



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

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Key rules of life and the fading cryosphere:**2 impacts in alpine lakes and streams**

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62

Abstract

64 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
66 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
68 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
70 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
72 thaws, alpine lakes and streams will experience major changes in temperature regimes,
absolute and relative inputs of solar radiation in ultraviolet and photosynthetically active
74 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
76 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
78 integrated global view of rapidly changing alpine environments. However, doing so will require
intensive interdisciplinary collaboration and international cooperation. More broadly, the alpine
80 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
82 ongoing global change across the daunting scope of diversity in Earth's biota and environments.
Keywords: rules of life; cryosphere; lakes; streams, glaciers;

84

86 **1. Introduction**

88 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
90 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
92 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
94 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
96 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).
98 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
100 communities poses an urgent challenge for ecologists and environmental scientists (Hotaling et
al., 2017a; Moser et al., 2019) because alpine aquatic ecosystems provide key services upon
102 which human well-being depends, especially for the inhabitants of mountain regions (Viviroli et
al., 2007).

104

To move beyond merely documenting ecological changes into making predictions requires a
106 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
108 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:

110 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.,
112 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
114 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
116 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
118 changes in the cryosphere but also to forecast their consequences.

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

122 *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
124 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
126 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
128 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
130 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
132 regimes, and habitat succession.

134 *2.2 Four key rules*

We propose four rules of life necessary for obtaining a fundamental and thus predictive

136 understanding of how aquatic biota and ecosystems in alpine environments will respond to a
changing cryosphere under ongoing climate change.

138 *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).

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

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

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

148

2.2.1 *Key rule 1: Temperature.*

150

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

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

154 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
156 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
158 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

160 point at which temperature becomes stressful, increasing temperature increases enzyme
activity, metabolic rate, and all biological rate processes that depend on metabolism, including
162 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
164 may not apply across narrower ranges of temperature and especially at low temperatures close
to the freezing point of water.

166

At low temperatures, organisms face unique challenges related to molecular flexibility,
168 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
170 (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.
172 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
174 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)
176 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
178 channels (Milner & Bailey, 1989; Clague & Evans, 2000; Brahney et al., 2010; Shugar et al.,
2017).

180

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

Likewise, likewise, cold-adapted membranes may fail at modestly high temperatures, with
186 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
188 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
190 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
192 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
194 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
196 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
198 habitats associated with snowpack or cold seeps and springs. Furthermore, recent studies
indicate that some cold-adapted insects have relatively broad temperature performance optima
200 (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
202 rules beyond temperature dependence may play an important role.

204 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
206 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-
208 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.

210 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
212 (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
214 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
216 altitudes and latitudes (Takeuchi et al., 2006; Lutz et al., 2016).

218 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.
220 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
222 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
224 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
226 regimes.

228 *2.2.2 Key rule 2: Wavelength dependence.*

230 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
232 (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
234 drives primary production whereas UVR can transform refractory organic matter (autochthonous

or terrestrially-derived) into energy resources through photodegradation, fueling ecosystem
236 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 &
238 Rose, 2010; Williamson et al., 2014, 2019).

240 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
242 (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
244 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,
246 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-
248 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
250 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
252 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
254 production (Engstrom et al., 2000; Williamson et al., 2001b).

256 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
258 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

260 increasingly concentrated in high elevation ice and snow due to sublimation and low
temperatures that slow contaminant degradation (Daly & Wania, 2005). This concentrating
262 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 &
264 Berenbaum, 1988). As terrestrial vegetation increases over the longer term with climate
warming, UVR-absorbing DOM inputs reduce UVR:PAR ratios, photodegradation of organic
266 matter, photoinhibition of photosynthesis, phototoxicity, and photodamage of DNA and other
cellular components (Figure 2) (Williamson et al., 2001a, b).

268
Ultimately, the loss of high UVR:PAR ecosystems as DOM increases with increasing terrestrial
270 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
272 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
274 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).

276
Several critical knowledge gaps provide a compelling need for further research to understand
278 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
280 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
282 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
284 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
286 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
288 trophic levels in the warming alpine cryosphere.

290 2.2.3 Key rule 3: *Biological stoichiometry.*

Due to a shared evolutionary history, organisms have a common biochemistry constructed from
292 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;
294 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
296 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.,
298 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
300 demands, inducing nutrient limitation that drives local diversity, community assembly, and
ecosystem dynamics. Stoichiometric plasticity and stoichiometric adaptations are key
302 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
304 acting upon the basic biochemical machinery of living organisms may also impose limits on
those stoichiometric responses (Zimmerman et al., 2014).

306

Taking a stoichiometric perspective on the living things that inhabit alpine lakes and streams
308 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,

310 depending on catchment geology, concentrations of available forms of P can increase, while
concentrations of dissolved inorganic and organic nitrogen decrease with increasing catchment
312 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
314 (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;
316 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
318 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).

320

Less is known about how shifts in snowpack regimes affect nutrient supplies to alpine lakes and
322 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
324 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
326 mobilization of accumulated nutrients in that snow. In addition, weathering of newly exposed
bedrock, which releases nutrients, should increase through both biological and physical
328 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
330 et al., 2015). This requires further research.

332 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
334 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-
336 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
338 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
340 species and disadvantage fast-growing organisms with high P requirements, especially in low P
supply environments (Elser et al., 2000; Kay et al., 2005).

342

A variety of research opportunities exist to gain a better understanding of stoichiometric
344 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
346 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
348 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
350 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
352 compared to related species from warmer habitats.

354 2.2.4 Key rule 4: Resource use efficiency.

356 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
358 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

360 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,
362 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
364 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
366 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.,
368 *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).

370

Resource use efficiency is also strongly linked to that of biodiversity. For example, according to
372 the biodiversity-ecosystem functioning hypothesis (Loreau et al., 2001), higher taxonomic
diversity is expected to increase RUE (Hooper et al., 2005). However, considering species
374 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
376 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
378 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
380 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
382 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
384 diversity, functionality and productivity within alpine ecosystems as the influence of the

386 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.

396
398 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.

404

2.3 Interactions among the key rules

406 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.,

410 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
412 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
414 (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
416 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).

418
Interactions among these key rules extend beyond stoichiometric dimensions. For example,
420 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).
422 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
424 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
426 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
428 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
430 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.
432 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

434 processes ultimately influence emergent resource use efficiency (Rule 4) in communities and
ecosystems under cryosphere change.

436

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

438 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

440 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

442 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

444 - 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

446 1) and to predict future transitions.

448 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

450 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.

452 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

454 land-use, climate, land-atmosphere interactions, microbial activity, and glacial drainage
patterns. Importantly, we need to document not only ongoing ecological responses to such

456 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,

458 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 UVR-

460 induced 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
462 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
464 (Hylander et al., 2009). Likewise, understanding fundamental temperature responses of
metabolism and performance, especially at low temperatures as water warms above its freezing
466 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.

468
To develop such a predictive, mechanistic understanding and to obtain broadly applicable
470 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
472 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
474 international attention. Furthermore, interdisciplinary integration across atmospheric, earth, and
life sciences is essential. Only with such integration can the most ecologically relevant
476 geophysical changes be identified and tracked and their impacts predicted from a foundation of
fundamental biological knowledge.

478
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820 **Figure Legends**

822 **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
824 aquatic alpine environments. Temperature modulates molecular processes connected to
metabolism and biosynthesis (Rule 1). Solar radiation modulates biotic responses in a
826 wavelength-dependent manner (Rule 2) via effects of photosynthetically active radiation (PAR)

on photosynthesis and consumer behavior while UVR drives photodamage and avoidance
828 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
830 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
832 organization and modulates the efficiency of transformations of energy and materials through
the ecological system (Rule 4).

834

Figure 2. (a) A schematic showing the sequence of expected changes in the light environment
836 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
838 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
840 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
842 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
844 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
846 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
848 contact with glacier), Little Esker (~10 years old), and Klotz Hills (~90 years old) lakes
(Williamson et al., 2001b).

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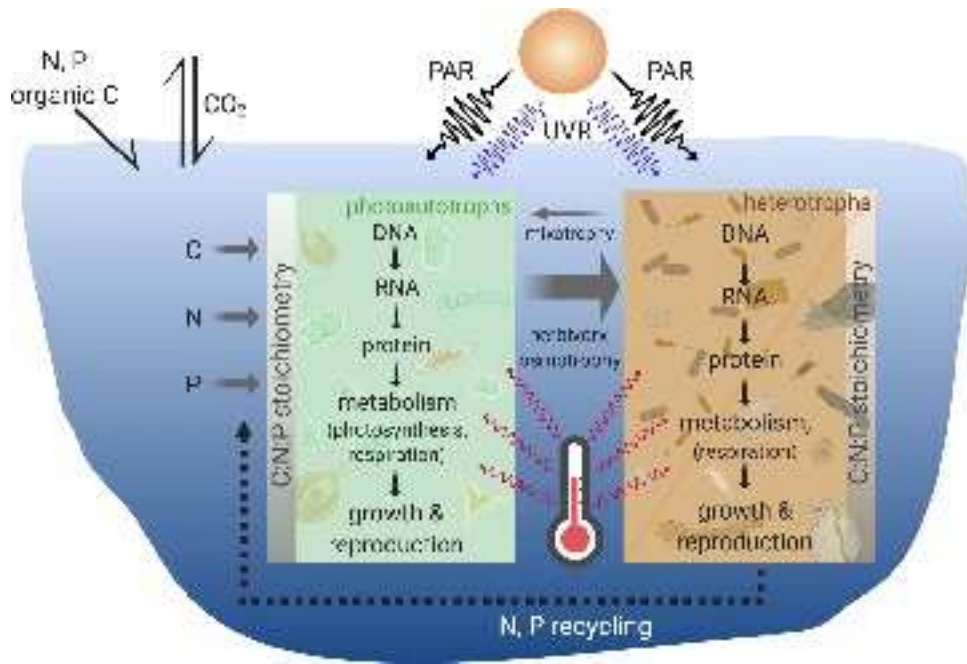
852 **Figure 3.** Predicted shifts in (a) nutrient supply and (b) biological demand of nutrients (i.e.,
stoichiometric ratios) as glaciers and permanent snowpack in the catchment fade. It is
854 anticipated that SRP will decline as DIN and DOC fluxes increase (Hood et al., 2009; Saros et
al., 2010). Cold, turbid systems with increased P availability and short growing seasons are
856 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-
858 limitation emerges.

860 **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
862 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
864 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,
866 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
868 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
870 (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
872 keystone taxa during the highly clear state. A similar trajectory may be followed in glacier-
dominated streams as turbidity conditions change.

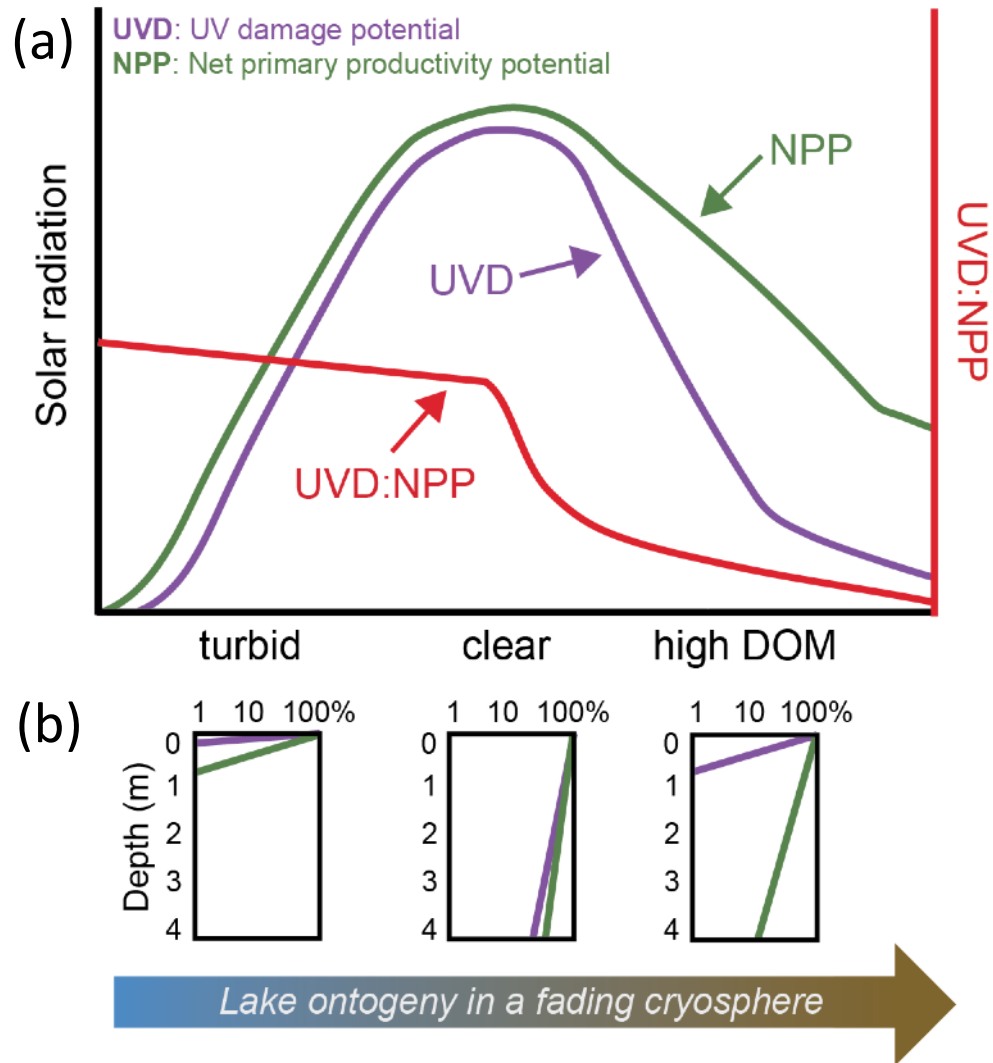
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Figure 5: Examples of differences in the phenology of exposure to (a) potentially damaging
876 UVR (320 nm, derived from a radiative transfer model), (b) surface water temperature (T), and

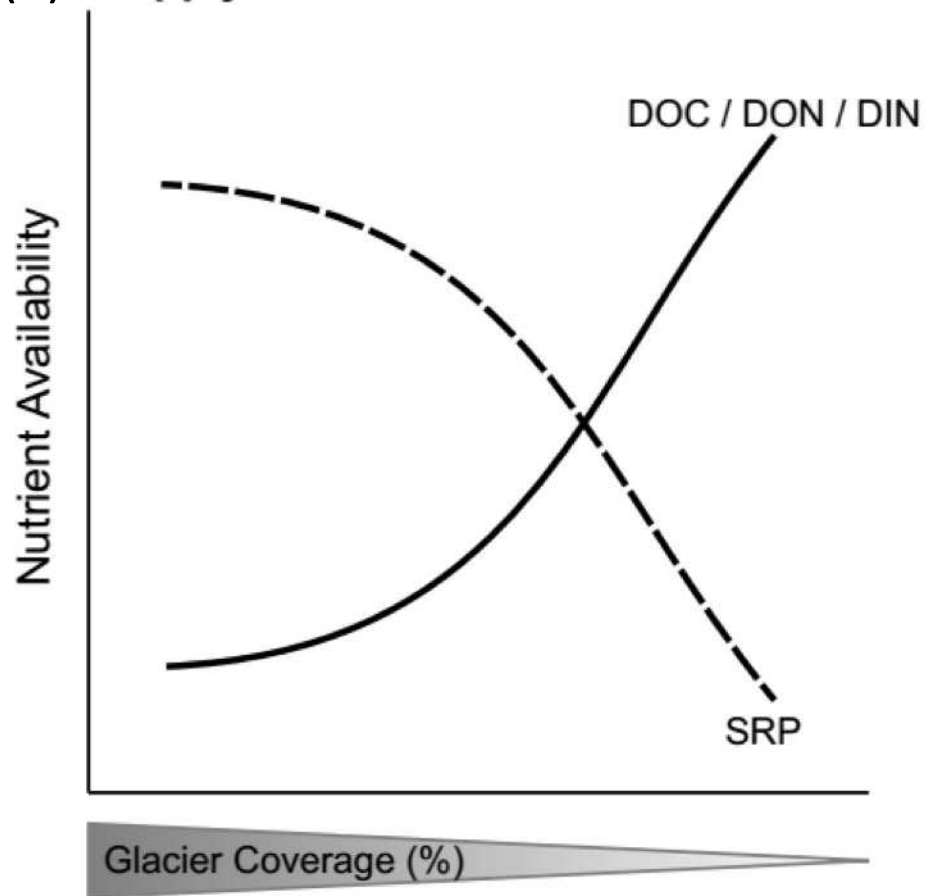
(c) the potential for UVR damage (UVR:T ratio) in a clear-water lowland temperate zone lake
878 (dashed lines, data from Williamson et al., 2002), and a high elevation temperate zone lake
(solid lines, 4,000 m, representing the Tibetan Plateau, the largest high elevation region in the
880 world). UVR 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
882 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.,
884 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
886 higher latitude boreal to polar regions.



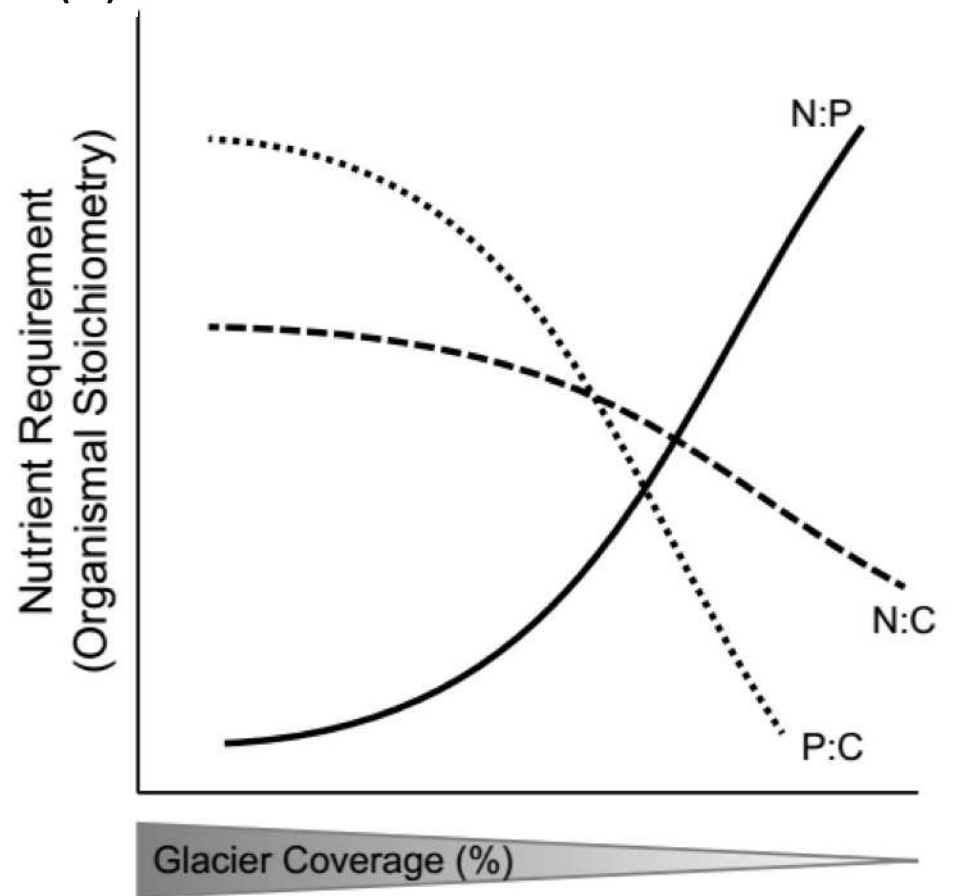
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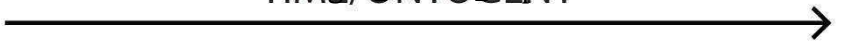
(a) Supply



(b) Demand



TIME/ONTOGENY

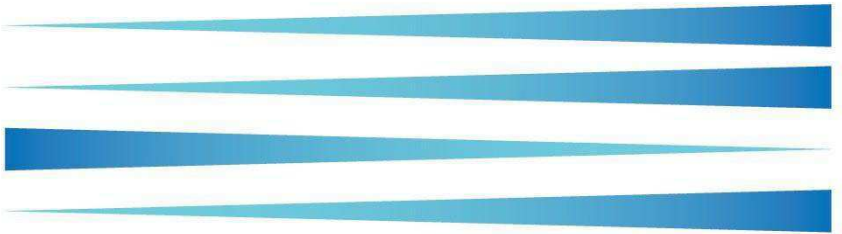


PAR

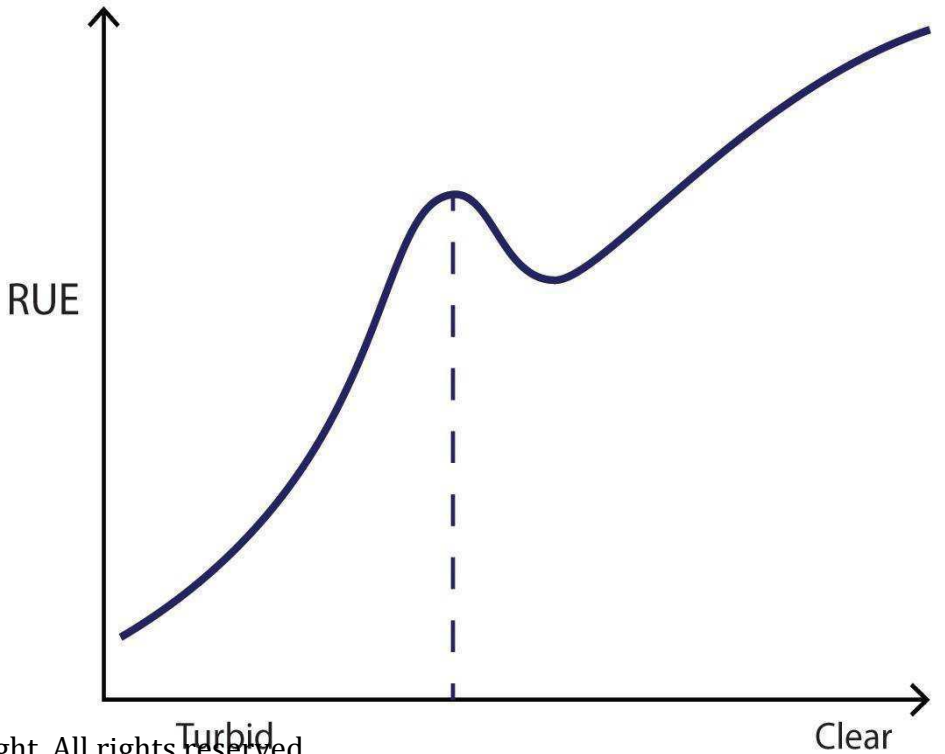
UV

P

DIN & DOC



Community Assembly



TIME/ONTOGENY

