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

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Running head: Cold rocky landforms as climate refugia

Abstract:

Mountains are global biodiversity hotspots where cold environments and their associated ecological communities are expected to shift upward and disappear as climates warm. Considerable research attention has been focused on the ecological effects of alpine glacier and snowfield recession and warming temperatures in aquatic and terrestrial habitats. However,

little attention has been devoted 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, stable terrestrial and aquatic habitats. Due to the insulating nature of debris cover and their internal ventilation patterns, CRLs are less responsive to atmospheric warming than alpine glaciers and snowfields. Here, we argue that CRLs represent global climate refugia for mountain biodiversity, offer guidelines for incorporating CRLs into management practice, 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 unique habitats associated with glaciers, permafrost, and seasonal snowpack (Hock *et al.* 2019). Globally, mountains are biodiversity hotspots (Rahbek *et al.* 2019) thanks in large part to high rates of local endemism driven by a combination of habitat isolation and adaptation to cold conditions (Smith & Weston 1990; Muhlfeld *et al.* 2020). Many microbes, plants, and animals in terrestrial and aquatic environments are associated with glaciers and other cold habitats (Lencioni 2018; Hotaling *et al.* 2019). Thus, the rapid contemporary warming of mountain ecosystems is projected to imperil cold-adapted biodiversity worldwide (Hotaling *et al.* 2017; Brighenti *et al.* 2019a).

As a result of climate warming, winter snowlines are moving higher, and melt seasons are shifting earlier and extending later (Hock *et al.* 2019). During warm periods, glaciers and snowfields are crucial for mountain hydrology as they yield large volumes of cold water and buffering the effects of climate warming, at least for aquatic biota (Fountain & Tangborn, 1985; Hotaling *et al.* 2017). Earlier melting and later accumulation of seasonal snow will extend harsh summer conditions when terrestrial and aquatic habitats are at their warmest and driest. In the long-term, ice-dominated features and their groundwater storage potential will fade, removing essential 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 will stress wetland and meadow vegetation, which may impact cold-adapted animals that depend on those habitats, creating additional stresses beyond rising temperature alone.

Although alpine glaciers and snowfields have received the bulk of scientific attention, these are not the only strongholds of cold conditions in mountain ecosystems. Mountains around the world harbor other landforms that also provide cold habitat conditions and high water-storage capacity (Figure 1). Among these, rock glaciers have received the most attention (Jones *et al.* 2018, 2019), but related features that similarly influence local habitats are also common. These include debris-covered glaciers, protalus ramparts (also called "valley-wall rock glaciers"), ice-embedded moraines, and talus slopes (Figure 2). Though considerable attention has been devoted to distinguishing among these features geomorphologically, a collective term is still missing (Millar & Westfall 2008). For efficiency, we refer to them herein as "cold rocky landforms" (CRLs). Structurally, CRLs have a surface mantle of rocky debris and interiors composed of ice and rock.

Cold rocky landforms are widespread in mountainous regions, present on every continent, and greatly outnumber more well-known alpine glaciers (Jones *et al.* 2018). Rocky mantles insulate and decouple CRL interiors from outside air and promote internal thermal regimes that enable ice accumulation and retention. With sub-freezing interiors, CRLs have the capacity to store percolated snowmelt as ice and release meltwater into springs and lakes during warm and dry periods (Jones *et al.* 2019; Hayashi 2020). 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 is on CRLs in mountain ecosystems, habitats exhibiting many of the same characteristics as CRLs—including the long-term persistence of subterranean ice—are present at lower elevations worldwide. For example, hundreds of "algific talus slope" sites exist in Iowa, USA, and are usually associated with north-facing, ice-filled caves (Nekola 1999). Thus, our arguments and conclusions likely extend beyond mountain ecosystems to include other forms of persistent cold habitats that depend on the long-term maintenance of subterranean ice.

Growing ecological evidence supports CRLs as key climate refugia—areas large enough to support a population of an imperiled species while their habitat is lost elsewhere due to climate change (Ashcroft 2010; Figure 2; Table S1). The potential for CRLs to serve as climate refugia is particularly important given their commonness in mountain ranges worldwide and the ongoing, rapid decline of alpine glaciers and snowfields. Here, we present a global synthesis of CRL ecology in mountain ecosystems, with an emphasis on their value as refugia for cold-adapted terrestrial and aquatic biodiversity under climate change. We offer strategies for identifying CRLs and integrating them into conservation and climate adaptation practices and conclude by highlighting standing questions for the field.

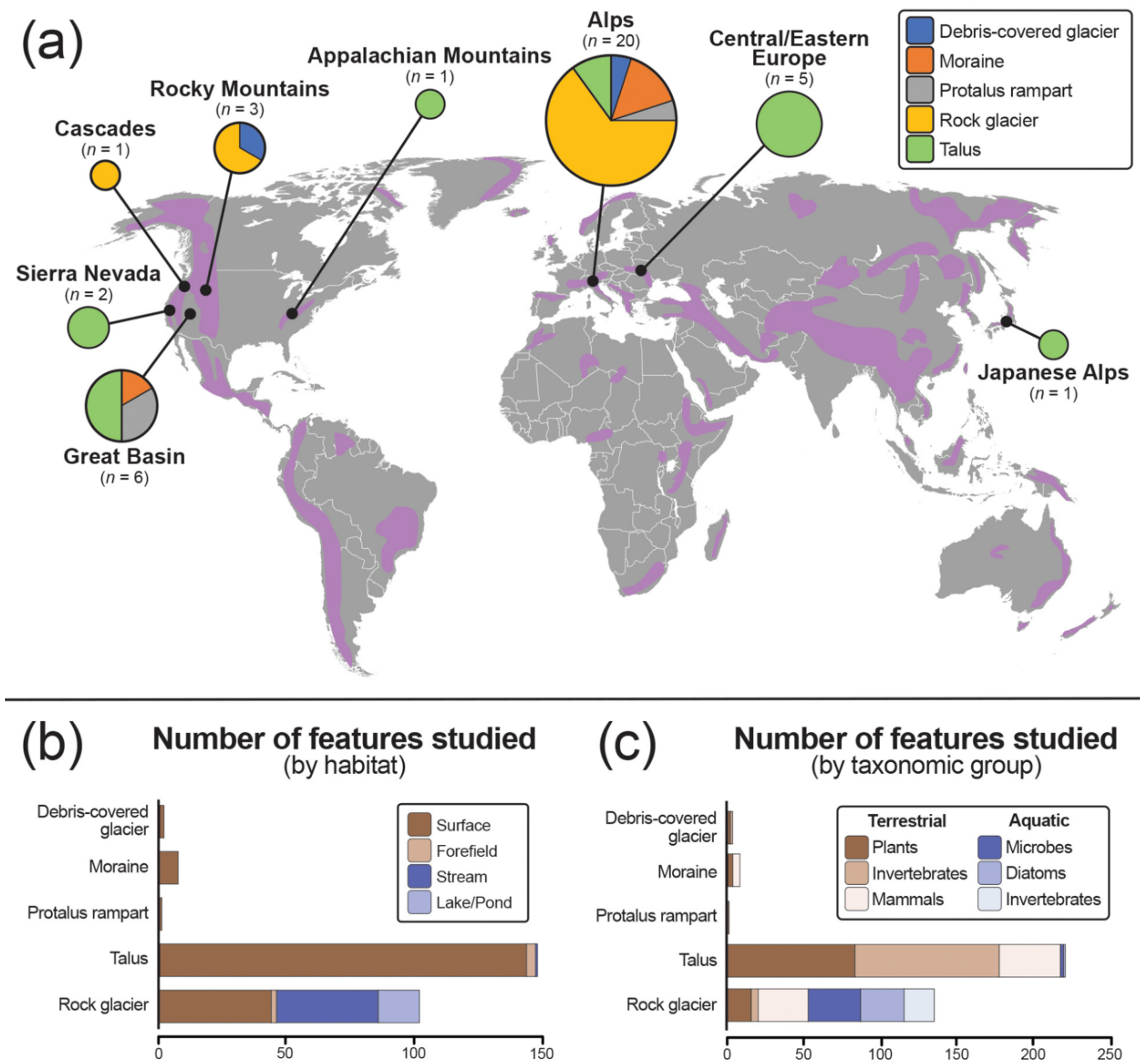

Figure 1. (a) Global distribution of ecological studies on cold rocky landforms in mountain ecosystems. Pie chart area reflects the total number of studies for a given region (given below each name). Purple shading indicates mountainous areas (adapted from Rahbek *et al.* 2019). The number of landforms investigated for each habitat and taxon are provided in (b) and (c), respectively. See Table S1 for complete details of the studies that were included in this figure.

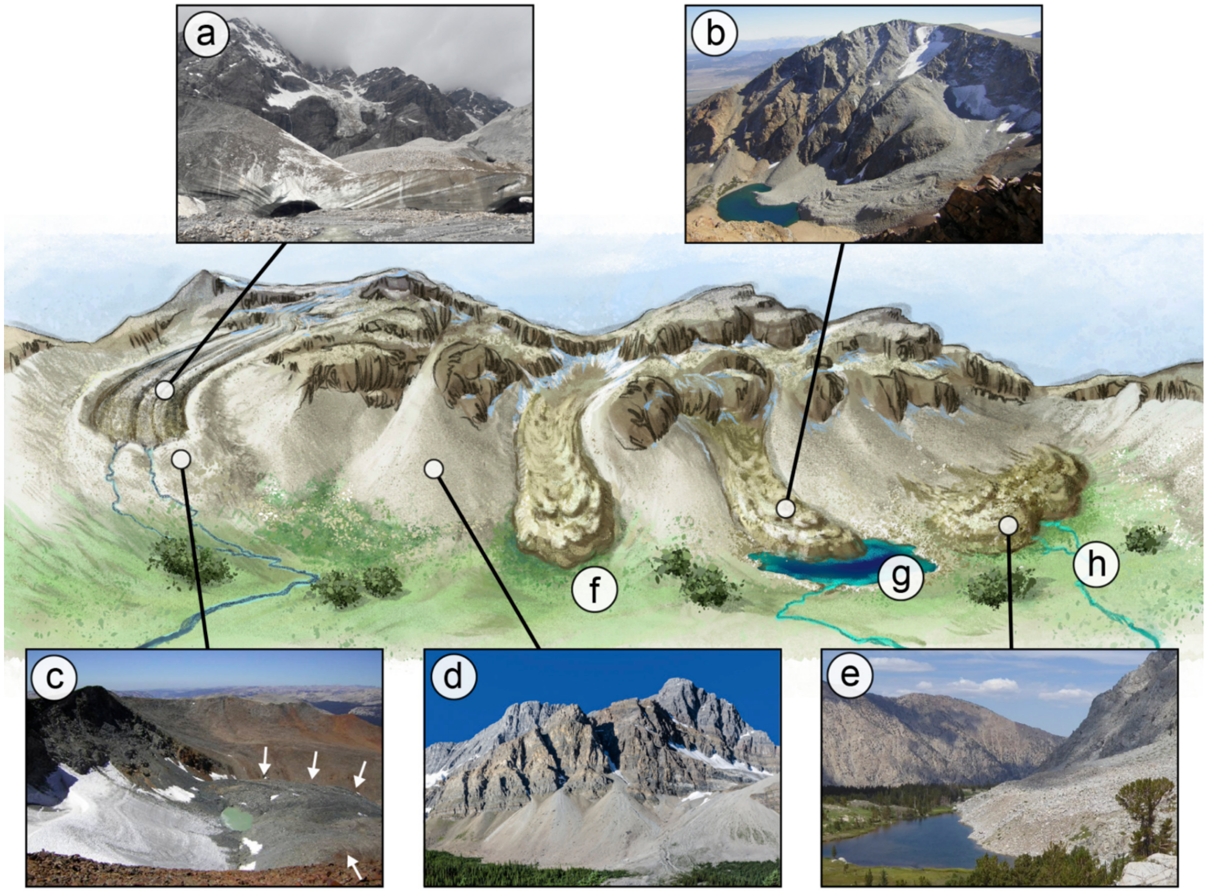

Figure 2. Cold rocky landforms (CRLs) have diverse origins and appearances. They are composed of rocky debris, ice, and water. (a) When an alpine glacier becomes covered with rock and soil, it transitions to a debris-covered glacier containing massive amounts of ice. The debris insulates the ice, reducing the rate of melt relative to debris-free glaciers. (b) Rock glaciers are masses of fragmented rock and ice that move downslope. They often develop when avalanches and snowmelt percolate into rocky debris at valley heads and re-freeze filling the void spaces with ice. (c) Moraines (white arrows in the image) are rocky deposits formed by glacial movement that can become embedded with ice as meltwater flows into their rocky debris and re-freezes but they typically do not move. (d) Talus slopes result from rockfall along valley walls, and while they may contain ice, they do not move or develop steepened fronts. (e) Protalus ramparts (sometimes referred to as valley-wall rock glaciers) form when ice develops within talus slopes such that they become over-steepened and move. CRLs commonly accumulate and deliver cold groundwater to (f) wet meadows, (g) lakes, and (h) springs. Under warming climates, active, moving CRLs become inactive when they no longer move, eventually becoming relict features when all ice is lost. See Supplementary Materials for additional images of different CRL types. Artwork in the panel center is courtesy of Vanessa Arrighi.

Cold habitats for biodiversity:

Terrestrial 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 temperatures, limited oxygen availability), instability of CRL mantles, routine avalanches, and rockfall make their surfaces particularly harsh environments. Nonetheless, many plants and animals persist on CRL surfaces and within CRL rocky matrices.

Vascular plants have been documented on rock glaciers and taluses in the Sierra Nevada, USA (Millar *et al.* 2015) and European Alps (Cannone & Gerdol 2003; Gobbi *et al.* 2014), as well as on debris-covered glaciers in the Alps (Caccianiga *et al.* 2011; Rieg *et al.* 2012). 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 common, with the latter typically represented by cold-hardy perennial species (Millar *et al.* 2015). Due to their unusually cold nature, plants have been observed on CRLs as far as 1000 m below their typical altitudinal zone (e.g., Fickert *et al.* 2007; Millar *et al.* 2015).

Arthropods are also common on and within CRLs (Table S1). Similar to plants, many arthropod species occur at lower elevations on CRLs than their typical distributions (e.g., Tampucci *et al.* 2017). CRLs can even harbor endemic arthropods. For instance, an endemic, cold-adapted pseudoscorpion is only known cold taluses 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 & Zacharada 1994).

An iconic CRL-dependent mammal is 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 temperatures, 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 survive in places where outside 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 (Smith *et al.* 1990). In addition to pikas, dozens of other mammals and birds also inhabit CRLs of North

America, including woodrats, weasels, chipmunks, and ground squirrels (Millar and Hickman, in review). In the Czech Republic, a small shrew (*Sorex minutus*) is endemic to taluses (Růžička & Zacharada 1994). CRLs are even crucial for wide-ranging, circumpolar carnivores such as wolverines (*Gulo gulo*), a species threatened by the effects of climate warming on seasonal snowpack. Indeed, taluses are so important to wolverines for prey caching that their presence defines the species' range limits (Inman *et al.* 2012).

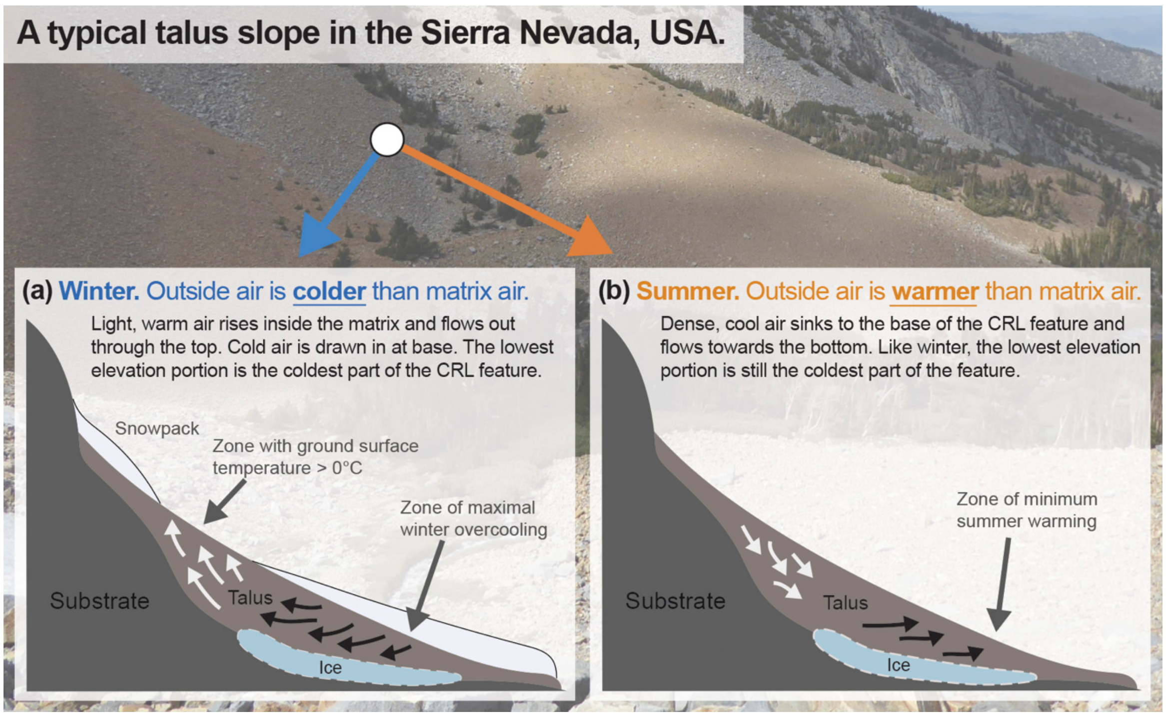

Figure 3. Unique properties and processes keep cold rocky landforms (CRLs) cold year-round. Natural convection internally ventilates the rocky matrix, creating a seasonally reversible circulation pattern (Morard *et al.* 2010). (a) In winter, outside air is colder than the air inside the CRL. As cold 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 of the landform, chilling adjacent forefields. This ventilation creates and sustains the relatively cold and stable conditions year-around within the CRL despite the absence of ground-ice on surrounding slopes. Cold interior temperatures freeze percolating snow meltwater 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.* 2016). CRLs can maintain their cool thermal properties even when ice is absent, such that relict forms still produce cool groundwater and springs (Jones *et al.* 2019). This mechanism also slows the response of CRLs to climate warming. 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.

Forefields and wet meadows

Cold air venting from the margins of CRLs in summer makes their forefields cooler than surrounding environments (Figure 3; Millar *et al.* 2014). Cold air and abundant groundwater combine to maintain cool wetland environments that are hot spots 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, 2015). Wet meadows 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 (e.g., Millar *et al.* 2015), making these habitats richer in biodiversity than areas not adjacent to CRLs. Vertebrates found on CRL surfaces also use adjacent wetlands. For instance, although pikas spend most of their time on the surface and interiors of CRLs, they often forage in adjacent habitat (Smith & Weston 1990).

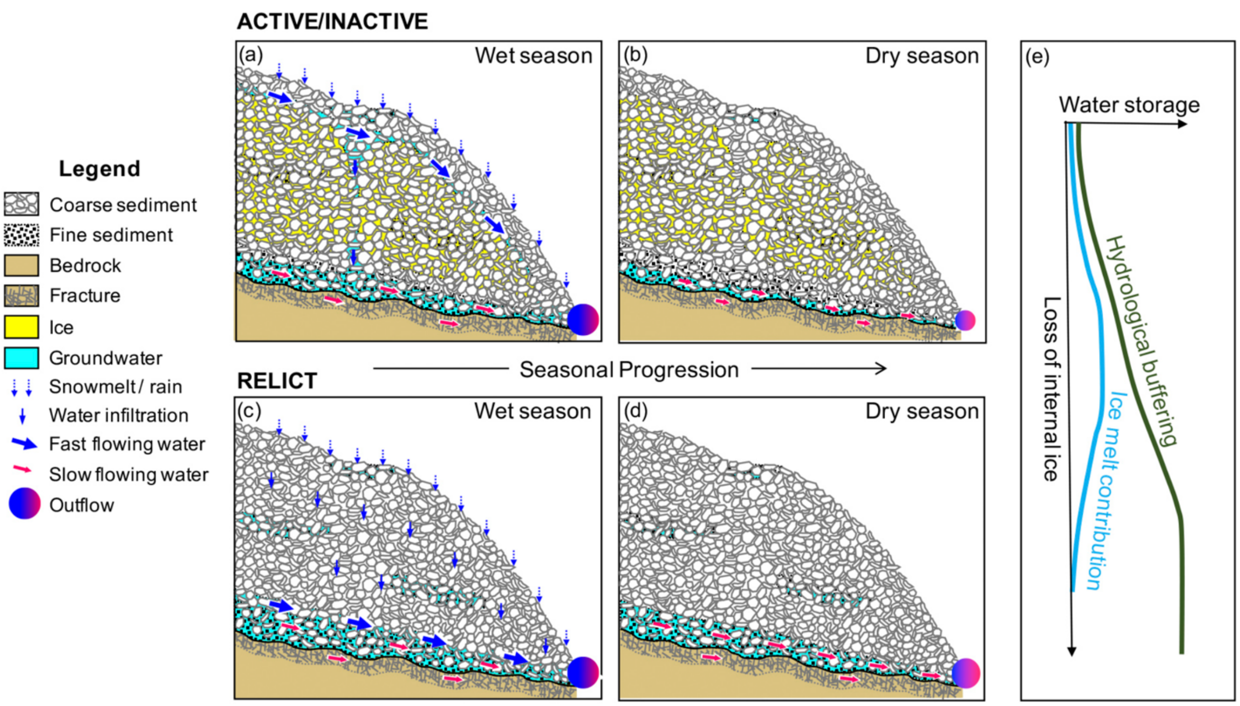

Figure 4. Cold rocky landforms (CRLs) act as mountain aquifers as they partially store groundwater in their mantles that is recharged by snowmelt and rainfall, and slowly release it into nearby habitats. These natural reservoirs greatly contribute to local water storage in areas once considered to be “teflon basins” where the water received from precipitation would be quickly exported to the lowlands (Hayashi 2020). When a CRL has ice filling up void spaces (a-b, active/inactive landforms), impermeable 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 as such 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, the 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

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 *et al*. 2019). Icy seeps have a unique combination of habitat conditions including persistently cold water, stable flows, low suspended sediments, and relatively high ionic concentrations. This combination of habitat conditions contrasts with meltwater streams sourced from alpine glaciers (cold but more variable thermal and flow conditions, high suspended sediments, low ions), true groundwater aquifers (springs with stable but warmer temperature), and seasonal snowpack (warmer and more variable temperatures, low ions).

Alpine streams have attracted ecological attention for several decades (reviewed by Hotaling *et al*. 2017), due in large part to concerns associated with the rapid shrinking of glaciers and seasonal snowpack. The disappearance of once-permanent alpine glaciers and snowfield sources is predicted to convert many headwaters from permanent to intermittent or result in the displacement of cold-adapted aquatic communities by upward-shifting assemblages intolerant of cold (e.g., Brighenti *et al*. 2019a; but see 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). It has become clear that the heterogeneity of hydrological source types in alpine headwaters have promoted the development of high beta (among-site) biodiversity in alpine streams (Finn *et al*. 2013). Until recently, CRLs were vastly underappreciated as an additional common source type, a key oversight given that they are substantially more resistant to climate change than alpine glaciers and snowfields.

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 *et al*. 2019; Tolotti *et al.* 2020), algal (Rotta *et al*. 2018), and macroinvertebrate diversity (Fell *et al.* 2017; Brighenti *et al.* 2019a; Tronstad *et al*. in press). However, whether icy seeps will serve as climate refugia as alpine glaciers and snowfields recede remains a pressing question. Essentially, 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 meltwater are key to occupancy, icy seeps are likely to act as climate refugia. The strongest evidence for this thus far comes from macroinvertebrates, which are ectothermic and represent the majority of animal biomass in alpine streams. In the European Alps (Brighenti *et al*. 2019a) and American Rockies (Tronstad *et al*. in press), 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 [e.g., midges of the *Diamesa latitarsis* group in the Alps (Lencioni 2018) and the stonefly *Zapada glacier* in the Rockies, Giersch *et al*. 2015)]. Furthermore, icy seeps exhibited greater local diversity than glacier-fed streams. While in need of more study, particularly beyond macroinvertebrates, our tentative conclusion is that the cold temperatures combined with the habitat stability of icy seeps will provide climate refugia for a substantial portions of alpine stream biodiversity.

Lakes and ponds

To date, most CRL-focused lake and pond research has focused on rock glacier-fed habitats. However, unlike nearby streams and an emphasis on temperature, the chemical composition of high mountain lakes has received considerable attention. High concentrations of ions (including nitrates, calcium, magnesium, and sulphates) and heavy metals, often exceeding drinking water limits, are common in rock glacier outflows (Williams *et al.* 2007; Colombo *et al.* 2018; Brighenti *et al.* 2019b). 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; Elser *et al.* 2009) in rock glacial waters, can enhance algal production (e.g., Slemmons and Saros, 2012), especially when compared with glacier-fed lakes where the high turbidity limits the algal growth (hindering light penetration in the water; 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 near shore 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 habitat and biodiversity 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.

When comparing mountain stream and lake ecosystems, the role of CRLs in driving climate refugia for freshwaters seems evident only for streams, whereas lakes, and their harsh, potentially CRL-influenced water chemistry may limit their viability as refugia. However, these conclusions are preliminary, as little is known about CRL-influenced freshwater ecology globally. Current knowledge is also based almost solely on active rock glaciers, with little known for other CRLs, whose outflow water chemistry appears to be less harsh than rock glaciers (Brighenti *et al.* 2019b).

Lessons from the past:

Considerable geomorphological, hydrological, and ecological evidence supports our 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. For instance, many plants and animals now restricted to CRLs were widespread during cold intervals of the Pleistocene, and thus have allowed cold-adapted species to persist for as long as 10,000 years during the Holocene (Růžička & Zacharada 1994; Fickert *et al.* 2007). 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 (Růžička & Zacharada 1994; Fickert *et al.* 2007). Thus, evidence from both the past and present strengthens our 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 *et al.* 2017).

Looking to the future:

Human pressures have substantial impacts on mountain ecosystems that can amplify the effects of climate change (Brighenti *et al.* 2019a). Often, species' capacities to respond to rapidly changing climates are 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 could change too quickly for them to adapt (LaSorte & Jetz 2010; Giersch *et al.* 2015). Thus, active conservation and climate-adaptation strategies are needed to prevent biodiversity loss (Millar *et al.* 2007). The identification, conservation, and restoration of potential climate-change refugia (Morelli *et al.* 2016, 2020) can provide protection for biodiversity without the risks associated with other approaches (e.g., translocation, Schwartz *et al.* 2012).

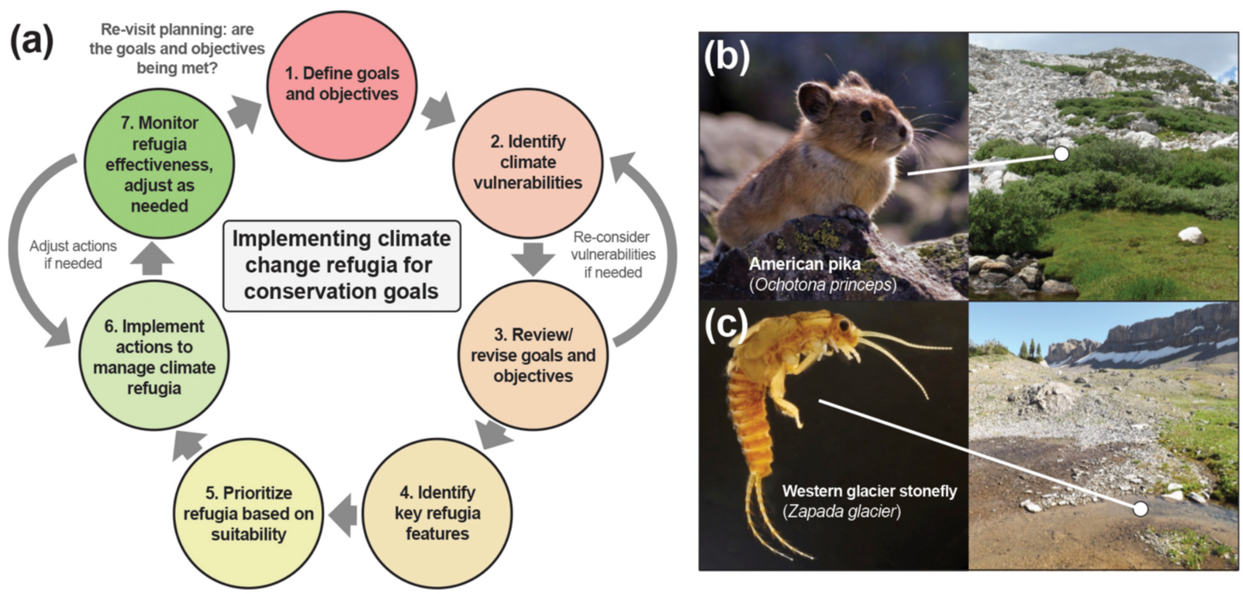

Figure 5. Managing cold rocky landforms (CRLs) as climate refugia. (a) We offer practical examples for implementing CRLs as climate refugia following the climate refugia conservation cycle from Morelli *et al.* (2016) for a terrestrial mammal (b; American pika) and an aquatic insect (c; the Western glacier stonefly). Step 1: Identify the species and relevant habitats to be prioritized for conservation. Future climate conditions should be evaluated (Step 2), along with species' presence, population size, availability of key habitat (e.g., forefield vegetation, American pika; cold water, Western glacier stonefly), and potential impacts (e.g., livestock grazing). Vulnerabilities should also be noted, including size and connectivity of habitats. American pika appear to persist longer in large, connected rocky patches. The Western glacier stonefly appears to prefer streams with cold water (< 8 °C) that originate from glaciers or CRLs. Step 3: Based on surveys and assessments, management objectives might need revision. Step 4: Identifying key CRL refugia can be achieved with remote sensing and field surveys. Step 5: A managed network of climate refugia should include core areas with optimal habitat which, if it contains CRLs and streams, could sustain both American pika and Western glacier stonefly populations. Step 6: Even in designated lands (e.g., national parks), specific climate-refugia management plans are important. For instance, if high-quality CRL patches do not have adequate connectivity, rocky walls along hiking trails can serve as

dispersal corridors for pikas. Further, given increasing recreation pressure, managers can divert recreational human and stock use away from key refugia. Step 7: Long-term monitoring of refugia is crucial for assessing conservation outcomes and reinforcing them. Since pikas are easily detected by sightings and vocalizations, their monitoring may not require wildlife biology expertise. Rather, citizen-science teams can be engaged, adding an educational element to the conservation plan. Although molecular data is needed to identify the Western glacier stonefly, research professionals and citizen scientists can still engage to collect community-level stream community data which could later be analyzed by experts.

However, identifying 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 *et al.* 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. Second, remote sensing-based assessments of *in situ* aquatic conditions are challenging. Quantifying thermal regimes, and biological and chemical settings of CRLs requires field-based surveys, ideally paired with longer term monitoring. Monitoring of water temperature may be a particularly inexpensive strategy for identifying CRL-based refugia, especially when combined with satellite imagery showing a lack of visible ice or snow upstream (Hotaling *et al.* 2019; Brighenti *et al.* 2019b). When considering the long-term viability of CRL-influenced climate refugia, the distribution and type of CRL is important. Solar exposure largely limits CRLs to north-facing slopes so these could be key areas for protected habitat. 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.

Owing to their climate change vulnerability (Hock *et al.* 2019), biotic monitoring of CRL and non-CRL habitats in mountain ecosystems is needed to identify biodiversity under threat and track population dynamics of focal species and communities. Networks of sites should be selected to represent different habitat types (terrestrial, wet meadow, aquatic) as “sentinels” of broader change. Building on the identification and mapping of CRLs, as well as accounting for resident biodiversity within them, 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 (Figure 6).

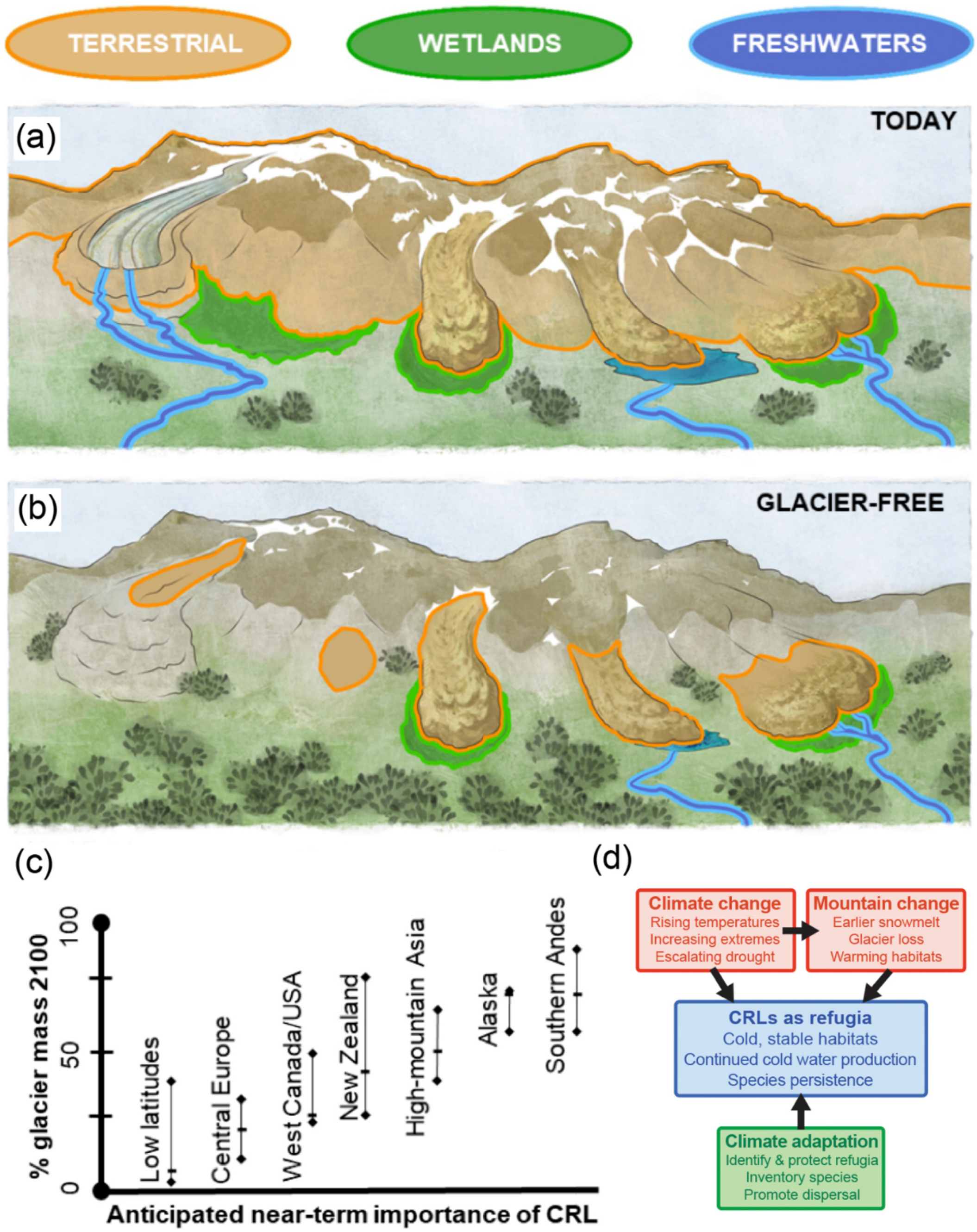

Figure 6. (a) Today, cold rocky landforms (CRLs) are key habitats for cold-adapted species, including those typical of higher elevations. (b) In the future, cold-adapted species may be restricted to CRLs because of alpine glacier and snowfield recession. (c) Species' impacts will likely occur at different timescales depending on the mountain range (for each area: upper limit = RCP2.6, lower limit = RCP8.4, median = RCP4.5; Hock *et al.* 2019). (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:

- How buffered against climate change are CRLs in terms of aquatic and terrestrial habitats? Are they receding more slowly than alpine glaciers and snowfields?
- Since aquatic habitats are naturally more decoupled from ambient warming than terrestrial environments due to the greater heat capacity of water, does the long-term persistence of cold-adapted species differ between aquatic and terrestrial habitats? Will terrestrial environments on CRLs lose sensitive species more rapidly than their freshwater counterparts under climate change? Or, conversely, since terrestrial species naturally experience more thermal variation than aquatic species, will terrestrial species associated with CRLs be more tolerant of changing conditions?
- Do different CRL types differ in their capacity to serve as climate refugia?
- Given their propensity for extreme water chemistry, are lakes and ponds influenced by rock glaciers limited in their capacity to serve climate refugia? And, if so, will lakes and ponds fed by other CRL types be better suited to this role?

Conclusions:

Both historical and contemporary studies on CRLs and the ecosystems they support lend considerable evidence to our thesis that these landforms will provide persistent future climate change 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 persistence of cold-adapted mountain species even under rapid climate change.

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