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

Stefano Brighenti[1,*], Scott Hotaling[2,*], Debra S. Finn[3], Andrew G. Fountain[4], Masaki Hayashi[5], David Herbst[6], Jasmine E. Saros[7], Lusha M. Tronstad[8], and Constance I. Millar[9]

Affiliations:

[1] Faculty of Science and Technology, Free University of Bozen-Bolzano, Bolzano, Italy
[2] School of Biological Sciences, Washington State University, Pullman, WA, USA
[3] Department of Biology, Missouri State University, Springfield, MO, USA
[4] Department of Geology, Portland State University, Portland, OR, USA
[5] Department of Geoscience, University of Calgary, Calgary, AB, Canada
[6] Sierra Nevada Aquatic Research Laboratory and Institute of Marine Sciences, University of California, Santa Cruz, CA, USA
[7] School of Biology and Ecology, Climate Change Institute, University of Maine, Orono, ME, USA
[8] Wyoming Natural Diversity Database, University of Wyoming, Laramie, WY, USA
[9] Pacific Southwest Research Station, USDA Forest Service, Albany, CA, USA
* *Contributed equally*

Correspondence:

Scott Hotaling, School of Biological Sciences, Washington State University, Pullman, WA, USA;
Phone: (828) 507-9950; Email: Scott.Hotaling@wsu.edu; ORCID: 0000-0002-5965-0986

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Abstract:

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

Introduction:

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

As a result of climate warming, winter snowlines are shifting to higher elevations, and melt seasons are beginning earlier and concluding later (Hock et al., 2019). During warm periods, glaciers and snowfields are crucial for mountain hydrology as they yield large volumes of cold water thereby buffering the effects of climate warming, at least for aquatic biota (Fountain & Tangborn, 1985; Hotaling et al., 2017). Through alterations to melt timing and seasonal snow accumulation, climate change will extend harsh summer conditions when terrestrial and aquatic habitats are at their warmest and driest (e.g., Riedel & Larrabee, 2016). In the long-term, ice-containing landforms (e.g., glaciers, snowfields, rock glaciers) and their water storage potential will fade, reducing habitat for cold-adapted species (Hock et al., 2019). As snow and ice recede, water temperatures will increase (Niedrist & Füreder, 2020) and formerly perennial streams may become intermittent or dry entirely (Herbst et al., 2019). Similarly, a reduction in groundwater input due to declines in snowmelt recharge (Hayashi, 2020) will stress wetland and meadow vegetation, which may impact cold-adapted animals that depend on them, creating additional stresses beyond rising temperature alone.

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

Cold rocky landforms are widespread in mountainous regions, present on every continent, and greatly outnumber more well-known alpine glaciers (Jones et al., 2018). Structurally, CRLs typically have a surface mantle of rocky debris and interiors composed of ice and rock. Their rocky mantles insulate and decouple CRL interiors from outside air and promote internal thermal regimes that support ice accumulation and retention (Morard et al., 2010). For these reasons, CRLs are expected to respond to climate change more slowly than their surface ice counterparts (Anderson et al., 2018; Stefaniak et al., 2020). With sub-freezing interiors, CRLs have the capacity to store percolated snowmelt and rain as ice, and release meltwater into springs and lakes during warm and dry periods (Hayashi, 2020; Jones et al., 2019). Thus, CRLs comprise and sustain key cold habitats in regions that are otherwise warm and dry, where winter snow is scarce or absent, and/or where glaciers and perennial snowfields are rare. For instance, in the semi-arid mountains of the Great Basin, USA, rock glaciers account for over 90% of the total water stored as ice (Millar & Westfall, 2019). While our focus here is on CRLs in mountain ecosystems, habitats exhibiting many of the same characteristics are present at lower elevations, including at mid-latitudes where average air temperatures are above freezing. Often called “algific talus slopes”, these habitats are Pleistocene relicts with persistent subsurface ice and associated cold surface conditions. Algific talus slopes have been documented in North America, Europe, and Asia (e.g., Kim et al., 2016; Nekola, 1999; Park et al., 2020; Růžička et al., 2012).

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

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

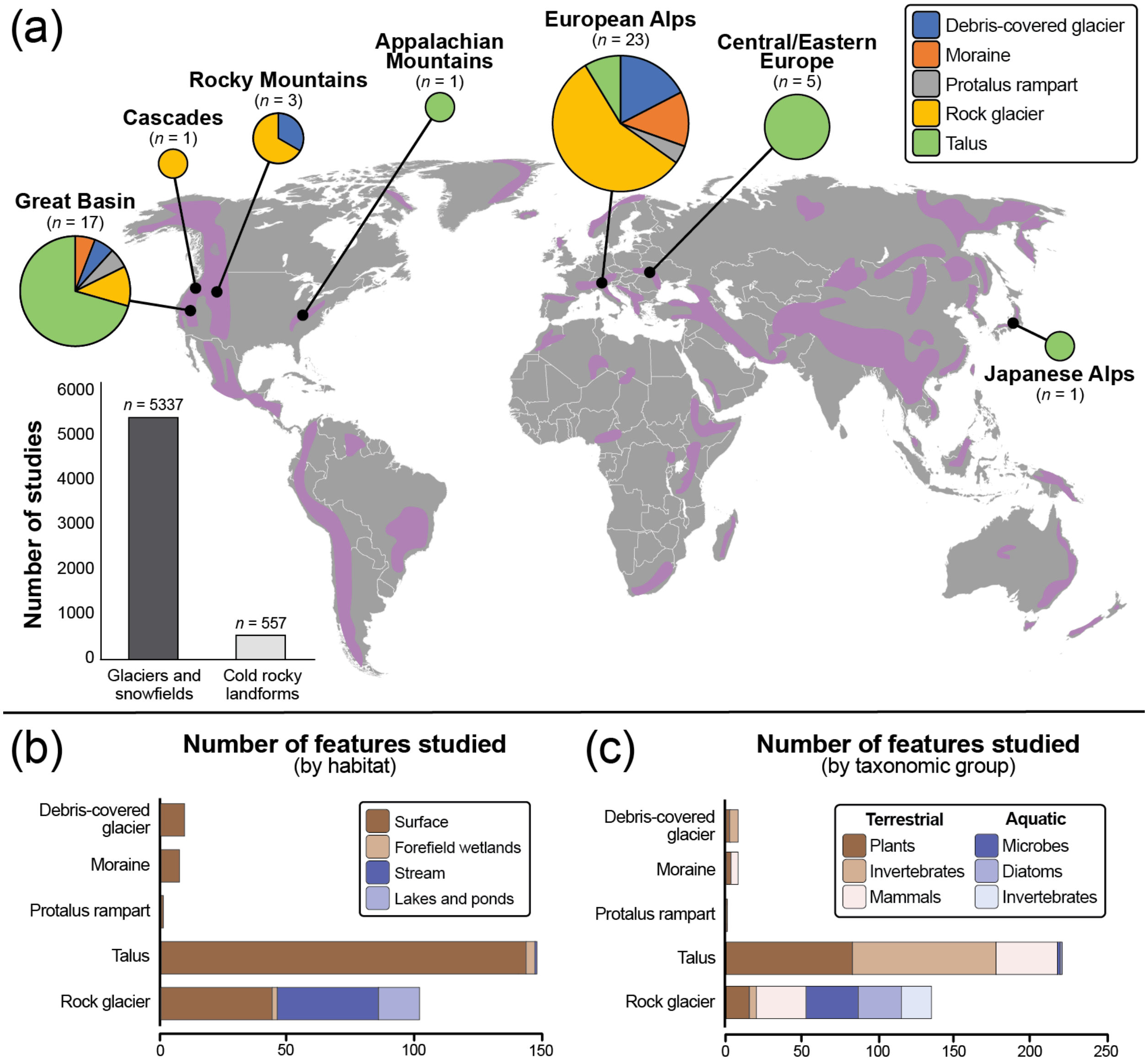


Figure 1. (a) A global representation of ecological studies on cold rocky landforms (CRLs) in mountain ecosystems. Pie chart area reflects the total number of studies for each montane region (given as *n* below each name). Purple shading indicates mountainous areas (adapted from Rahbek et al., 2019).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

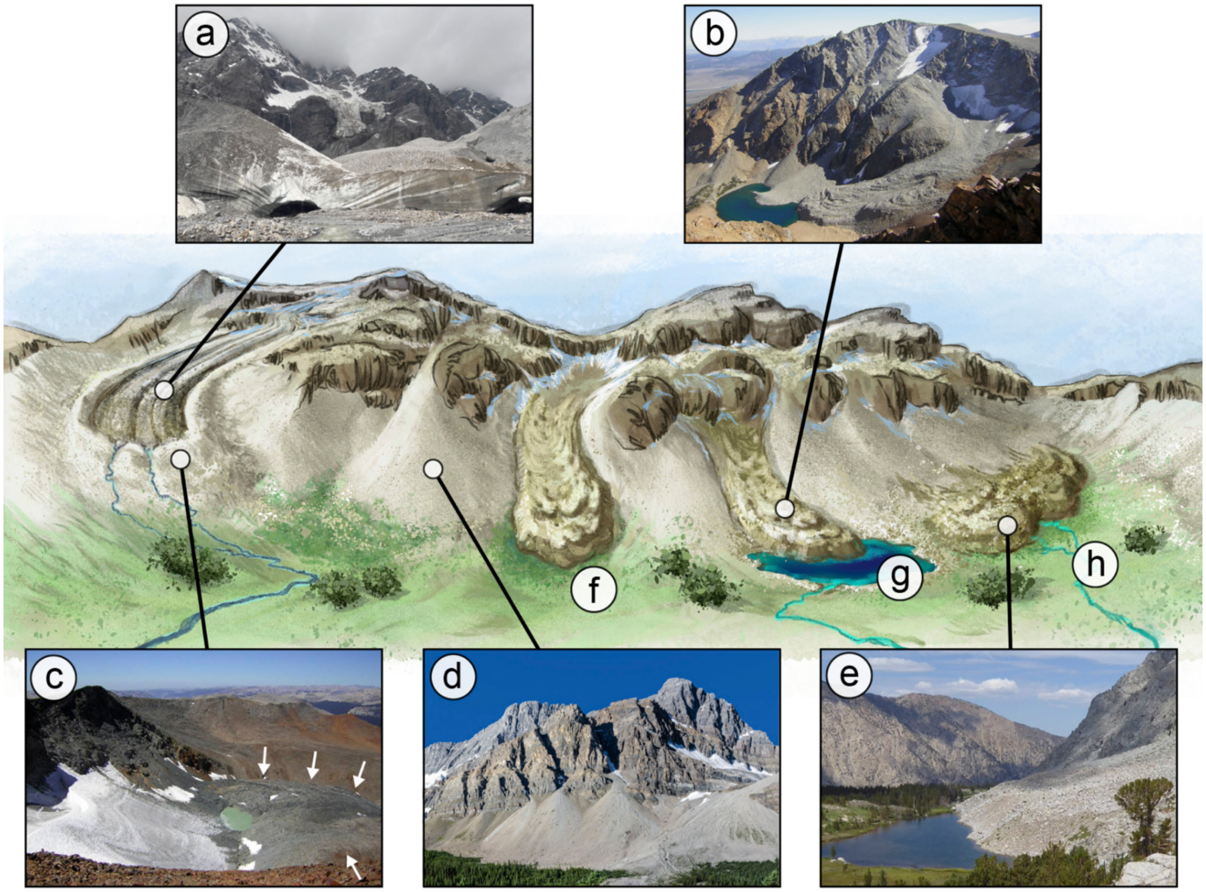


Figure 2. Cold rocky landforms (CRLs) are composed of rocky debris, ice, and water, and have diverse origins and appearances. When an alpine glacier becomes covered with rock and soil, it transitions to a (a) debris-covered glacier which still contains substantial amounts of ice. The debris cover insulates 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.

Cold habitats for biodiversity:

Surface habitats

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

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

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

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

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

Forefield wetlands

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

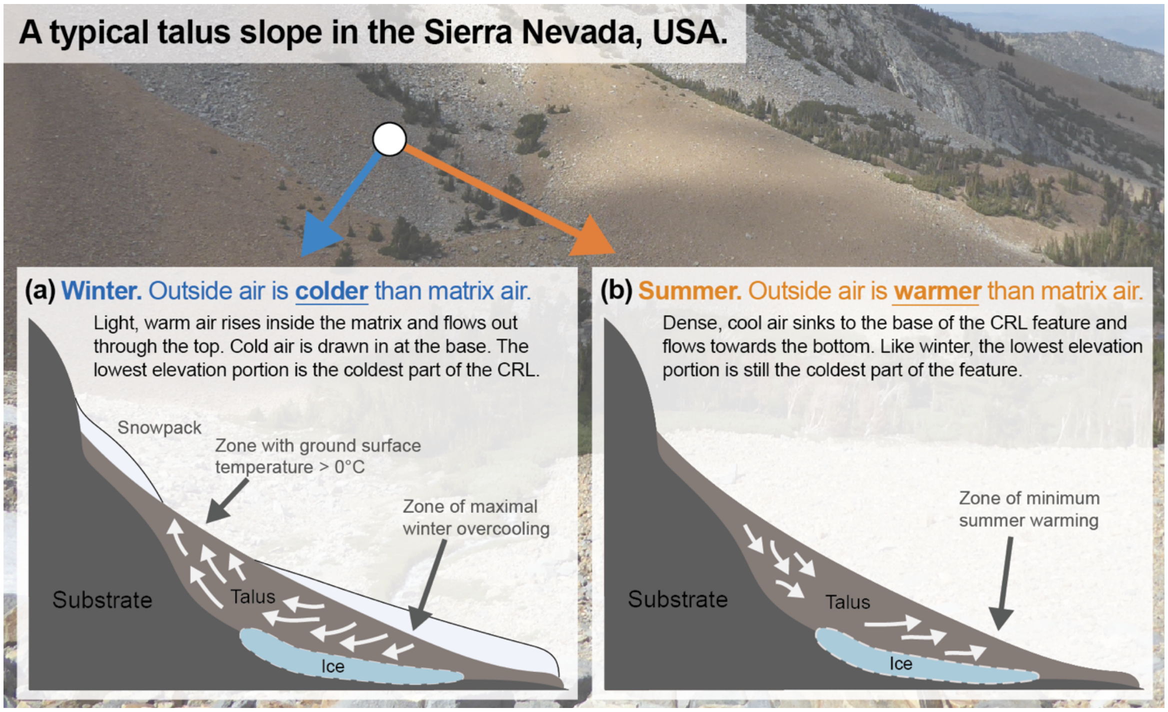


Figure 3. Unique properties and processes keep cold rocky landforms (CRLs) cold year-round. Natural convection ventilates the rocky matrix, creating a seasonally reversible circulation pattern (Morard et al., 2010). (a) In winter, outside air is colder than air inside the CRL. As cold air is drawn in 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).

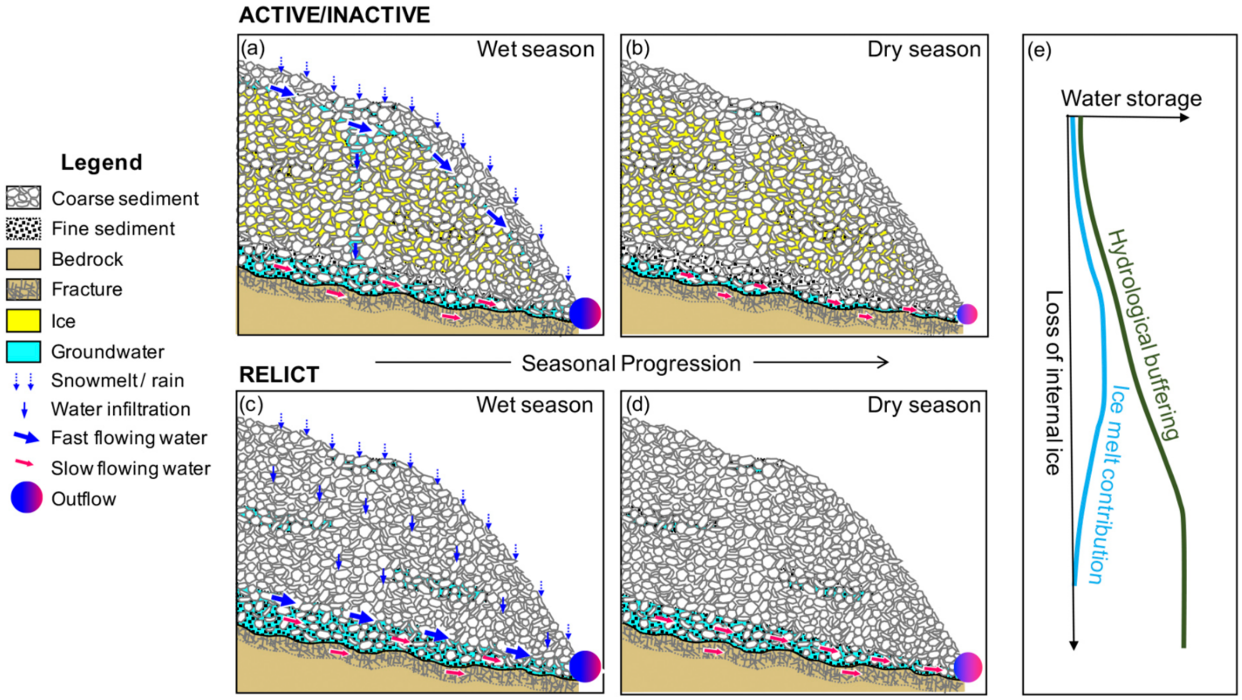


Figure 4. Cold rocky landforms (CRLs) act as mountain aquifers as they partially store groundwater in their mantles that is recharged by snowmelt and rainfall, and slowly release it into nearby habitats. These natural reservoirs greatly contribute to local water storage in areas once considered to be "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.

Streams

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

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

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

Lakes and ponds

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

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

Lessons from the past:

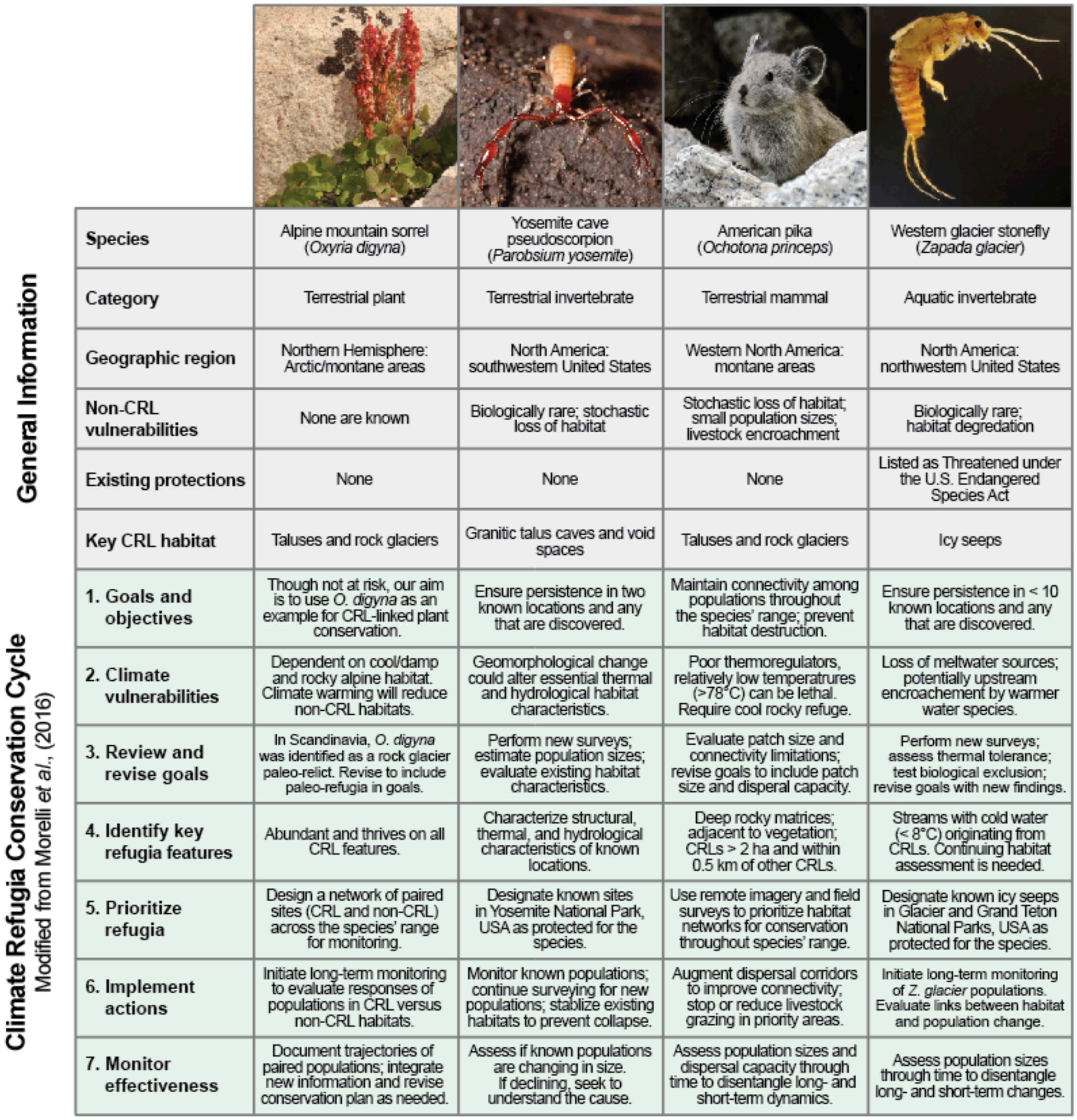
Geomorphological, hydrological, and ecological evidence supports the thesis that CRLs can offset warming and water shortages in mountain ecosystems, and act as global climate refugia for cold-adapted terrestrial and aquatic biota (Figures 1-2). Paleohistoric studies highlight the long-term stability and refugial nature of CRLs, allowing cold-adapted species to persist for as long as 10,000 years during the Holocene. For instance, on both debris-covered glaciers in western North America and taluses of central Europe, plants and arthropods that were widespread during cold intervals of the Pleistocene are now restricted to CRLs (Fickert et al., 2007; Růžička & Zacharda, 1994). This paleo-refugia hypothesis suggests that as climates warmed after the last glacial period, cold-adapted species were generally forced to track suitable habitat conditions to higher latitudes and/or elevations. CRLs, however, maintained cooler conditions and persisted as cold habitat islands. Today, we see continuing evidence of this pattern with elevationally or latitudinally disjunct populations of some species in CRL-linked habitats (Fickert et al., 2007; Růžička & Zacharda, 1994). Thus, evidence from both the past and present strengthens the prediction that CRLs will sustain long-lasting cold refugia under contemporary climate change (Caccianiga et al., 2011; Gobbi et al., 2014; Millar et al., 2015; Tampucci, Gobbi, et al., 2017; but see Karjalainen et al., 2020).

Looking to the future:

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

However, identifying *in situ* habitats that will retain cold conditions and serve as climate refugia can be difficult (Figure 5; Morelli et al., 2020; Morelli et al., 2016). While advances have been made in predicting topographic and landscape features that support cool micro-climates (Dobrowski, 2011), CRLs can be readily identified via satellite imagery and aerial photography due to their distinct geomorphology (e.g., Cremonese et al., 2011). For aquatic habitats, however, remote sensing has practical limitations. First, while CRL-associated lakes and ponds can be readily detected by satellite imagery when seasonal snow is minimized, icy seeps are typically small and easily overlooked. Subsurface flows and the presence of potentially key aquifers are also impossible to detect with satellite imagery. Second, remote sensing-based assessments of *in situ* aquatic conditions are limited. Quantifying thermal regimes as well as the biological and chemical settings of CRLs thus requires field-based surveys, ideally paired with long-term monitoring. Indeed, measuring water temperature may be an inexpensive tool for identifying CRL-based refugia, especially when combined with satellite imagery showing a lack of visible ice or snow upstream (Brighenti, Tolotti, Bruno, Engel, et al., 2019; Hotaling, Foley, et al., 2019). When considering the long-term viability of CRL-influenced climate refugia, the distribution and type of CRL is important. Microclimatological factors such as solar exposure and snow accumulation favors the occurrence of CRLs on north-facing slopes or slopes subjected to wind scouring of snow (Wagner et al., 2019). Therefore, slope aspect and physical setting in relation to microclimate can be used to identify key areas for protected habitat (Millar & Westfall, 2019). Along with aspect, the composition of CRLs in terms of ice content and their topography may also affect how they sustain flows to downstream biological communities when other sources are lost (Hayashi, 2020).

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



General Information	**Species**	Alpine mountain sorrel (*Oxyria digyna*)	Yosemite cave pseudoscorpion (*Parobsium yosemite*)	American pika (*Ochotona princeps*)	Western glacier stonefly (*Zapada glacier*)
	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 degredation
	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
Climate Refugia Conservation Cycle Modified from Morelli *et al.*, (2016)	**1. Goals and objectives**	Though not at risk, our aim is to use *O. digyna* 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 temperatrures (>78°C) can be lethal. Require cool rocky refuge.	Loss of meltwater sources; potentially upstream encroachement by warmer water species.
	3. Review and revise goals	In Scandinavia, *O. digyna* 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 disperal 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; stablize existing habitats to prevent collapse.	Augment dispersal corridors to improve connectivity; stop or reduce livestock grazing in priority areas.	Initiate long-term monitoring of *Z. glacier* 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.

Figure 5. Practical examples of how cold rocky landforms (CRLs) can be used in management for representative species from terrestrial and aquatic habitats and a range of taxonomic groups. The Climate Refugia Conservation Cycle used as guidance here is modified from Morelli et al. (2016). Photograph credits (left to right): Jan Nachlinger, Jean Krejca/Zara Environmental LLC, Marshal Hedin, Joe Giersch.

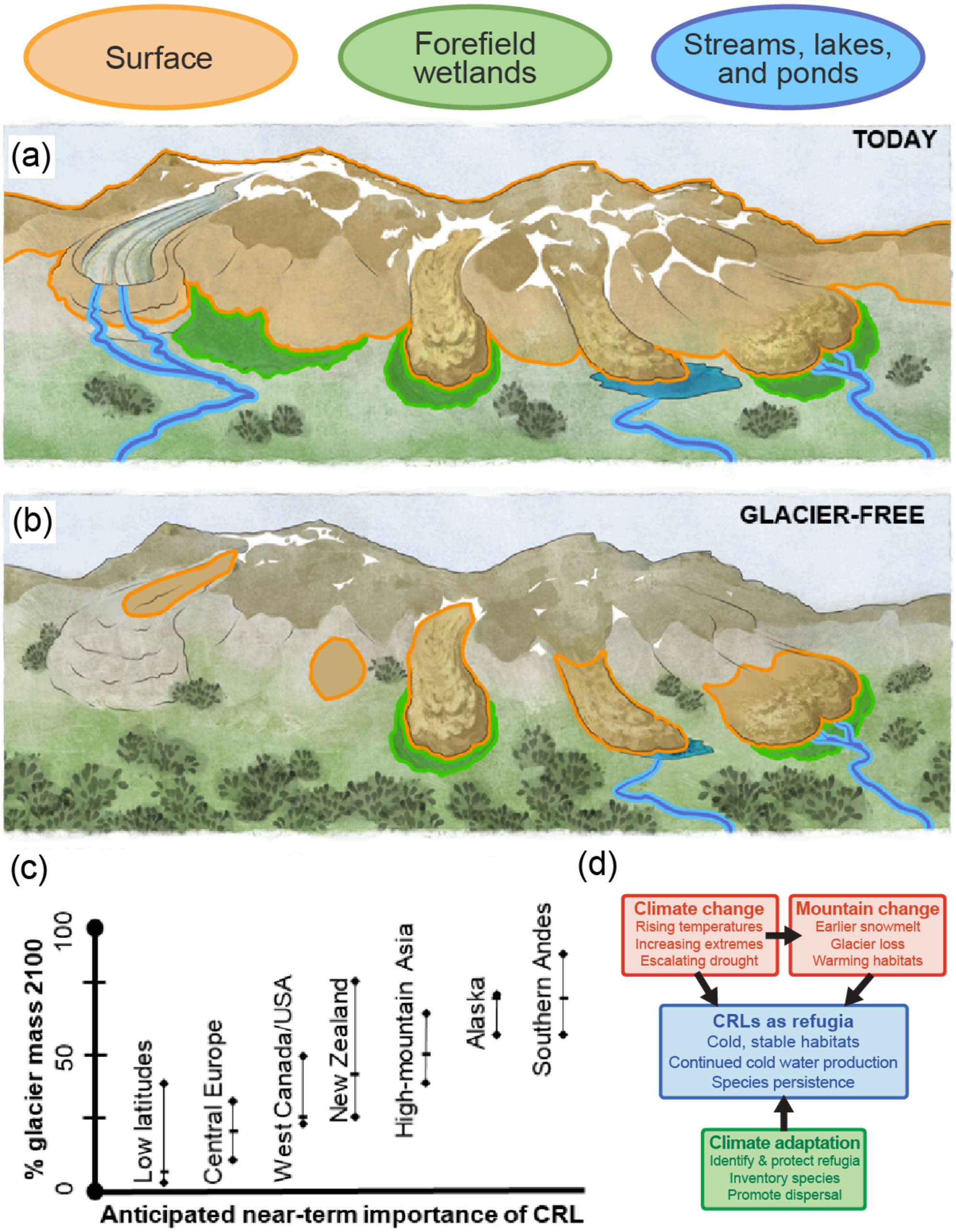


Figure 6. (a) Today, cold rocky landforms (CRLs) are key habitats for cold-adapted species, including those typical of higher elevations and latitudes. (b) In the future, cold-adapted species may be restricted to CRLs because of alpine glacier and snowfield recession. (c) The value of CRLs in a given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

Future research:

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

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

Conclusions:

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

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Author contributions:

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

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