Biodiversity under threat in glacier-fed river systems

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Freshwater biodiversity is under threat across the globe[1], with climate change being a significant contributor[2,3]. One impact of climate change is the rapid shrinking of glaciers[4], resulting in a reduction in glacial meltwater contribution to river flow in glaciated catchments[5,6]. These changes potentially affect the biodiversity of specialized glacier-fed river communities[7]. Perhaps surprisingly then, while freshwater biodiversity is a major conservation priority[3], the effect 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, while 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 currently 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 increase 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 along[8] and

between rivers with varying glacial contribution to flow[6]. 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. Because 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 mountain 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

biodiversity[10].

In this analysis we assembled datasets on macroinvertebrates, a group of organisms

which 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; 1)

were available from a large number of river sites within relatively confined geographical regions,

2) covered a wide range in glacial influence (percentage of glacier cover in the catchment from 0

to 100 %), and 3) were subject to similar sampling techniques among sites within regions. Meta-

datasets 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[11,12,13,14], 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 shrinkage[15]. The fauna were identified with

varying taxonomic resolution (see Methods), but standardized within datasets before each

analyses. 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 datasets, all values of α- and β- diversity were standardised to the mean value of the group of sites with zero % glacial cover in the catchment (GCC). We used nonparametric fitting techniques (Lowess smoothing function) to determine the shape of the response curves of macroinvertebrate diversity metrics (α-, β-, and γ-diversity) to % GCC. For the three metrics and the three regions, these fits produced a near-random distribution of residuals on XY 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 performed on species data exclusively, and localities with lower resolution data were eliminated because higher level taxonomic groups such as e.g. 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 (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 due to biogeography. Further, high mountain habitats often represent isolated islands which restrict immigration, increasing the likelihood of speciation, leading to a high degree of endemism[16], 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 currently known endemic species adapted to glacier-fed rivers, such as the caddisfly *Rhyacophila angelieri* in the French

Pyrenees[7] and the stonefly *Zapada glacier* in Montana[17]. Also, in addition to the potential loss of higher taxonomic levels such as genera[16], 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 catchments[18].

Beta-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 conditions[19]. Nevertheless, we found that beta-diversity increased towards sites with high % GCC (i.e. 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 beta-diversity, we standardized to family level for the Ecuadorian and European Alpine datasets (sub-family 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 beta-diversity pattern is due to proportionally more families occurring sporadically (i.e. patchily distributed) in sites with high compared to low % GCC. Isolated and sporadically occurring populations face elevated risk of local extinction. These results concur with previous work showing that, *between* regions, beta-diversity increases and similarity decreases towards higher glacial influence [20].

In contrast to the general assumption that local richness increases monotonically with decreasing glacial cover in the catchment[7], our 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 vs. quadratic-like models (see Methods), were fitted to the data. For the same reasons as

stated above, the analysis of α-diversity was performed 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 macroinvertebrates[21]. 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 Alps[22]. This result implies that glacial retreat will enhance

local richness in those reaches in the river that have more than 5-30 % GCC, while glacial retreat

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 altitudes[23]. A potential

ecological mechanism behind this peak in local richness can be hypothesised from the

intermediate disturbance hypothesis[24]: 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 (i.e. snow melt, rain and/or

groundwater-fed, see Fig. 4) creates intermediate disturbance which maximizes diversity because

superior competitors cannot dominate and co-exist with opportunistic species.

The three analyses undertaken here on a global meta-dataset 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 mountain 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 melt water 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 documented in some regions[7], and we expect that

species have been lost, beta-diversity decreased and maximum local richness reduced in glacier-

fed catchments worldwide.

While two of the study regions in this analysis use sites arrayed spatially but with

different % GCC to infer temporal changes, the clear concordance in patterns to the temporal

dataset 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 Alps [26] and French Pyrenees[7] but did not consider

responses across the entire spectrum of % GCC. Similar changes to aquatic biodiversity and

associated ecosystem functioning and services can be expected in glacial alpine and Arctic 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 decomposition[28]. However, the ecological roles of most of

the threatened species in glacial 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, suggest that strategic conservation should take a holistic

approach that includes both invertebrate and vertebrate aquatic species.

Methods

The Ecuadorian Andes dataset was collected from the Antisana Ecological Reserve and included 49 sites located between 3917 – 4853 m a.s.l. Sites were sampled once (between 2008 and 2010) using a Surber sampler (5 replicates; 0.05m^2; 500μm mesh), with 17 sites identified to species (or morphospecies) level, and an additional 32 sites only to family (or sub-family) (Dangles & Jacobsen, unpublished data). The dataset from Europe was composed of four published works[11,12,13,14], in total comprising 34 sites in the Italian and Swiss Alps. These streams were located between 1300 and 2830 m a.s.l. and all sites were sampled several times during different seasons using comparable quantitative techniques. From this dataset, samples from 14 sites were identified to species level for most groups, and 20 additional sites to family (or sub-family) level. The third dataset 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 meltwater 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; 0.1m^2; 300μm mesh), except for 1978-1985, 1987, 1995 and 2003, giving a total of 20 sample-years[15]. Most groups in the Wolf Point Creek samples were identified to species level (particularly chironomids). For all three datasets, some none-insect groups such as Oligochaeta were not identified further than Order.

In the original datasets either distance from the glacier terminus or percent glacial cover in the catchment (% GCC) were used as measures of glacial influence at specific stream sites. To allow the inclusion of the temporal dataset from Alaska we chose the latter for our analysis.

Therefore, in order to work with a common independent variable across datasets we converted those expressed as distance[11,12,13] to % GCC. This was done by using eight stream sites in the Swiss[11,14] and Austrian Alps[29] for which distance from glacier, glacier size (km^2) and % GCC were known. The conversion followed two steps; first the Glacial Index (*GI*) based on distance from the glacier and size of the glacier[20] was calculated for each of the eight sites. We then established the relationship between *GI* and % GCC: % GCC = $20.996e^{1.461GI}$, r^2 = 0.98. This relationship was used to estimate % 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 % GCC, and registered the number of species at each site that were found at higher, but not at lower % GCC. These counts were then accumulated.

Taxon-turnover was calculated among sites in distinct groups, which augments the number of sites required. Thus, in order to use all available sites, this analysis was performed on family (sub-family in the case of Chironomidae, Diptera) instead of species data. Each of these site groups covered a range in % GCC. However, as the density and distribution of sites along the % GCC gradient was irregular and differed among datasets, the number of sites in the established groups varied (from 3 to 26 sites) and represented different mean values and range widths of % GCC (from 0 to 22 %). For each group we calculated a measure of β-diversity or taxon turnover as γ_3/α_{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 10000 times, and α_{mean} was the mean number of taxa per site in the group.

We fitted diversity vs. % 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 vs. quadratic-like models) was performed using 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 both 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 1) 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, analyzed 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. Correspondence and requests for materials should be addressed to D.J. and O.D.

Figure legends

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 approx. 50 %. Each data point represents a river site and lines are Lowess fits.

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.

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 % glacial cover in the catchment. 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.

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 Dean Jacobsen).

- European Alps
- Ecuadorian Andes
- Alaskan Coastal Range

Indexed taxon richness

Glacier cover in catchment (%)