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Global evidence that cold rocky landforms support icy springs in warming mountains

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Global evidence that cold rocky landforms support icy springs in warming

2 mountains

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Abstract

Climate change is reducing the extent of cold aquatic habitats and their unique biodiversity in mountain areas. However, a variety of cold rocky landforms (CRLs) are thermally buffered and feed cold springs (< 2°C) that may represent climate refugia for cold-adapted organisms. These landforms, hitherto overlooked by freshwater research, include rock glaciers, debriscovered glaciers, talus slopes, protalus ramparts, and young moraines. Here, we investigated the warm-season water temperature of 228 springs from clean (ice) glaciers, CRLs, and reference slopes (not sourced by any of these features) in 13 mountain ranges of Europe, South America, and North America. Only springs from glaciers (90%) and CRLs (45%) had average stream temperatures below the thermal optimum for coldwater organisms of 2°C. Springs fed by CRLs were 3-5°C (up to 9°C) colder than those from nearby reference slopes. In general, cold springs were rarer in mediterranean/semi-arid climates than in temperate and sub-polar climates. Landforms comprising barren and coarse rocky surfaces or ice/rock mix, having a simple or absent soil/vegetation structure, and higher likelihood of permafrost more often supported cold springs. When water temperatures were compared to air temperature, most CRL springs were thermally buffered against warm periods, cumulative heat, and daily temperature fluctuations. With cold conditions maintained in a variety of climates and mountain landscapes, CRL springs in mountains likely have high conservation value. We call for integrated ecological and hydrological research for these ecosystems, aimed at understanding their potential as climate refugia.

Keywords: icy seeps, ice-embedded moraine, talus, coarse blocky surface, ice-rock features, climate change, cold habitats

1. Introduction

- Loss of cold habitats is a major, ongoing impact of climate change (Hock et al., 2019).
- Increasing air temperature, prolonged summers, reduced snow volumes and persistence,
- and shrinking glaciers are causing widespread warming of stream habitats in mountain
- areas. From 2000-2020, observed warming of mountain streams has been ~1.9-2.7 °C per
- decade, and this warming is associated with the loss of cold-adapted biodiversity (Giersch et
- al., 2015; Niedrist and Füreder, 2020; Lencioni et al., 2022; Wilkes et al., 2023; Fahy et al.,
- 61 2024).
- 62 Given the ongoing decline of cold habitats, "cold rocky landforms" (CRLs) have emerged as
- the subject of considerable research (e.g., Brighenti et al., 2021). These strongholds of cold
- conditions occur extensively in glacierized landscapes (Ballantyne, 2002; Bollati et al., 2023)
- as well as in areas that lack clean-ice glaciers (Millar and Westfall, 2008; 2019; Reato et al.,
- 2021; Oliva et al., 2022). CRLs include rock glaciers (Janke and Bolch, 2023), debris-covered
- 67 glaciers (Mayr and Hagg, 2019), ice-cored moraines (Ravanel et al., 2018; Altman et al.,
- 68 2020), talus slopes and cones (Millar et al., 2014; Curry, 2023), block streams (Şerban et al.,
- 69 2019), protalus/pronival ramparts (Hedding, 2011; Colucci et al., 2016), and ice caves
- 70 (Luetscher and Jeannin, 2004; Obleitner et al., 2024).
- 71 Embedded ice, a thick cover of rocky debris that enhances dispersive heat fluxes, and/or
- 72 unique air ventilation processes are typical of these landforms (Delaloye and Lambiel, 2005;
- 73 Wagner et al., 2019; Amschwand et al., 2024), and make their local conditions considerably
- 74 colder than surrounding environments (Brighenti et al., 2021). These cooling mechanisms
- 75 can still be active even when little or no embedded ice exists in the CRL (Harrington et al.,
- 76 2018; Colucci et al., 2019; Winkler et al., 2016). Thus, CRLs are predicted to act as climate
- 77 refugia for cold-adapted terrestrial and aquatic species (Millar et al., 2015; Tampucci et al.,
- 78 2017; Brighenti et al., 2021).
- 79 However, studies on the role of CRLs in shaping cold aquatic ecosystems are relatively few,
- 80 especially when compared to investigations about the influence of CRLs on ground
- temperature and energy balance (see Amschwand et al., 2024). Indeed, CRLs often support
- springs (Millar et al., 2013) that have been referred to as "icy seeps" (Hotaling et al., 2019),
- due to their very cold waters (< 2°C). CRL springs provide suitable thermal habitat for cold-
- adapted species of invertebrates (Brighenti et al., 2020; Tronstad et al., 2020; Reato et al.,
- 85 2023; Martini et al., 2024) and microbes (Hotaling et al., 2019; Tolotti et al., 2020; 2024).

These may also include species that were previously thought as exclusive dwellers of glacier springs (Martini et al., 2024). While the occurrence of such smaller organisms was hitherto demonstrated for spring systems only, CRLs can have strong cooling effects on downstream systems as well, hence expanding the stream network suitable for climatically vulnerable fish and other alpine aquatic fauna (Harrington et al., 2017). Not all CRLs, however, support cold aquatic habitats. For example, relict forms without embedded ice, features on a sunny south-facing aspect, or those with surfaces entirely covered with soil and vegetation can have relatively warm springs emanating from them (e.g., > 6°C; Carturan et al., 2024). Likewise, even springs not influenced by CRLs or glaciers can still be 1-3°C in favourable settings (Küry et al., 2017). Therefore, quantifying the prevalence of cold springs among CRLs and identifying their specific thermal features, is of paramount importance for freshwater research and conservation. Here we examine water temperature during the warm season for 228 springs in 13 mountain ranges on three continents (Europe, North America, and South America) aiming to: i) analyse differences in the occurrence of cold springs among clean-ice glaciers, CRLs, and reference slopes, ii) determine if springs originating from CRLs are colder than those from reference slopes, iii) identify the environmental drivers associated with cold springs. Finally, we propose an approach on how to identify cold springs to assist further ecological

2. Methods

2.1 Field activities

studies and conservation.

We investigated 228 mountain springs located in the Western and Eastern European Alps, Central Europe (Rhoen), North America (Sierra Nevada, Canadian Rocky Mountains, Teton Range, and Wasatch Mountains), and South America (Patagonian Andes). These regions span diverse landscapes, geologies, climates, and prevalence of paraglacial and periglacial dynamics (Figure 1; Supplementary 1; Supplementary dataset).

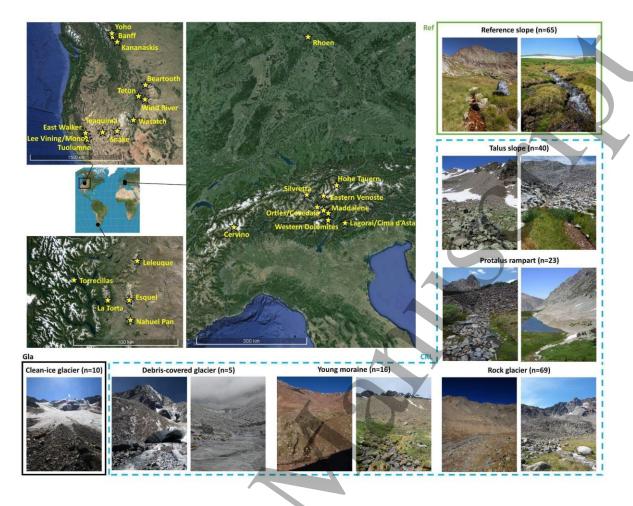


Figure 1. Geographical location of the mountain ranges (world atlas and zooming boxes) investigated and representative pictures of different landform types (border images), with different categories (Gla = clean glaciers, CRL = cold rocky landforms, Ref = reference slopes) framed in different colours. The names of different mountain areas are shown in yellow. See Table 1 for further information on single landform types.

We classified landform types based on the available geological maps or specific studies (Supplementary 2) and defined three landform categories: clean (ice) glaciers, cold rocky landforms (CRLs), and reference slopes (Table 1). Additionally, we distinguished five types of CRLs (Brighenti et al., 2021): debris-covered glaciers, young moraines, talus slopes, protalus ramparts, and rock glaciers. Reference slopes were depositional units with no apparent potential to generate cooling mechanisms (Table 1). Within each mountain range, the difference in elevation among springs was < 500 m and the distance between the sampling location and the water outflow was < 50 m (Supplementary dataset).

Table 1. List of the different landform categories (acronyms in parentheses) used in this study, with definition and key references. CRL = cold rocky landforms. We acknowledge that distinguishing different landforms can be challenging, and

that debates persist regarding different classifications and genesis processes (e.g., Clark et al., 1998; Millar & Westfall, 2008; Berthling, 2011; Scapozza, 2015; Anderson et al., 2019); however, these issues were outside from the scope of this work.

Category	Landform and definition
Clean-ice glacier (Gla)	Glacier with little debris-cover in thickness and extent
CRL	Debris-covered glacier (DCG). Glacier where the ablation zone is continuously
	covered with rock debris across the entire width (Mayr and Hagg, 2018)
CRL	Young moraine (MO). Glacial deposit formed during the Little Ice Age or later. These
	landforms are often ice-embedded (Langston et al., 2011; Ravanel et al., 2018)
CRL	Talus slope (TAL) . These features, often referred to as scree slopes, are frequently
	cone-shaped (talus cones) (Curry, 2023) Here, we include in this classification also
	boulder/block streams (Şerban et al., 2019)
CRL	Protalus rampart (PR). Also referred to as "pronival rampart" or "protalus lobe",
	elongated rocky landform mostly originating from avalanche processes at the foot of
	taluses (Hedding, 2011; Scapozza, 2015; Colucci et al., 2016).
CRL	Rock glacier (RG). Rocky landform showing evidence of deformation by ice-driven
	creeping activity (Janke and Bolch, 2023)
Reference slope (Ref)	Reference slopes represent depositional units with no apparent potential to generate
	cooling mechanisms. They are represented by unconsolidated deposits of glacial
	(tills), colluvial, or alluvial origin that are mainly composed or are embedded with fine
	sediments. They include: wet meadows (Reato et al., 2019), solifluction and
	gelifluction lobes, fluvio-glacial and debris-flow deposits, alluvial fans, landslides, and
	in general landforms fully covered with soil and vegetation. We also included in this
	category karstic rocks not influenced by ice caves and springs where CRLs covered
	only a minor fraction of the catchment (< 5%). These landforms belong to the fine
	sediment system of mountain areas, i.e., the slopes mantled by soil and fine
	sediments (Barsch and Caine, 1984).

During 2021 and 2023, we instrumented 104 springs with temperature loggers recording at 0.5–4 hour intervals. The same springs and additional 124 springs not instrumented with dataloggers were investigated with hand-held probes during 1–8 visits. The same model of datalogger and/or type of probe was generally used in the same region (Supplementary dataset).

Measurements were recorded during July-September in the northern hemisphere, and January-March in the southern hemisphere. During these months, the cooling effect from latent heat of snowmelt is generally lowest and the annual influence from solar radiation is the greatest. Hence, the difference between cold and warm springs is larger during this period (Millar et al., 2013; Küry et al., 2017; Brighenti et al. 2019).

2.2 Data analysis

We used Google Earth Pro software and field observations to calculate the main topographic, geographic, geomorphologic features of the springs, the landforms from which they originate, and the catchments in which they occurred (Table 2).

Table 2. Main variables estimated for each spring and related landform.

Variable	Type of variable	Definition and levels
Köppen climate	Categorical	Based on high-resolution (0.1° × 0.1° grid) map of the Köppen-Geiger
classes		climate classification (Peel et al., 2007). See Table S1.2.
Slope aspect	Categorical	Based on the local azimuth. Sunny (SE, S, SW in the Northern Hemisphere; NE, N, NW in the Southern Hemisphere), Intermediate (W, E), Shady (NE, N, NW; SE, S, SW)
Permafrost	Categorical	Based on the global Permafrost Zonation Index (Gruber et al., 2012).
likelihood		Prevalent class in the catchment upstream of the spring. Six classes: 0
		(permafrost absent), 1 (unlikely), 2 (likely), 3 (very likely), 4 (probable), 5 (certain).
Spring	Continuous	Elevation (Ele; m a.s.l.), distance from the landform front (Dist; m)
Slope upstream		Categorical. Main aspect: Cool facing (N, NW, NE in the northern
from the spring		hemisphere, S, SW, SE in the southern hemisphere), intermediate (E, W), warm-facing (other orientations)
Dominant clast	Categorical	Estimated in the field: Ice-lithic mix (only for clean and debris-covered
size of the		glaciers); Fine (fine-grained lithic: soil, sandy and gravelly material Φ < 5
landform		cm); Small (Stones 5 – 30 cm); Medium (boulders 30 cm - 1 m); Large
		(boulders 1 - 3 m); Very large (boulders > 3 m).
Soil cover on	Categorical	Estimated in the field. Soil and vegetation covering the landform:
the landform		Scarce/absent (<5%); Patchy (5-30%); Sparse (30-60%); Extensive (60-90%); Continuous (90-100%)
Vegetation type	Categorical	Estimated in the field. Dominant vegetation covering the landform and the surrounding area: Absent (only lichens and mosses); Alpine grassland;
		Alpine grassland and (secondary) shrubs; Grass, shrubs (codominant) and
		trees; Trees, shrubs (codominant) and grass

We calculated the average water temperature of the reference period (T_{avg}) for each spring. Because we combined logger data with hand-probe measurements taken during different times in the season, we first conducted a sensitivity analysis and found only slight, nonsignificant differences in T_{avg} between the measurement types (Supplementary 3). We calculated the index of thermal offset (°C) as the difference between T_{avg} of each spring and the median T_{avg} of all reference slope springs located within the same catchment (n = 120 springs) or mountain massif (n = 97). For springs without reference locations (n = 12), thermal offset was not calculated. Negative and positive values of the thermal offset indicated colder and warmer conditions at the CRL and glacier spring relative to a hypothetical reference slope spring.

We used T_{avg} to investigate the frequency of cold (< 2°C), cool (2–4°C), and warm (> 4°C) springs. The 2°C threshold represents the value below which glacier-specialized invertebrates and microbes have been found in previous studies on CRL springs (Giersch et al., 2017; Tronstad et al., 2020; Tolotti et al., 2020; Martini et al., 2024) and defines the

temperature limit of proglacial stream habitats (metakryal; e.g., Lencioni, 2018). The 4°C threshold represents the temperature below which meltwater-specialized biodiversity is still found (Hotaling et al., 2019; Tronstad et al., 2020) and defines the limit of glacier-fed stream habitats (hypokryal; Ward, 1999; Lencioni, 2018). To estimate the environmental drivers of cold springs, we used regression trees technique (a supervised machine learning method; see Breiman, 2017). We used the package rpart (Therneau et al., 2023) to build one tree based on Tavg and one tree based on thermal offset (response variables) using as categorical predictors the following variables: Köppen climate classes, landform clast size, soil/vegetation cover, vegetation structure, permafrost likelihood, and slope aspect (Table 1). We complemented the trees by providing the statistical significance of pairwise comparisons at each node, and added information on the relative frequency of cold springs in each branch/leaf (Supplementary 4 for details). Based on the available time series (without any gaps) of water temperature during the reference period (n = 84), we calculated the average daily standard deviation (daily fluctuation index, °C) and the standard deviation of daily water temperature over the warm season (seasonal fluctuation index, °C). To estimate the spring thermal response to warm periods, we designed a warm-period response index (°C), which represents the thermal response of water temperature to warm atmospheric periods, identified based on daily air temperature (°C) series from the closest weather station (Supplementary 5). To do this, we first calculated the thermal anomaly index as [(A_{day}-A_{avg}) / A_{sd}] for each day and spring, where A_{avg} and A_{sd} are the mean and standard deviation values of daily air temperature during the warm season (1 July-30 September; no continuous data was available from the Southern Hemisphere), and A_{day} is the mean air temperature of the day of interest. Based on the thermal anomaly index, we identified the warm period as the warmest period occurring during the month of August (i.e., the warmest month during which latent heat of snowmelt is least likely in the Northern Hemisphere; no time series available for the Southern Hemisphere) with an index > 1 for at least three consecutive days. Then, the warm-period response index was calculated as [W_{max}-W₀], where W_{max} (°C) is the maximum daily water temperature reached during the warm period and including the following 7 days (to account for a potential lagged response), and W₀ is the daily water temperature during the day prior to the onset of the warm period.

Finally, to visualize the relation among thermal indices and springs from different landform categories, we performed a principal component analysis (PCA) using the R packages factominer (Husson et al., 2024) and factextra (Kassambara and Mundt, 2017).

3. RESULTS

3.1 Cold springs frequency, water temperature, and thermal offset among landforms

 T_{avg} and the thermal offset were higher in reference slope springs versus those from CRLs and clean-ice glaciers (Figure 2b). In springs, from each type of landform category, T_{avg} increased from high-elevation polar/subpolar (ET/Dfc; Köppen classes), to humid continental/oceanic (Dfb, Dsb, Cfb), and mediterranean/semiarid (Csb, Csa, Bsk) climates (Table 3). Overall, springs from all CRL categories and clean glaciers had significantly lower T_{avg} and thermal offset compared with those from reference slopes (p < 0.001). Among landform types, T_{avg} and thermal offset significantly differed (p < 0.05) among clean-ice glaciers, debris-covered glaciers and/or rock glaciers, and talus slopes (Figure 2c). Indeed, landform type was strongly related to temperature since 90% of springs draining clean glaciers, 45% sourced from CRLs, and 0% of springs from reference slopes, were cold (< 2 °C; based on T_{avg}). Among CRLs, the percentage of cold springs was larger in polar/subpolar (60%) and humid continental/oceanic (48%) climates than in mediterranean/semiarid (25%) climates (Figure 2; Table 3).

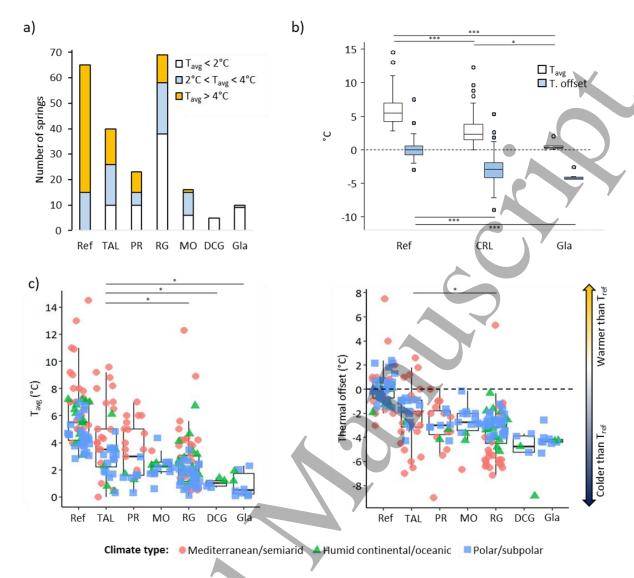


Figure 2. Occurrence of cold springs, their water temperature and thermal offset. a) Occurrence of cold ($< 2^{\circ}$ C), cool ($2 - 4^{\circ}$ C), and warm ($> 4^{\circ}$ C) springs for each landform category. b) Boxplots of T_{avg} and thermal offset at different categories, with connectors showing significant differences (* p < 0.05, *** p < 0.001) of T_{avg} (upper connectors) and thermal offset (lower ones). c) Boxplots with jitter points, categorised by climate type, of T_{avg} and thermal offset at different landform categories. Negative and positive values of thermal offset indicate colder and warmer T_{avg} of a spring when compared with that of its reference slope counterpart (T_{ref}). Pairwise comparisons between reference slope springs and all other categories are all significant (p < 0.01), and are not shown. NOTES: see Table 1 for the meaning of acronyms. Pairwise comparisons are based on Kruskal-Wallis tests and post-hoc comparisons with adjusted Dunn's test and Bonferroni corrections.



Table 3. Mean and standard deviation of T_{avg} at different climates (merged from Köppen climate classes) and landform categories. For each of these climates, CRL springs had significantly lower T_{avg} than reference slopes (p<0.001). CRL springs in mediterranean/semiarid climates had higher T_{avg} than those in polar/subpolar (p<0.001) and in humid continental/oceanic (p=0.007) climates. For reference slope springs, significant differences were found only between mediterranean/semiarid and polar/subpolar climates (p<0.001).

	Polar/subpolar	Humid continental/oceanic	Mediterranean/semiarid
	T _{avg} (°C)	T _{avg} (°C)	T _{avg} (°C)
1. Clean-ice glacier (Gla)	0.9 ± 0.9	-	A
2. Cold rocky landform (CRL)	1.9 ± 1.0	2.4 ± 1.4	4.2 ± 2.6
2.1 Debris-covered glacier (DCG)	0.8 ± 0.1	1.2 ± 0.2	<u>'-</u>
2.2 Young moraine (MO)	2.2 ± 0.9	2.3 ± 0.3	3.4
2.3 Rock glacier (RG)	1.6 ± 0.8	2.6 ± 1.5	3.4 ± 2.8
2.4 Protalus rampart (PR)	1.6 ± 0.8	1.5 ± 0.3	4.5 ± 1.6
2.5 Talus slopes (TAL)	2.7 ± 1.1	2.6 ± 2.3	5.1 ± 2.9
3. Reference slope (Ref)	4.5 ± 1.1	5.8 ± 1.4	7.5 ± 2.7

3.2 Environmental characteristics of cold springs

The regression tree analysis resulted in different tree structures and different importance of predictors between Tavg and thermal offset response variables (Figure 3). For Tavg, the likelihood of cold springs was greater for colder climates (first node), where soil and vegetation cover was sparse or absent (second node), and where the vegetation structure was simple or absent (third node). In the same climates, extensive or continuous soil/vegetation cover was associated with a much lower frequency of cold springs. In contrast, for mediterranean/semiarid climates, the likelihood of cold springs was related more to larger clast size of the landforms (second node) and to the likelihood of permafrost (third node), while lower vegetation cover (fourth node) was more related to cold spring presence (Figure 3a). For thermal offset (Figure 3b), clast size of the landform (first node) was by far the most important predictor (Figure 3c), with larger clasts more likely reflecting negative thermal offset. Simple vegetation structure (second node) was related to stronger thermal offset, especially for the absent/sparse class than intermediate classes of permafrost conditions (third node). In the latter, absent/sparse soil cover (fourth node) was related to higher thermal offset than extensive/continuous soil cover.

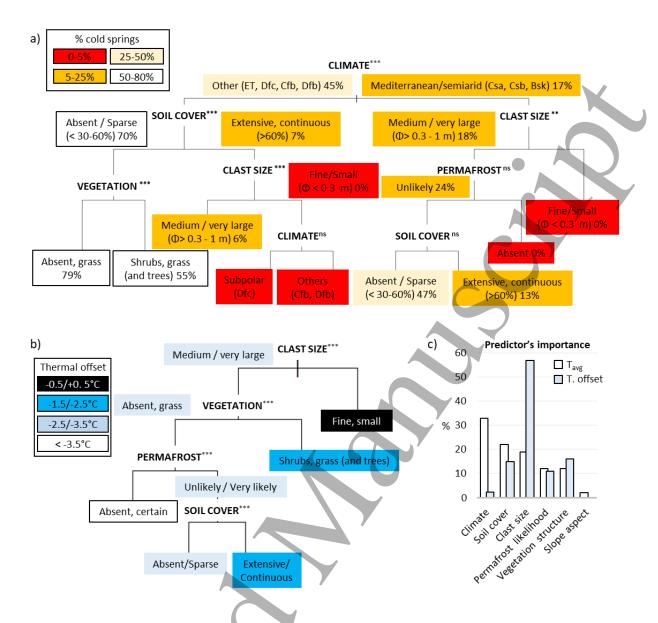


Figure 3. Results of the regression trees. a) Tree based on T_{avg} (°C) as response variable. For each node of the tree diagram, the percentage of cold springs (< 2°C) is highlighted for the lower branches (with colours representing percentage ranges; see upper box legend), and the significance of the pairwise comparison (Mann-Whitney test) is provided (*p<0.05, **p<0.01, ***p<0.001). b) Regression tree based on the thermal offset (°C) as response variable with pairwise comparisons at each node. Different colours of the branches indicate different thermal offset ranges calculated as average values at each branch. NOTE: "medium/large" clast size also includes ice/lithic mix (Debris-covered and clean glaciers). c) Relative importance of the predictors in the two trees. NOTE: For the thermal offset, predictor's importance of slope aspect < 1%.

3.3 Temperature variability and practical implications

When accounting for the temporal variability of water temperature, daily and seasonal fluctuations indices were generally lower in CRL than in reference slopes, yet these differences were not significant. The warm-period response index increased progressively from CRL to reference slope and clean glacier springs, with the latter category having a large variability of the index (Figure 4a). Among CRLs, most young moraines had a negative

response to warm periods relating to a decreasing trend of water temperature from early to late summer, which remained unaltered during the warm period. The warm-period response index was significantly lower in polar/subpolar climates (Dfc) than in humid temperate/continental and mediterranean/semiarid climates (p < 0.001). In reference slope springs, the indices of seasonal and daily fluctuations and the index of response to warm periods did not differ significantly among climate categories. No variables were significant when attempting regression trees with the three indices as response variables.

Our PCA analysis supported a bidimensional space (explaining 78% of the variance) where the three indices were positively related to the first component, and T_{avg} and thermal offset were positively related to the second one. Within the PCA space, landform categories are generally clustered along PC2 and more uniformly distributed along the PC1 (Figure 4b).

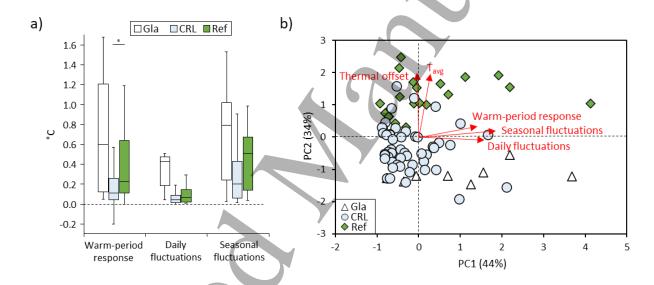


Figure 4. Indices of temporal variations of water temperature and their relation with temperature variables. a) Boxplots of the indices of warm-period response, daily fluctuations, and seasonal fluctuations in glacier, CRL, and reference slope springs (outliers removed to aid visualization). b) PCA biplot of the thermal variables with springs categories highlighted. The two components were extracted based on an Eigenvalue larger than 1.

4. Discussion

Cold rocky landforms are overlooked strongholds for cold spring habitats in mountain ecosystems. While prior research has focused mainly on rock glaciers, we provide evidence that other landforms can also support cold water in a variety of landscapes and climates. The main factors making CRLs act as "hydrological refrigerators" in all climate categories

were: large clast size of the surface, low soil cover, poor vegetation structure, and higher likelihood of permafrost.

4.1 Cold meltwater contribution of springs related to ice

Ice meltwater in clean-ice glaciers, debris-covered glaciers, and ice-cored young moraines (Lukas, 2011; Gärtner-Roer and Bast, 2019) is likely the main cooling agent of spring waters. This is likely because of the predominant influence from latent heat of melting ice and snow (i.e., meltwater has an initial temperature of 0°C), as well as the flow of water in contact with ice (conductive fluxes; Outcalt et al., 1990). For moraine waters, we hypothesize that hydrological subsurface connections with glaciers (Hayashi, 2020) or permafrost-rich areas located upstream represent the main cooling processes. This was supported by a decreasing trend of water temperature from early to late summer that might be explained by a progressive activation and increase of these hydrological connections. In rock glaciers, protalus ramparts, and talus slopes, similar water pathways with permafrost and (at some locations) clean-ice glaciers may occur (e.g., Brighenti et al., 2019; Wagner et al., 2021).

4.2 Landform structure enhances cooling mechanisms

A unique air circulation regime is likely the most important driver of air cooling within CRLs (Delaloye and Lambiel, 2005; Morard et al., 2010; Millar et al., 2014; Germain and Milot, 2024; Amschwand et al., 2024; Wiegand and Kneisel, 2024). While these cooling processes have been investigated for their ability to promote permafrost, the same mechanisms may also cool the water seeping through the landform, and thus maintaining cool internal aquifers (Jones et al., 2019; Zegers et al., 2024). This air circulation is active only when the upper and the lower portions of the landform are connected with each other and the atmosphere. As such, a blocky-clast composition ensures the presence of voids and air circulation within the landform, whereas the barren surface allows for efficient exchange with the atmosphere (Carturan et al., 2024). Notably, these processes can be responsible for the export of ~90% of the incoming heat, hence protecting ground ice from melting (Amschwand et al., 2024). The presence of snow and ice is an additional driver of cooling. The longer persistence of snow cover among the boulders, including enhanced cold surfaces, can further insulate the landform interior, providing water cooling through conduction and latent heat release throughout summer (Stoy et al., 2018).

Overall, these intercorrelated cooling processes, which are more intense in ice-rich landforms, thermally shield air and water against the external atmosphere. The presence of perennial ice is generally related to low water temperatures at springs from rock glaciers (Carturan et al., 2024). Spring water temperature is considered the most reliable hydrological proxy for ground-ice occurrence in mountain areas (e.g., Haeberli, 1975; Strozzi et al., 2004; Carturan et al., 2016). The occurrence and extent of perennial ice is difficult to measure in CRLs, requiring surface temperature measurement under snow cover, geophysical investigations, or borehole drilling, that are often not feasible in remote settings. Visual estimations and remote sensing allow for assessment in actively moving rock glaciers (implying embedded ice), and not in inactive rock glaciers that can still contain perennial ice, nor in taluses and other immobile landforms. However, our work highlights that the visual estimations of key parameters (clast size, vegetation type and extent) might be more useful than the identification of ice when surveying for cold springs.

4.3 Springs from CRLs are colder than those from reference slopes

CRL springs were 3-5°C (and up to 9°C) colder than reference slope springs; this difference increased from polar/subpolar to temperate and mediterranean climates. This implies that even though cold springs are relatively rare in these climates, the cooling capacity of CRLs is maintained and where present, is even more important than in colder climates. For this reason, a stronger thermal offset was identified in areas with either continuous or absent permafrost. In areas of homogeneous permafrost presence or absence, large clast size and vegetation structure are sufficient indicators of cooling mechanisms. In contrast, where permafrost occurrence is spatially heterogeneous (intermediate classes in our analysis), an additional indicator is the total cover of soil/vegetation as it has an impact on air ventilation. It should be noted that the groundwaters examined in this study are sourced by local systems within unconsolidated sediments or a relatively thin zone of regolith, not from deeper bedrock aquifers. Therefore, they represent the local thermal condition of the areas directly upstream of the springs.

4.4 Buffered response to warm periods

Springs from CRLs had an attenuated response to warm periods compared to those from reference slopes yet, seasonal and daily variability of water temperature were comparable

between the two groups. CRLs are considered to be shallow aquifers in mountain areas (Hayashi, 2020), where the same drivers that enhance cold air conditions (air circulation, blocky surfaces, ice presence) might also buffer thermal response of associated springs to warm events. In contrast, springs from reference slopes may have relatively shallow (e.g., seepage from lakes) or deep (e.g., mountain block recharge) water pathways, resulting in a more variable physical distance between subsurface flows and the atmosphere (Hayashi, 2020; Somers and McKenzie, 2020). Thus, the stronger response to warm periods in reference slope springs might be related to the fact that we investigated headwater areas, where groundwater is less likely to originate from deep pathways (Somers and McKenzie, 2020) and, as such, is more responsive to atmospheric temperature. These different drivers of thermal stability in CRL versus reference slope springs may also reflect their sensitivity to climate warming. While non-CRL aquifers are influenced by increasing air temperatures (Jyväsjärvi et al., 2015; Mastrocicco et al., 2019; Bastiancich et al., 2022), particularly at higher elevations (Niedrist and Füreder, 2020), CRLs and their spring waters are more thermally decoupled from atmospheric conditions (Harris and Pederson, 1998; Morard et al., 2010), which is a fundamental prerequisite for their refugial role.

4.5 Identification of cold springs for ecological studies and biodiversity conservation

Increasingly, research is showing that springs from intact rock glaciers are suitable habitats for cold-adapted ecological communities (see Brighenti et al., 2021). Even though water temperature is just one of several variables characterising stream habitats, cold waters (< 2°C) appear to be a prerequisite for the occurrence of certain cold-adapted species, including those that were previously considered to occur only in clean-ice glacier springs (Martini et al., 2024). However, some cold-adapted microbes and invertebrates may find suitable habitat conditions in slightly warmer waters (cool springs, < 4°C; Hotaling et al., 2019; Tronstad et al., 2020; Reato et al., 2023) that are more frequent in CRLs, and in reference slopes outside mediterranean/semiarid climates. The capacity of CRL spring habitats to support glacial-spring specialists and cold-adapted species in the long term remains to be investigated.

Our study offers preliminary guidance for ecological research aimed at identifying climate refugia for cold-adapted organisms. Where prior knowledge is lacking, barren landforms

composed of large rock clasts and surrounded by barren rock or grasslands should be investigated, and possibly prioritised for conservation. Non-invasive methods based on e-DNA may be used to study spring communities and help identify CRL habitats where target species dwell, allowing investigations over large spatial scales (Carraro et al., 2020). However, the identification of refugia should be done in parallel with the development of a sustainable water management plan to avoid local stressors that hinder the survival of sensitive organisms (Morelli et al., 2020; Keppel et al., 2024).

5. Conclusions

In this study, we found that CRLs can persistently source cold waters in several mountain ranges across the globe. Indeed, the investigated CRL springs are significantly colder than those that do not originate from CRLs, and have buffered responses to warm periods. Given the abundance and widespread distribution of cold rocky landforms, we encourage future work to address three research priorities.

First, we need long-term records of water temperature in CRL springs to understand if they are warming and how fast, especially when compared with springs from reference slopes. Even for these reference springs, little is known on the likely different influence of climate change between those resulting from shallow aquifers and those from deep bedrock aquifers. It could be hypothesised that the former type of springs, although very rare at high elevations, is less responsive to short-term variations of air temperature and as such it is more suitable for cold-adapted organisms (depending on the local mean annual air temperature). Second, studies should address the hydrological persistence of CRL springs, because the suitability of cold springs to act as refugia is related to the supply of water and CRL spring discharge is often low (Martini et al., 2024). Given the projected frequency of dry spells (Felsche et al., 2024), droughts and flow intermittency may become strong ecological drivers (Chanut et al., 2023; Leathers et al., 2023). Understanding the hydrological capacity of CRLs in scenarios of reduced water availability is of paramount importance to sustainable conservation of mountain springs, particularly in arid and semi-arid climates. Third, the suitability of CRL springs for coldwater specialists is a promising yet relatively unexplored

field of research as most studies on alpine river ecology focus on glaciers (Milner et al., 2017).

New ecological studies may broaden the geomorphological perspective of CRL springs, so far restricted to rock glaciers, and investigate different types of landforms that remain overlooked in hydrological (e.g., protalus ramparts, ice caves; Hotaling et al., 2019; Tronstad et al., 2020; Latella and Brighenti, 2024) and ecological (young moraines, protalus ramparts) research. Investigating the extent of coldwater habitat downstream from the CRL spring sources may shed light on the availability of appropriate conditions for survival of coldadapted species (Harrington et al., 2017). These may be isolated and limited in extent, leading to localized populations that are particularly prone to local extinction. Acknowledging the ecological importance of water temperature (Bonacina et al., 2023), extending the investigations to other characteristics of the habitat (water chemistry, channel stability, and food availability) and the community (e.g., species interactions, primary production) is of paramount importance in identifying the key set of conditions that allow cold-adapted species to survive (e.g., Martini et al., 2024). Although rising temperatures in streams and rivers are a consequence of a warming climate, human disturbances also contribute to the decline in the abundance of cold-water organisms (Birrell et al., 2019). The conservation of cold springs as climate refugia would benefit from interdisciplinary research among social, economic, and natural sciences, and from an improved understanding of the relationship between geomorphological drivers, habitat conditions, and cold-adapted biodiversity.

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References

- 447 Altmann, M., Piermattei, L., Haas, F., Heckmann, T., Fleischer, F., Rom, J., ... & Becht, M.
- 448 (2020). Long-term changes of morphodynamics on little ice age lateral moraines and the
- resulting sediment transfer into mountain streams in the Upper Kauner Valley, Austria.
- *Water*, 12(12), 3375. https://doi.org/10.3390/w12123375
- 451 Amschwand, D., Scherler, M., Hoelzle, M., Krummenacher, B., Haberkorn, A., Kienholz, C., &
- 452 Gubler, H. (2024). Surface heat fluxes at coarse blocky Murtèl rock glacier (Engadine,
- 453 eastern Swiss Alps). The Cryosphere, 18(4), 2103-2139. https://doi.org/10.5194/tc-18-2103-
- 454 <u>2024</u>
- 455 Ballantyne, C. K. (2002). Paraglacial geomorphology. Quaternary Science Reviews, 21(18-19),
- 456 1935-2017. https://doi.org/10.1016/S0277-3791(02)00005-7
- 457 Bastiancich, L., Lasagna, M., Mancini, S., Falco, M., & De Luca, D. A. (2021). Temperature and
- discharge variations in natural mineral water springs due to climate variability: a case study
- in the Piedmont Alps (NW Italy). *Environmental geochemistry and health*, 1-24.
- 460 https://doi.org/10.1007/s10653-021-00864-8
- Barsch, D., & Caine, N. (1984). The nature of mountain geomorphology. *Mountain Research*
- 462 and Development, 287-298. https://doi.org/10.2307/3673231
- 463 Bearzot, F., Colombo, N., Cremonese, E., di Cella, U. M., Drigo, E., Caschetto, M., ... &
- 464 Rossini, M. (2023). Hydrological, thermal, and chemical influence of an intact rock glacier
- discharge on mountain stream water. Science of The Total Environment, 876, 162777.
- 466 <u>https://doi.org/10.1016/j.scitotenv.2023.162777</u>
- 467 Birrell, J. H., Meek, J. B., & Nelson, C. R. (2019). Decline of the Giant Salmonfly Pteronarcys
- 468 californica Newport, 1848 (Plecoptera: Pteronarcyidae) in the Provo River, Utah, USA.
- *Illiesia*, 15(5), 53-97. https://doi.org/10.25031/2019/15.05
- Bollati, I. M., Viani, C., Masseroli, A., Mortara, G., Testa, B., Tronti, G., ... & Reynard, E.
- 471 (2023). Geodiversity of proglacial areas and implications for geosystem services: A
- 472 review. *Geomorphology*, 421, 108517. https://doi.org/10.1016/j.geomorph.2022.108517

- Bonacina, L., Fasano, F., Mezzanotte, V., & Fornaroli, R. (2023). Effects of water temperature
- on freshwater macroinvertebrates: A systematic review. Biological Reviews, 98(1), 191-221.
- 475 <u>https://doi.org/10.1111/brv.12903</u>
- Böckli, L., Brenning, A., Gruber, S., and Noetzli, J. (2012). Permafrost distribution in the
- 477 European Alps: calculation and evaluation of an index map and summary statistics. The
- *Cryosphere*, *6*, 807–820, https://doi.org/10.5194/tc-6-807-2012
- 479 Breiman, L. (2017). Classification and regression trees. Chapman and Hall/CRC, New York
- 480 (USA). 368 pp. https://doi.org/10.1201/9781315139470
- Brighenti, S., Tolotti, M., Bruno, M. C., Engel, M., Wharton, G., Cerasino, L., ... & Bertoldi, W.
- 482 (2019). After the peak water: the increasing influence of rock glaciers on alpine river
- 483 systems. *Hydrological Processes*, *33*(21), 2804-2823. https://doi.org/10.1002/hyp.13533
- 484 Brighenti, S., Tolotti, M., Bertoldi, W., Wharton, G., & Bruno, M. C. (2021). Rock glaciers and
- paraglacial features influence stream invertebrates in a deglaciating Alpine area. Freshwater
- 486 Biology, 66(3), 535-548. https://doi.org/10.1111/fwb.13658
- Brighenti, S., Hotaling, S., Finn, D. S., Fountain, A. G., Hayashi, M., Herbst, D., ... & Millar, C. I.
- 488 (2021). Rock glaciers and related cold rocky landforms: Overlooked climate refugia for
- mountain biodiversity. *Global Change Biology*, 27(8), 1504-1517.
- 490 https://doi.org/10.1111/gcb.15510
- 491 Carraro, L., Mächler, E., Wüthrich, R., & Altermatt, F. (2020). Environmental DNA allows
- 492 upscaling spatial patterns of biodiversity in freshwater ecosystems. *Nature Communications*,
- 493 11, 3585. https://doi.org/10.1038/s41467-020-17337-8
- 494 Carturan, L., Zuecco, G., Seppi, R., Zanoner, T., Borga, M., Carton, A., & Dalla Fontana, G.
- 495 (2016). Catchment-scale permafrost mapping using spring water characteristics. *Permafrost*
- 496 and Periglacial Processes, 27(3), 253-270. https://doi.org/10.1002/ppp.1875
- 497 Carturan, L., Zuecco, G., Andreotti, A., Boaga, J., Morino, C., Pavoni, M., ... & Zumiani, M.
- 498 (2024). Spring-water temperature suggests widespread occurrence of Alpine permafrost in
- 499 pseudo-relict rock glaciers. The Cryosphere, 18, 5713–5733. https://doi.org/10.5194/tc-18-
- 500 <u>5713-2024</u>

- 501 Chanut, P. C., Drost, A., Siebers, A. R., Paillex, A., & Robinson, C. T. (2023). Flow
- intermittency affects structural and functional properties of macroinvertebrate
- communities in alpine streams. Freshwater Biology, 68(2), 212-228.
- 504 https://doi.org/10.1111/fwb.14018
- 505 Christensen, C. W., Hayashi, M., & Bentley, L. R. (2020). Hydrogeological characterization of
- an alpine aquifer system in the Canadian Rocky Mountains. Hydrogeology journal, 28(5),
- 507 1871. https://doi.org/10.1007/s10040-020-02153-7
- Colucci, R. R., Boccali, C., Žebre, M., & Guglielmin, M. (2016). Rock glaciers, protalus
- ramparts and pronival ramparts in the south-eastern Alps. *Geomorphology*, 269, 112-121.
- 510 <u>https://doi.org/10.1016/j.geomorph.2016.06.039</u>
- Colucci, R. R., Forte, E., Žebre, M., Maset, E., Zanettini, C., & Guglielmin, M. (2019). Is that a
- relict rock glacier?. *Geomorphology*, 330, 177-189.
- 513 https://doi.org/10.1016/j.geomorph.2019.02.002
- 514 Curry, A. M. (2023). Talus slopes. Reference Module in Earth Systems and Environmental
- *Sciences*. https://doi.org/10.1016/B978-0-323-99931-1.00047-7
- 516 Delaloye, R., & Lambiel, C. (2005). Evidence of winter ascending air circulation throughout
- talus slopes and rock glaciers situated in the lower belt of alpine discontinuous permafrost
- 518 (Swiss Alps). Norsk Geografisk Tidsskrift-Norwegian Journal of Geography, 59(2), 194-203.
- 519 https://doi.org/10.1080/00291950510020673
- 520 Fahy, J. C., Demierre, E., & Oertli, B. (2024). Long-term monitoring of water temperature and
- 521 macroinvertebrates highlights climate change threat to alpine ponds in protected
- areas. *Biological Conservation*, 290, 110461. https://doi.org/10.1016/j.biocon.2024.110461
- Felsche, E., Böhnisch, A., Poschlod, B., & Ludwig, R. (2024). European hot and dry summers
- are projected to become more frequent and expand northwards. Communications Earth &
- 525 Environment, 5(1), 410. https://doi.org/10.1038/s43247-024-01575-5
- 526 Giersch, J. J., Jordan, S., Luikart, G., Jones, L. A., Hauer, F. R., & Muhlfeld, C. C. (2015).
- 527 Climate-induced range contraction of a rare alpine aquatic invertebrate. Freshwater Science,
- 528 34(1), 53-65. https://doi.org/10.1086/679490

- 529 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),
- 531 2577-2589. https://doi.org/10.1111/gcb.13565
- 532 Gärtner-Roer, I., & Bast, A. (2019). (Ground) ice in the proglacial zone. Geomorphology of
- 533 Proglacial Systems: Landform and Sediment Dynamics in Recently Deglaciated Alpine
- *Landscapes*, 85-98. https://doi.org/10.1007/978-3-319-94184-4-6
- Germain, D., & Milot, J. F. (2024). An overcooled coarse-grained talus slope at low elevation:
- New insights on air circulation and environmental impacts, Cannon Cliff, New Hampshire,
- 537 USA. Earth Surface Processes and Landforms, 49(5), 1705-1720.
- 538 <u>https://doi.org/10.1002/esp.5792</u>
- 539 Glas, R., Lautz, L., McKenzie, J., Moucha, R., Chavez, D., Bryan, M., & Lane Jr, J. W. (2019).
- 540 Hydrogeology of an alpine talus aquifer: Cordillera Blanca, Peru. Hydrogeology
- *Journal*, 27(6), 2137-2154. https://doi.org/10.1007/s10040-019-01982-5
- Gruber, S. (2012). Derivation and analysis of a high-resolution estimate of global permafrost
- zonation. *The Cryosphere*, *6*(1), 221-233. https://doi.org/10.5194/tc-6-221-2012
- Haeberli, W. (1975). Untersuchungen zur Verbreitung von Permafrost zwischen Flüelapass
- 545 und Piz Grialetsch (Graubünden) (p. 221). Versuchsanstalt für Wasserbau, Hydrologie und
- 546 Glaziologie an der ETH.
- Harrington, J. S., Hayashi, M., & Kurylyk, B. L. (2017). Influence of a rock glacier spring on the
- 548 stream energy budget and cold-water refuge in an alpine stream. *Hydrological*
- *Processes*, *31*(26), 4719-4733. https://doi.org/10.1002/hyp.11391
- Harrington, J. S., Mozil, A., Hayashi, M., & Bentley, L. R. (2018). Groundwater flow and
- storage processes in an inactive rock glacier. *Hydrological Processes*, 32(20), 3070-3088.
- 552 https://doi.org/10.1002/hyp.13248
- Harris, S. A., & Pedersen, D. E. (1998). Thermal regimes beneath coarse blocky
- materials. *Permafrost and periglacial processes*, *9*(2), 107-120.
- 555 https://doi.org/10.1002/(SICI)1099-1530(199804/06)9:2<107::AID-PPP277>3.0.CO;2-G

- Hayashi, M. (2020). Alpine hydrogeology: The critical role of groundwater in sourcing the
- headwaters of the world. *Groundwater*, 58(4), 498-510.
- 558 <u>https://doi.org/10.1111/gwat.12965</u>
- He, J., & Hayashi, M. (2023). Field observation and mathematical representation of the
- 560 hydrogeological function of alpine landforms in the Canadian Rockies. Hydrological
- *Processes*, *37*(5), e14881. https://doi.org/10.1002/hyp.14881
- 562 Hedding, D. W. (2011). Pronival rampart and protalus rampart: a review of
- 563 terminology. *Journal of Glaciology*, *57*(206), 1179-1180.
- 564 <u>https://doi.org/10.3189/002214311798843241</u>
- Hedding, D. W. (2016). Pronival ramparts: A review. *Progress in Physical Geography*, 40(6),
- 566 835-855. https://doi.org/10.1177/0309133316678148
- Hock, R., Rasul, G., Adler, C., Caceres, B., Gruber, S. et al (2019). High Mountain Areas. In:
- Portner H. O., Roberts, D. C., Masson-Delmotte, V., Zhai, P., Tignor, M., Poloczanska, E.,
- Mintenbeck, K., Alegría, A., Nicolai. M., Okem, A., Petzold, J., Rama, B., & Weyer, N. M.
- 570 (eds.). IPCC Special Report on the Ocean and Cryosphere in a Changing Climate.
- 571 https://www.ipcc.ch/site/assets/uploads/sites/3/2019/11/06 SROCC Ch02 FINAL.pdf.
- 572 Hotaling, S., Foley, M. E., Zeglin, L. H., Finn, D. S., Tronstad, L. M., Giersch, J. J., ... &
- 573 Weisrock, D. W. (2019). Microbial assemblages reflect environmental heterogeneity in
- alpine streams. Global Change Biology, 25(8), 2576-2590.
- 575 https://doi.org/10.1111/gcb.14683
- Husson, F., Josse, J., Le, S., & Mazet, J. (2024). Package 'factominer' version
- 577 2.11. Multivariate Exploratory Data Analysis and Data Mining. http://factominer.free.fr
- Janke, J. R., & Bolch, T. (2021). Rock glaciers. Reference module in Earth systems and
- *environmental sciences*. https://doi.org/10.1016/B978-0-12-818234-5.00187-5
- Jones, D. B., Harrison, S., Anderson, K., & Whalley, W. B. (2019). Rock glaciers and mountain
- 581 hydrology: A review. *Earth-Science Reviews*, 193, 66-90.
- 582 https://doi.org/10.1016/j.earscirev.2019.04.001

- Jyväsjärvi, J., Marttila, H., Rossi, P. M., Ala-Aho, P., Olofsson, B. O., Nisell, J., ... & Muotka, T.
- 584 (2015). Climate-induced warming imposes a threat to north European spring
- ecosystems. *Global Change Biology*, *21*(12), 4561-4569. https://doi.org/10.1111/gcb.13067
- 586 Kassambara, A., & Mundt, F. (2017). Package 'factoextra' version 1.0.3. Extract and visualize
- the results of multivariate data analyses, 76(2).
- 588 http://www.sthda.com/english/rpkgs/factoextra
- Keppel, G., Stralberg, D., Morelli, T. L., & Bátori, Z. (2024). Managing climate-change refugia
- to prevent extinctions. *Trends in Ecology & Evolution*, *39*(9), 800-808.
- 591 <u>https://doi.org/10.1016/j.tree.2024.05.002</u>
- Küry, D., Lubini, V., & Stucki, P. (2017). Temperature patterns and factors governing thermal
- response in high elevation springs of the Swiss Central Alps. Hydrobiologia, 793(1), 185-197.
- 594 https://doi.org/10.1007/s10750-016-2918-0
- Langston, G., Bentley, L. R., Hayashi, M., McClymont, A., & Pidlisecky, A. (2011). Internal
- 596 structure and hydrological functions of an alpine proglacial moraine. *Hydrological*
- 597 processes, 25(19), 2967-2982. https://doi.org/10.1002/hyp.8144
- Latella, L., and Brighenti, S. (2024). Exploring Ice Cave Biodiversity in Northeastern Italy.
- 599 Diversity, 16(7), 364. https://doi.org/10.3390/d16070364
- Leathers, K., Herbst, D., Safeeq, M., & Ruhi, A. (2023). Dynamic, downstream-propagating
- thermal vulnerability in a mountain stream network: Implications for biodiversity in the face
- of climate change. *Limnology and Oceanography*, 68, S101-S114.
- 603 https://doi.org/10.1002/lno.12264
- 604 Lencioni, V. (2018). Glacial influence and stream macroinvertebrate biodiversity under
- climate change: Lessons from the Southern Alps. Science of the Total Environment, 622, 563-
- 606 575. https://doi.org/10.1016/j.scitotenv.2017.11.266
- 607 Lencioni, V., Stella, E., Zanoni, M. G., & Bellin, A. (2022). On the delay between water
- temperature and invertebrate community response to warming climate. Science of the Total
- 609 Environment, 837, 155759. https://doi.org/10.1016/j.scitotenv.2022.155759

- 610 Luetscher, M., & Jeannin, P. Y. (2004). A process-based classification of alpine ice
- 611 caves. *Theoretical and Applied Karstology*, 17(5), 5-10.
- 612 Lukas, S. (2012). Processes of annual moraine formation at a temperate alpine valley glacier:
- 613 insights into glacier dynamics and climatic controls. *Boreas*, 41(3), 463-480.
- 614 https://doi.org/10.1111/j.1502-3885.2011.00241.x
- Martini, J., Brighenti, S., Vanek, M., Schwingshackl, T., Vallefuoco, F., Scotti, A., ... & Bottarin,
- R. (2024). Rock glacier springs: cool habitats for species on the edge. *Biodiversity and*
- *Conservation*, 1-26. https://doi.org/10.1007/s10531-024-02937-3
- Mastrocicco, M., Busico, G., & Colombani, N. (2019). Deciphering interannual temperature
- variations in springs of the Campania region (Italy). Water, 11(2), 288.
- 620 <u>https://doi.org/10.3390/w11020288</u>
- Mayr, E., & Hagg, W. (2019). Debris-covered glaciers. *Geomorphology of Proglacial Systems:*
- 622 Landform and Sediment Dynamics in Recently Deglaciated Alpine Landscapes, 59-71.
- 623 https://doi.org/10.1007/978-3-319-94184-4 4
- 624 Millar, C. I., & Westfall, R. D. (2008). Rock glaciers and related periglacial landforms in the
- 625 Sierra Nevada, CA, USA; inventory, distribution and climatic relationships. *Quaternary*
- 626 International, 188(1), 90-104. https://doi.org/10.1016/j.quaint.2007.06.004
- 627 Millar, C. I., & Westfall, R. D. (2019). Geographic, hydrological, and climatic significance of
- 628 rock glaciers in the Great Basin, USA. Arctic, Antarctic, and Alpine Research, 51(1), 232-249.
- 629 https://doi.org/10.1080/15230430.2019.1618666
- 630 Millar, C. I., Westfall, R. D., & Delany, D. L. (2013). Thermal and hydrologic attributes of rock
- 631 glaciers and periglacial talus landforms: Sierra Nevada, California, USA. Quaternary
- 632 International, 310, 169-180. https://doi.org/10.1016/j.quaint.2012.07.019
- 633 Millar, C.I., D. Westfall, R., & Delany, D.L. (2014). Thermal regimes and snowpack relations of
- 634 periglacial talus slopes, Sierra Nevada, California, USA. Arctic, Antarctic, and Alpine
- 635 Research, 46(2), 483-504. https://doi.org/10.1657/1938-4246-46.2.483
- 636 Millar, C. I., Westfall, R. D., Evenden, A., Holmquist, J. G., Schmidt-Gengenbach, J., Franklin,
- 637 R. S., ... & Delany, D. L. (2015). Potential climatic refugia in semi-arid, temperate mountains:

- Plant and arthropod assemblages associated with rock glaciers, talus slopes, and their
- 639 forefield wetlands, Sierra Nevada, California, USA. Quaternary International, 387, 106-121.
- 640 <u>https://doi.org/10.1016/j.quaint.2013.11.003</u>
- 641 Milner, A. M., Khamis, K., Battin, T. J., Brittain, J. E., Barrand, N. E., Füreder, L., ... & Brown, L.
- 642 E. (2017). Glacier shrinkage driving global changes in downstream systems. *Proceedings of*
- 643 the National Academy of Sciences, 114(37), 9770-9778.
- 644 <u>https://doi.org/10.1073/pnas.1619807114</u>
- Morard, S., Delaloye, R., & Lambiel, C. (2010). Pluriannual thermal behavior of low elevation
- cold talus slopes in western Switzerland. *Geographica Helvetica*, *65*(2), 124-134.
- 647 <u>https://doi.org/10.5194/gh-65-124-2010</u>
- Morelli, T. L., Barrows, C. W., Ramirez, A. R., Cartwright, J. M., Ackerly, D. D., Eaves, T. D., ...
- & Thorne, J. H. (2020). Climate-change refugia: Biodiversity in the slow lane. Frontiers in
- 650 Ecology and the Environment, 18(5), 228-234. https://doi.org/10.1002/fee.2189
- Muir, D. L., Hayashi, M., & McClymont, A. F. (2011). Hydrological storage and transmission
- characteristics of an alpine talus. *Hydrological Processes*, 25(19), 2954-2966.
- 653 <u>https://doi.org/10.1002/hyp.8060</u>
- Niedrist, G. H., & Füreder, L. (2021). Real-time warming of alpine streams:(re) defining
- invertebrates' temperature preferences. River Research and Applications, 37(2), 283-293.
- 656 https://doi.org/10.1002/rra.3638
- Obleitner, F., Trüssel, M., & Spötl, C. (2024). Climate warming detected in caves of the
- 658 European Alps. Scientific Reports, 14(1), 27435. https://doi.org/10.1038/s41598-024-78658-
- 659 <u>y</u>
- Outcalt, S. I., Nelson, F. E., & Hinkel, K. M. (1990). The zero-curtain effect: Heat and mass
- transfer across an isothermal region in freezing soil. Water Resources Research, 26(7), 1509-
- 662 1516. https://doi.org/10.1029/WR026i007p01509
- Peel, M. C., Finlayson, B. L., & McMahon, T. A. (2007). Updated world map of the Köppen-
- 664 Geiger climate classification. *Hydrology and earth system sciences*, 11(5), 1633-1644.
- 665 https://doi.org/10.5194/hess-11-1633-2007

- Oliva, M., Nývlt, D., & Fernández-Fernández, J. M. (2022). Periglacial Landscapes of Europe.
- Springer Nature Switzerland. 523 pp. https://doi.org/10.1007/978-3-031-14895-8
- Ravanel, L., Duvillard, P. A., Jaboyedoff, M., & Lambiel, C. (2018). Recent evolution of an ice-
- 669 cored moraine at the Gentianes Pass, Valais Alps, Switzerland. Land Degradation &
- 670 Development, 29(10), 3693-3708. https://doi.org/10.1002/ldr.3088
- Reato, A., Carol, E. S., Cottescu, A., & Martínez, O. A. (2021). Hydrological significance of
- 672 rock glaciers and other periglacial landforms as sustenance of wet meadows in the
- Patagonian Andes. Journal of South American Earth Sciences, 111, 103471.
- 674 <u>https://doi.org/10.1016/j.jsames.2021.103471</u>
- Reato, A., Borzi, G., Martínez, O. A., & Carol, E. (2022). Role of rock glaciers and other high-
- altitude depositional units in the hydrology of the mountain watersheds of the Northern
- Patagonian Andes. Science of the Total Environment, 824, 153968.
- 678 https://doi.org/10.1016/j.scitotenv.2022.153968
- Reato, A., Martínez, N. R., Epele, B. L., Borzi, G., & Carol, E. (2024). Rock glacier and
- solifluction lobes groundwater as nutrient sources and refugia for unique macroinvertebrate
- assemblages in a mountain ecosystem of the North Patagonian Andes. Aquatic Sciences,
- 682 86(1), 11. https://doi.org/10.1007/s00027-023-01025-y
- Roy, J. W., & Hayashi, M. (2009). Multiple, distinct groundwater flow systems of a single
- 684 moraine–talus feature in an alpine watershed. *Journal of Hydrology*, 373(1-2), 139-150.
- 685 https://doi.org/10.1016/j.jhydrol.2009.04.018
- 686 Scapozza, C. (2015). Investigation on protalus ramparts in the Swiss Alps. *Geographica*
- *Helvetica*, 70(2), 135-139. https://doi.org/10.5194/gh-70-135-2015
- Serban, R. D., Onaca, A., Serban, M., & Urdea, P. (2019). Block stream characteristics in
- 689 Southern Carpathians (Romania). Catena, 178, 20-31.
- 690 https://doi.org/10.1016/j.catena.2019.03.003
- 691 Shepherd, N., Bergstrom, A., Carling, G., Coombs, M., Bickmore, B., & Hotaling, S. (2024).
- 692 Water temperature and conductivity, Dinwoody Creek glacial watershed, Wind River Range,
- 693 Wyoming, summer 2018, *HydroShare*.
- 694 https://doi.org/10.4211/hs.4c61ac51067e452aaeda64c2dcecb306

- 695 Somers, L. D., & McKenzie, J. M. (2020). A review of groundwater in high mountain
- 696 environments. Wiley Interdisciplinary Reviews: Water, 7(6), e1475.
- 697 <u>https://doi.org/10.1002/wat2.1475</u>
- 698 Stoy, P. C., Peitzsch, E., Wood, D., Rottinghaus, D., Wohlfahrt, G., Goulden, M., & Ward, H.
- 699 (2018). On the exchange of sensible and latent heat between the atmosphere and melting
- 700 snow. *Agricultural and Forest Meteorology*, 252, 167-174.
- 701 <u>https://doi.org/10.1016/j.agrformet.2018.01.028</u>
- Strozzi, T., Kääb, A., & Frauenfelder, R. (2004). Detecting and quantifying mountain
- 703 permafrost creep from in situ inventory, space-borne radar interferometry and airborne
- digital photogrammetry. *International Journal of Remote Sensing*, 25(15), 2919-2931.
- 705 <u>https://doi.org/10.1080/0143116042000192330</u>
- Tampucci, D., Gobbi, M., Marano, G., Boracchi, P., Boffa, G., Ballarin, F., ... & Caccianiga, M.
- 707 (2017). Ecology of active rock glaciers and surrounding landforms: climate, soil, plants and
- 708 arthropods. Boreas, 46(2), 185-198. https://doi.org/10.1111/bor.12219
- Therneau, T., Atkinson, B., Ripley, B., & Ripley, M. B. (2023). Package 'rpart'. Available
- online: cran. ma. ic. ac. uk/web/packages/rpart/rpart. pdf (accessed on 20 September 2023).
- Tolotti, M., Cerasino, L., Donati, C., Pindo, M., Rogora, M., Seppi, R., & Albanese, D. (2020).
- 712 Alpine headwaters emerging from glaciers and rock glaciers host different bacterial
- 713 communities: Ecological implications for the future. Science of the Total Environment, 717,
- 714 137101. https://doi.org/10.1016/j.scitotenv.2020.137101
- Tolotti, M., Brighenti, S., Bruno, M. C., Cerasino, L., Pindo, M., Tirler, W., & Albanese, D.
- 716 (2024). Ecological "Windows of opportunity" influence biofilm prokaryotic diversity
- 717 differently in glacial and non-glacial Alpine streams. Science of The Total Environment,
- 718 173826. https://doi.org/10.1016/j.scitotenv.2024.173826
- 719 Tronstad, L. M., Hotaling, S., Giersch, J. J., Wilmot, O. J., & Finn, D. S. (2020). Headwaters fed
- by subterranean ice: potential climate refugia for mountain stream communities?. Western
- *North American Naturalist*, *80*(3), 395-407. https://doi.org/10.3398/064.080.0311
- Wagner, T., Pauritsch, M., Mayaud, C., Kellerer-Pirklbauer, A., Thalheim, F., & Winkler, G.
- 723 (2019). Controlling factors of microclimate in blocky surface layers of two nearby relict rock

724	glaciers (Niedere Tauern Range, Austria). Geografiska Annaler: Series A, Physical
725	Geography, 101(4), 310-333. https://doi.org/10.1080/04353676.2019.1670950
726 727 728	Wagner, T., Seelig, S., Krainer, K., & Winkler, G. (2021). Storage-discharge characteristics of an active rock glacier catchment in the Innere Ölgrube, Austrian Alps. <i>Hydrological Processes</i> , <i>35</i> (5), e14210. https://doi.org/10.1002/hyp.14210
729	Ward, J. V. (1994). Ecology of alpine streams. Freshwater biology, 32(2), 277-294.
730	https://doi.org/10.1111/j.1365-2427.1994.tb01126.x
731	Wiegand, T., & Kneisel, C. (2024). Monitoring of thermal conditions and snow dynamics at
732	periglacial block accumulations in a low mountain range in central Germany. Earth Surface
733	Processes and Landforms. https://doi.org/10.1002/esp.5998
734	Wilkes, M. A., Carrivick, J. L., Castella, E., Ilg, C., Cauvy-Fraunié, S., Fell, S. C., & Brown, L. E.
735	(2023). Glacier retreat reorganizes river habitats leaving refugia for Alpine invertebrate
736	biodiversity poorly protected. <i>Nature Ecology & Evolution</i> , 7(6), 841-851.
737	https://doi.org/10.1038/s41559-023-02061-5
738	Winkler, G., Wagner, T., Pauritsch, M., Birk, S., Kellerer-Pirklbauer, A., Benischke, R., &
739	Hergarten, S. (2016). Identification and assessment of groundwater flow and storage
740	components of the relict Schöneben Rock Glacier, Niedere Tauern Range, Eastern Alps
741	(Austria). <i>Hydrogeology Journal</i> , 24(4), 937. https://doi.org/10.1007/s10040-015-1348-9
742	Zegers, G., Hayashi, M., & Pérez-Illanes, R. (2024). Improved permafrost modeling in
743	mountain environments by including air convection in a hydrological model. EGUsphere,
744	2024, 1-31. https://doi.org/10.5194/egusphere-2024-2575