


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

Stefano Brighenti<sup>1</sup> | Scott Hotaling<sup>2</sup>  | Debra S. Finn<sup>3</sup> | Andrew G. Fountain<sup>4</sup> | Masaki Hayashi<sup>5</sup> | David Herbst<sup>6</sup> | Jasmine E. Saros<sup>7</sup> | Lusha M. Tronstad<sup>8</sup> | Constance I. Millar<sup>9</sup> 

<sup>1</sup>Faculty of Science and Technology, Free University of Bozen-Bolzano, Bolzano, Italy

<sup>2</sup>School of Biological Sciences, Washington State University, Pullman, WA, USA

<sup>3</sup>Department of Biology, Missouri State University, Springfield, MO, USA

<sup>4</sup>Department of Geology, Portland State University, Portland, OR, USA

<sup>5</sup>Department of Geoscience, University of Calgary, Calgary, AB, Canada

<sup>6</sup>Sierra Nevada Aquatic Research Laboratory and Institute of Marine Sciences, University of California, Santa Cruz, CA, USA

<sup>7</sup>School of Biology and Ecology, Climate Change Institute, University of Maine, Orono, ME, USA

<sup>8</sup>Wyoming Natural Diversity Database, University of Wyoming, Laramie, WY, USA

<sup>9</sup>Pacific Southwest Research Station, USDA Forest Service, Albany, CA, USA

## Correspondence

Scott Hotaling, School of Biological Sciences, Washington State University, Pullman, WA, USA.  
Email: Scott.Hotaling@wsu.edu

## Funding information

NSF, Grant/Award Number: OPP-1906015; U.S. Forest Service

## Abstract

Mountains are global biodiversity hotspots where cold environments and their associated ecological communities are 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 show that CRLs will likely act as key climate refugia for terrestrial and aquatic biodiversity in mountain ecosystems, offer guidelines for incorporating CRLs into conservation practices, and identify areas for future research.

## KEYWORDS

alpine stream, biodiversity monitoring, climate adaptation, climate change ecology, debris-covered glacier, icy seeps, mountain hydrology, talus slope

## 1 | 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 snow (Hock et al., 2019). Globally, mountains are biodiversity hotspots (Rahbek et al., 2019) due to high

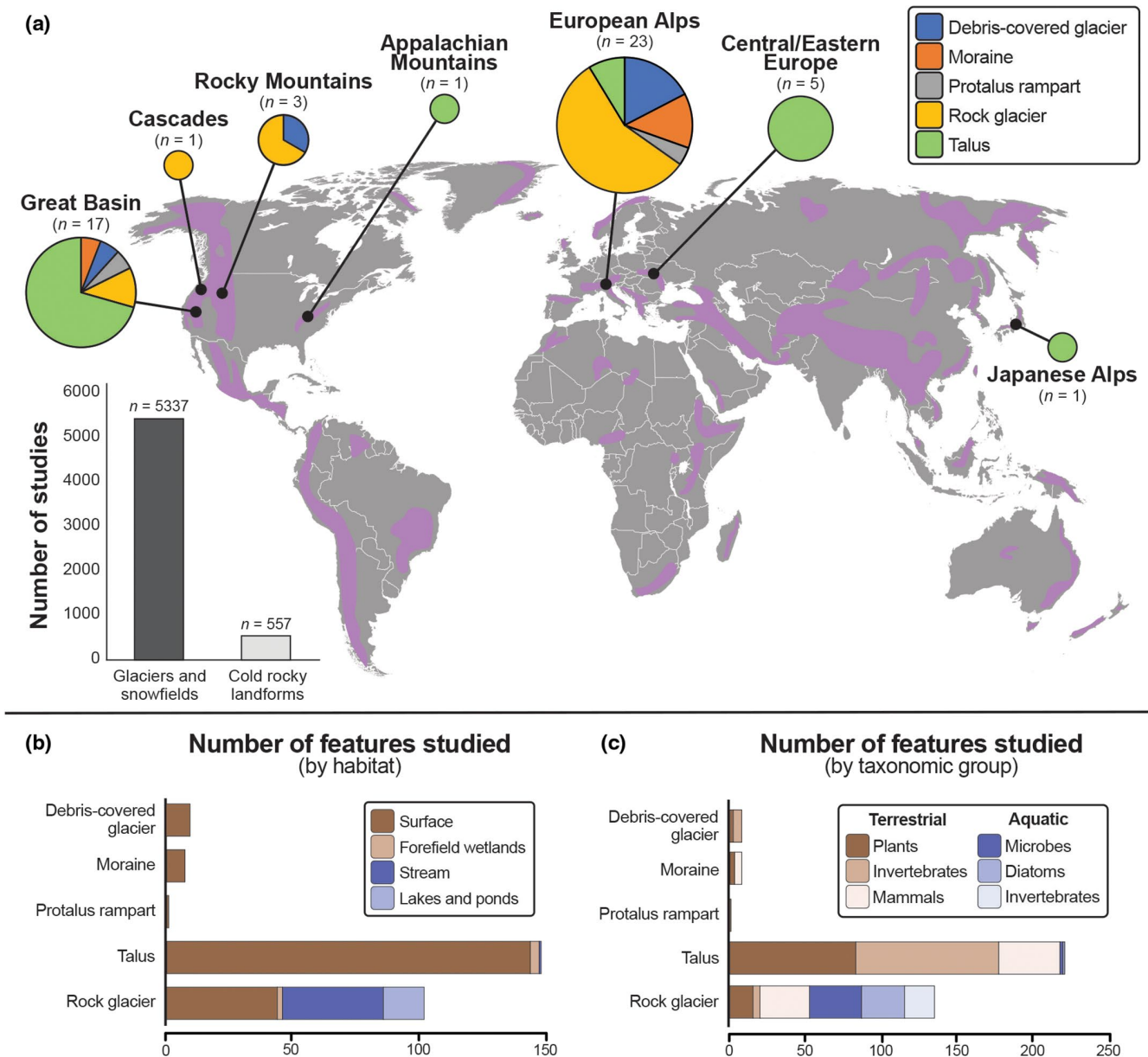
rates of local endemism driven by a combination of habitat isolation and adaptation to cold conditions (Muhlfeld et al., 2020; Smith & Weston, 1990). Many microbes, plants, and animals in terrestrial and aquatic environments are associated with glaciers and other cold habitats (Gobbi & Lencioni, 2020; Hågvær et al., 2020; Hotaling, Foley, et al., 2019; Lencioni, 2018). Thus, the rapid contemporary warming of mountain ecosystems is projected to threaten cold-adapted biodiversity worldwide (Brighenti, Tolotti, Bruno, Wharton,

Stefano Brighenti and Scott Hotaling contributed equally.

et al., 2019; Hågvær et al., 2020; Hotaling et al., 2017, 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 ending 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 habitats are at their warmest and driest (e.g., Riedel & Larrabee, 2016). In the long term under continued warming, all ice-containing landforms (e.g., glaciers, snowfields, and even rock glaciers) will lose their persistent ice and their water storage potential will fade, reducing habitat for cold-adapted species (Hock et al., 2019). As snow and ice recede, water temperatures increase (e.g., Niedrist & Füreder, 2020) and formerly perennial streams may become intermittent or dry entirely (Herbst et al., 2019). Similarly, a reduction in groundwater input



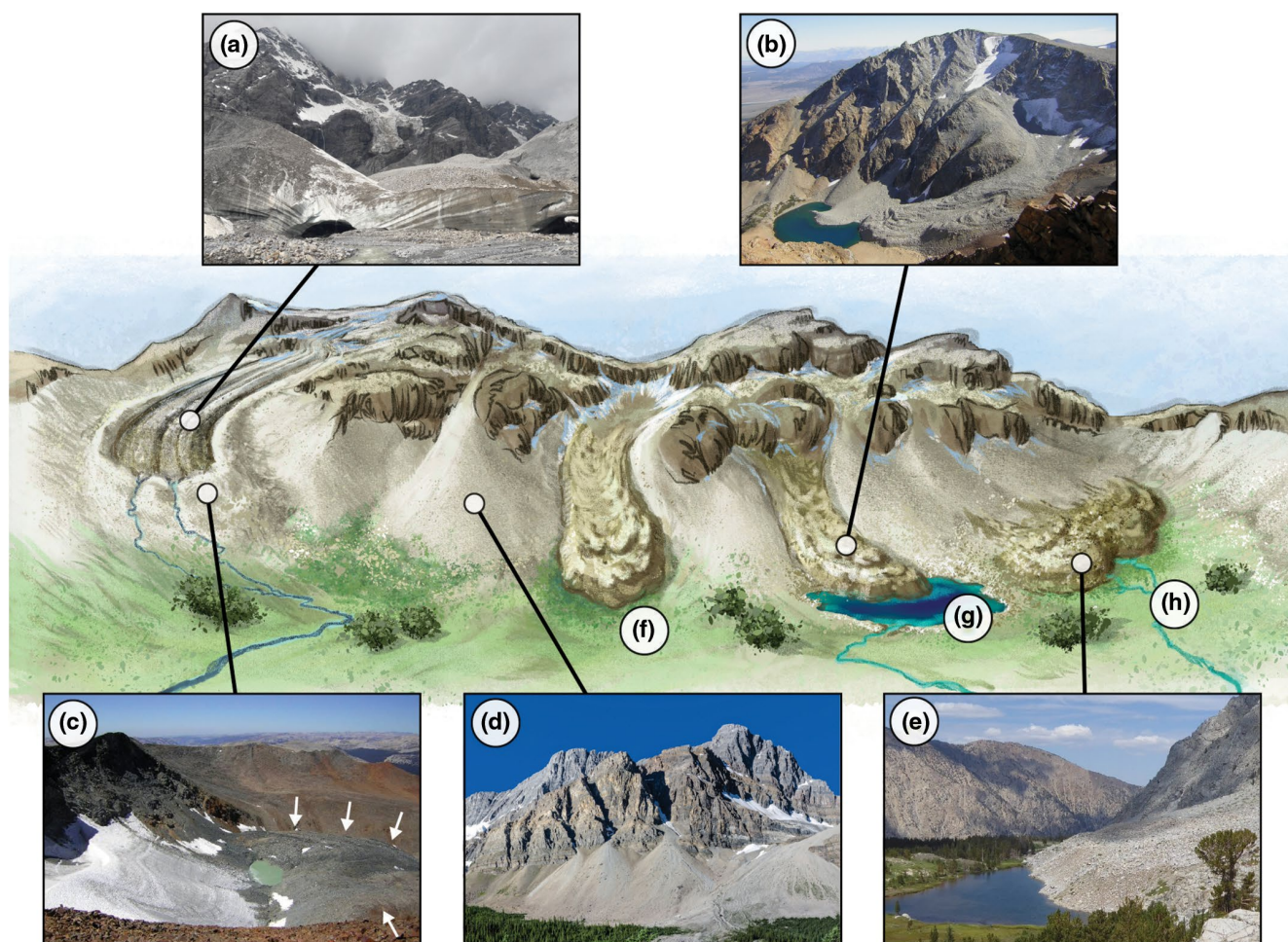
**FIGURE 1** (a) A global representation of ecological studies on cold rocky landforms (CRLs) in mountain ecosystems. Pie chart area reflects the total number of studies for each montane region (given as  $n$  below each name). Purple shading indicates mountainous areas (adapted from Rahbek et al., 2019). 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 CRLs investigated for each habitat and taxonomic group 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 are defined are provided in the Supporting information, primarily in Table S1

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 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, 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 plenty of 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 of alpine glaciers and snowfields outnumber those on CRLs by approximately 10:1 (Figure 1a).

Cold rocky landforms are widespread in mountainous regions, present on every continent, and greatly outnumber 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,



**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, and/or water percolating into rocky debris and refreezing within the matrix. (c) Moraines (white arrows in the image) are deposited by glaciers and 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. 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 Supporting information 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



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 its melt 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 (Nekola, 1999). Algific talus slopes have been documented in North America, Europe, and Asia (e.g., Kim et al., 2016; Nekola, 1999; Park et al., 2020; Růžicka 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 ubiquitous 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 potential climate refugia for cold-adapted terrestrial and aquatic biodiversity. 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 CRLs to act 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), entomologists (e.g., Tampucci, Gobbi, et al., 2017), mammalogists (e.g., 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 and (2) to 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.

## 2 | COLD HABITATS FOR BIODIVERSITY

### 2.1 | 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, intense solar radiation, reduced oxygen availability; Birrell et al., 2020; Elser et al., 2020), instability of CRL mantles, 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).

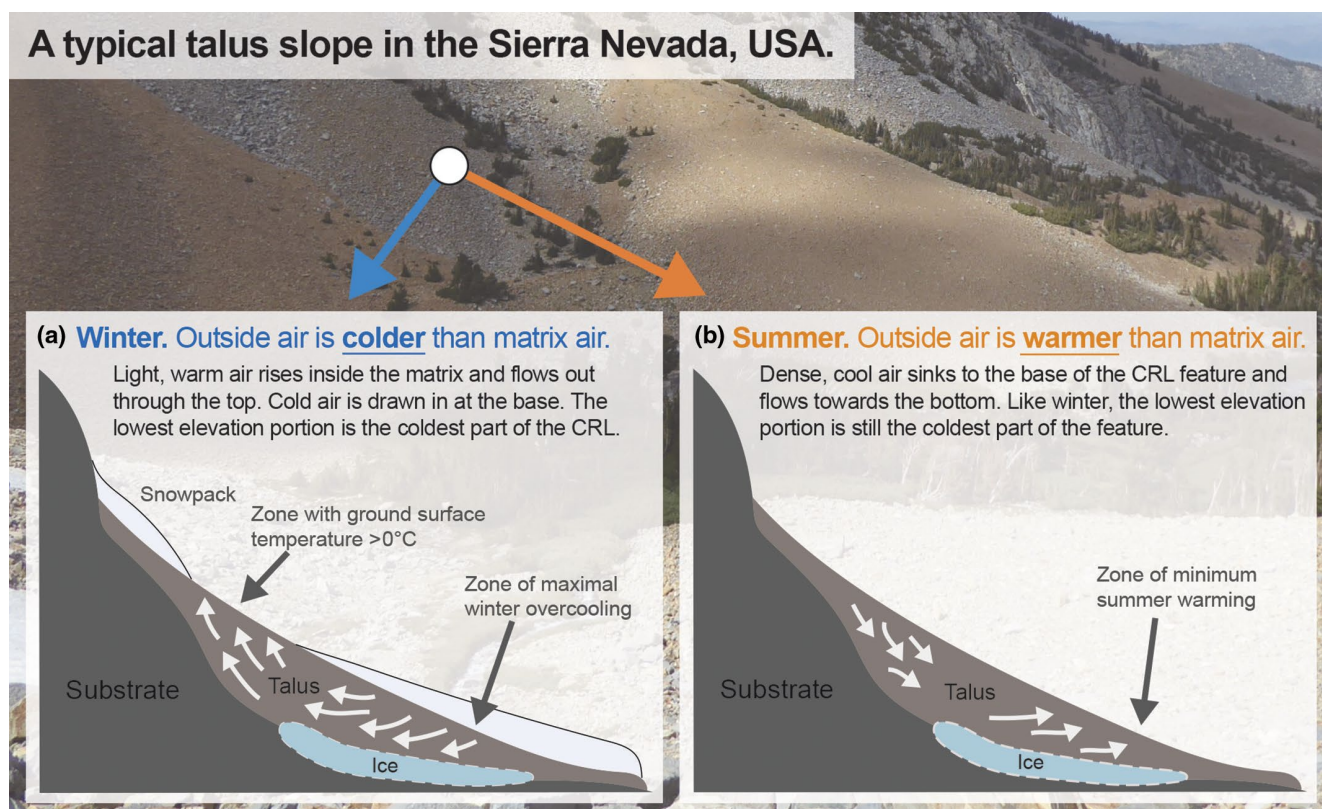
Arthropods are also common on and within CRLs. While no synthesis of arthropod diversity on CRLs has been performed, targeted studies—primarily from the European Alps and North America—have revealed a rich diversity of beetles, mites, spiders, and pseudoscorpions (Table S1; Gobbi et al., 2011, 2014; Gude et al., 2003; Růžicka & Zacharda, 1994; Tampucci, Azzoni, et al., 2017; Tampucci, Gobbi, et al., 2017). Similar to plants, many arthropods occur on CRLs at elevations lower than their typical distributions (Tampucci, Gobbi, et al., 2017). CRLs also 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 (Růžicka & 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 elevations 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 in 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 talus presence may define the species' range limits (Inman et al., 2012).

## 2.2 | 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 frequent droughts (Millar et al., 2014, 2015). Wet meadows act as intermediate habitats between terrestrial and aquatic ecosystems, sharing characteristics of both. Forefield wetlands associated with CRLs support a variety of plants and arthropods (Millar et al., 2015). Similar to surface CRL



**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 can also freeze percolating snowmelt and rain, resupplying the ice that melts later in the summer. Ice gain and loss within CRLs are not well documented, but melt rates are estimated to be ~10–100 times less than for alpine glaciers due to the insulation afforded by their rocky mantle (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). Diagrams modified from Morard et al. (2010)

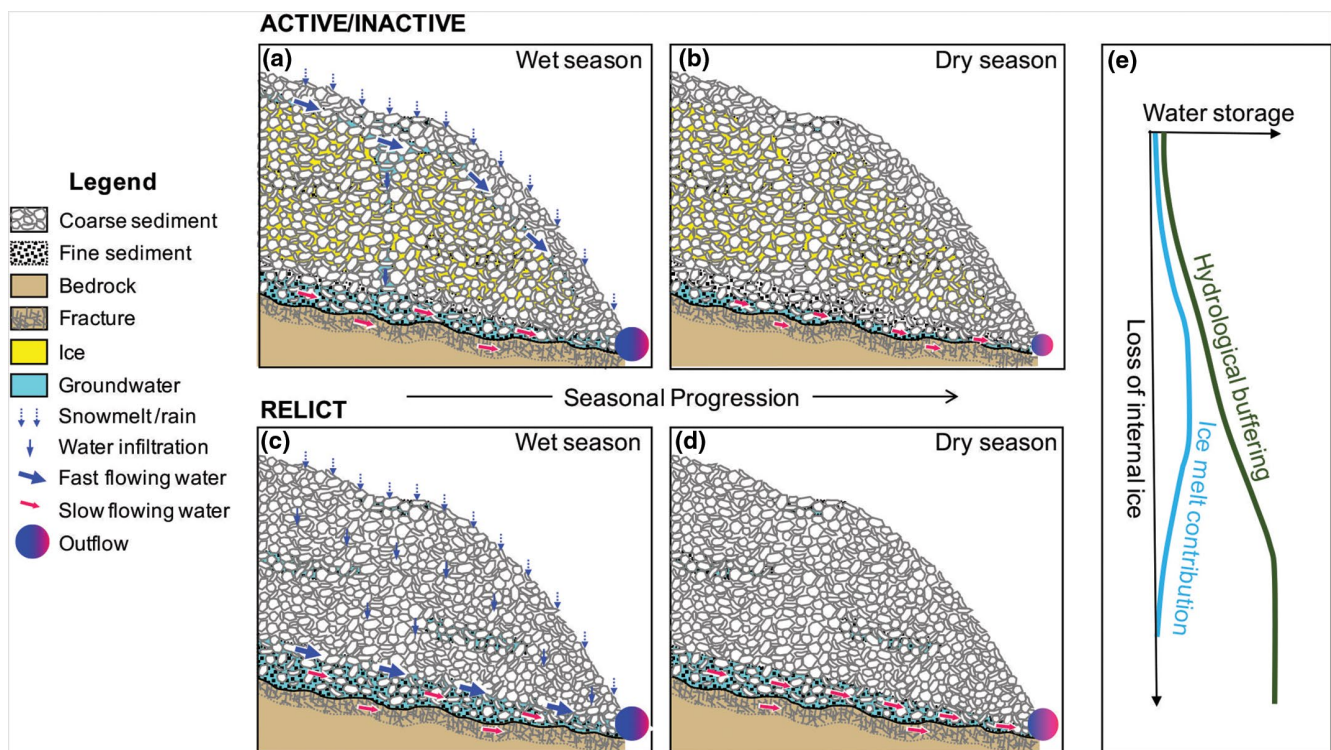
biota, species typical of higher elevations are commonly found in forefield wetlands of CRLs, making these habitats richer in biodiversity than areas not adjacent to CRLs (Millar et al., 2015). Vertebrates found on CRL surfaces also use adjacent wetlands. For instance, although pikas spend near the surface of CRLs, they often forage in adjacent habitats (Smith & Weston, 1990).

## 2.3 | 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 snowpacks. 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 disproportionately 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 represent key aquifers in high-mountain landscapes (Figure 4; Hayashi, 2020). Often, water 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



**FIGURE 4** Cold rocky landforms (CRLs) act as mountain aquifers by partially storing groundwater in their mantles—which is recharged by snowmelt and rainfall—and slowly releasing 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 voids within a CRL are filled by ice (a–b; active = moving, inactive = no longer moving), the ice does not allow water to flow through, causing relatively fast flow of groundwater. 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 and d, relict landforms). (e) As landforms transition to relicts under climate change, their water storage capacity increases 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 and 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 where droughts are common



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 ionic concentrations, unstable channels), true groundwater aquifers (springs with stable channels but warmer temperatures), and seasonal snowpack (warmer and more variable temperatures, low ionic concentrations; 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 habitat conditions are distinct enough between icy seeps and streams fed by alpine glaciers and snowfields in the same area, 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 keys 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., 2020; 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. For instance, 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 levels of diversity than nearby glacier-fed streams (Tronstad et al., 2020), including cold-adapted species that are not found in glacier-fed streams of the same area (Brighenti et al., 2020). Icy seeps can also provide critical habitat for fish of conservation concern such as the westslope cutthroat trout in western North America (Harrington et al., 2017). Although more research is required, the cold, stable aquatic habitat of icy seeps may provide climate refugia for a substantial portion of alpine stream biodiversity.

## 2.4 | 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 sulfates) 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 have 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 CRLs 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 has 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 hinder the potential for CRLs to bolster climate refugia in mountain lake and pond ecosystems.

## 3 | LESSONS FROM THE PAST

Geomorphological, hydrological, and ecological evidence supports the thesis that CRLs may offset warming and water shortages in mountain ecosystems, and act as global climate refugia for cold-adapted terrestrial and aquatic biota (e.g., Anderson et al., 2018; Hayashi, 2020; Hotaling, Foley, et al., 2019; Figures 1 and 2). Paleohistoric studies also highlight the potential for 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; Růžicka & 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).

#### 4 | 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

General Information



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.

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

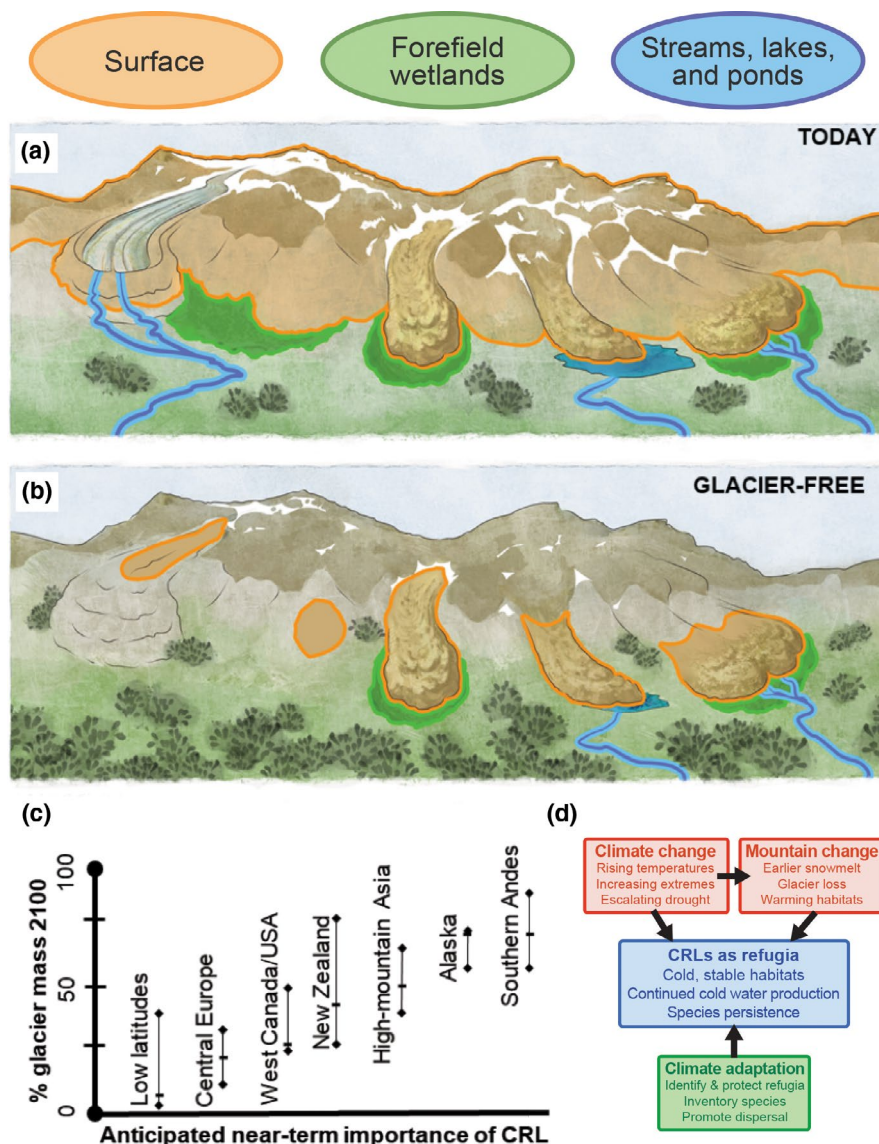
**FIGURE 5** Practical examples of how cold rocky landforms (CRLs) can be used in management for representative species from terrestrial and aquatic habitats and a range of taxonomic groups. The Climate Refugia Conservation Cycle used as guidance here is modified from Morelli et al. (2016). Photograph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



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 refugia within a species' existing range can provide biodiversity protection without the risks associated with other solutions (Morelli et al., 2016, 2020). 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). Managed relocation (also referred to as "assisted migration") raises a host of ecological and ethical 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., 2016, 2020). While advances have been made in predicting topographic and landscape features that support cool micro-climates (Dobrowski, 2011), CRLs can often be identified via satellite imagery and aerial photography due to their distinct geomorphology (e.g., Cremonese et al., 2011). Maps of permafrost distributions may also be useful when seeking to identify CRLs (e.g., Boeckli et al., 2012). 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

**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 mountain 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), that is, 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



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 are important. Microclimatological factors such as solar exposure and snow accumulation favor 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 the vulnerability of mountain ecosystems to climate change (Hock et al., 2019), biotic monitoring of both CRL and nearby non-CRL habitats is needed to identify the biodiversity that is 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, and 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 that will determine the success of CRLs as climate refugia given uncertain climate change scenarios and increasing local pressures from human activities (Figures 5 and 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.

## 5 | FUTURE RESEARCH

We encourage research in the emerging field of CRL-based climate refugia which would benefit from multidisciplinary expertise in 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 habitat 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?

## 6 | 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 contemporary climate change.

## ACKNOWLEDGEMENTS

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

## AUTHORS' 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.

## DATA AVAILABILITY STATEMENT

All data included in this article are publicly available and included in this study's Supporting information.

## ORCID

Scott Hotaling  <https://orcid.org/0000-0002-5965-0986>

Constance I. Millar  <https://orcid.org/0000-0003-1761-0027>

## REFERENCES

Alexander, J. M., Chalmardier, L., Lenoir, J., Burgess, T. I., Essl, F., Haider, S., Kueffer, C., McDougall, K., Milbau, A., Nuñez, M. A., Pauchard,

- A., Rabitsch, W., Rew, L. J., Sanders, N. J., & Pellissier, L. (2018). Lags in the response of mountain plant communities to climate change. *Global Change Biology*, 24(2), 563–579. <https://doi.org/10.1111/gcb.13976>
- Anderson, R. S., Anderson, L. S., Armstrong, W. H., Rossi, M. W., & Crump, S. E. (2018). Glaciation of alpine valleys: The glacier-debris-covered glacier-rock glacier continuum. *Geomorphology*, 311, 127–142. <https://doi.org/10.1016/j.geomorph.2018.03.015>
- Ashcroft, M. B. (2010). Identifying refugia from climate change. *Journal of Biogeography*, 37(8), 1407–1413. <https://doi.org/10.1111/j.1365-2699.2010.02300.x>
- Benn, D., & Evans, D. J. (2014). *Glaciers and glaciation*. Routledge.
- Birrell, J. H., Shah, A. A., Hotaling, S., Giersch, J. J., Williamson, C. E., Jacobsen, D., & Woods, H. A. (2020). Insects in high-elevation streams: Life in extreme environments imperiled by climate change. *Global Change Biology*, 26, 6667–6684. <https://doi.org/10.1111/gcb.15356>
- Boeckli, L., Brenning, A., Gruber, S., & Noetzli, J. (2012). Permafrost distribution in the European Alps: calculation and evaluation of an index map and summary statistics. *The Cryosphere*, 6(4), 807–820. <https://doi.org/10.5194/tc-6-807-2012>
- Brighenti, S., Tolotti, M., Bertoldi, M., Wharton, G., & Bruno, M. C. (2020). Rock glaciers and paraglacial features influence stream invertebrates in a deglaciating alpine area. *Freshwater Biology*. <https://doi.org/10.1111/fwb.13658>
- Brighenti, S., Tolotti, M., Bruno, M. C., Engel, M., Wharton, G., Cerasino, L., Mair, V., & Bertoldi, W. (2019). After the peak water: the increasing influence of rock glaciers on alpine river systems. *Hydrological Processes*, 33(21), 2804–2823. <https://doi.org/10.1002/hyp.13533>
- Brighenti, S., Tolotti, M., Bruno, M. C., Wharton, G., Pusch, M. T., & Bertoldi, W. (2019). Ecosystem shifts in Alpine streams under glacier retreat and rock glacier thaw: A review. *Science of the Total Environment*, 675, 542–559. <https://doi.org/10.1016/j.scitotenv.2019.04.221>
- Brown, L. E., Hannah, D. M., & Milner, A. M. (2007). Vulnerability of alpine stream biodiversity to shrinking glaciers and snowpacks. *Global Change Biology*, 13(5), 958–966. <https://doi.org/10.1111/j.1365-2486.2007.01341.x>
- Burga, C. A., Frauenfelder, R., Ruffet, J., Hoelzle, M., & Kääb, A. (2004). Vegetation on Alpine rock glacier surfaces: A contribution to abundance and dynamics on extreme plant habitats. *Flora-Morphology, Distribution, Functional Ecology of Plants*, 199(6), 505–515. <https://doi.org/10.1078/0367-2530-00179>
- Caccianiga, M., Andreis, C., Diolaiuti, G., D'Agata, C., Mihalcea, C., & Smiraglia, C. (2011). Alpine debris-covered glaciers as a habitat for plant life. *The Holocene*, 21(6), 1011–1020. <https://doi.org/10.1177/0959683611400219>
- Cannone, N., & Gerdol, R. (2003). Vegetation as an ecological indicator of surface instability in rock glaciers. *Arctic, Antarctic, and Alpine Research*, 35(3), 384–390. [https://doi.org/10.1657/1523-0430\(2003\)035\[0384:VA AEIO\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2003)035[0384:VA AEIO]2.0.CO;2)
- Chapman, J. A., & Flux, J. E. (1990). *Rabbits, hares and pikas: status survey and conservation action plan*. IUCN.
- Cokendolpher, J. C., & Krejca, J. K. (2010). A new cavernicolous *Parobisium* Chamberlin 1930 (*Pseudoscorpiones: neobisiidae*) from Yosemite National Park, USA (Vol. 297). Museum of Texas Tech University. <https://doi.org/10.5962/bhl.title.156953>
- Colombo, N., Salerno, F., Gruber, S., Freppaz, M., Williams, M., Fratianni, S., & Giardino, M. (2018). Impacts of permafrost degradation on inorganic chemistry of surface fresh water. *Global and Planetary Change*, 162, 69–83. <https://doi.org/10.1016/j.gloplacha.2017.11.017>
- Cremonese, E., Gruber, S., Phillips, M., Pogliotti, P., Böckli, L., Noetzli, J., Suter, C., Bodin, X., Crepaz, A., & Kellerer-Pirklbauer, A. (2011). An inventory of permafrost evidence for the European Alps. *The Cryosphere*, 5, 651–657. <https://doi.org/10.5194/tc-5-651-2011>
- Dobrowski, S. Z. (2011). A climatic basis for microrefugia: The influence of terrain on climate. *Global Change Biology*, 17(2), 1022–1035. <https://doi.org/10.1111/j.1365-2486.2010.02263.x>
- Elser, J. J., Andersen, T., Baron, J. S., Bergström, A.-K., Jansson, M., Kyle, M., Nydick, K. R., Steger, L., & Hessen, D. O. (2009). Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. *Science*, 326(5954), 835–837. <https://doi.org/10.1126/science.1176199>
- Elser, J. J., Wu, C., González, A. L., Shain, D. H., Smith, H. J., Sommaruga, R., Williamson, C. E., Brahney, J., Hotaling, S., Vanderwall, J., Yu, J., Aizen, V., Aizen, E., Battin, T. J., Camassa, R., Feng, X., Jiang, H., Lu, L., Qu, J. J., ... Saros, J. E. (2020). Key rules of life and the fading cryosphere: Impacts in alpine lakes and streams. *Global Change Biology*, 26, 6644–6656. <https://doi.org/10.1111/gcb.15362>
- Fegel, T. S., Baron, J. S., Fountain, A. G., Johnson, G. F., & Hall, E. K. (2016). The differing biogeochemical and microbial signatures of glaciers and rock glaciers. *Journal of Geophysical Research: Biogeosciences*, 121(3), 919–932. <https://doi.org/10.1002/2015JG003236>
- Fell, S. C., Carrivick, J. L., & Brown, L. E. (2017). The multitrophic effects of climate change and glacier retreat in mountain rivers. *BioScience*, 67(10), 897–911. <https://doi.org/10.1093/biosci/bix107>
- Fell, S. C., Carrivick, J. L., Kelly, M. G., Füreder, L., & Brown, L. E. (2018). Declining glacier cover threatens the biodiversity of alpine river diatom assemblages. *Global Change Biology*, 24(12), 5828–5840. <https://doi.org/10.1111/gcb.14454>
- Fickert, T., Friend, D., Grüniger, F., Molnia, B., & Richter, M. (2007). Did debris-covered glaciers serve as Pleistocene refugia for plants? A new hypothesis derived from observations of recent plant growth on glacier surfaces. *Arctic, Antarctic, and Alpine Research*, 39(2), 245–257. [https://doi.org/10.1657/1523-0430\(2007\)39\[245:DDGSAP\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2007)39[245:DDGSAP]2.0.CO;2)
- Finn, D. S., Khamis, K., & Milner, A. M. (2013). Loss of small glaciers will diminish beta diversity in Pyrenean streams at two levels of biological organization. *Global Ecology and Biogeography*, 22(1), 40–51. <https://doi.org/10.1111/j.1466-8238.2012.00766.x>
- Finn, D. S., Räsänen, K., & Robinson, C. T. (2010). Physical and biological changes to a lengthening stream gradient following a decade of rapid glacial recession. *Global Change Biology*, 16(12), 3314–3326. <https://doi.org/10.1111/j.1365-2486.2009.02160.x>
- Fountain, A. G., & Tangborn, W. V. (1985). The effect of glaciers on streamflow variations. *Water Resources Research*, 21(4), 579–586. <https://doi.org/10.1029/WR021i004p00579>
- Gentili, R., Baroni, C., Caccianiga, M., Armiraglio, S., Ghiani, A., & Citterio, S. (2015). Potential warm-stage microrefugia for alpine plants: Feedback between geomorphological and biological processes. *Ecological Complexity*, 21, 87–99. <https://doi.org/10.1016/j.ecocom.2014.11.006>
- Gentili, R., Baroni, C., Panigada, C., Rossini, M., Tagliabue, G., Armiraglio, S., Citterio, S., Carton, A., & Salvatore, M. C. (2020). Glacier shrinkage and slope processes create habitat at high elevation and microrefugia across treeline for alpine plants during warm stages. *Catena*, 193, 104626. <https://doi.org/10.1016/j.catena.2020.104626>
- Giersch, J. J., Hotaling, S., Kovach, R. P., Jones, L. A., & Muhlfeld, C. C. (2017). Climate-induced glacier and snow loss imperils alpine stream insects. *Global Change Biology*, 23(7), 2577–2589. <https://doi.org/10.1111/gcb.13565>
- Giersch, J. J., Jordan, S., Luikart, G., Jones, L. A., Hauer, F. R., & Muhlfeld, C. C. (2015). Climate-induced range contraction of a rare alpine aquatic invertebrate. *Freshwater Science*, 34(1), 53–65. <https://doi.org/10.1086/679490>
- Gobbi, M., Ballarin, F., Compostella, C., Lencioni, V., Seppi, R., Tampucci, D., & Caccianiga, M. (2014). Physical and biological features of an active rock glacier in the Italian Alps. *The Holocene*, 24(11), 1624–1631. <https://doi.org/10.1177/0959683614544050>
- Gobbi, M., Isaia, M., & De Bernardi, F. (2011). Arthropod colonisation of a debris-covered glacier. *The Holocene*, 21(2), 343–349. <https://doi.org/10.1177/0959683610374885>



- Gobbi, M., & Lencioni, V. (2020). Glacial biodiversity: Lessons from ground-dwelling and aquatic insects. In *Glaciers*: IntechOpen. <https://doi.org/10.5772/intechopen.92826>
- Gude, M., Dietrich, S., Mäusbacher, R., Hauck, C., Molenda, R., Ruzicka, V., & Zacharda, M. (2003). Probable occurrence of sporadic permafrost in non-alpine scree slopes in central Europe. *Proceedings of the 8th International Conference on Permafrost*.
- Haeberli, W., Schaub, Y., & Huggel, C. (2017). Increasing risks related to landslides from degrading permafrost into new lakes in de-glaciating mountain ranges. *Geomorphology*, 293, 405–417. <https://doi.org/10.1016/j.geomorph.2016.02.009>
- Hågvær, S., Gobbi, M., Kaufmann, R., Ingimarsdóttir, M., Caccianiga, M., Valle, B., Pantini, P., Fanciulli, P. P., & Vater, A. (2020). Ecosystem birth near melting glaciers: A review on the pioneer role of ground-dwelling arthropods. *Insects*, 11(9), 644. <https://doi.org/10.3390/insects11090644>
- Harrington, J. S., Hayashi, M., & Kurylyk, B. L. (2017). Influence of a rock glacier spring on the stream energy budget and cold-water refuge in an alpine stream. *Hydrological Processes*, 31(26), 4719–4733. <https://doi.org/10.1002/hyp.11391>
- Hayashi, M. (2020). Alpine hydrogeology: The critical role of groundwater in sourcing the headwaters of the world. *Groundwater*, 58(4), 498–510. <https://doi.org/10.1111/gwat.12965>
- Herbst, D. B., Cooper, S. D., Medhurst, R. B., Wiseman, S. W., & Hunsaker, C. T. (2018). A comparison of the taxonomic and trait structure of macroinvertebrate communities between the riffles and pools of montane headwater streams. *Hydrobiologia*, 820(1), 115–133. <https://doi.org/10.1007/s10750-018-3646-4>
- Herbst, D. B., Cooper, S. D., Medhurst, R. B., Wiseman, S. W., & Hunsaker, C. T. (2019). Drought ecohydrology alters the structure and function of benthic invertebrate communities in mountain streams. *Freshwater Biology*, 64(5), 886–902. <https://doi.org/10.1111/fwb.13270>
- Hock, R., Rasul, G., Adler, C., Cáceres, B., Gruber, S., Hirabayashi, Y., Jackson, M., Kääb, A., Kang, S., Kutuzov, S., Milner, A. M., Molau, U., Morin, S., Orlove, B., Steltzer, H., Simon, A., Arenson, L., Banerjee, S., Barr, I., ... Zhang, Y. (2019). High mountain areas. *The Intergovernmental Panel on Climate Change (IPCC)*, 2, 1–94.
- Hotaling, S., Finn, D. S., Giersch, J. J., Weisrock, D. W., & Jacobsen, D. (2017). Climate change and alpine stream biology: Progress, challenges, and opportunities for the future. *Biological Reviews*, 92(4), 2024–2045. <https://doi.org/10.1111/brv.12319>
- Hotaling, S., Foley, M. E., Zeglin, L. H., Finn, D. S., Tronstad, L. M., Giersch, J. J., Muhlfeld, C. C., & Weisrock, D. W. (2019). Microbial assemblages reflect environmental heterogeneity in alpine streams. *Global Change Biology*, 25(8), 2576–2590. <https://doi.org/10.1111/gcb.14683>
- Hotaling, S., Giersch, J. J., Finn, D. S., Tronstad, L. M., Jordan, S., Serpa, L. E., Call, R. G., Muhlfeld, C. C., & Weisrock, D. W. (2019). Congruent population genetic structure but differing depths of divergence for three alpine stoneflies with similar ecology, geographic distributions, and climate change threats. *Freshwater Biology*, 64, 335–347. <https://doi.org/10.1111/fwb.13223>
- Hotaling, S., Shah, A. A., McGowan, K. L., Tronstad, L. M., Giersch, J. J., Finn, D. S., Woods, H. A., Dillon, M. E., & Kelley, J. L. (2020). Mountain stoneflies may tolerate warming streams: evidence from organismal physiology and gene expression. *Global Change Biology*, 10, 5524–5538. <https://doi.org/10.1111/gcb.15294>
- Hotaling, S., Wimberger, P. H., Kelley, J. L., & Watts, H. E. (2020). Macroinvertebrates on glaciers: A key resource for terrestrial food webs? *Ecology*, 101(4), e02947. <https://doi.org/10.1002/ecy.2947>
- Ilyashuk, B. P., Ilyashuk, E. A., Psenner, R., Tessadri, R., & Koinig, K. A. (2014). Rock glacier outflows may adversely affect lakes: Lessons from the past and present of two neighboring water bodies in a crystalline-rock watershed. *Environmental Science & Technology*, 48(11), 6192–6200. <https://doi.org/10.1021/es500180c>
- Inman, R. M., Magoun, A. J., Persson, J., & Mattisson, J. (2012). The wolverine's niche: Linking reproductive chronology, caching, competition, and climate. *Journal of Mammalogy*, 93(3), 634–644. <https://doi.org/10.1644/11-MAMM-A-319.1>
- Jones, D. B., Harrison, S., Anderson, K., & Betts, R. (2018). Mountain rock glaciers contain globally significant water stores. *Scientific Reports*, 8(1), 2834. <https://doi.org/10.1038/s41598-018-21244-w>
- Jones, D. B., Harrison, S., Anderson, K., & Whalley, W. B. (2019). Rock glaciers and mountain hydrology: A review. *Earth-science Reviews*, 193, 66–90. <https://doi.org/10.1016/j.earscirev.2019.04.001>
- Karjalainen, O., Luoto, M., Aalto, J., Etzelmüller, B., Grosse, G., Jones, B. M., Lilleøren, K. S., & Hjort, J. (2020). High potential for loss of permafrost landforms in a changing climate. *Environmental Research Letters*, 15(10), 104065. <https://doi.org/10.1088/1748-9326/abafd5>
- Kavanaugh, D. H. (1979). Investigations on present climatic refugia in North America through studies on the distributions of carabid beetles: Concepts, methodology and prospectus. In T. L. Erwin, G. E. Ball, D. R. Whitehead, & A. L. Halpern (Eds.), *Carabid beetles: Their evolution, natural history, and classification* (pp. 369–381). Springer.
- Khamis, K., Hannah, D. M., Clarvis, M. H., Brown, L. E., Castella, E., & Milner, A. M. (2014). Alpine aquatic ecosystem conservation policy in a changing climate. *Environmental Science & Policy*, 43, 39–55. <https://doi.org/10.1016/j.envsci.2013.10.004>
- Kim, J.-S., Chung, J.-M., Kim, J.-H., Lee, W., Lee, B.-Y., & Pak, J.-H. (2016). Floristic study and conservation management strategies of algal talus slopes on the Korean peninsula. *Korean Journal of Plant Taxonomy*, 46(2), 213–246. <https://doi.org/10.11110/kjpt.2016.46.2.213>
- Krainer, K., Bressan, D., Dietre, B., Haas, J. N., Hajdas, I., Lang, K., Mair, V., Nickus, U., Reidl, D., Thies, H., & Tonidandel, D. (2015). A 10,300-year-old permafrost core from the active rock glacier Lazaun, southern Ötztal Alps (South Tyrol, northern Italy). *Quaternary Research*, 83(2), 324–335. <https://doi.org/10.1016/j.yqres.2014.12.005>
- La Sorte, F. A., & Jetz, W. (2010). Projected range contractions of montane biodiversity under global warming. *Proceedings of the Royal Society B*, 277(1699), 3401–3410. <https://doi.org/10.1098/rspb.2010.0612>
- Lencioni, V. (2018). Glacial influence and stream macroinvertebrate biodiversity under climate change: Lessons from the Southern Alps. *Science of the Total Environment*, 622, 563–575. <https://doi.org/10.1016/j.scitotenv.2017.11.266>
- Mania, I., Gorra, R., Colombo, N., Freppaz, M., Martin, M., & Anesio, A. M. (2019). Prokaryotic diversity and distribution in different habitats of an alpine rock glacier-pond system. *Microbial Ecology*, 78(1), 70–84. <https://doi.org/10.1007/s00248-018-1272-3>
- Millar, C. I., D. Westfall, R., & Delany, D. L. (2014). Thermal regimes and snowpack relations of periglacial talus slopes, Sierra Nevada, California, USA. *Arctic, Antarctic, and Alpine Research*, 46(2), 483–504. <https://doi.org/10.1657/1938-4246-46.2.483>
- Millar, C. I., Delany, D. L., Hersey, K. A., Jeffress, M. R., Smith, A. T., Van Gunst, K. J., & Westfall, R. D. (2018). Distribution, climatic relationships, and status of American pikas (*Ochotona princeps*) in the Great Basin, USA. *Arctic, Antarctic, and Alpine Research*, 50(1), e1436296. <https://doi.org/10.1080/15230430.2018.1436296>
- Millar, C. I., & Hickman, K. (in press). Camera traps provide insights into American pika site occupancy, behavior, thermal relations and associated wildlife diversity. *Western North American Naturalist*.
- Millar, C. I., Stephenson, N. L., & Stephens, S. L. (2007). Climate change and forests of the future: Managing in the face of uncertainty. *Ecological Applications*, 17(8), 2145–2151. <https://doi.org/10.1890/06-1715.1>
- Millar, C. I., & Westfall, R. D. (2008). Rock glaciers and related periglacial landforms in the Sierra Nevada, CA, USA; inventory, distribution and climatic relationships. *Quaternary International*, 188(1), 90–104. <https://doi.org/10.1016/j.quaint.2007.06.004>
- Millar, C. I., & Westfall, R. D. (2019). Geographic, hydrological, and climatic significance of rock glaciers in the Great Basin, USA.

- Arctic, Antarctic, and Alpine Research, 51(1), 232–249. <https://doi.org/10.1080/15230430.2019.1618666>
- Millar, C. I., Westfall, R. D., Evenden, A., Holmquist, J. G., Schmidt-Gengenbach, J., Franklin, R. S., Nachlinger, J., & Delany, D. L. (2015). Potential climatic refugia in semi-arid, temperate mountains: Plant and arthropod assemblages associated with rock glaciers, talus slopes, and their forefield wetlands, Sierra Nevada, California, USA. *Quaternary International*, 387, 106–121. <https://doi.org/10.1016/j.quaint.2013.11.003>
- Morard, S., Delaloye, R., & Lambiel, C. (2010). Pluriannual thermal behaviour of low elevation cold talus slopes in western Switzerland. *Geographica Helvetica*, 65, 124–134. <https://doi.org/10.5194/ggh-65-124-2010>
- Morelli, T. L., Barrows, C. W., Ramirez, A. R., Cartwright, J. M., Ackerly, D. D., Eaves, T. D., Ebersole, J. L., Krawchuk, M. A., Letcher, B. H., Mahalovich, M. F., Meigs, G. W., Michalak, J. L., Millar, C. I., Quiñones, R. M., Stralberg, D., & Thorne, J. H. (2020). Climate-change refugia: Biodiversity in the slow lane. *Frontiers in Ecology and the Environment*, 18(5), 228–234. <https://doi.org/10.1002/fee.2189>
- Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T., Lundquist, J. D., Millar, C. I., Maher, S. P., Monahan, W. B., Nydick, K. R., Redmond, K. T., Sawyer, S. C., Stock, S., & Beissinger, S. R. (2016). Managing climate change refugia for climate adaptation. *PLoS One*, 11(8), e0159909. <https://doi.org/10.1371/journal.pone.0159909>
- Muhlfeld, C. C., Cline, T. J., Giersch, J. J., Peitzsch, E., Florentine, C., Jacobsen, D., & Hotaling, S. (2020). Specialized meltwater biodiversity persists despite widespread deglaciation. *Proceedings of the National Academy of Sciences of the United States of America*, 117, 12208–12214. <https://doi.org/10.1073/pnas.2001697117>
- Nekola, J. C. (1999). Paleoreugia and neoreugia: The influence of colonization history on community pattern and process. *Ecology*, 80(8), 2459–2473. [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)
- Niedrist, G. H., & Füreder, L. (2020). Real-time warming of alpine streams: (re)defining invertebrates' temperature preferences. *River Research and Applications*, 1–11. <https://doi.org/10.1002/rra.3638>
- Park, J. S., Kim, D.-K., Kim, C. S., Oh, S., Kim, K.-H., & Oh, S.-O. (2020). The first finding of the lichen *Solorina saccata* at an algalic talus slope in Korea. *Mycobiology*, 48(4), 276–287. <https://doi.org/10.1080/12298093.2020.1785729>
- Rahbek, C., Borregaard, M. K., Colwell, R. K., Dalsgaard, B., Holt, B. G., Morueta-Holme, N., Nogues-Bravo, D., Whittaker, R. J., & Fjeldså, J. (2019). Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science*, 365(6458), 1108–1113. <https://doi.org/10.1126/science.aax0149>
- Ren, Z., Martyniuk, N., Oleksy, I. A., Swain, A., & Hotaling, S. (2019). Ecological stoichiometry of the mountain cryosphere. *Frontiers in Ecology and Evolution*, 7, 360. <https://doi.org/10.3389/fevo.2019.00360>
- Ricciardi, A., & Simberloff, D. (2009). Assisted colonization is not a viable conservation strategy. *Trends in Ecology & Evolution*, 24(5), 248–253. <https://doi.org/10.1016/j.tree.2008.12.006>
- Riedel, J. L., & Larrabee, M. A. (2016). Impact of recent glacial recession on summer streamflow in the Skagit River. *Northwest Science*, 90(1), 5–22. <https://doi.org/10.3955/046.090.0103>
- Rieg, L., Sailer, R., Stötter, J., & Burger, D. (2012). Vegetation cover on alpine rock glaciers in relation to surface velocity and substrate. *Proceedings of the Tenth International Conference on Permafrost*.
- Robinson, C., Tonolla, D., Imhof, B., Vukelic, R., & Uehlinger, U. (2016). Flow intermittency, physico-chemistry and function of headwater streams in an Alpine glacial catchment. *Aquatic Sciences*, 78(2), 327–341. <https://doi.org/10.1007/s00027-015-0434-3>
- Rotta, F., Cerasino, L., Occhipinti-Ambrogi, A., Rogora, M., Seppi, R., & Tolotti, M. (2018). Diatom diversity in headwaters influenced by permafrost thawing: First evidence from the Central Italian Alps. *Advances in Oceanography and Limnology*, 9(2). <https://doi.org/10.4081/aiol.2018.7929>
- Růžička, V., & Zacharda, M. (1994). Arthropods of stony debris in the Krkonoše Mountains, Czech Republic. *Arctic, Antarctic, and Alpine Research*, 26(4), 332–338. <https://doi.org/10.1080/00040851.1994.12003077>
- Růžička, V., Zacharda, M., Němcová, L., Šmilauer, P., & Nekola, J. C. (2012). Periglacial microclimate in low-altitude scree slopes supports relict biodiversity. *Journal of Natural History*, 46(35–36), 2145–2157. <https://doi.org/10.1080/00222933.2012.707248>
- Sasaki, H. (1986). Air and soil temperature affecting the distribution of plants on a wind-hole site. *Ecological Review = Seitaiyaku Kenkyu*, 21(1), 21.
- Schwartz, M. W., Hellmann, J. J., McLachlan, J. M., Sax, D. F., Borevitz, J. O., Brennan, J., Camacho, A. E., Ceballos, G., Clark, J. R., Doremus, H., Early, R., Etterson, J. R., Fielder, D., Gill, J. L., Gonzalez, P., Green, N., Hannah, L., Jamieson, D. W., Javeline, D., ... Zellmer, S. (2012). Managed relocation: Integrating the scientific, regulatory, and ethical challenges. *BioScience*, 62(8), 732–743. <https://doi.org/10.1525/bio.2012.62.8.6>
- Shah, A. A., Dillon, M. E., Hotaling, S., & Woods, H. A. (2020). High elevation insect communities face shifting ecological and evolutionary landscapes. *Current Opinion in Insect Science*, 41, 1–6. <https://doi.org/10.1016/j.cois.2020.04.002>
- Siebers, A. R., Paillex, A., & Robinson, C. T. (2019). Flow intermittency influences the trophic base, but not the overall diversity of alpine stream food webs. *Ecography*, 42(9), 1523–1535. <https://doi.org/10.1111/ecog.04597>
- Slemmons, K. E. H., & Saros, J. E. (2012). Implications of nitrogen-rich glacial meltwater for phytoplankton diversity and productivity in alpine lakes. *Limnology and Oceanography*, 57(6), 1651–1663. <https://doi.org/10.4319/lo.2012.57.6.1651>
- Smith, A. T., & Weston, M. L. (1990). Ochotona princeps. *Mammalian Species*, (352), 1–8. <https://doi.org/10.2307/3504319>
- Stefaniak, A., Robson, B., Cook, S., Clutterbuck, B., Midgley, N., & Labadz, J. (2020). Mass balance and surface evolution of the debris-covered Miage Glacier, 1990–2018. *Geomorphology*, 373, 107474. <https://doi.org/10.1016/j.geomorph.2020.107474>
- Stibal, M., Bradley, J. A., Edwards, A., Hotaling, S., Zawierucha, K., Rosvold, J., Lutz, S., Cameron, K. A., Mikucki, J. A., Kohler, T. J., Šabacká, M., & Anesio, A. M. (2020). Glacial ecosystems are essential to understanding biodiversity responses to glacier retreat. *Nature Ecology & Evolution*, 4(5), 686–687. <https://doi.org/10.1038/s41559-020-1163-0>
- Tampucci, D., Azzoni, R. S., Boracchi, P., Citterio, C., Compostella, C., Diolaiuti, G., Isaia, M., Marano, G., Smiraglia, C., Gobbi, M., & Caccianiga, M. (2017). Debris-covered glaciers as habitat for plant and arthropod species: Environmental framework and colonization patterns. *Ecological Complexity*, 32, 42–52. <https://doi.org/10.1016/j.ecocom.2017.09.004>
- Tampucci, D., Boffa, G., Mangili, F., Gobbi, M., & Caccianiga, M. (2015). Vegetation outlines of two active rock glaciers with contrasting lithology. *Plant Sociology*, 52, 9–18. <https://doi.org/10.7338/pls2015521/02>
- Tampucci, D., Gobbi, M., Marano, G., Boracchi, P., Boffa, G., Ballarin, F., Pantini, P., Seppi, R., Compostella, C., & Caccianiga, M. (2017). Ecology of active rock glaciers and surrounding landforms: Climate, soil, plants and arthropods. *Boreas*, 46(2), 185–198. <https://doi.org/10.1111/bor.12219>
- Thaler, B., Tait, D., & Tolotti, M. (2015). Permafrost und seine Auswirkungen auf die Ökologie von Hochgebirgsseen. *GEO.ALP*, 12, 183–234.
- Tolotti, M., Cerasino, L., Donati, C., Pindo, M., Rogora, M., Seppi, R., & Albanese, D. (2020). Alpine headwaters emerging from glaciers and rock glaciers host different bacterial communities: Ecological

- implications for the future. *Science of the Total Environment*, 717, 137101. <https://doi.org/10.1016/j.scitotenv.2020.137101>
- Tronstad, L. M., Hotaling, S., Giersch, J. J., Wilmot, O. J., & Finn, D. S. (2020). Headwater streams fed by subterranean ice: Potential climate refugia for mountain communities? *Western North American Naturalist*, 3, 11.
- Wagner, T., Pauritsch, M., Mayaud, C., Kellerer-Pirklbauer, A., Thalheim, F., & Winkler, G. (2019). Controlling factors of microclimate in blocky surface layers of two nearby relict rock glaciers (Niedere Tauern Range, Austria). *Geografiska Annaler: Series A, Physical Geography*, 101(4), 310–333. <https://doi.org/10.1080/04353676.2019.1670950>
- Ward, J. (1994). Ecology of alpine streams. *Freshwater Biology*, 32(2), 277–294. <https://doi.org/10.1111/j.1365-2427.1994.tb01126.x>
- Wilhelm, L., Singer, G. A., Fasching, C., Battin, T. J., & Besemer, K. (2013). Microbial biodiversity in glacier-fed streams. *The ISME Journal*, 7(8), 1651–1660. <https://doi.org/10.1038/ismej.2013.44>
- Williams, M., Knauf, M., Cory, R., Caine, N., & Liu, F. (2007). Nitrate content and potential microbial signature of rock glacier outflow,

Colorado Front Range. *Earth Surface Processes and Landforms*, 32(7), 1032–1047. <https://doi.org/10.1002/esp.1455>

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Brighenti S, Hotaling S, Finn DS, et al. Rock glaciers and related cold rocky landforms: Overlooked climate refugia for mountain biodiversity. *Glob Change Biol*. 2021;00:1–14. <https://doi.org/10.1111/gcb.15510>