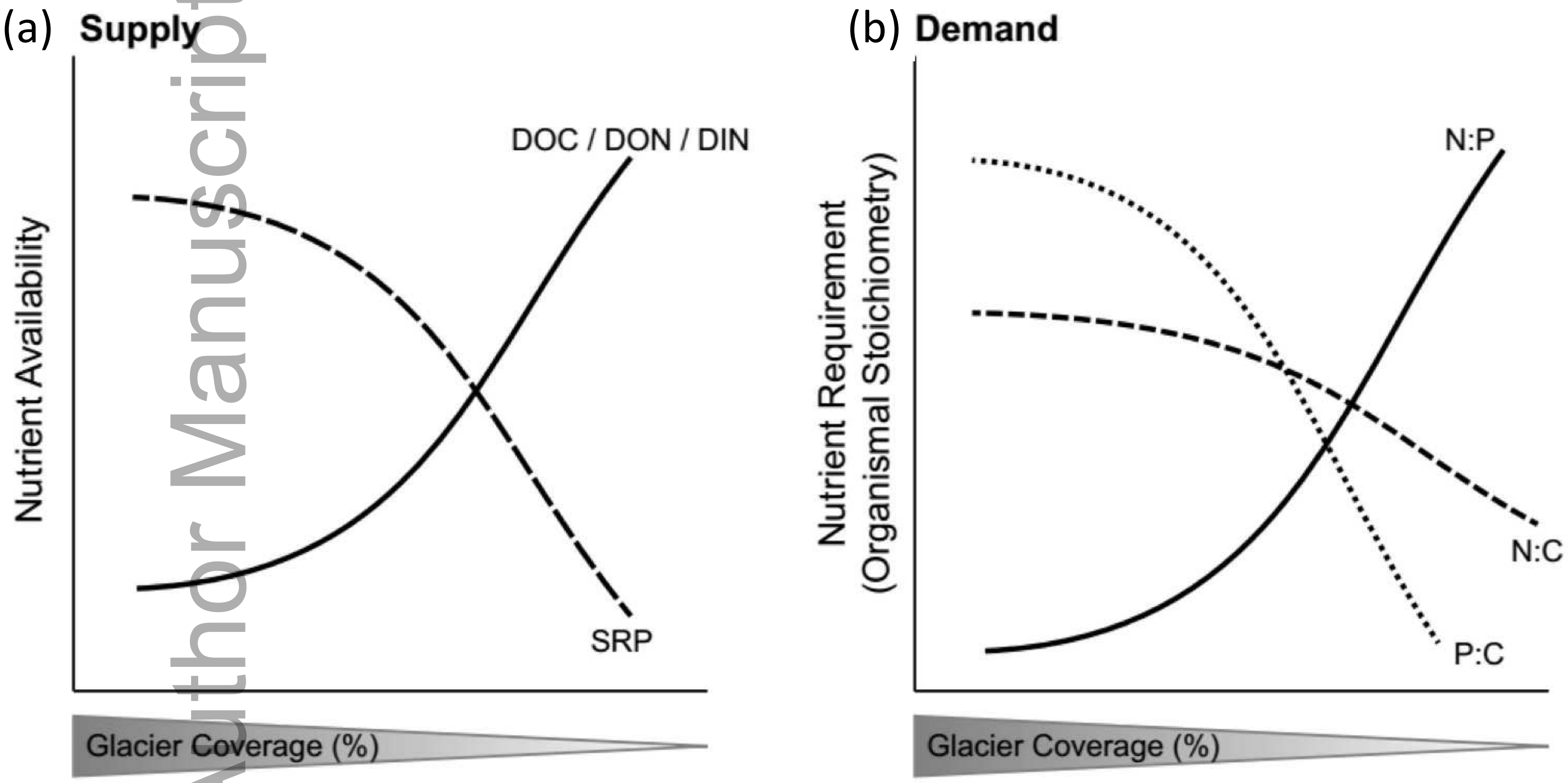
Figure 5: Examples of differences in the phenology of exposure to (a) potentially damaging UVR (320 nm, derived from a radiative transfer model), (b) surface water temperature (T), and

(c) the potential for UVR damage (UVR:T ratio) in a clear-water lowland temperate zone lake (dashed lines, data from Williamson et al., 2002), and a high elevation temperate zone lake (solid lines, 4,000 m, representing the Tibetan Plateau, the largest high elevation region in the world). UVR exposure in the alpine lake is estimated by using the data from the lowland lake and an 11% increase per 1000 m in 320 nm solar UVR (Blumthaler et al., 1997). Alpine surface water temperatures are hypothetical, based on ice-out soon after the summer solstice. Temperature data are from multiple temperate-zone alpine lakes around the world (C.E.W., unpublished data). Incident UVR will increase, and seasonal variations in UVR and T decrease with decreasing latitude into more tropical regions, while the reverse patterns will be observed in higher latitude boreal to polar regions.

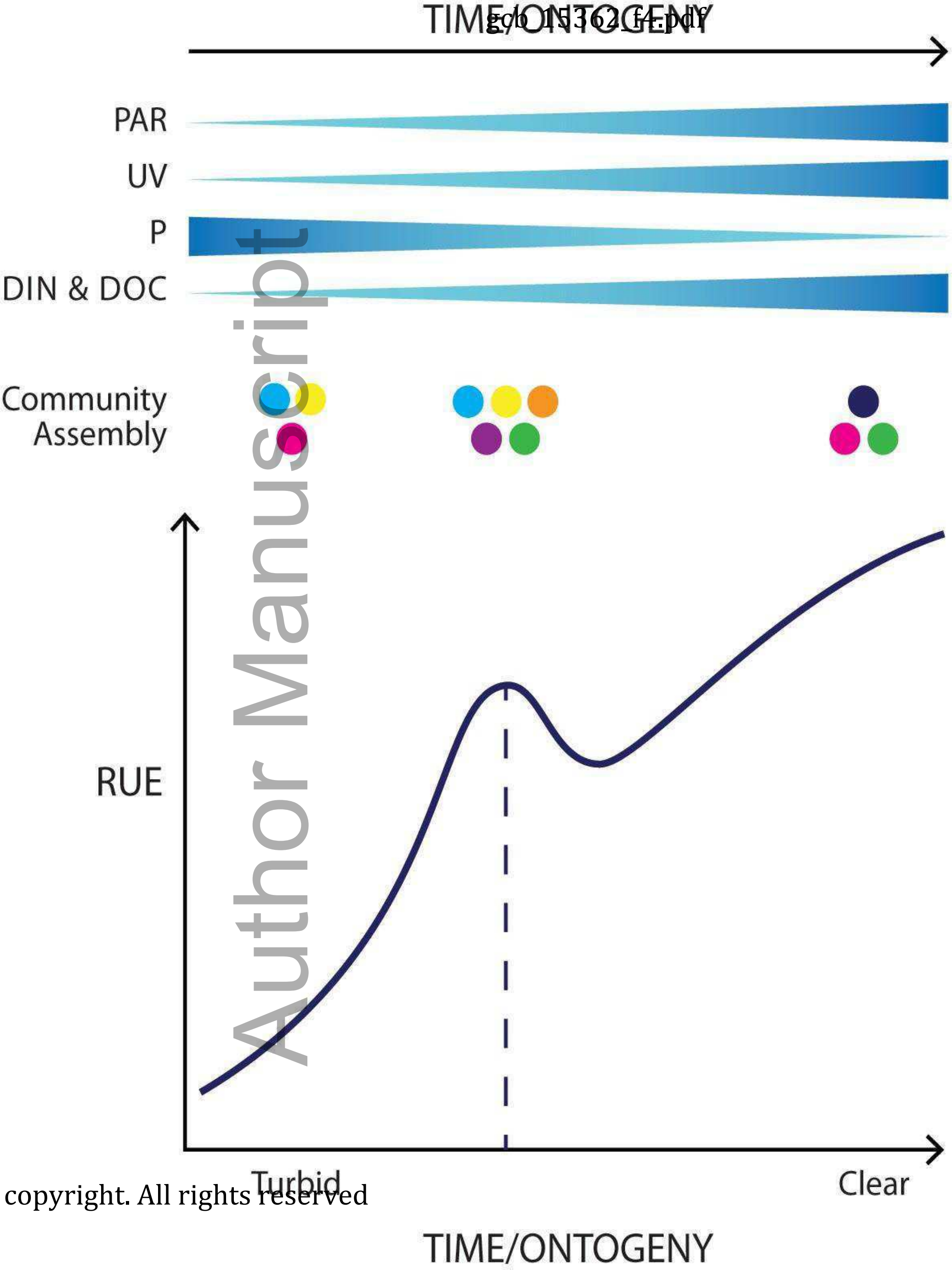


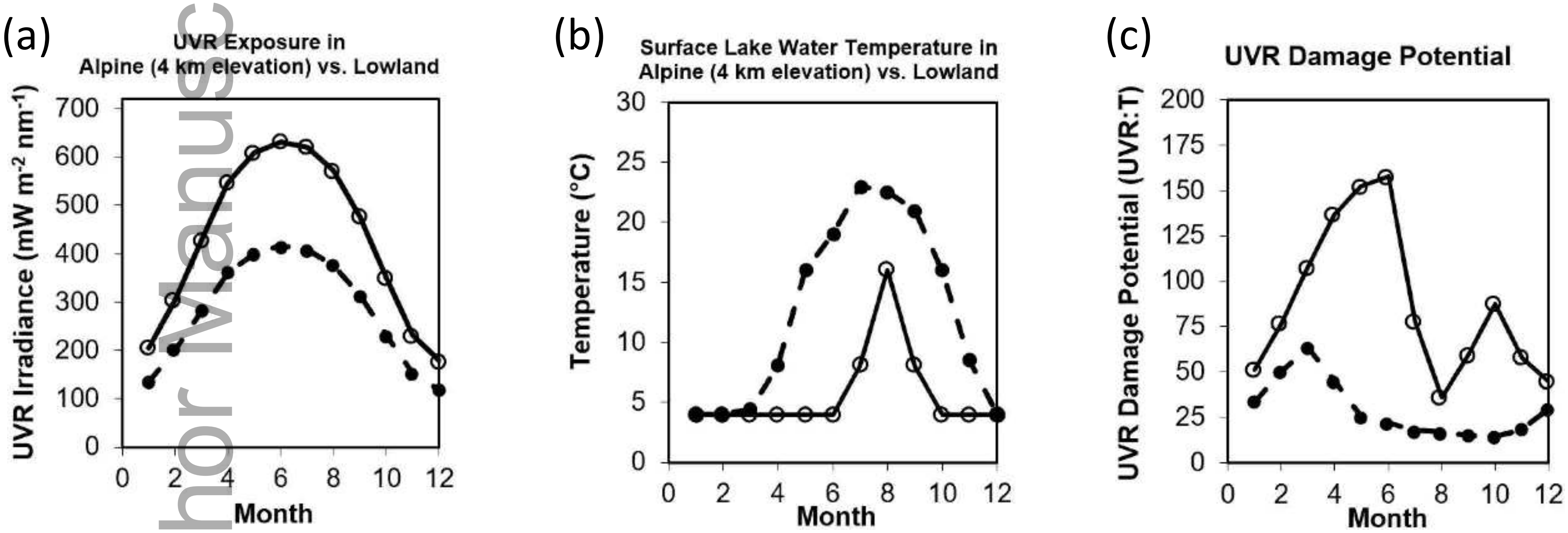
gcb_15362_f1.png


(a)
UVD: UV damage potential
NPP: Net primary productivity potential
Solar radiation
UVD:NPP
NPP
UVD
UVD:NPP
turbid
clear
high DOM
(b)
Depth (m)
1 10 100%
0
1
2
3
4
1 10 100%
0
1
2
3
4
1 10 100%
0
1
2
3
4
Lake ontogeny in a fading cryosphere


(a) Supply
Nutrient Availability
DOC / DON / DIN
SRP
Glacier Coverage (%)
(b) Demand
Nutrient Requirement (Organismal Stoichiometry)
N:P
N:C
P:C
Glacier Coverage (%)

gcb_15362_f4.pdf




(a)
UVR Exposure in
Alpine (4 km elevation) vs. Lowland
UVR Irradiance (mW m-2 nm-1)
0
100
200
300
400
500
600
700
0
2
4
6
8
10
12
Month
(b)
Surface Lake Water Temperature in
Alpine (4 km elevation) vs. Lowland
Temperature (°C)
0
5
10
15
20
25
30
0
2
4
6
8
10
12
Month
(c)
UVR Damage Potential
UVR Damage Potential (UVR:T)
0
25
50
75
100
125
150
175
200
0
2
4
6
8
10
12
Month