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Supplementary material for this article is available [online](#)

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, debris-covered 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 °C–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.

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 °C– 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* 2024).

Given the ongoing decline of cold habitats, ‘cold rocky landforms’ (CRLs) have emerged as the subject of considerable research (e.g. Brighenti *et al* 2021a). 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 2021), debris-covered glaciers (Mayr and Hagg 2019), ice-cored moraines (Altman *et al* 2020, Ravelin *et al* 2018), talus slopes and cones (Millar *et al* 2014, Curry 2023), block streams (Şerban *et al* 2019), protalus/pronival ramparts (Hedding 2011, Hedding 2016, Colucci *et al* 2016), and ice caves (Luetscher and Jeannin 2017, Obleitner *et al* 2024).

Embedded ice, a thick cover of rocky debris that enhances dispersive heat fluxes, and/or unique air ventilation processes are typical of these landforms (Delaloye and Lambiel 2005, Wagner *et al* 2019, Amschwand *et al* 2024), and make their local conditions considerably colder than surrounding environments (Brighenti *et al* 2021a). These cooling mechanisms can still be active even when little or no embedded ice exists in the CRL (Winkler *et al* 2016, Harrington *et al* 2018, Colucci *et al* 2019). Thus, CRLs are predicted to act as climate refugia for cold-adapted terrestrial and aquatic species (Millar *et al* 2015, Tampucci *et al* 2017, Brighenti *et al* 2021a).

However, studies on the role of CRLs in shaping cold aquatic ecosystems are relatively few, 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* 2021b, Tronstad *et al*

2020, Reato *et al* 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 (Bearzot *et al* 2023), hence expanding the stream network suitable for climatically vulnerable fish and other alpine aquatic fauna (Harrington *et al* 2017).

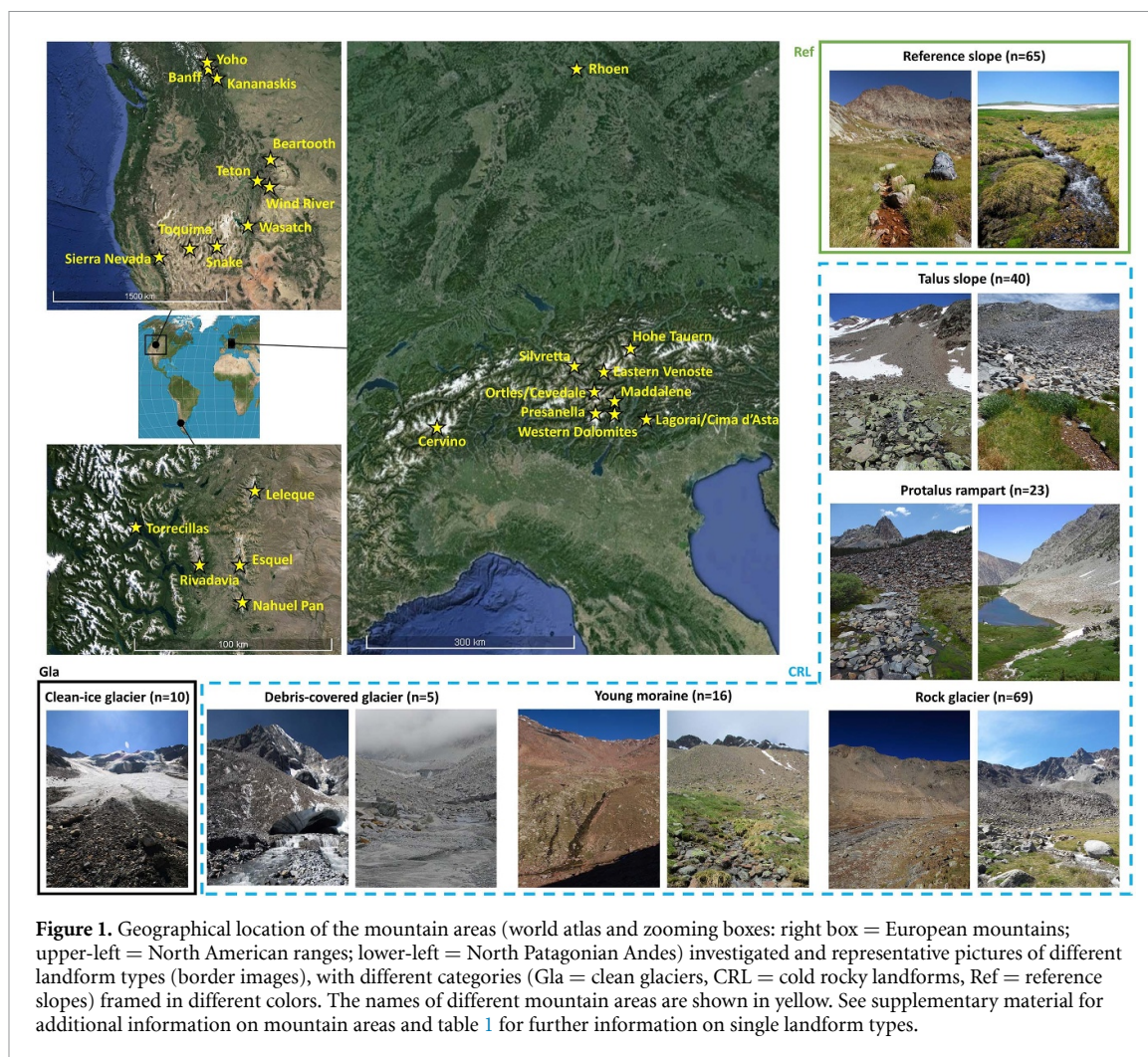
Not all CRLs, however, support cold aquatic habitats. For example, relict forms without embedded ice, features on a sunny aspect, or those with surfaces entirely covered with soil and vegetation, can have relatively warm springs emanating from them (e.g. > 6 °C; Carturan *et al* 2024; Berzescu *et al* 2025). Likewise, even springs not influenced by CRLs or glaciers can still be 1 °C– 3 °C in favorable 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) analyze 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 studies and conservation.

2. Methods

2.1. Field activities

We investigated 228 springs located in the following mountain ranges: Canadian Rocky Mountains, Beartooth Mountains, Teton Range, Wind River Range, Wasatch Range, Snake Range, Toquima Range, Sierra Nevada (North America); North Patagonian Andes (South America); Central German Uplands, Western and Eastern European Alps, and Dolomites (Europe). These ranges span diverse landscapes, geologies, climates, and prevalence of paraglacial and periglacial dynamics (figure 1; supplementary 1; supplementary dataset).



We classified landform types based on the available geological maps or specific studies (supplementary 2) and defined three landform categories: clean (ice) glaciers, CRLs, and reference slopes (table 1). Additionally, we distinguished five types of CRLs (Brighenti *et al* 2021a): 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).

During 2021 and 2023, we instrumented 104 springs with temperature loggers recording at 0.5–4 h 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 snow-melt 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).

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 ($^{\circ}\text{C}$) 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

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 and Westfall 2008, Berthling 2011, Scapozza 2015, Anderson *et al* 2018); 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 <i>et al</i> 2011, Ravelin <i>et al</i> 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 <i>et al</i> 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 <i>et al</i> 2016)
CRL	Rock glacier (RG) . Rocky landform showing evidence of deformation by ice-driven creeping activity (Janke and Bolch 2021)
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 of or are embedded with fine sediments. They include: wet meadows (Reato <i>et al</i> 2021, 2022), 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)

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

Variable	Type of variable	Definition and levels
Köppen climate classes	Categorical	Based on high-resolution ($0.1^\circ \times 0.1^\circ$ grid) map of the Köppen-Geiger climate classification (Peel <i>et al</i> 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 (other orientations)
Permafrost likelihood	Categorical	Based on the global Permafrost Zonation Index (Gruber <i>et al</i> 2012). 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)
Dominant clast size of the landform	Categorical	Estimated in the field: Ice-lithic mix (only for clean and debris-covered glaciers); fine (fine-grained lithic: soil, sandy and gravelly material $\Phi < 5$ 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 the landform	Categorical	Estimated in the field. Soil and vegetation covering 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

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 °C– 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, Tolotti et al 2020, Tronstad 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 1994, Lencioni 2018).

To estimate the environmental drivers of cold springs, we used a 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 T_{avg} 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 $[(A_{\text{day}} - A_{\text{avg}}) / A_{\text{sd}}]$ 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 were 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 $[W_{\text{max}} - W_0]$, where W_{max} (°C) is the maximum daily water temperature reached during the warm period and including the following 7 d (to account for a potential lagged response), and W_0 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 *factminer* (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 2(b)). 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 2(c)). 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).

3.2. Environmental characteristics of cold springs

The regression tree analysis resulted in different tree structures and different importance of predictors between T_{avg} and thermal offset response variables (figure 3). For T_{avg} , 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

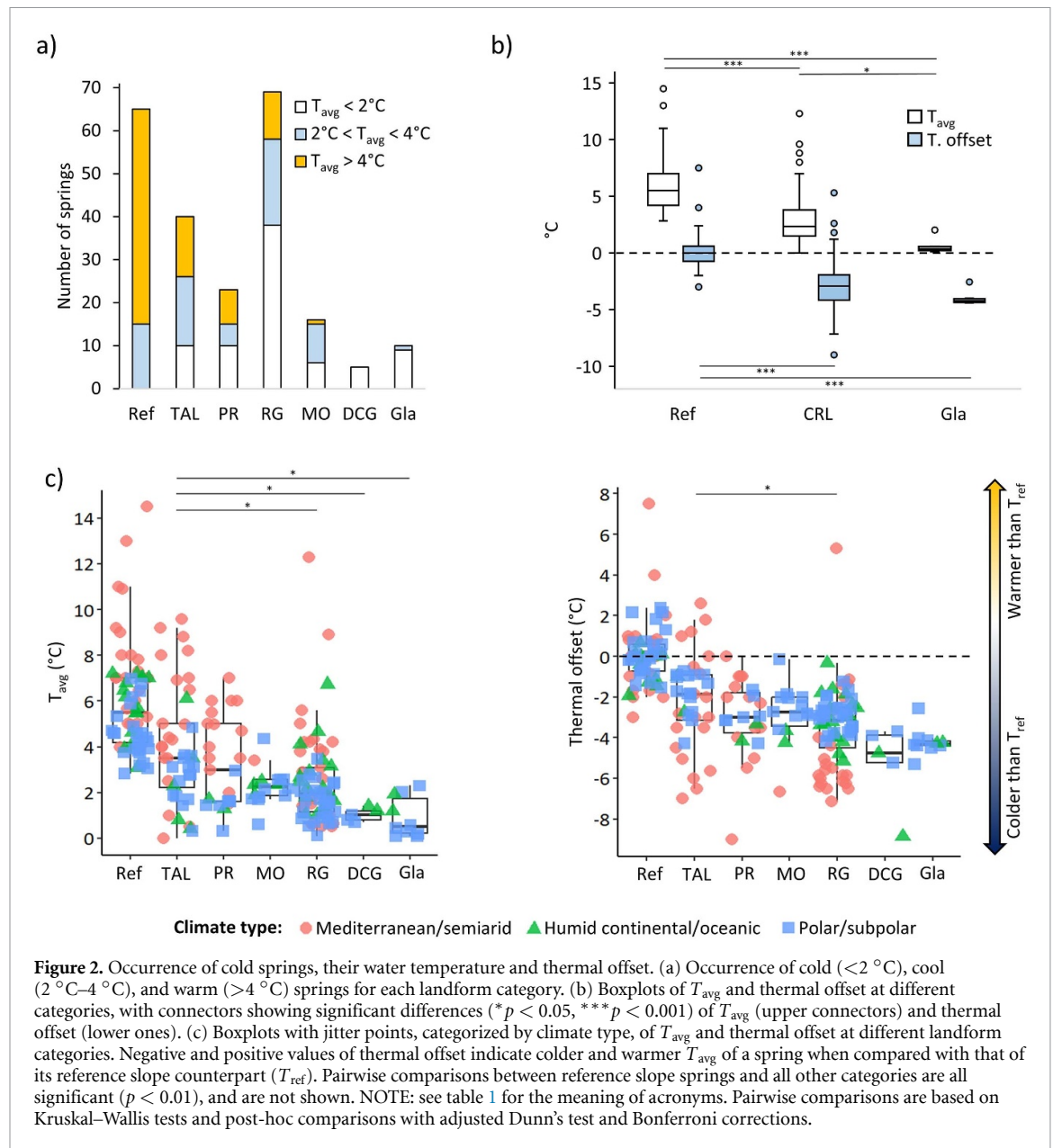
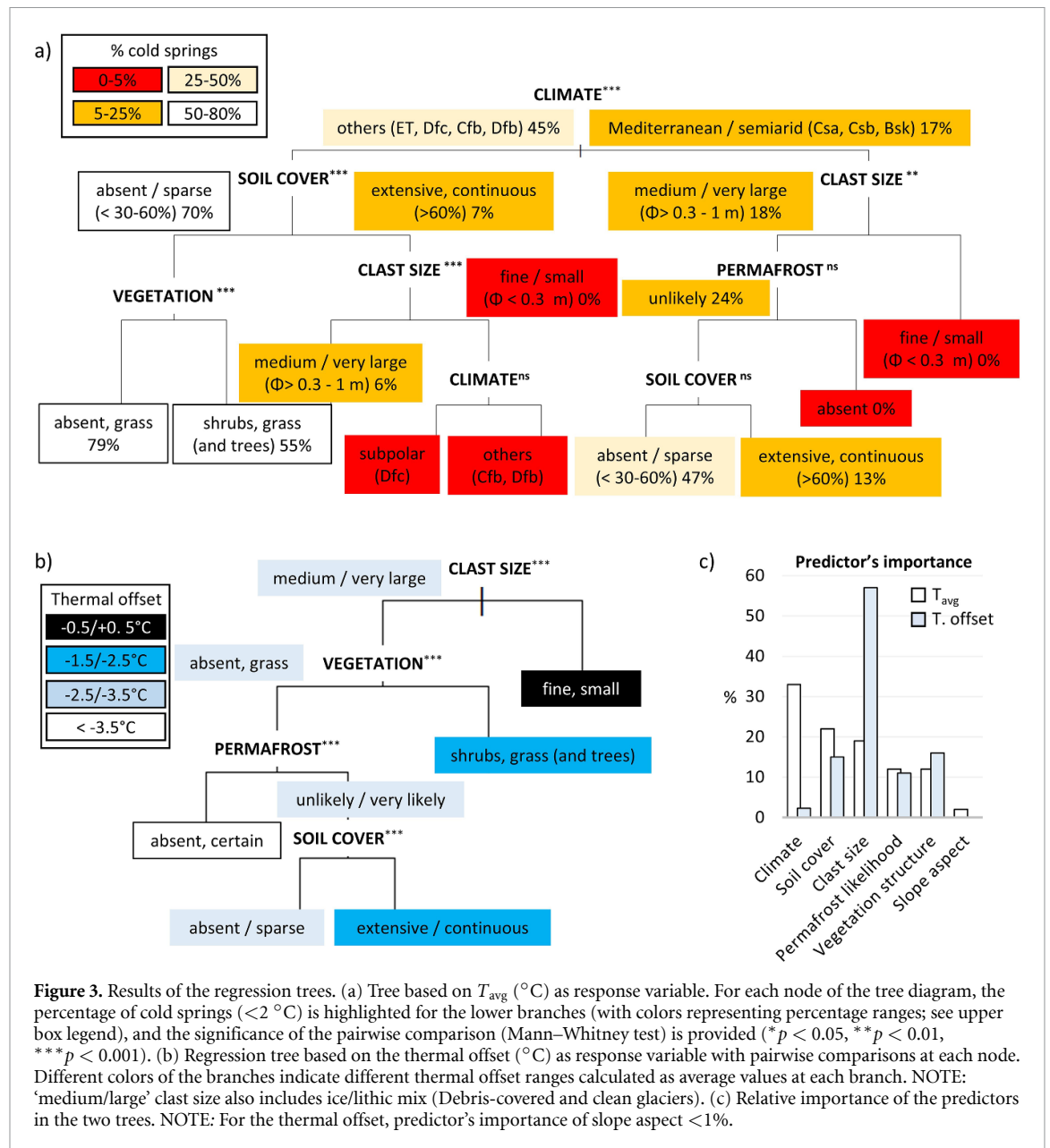


Table 3. Mean and standard deviation of T_{avg} at different climates (merged from Köppen climate classes) and landform categories. For each of these climates, CRL springs had significantly lower T_{avg} than reference slopes ($p < 0.001$). CRL springs in Mediterranean/semiarid climates had higher T_{avg} 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 T_{avg} ($^{\circ}\text{C}$)	Humid continental/oceanic T_{avg} ($^{\circ}\text{C}$)	Mediterranean/semiarid T_{avg} ($^{\circ}\text{C}$)
1. Clean-ice glacier (Gla)	0.9 ± 0.9	—	—
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	—
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



size of the landforms (second node) and to the likelihood of permafrost (third node), while lower soil cover (fourth node) was more related to cold spring presence (figure 3(a)).

For thermal offset (figure 3(b)), clast size of the landform (first node) was by far the most important predictor (figure 3(c)), 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.

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 large variability of the index (figure 4(a)). 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

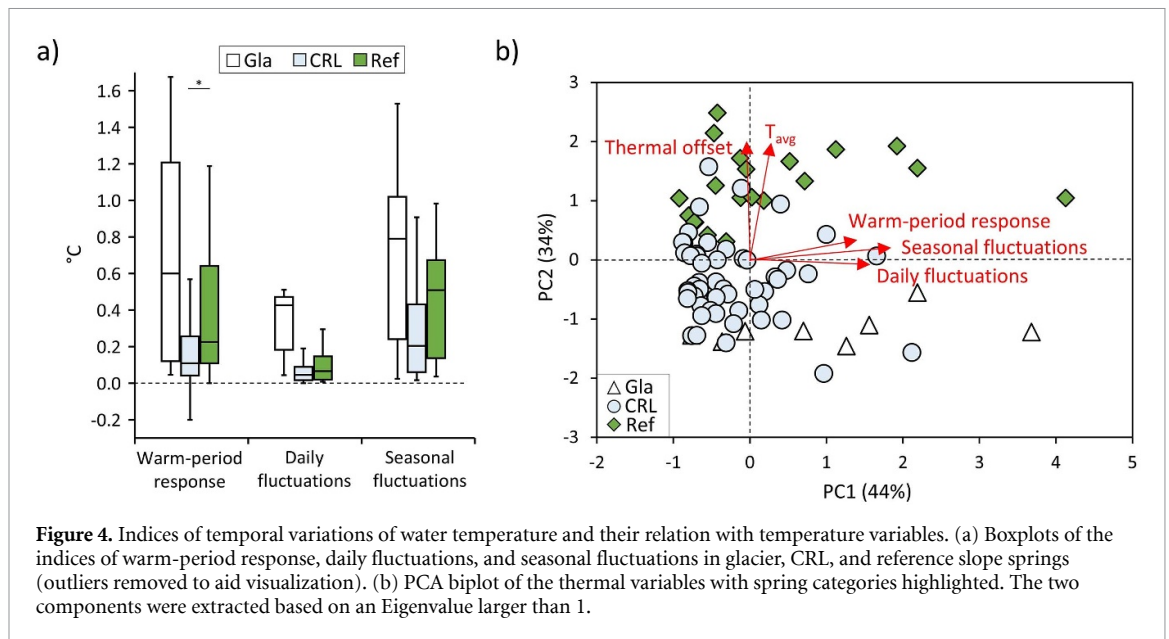


Figure 4. Indices of temporal variations of water temperature and their relation with temperature variables. (a) Boxplots of the indices of warm-period response, daily fluctuations, and seasonal fluctuations in glacier, CRL, and reference slope springs (outliers removed to aid visualization). (b) PCA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

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 4(b)).

4. Discussion

CRLs 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 2012, 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 or persistent snow/ice fields 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, Amschwand *et al* 2024, Germain and Milot 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 $\sim 90\%$ 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. Haerberli 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 $3\text{ }^{\circ}\text{C}$ – $5\text{ }^{\circ}\text{C}$ (and up to $9\text{ }^{\circ}\text{C}$) 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* 2021), particularly at higher elevations (Niedrist and Füreder 2021), CRLs and their spring waters are more thermally decoupled from atmospheric conditions (Harris and Pederson 1998, Morard *et al* 2010, Berzescu *et al* 2025), 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* 2021a). Even though water temperature is just one of several variables characterizing stream habitats, cold waters ($<2\text{ }^{\circ}\text{C}$) 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, $<4\text{ }^{\circ}\text{C}$; 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 prioritized 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 CRLs, 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 hypothesized that the latter 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. proglacial ramparts, ice caves; Hotaling *et al*

2019, Tronstad *et al* 2020, Latella and Brighenti 2024) and ecological (young moraines, proglacial 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 cold-adapted 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.

Data availability statement

All data that support the findings of this study are included within the article (and any supplementary files).

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