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

8  
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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).

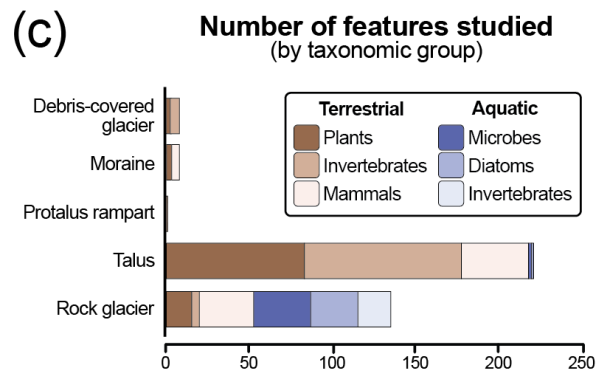
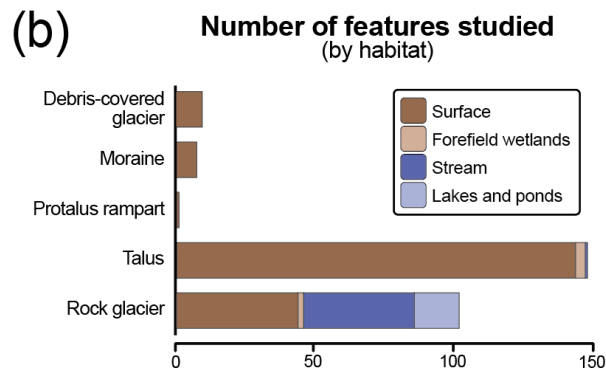
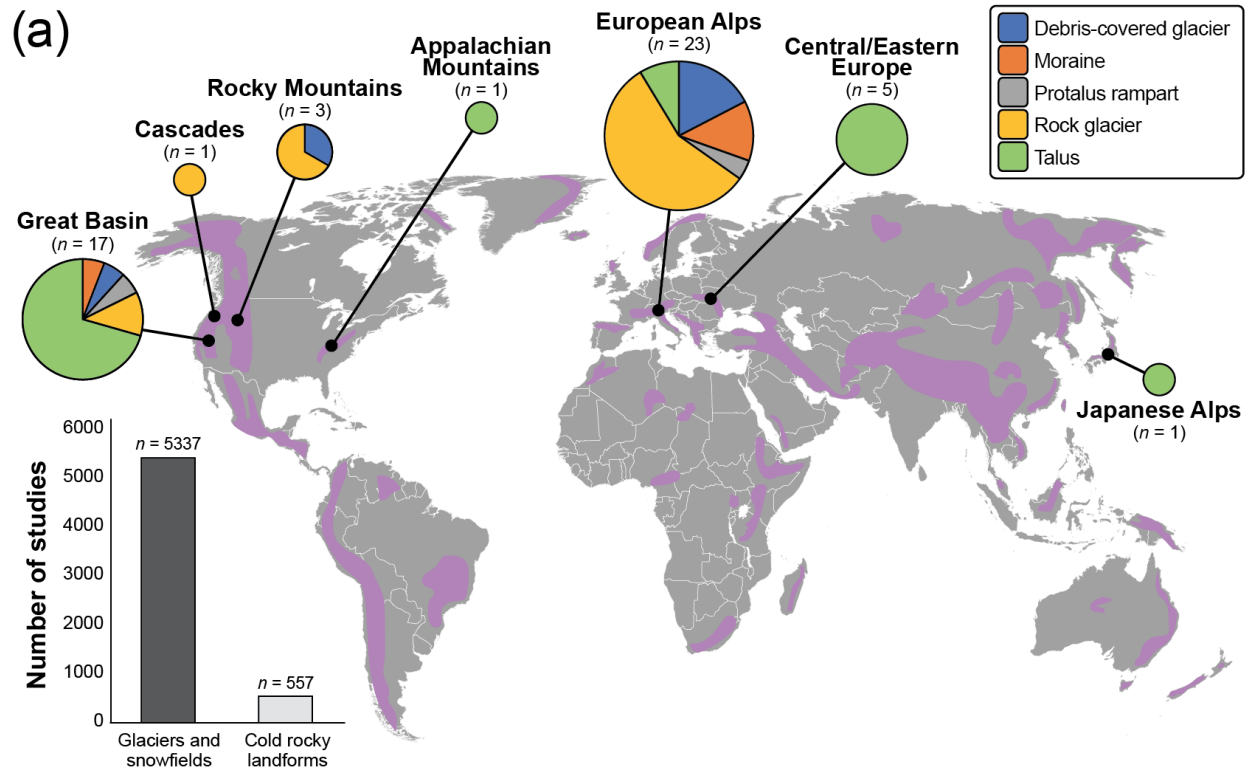
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93 Cold rocky landforms are widespread in mountainous regions, present on every continent, and  
94 greatly outnumber more well-known alpine glaciers (Jones et al., 2018). Structurally, CRLs  
95 typically have a surface mantle of rocky debris and 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).

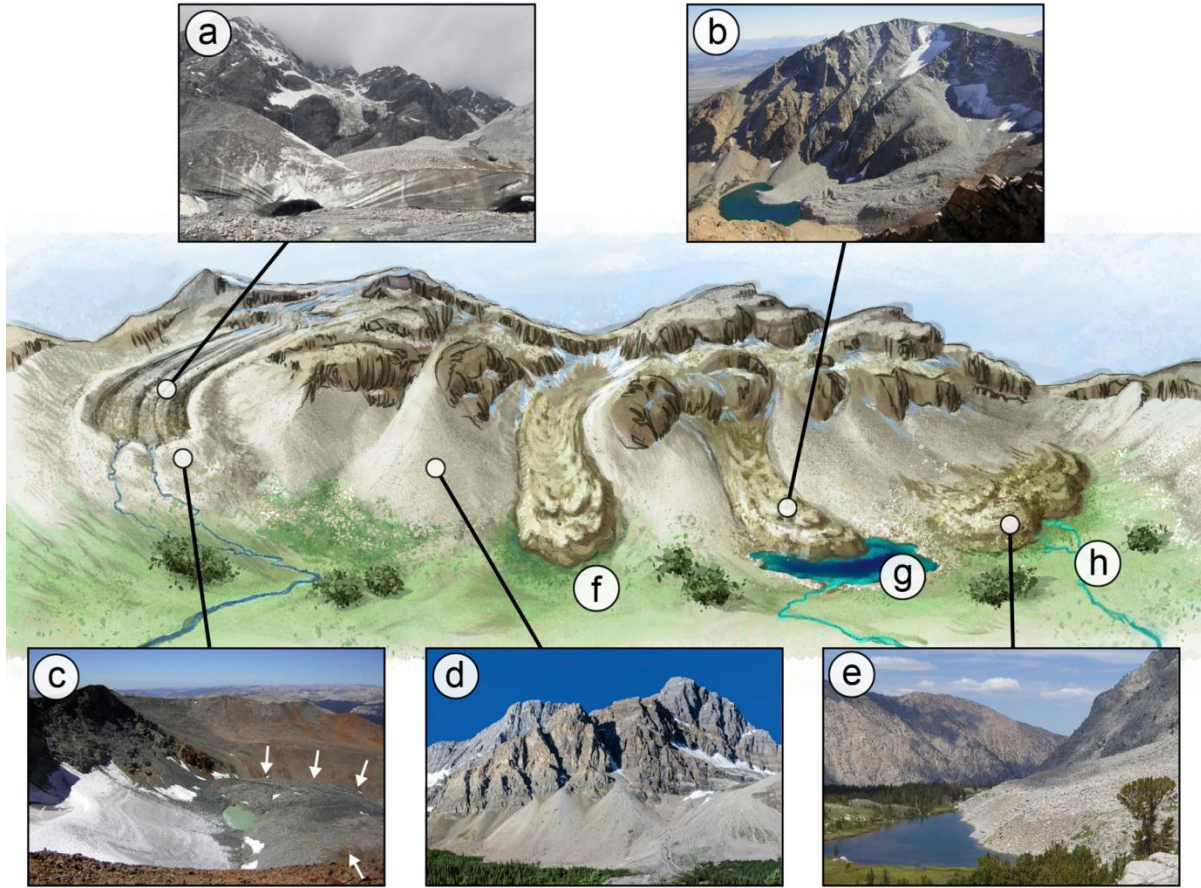
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113 One strategy for mitigating the effects of climate change on biodiversity is the identification and  
114 management of climate refugia (Morelli et al., 2020). Climate refugia are areas large enough to  
115 support populations of imperiled species 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.



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**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).

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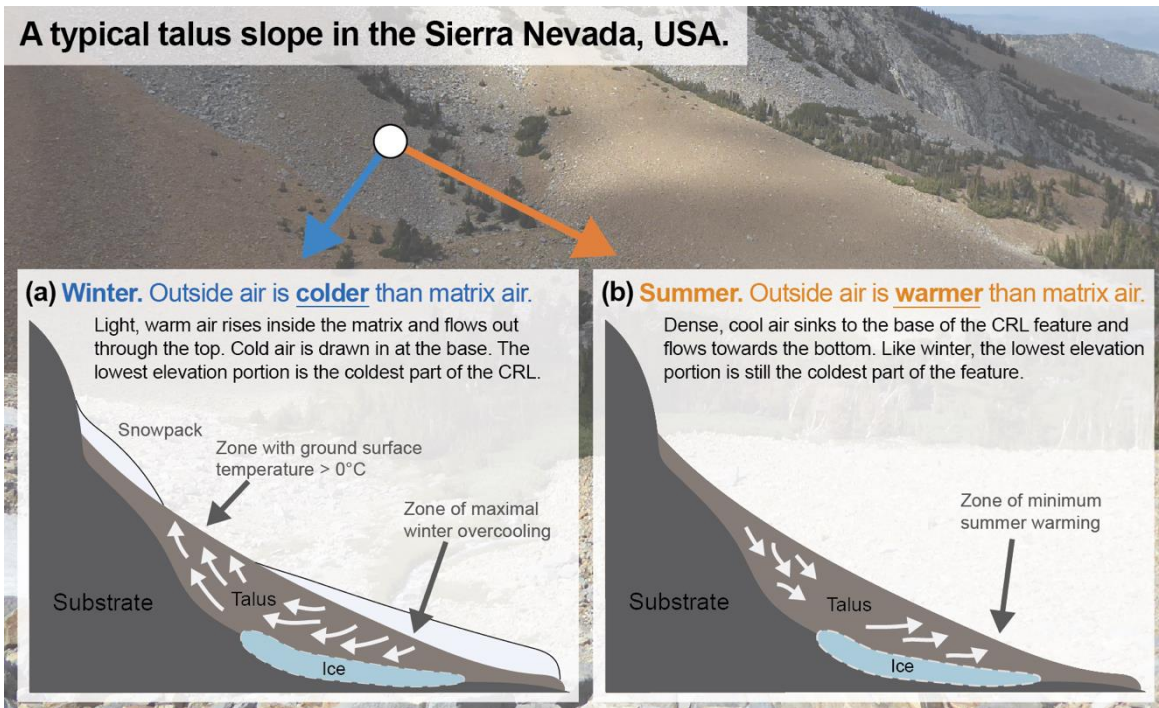
207 CRLs are important to the life history of many mammals and other vertebrates, including the  
208 iconic CRL-dependent mammal, the American pika (*Ochotona princeps*), a small relative of  
209 rabbits that is widespread in western North America (Smith & Weston, 1990). Pikas are poor  
210 thermoregulators 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).

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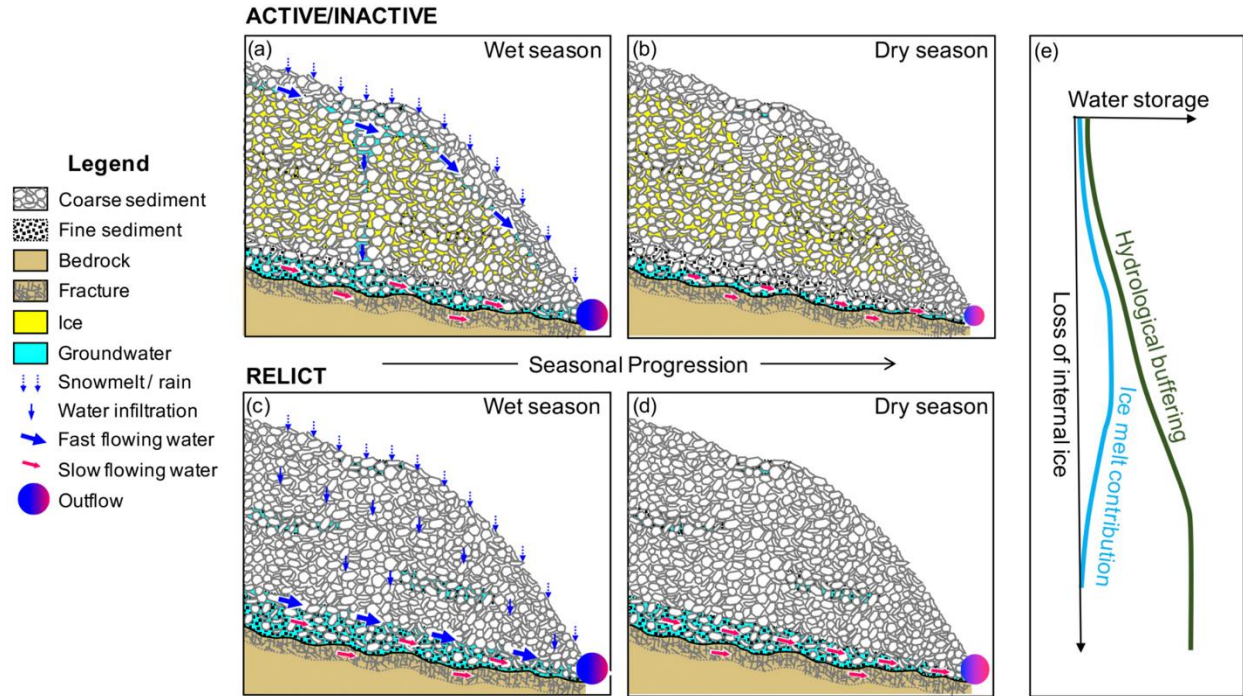
#### 224 *Forefield wetlands*

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).



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**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  $\sim 10$ - $100$  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).



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256

257 **Figure 4.** Cold rocky landforms (CRLs) act as mountain aquifers as they partially store groundwater in  
 258 their mantles that is recharged by snowmelt and rainfall, and slowly release it into nearby habitats. These  
 259 natural reservoirs greatly contribute to local water storage in areas once considered to be “teflon basins”  
 260 where precipitation would be quickly exported to the lowlands (Hayashi, 2020). When a CRL has ice filling  
 261 voids (a-b; active = moving, inactive = no longer moving), the ice does not allow water to flow through,  
 262 causing relatively fast flow of groundwater over the ice surface. Some groundwater may still flow through  
 263 to the CRL bottom and the base may be underlain by fractured bedrock that conducts water. (b)  
 264 Groundwater at the base has relatively slow flow and sustains outflows into springs and nearby habitats  
 265 even during dry periods. Many CRLs formed when the climate was much colder than the present and do  
 266 not contain internal ice (c-d, relict landforms). (e) As landforms transition to relicts under climate change,  
 267 their water storage capacity will increase as more snowmelt and rainwater infiltrates (e.g., c) and flows  
 268 through the coarse sediments near the bottom (fast flow), and the fine sediments and fractured rock in the  
 269 bottom zone (slow flow). In relict CRLs, increased water storage in the bottom layer sustains a higher  
 270 amount of dry-season outflow into springs. For this reason, relict landforms may actually have an  
 271 increased capacity for hydrological buffering when compared to those with internal ice (d-e). The  
 272 meltwater contribution from internal ice generally represents a relatively minor fraction (less than 5%) of  
 273 dry-season groundwater discharge from CRLs (Krainer et al., 2015). However, this fraction will become  
 274 increasingly important during drier and warmer summers, particularly in semi-arid mountain regions where  
 275 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)

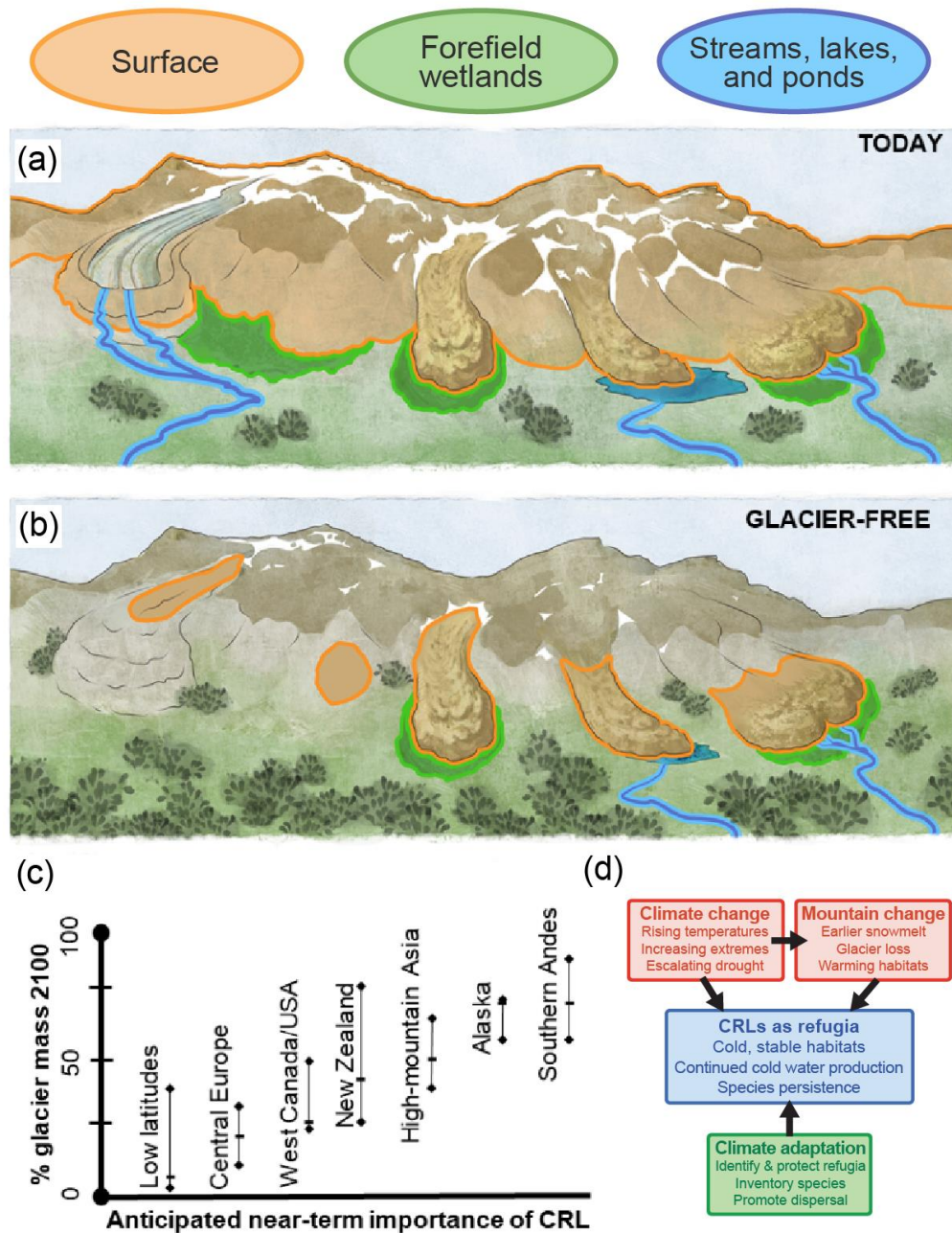
				
<b>Species</b>	Alpine mountain sorrel ( <i>Oxyria digyna</i> )	Yosemite cave pseudoscorpion ( <i>Parobisium yosemite</i> )	American pika ( <i>Ochotona princeps</i> )	Western glacier stonefly ( <i>Zapada glacier</i> )
<b>Category</b>	Terrestrial plant	Terrestrial invertebrate	Terrestrial mammal	Aquatic invertebrate
<b>Geographic region</b>	Northern Hemisphere: Arctic/montane areas	North America: southwestern United States	Western North America: montane areas	North America: northwestern United States
<b>Non-CRL vulnerabilities</b>	None are known	Biologically rare; stochastic loss of habitat	Stochastic loss of habitat; small population sizes; livestock encroachment	Biologically rare; habitat degradation
<b>Existing protections</b>	None	None	None	Listed as Threatened under the U.S. Endangered Species Act
<b>Key CRL habitat</b>	Taluses and rock glaciers	Granitic talus caves and void spaces	Taluses and rock glaciers	Icy seeps
<b>1. Goals and objectives</b>	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.
<b>2. Climate vulnerabilities</b>	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.
<b>3. Review and revise goals</b>	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.
<b>4. Identify key refugia features</b>	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.
<b>5. Prioritize refugia</b>	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.
<b>6. Implement actions</b>	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.
<b>7. Monitor effectiveness</b>	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

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499 S.H., D.S.F., and C.I.M. conceived of the manuscript. S.B., S.H., and C.I.M. wrote the  
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501 contributed edits to the final version and approved it for submission.

502

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