Specialized meltwater biodiversity persists despite widespread deglaciation

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Glaciers are important drivers of environmental heterogeneity and biological diversity across mountain landscapes. Worldwide, glaciers are receding rapidly due to climate change, with important consequences for biodiversity in mountain ecosystems. However, the effects of glacier loss on biodiversity have never been quantified across a mountainous region, primarily due to a lack of adequate data at large spatial and temporal scales. Here, we combine high-resolution biological and glacier change (ca. 1850–2015) datasets for Glacier National Park, USA, to test the prediction that glacier retreat reduces biodiversity in mountain ecosystems through the loss of uniquely adapted meltwater stream species. We identified a specialized cold-water invertebrate community restricted to the highest elevation streams primarily below glaciers, but also snowfields and groundwater springs. We show that this community and endemic species have unexpectedly persisted in cold, high-elevation sites, even in catchments that have not been glaciated in ∼170 y. Future projections suggest substantial declines in suitable habitat, but not necessarily loss of this community with the complete disappearance of glaciers. Our findings demonstrate that high-elevation streams fed by snow and other cold-water sources continue to serve as critical climate refugia for mountain biodiversity even after glaciers disappear.

mountain streams | glacier loss | biodiversity | invertebrate communities | climate change

Mountain regions are rich in biodiversity, harboring high levels of species richness and endemism (1). The generation and maintenance of mountain biodiversity ultimately depends on geological and climatic processes that promote habitat heterogeneity across these dynamic landscapes (2). Glaciers and other meltwater sources enhance habitat heterogeneity of mountainous regions by shaping local geomorphology and providing cold meltwater to downstream ecosystems (2–4). However, glaciers are rapidly shrinking and disappearing due to global warming (5–8), and these trends are predicted to accelerate over the coming decades (5, 9). Glacier loss is considered a major threat to biodiversity in mountain regions worldwide (2, 10, 11), yet direct, quantitative tests of how glacier retreat affects biodiversity across a range of spatial scales are scarce (12, 13).

The rapid decline of mountain glaciers reduces meltwater contributions to downstream ecosystems, altering flow regimes, increasing water temperatures, and ultimately homogenizing stream habitats (3, 14). Glacier loss is expected to increase local diversity within streams as more diverse, warmer-water communities shift upstream, but decrease regional diversity as unique glacier-dependent species and communities are lost (15, 16). Global predictions suggest that 11–38% of species will be lost following complete disappearance of glaciers in a region (15). Here, we explicitly test the prediction that glacier recession reduces stream biodiversity through the loss of specialized meltwater species across a large mountainous region.

We conducted this test in Glacier National Park (GNP), Montana, a protected landscape (e.g., World Heritage Site and Biosphere Reserve) that has experienced widespread glacier loss since the end of the Little Ice Age (LIA, ca. 1850; Fig. 1). Like many mountain ranges worldwide, this region harbors an extensive network of high-elevation streams that are highly heterogenous in terms of hydrologic source contributions, temperature, and flow regimes across small spatial extents (<1 km). These habitat mosaics support diverse biological communities with high levels of endemism, including two stoneflies (*Lednia tumana* and *Zapada glacier*) that were recently listed under the US Endangered Species Act exclusively due to climate change-induced glacier and snow loss (17, 18). Of the 146 glaciers present at the end of the LIA, only 35% persisted through 2005 (19), with complete deglaciation predicted by 2100 (5). We focused on alpine stream invertebrates because they are constrained to the highest elevations of aquatic habitats and are considered a "canary in the coal mine" for climate-induced biodiversity loss in mountain ecosystems (20). They are also key components of freshwater communities, performing vital roles in

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Significance

Glaciers are retreating rapidly due to climate change, and these changes are predicted to reduce biodiversity in mountain ecosystems through the loss of specialized meltwater species. However, direct observations of how glacier change affects biological communities living in mountain streams are scarce. Here, we show that a specialized cold-water invertebrate community has unexpectedly persisted in cold, high-elevation streams despite widespread glacier loss and habitat reductions in Glacier National Park since the Little Ice Age (ca. 1850). Although shrinking habitat and increased fragmentation pose significant risks to these range-restricted species, our results demonstrate that specialized meltwater communities may be more resilient to glacier recession than previously thought.

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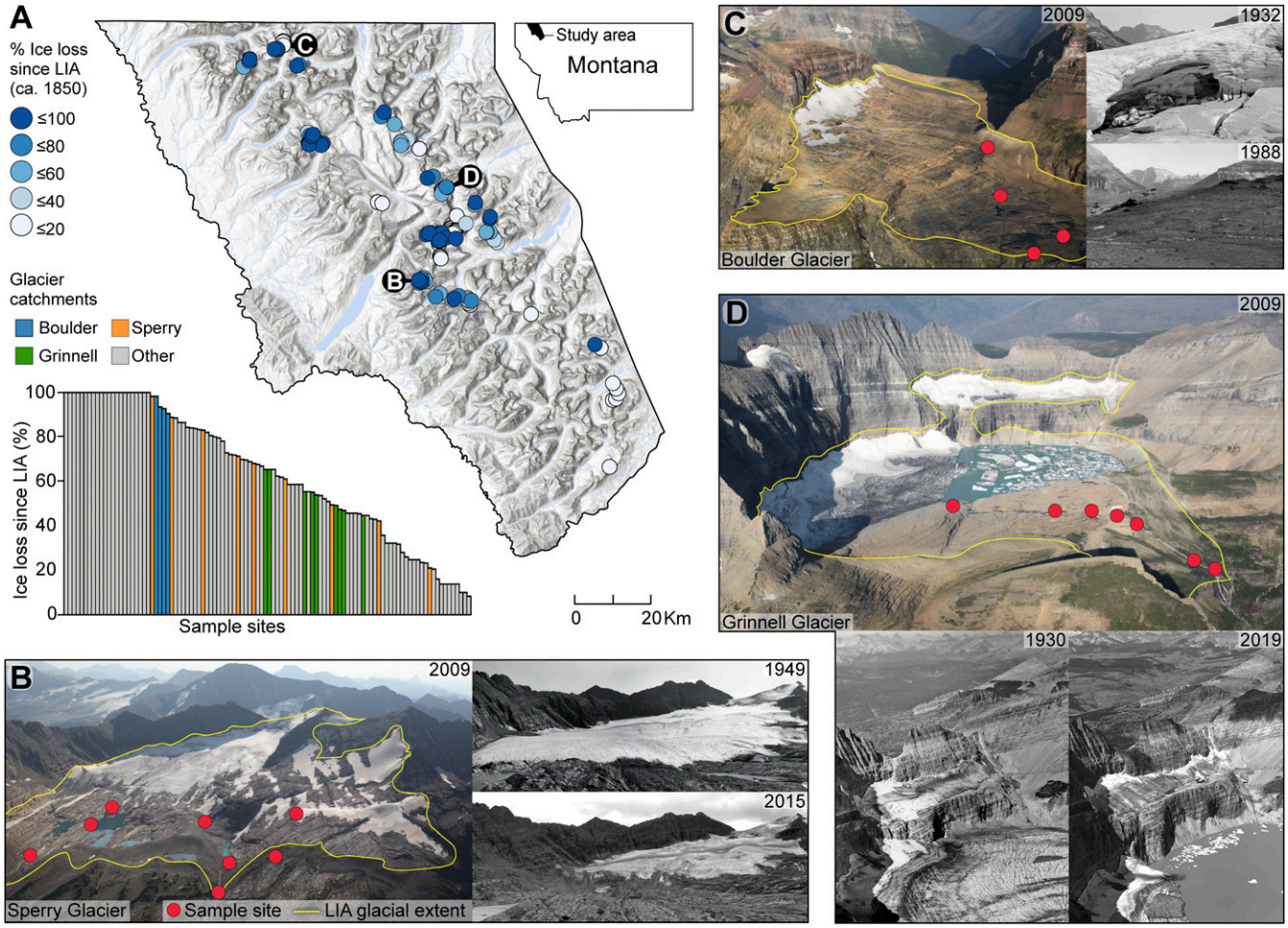

Fig. 1. Glaciers have rapidly receded in GNP since the LIA. (*A*) Map and histogram of glacial loss for all 129 sampling sites (colored circles) since the end of the LIA (ca. 1850). White to dark shading represents topographic relief. Sampling sites (red points), LIA glacier extent (yellow), and historical photos of glacier loss in Sperry (*B*), Boulder (*C*), Grinnell (*D*) basins are shown. Sites where glaciers were absent in LIA are not included in the histogram.

ecosystem functioning, such as organic matter decomposition and nutrient cycling.

Using high-resolution satellite imagery, we quantified change in glacier cover by mapping the area of present-day glaciers (ca. 2015) and analyzing their maximum at the end of the LIA (18, 19, 21). We quantified the abundance and diversity of stream invertebrate communities at 129 sites (within and across streams) in 36 catchments with varying levels of contemporary glacial influence (percentage of present-day glacier cover, 0–91%) and glacier loss since the LIA (8–100%) (22). Sample sites spanned a range of water sources (glacier, snowfield, and groundwater spring), summer water temperatures (1–10 °C), elevations (1,507–2,431 m), and distances to source (1–3,853 m). We identified distinct invertebrate communities using latent Dirichlet allocation (LDA) (23), a probabilistic hierarchical cluster analysis, with no a priori habitat information included. We then evaluated how a suite of geomorphic, topographic, and climatic variables influence both current and future relative abundance of a specialized cold-water community. Our study tests the relationship between present-day community composition and glacial retreat for an entire mountain ecosystem.

Results

Current glacier cover strongly influenced the diversity and composition of stream invertebrate communities across catchments (Fig. 2). Local taxonomic richness was higher in catchments with reduced glacial cover and warmer water temperatures (Fig. 2). These findings are consistent with previous studies (15, 16, 24, 25). Taxonomic differences (dissimilarity) between individual sites and the regional species pool (β-diversity) was higher among sites with greater glacial cover and colder water temperatures. Spatial turnover of taxa accounted for 98.5% of overall beta-diversity among sites, demonstrating that glaciated reaches support distinct communities (*SI Appendix*, Table S2). These results also indicate that local increases in species diversity may come at the expense of regional species diversity as glacier-dependent species are lost and high-elevation streams become environmentally and taxonomically homogenized (15). However, there was significant variation in community diversity among sites without glaciers, suggesting environmental conditions supporting distinct communities may exist elsewhere on the landscape.

We identified a total of 113 taxa in the region's high-elevation species pool that cluster in two distinct communities that commonly cooccur within streams (Fig. 3). One community included species commonly associated with glacier-fed streams, such as the snow midges *Diamesa*, the endangered meltwater stonefly *L. tumana*, and the blind glacier amphipod *Stygobromus glacialis*, many of which are also presumed to be imperiled endemics (18) (Fig. 3 *A* and *B*). This community (hereafter "cold-water community") occupied high-elevation streams immediately below glaciers, perennial snowfields, and springs. The relative abundance of the cold-water community generally increased with

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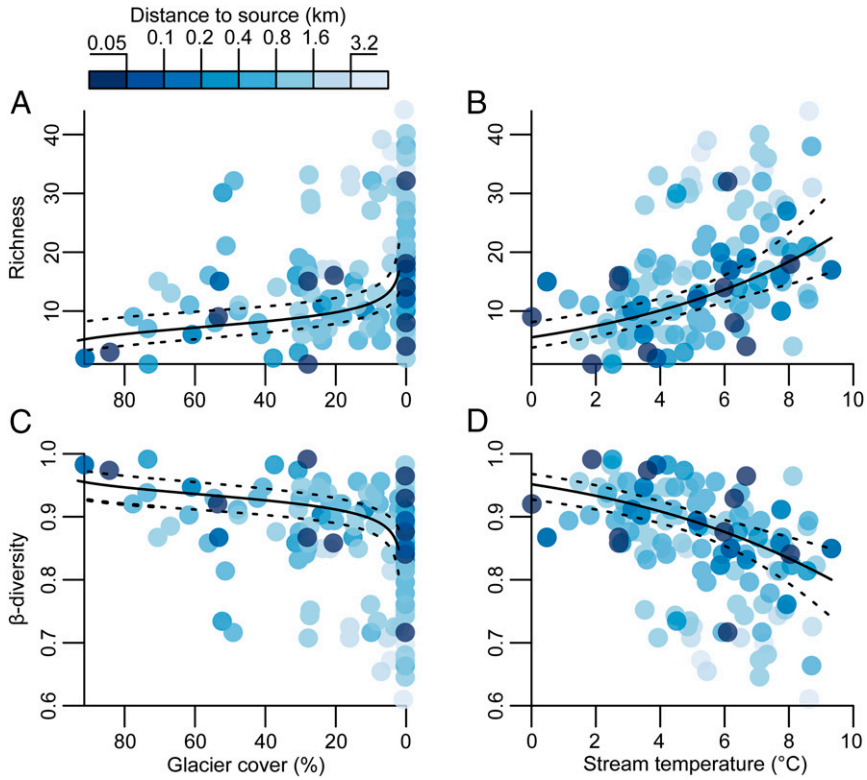

Fig. 2. Glacier cover influences the diversity of mountain stream communities. Taxonomic richness and community diversity of stream macroinvertebrates as a function of glacier cover (*A* and *C*) and water temperature (*B* and *D*). Taxon turnover (β-diversity) between sites and the regional species pool is influenced by glacier cover (*C*) and water temperature (*D*). Solid lines are predictions from the best fit linear mixed effects regressions and dotted lines indicate 95% CIs (*SI Appendix*, Table S1).

glacial cover and decreased with distance to stream source (Fig. 3 *C* and *D*). However, this community was also found in streams fed by snow and groundwater, but in relatively shorter reaches and closer to the source (Fig. 3*D*). These results show that glacial meltwater contributions extend the habitat of the cold-water community, but suitable conditions also exist in nonglaciated catchments.

The cold-water community was also present in high abundance (>80%) in catchments where glaciers were absent (35%) or lost (39%) since the end of the LIA (Fig. 3*E*), and abundance was not influenced by the amount of glacier loss (*SI Appendix*, Fig. S1). In these nonglacial catchments, the cold-water community was retained primarily in the coldest sites supplied by seasonal and multiyear snowpack and groundwater sources (Fig. 3*F*). However, there was still some unexplained variation, suggesting other physical (e.g., flow, turbidity) and biological (e.g., competition, founder effects) factors may have influenced their persistence (13). Importantly, 110 of the 113 taxa (>97%) were found in streams not fed by a present-day glacier, demonstrating that the vast majority of the regional high-elevation species pool are not glacier-obligates. These results do not support the prediction that contemporary glacier loss substantially reduces regional biodiversity through the loss of glacier-obligate species.

Despite persistence of the cold-water community in nonglacial streams, future climate change is predicted to further reduce the extent of suitable habitats supporting this range-restricted cold-water community (Fig. 4). We modeled future habitat conditions and the relative abundance of the cold-water community under future stream temperature warming (representative concentration pathway [RCP] 4.5 and RCP 8.5) and complete glacier loss scenarios. Our projections suggest a 70–80% decline in suitable habitat supporting a high relative abundance of the cold-water community by the end of the century (Fig. 4). Therefore, while cold-water communities are expected to persist despite glacier recession, these climate-induced changes will still reduce habitats supporting this specialized community in high-elevation mountain streams.

Discussion

Our results show that a specialized invertebrate community and its endemic species has persisted despite widespread deglaciation since the LIA glacial maximum. Cold water was the primary driver influencing the abundance of this unique community across glacial and nonglacial streams. Together, our results portend significant upstream range contractions but not necessarily loss of specialized meltwater communities with shrinkage and disappearance of glaciers.

Surprisingly, we found that the vast majority of regional taxonomic diversity was seemingly not lost following deglaciation. However, present-day persistence of specialized meltwater communities may reflect a temporal lag (i.e., climate debt) while erosion of genetic diversity, encounters with downstream competitors, or physiological mismatches between thermal optimal and in situ conditions accumulate and eventually drive local extirpations and extinction (24). For many range-restricted species, especially mountaintop communities, shifts to higher elevations are not possible, and dispersal may be limited by habitat connectivity and ability (26–29). Therefore, habitat loss and fragmentation will likely lead to increased isolation, reduced gene flow, and loss of genetic diversity (30, 31). Analogous distributional shifts to higher latitudes have been observed for a variety of taxa in response to climate change (32), but for many cold-adapted species, space for tracking suitable habitat conditions may be limited at the highest elevations and latitudes of the

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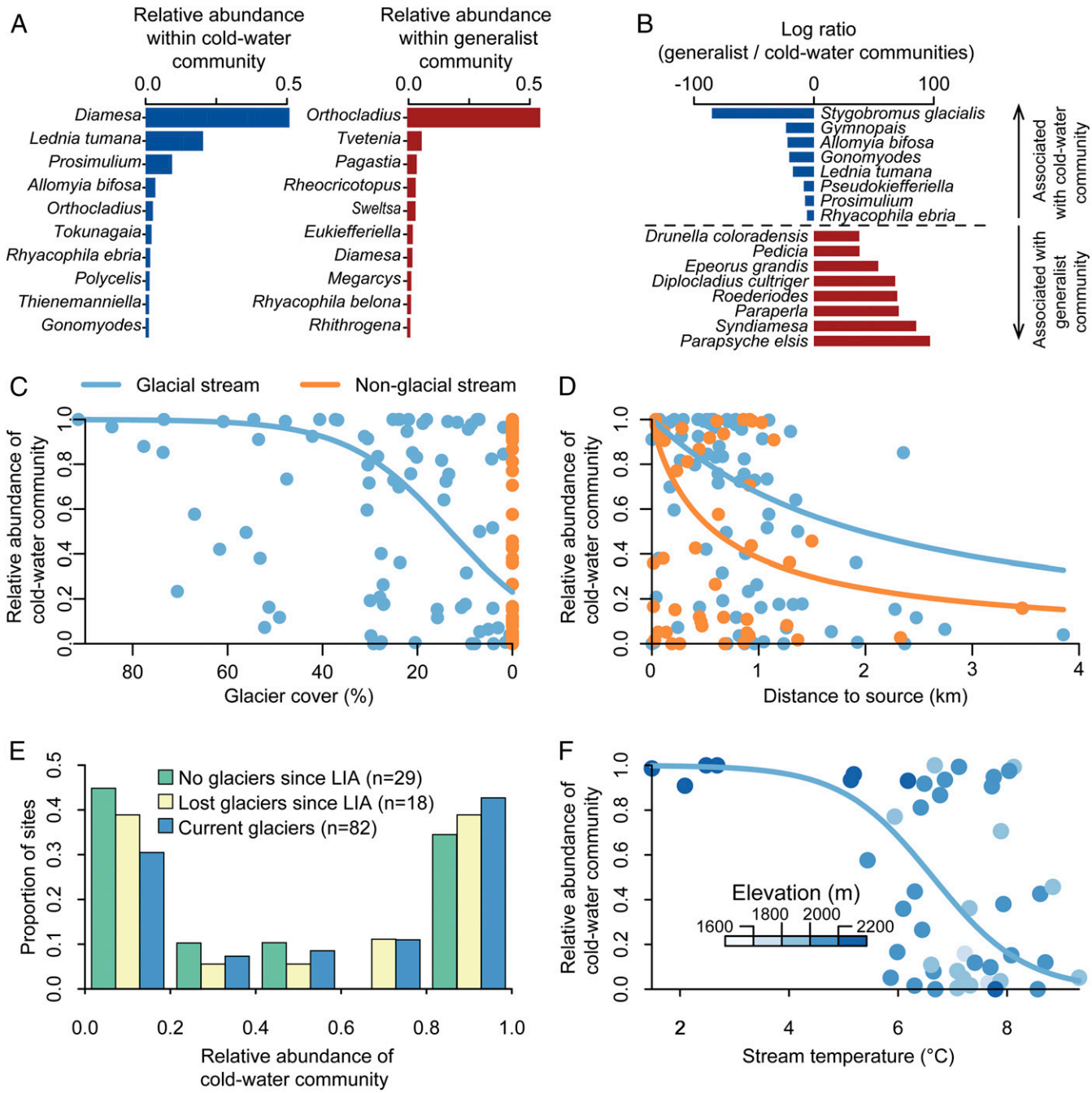

Fig. 3. A specialized cold-water community persists in both glacial and nonglacial streams. (*A*) Relative abundances of the most represented taxa in each of two distinct communities of alpine invertebrates identified by LDA (*SI Appendix*, Table S3). (*B*) The strength of association (magnitude of log-ratio) between taxa and a specific community. (*C*) The relative abundance of the cold-water community across sites with varying glacier cover (blue), including sites without glaciers (orange). (*D*) The relative abundance of the cold-water community as a function of distance to source in glacial (blue) and nonglacial streams (orange). (*E*) A histogram of the relative abundances of the cold-water community across sites that had no glaciers (green), lost their glaciers (yellow), or experienced glacier decline (blue) since the end of the LIA. (*F*) The relative abundance of the cold-water community as a function of stream temperature in sites where glaciers have been absent or that have lost glaciers since the end of the LIA; Lines (blue and orange) in all panels are model averaged predictions from linear mixed effects models (*SI Appendix*, Tables S4 and S5).

globe (33). Erosion of genetic and population diversity—critical elements of ecological diversity—may have severe consequences for resiliency and adaptation of range-restricted communities facing rapid environmental change.

Ultimately, the long-term viability of specialized cold-water communities will likely depend on the persistence of ice and seasonal snow on mountain landscapes. As warming continues, some mountain glaciers may persist as very small remnants, depending on local climatic conditions and topographic processes (e.g., avalanches, wind redistribution of snow, and shading), yet many will continue to shrink and soon disappear (5). As mountain catchments lose glaciers, seasonal snow will be an increasingly important cold-water source. Despite the recent general decline in mountain snowpack across the western United States (34), some of the highest elevations experienced stable or increasing trends, and projections suggest that snow will likely

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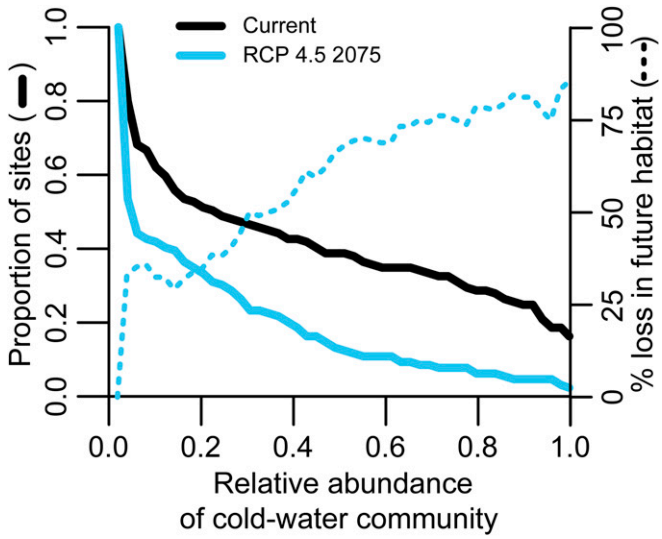

Fig. 4. Climate change will likely shrink habitats supporting abundant cold-water communities. Model predicted cumulative distributions of sites supporting the cold-water community under current (black) and future climate (blue) conditions (corresponding percent reductions are dashed lines). Predictions were made using model averaging across linear mixed effects models relating elevation, distance to source, temperature, and glacial cover to the current distribution of the cold-water community (*SI Appendix*, Table S6).

persist into the next century (35, 36). Regardless of the precise timing and magnitude of future ice and snow changes, our findings demonstrate that high-elevation streams fed by seasonal and multiyear snow, remnant ice, and other cold groundwater sources (e.g., subterranean ice) will continue to serve as critical climate refugia for regional mountain biodiversity after glaciers disappear.

Climate change impacts on mountain biodiversity remain complex and uncertain. More work is needed to understand how different dimensions of ecological diversity (e.g., habitat variation, genetic diversity, locally adapted communities) are affected by climate-induced glacier loss in high-elevation mountain ecosystems. Conservation of mountain biodiversity with climate change will require protecting high-elevation landscapes, while addressing the root causes of global warming.

Materials and Methods

Study Area. GNP is designated as a World Heritage Site, International Peace Park, and Biosphere Reserve and encompasses ∼4,099 km^2 in northwest Montana, USA. Geologic evidence shows that ∼20,000 y ago, at the Last Glacial Maximum, GNP was almost completely covered by glacier ice (37). Approximately 11,500 y ago, GNP was nearly ice free, and since ∼6,500 y ago, small glaciers have been present and active (38). The most recent ice advance culminated with the Little Ice Age (LIA) glacial maxima near the mid-19th century, around 1850 (19). GNP glacier advance and retreat over recent centuries has been tied to regional climate drivers (39).

Invertebrate Sampling. We quantitatively sampled alpine stream benthic macroinvertebrate communities at 129 sites along 58 streams in GNP. Our nested sampling design included longitudinal sampling within streams and multiple streams within drainages (Fig. 1) and covered a large portion of GNP, including 20 of 60 possible HUC12 units. The elevation of sampling sites ranged from 1,474 to 2,431 m (mean 1,979 m); 52 sites were at or above the permanent tree line (∼2,100 m). Replicate macroinvertebrate samples were collected at each site (mean 8.6, SD 3.2) using a Surber sampler (area 0.09 m^2, 250 μm) and preserved with 95% ethanol (18). Macroinvertebrates were sorted, counted, and identified to the lowest taxonomic level, typically to the genus and species levels (*SI Appendix*, Table S3), by expert aquatic macroinvertebrate taxonomists (40). Number of individuals per square meter was calculated based on the fractions subsampled and total area sampled (40).

Assessing Glacier Change since the LIA. Contemporary glaciers and multiyear snow features were digitized from satellite imagery (2003, 2005, and 2015) using ArcGIS version 10.2 (18). We used glacial catchment coverage (GCC) as a measure of glacial influence by calculating the proportion of total upstream watershed area covered by glaciers for each sample site. LIA ice extent was documented in the glacier polygon dataset (19). LIA glacier extent was reconstructed by digitally tracing LIA moraines and cirque headwalls visible in 30-cm resolution, multispectral, pansharpened Digital Globe WorldView satellite imagery collected in late summer 2014, 2015, and 2016 (19). Additional snowfield perimeters were refined using National Aerial Photography Program imagery from September 2003, a record year for wildfires in GNP. Mean LIA glacier margin uncertainty was less than 3%. We calculated change in areal glacial cover since the LIA glacial maxima by comparing our contemporary glacier coverage dataset (18) to the LIA glacier polygon dataset (19).

High-Elevation Stream Digitization. Streams were digitized to extend the National Hydrologic Dataset to the alpine zone using 1-m resolution NAIP 2005 satellite imagery. Streams fed by glaciers were coded as such, and all other streams were coded as nonglacial. Drainage area above each site was calculated using 10-m Digital Elevation Model data. Watershed boundaries were refined based upon visible drainage channels using 0.6-m resolution satellite imagery (DigitalGlobe) accessed through ArcGIS World Imagery. Distances to stream source, glacier cover, and watershed area were calculated in ArcGIS. The Tabulate Intersection tool in ArcGIS was used to calculate glacier and ice cover per drainage and percentage of glacier and ice cover for each site.

Stream Temperature Modeling. Mean August temperatures were predicted for each site using a generalized linear model parameterized with air temperature, elevation, slope, aspect, and glacier predictor variables (r = 0.84 and root-mean-square error = 1.35 °C) using the modeling approach described in refs. 18 and 39. Briefly, for the baseline (current) model simulations, mean August air temperature surfaces (Daymet) were summarized for the present-day period (1986–2005) and used to predict average monthly temperatures. To predict future conditions, gridded monthly air temperature changes from two RCP scenarios, RCP 4.5 and RCP 8.5 (1-km resolution), from the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (41), were summarized for the future period 2066–2085 (2075). These scenarios span a range of greenhouse gas emission scenarios between moderate (RCP 4.5) and extreme scenarios (RCP 8.5). These surfaces were then added to the baseline surfaces and used in a delta-change approach to assess future air temperature warming effects on stream temperatures. Glacier effects were removed from future stream temperature predictions under the climate warming prediction that the glaciers will be gone by the end of the century (5).

Data Analysis. We used the quantitative sampling described above to calculate relative abundance of taxa at each site and characterize biodiversity in our dataset. To calculate taxon turnover (β-diversity), we used Jaccard's dissimilarity index to measure taxon differences between each site and the regional taxon pool (an aggregate of all sites). This metric ranges from zero (complete overlap in species composition) to one (complete mismatch in species composition). We also decomposed beta-diversity into spatial turnover and nestedness components using multisite dissimilarity following (42) (*SI Appendix*, Table S2). We calculated the relative importance of spatial turnover by calculating its percentage of the overall beta-diversity. Richness and β-diversity were calculated across sites using the lowest taxonomic resolution possible. However, because not all taxa were identified to species, our measures of richness and turnover are conservative. All diversity and turnover metrics were calculated in R (43) with the "vegan" package, and decomposition of beta-diversity was carried out using the "betapart" package.

We tested for relationships between measures of biodiversity (e.g., richness, β-diversity) and site attributes (e.g., GCC, elevation, distance-to-source, temperature) using linear mixed effects models (*SI Appendix*, Table S1). For each model set, we tested different random effects structures to account for our nested sampling design following the procedure outlined in ref. 44. For species richness, we used rarefaction to construct individual-based species accumulation curves to account for any potential biases in the estimates of richness across sites (45). We found no difference in the effects of glacier cover and stream temperature between the raw and rarified estimates of

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richness. Therefore, we used the raw estimates of richness for these models. Across all models, distance-to-source and richness were log-transformed to ensure normality. Similarly, β-diversity and GCC were logit-transformed prior to analysis. We added 0.01 to GCC prior to transformation to account for zero values. All models were estimated in R using the "lme4" package. Model performance and selection were evaluated using Akaike's Information Criterion corrected for sample size (AICc).

We classified macroinvertebrate communities into distinct component communities based on the relative abundance of different taxa using the probabilistic classification model, LDA (23). This classification is computed using only the relative abundance of taxa at different sites; therefore, the LDA-generated component communities are not informed by any environmental variables. Output from LDA includes the relative abundance of each component community for each site and the relative abundance of each taxa within the component communities (Fig. 3 *A* and *B* and *SI Appendix*, Table S3). LDA component communities were estimated using the VEM algorithm in the "topicmodels" package in R. LDA requires integer counts of taxa, therefore we multiplied our density (number of individuals $\times$ m^{-2}) by 10^3 and rounded to the nearest integer, which maintains the integrity of rare taxa in the analysis. Using different factors ranging from 10 to 10^5 had no impact on the classification into component communities. Similar to other clustering algorithms (e.g., *k*-means), the number of component communities is specified a priori. We classified macroinvertebrates into two component communities (*SI Appendix*, Table S3), which adhered to expectations of experts in the distribution of alpine macroinvertebrates (e.g., J.J.G.) and were clearly differentiated across habitat variables. We specified these two component communities as the "cold-water" and "generalist" communities. We also estimated LDA models with three or more a priori component communities, and the cold-water community remained unchanged.

To identify specific taxa that may be glacial-obligates and to directly compare estimates of the reliance of the regional taxonomic pool on glaciers (15), we compared taxon presence data from glacial (>0% ice cover) sites to nonglacial sites. We only included well-represented taxa that were found in three or more sites (>3% of sites sampled). Three taxa (*Gymnopais*, *Bolshecapnia*, and *Neothremma*) were found in glacial streams but not in nonglacial streams. We also tested the sensitivity of this result to different thresholds of site number. Of taxa found in two or more sites, seven taxa (*Gymnopais, Limonia, Baetis tricaudatus, Suwallia, Cryptochia, Bolshecapnia,* and *Neothremma*) were only found in glacial streams. Only one taxon (*Gymnopais*) was found in more than four or more sites that were only glacier-fed.

We tested for the influence of GCC and distance to source on the relative abundance of the cold-water and generalist communities, again using linear mixed effects models (Fig. 3 *C* and *D* and *SI Appendix*, Table S4). To test for differences in habitat extent in glacial and nonglacial streams, we included a binary glacial stream variable (ice cover > 0%) in regressions including distance-to-source (Fig. 3*D* and *SI Appendix*, Table S4). All models included a random intercept for drainage to account for repeated sampling within drainages. Model fits presented in Fig. 3 are model averaged predictions based on model weights (*SI Appendix*, Tables S4 and S5).

To forecast suitable habitat conditions for the cold-water community into the future, we fit linear mixed effects models including stream temperature, elevation, distance to stream source, and GCC to the current distribution and relative abundance of the cold-water community across sites (*SI Appendix*, Table S6). A number of models had similar AICc support; therefore, we used model averaging based on model weights (46) to make future predictions. We reduced the candidate model set to only include models with ΔAICc < 4 and then calculated model weights for the top model set. Predictions were made for each model using future estimates of temperature and glacier cover, and a weighted average prediction was calculated using model weights (*SI Appendix*, Fig. S2). We predicted future habitat and relative abundance of the cold-water community under two emissions scenarios, RCP 4.5 and RCP 8.5. Future stream temperatures were based on an empirically derived temperature model for both emission scenarios (see *Stream Temperature Modeling* above) (47). For both future scenarios, we assumed 0% glacier cover for all sites. Modeled stream temperature predictions were very similar for the RCP 4.5 and RCP 8.5 emission scenarios (average of 0.6 °C), resulting in similar estimates of future habitat loss, which were driven primarily by the glacier effect. Therefore, for simplicity we provide only the results of the RCP 4.5 scenario (Fig. 4).

Data Availability. The stream invertebrate data and contemporary glacier data used in this study have been deposited in ScienceBase (https://doi.org/10.5066/P9RCMMKL). The R code for all statistical analyses used in this study have been deposited in GitHub (https://github.com/tjcline/AlpineBugs_PNAS2020).

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