

Biodiversity under threat in glacier-fed river systems

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Freshwater biodiversity is under threat across the globe¹, with climate change being a significant contributor^{2,3}. One impact of climate change is the rapid shrinking of glaciers⁴, resulting in a reduction in glacial meltwater contribution to river flow in many glacierized catchments^{5,6}. These changes potentially affect the biodiversity of specialized glacier-fed river communities⁷. Perhaps surprisingly then, although freshwater biodiversity is a major conservation priority³, the effects of shrinkage and disappearance of glaciers on river biodiversity have hitherto been poorly quantified. Here we focus on macroinvertebrates (mainly insect larvae) and demonstrate that local (α) and regional (γ) diversity, as well as turnover among reaches (β -diversity), will be consistently reduced by the shrinkage of glaciers. We show that 11–38% of the regional species pools, including endemics, can be expected to be lost following complete disappearance of glaciers in a catchment, and steady shrinkage is likely to reduce taxon turnover in proglacial river systems and local richness at downstream reaches where glacial cover in the catchment is less than 5–30%. Our analysis demonstrates not only the vulnerability of local biodiversity hotspots but also that extinction will probably greatly exceed the few known endemic species in glacier-fed rivers.

The cold, turbid melt waters of glacier-fed rivers are a feature of many mountainous areas. These rivers carry high suspended sediment loads, tumbling down moraines, valleys and often over terrain little affected by human activities. On a global scale, glacier-fed river systems often sustain alpine wetlands, reduce the variability of flows in the adjacent lowlands and form the headwaters of some of the world's greatest rivers. With distance downstream, the influence of glacial runoff diminishes. The increases in channel stability and water temperature with distance from the glacier are thought to be the two main driving factors for the change in aquatic biodiversity along⁸ and between rivers with varying glacial contribution to flow⁶. Proglacial reaches, the zone immediately in front of a glacier's terminus or 'snout', are probably one of the harshest environments in nature (except where a proglacial lake is present) and at the limit for most aquatic life. However, the diversity of aquatic macroinvertebrates usually increases with distance from the glacier and decreasing glacial contribution to river flow^{8,9}, and many of these environments support unique and rare species. As a result of the apparent 'low' biodiversity, and minimal knowledge regarding the distribution of alpine aquatic species, glacier-fed rivers have received negligible attention from conservationists. Here we describe

how freshwater biodiversity in glacierized catchments will decline significantly with the shrinkage and disappearance of glaciers, thereby adding a new dimension to the important and timely issue surrounding the effects of climate change on biodiversity¹⁰.

In this analysis we assembled data sets on macroinvertebrates, a group of organisms that have been well studied with relatively well-known environmental requirements, and can therefore be considered as a 'model' group. Data were subject to the following requirements: were available from a large number of river sites within relatively confined geographical regions or collected over time as glacier coverage declined; covered a wide range in glacial influence (percentage of glacier cover in the catchment (GCC) from 0 to 100%); and were subject to similar sampling techniques among sites within regions. Meta-data-sets fulfilling these criteria were assembled from three different continents: 49 river sites in the Ecuadorian Andes (unpublished data), 34 sites in the Swiss and Italian Alps^{11–14} and a temporal study comprising 20 sampling occasions at a river in the Coastal Range Mountains of southeast Alaska over nearly three decades of glacial shrinkage¹⁵. The fauna were identified with varying taxonomic resolution (see Methods), but standardized within data sets before each analysis. We analysed how three key and complementary biodiversity elements (regional taxon richness, γ -diversity; taxon turnover, β -diversity; and local taxon richness, α -diversity) responded to the shrinkage of mountain glaciers. To facilitate the comparison between data sets, all values of α - and β -diversity were standardized to the mean value of the group of sites with 0% GCC. We used non-parametric fitting techniques (Lowess smoothing function) to determine the shape of the response curves of macroinvertebrate diversity metrics (α -, β - and γ -diversity) to percentage of GCC. For the three metrics and the three regions, these fits produced a near-random distribution of residuals on X – Y plots.

Loss of regional species richness is a primary concern in terms of preserving biodiversity, because it is the variable that most explicitly reflects extinction risk. The analysis of potential loss of regional richness was carried out on species data exclusively, and localities with lower-resolution data were eliminated because higher-level taxonomic groups such as for example families of macroinvertebrates have relatively wide distributions within rivers. Our analysis showed that several species occurring in rivers in catchments with high glacial cover begin to disappear from the community at 30–50% GCC, and 9–14 species are predicted to be lost with the complete disappearance of glaciers in each region

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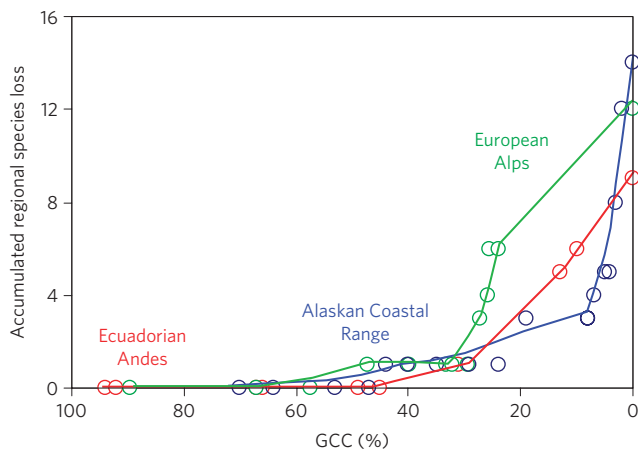


Figure 1 | Accumulated loss of regional species richness (γ diversity) as a function of glacial cover. Obligate glacial river macroinvertebrates begin to disappear from assemblages when glacial cover in the catchment drops below approximately 50%. Each data point represents a river site and lines are Lowess fits.

(Fig. 1), corresponding to 11, 16 and 38% of the total species richness, respectively, in the three study regions in Ecuador, the Alps and Alaska. These species differed between the three regions owing to biogeography. Furthermore, high mountain habitats often represent isolated islands that restrict immigration, increasing the likelihood of speciation, leading to a high degree of endemism¹⁶, but also increasing the risk of local extinction. In consequence, a significant global decline in the number of mountain glaciers may lead not only to local or regional extinction of aquatic macroinvertebrates, but also to the extinction of endemics. This highlights that potential extinction may go far beyond the few known endemic species adapted to glacier-fed rivers, such as the caddisfly *Rhyacophila angelieri* in the French Pyrenees⁷ and the stonefly *Zapada glacier* in Montana¹⁷. Furthermore, in addition to the potential loss of higher taxonomic levels such as genera¹⁶, recent work has shown that the loss of genetic diversity among cryptic species due to climate change greatly exceeds that of morphospecies for aquatic insects in alpine catchments¹⁸.

β -diversity (or taxon turnover) is generally expected to be low among harsh sites (such as proglacial rivers) because few species from the potential regional species pool are adapted to survive the harsh environmental conditions¹⁹. Nevertheless, we found that β -diversity increased towards sites with a high percentage of GCC (that is, the harshest sites) in the three regions ($r = 0.868$ for Ecuador, $r = 0.792$ for the Alps, $r = 0.828$ for Alaska, $P < 0.001$ for all regions, Spearman rank test; Fig. 2). To include all available sites in our analysis of β -diversity, we standardized to family level for the Ecuadorian and European alpine data sets (subfamily for Chironomidae; non-biting midges); an approach that should generate very conservative estimates of turnover. However, as macroinvertebrate assemblages at high GCC typically consist exclusively of species within the same two or three subfamilies of Chironomidae, the pattern of higher turnover towards high GCC could be even more pronounced at the species level. The observed β -diversity pattern is due to proportionally more families occurring sporadically (that is, patchily distributed) in sites with a high, compared with a low, percentage of GCC. Isolated and sporadically occurring populations face an elevated risk of local extinction. These results concur with previous work showing that, between regions, β -diversity increases and similarity decreases towards higher glacial influence²⁰.

In contrast to the general assumption that local richness increases monotonically with decreasing GCC (ref. 7), our

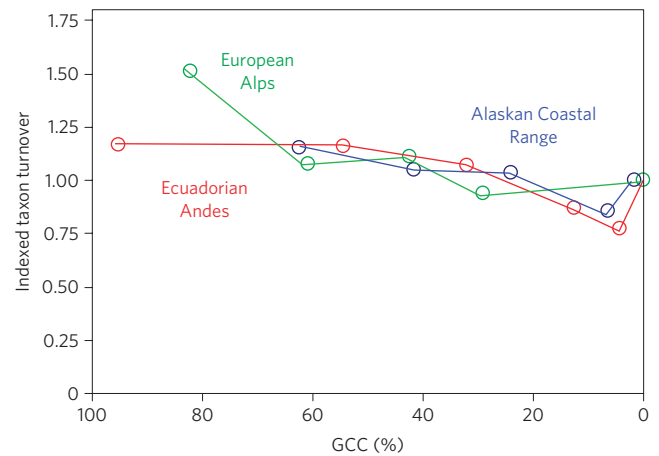


Figure 2 | Taxon turnover (β diversity) as a function of glacial cover. The data shown are for species turnover (Alaska) and family turnover (Ecuador and Alps). Assemblages at river sites close to glaciers are more spatially variable than those at sites with less glacial influence. Data are indexed to 1 at non-glacial sites (0% glacial cover). Each data point represents a river site and lines are Lowess fits.

results indicate that low glacial influence enhances local diversity in mountain rivers. For the three regions, local richness was maximized at 5–30% GCC (Fig. 3). The validity of this α -diversity peak was statistically confirmed for the three regions using model selection analysis in which two competing categories of models, linear-like models versus quadratic-like models (see Methods), were fitted to the data. For the same reasons as stated above, the analysis of α -diversity was carried out on family data for the Ecuadorian and European alpine sites. However, patterns in species richness are usually quite closely correlated with family richness of stream macroinvertebrates²¹. Moreover, this globally consistent pattern of peaking family richness at above zero GCC is supported by an independent data set at higher taxonomic resolution from the Austrian Alps²². This result implies that glacial retreat will enhance local richness in those reaches in the river that have more than 5–30% GCC, whereas it will reduce richness at reaches further downstream with less than 5–30% GCC. Complete disappearance of glaciers in a catchment will extinguish potential local diversity hotspots. This is a most intriguing pattern, which is even more conspicuous if we take into account that family richness, even in non-glacial rivers, usually increases towards lower altitudes²³. A potential ecological mechanism behind this peak in local richness can be predicted from the intermediate disturbance hypothesis²⁴: turbid glacier-fed rivers, with low water temperature and solute concentrations and varying hydrological regimes restrict the fauna to a few specialized species, but further downstream on mixing with warmer, clearer water (that is, snow melt, rain and/or groundwater-fed, see Fig. 4) creates intermediate disturbance that maximizes diversity because superior competitors cannot dominate and co-exist with opportunistic species.

The three analyses undertaken here on a global meta-data-set of river macroinvertebrates showed concurrently that the continued shrinkage of glaciers will have negative effects on fundamental elements of biodiversity. Our results do not require that rivers cease to flow with the complete disappearance of glaciers, because most will continue to be sourced from melting snow, rainfall and groundwater reserves, but clearly the reduction in ice extent will lead to significant changes in hydrological and water-quality regimes^{6,25}. This study has demonstrated that decreases in glacial meltwater contribution to the flow of mountain river systems will affect the distribution of aquatic diversity; increasing at some reaches but decreasing at others. These changes have already been

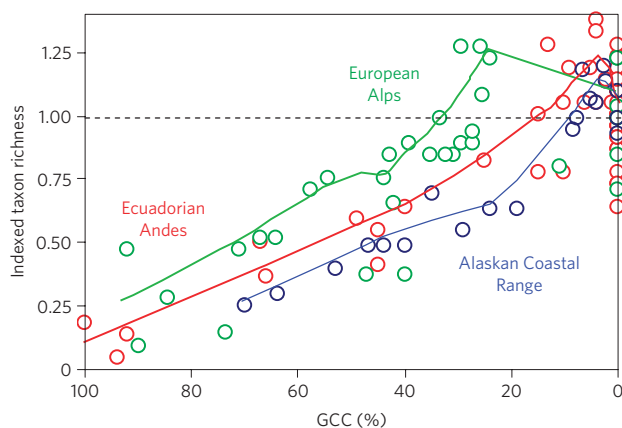


Figure 3 | Local richness (α diversity) as a function of glacial cover. The data shown are for species richness (Alaska) and family richness (Ecuador and Alps). Local taxon richness peaks at 5–30% GCC. Data are indexed to 1, indicated by the horizontal dashed line, at non-glacial sites (0% glacial cover). Each data point represents a river site and lines are Lowess fits.

documented in some regions⁷, and we expect that species have been lost, β -diversity decreased and maximum local richness reduced in glacier-fed catchments worldwide.

Although two of the study regions in this analysis use sites arrayed spatially but with different percentages of GCC to infer temporal changes, the clear concordance in patterns to the temporal data set from Alaska strengthens predictions regarding the effect of glacial shrinkage and disappearance for future biodiversity. Other temporal studies have documented biological responses to shrinking glaciers in the Swiss Alps²⁶ and French Pyrenees⁷ but did not consider responses across the entire spectrum of percentage of GCC. Similar changes to aquatic biodiversity and associated ecosystem functioning and services can be expected in glacially influenced river systems across the world.

Extinction at the local and regional scale, as well as loss of endemic species and/or genera of aquatic macroinvertebrates, is clearly undesirable from a conservation perspective. It is also worrying because the macroinvertebrate community plays a key role in ecosystem functioning^{2,27} such as organic matter decomposition²⁸. However, the ecological roles of most of the threatened species in glacier-fed rivers are unknown, and possible consequences for higher trophic levels such as fish, amphibians, birds and mammals (which perhaps are more appreciated by humans) are, at present, difficult to predict. These knowledge gaps, and the potential threats to biodiversity demonstrated by our study, indicate that strategic conservation should take a holistic approach that includes both invertebrate and vertebrate aquatic species.

Methods

The Ecuadorian Andes data set was collected from the Antisana Ecological Reserve and included 49 sites located between 3,917 and 4,853 m a.s.l. Sites were sampled once (between 2008 and 2010) using a Surber sampler (5 replicates; 0.05 m²; 500 μ m mesh), with 17 sites identified to species (or morphospecies) level, and a further 32 sites only to family (or subfamily; O.D. and D.J., unpublished data). The data set from Europe was composed of four published works^{11–14}, in total comprising 34 sites in the Italian and Swiss Alps. These streams were located between 1,300 and 2,830 m a.s.l. and all sites were sampled several times during different seasons using comparable quantitative techniques. From this data set, samples from 14 sites were identified to species level for most groups, and 20 further sites to family (or subfamily) level. The third data set represented a temporal study of one site on Wolf Point Creek, located 0.75 km from its mouth and 15 m a.s.l. in the Coastal Range of Glacier Bay National Park, southeast Alaska. Wolf Point Creek was fed by melt water from the Muir glacial remnant until this completely disappeared in 2005. During the period from 1977 to 2007, macroinvertebrates were collected annually using Surber nets (10 replicates; 0.1 m²; 300 μ m mesh), except for 1978–1985, 1987, 1995 and 2003, giving a total of 20 sample years¹⁵. Most groups in the Wolf Point Creek samples were identified to species level



Figure 4 | Confluence of glacier-fed (left) and spring-fed streams in Ecuador. These confluence zones of different river types produce local spikes in taxon richness (photo by D. Jacobsen).

(particularly chironomids). For all three data sets, some non-insect groups such as Oligochaeta were not identified further than order.

In the original data sets, either distance from the glacier terminus or percentage of GCC was used as the measure of glacial influence at specific stream sites. To allow the inclusion of the temporal data set from Alaska we chose the latter for our analysis. Therefore, to work with a common independent variable across data sets we converted those expressed as distance^{11–13} to percentage of GCC. This was done by using eight stream sites in the Swiss^{11,14} and Austrian Alps²⁹ for which distance from glacier, glacier size (km²) and percentage of GCC were known. The conversion followed two steps. First, the glacial index based on distance from the glacier and size of the glacier²⁰ was calculated for each of the eight sites. We then established the relationship between the glacial index (GI) and percentage of GCC: percentage of GCC = $20.996e^{1.461GI}$, $r^2 = 0.98$. This relationship was used to estimate the percentage of GCC of the sites for which only distance from glacier and size of glacier were known.

To determine accumulated regional species loss within each of the three regions we analysed species lists from the above-mentioned studies, with sites arranged in order of decreasing percentage of GCC, and registered the number of species at each site that were found at higher, but not at lower, percentages of GCC. These counts were then accumulated.

Taxon turnover was calculated among sites in distinct groups, which augments the number of sites required. Thus, to use all available sites, this analysis was carried out on family (subfamily in the case of Chironomidae, Diptera) instead of species data. Each of these site groups covered a range in percentage of GCC. However, as the density and distribution of sites along the percentage of GCC gradient were irregular and differed among data sets, the number of sites in the established groups varied (from 3 to 26 sites) and represented different mean values and range widths of percentage of GCC (from 0 to 22%). For each group we calculated a measure of β -diversity or taxon turnover as $\gamma_3/\alpha_{\text{mean}}$, where γ_3 was the total number of taxa at three sites (which was the lowest number of sites in any of the groups) randomized 10,000 times, and α_{mean} was the mean number of taxa per site in the group.

We fitted diversity versus percentage of GCC data using a Lowess smoothing function (a locally weighted polynomial regression) with a tension of 0.4 and a number of dimensions fixed at 2. To assess the validity of the α -diversity peak revealed by the Lowess fit, model selection analysis (linear-like versus quadratic-like models) was carried out using a corrected Akaike information criterion (AIC_c), which is recommended for small sample sizes. The model with the lowest AIC_c was retained. We used the likelihood ratio test (LRT) to test for the difference between the two models. Results showed that, for the three regions, the best quadratic model (in our case a log-normal model) had lower AIC_c values than the best linear model (Supplementary Table S1) and that these differences were significant (LRT > 4.50, $P < 0.05$ for all comparisons).

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Author contributions

D.J. and O.D. collected the Ecuadorian data, conceived the study, analysed the data and led the writing of the paper. A.M.M. and L.E.B. collected the Alaska data and contributed to the writing of the manuscript. D.J. and O.D. contributed equally to the study.

Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/natureclimatechange. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to D.J. or O.D.