

1-6-2021

Rock Glaciers and Related Cold Rocky Landforms: Overlooked Climate Refugia for Mountain Biodiversity

Stefano Brighenti
Free University of Bozen-Bolzano

Scott Hotaling
Washington State University

Debra S. Finn
Missouri State University

Andrew G. Fountain
Portland State University, andrew@pdx.edu

Masaki Hayashi
University of Calgary

Follow this and additional works at: https://pdxscholar.library.pdx.edu/geology_fac



See next page for additional authors
Part of the [Geology Commons](#), and the [Glaciology Commons](#)

Let us know how access to this document benefits you.

Citation Details

Published as: Brighenti, S., Hotaling, S., Finn, D. S., Fountain, A. G., Hayashi, M., Herbst, D., Saros, J. E., Tronstad, L. M., & Millar, C. I. (2021). Rock glaciers and related cold rocky landforms: Overlooked climate refugia for mountain biodiversity. *Global Change Biology*, gcb.15510. <https://doi.org/10.1111/gcb.15510>

This Post-Print is brought to you for free and open access. It has been accepted for inclusion in Geology Faculty Publications and Presentations by an authorized administrator of PDXScholar. Please contact us if we can make this document more accessible: pdxscholar@pdx.edu.

Authors

Stefano Brighenti, Scott Hotaling, Debra S. Finn, Andrew G. Fountain, Masaki Hayashi, David Herbst, Jasmine E. Saros, Lusha M. Tronstad, and Constance I. Millar

1 **This manuscript is now published in *Global Change Biology*. Please cite as:** Brighenti, S.,
2 Hotaling, S., Finn, D.S., Fountain, A.G., Hayashi, M., Herbst, D., Saros, J.E., Tronstad, L.M. and
3 Millar, C.I. (2021), Rock glaciers and related cold rocky landforms: overlooked climate refugia for
4 mountain biodiversity. *Glob Change Biology*. <https://doi.org/10.1111/gcb.15510>
5

6 **Rock glaciers and related cold rocky landforms: overlooked climate refugia for mountain**
7 **biodiversity**

8
9 Stefano Brighenti^{1,*}, Scott Hotaling^{2,*}, Debra S. Finn³, Andrew G. Fountain⁴, Masaki Hayashi⁵,
10 David Herbst⁶, Jasmine E. Saros⁷, Lusha M. Tronstad⁸, and Constance I. Millar⁹
11

12 **Affiliations:**

13 ¹ Faculty of Science and Technology, Free University of Bozen-Bolzano, Bolzano, Italy

14 ² School of Biological Sciences, Washington State University, Pullman, WA, USA

15 ³ Department of Biology, Missouri State University, Springfield, MO, USA

16 ⁴ Department of Geology, Portland State University, Portland, OR, USA

17 ⁵ Department of Geoscience, University of Calgary, Calgary, AB, Canada

18 ⁶ Sierra Nevada Aquatic Research Laboratory and Institute of Marine Sciences, University of
19 California, Santa Cruz, CA, USA

20 ⁷ School of Biology and Ecology, Climate Change Institute, University of Maine, Orono, ME,
21 USA

22 ⁸ Wyoming Natural Diversity Database, University of Wyoming, Laramie, WY, USA

23 ⁹ Pacific Southwest Research Station, USDA Forest Service, Albany, CA, USA

24 * *Contributed equally*
25

26 **Correspondence:**

27 Scott Hotaling, School of Biological Sciences, Washington State University, Pullman, WA, USA;

28 Phone: (828) 507-9950; Email: Scott.Hotaling@wsu.edu; ORCID: 0000-0002-5965-0986
29

30 **Keywords:** icy seeps, global change biology, mountain hydrology, alpine stream, biodiversity
31 monitoring, climate change ecology, talus slope, debris-covered glacier
32

33 **Running head:** Cold rocky landforms as climate refugia
34

35 **Abstract:**

36 Mountains are global biodiversity hotspots where cold environments and their associated
37 ecological communities are predicted to be threatened by climate warming. Considerable
38 research attention has been devoted to understanding the ecological effects of alpine glacier
39 and snowfield recession. However, much less attention has been given to identifying climate
40 refugia in mountain ecosystems where present-day environmental conditions will be maintained,
41 at least in the near-term, as other habitats change. Around the world, montane communities of
42 microbes, animals, and plants live on, adjacent to, and downstream of rock glaciers and related
43 cold rocky landforms (CRL). These geomorphological features have been overlooked in the
44 ecological literature despite being extremely common in mountain ranges worldwide with a
45 propensity to support cold and stable habitats for aquatic and terrestrial biodiversity. CRLs are
46 less responsive to atmospheric warming than alpine glaciers and snowfields due to the
47 insulating nature and thermal inertia of their debris cover paired with their internal ventilation
48 patterns. Thus, CRLs are likely to remain on the landscape after adjacent glaciers and
49 snowfields have melted, thereby providing longer-term cold habitat for biodiversity living on and
50 downstream of them. Here, we argue that CRLs will act as climate refugia for terrestrial and
51 aquatic biodiversity in mountain ranges worldwide, offer guidelines for incorporating CRLs into
52 conservation practices, and identify key areas where future research is needed.

53

54 **Introduction:**

55 In high mountain areas, climate warming is proceeding 2-3 times faster than the global average,
56 imperiling habitats associated with glaciers, permafrost, and seasonal snowpacks (Hock et al.,
57 2019). Globally, mountains are biodiversity hotspots (Rahbek et al., 2019) due to high rates of
58 local endemism driven by a combination of habitat isolation and adaptation to cold conditions
59 (Muhlfeld et al., 2020; Smith & Weston, 1990). Many microbes, plants, and animals in terrestrial
60 and aquatic environments are associated with glaciers and other cold habitats (Gobbi &
61 Lencioni, 2020; Hågvar et al., 2020; Hotaling, Foley, et al., 2019; Lencioni, 2018). Thus, the
62 rapid contemporary warming of mountain ecosystems is projected to imperil cold-adapted
63 biodiversity worldwide (Brighenti, Tolotti, Bruno, Wharton, et al., 2019; Hågvar et al., 2020;
64 Hotaling et al., 2017; Hotaling, Wimberger, et al., 2020; Millar et al., 2018; Stibal et al., 2020).

65

66 As a result of climate warming, winter snowlines are shifting to higher elevations, and melt
67 seasons are beginning earlier and concluding later (Hock et al., 2019). During warm periods,
68 glaciers and snowfields are crucial for mountain hydrology as they yield large volumes of cold
69 water thereby buffering the effects of climate warming, at least for aquatic biota (Fountain &

70 Tangborn, 1985; Hotaling et al., 2017). Through alterations to melt timing and seasonal snow
71 accumulation, climate change will extend harsh summer conditions when terrestrial and aquatic
72 habitats are at their warmest and driest (e.g., Riedel & Larrabee, 2016). In the long-term, ice-
73 containing landforms (e.g., glaciers, snowfields, rock glaciers) and their water storage potential
74 will fade, reducing habitat for cold-adapted species (Hock et al., 2019). As snow and ice recede,
75 water temperatures will increase (Niedrist & Füreder, 2020) and formerly perennial streams may
76 become intermittent or dry entirely (Herbst et al., 2019). Similarly, a reduction in groundwater
77 input due to declines in snowmelt recharge (Hayashi, 2020) will stress wetland and meadow
78 vegetation, which may impact cold-adapted animals that depend on them, creating additional
79 stresses beyond rising temperature alone.

80

81 Although alpine glaciers and snowfields have received the bulk of scientific attention, they are
82 not the only strongholds of cold conditions in mountain ecosystems. Mountains around the world
83 harbor other landforms that also support cold habitats with considerable water-storage capacity
84 (Figure 1; Jones et al., 2018). Among these, rock glaciers have received the most attention
85 (Figure 1A; Jones et al., 2018; Jones et al., 2019), but related features are also common
86 including debris-covered glaciers, protalus ramparts (also called “valley-wall rock glaciers”), ice-
87 cored moraines, and cold talus slopes (Figure 2). Though considerable focus has been devoted
88 to distinguishing among these features geomorphologically, a collective term is still missing
89 (Millar & Westfall, 2008). For efficiency, we refer to them as “cold rocky landforms” (CRLs).
90 From an ecological perspective, studies focusing on alpine glaciers and snowfields outnumber
91 those on CRLs by approximately 10:1 (Figure 1).

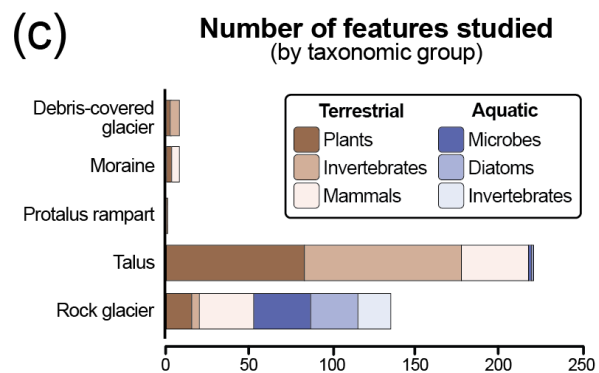
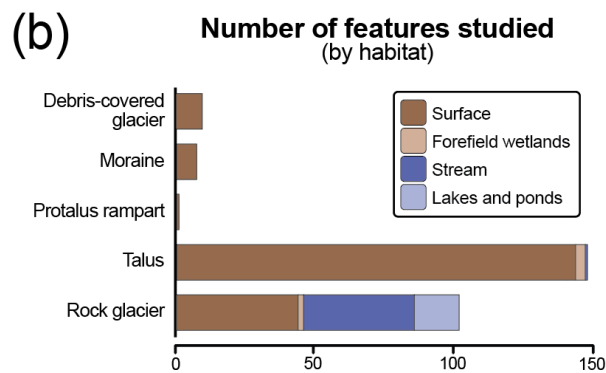
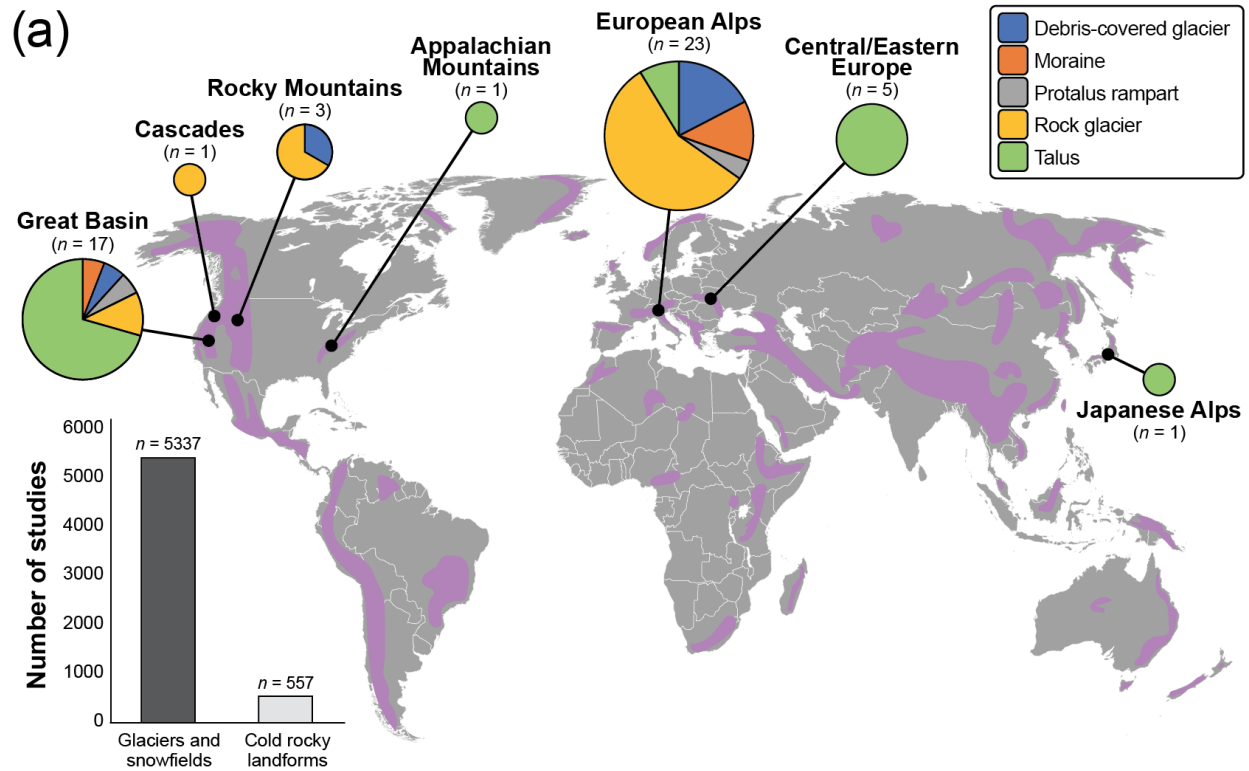
92

93 Cold rocky landforms are widespread in mountainous regions, present on every continent, and
94 greatly outnumber more well-known alpine glaciers (Jones et al., 2018). Structurally, CRLs
95 typically have a surface mantle of rocky debris and interiors composed of ice and rock. Their
96 rocky mantles insulate and decouple CRL interiors from outside air and promote internal thermal
97 regimes that support ice accumulation and retention (Morard et al., 2010). For these reasons,
98 CRLs are expected to respond to climate change more slowly than their surface ice
99 counterparts (Anderson et al., 2018; Stefaniak et al., 2020). With sub-freezing interiors, CRLs
100 have the capacity to store percolated snowmelt and rain as ice, and release meltwater into
101 springs and lakes during warm and dry periods (Hayashi, 2020; Jones et al., 2019). Thus, CRLs
102 comprise and sustain key cold habitats in regions that are otherwise warm and dry, where
103 winter snow is scarce or absent, and/or where glaciers and perennial snowfields are rare. For

104 instance, in the semi-arid mountains of the Great Basin, USA, rock glaciers account for over
105 90% of the total water stored as ice (Millar & Westfall, 2019). While our focus here is on CRLs in
106 mountain ecosystems, habitats exhibiting many of the same characteristics are present at lower
107 elevations, including at mid-latitudes where average air temperatures are above freezing. Often
108 called “algific talus slopes”, these habitats are Pleistocene relicts with persistent subsurface ice
109 and associated cold surface conditions. Algific talus slopes have been documented in North
110 America, Europe, and Asia (e.g., Kim et al., 2016; Nekola, 1999; Park et al., 2020; Růžička et
111 al., 2012).

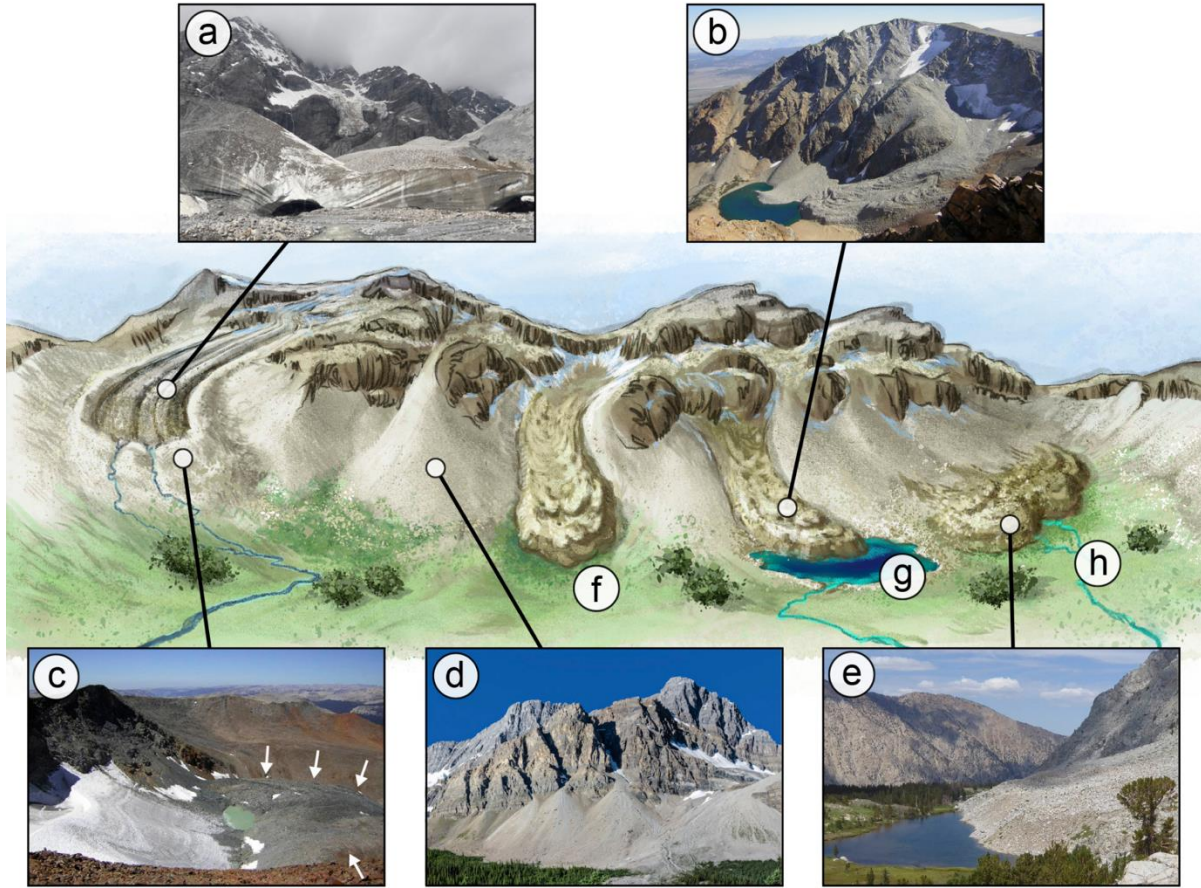
112
113 One strategy for mitigating the effects of climate change on biodiversity is the identification and
114 management of climate refugia (Morelli et al., 2020). Climate refugia are areas large enough to
115 support populations of imperiled species while their habitat is lost elsewhere due to climate
116 change (Figure 2, Table S1; Ashcroft, 2010). Growing ecological evidence, including the
117 presence of relict populations of a variety of organisms on lower elevation algific talus slopes
118 (e.g., Nekola, 1999), supports the hypothesis that CRLs will act as climate refugia in mountain
119 ecosystems. This potential is particularly striking when the prevalence of CRLs in mountain
120 ranges around the world is considered. Indeed, CRLs are ubiquitous at higher elevations
121 worldwide (Figure 1, Table S1; Jones et al., 2019) and are likely to maintain refugial cold habitat
122 following the rapid decline of alpine glaciers and snowfields.

123
124 Here, we present a global perspective of CRL ecology in mountain ecosystems, with an
125 emphasis on their value as refugia for cold-adapted terrestrial and aquatic biodiversity under
126 climate change. It is important to note that we are not the first to recognize the value of CRLs for
127 biodiversity. Indeed, Kavanaugh (1979) noted the potential for these landforms to serve as
128 refugia for high-elevation carabid beetles over 40 years ago. This potential has also been
129 highlighted by botanists (e.g., Gentili et al., 2015), mammologists (Millar et al., 2018), and very
130 recently, by alpine stream ecologists (e.g., Hotaling, Foley, et al., 2019). In this article, we have
131 two overarching goals: (1) to illustrate the refugial potential of CRLs under contemporary climate
132 change for a wide range of taxa in terrestrial and aquatic habitats. (2) Provide clear, actionable
133 guidance for identifying and integrating CRLs into conservation and climate adaptation
134 practices. We begin by providing a synthetic—but not exhaustive—overview of CRL ecosystems
135 and the biodiversity they contain. We then discuss how CRLs can be integrated into climate
136 adaptation practices and conclude by highlighting standing questions for the field.



137

138 **Figure 1.** (a) A global representation of ecological studies on cold rocky landforms (CRLs) in mountain
 139 ecosystems. Pie chart area reflects the total number of studies for each montane region (given as n
 140 below each name). Purple shading indicates mountainous areas (adapted from Rahbek et al., 2019). The
 141 inset vertical bar chart shows the difference in the number of studies that have focused on glaciers and
 142 snowfields versus CRLs according to a comprehensive Web of Science literature search within the
 143 category “mountain ecology.” The number of landforms investigated for each habitat and taxon are
 144 provided in (b) and (c), respectively, with one exception: a disproportionate number of studies have
 145 focused on CRLs providing habitat for American pika and thus, for visualization purposes, only ~5-10% of
 146 American pika features are included. Complete details of the studies underlying this figure, the methods
 147 used to obtain the data, and how montane regions were defined are provided in the Supplementary
 148 Materials, primarily in Table S1.



149
 150
 151
 152
 153
 154
 155
 156
 157
 158
 159
 160
 161
 162
 163
 164
 165
 166
 167
 168

Figure 2. Cold rocky landforms (CRLs) are composed of rocky debris, ice, and water, and have diverse origins and appearances. When an alpine glacier becomes covered with rock and soil, it transitions to a (a) debris-covered glacier which still contains substantial amounts of ice. The debris cover insulates the ice, reducing its rate of melt relative to debris-free glaciers (Anderson et al., 2018). (b) Rock glaciers are masses of fragmented rock and ice that move downslope. Rock glacier genesis can be varied, including progression from debris-covered glaciers, the formation of ice within rocky debris under permafrost conditions, or rain/snowmelt percolating into rocky debris and refreezing within the matrix. (c) Moraines (white arrows in the image) are rocky landforms deposited by glaciers. Moraines can preserve a core of glacier ice or develop an ice core as water flows into their rocky debris and refreezes. (d) Talus slopes result from rockfall along valley walls, and while they may contain ice from percolating and freezing water, they do not move or develop steepened fronts. (e) Protalus ramparts (sometimes referred to as valley-wall rock glaciers) often develop at the base of talus slopes where avalanche debris accumulate and bury snow. After burial, the snow can be preserved and transformed into ice, causing protalus ramparts to move. CRLs commonly accumulate and deliver cold groundwater to (f) forefield wetlands, (g) lakes, and (h) springs. Under climate change, active CRLs become inactive when they no longer move, eventually becoming relict features when all ice is lost. For additional images and discussion of CRLs see this study's Supplementary Materials as well as Millar and Westfall (2008), Benn and Evans (2014), Anderson et al. (2018), and Jones et al. (2019). Center artwork courtesy of Vanessa Arrighi.

169 **Cold habitats for biodiversity:**

170 *Surface habitats*

171 The surfaces of CRLs are typically boulder-strewn and heterogeneous, and include dry, rocky
172 ridges, sediment-filled depressions and unstable, shifting margins (Figure 2). Paired with the
173 environmental challenges that already stem from high-elevation habitat in mountain ecosystems
174 (e.g., extreme cold, reduced oxygen availability; Birrell et al., 2020; Elser et al., 2020), instability
175 of CRL mantles, intense solar radiation, routine avalanches, and rockfall make their surfaces
176 particularly harsh environments. For temperature, cold is not the only risk. On many CRLs,
177 organisms must contend with large thermal swings between night and day (Tampucci, Azzoni,
178 et al., 2017). Nonetheless, an array of plants and animals persist on CRL surfaces and within
179 their rocky matrices.

180
181 Vascular plants are common on CRLs (reviewed by Gentili et al., 2015) and include species
182 such as the wide-ranging mountain sorrel (*Oxyria digyna*) that inhabits CRLs throughout the
183 Northern Hemisphere. Plant-focused CRL studies have been performed on combinations of
184 CRL types and locations worldwide, ranging from rock glaciers and taluses in the Sierra
185 Nevada, USA (Millar et al., 2015) and European Alps (Cannone & Gerdol, 2003; Gobbi et al.,
186 2014) to debris-covered glaciers in the European Alps (Caccianiga et al., 2011; Rieg et al.,
187 2012; Tampucci et al., 2015). Plants on CRL surfaces are often found in cool soil patches that
188 are scattered and shallow (e.g., Burga et al., 2004; Gobbi et al., 2014; Millar et al., 2015; Table
189 S1). Both pioneering vegetation (e.g., bryophytes; Gobbi et al., 2014) and herbs and shrubs
190 (Burga et al., 2004; Cannone & Gerdol, 2003) are typical, with the latter often represented by
191 cold-hardy perennial species (Millar et al., 2015). Due to their cold nature versus surrounding
192 habitats, plants have been observed on CRLs as far as 1200 m below their typical altitudinal
193 zone (Fickert et al., 2007; Gentili et al., 2020; Millar et al., 2015).

194
195 Arthropods are also common on and within CRLs. While no synthesis of arthropod diversity on
196 CRLs has been performed, targeted studies—primarily from the European Alps and North
197 America—have revealed a rich diversity of beetles, mites, spiders, and pseudoscorpions (Table
198 S1; Gobbi et al., 2014; Gobbi et al., 2011; Gude et al., 2003; Růžička & Zacharda, 1994;
199 Tampucci, Azzoni, et al., 2017; Tampucci, Gobbi, et al., 2017). Similar to plants, many
200 arthropods also occur at lower elevations on CRLs than their typical distributions (Tampucci,
201 Gobbi, et al., 2017). CRLs can even harbor endemic arthropods. For instance, a cold-adapted
202 pseudoscorpion (*Parobsium yosemite*) is only known from cold talus caves in the Sierra

203 Nevada, USA, and is presumed to have evolved *in situ* (Cokendolpher & Krejca, 2010),
204 highlighting the potential for long-term stability of environmental conditions associated with
205 CRLs (Růžička & Zacharda, 1994).

206

207 CRLs are important to the life history of many mammals and other vertebrates, including the
208 iconic CRL-dependent mammal, the American pika (*Ochotona princeps*), a small relative of
209 rabbits that is widespread in western North America (Smith & Weston, 1990). Pikas are poor
210 thermoregulators and do not tolerate warm conditions, dying after prolonged exposure to
211 temperatures above 25°C (Smith & Weston, 1990). The near-surface interiors of CRLs,
212 however, provide cold micro-climates that allow pikas to persist in places where ambient
213 conditions are often untenable, including lower elevation sites atypical of the species (Millar et
214 al., 2018). Globally, at least 15 *Ochotona* species are restricted to cold CRL micro-climates
215 (Chapman & Flux, 1990). In addition to pikas, dozens of other mammals and birds inhabit CRLs
216 of North America, including woodrats, weasels, chipmunks, and ground squirrels (Millar &
217 Hickman, in press). In the Czech Republic, a small shrew (*Sorex minutus*) is endemic to taluses
218 (Růžička & Zacharda, 1994). CRLs are even crucial for wide-ranging, circumpolar carnivores
219 such as wolverines (*Gulo gulo*), a species threatened under the U.S. Endangered Species Act
220 due to climate change as their distributions are highly correlated with the presence of persistent
221 spring snowpack. Indeed, taluses are so important to wolverines for prey caching that their
222 presence appears to define the species' range limits (Inman et al., 2012).

223

224 *Forefield wetlands*

225 Cold air venting from the margins of CRLs in summer makes their forefields cooler than
226 surrounding environments (Figure 3; Sasaki, 1986). Cold air and abundant groundwater
227 combine to maintain cool wetland environments that are hotspots of biotic diversity in mountain
228 ecosystems (Hayashi, 2020), especially in semi-arid regions where they persist despite long
229 summers and common droughts (Millar et al., 2014; Millar et al., 2015). Wet meadows are
230 intermediate habitats between terrestrial and aquatic habitats, sharing characteristics of both.
231 Forefield wetlands associated with CRLs support a variety of plants and arthropods (Millar et al.,
232 2015). Similar to surface CRL biota, species typical of higher elevations are commonly found in
233 forefield wetlands of CRLs, making these habitats richer in biodiversity than areas not adjacent
234 to CRLs (Millar et al., 2015). Vertebrates found on CRL surfaces also use adjacent wetlands.
235 For instance, although pikas spend most of their time on the surface of CRLs, they often forage
236 in adjacent habitats (Smith & Weston, 1990).

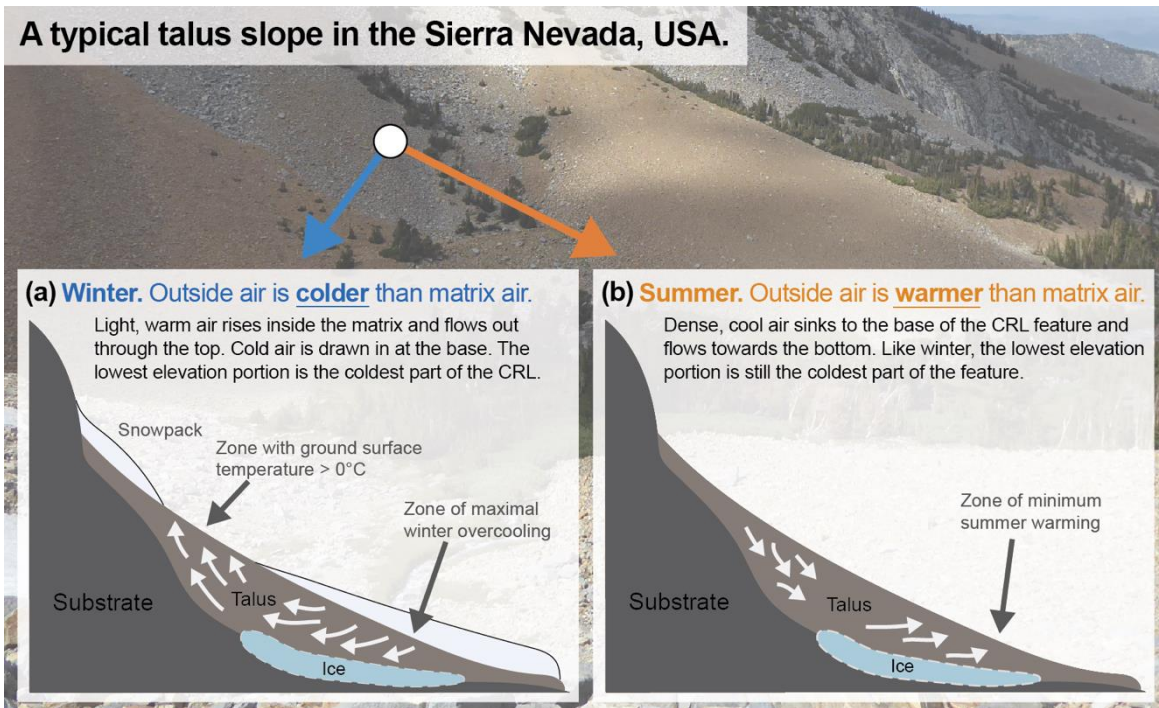
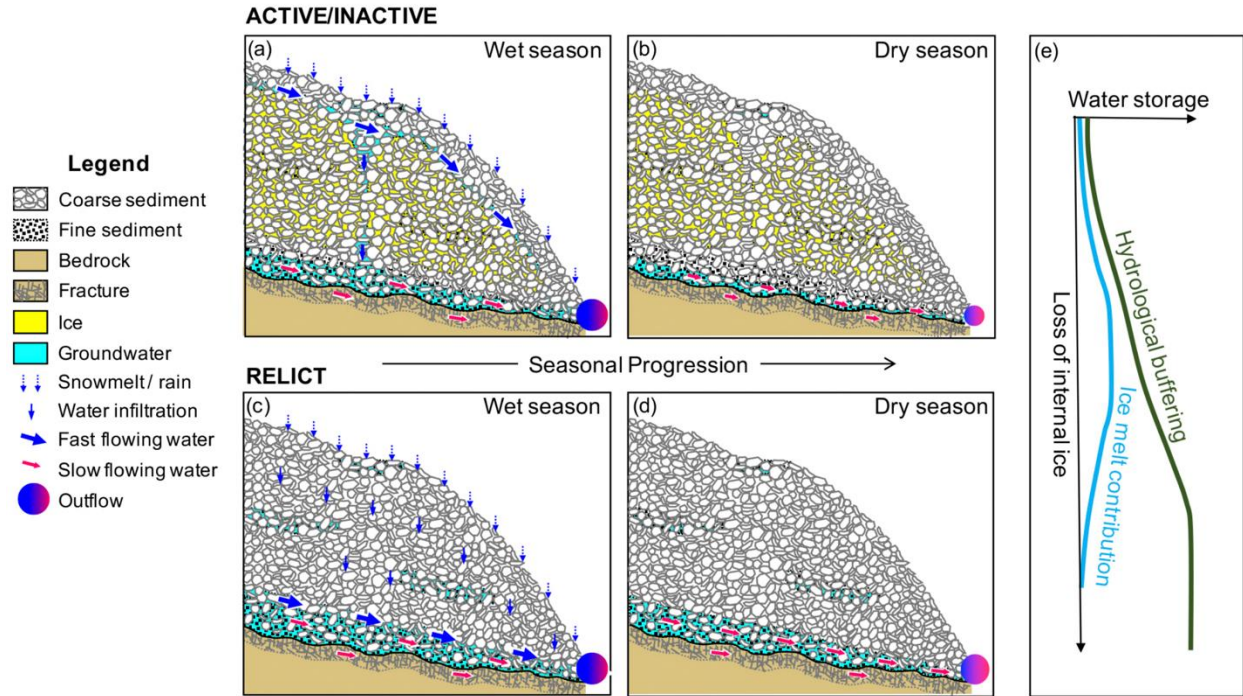
238
239

Figure 3. Unique properties and processes keep cold rocky landforms (CRLs) cold year-round. Natural convection ventilates the rocky matrix, creating a seasonally reversible circulation pattern (Morard et al., 2010). (a) In winter, outside air is colder than air inside the CRL. As cold air is drawn in at the base, it warms, and ascends upslope within the rocky matrix. (b) In summer, the atmosphere is warmer than air in the CRL and the flow reverses: cold, dense air sinks within the matrix and flows out at the base, chilling adjacent forefields. In both (a) and (b) white arrows indicate the direction of air flow. These ventilation patterns sustain cold and stable conditions year-around within the CRL despite the absence of ground-ice on surrounding slopes. Cold interiors freeze percolating snowmelt and rain, resupplying the ice that melts later in the summer. Ice gain and loss within CRLs is not well documented, but melt rates are estimated to be ~10-100 times less than for alpine glaciers due to the insulation afforded by the blanket of rocky boulders (Haeberli et al., 2017). CRLs can also maintain their cool thermal properties even when ice is absent, such that relict forms still support cool groundwater and springs (Jones et al., 2019). The summer versus winter distinction depicted in this panel largely stems from the fact that the bulk of CRL research has occurred at temperate to high latitudes. Thermal regimes within CRLs in tropical regions remain unknown. Diagrams modified from Morard et al. (2010).



255
 256
 257
 258
 259
 260
 261
 262
 263
 264
 265
 266
 267
 268
 269
 270
 271
 272
 273
 274
 275

Figure 4. Cold rocky landforms (CRLs) act as mountain aquifers as they partially store groundwater in their mantles that is recharged by snowmelt and rainfall, and slowly release it into nearby habitats. These natural reservoirs greatly contribute to local water storage in areas once considered to be “teflon basins” where precipitation would be quickly exported to the lowlands (Hayashi, 2020). When a CRL has ice filling voids (a-b; active = moving, inactive = no longer moving), the ice does not allow water to flow through, causing relatively fast flow of groundwater over the ice surface. Some groundwater may still flow through to the CRL bottom and the base may be underlain by fractured bedrock that conducts water. (b) Groundwater at the base has relatively slow flow and sustains outflows into springs and nearby habitats even during dry periods. Many CRLs formed when the climate was much colder than the present and do not contain internal ice (c-d, relict landforms). (e) As landforms transition to relicts under climate change, their water storage capacity will increase as more snowmelt and rainwater infiltrates (e.g., c) and flows through the coarse sediments near the bottom (fast flow), and the fine sediments and fractured rock in the bottom zone (slow flow). In relict CRLs, increased water storage in the bottom layer sustains a higher amount of dry-season outflow into springs. For this reason, relict landforms may actually have an increased capacity for hydrological buffering when compared to those with internal ice (d-e). The meltwater contribution from internal ice generally represents a relatively minor fraction (less than 5%) of dry-season groundwater discharge from CRLs (Krainer et al., 2015). However, this fraction will become increasingly important during drier and warmer summers, particularly in semi-arid mountain regions where droughts are common.

276 *Streams*

277 Alpine streams have attracted ecological attention for several decades (reviewed by Hotaling et
278 al., 2017), due in large part to concerns about the rapid shrinking of glaciers and seasonal
279 snowpack. The disappearance of once-perennial alpine glaciers and snowfield sources is
280 predicted to convert many headwaters from permanent to intermittent flows (Robinson et al.,
281 2016; Siebers et al., 2019) or result in the displacement of cold-adapted aquatic communities by
282 upstream-shifting warmer water assemblages (e.g., Brighenti, Tolotti, Bruno, Wharton, et al.,
283 2019; Finn et al., 2010; but see, Hotaling, Shah, et al., 2020; Muhlfeld et al., 2020). More
284 frequent snow drought is also expected to disproportionately reduce in-stream habitat types
285 associated with higher levels of biodiversity (e.g., riffles, Herbst et al., 2018). The heterogeneity
286 of hydrological sources in alpine headwaters has promoted high beta (among-site) diversity in
287 alpine streams from genetic diversity to invertebrates (Fell et al., 2018; Finn et al., 2013;
288 Hotaling, Giersch, et al., 2019; Wilhelm et al., 2013). Until recently, CRLs were vastly
289 underappreciated as an additional common source type, a crucial oversight given their
290 hydrology (Figure 4) and greater resistance to climate change versus alpine glaciers and
291 snowfields.

292
293 CRLs store substantial volumes of percolated water as ice and serve as aquifers in high
294 mountain landscapes (Figure 4; Hayashi, 2020). Often, meltwater emerges from CRLs as
295 springs that have been termed “icy seeps” (Hotaling, Foley, et al., 2019). Icy seeps have a
296 unique combination of habitat conditions including persistently cold water, stable flows, low
297 suspended sediments, stable channels, and relatively high ionic concentrations (Brighenti,
298 Tolotti, Bruno, Engel, et al., 2019; Hotaling, Foley, et al., 2019). This combination of habitat
299 conditions contrasts with streams sourced from alpine glaciers (cold but more variable thermal
300 and flow conditions, high suspended sediments, low ions, unstable channels), true groundwater
301 aquifers (springs with stable but warmer temperatures), and seasonal snowpack (warmer and
302 more variable temperatures, low ions; Birrell et al., 2020; Hotaling, Foley, et al., 2019; Ward,
303 1994). The heterogeneity of alpine streams resulting from varying hydrological source
304 contributions has been linked to differences in community structure for microbes (Feghel et al.,
305 2016; Hotaling, Foley, et al., 2019), diatoms (Fell et al., 2018), and invertebrates (Brown et al.,
306 2007; Giersch et al., 2017; Tronstad et al., 2020).

307
308 The impact of CRL-sourced headwaters on regional-scale biodiversity remains poorly
309 understood, but there is mounting evidence that icy seeps contain unique microbial (Feghel et al.,

2016; Hotaling, Foley, et al., 2019; Tolotti et al., 2020), algal (Rotta et al., 2018), and macroinvertebrate diversity (Brighenti, Tolotti, Bruno, Wharton, et al., 2019; Fell et al., 2017; Tronstad et al., 2020). However, whether icy seeps will serve as climate refugia as alpine glaciers and snowfields recede remains a pressing question. If local conditions are different enough between icy seeps and streams fed by alpine glaciers and snowfields, it is possible that a significant proportion of extant alpine stream biodiversity will still perish with the disappearance of these meltwater sources. However, if habitat persistence and cold water are key to occupancy, icy seeps will act as climate refugia. The strongest evidence for this thus far comes from macroinvertebrates, which represent the majority of animal biomass in alpine streams. In the European Alps (Brighenti et al., in press; Brighenti, Tolotti, Bruno, Wharton, et al., 2019) and American Rockies (Tronstad et al., 2020), macroinvertebrate communities in icy seeps contain many taxa that are common in nearby glacier- and snowmelt-fed streams. Notably, icy seeps in both regions contained healthy populations of taxa previously thought to occur only in the harsh conditions of glacier-fed streams such as midges of the *Diamesa latitarsis* group in the Alps (Lencioni, 2018) and the stonefly *Zapada glacier* in the Rockies (Hotaling, Giersch, et al., 2019; Tronstad et al., 2020). Furthermore, icy seeps can harbor greater local diversity than glacier-fed streams (Tronstad et al., 2020), including cold-adapted species that are not found in glacier-fed streams in the same area (Brighenti et al., in press). Icy seeps can also provide critical habitat for fish of conservation concern such as the westslope cutthroat trout in western Canada (Harrington et al., 2017). Although more research is required, our tentative conclusion is that the cold, stable aquatic habitat of icy seeps will provide climate refugia for a substantial portion of alpine stream biodiversity.

332

333 *Lakes and ponds*

334 Mountain lakes and ponds are more likely to be influenced by multiple hydrological sources than streams in the same areas and thus, their hydrology and resulting water chemistry are particularly complex (Ren et al., 2019). To date, most CRL-focused lake and pond research has focused on rock glacier-fed habitats. Thus far it appears that water chemistry, rather than temperature, is the overriding environmental driver in high mountain lake ecosystems. High concentrations of ions (including nitrates, calcium, magnesium, and sulphates) and heavy metals, often exceeding drinking water limits, appear common in rock glacier outflows (Brighenti, Tolotti, Bruno, Engel, et al., 2019; Colombo et al., 2018; Williams et al., 2007). High metal concentrations promote sublethal effects on lake biodiversity, as shown by a high prevalence of mouth deformities in the midge *Pseudodiamesa nivosa* in a rock glacial lake of

344 the Italian Alps (Ilyashuk et al., 2014). High concentrations of nitrogen (in particular nitrates, a
345 limiting nutrient in mountain lakes and streams, Elser et al., 2009) in rock glacier-fed waters, can
346 enhance algal production (Slemmons & Saros, 2012), especially when compared with alpine
347 glacier-fed lakes where high turbidity limits algal growth by hindering light penetration (Elser et
348 al., 2020).

349

350 It is unclear if CRL will promote refugia in lakes and ponds similar to that of alpine streams. For
351 instance, while microbial diversity typical of glacier-fed lakes has been observed in rock glacier-
352 fed water bodies (Mania et al., 2019), only one study has made a direct comparison. In the
353 Italian Alps, primary producer communities are comparable between lakes influenced by rock
354 glaciers and those not influenced by them (Thaler et al., 2015). In contrast, the nearshore zone
355 of rock glacier-fed lakes have lower invertebrate diversity than typical high-mountain lakes, with
356 resident communities mainly composed of species tolerant of high metal concentrations (Thaler
357 et al., 2015). How CRLs shape mountain lake ecosystems remains underexplored, and in
358 particular, it is unclear if the unique chemical compositions of CRL-influenced lakes and ponds
359 observed in the Alps are unique to that region or common globally, a key question when
360 considering whether their chemical compositions hinders the potential for CRLs to bolster
361 climate refugia in mountain lakes and ponds.

362

363 **Lessons from the past:**

364 Geomorphological, hydrological, and ecological evidence supports the thesis that CRLs can
365 offset warming and water shortages in mountain ecosystems, and act as global climate refugia
366 for cold-adapted terrestrial and aquatic biota (Figures 1-2). Paleohistoric studies highlight the
367 long-term stability and refugial nature of CRLs, allowing cold-adapted species to persist for as
368 long as 10,000 years during the Holocene. For instance, on both debris-covered glaciers in
369 western North America and taluses of central Europe, plants and arthropods that were
370 widespread during cold intervals of the Pleistocene are now restricted to CRLs (Fickert et al.,
371 2007; Růžička & Zacharda, 1994). This paleo-refugia hypothesis suggests that as climates
372 warmed after the last glacial period, cold-adapted species were generally forced to track
373 suitable habitat conditions to higher latitudes and/or elevations. CRLs, however, maintained
374 cooler conditions and persisted as cold habitat islands. Today, we see continuing evidence of
375 this pattern with elevationally or latitudinally disjunct populations of some species in CRL-linked
376 habitats (Fickert et al., 2007; Růžička & Zacharda, 1994). Thus, evidence from both the past
377 and present strengthens the prediction that CRLs will sustain long-lasting cold refugia under

378 contemporary climate change (Caccianiga et al., 2011; Gobbi et al., 2014; Millar et al., 2015;
379 Tampucci, Gobbi, et al., 2017; but see Karjalainen et al., 2020).

380

381 **Looking to the future:**

382 Human pressures have substantial impacts on mountain ecosystems that can amplify the
383 effects of climate change (Brighenti, Tolotti, Bruno, Wharton, et al., 2019). Often, species'
384 capacities to respond to rapid climate change is impeded by anthropogenic obstacles to
385 dispersal, such as land or water development and/or habitat fragmentation (Alexander et al.,
386 2018). In other cases, species run out of habitat to disperse into or conditions change too
387 quickly for them to adapt (Giersch et al., 2015; La Sorte & Jetz, 2010). Thus, active
388 conservation and climate-adaptation strategies are needed to prevent biodiversity loss (Millar et
389 al., 2007). The identification, conservation, and restoration of *in situ* climate-change refugia
390 within a species' existing range can provide biodiversity protection without the risks associated
391 with other solutions (Morelli et al., 2020; Morelli et al., 2016). For example, a common solution
392 for maintaining biodiversity under climate change is the use of managed relocation, where
393 species, population, or genotypes are moved to suitable habitat outside of their historical
394 distributions (Schwartz et al., 2012). The use of managed relocation (also referred to as
395 "assisted migration") raises a host of ecological concerns, chief of which are the unintended,
396 unpredictable consequences associated with bringing species into a new habitat (akin to the
397 known consequences of invasive species worldwide, Ricciardi & Simberloff, 2009).

398

399 However, identifying *in situ* habitats that will retain cold conditions and serve as climate refugia
400 can be difficult (Figure 5; Morelli et al., 2020; Morelli et al., 2016). While advances have been
401 made in predicting topographic and landscape features that support cool micro-climates
402 (Dobrowski, 2011), CRLs can be readily identified via satellite imagery and aerial photography
403 due to their distinct geomorphology (e.g., Cremonese et al., 2011). For aquatic habitats,
404 however, remote sensing has practical limitations. First, while CRL-associated lakes and ponds
405 can be readily detected by satellite imagery when seasonal snow is minimized, icy seeps are
406 typically small and easily overlooked. Subsurface flows and the presence of potentially key
407 aquifers are also impossible to detect with satellite imagery. Second, remote sensing-based
408 assessments of *in situ* aquatic conditions are limited. Quantifying thermal regimes as well as the
409 biological and chemical settings of CRLs thus requires field-based surveys, ideally paired with
410 long-term monitoring. Indeed, measuring water temperature may be an inexpensive tool for
411 identifying CRL-based refugia, especially when combined with satellite imagery showing a lack





412 of visible ice or snow upstream (Brighenti, Tolotti, Bruno, Engel, et al., 2019; Hotaling, Foley, et
413 al., 2019). When considering the long-term viability of CRL-influenced climate refugia, the
414 distribution and type of CRL is important. Microclimatological factors such as solar exposure
415 and snow accumulation favors the occurrence of CRLs on north-facing slopes or slopes
416 subjected to wind scouring of snow (Wagner et al., 2019). Therefore, slope aspect and physical
417 setting in relation to microclimate can be used to identify key areas for protected habitat (Millar
418 & Westfall, 2019). Along with aspect, the composition of CRLs in terms of ice content and their
419 topography may also affect how they sustain flows to downstream biological communities when
420 other sources are lost (Hayashi, 2020).

421
422 Owing to their climate change vulnerability (Hock et al., 2019), biotic monitoring of both CRL
423 and nearby non-CRL habitats in mountain ecosystems is needed to identify biodiversity under
424 threat and track population dynamics as conditions change (Figure 5). Networks of monitoring
425 sites should be selected to represent different habitat types (surface, wetland, aquatic) as
426 “sentinels” of broader change. Building on the identification and mapping of CRLs, as well as
427 accounting for resident biodiversity, active climate-adaptation practices can also be
428 implemented. Indeed, successful implementation of climate-adaptation strategies may be the
429 key factor underlying the success of CRLs as climate refugia given uncertain climate change
430 scenarios and increasing local pressures from human activities (Figures 5-6). When developing
431 CRL-focused strategies for climate-adaptation in mountain ecosystems, new ideas should be
432 considered in the context of both existing frameworks and local, regional, and national
433 governance policies. For instance, Khamis et al. (2014) considered conservation aims for alpine
434 rivers within the framework of the European Union, highlighting a need for policy shifts from
435 species-centric to more holistic ecosystem conservation practices. This premise applies broadly
436 to CRL conservation, as do their recommendations for conservation strategies to focus on
437 connectivity within and between alpine river basins and the need for reducing anthropogenic
438 stressors.

439

General Information

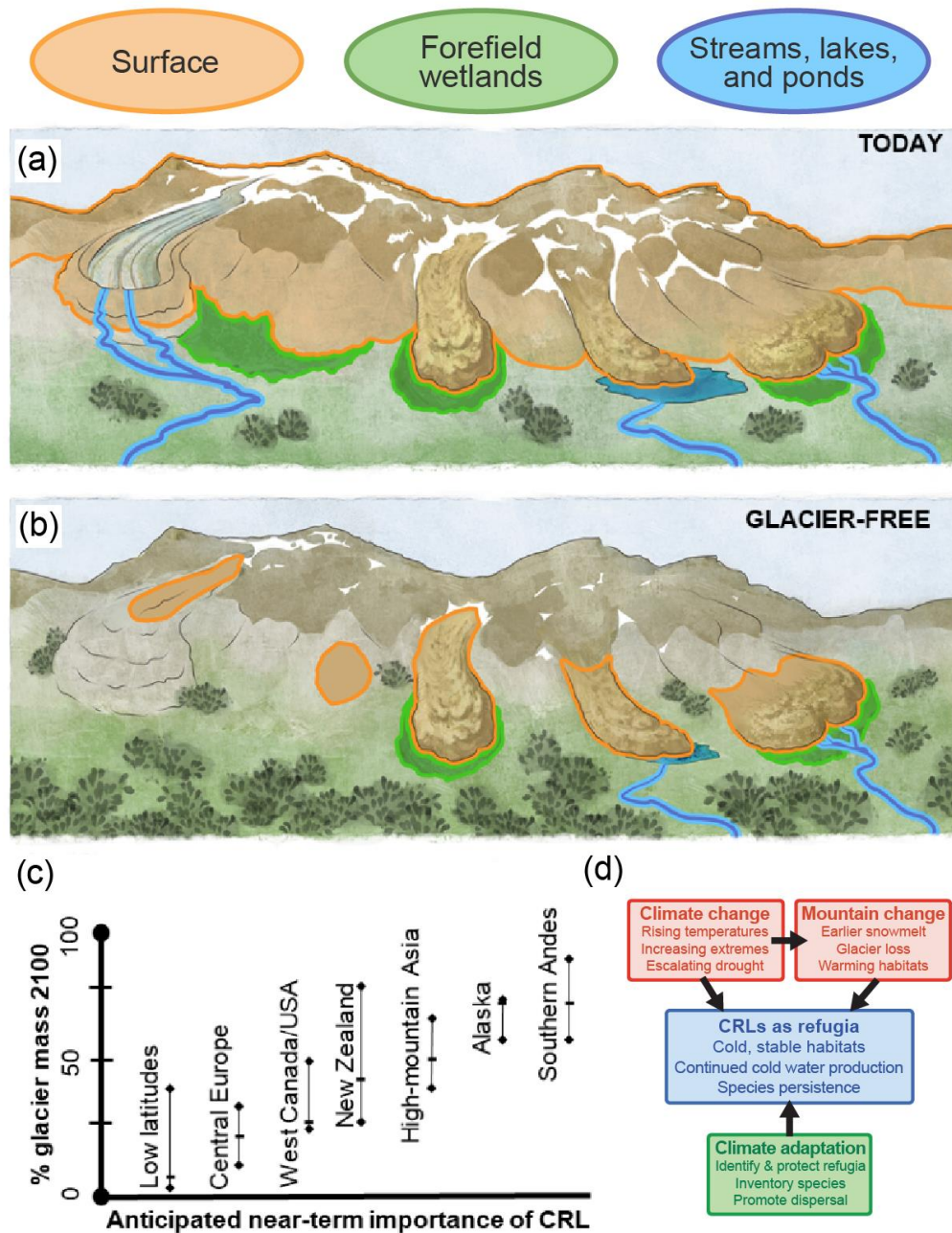
Climate Refugia Conservation Cycle
Modified from Morelli et al., (2016)

				
Species	Alpine mountain sorrel (<i>Oxyria digyna</i>)	Yosemite cave pseudoscorpion (<i>Parobisium yosemite</i>)	American pika (<i>Ochotona princeps</i>)	Western glacier stonefly (<i>Zapada glacier</i>)
Category	Terrestrial plant	Terrestrial invertebrate	Terrestrial mammal	Aquatic invertebrate
Geographic region	Northern Hemisphere: Arctic/montane areas	North America: southwestern United States	Western North America: montane areas	North America: northwestern United States
Non-CRL vulnerabilities	None are known	Biologically rare; stochastic loss of habitat	Stochastic loss of habitat; small population sizes; livestock encroachment	Biologically rare; habitat degradation
Existing protections	None	None	None	Listed as Threatened under the U.S. Endangered Species Act
Key CRL habitat	Taluses and rock glaciers	Granitic talus caves and void spaces	Taluses and rock glaciers	Icy seeps
1. Goals and objectives	Though not at risk, our aim is to use <i>O. digyna</i> as an example for CRL-linked plant conservation.	Ensure persistence in two known locations and any that are discovered.	Maintain connectivity among populations throughout the species' range; prevent habitat destruction.	Ensure persistence in < 10 known locations and any that are discovered.
2. Climate vulnerabilities	Dependent on cool/damp and rocky alpine habitat. Climate warming will reduce non-CRL habitats.	Geomorphological change could alter essential thermal and hydrological habitat characteristics.	Poor thermoregulators, relatively low temperatures (>78°C) can be lethal. Require cool rocky refuge.	Loss of meltwater sources; potentially upstream encroachment by warmer water species.
3. Review and revise goals	In Scandinavia, <i>O. digyna</i> was identified as a rock glacier paleo-relict. Revise to include paleo-refugia in goals.	Perform new surveys; estimate population sizes; evaluate existing habitat characteristics.	Evaluate patch size and connectivity limitations; revise goals to include patch size and dispersal capacity.	Perform new surveys; assess thermal tolerance; test biological exclusion; revise goals with new findings.
4. Identify key refugia features	Abundant and thrives on all CRL features.	Characterize structural, thermal, and hydrological characteristics of known locations.	Deep rocky matrices; adjacent to vegetation; CRLs > 2 ha and within 0.5 km of other CRLs.	Streams with cold water (< 8°C) originating from CRLs. Continuing habitat assessment is needed.
5. Prioritize refugia	Design a network of paired sites (CRL and non-CRL) across the species' range for monitoring.	Designate known sites in Yosemite National Park, USA as protected for the species.	Use remote imagery and field surveys to prioritize habitat networks for conservation throughout species' range.	Designate known icy seeps in Glacier and Grand Teton National Parks, USA as protected for the species.
6. Implement actions	Initiate long-term monitoring to evaluate responses of populations in CRL versus non-CRL habitats.	Monitor known populations; continue surveying for new populations; stabilize existing habitats to prevent collapse.	Augment dispersal corridors to improve connectivity; stop or reduce livestock grazing in priority areas.	Initiate long-term monitoring of <i>Z. glacier</i> populations. Evaluate links between habitat and population change.
7. Monitor effectiveness	Document trajectories of paired populations; integrate new information and revise conservation plan as needed.	Assess if known populations are changing in size. If declining, seek to understand the cause.	Assess population sizes and dispersal capacity through time to disentangle long- and short-term dynamics.	Assess population sizes through time to disentangle long- and short-term changes.

440

441 **Figure 5.** Practical examples of how cold rocky landforms (CRLs) can be used in management for
 442 representative species from terrestrial and aquatic habitats and a range of taxonomic groups. The
 443 Climate Refugia Conservation Cycle used as guidance here is modified from Morelli et al. (2016).

444 Photograph credits (left to right): Jan Nachlinger, Jean Krejca/Zara Environmental LLC, Marshal Hedin,
 445 Joe Giersch.



447

448 **Figure 6.** (a) Today, cold rocky landforms (CRLs) are key habitats for cold-adapted species, including
 449 those typical of higher elevations and latitudes. (b) In the future, cold-adapted species may be restricted
 450 to CRLs because of alpine glacier and snowfield recession. (c) The value of CRLs in a given range will
 451 likely depend on the timeline to deglaciation. Thus, CRLs will not be as crucial as near-term refugia in
 452 mountain areas further to the right on the x-axis versus those to the left. The projections for percent
 453 glacier mass in 2100 (y-axis) are based on Representative Concentration Pathways (RCP), i.e., climate
 454 warming according to standard greenhouse gas emission scenarios [upper limits = RCP2.6 (less
 455 warming), lower limit = RCP8.4 (most warming), median = RCP4.5 (intermediate warming); see Hock et
 456 al. (2019) for additional details]. (d) Suitability of CRLs as climate refugia will depend on the interplay
 457 between climate and mountain change and climate adaptation strategies. Artwork in (a) and (b) by
 458 Vanessa Arrighi.

459 **Future research:**

460 We encourage research in the emerging field of CRL-based climate refugia, which would benefit
461 from multidisciplinary expertise including, but not limited to, geology, ecology, hydrology, and
462 climate-adaptation science. We call for a coordinated, international CRL monitoring network to
463 be established that encompasses many mountain ranges and habitat types around the world.
464 Such a network would promote long-term ecological studies, generate key data for testing
465 whether CRLs will act as climate refugia at local to global scales, and help address major
466 questions including:

467

- 468 • Do CRL types differ in their capacity to act as climate refugia in aquatic and terrestrial
469 habitats?
- 470 • Are CRLs receding more slowly than alpine glaciers and snowfields? Do slower rates of
471 change extend to CRL-linked ecosystems?
- 472 • Since aquatic habitats are naturally more decoupled from ambient warming than
473 terrestrial environments due to the greater heat capacity of water (Shah et al., 2020), will
474 the long-term persistence of cold-adapted species differ between CRL-linked aquatic
475 and terrestrial habitats?
- 476 • Given observations of relatively extreme water chemistry in lakes and ponds influenced
477 by rock glaciers, will these habitats be limited in their capacity to serve as climate
478 refugia? And, if so, will lakes and ponds fed by other CRL types be better suited to
479 acting as refugia?
- 480 • From a geographic perspective, what capacity do CRLs have to support climate refugia
481 in lesser studied (e.g., tropical) mountain ranges? Beyond mountain ecosystems at
482 lower elevations?

483

484 **Conclusions:**

485 Both historical and contemporary studies on CRLs lend support to the thesis that CRLs will
486 provide near-term climate refugia for mountain biodiversity. However, there is a pressing need
487 for more CRL research, particularly from long-term ecological perspectives. Active climate-
488 adaptation strategies at local scales may augment the natural refugial character of CRLs,
489 offering hope for cold-adapted mountain biodiversity under rapid climate change.

490

491 **Acknowledgements:**

492 This manuscript stemmed from discussions at the 2019 Society for Freshwater Science Annual
493 Meeting in Salt Lake City, UT. S.H. was supported by NSF award #OPP-1906015. C.I.M. was
494 supported by U.S. Forest Service operating funds. We thank Toni Lyn Morelli and two
495 anonymous reviewers for comments that improved the manuscript. We also thank Vanessa
496 Arrighi for providing the artwork in Figures 2 and 6.

497

498 **Author contributions:**

499 S.H., D.S.F., and C.I.M. conceived of the manuscript. S.B., S.H., and C.I.M. wrote the
500 manuscript with considerable input from A.G.F., M.H., D.H., J.E.S., and L.M.T. All authors
501 contributed edits to the final version and approved it for submission.

502

503 **References:**

504 Alexander, J. M., Chalmandrier, L., Lenoir, J., Burgess, T. I., Essl, F., Haider, S., Kueffer, C.,
505 McDougall, K., Milbau, A., & Nuñez, M. A. (2018). Lags in the response of mountain
506 plant communities to climate change. *Global Change Biology*, 24(2), 563-579.

507 <https://doi.org/10.1111/gcb.13976>

508 Anderson, R. S., Anderson, L. S., Armstrong, W. H., Rossi, M. W., & Crump, S. E. (2018).
509 Glaciation of alpine valleys: The glacier–debris-covered glacier–rock glacier continuum.
510 *Geomorphology*, 311, 127-142. <https://doi.org/10.1016/j.geomorph.2018.03.015>

511 Ashcroft, M. B. (2010). Identifying refugia from climate change. *Journal of Biogeography*, 37(8),
512 1407-1413. <https://doi.org/10.1111/j.1365-2699.2010.02300.x>

513 Benn, D., & Evans, D. J. (2014). *Glaciers and glaciation*. Routledge.

514 Birrell, J. H., Shah, A. A., Hotaling, S., Giersch, J. J., Williamson, C. E., Jacobsen, D., & Woods,
515 H. A. (2020). Insects in high-elevation streams: Life in extreme environments imperiled
516 by climate change. *Global Change Biology*, 26, 6667-6684.

517 <https://doi.org/10.1111/gcb.15356>

518 Brighenti, S., Tolotti, M., Bertoldi, M., Wharton, G., & Bruno, M. C. (in press). Rock glaciers and
519 paraglacial features influence stream invertebrates in a deglaciating alpine area.

520 *Freshwater Biology*. <https://doi.org/10.1111/fwb.13658>

521 Brighenti, S., Tolotti, M., Bruno, M. C., Engel, M., Wharton, G., Cerasino, L., Mair, V., & Bertoldi,
522 W. (2019). After the peak water: the increasing influence of rock glaciers on alpine river
523 systems. *Hydrological Processes*, 33(21), 2804-2823. <https://doi.org/10.1002/hyp.13533>

524 Brighenti, S., Tolotti, M., Bruno, M. C., Wharton, G., Pusch, M. T., & Bertoldi, W. (2019).
525 Ecosystem shifts in Alpine streams under glacier retreat and rock glacier thaw: A review.
526 *Science of The Total Environment*, 675, 542-559.
527 <https://doi.org/10.1016/j.scitotenv.2019.04.221>

528 Brown, L. E., Hannah, D. M., & Milner, A. M. (2007). Vulnerability of alpine stream biodiversity to
529 shrinking glaciers and snowpacks. *Global Change Biology*, 13(5), 958-966.
530 <https://doi.org/10.1111/j.1365-2486.2007.01341.x>

531 Burga, C. A., Frauenfelder, R., Ruffet, J., Hoelzle, M., & Kääb, A. (2004). Vegetation on Alpine
532 rock glacier surfaces: a contribution to abundance and dynamics on extreme plant
533 habitats. *Flora-Morphology, Distribution, Functional Ecology of Plants*, 199(6), 505-515.
534 <https://doi.org/10.1078/0367-2530-00179>

535 Caccianiga, M., Andreis, C., Diolaiuti, G., D'Agata, C., Mihalcea, C., & Smiraglia, C. (2011).
536 Alpine debris-covered glaciers as a habitat for plant life. *The Holocene*, 21(6), 1011-
537 1020. <https://doi.org/10.1177%2F0959683611400219>

538 Cannone, N., & Gerdol, R. (2003). Vegetation as an ecological indicator of surface instability in
539 rock glaciers. *Arctic, Antarctic, and Alpine Research*, 35(3), 384-390.
540 [https://doi.org/10.1657/1523-0430\(2003\)035\[0384:VAAEIO\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2003)035[0384:VAAEIO]2.0.CO;2)

541 Chapman, J. A., & Flux, J. E. (1990). *Rabbits, hares and pikas: status survey and conservation*
542 *action plan*. IUCN.

543 Cokendolpher, J. C., & Krejca, J. K. (2010). *A new cavernicolous Parobisium Chamberlin 1930*
544 *(Pseudoscorpiones: neobisiidae) from Yosemite National Park, USA (Vol. 297)*. Museum
545 of Texas Tech University. <https://doi.org/10.5962/bhl.title.156953>

546 Colombo, N., Salerno, F., Gruber, S., Freppaz, M., Williams, M., Fratianni, S., & Giardino, M.
547 (2018). Impacts of permafrost degradation on inorganic chemistry of surface fresh water.
548 *Global and Planetary Change*, 162, 69-83.
549 <https://doi.org/10.1016/j.gloplacha.2017.11.017>

550 Cremonese, E., Gruber, S., Phillips, M., Pogliotti, P., Böckli, L., Noetzli, J., Suter, C., Bodin, X.,
551 Crepaz, A., & Kellerer-Pirklbauer, A. (2011). An inventory of permafrost evidence for the
552 European Alps. *The Cryosphere*, 5, 651-657. [https://doi.org/doi.org/10.5194/tc-5-651-](https://doi.org/doi.org/10.5194/tc-5-651-2011)
553 [2011](https://doi.org/doi.org/10.5194/tc-5-651-2011)

554 Dobrowski, S. Z. (2011). A climatic basis for microrefugia: the influence of terrain on climate.
555 *Global Change Biology*, 17(2), 1022-1035. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2486.2010.02263.x)
556 [2486.2010.02263.x](https://doi.org/10.1111/j.1365-2486.2010.02263.x)

557 Elser, J. J., Andersen, T., Baron, J. S., Bergström, A.-K., Jansson, M., Kyle, M., Nydick, K. R.,
558 Steger, L., & Hessen, D. O. (2009). Shifts in lake N:P stoichiometry and nutrient
559 limitation driven by atmospheric nitrogen deposition. *Science*, 326(5954), 835-837.
560 <https://doi.org/10.1126/science.1176199>

561 Elser, J. J., Wu, C., González, A. L., Shain, D. H., Smith, H. J., Sommaruga, R., Williamson, C.
562 E., Brahney, J., Hotaling, S., Vanderwall, J., Yu, J., Aizen, V., Aizen, E., Battin, T. J.,
563 Camassa, R., Feng, X., Jiang, H., Lu, L., Qu, J. J., Ren, Z., Wen, J., Woods, H. A.,
564 Xiong, X., Xu, J., Yu, G., Harper, J. T., & Saros, J. E. (2020). Key rules of life and the
565 fading cryosphere: Impacts in alpine lakes and streams. *Global Change Biology*, 26,
566 6644-6656. <https://doi.org/10.1111/qcb.15362>

567 Feghel, T. S., Baron, J. S., Fountain, A. G., Johnson, G. F., & Hall, E. K. (2016). The differing
568 biogeochemical and microbial signatures of glaciers and rock glaciers. *Journal of*
569 *Geophysical Research: Biogeosciences*, 121(3), 919-932.
570 <https://doi.org/10.1002/2015JG003236>

571 Fell, S. C., Carrivick, J. L., & Brown, L. E. (2017). The multitrophic effects of climate change and
572 glacier retreat in mountain rivers. *BioScience*, 67(10), 897-911.
573 <https://doi.org/10.1093/biosci/bix107>

574 Fell, S. C., Carrivick, J. L., Kelly, M. G., Füreder, L., & Brown, L. E. (2018). Declining glacier
575 cover threatens the biodiversity of alpine river diatom assemblages. *Global Change*
576 *Biology*, 24(12), 5828-5840. <https://doi.org/10.1111/gcb.14454>

577 Fickert, T., Friend, D., Grüniger, F., Molnia, B., & Richter, M. (2007). Did debris-covered
578 glaciers serve as Pleistocene refugia for plants? A new hypothesis derived from
579 observations of recent plant growth on glacier surfaces. *Arctic, Antarctic, and Alpine*
580 *Research*, 39(2), 245-257. [https://doi.org/10.1657/1523-
581 0430\(2007\)39\[245:DDGSAP\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2007)39[245:DDGSAP]2.0.CO;2)

582 Finn, D. S., Khamis, K., & Milner, A. M. (2013). Loss of small glaciers will diminish beta diversity
583 in Pyrenean streams at two levels of biological organization. *Global Ecology and*
584 *Biogeography*, 22(1), 40-51. <https://doi.org/10.1111/j.1466-8238.2012.00766.x>

585 Finn, D. S., Räsänen, K., & Robinson, C. T. (2010). Physical and biological changes to a
586 lengthening stream gradient following a decade of rapid glacial recession. *Global*
587 *Change Biology*, 16(12), 3314-3326. <https://doi.org/10.1111/j.1365-2486.2009.02160.x>

588 Fountain, A. G., & Tangborn, W. V. (1985). The effect of glaciers on streamflow variations.
589 *Water Resources Research*, 21(4), 579-586. <https://doi.org/10.1029/WR021i004p00579>

590 Gentili, R., Baroni, C., Caccianiga, M., Armiraglio, S., Ghiani, A., & Citterio, S. (2015). Potential
591 warm-stage microrefugia for alpine plants: Feedback between geomorphological and
592 biological processes. *Ecological Complexity*, 21, 87-99.
593 <https://doi.org/10.1016/j.ecocom.2014.11.006>

594 Gentili, R., Baroni, C., Panigada, C., Rossini, M., Tagliabue, G., Armiraglio, S., Citterio, S.,
595 Carton, A., & Salvatore, M. C. (2020). Glacier shrinkage and slope processes create
596 habitat at high elevation and microrefugia across treeline for alpine plants during warm
597 stages. *Catena*, 193, 104626. <https://doi.org/10.1016/j.catena.2020.104626>

598 Giersch, J. J., Hotaling, S., Kovach, R. P., Jones, L. A., & Muhlfeld, C. C. (2017). Climate -
599 induced glacier and snow loss imperils alpine stream insects. *Global Change Biology*,
600 23(7), 2577-2589. <https://doi.org/10.1111/gcb.13565>

601 Giersch, J. J., Jordan, S., Luikart, G., Jones, L. A., Hauer, F. R., & Muhlfeld, C. C. (2015).
602 Climate-induced range contraction of a rare alpine aquatic invertebrate. *Freshwater*
603 *Science*, 34(1), 53-65. <https://doi.org/10.1086/679490>

604 Gobbi, M., Ballarin, F., Compostella, C., Lencioni, V., Seppi, R., Tampucci, D., & Caccianiga, M.
605 (2014). Physical and biological features of an active rock glacier in the Italian Alps. *The*
606 *Holocene*, 24(11), 1624-1631. <https://doi.org/10.1177%2F0959683614544050>

607 Gobbi, M., Isaia, M., & De Bernardi, F. (2011). Arthropod colonisation of a debris-covered
608 glacier. *The Holocene*, 21(2), 343-349. <https://doi.org/10.1177%2F0959683610374885>

609 Gobbi, M., & Lencioni, V. (2020). Glacial Biodiversity: Lessons from ground-dwelling and
610 aquatic insects. In *Glaciers*. IntechOpen. <https://doi.org/10.5772/intechopen.92826>

611 Gude, M., Dietrich, S., Mäusbacher, R., Hauck, C., Molenda, R., Ruzicka, V., & Zacharda, M.
612 (2003). Probable occurrence of sporadic permafrost in non-alpine scree slopes in central
613 Europe. Proceedings of the 8th International Conference on Permafrost,

614 Haeberli, W., Schaub, Y., & Huggel, C. (2017). Increasing risks related to landslides from
615 degrading permafrost into new lakes in de-glaciating mountain ranges. *Geomorphology*,
616 293, 405-417. <https://doi.org/10.1016/j.geomorph.2016.02.009>

617 Hågvar, S., Gobbi, M., Kaufmann, R., Ingimarsdóttir, M., Caccianiga, M., Valle, B., Pantini, P.,
618 Fanciulli, P. P., & Vater, A. (2020). Ecosystem Birth Near Melting Glaciers: A Review on
619 the Pioneer Role of Ground-Dwelling Arthropods. *Insects*, 11(9), 644.
620 <https://doi.org/10.3390/insects11090644>

621 Harrington, J. S., Hayashi, M., & Kurylyk, B. L. (2017). Influence of a rock glacier spring on the
622 stream energy budget and cold - water refuge in an alpine stream. *Hydrological*
623 *Processes*, 31(26), 4719-4733. <https://doi.org/10.1002/hyp.11391>

624 Hayashi, M. (2020). Alpine hydrogeology: The critical role of groundwater in sourcing the
625 headwaters of the world. *Groundwater*, 58(4), 498-510.
626 <https://doi.org/10.1111/gwat.12965>

627 Herbst, D. B., Cooper, S. D., Medhurst, R. B., Wiseman, S. W., & Hunsaker, C. T. (2018). A
628 comparison of the taxonomic and trait structure of macroinvertebrate communities
629 between the riffles and pools of montane headwater streams. *Hydrobiologia*, 820(1),
630 115-133. <https://doi.org/10.1007/s10750-018-3646-4>

631 Herbst, D. B., Cooper, S. D., Medhurst, R. B., Wiseman, S. W., & Hunsaker, C. T. (2019).
632 Drought ecohydrology alters the structure and function of benthic invertebrate
633 communities in mountain streams. *Freshwater Biology*, 64(5), 886-902.
634 <https://doi.org/10.1111/fwb.13270>

635 Hock, R., Rasul, G., Adler, C., Cáceres, B., Gruber, S., Hirabayashi, Y., Jackson, M., Kääb, A.,
636 Kang, S., Kutuzov, S., Milner, A. M., Molau, U., Morin, S., Orlove, B., Steltzer, H., Simon,
637 A., Arenson, L., Banerjee, S., Barr, I., Børquez, R., Brown, L. E., Cao, B., Carey, M.,
638 Cogley, J. G., Fischlin, A., de Sherbinin, A., Eckert, N., Geertsema, M., Hagenstand, M.,
639 Honsberg, M., Hood, E., Huss, M., Zamora, E. J., Kotlarski, S., Lefeuvre, P., Moreno, J.
640 I. L., Lundquist, J., McDowell, G., Mills, S., Mou, C., Nepal, S., Noetzli, J., Palazzi, E.,
641 Pepin, N., Rixen, C., Shahgedanova, M., Skiles, S. M., Vincent, C., Viviroli, D.,
642 Weyhenmeyer, G., Pasang, Y. S., Weyer, N., Wouters, B., Yasunari, T., You, Q., &
643 Zhang, Y. (2019). High mountain areas. *The Intergovernmental Panel on Climate*
644 *Change (IPCC)*, 2, 1-94.

645 Hotaling, S., Finn, D. S., Giersch, J. J., Weisrock, D. W., & Jacobsen, D. (2017). Climate
646 change and alpine stream biology: progress, challenges, and opportunities for the future.
647 *Biological Reviews*, 92(4), 2024-2045. <https://doi.org/10.1111/brv.12319>

648 Hotaling, S., Foley, M. E., Zeglin, L. H., Finn, D. S., Tronstad, L. M., Giersch, J. J., Muhlfeld, C.
649 C., & Weisrock, D. W. (2019). Microbial assemblages reflect environmental
650 heterogeneity in alpine streams. *Global Change Biology*, 25(8), 2576-2590.
651 <https://doi.org/10.1111/gcb.14683>

652 Hotaling, S., Giersch, J. J., Finn, D. S., Tronstad, L. M., Jordan, S., Serpa, L. E., Call, R. G.,
653 Muhlfeld, C. C., & Weisrock, D. W. (2019). Congruent population genetic structure but

654 differing depths of divergence for three alpine stoneflies with similar ecology, geographic
655 distributions, and climate change threats. *Freshwater Biology*, 64, 335-347.
656 <https://doi.org/10.1111/fwb.13223>

657 Hotaling, S., Shah, A. A., McGowan, K. L., Tronstad, L. M., Giersch, J. J., Finn, D. S., Woods,
658 H. A., Dillon, M. E., & Kelley, J. L. (2020). Mountain stoneflies may tolerate warming
659 streams: evidence from organismal physiology and gene expression. *Global Change*
660 *Biology*, 10, 5524-5538. <https://doi.org/10.1111/gcb.15294>

661 Hotaling, S., Wimberger, P. H., Kelley, J. L., & Watts, H. E. (2020). Macroinvertebrates on
662 glaciers: a key resource for terrestrial food webs? *Ecology*, 101(4), e02947.
663 <https://doi.org/10.1002/ecy.2947>

664 Ilyashuk, B. P., Ilyashuk, E. A., Psenner, R., Tessadri, R., & Koinig, K. A. (2014). Rock glacier
665 outflows may adversely affect lakes: lessons from the past and present of two
666 neighboring water bodies in a crystalline-rock watershed. *Environmental science &*
667 *technology*, 48(11), 6192-6200. <https://doi.org/10.1021/es500180c>

668 Inman, R. M., Magoun, A. J., Persson, J., & Mattisson, J. (2012). The wolverine's niche: linking
669 reproductive chronology, caching, competition, and climate. *Journal of Mammalogy*,
670 93(3), 634-644. <https://doi.org/10.1644/11-MAMM-A-319.1>

671 Jones, D. B., Harrison, S., Anderson, K., & Betts, R. (2018). Mountain rock glaciers contain
672 globally significant water stores. *Sci Rep*, 8(1), 2834. <https://doi.org/10.1038/s41598-018-21244-w>

673

674 Jones, D. B., Harrison, S., Anderson, K., & Whalley, W. B. (2019). Rock glaciers and mountain
675 hydrology: A review. *Earth-science reviews*, 193, 66-90.
676 <https://doi.org/10.1016/j.earscirev.2019.04.001>

677 Karjalainen, O., Luoto, M., Aalto, J., Etzelmüller, B., Grosse, G., Jones, B. M., Lilleøren, K. S., &
678 Hjort, J. (2020). High potential for loss of permafrost landforms in a changing climate.
679 *Environmental Research Letters*, 15(10), 104065. <https://doi.org/10.1088/1748-9326/abafd5>

680

681 Kavanaugh, D. H. (1979). Investigations on present climatic refugia in North America through
682 studies on the distributions of carabid beetles: concepts, methodology and prospectus.
683 In *Carabid Beetles* (pp. 369-381). Springer.

684 Khamis, K., Hannah, D. M., Clarvis, M. H., Brown, L. E., Castella, E., & Milner, A. M. (2014).
685 Alpine aquatic ecosystem conservation policy in a changing climate. *Environmental*
686 *Science & Policy*, 43, 39-55. <https://doi.org/10.1016/j.envsci.2013.10.004>

687 Kim, J.-S., Chung, J.-M., Kim, J.-H., Lee, W., Lee, B.-Y., & Pak, J.-H. (2016). Floristic study and
688 conservation management strategies of algific talus slopes on the Korean peninsula.
689 *Korean Journal of Plant Taxonomy*, 46(2), 213-246.
690 <https://doi.org/10.11110/kjpt.2016.46.2.213>

691 Krainer, K., Bressan, D., Dietre, B., Haas, J. N., Hajdas, I., Lang, K., Mair, V., Nickus, U., Reidl,
692 D., & Thies, H. (2015). A 10,300-year-old permafrost core from the active rock glacier
693 Lazaun, southern Ötztal Alps (South Tyrol, northern Italy). *Quaternary Research*, 83(2),
694 324-335. <https://doi.org/10.1016/j.yqres.2014.12.005>

695 La Sorte, F. A., & Jetz, W. (2010). Projected range contractions of montane biodiversity under
696 global warming. *Proceedings of the Royal Society B*, 277(1699), 3401-3410.
697 <https://doi.org/10.1098/rspb.2010.0612>

698 Lencioni, V. (2018). Glacial influence and stream macroinvertebrate biodiversity under climate
699 change: Lessons from the Southern Alps. *Science of The Total Environment*, 622, 563-
700 575. <https://doi.org/10.1016/j.scitotenv.2017.11.266>

701 Mania, I., Gorra, R., Colombo, N., Freppaz, M., Martin, M., & Anesio, A. M. (2019). Prokaryotic
702 diversity and distribution in different habitats of an alpine rock glacier-pond system.
703 *Microbial Ecology*, 78(1), 70-84. <https://doi.org/10.1007/s00248-018-1272-3>

704 Millar, C. I., D. Westfall, R., & Delany, D. L. (2014). Thermal regimes and snowpack relations of
705 periglacial talus slopes, Sierra Nevada, California, USA. *Arctic, Antarctic, and Alpine*
706 *Research*, 46(2), 483-504. <https://doi.org/10.1657/1938-4246-46.2.483>

707 Millar, C. I., Delany, D. L., Hersey, K. A., Jeffress, M. R., Smith, A. T., Van Gunst, K. J., &
708 Westfall, R. D. (2018). Distribution, climatic relationships, and status of American pikas
709 (*Ochotona princeps*) in the Great Basin, USA. *Arctic, Antarctic, and Alpine Research*,
710 50(1), e1436296. <https://doi.org/10.1080/15230430.2018.1436296>

711 Millar, C. I., & Hickman, K. (in press). Camera traps provide insights into American pika site
712 occupancy, behavior, thermal relations and associated wildlife diversity. *Western North*
713 *American Naturalist*.

714 Millar, C. I., Stephenson, N. L., & Stephens, S. L. (2007). Climate change and forests of the
715 future: managing in the face of uncertainty. *Ecological Applications*, 17(8), 2145-2151.
716 <https://doi.org/10.1890/06-1715.1>

717 Millar, C. I., & Westfall, R. D. (2008). Rock glaciers and related periglacial landforms in the
718 Sierra Nevada, CA, USA; inventory, distribution and climatic relationships. *Quaternary*
719 *International*, 188(1), 90-104. <https://doi.org/10.1016/j.quaint.2007.06.004>

- 720 Millar, C. I., & Westfall, R. D. (2019). Geographic, hydrological, and climatic significance of rock
721 glaciers in the Great Basin, USA. *Arctic, Antarctic, and Alpine Research*, 51(1), 232-249.
722 <https://doi.org/10.1080/15230430.2019.1618666>
- 723 Millar, C. I., Westfall, R. D., Evenden, A., Holmquist, J. G., Schmidt-Gengenbach, J., Franklin,
724 R. S., Nachlinger, J., & Delany, D. L. (2015). Potential climatic refugia in semi-arid,
725 temperate mountains: Plant and arthropod assemblages associated with rock glaciers,
726 talus slopes, and their forefield wetlands, Sierra Nevada, California, USA. *Quaternary*
727 *International*, 387, 106-121. <https://doi.org/10.1016/j.quaint.2013.11.003>
- 728 Morard, S., Delaloye, R., & Lambiel, C. (2010). Pluriannual thermal behaviour of low elevation
729 cold talus slopes in western Switzerland. *Geographica Helvetica*, 65, 124-134.
730 <https://doi.org/10.5194/gh-65-124-2010>
- 731 Morelli, T. L., Barrows, C. W., Ramirez, A. R., Cartwright, J. M., Ackerly, D. D., Eaves, T. D.,
732 Ebersole, J. L., Krawchuk, M. A., Letcher, B. H., & Mahalovich, M. F. (2020). Climate -
733 change refugia: biodiversity in the slow lane. *Frontiers in Ecology and the Environment*,
734 18(5), 228-234. <https://doi.org/10.1002/fee.2189>
- 735 Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T.,
736 Lundquist, J. D., Millar, C. I., Maher, S. P., & Monahan, W. B. (2016). Managing climate
737 change refugia for climate adaptation. *PLoS One*, 11(8), e0159909.
738 <https://doi.org/10.1371/journal.pone.0159909>
- 739 Muhlfeld, C. C., Cline, T. J., Giersch, J. J., Peitzsch, E., Florentine, C., Jacobsen, D., &
740 Hotaling, S. (2020). Specialized meltwater biodiversity persists despite widespread
741 deglaciation. *Proceedings of the National Academy of Sciences*, 117, 12208-12214.
742 <https://doi.org/10.1073/pnas.2001697117>
- 743 Nekola, J. C. (1999). Paleorefugia and neorefugia: the influence of colonization history on
744 community pattern and process. *Ecology*, 80(8), 2459-2473.
745 [https://doi.org/10.1890/0012-9658\(1999\)080\[2459:PANTIO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[2459:PANTIO]2.0.CO;2)
- 746 Niedrist, G. H., & Füreder, L. (2020). Real - time warming of alpine streams: (re)defining
747 invertebrates' temperature preferences. *River Research and Applications*, 1-11.
748 <https://doi.org/10.1002/rra.3638>
- 749 Park, J. S., Kim, D.-K., Kim, C. S., Oh, S., Kim, K.-H., & Oh, S.-O. (2020). The First Finding of
750 the Lichen *Solorina saccata* at an Algific Talus Slope in Korea. *Mycobiology*, 48(4), 276-
751 287. <https://doi.org/10.1080/12298093.2020.1785729>

752 Rahbek, C., Borregaard, M. K., Colwell, R. K., Dalsgaard, B., Holt, B. G., Morueta-Holme, N.,
753 Nogues-Bravo, D., Whittaker, R. J., & Fjeldså, J. (2019). Humboldt's enigma: What
754 causes global patterns of mountain biodiversity? *Science*, 365(6458), 1108-1113.
755 <https://doi.org/10.1126/science.aax0149>

756 Ren, Z., Martyniuk, N., Oleksy, I. A., Swain, A., & Hotaling, S. (2019). Ecological stoichiometry
757 of the mountain cryosphere. *Frontiers in Ecology and Evolution*, 7, 360.
758 <https://doi.org/10.3389/fevo.2019.00360>

759 Ricciardi, A., & Simberloff, D. (2009). Assisted colonization is not a viable conservation strategy.
760 *Trends in Ecology & Evolution*, 24(5), 248-253.
761 <https://doi.org/10.1016/j.tree.2008.12.006>

762 Riedel, J. L., & Larrabee, M. A. (2016). Impact of recent glacial recession on summer
763 streamflow in the Skagit River. *Northwest Science*, 90(1), 5-22.
764 <https://doi.org/10.3955/046.090.0103>

765 Rieg, L., Sailer, R., Stötter, J., & Burger, D. (2012). Vegetation cover on alpine rock glaciers in
766 relation to surface velocity and substrate. Proceedings of the Tenth International
767 Conference on Permafrost,

768 Robinson, C., Tonolla, D., Imhof, B., Vukelic, R., & Uehlinger, U. (2016). Flow intermittency,
769 physico-chemistry and function of headwater streams in an Alpine glacial catchment.
770 *Aquatic sciences*, 78(2), 327-341. <https://doi.org/10.1007/s00027-015-0434-3>

771 Rotta, F., Cerasino, L., Occhipinti-Ambrogi, A., Rogora, M., Seppi, R., & Tolotti, M. (2018).
772 Diatom diversity in headwaters influenced by permafrost thawing: First evidence from
773 the Central Italian Alps. *Advances in Oceanography and Limnology*.
774 <https://doi.org/10.4081/aiol.2018.7929>

775 Růžička, V., & Zacharda, M. (1994). Arthropods of stony debris in the Krkonoše Mountains,
776 Czech Republic. *Arctic, Antarctic, and Alpine Research*, 26(4), 332-338.
777 <https://doi.org/10.1080/00040851.1994.12003077>

778 Růžička, V., Zacharda, M., Němcová, L., Šmilauer, P., & Nekola, J. C. (2012). Periglacial
779 microclimate in low-altitude scree slopes supports relict biodiversity. *Journal of Natural*
780 *History*, 46(35-36), 2145-2157. <https://doi.org/10.1080/00222933.2012.707248>

781 Sasaki, H. (1986). Air and soil temperature affecting the distribution of plants on a wind-hole
782 site. *Ecological Review = Seitaiyaku Kenkyu*, 21(1), 21.

783 Schwartz, M. W., Hellmann, J. J., McLachlan, J. M., Sax, D. F., Borevitz, J. O., Brennan, J.,
784 Camacho, A. E., Ceballos, G., Clark, J. R., & Doremus, H. (2012). Managed relocation:

785 integrating the scientific, regulatory, and ethical challenges. *BioScience*, 62(8), 732-743.
786 <https://doi.org/10.1525/bio.2012.62.8.6>

787 Shah, A. A., Dillon, M. E., Hotaling, S., & Woods, H. A. (2020). High elevation insect
788 communities face shifting ecological and evolutionary landscapes. *Current Opinion in*
789 *Insect Science*, 41, 1-6. <https://doi.org/10.1016/j.cois.2020.04.002>

790 Siebers, A. R., Paillex, A., & Robinson, C. T. (2019). Flow intermittency influences the trophic
791 base, but not the overall diversity of alpine stream food webs. *Ecography*, 42(9), 1523-
792 1535. <https://doi.org/10.1111/ecog.04597>

793 Slemmons, K. E. H., & Saros, J. E. (2012). Implications of nitrogen-rich glacial meltwater for
794 phytoplankton diversity and productivity in alpine lakes. *Limnology and Oceanography*,
795 57(6), 1651-1663. <https://doi.org/10.4319/lo.2012.57.6.1651>

796 Smith, A. T., & Weston, M. L. (1990). *Ochotona princeps*. *Mammalian species*(352), 1-8.

797 Stefaniak, A., Robson, B., Cook, S., Clutterbuck, B., Midgley, N., & Labadz, J. (2020). Mass
798 balance and surface evolution of the debris-covered Miage Glacier, 1990-2018.
799 *Geomorphology*, 373, 107474. <https://doi.org/10.1016/j.geomorph.2020.107474>

800 Stibal, M., Bradley, J. A., Edwards, A., Hotaling, S., Zawierucha, K., Rosvold, J., Lutz, S.,
801 Cameron, K. A., Mikucki, J. A., & Kohler, T. J. (2020). Glacial ecosystems are essential
802 to understanding biodiversity responses to glacier retreat. *Nature ecology & evolution*,
803 4(5), 686-687. <https://doi.org/10.1038/s41559-020-1163-0>

804 Tampucci, D., Azzoni, R. S., Boracchi, P., Citterio, C., Compostella, C., Diolaiuti, G., Isaia, M.,
805 Marano, G., Smiraglia, C., & Gobbi, M. (2017). Debris-covered glaciers as habitat for
806 plant and arthropod species: Environmental framework and colonization patterns.
807 *Ecological Complexity*, 32, 42-52. <https://doi.org/10.1016/j.ecocom.2017.09.004>

808 Tampucci, D., Boffa, G., Mangili, F., Gobbi, M., & Caccianiga, M. (2015). Vegetation outlines of
809 two active rock glaciers with contrasting lithology. *Plant Sociology*, 52, 9-18.
810 <https://doi.org/10.7338/pls2015521/02>

811 Tampucci, D., Gobbi, M., Marano, G., Boracchi, P., Boffa, G., Ballarin, F., Pantini, P., Seppi, R.,
812 Compostella, C., & Caccianiga, M. (2017). Ecology of active rock glaciers and
813 surrounding landforms: climate, soil, plants and arthropods. *Boreas*, 46(2), 185-198.
814 <https://doi.org/10.1111/bor.12219>

815 Thaler, B., Tait, D., & Tolotti, M. (2015). Permafrost und seine Auswirkungen auf die Ökologie
816 von Hochgebirgsseen. *GEO.ALP*, 12, 183-234.

817 Tolotti, M., Cerasino, L., Donati, C., Pindo, M., Rogora, M., Seppi, R., & Albanese, D. (2020).
818 Alpine headwaters emerging from glaciers and rock glaciers host different bacterial

819 communities: Ecological implications for the future. *Science of The Total Environment*,
820 717, 137101. <https://doi.org/10.1016/j.scitotenv.2020.137101>

821 Tronstad, L. M., Hotaling, S., Giersch, J. J., Wilmot, O. J., & Finn, D. S. (2020). Headwater
822 streams fed by subterranean ice: potential climate refugia for mountain communities?
823 *Western North American Naturalist*, 3, 11.

824 Wagner, T., Pauritsch, M., Mayaud, C., Kellerer-Pirklbauer, A., Thalheim, F., & Winkler, G.
825 (2019). Controlling factors of microclimate in blocky surface layers of two nearby relict
826 rock glaciers (Niedere Tauern Range, Austria). *Geografiska Annaler: Series A, Physical*
827 *Geography*, 101(4), 310-333. <https://doi.org/10.1080/04353676.2019.1670950>

828 Ward, J. (1994). Ecology of alpine streams. *Freshwater Biology*, 32(2), 277-294.
829 <https://doi.org/10.1111/j.1365-2427.1994.tb01126.x>

830 Wilhelm, L., Singer, G. A., Fasching, C., Battin, T. J., & Besemer, K. (2013). Microbial
831 biodiversity in glacier-fed streams. *The ISME journal*, 7(8), 1651-1660.
832 <https://doi.org/10.1038/ismej.2013.44>

833 Williams, M., Knauf, M., Cory, R., Caine, N., & Liu, F. (2007). Nitrate content and potential
834 microbial signature of rock glacier outflow, Colorado Front Range. *Earth Surface*
835 *Processes and Landforms*, 32(7), 1032-1047. <https://doi.org/10.1002/esp.1455>
836