Glacier shrinkage driving global changes in downstream ecosystems

Alexander M. Milner[1a,b], Kieran Khamis[a], Tom J. Battin[c], John E. Brittain[d], Nicholas E. Barrand[a], Leo Fuereder[e] Sophie Cauvy-Fraunie[f], Gísli Már Gíslason[g], Dean Jacobsen[h], David M. Hannah[a], Andrew J. Hodson[i], Eran Hood[j], Valeria Lencioni[k], Jón S. Ólafsson[l], Christopher T. Robinson[m], Martyn Tranter[n], and Lee E. Brown[o]

[a]School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham B15 2TT, UK; [b]Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775, USA; [c]Civil and Environmental Engineering, Ecole Polytechnique Fédérale de Lausanne (EPFL), CH-1015 Lausanne, Switzerland; [d]Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, 0318 Oslo, Norway; [e]River Ecology and Conservation Research, Institute of Ecology, University of Innsbruck, Technikerstr. 25, A-6020 Innsbruck, Austria; [f]Institut de Recherche pour le Développement (IRD), UMR EGCE, IRD-247 CNRS-UP Sud-9191, Avenue de la Terrasse, Bâtiment 13, 91198 Gif-sur Yvette, France; [g]Institute of Life and Environmental Sciences, University of Iceland, IS-101, Reykjavik, Iceland; [h]Freshwater Biological Laboratory Dept. of Biology, University of Copenhagen, Universitetsparken 4, 2100 Copenhagen, Denmark; [i]Department of Geography, The University of Sheffield, Sheffield S10 2TN, UK; [j]Department of Natural Science, University of Alaska Southeast, 11120 Glacier Hwy Juneau, AK 99801, USA; [k]Invertebrate Zoology and Hydrobiology Department, MUSE-Museo delle Scienze, Corso del Lavoro e della Scienza 3, I-38123 Trento, Italy; [l]Marine and Freshwater Research Institute, Skúlagata 4, IS 101 Reykjavík, Iceland; [m]EAWAG, Überlandstrasse 133, 8600 Dübendorf, Switzerland; [n]Bristol Glaciology Centre, Geographical Sciences, University of Bristol, Bristol BS8 1SS, UK; [o]School of Geography and water@leeds, University of Leeds, Leeds LS2 9JT, UK.

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The glaciers that presently comprise 10% of the world's land surface are shrinking rapidly across most parts of the world with cascading impacts to downstream ecosystems. Changes in hydrology and hydro-morphology due to climate-induced glacier loss are projected to be the greatest of any hydrological system, with major implications for riverine and near-shore marine environments. Glaciers impart unique footprints on river flow at times when other water sources are low. Here we review the current evidence of how glacier shrinkage will alter hydrological regimes, sediment transport, and biogeochemical and contaminant fluxes from rivers to oceans which will profoundly influence the natural environment and the ecosystem services that glacier-fed rivers provide to humans, particularly provision of water for agriculture, hydropower and consumption. We conclude that human society must plan adaptation and mitigation measures for the full breadth of impacts in all affected regions due to glacier shrinkage.

Keywords; Glacier, runoff, biogeochemistry, biodiversity, ecosystem services

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Significance Statement

Glaciers melt is accelerating due to global warming in many parts of the world with the resultant hydrological changes some of the greatest projected for any ecosystem. This synthesis evaluates and contrasts the wide-ranging effects of glacier retreat on downstream biogeochemistry, contaminant delivery and transport, community ecology, and critical ecosystem functions and services, including provision of water and food, regulation of water quality and hazards, and cultural elements including tourism and religion. We develop new conceptual understanding of the major shifts envisaged this century for these important features of aquatic systems downstream from glaciers. Adaptive management strategies are outlined to mitigate the societal impact of these profound changes in glacial runoff, with key ecosystem service trade-offs and priority research areas identified to inform these strategies.

Global-scale understanding of glacier mass loss has improved significantly in the past decade, principally via advances in satellite remote-sensing instrumentation and processing. Previous estimates of mass loss were extrapolated from sparsely distributed *in situ* observations (1), whereas field measurements are now combined routinely with globally complete glacier inventories (2) and direct measurements of volume and mass change from satellite altimetry and gravimetry to provide accurate estimates of global glacier mass change (3). The most recent estimate of glacier change indicates a mass loss rate of 259 ± 28 Gt yr^{-1} between 2003 and 2009 (3) with global runoff from glaciers exceeding 1350 km^3 yr^{-1} (4). Research to date on the associated downstream impacts of this glacier mass loss has focused largely on sea-level rise (e.g. Gardner et al., 2013), and to a lesser extent, water availability and runoff (5, 6,7). The scale of ice loss worldwide means there is an urgent need to comprehensively evaluate the broader spectrum of downstream effects on freshwater and near-shore marine systems. This increased understanding is vital to aid planning for adaptation and mitigation measures in the most significantly affected environments and regions.

The largest individual contributions to global glacier mass loss come from the glaciers of the Gulf of Alaska, the Canadian Arctic, and the ice sheet peripheries of Greenland and Antarctica. However, the glaciers with the most negative mass balances are located in the European Alps and at low latitudes in the South American Andes (3). In the European Alps, atmospheric warming has been pronounced in the last 30 years, especially during the summer months (8), which, when combined with decreased snowfall (9), has led to a 54% loss of ice area since 1850 (10). Current projections of alpine ice loss suggest that just 4-13% of the 2003 ice area will remain by 2100 in Europe (10A). Similarly, Bolivian glaciers have lost nearly 50% of their mass in the last 50 years (11) and in western Canada glacier ice volume relative to 2005 is projected to decrease by 70 ± 10% by 2100 (12). Glaciers in the Ganges, Indus and Brahmaputra river basins of the Himalaya are currently losing 24 ± 2 Gt yr^{-1} of ice (13), equivalent to around 10% of the global glacier mass loss between 2003 and 2009 (3). Climate-driven changes in glacier volume will have far-reaching consequences for downstream ecosystems, including rivers, lakes and the coastal zones of major oceans, and the human populations that depend on them (Pritchard 2017). Our synthesis demonstrates that glacier shrinkage can be expected to alter the timing, magnitude and frequency of downstream discharge, sediment transport and the speciation of nutrients and other solutes.

The downstream impacts of these climate-induced shifts along the continuum from glaciers to rivers to the ocean are only beginning to be understood. Impacts affect various ecosystem levels ranging from perturbed food web dynamics (14), loss of biodiversity (15,16), and shifts in biogeochemical and sediment fluxes (17, 18). Glacier shrinkage also will have important implications for the ecosystem services that glacier-fed rivers provide, particularly in regions where glacier runoff is integral to multiple human activities, such as farming, energy production, water quality and tourism. The scale of potential changes faced by society is immense. For example, Himalayan glaciers alone provide water to 20% of the global population, or 1.4 billion people, in countries such as India, Nepal and China (19). In this perspectives article we have developed (OR examined) multiple lines of evidence from glacier-fed systems globally, to develop a framework to synthesize existing information and expert understanding about how glacier shrinkage and changes in runoff regimes will impact downstream ecosystems and human society. We have developed new integrated models of how discharge, nutrients, ecological communities and ecosystem services respond as glacial cover decreases over time with ongoing climate warming (Figure 1). Building on this new framework, we present a globally integrated perspective into the complex adaptation decisions required, with respect to changing ecosystem services and associated societal adaptations within glacierized areas.

Hydrological and geomorphological implications of glacier melt

Estimating the quantity and timing of melt-water runoff in relation to glacier mass-balance is a major challenge due to complex hydroclimatological interactions across different spatial scales and climatic zones (7). A significant amount of what is considered “glacial” runoff is sourced from the melt of annual snowfall that passes over or on the surface of the glacial ice, which will still occur in the absence of a glacier. However snowmelt dominated systems have a more variable and temporally constrained hydrological regime in terms of timing and quantity when compared to glacially dominated systems. Glacier melt does not cease and will keep flowing as long as there is energy for melt because of the infinite (on an annual basis) glacier ice reservoir. Hence, the loss or substantial reduction of glacial ice will lead to distinct changes in the timing and magnitude of peaks in the hydrological regime (20). Glacial ice-melt runoff typically peaks during summer in mid-high latitude regions (21), when runoff from other sources is typically low, thereby buffering dry-season stream discharge from precipitation and snowmelt variability (Figure 2a high glacier cover; 22,23) and preventing drought in certain regions e.g. Asia (Pritchard 2017). Over longer time scales, regions with extensive glacier cover, such as the NE Canadian Arctic and Svalbard, are predicted to see an initial increase in annual glacier runoff (4) due to the earlier disappearance of the reflective snow cover and the exposure of ice with lower surface albedo. However, this initial bulk discharge increase (Figure 1a) will be followed by reduced annual runoff due to the ensuing decrease in glacier volume (24, 25), as is presently observed with smaller glaciers. During the coming century, total runoff from glaciers will decrease in most regions (Figure 1a) and river flow in summer will become more sensitive to summer precipitation events, particularly if these events become more extreme with climate change (Figure 2a). For example, analyses in Alaska suggest overall that, loss of glaciers will decrease total catchment runoff by the order of 10-20% (26). However, modeling indicates that geographically there are likely to be significant differences in the hydrological response of high altitude catchments, with runoff in the Chilean Andes likely to decrease sharply this century, whereas runoff and thereby water availability will increase and show less seasonality in the Nepalese Himalaya (7).

In alpine and high latitude watersheds with low glacial influence, river flows in spring and fall will be higher with more variability (e.g. Figure 2d) than when glacier cover is intermediate or high (e.g. Figure 2c). This is due to a combination of the earlier onset of snow melt and an increased fraction of winter precipitation falling as rain with climate warming (Figure 2a; 27). Consequently, the hydrological regime in many temperate and arctic glacier-fed streams and rivers will shift from being deterministic and predictable to stochastic (Figure 1a), as the predictable late summer glacier melt is replaced by less predictable rainfall events and snowmelt runoff regimes increasing short-term flow variability (Figure 2b). Clearly, this will have major implications for downstream ecosystem processes and ecological communities given the known importance of predictable annual flow pulses for river biodiversity (28). However this can vary according to region; for example in the Himalaya precipitation from the Monsoon system provides a deterministic element to the annual flow cycle (Hannah et al. 2005a) although the year-to-year variability in this flow will increase without the buffering capacity of glacial runoff (Hannah et al 2005b). Equatorial systems typically have no seasonality but high diurnal variability (75?). These systems are ablation driven with no snow accumulation so the quantity of meltwater will decrease over time and the magnitude of the diurnal variability will gradually decrease.

With reduced glacial runoff, water temperature in summer will increase downstream due to (1) an increase in atmospheric energy receipt with warmer air temperature (although radiation could be reduced by increased cloudiness); (2) a decline in the relative contribution of cold water from glacial melt; and (3) the reduced heat capacity of rivers with lower flow (29). Concomitantly, bedload and suspended sediment transport are expected to decrease in the long term as glacial runoff becomes reduced and erosion decreases (30). The resultant decrease in turbidity will increase light penetration to the bed of streams and rivers with implications for primary production and the photochemical transformation of organic matter (30), enhanced by increased channel stability where braiding of river channels is less (31).

In Nepal and Greenland, basins have formed between the glacier and the lateral or end moraines with rapid ice recession in recent times. Stagnant ice in these basins may melt to form glacial lakes, which can grow rapidly in size (32, 33, 34) and catastrophically discharge as a glacial lake outburst flood thereby representing a major hydrohazard to downstream areas. Such hydrohazards are predicted to increase with ongoing glacier recession in heavily glacierized regions (35), leading to significant societal impacts via loss of life and damage to land, property and infrastructure (36)

Glacier retreat is likely to expose new areas of unconsolidated glacial sediments and to destabilize slopes in many areas (37), creating the potential for a short-term increase in sediment yields from glacial basins. On steeper slopes where vegetation cannot be established sediment yields will be longer (Klaar et al. 2015). An unexpected consequence of a reduction in glacier volume in polar areas may be a decrease in sediment yield from glaciers undergoing changes in their thermal regime (38). Ice overburden pressure and heat release by deformation and strain heating will be reduced by glacier thinning, potentially reducing the energy available for subglacial erosion, especially in cases where the energy loss causes a reduction in basal sliding. Ultimately, thinning glaciers may even freeze onto the bed. However, this decrease in sediment yield may be compensated by mobilization of paraglacial sedimentary materials from thermo-erosion of ice-cored moraines and increased prevalence of ice-marginal landslides and debris flows (39). The net result is that a shift from glacial to paraglacial-dominated mountain catchments will occur, which in the short term (coming decades) will increase sediment supply and associated geohazards within mountain ranges (Figure 1a).

Biogeochemical fluxes and cycling

There have been major discoveries in recent years regarding glacier-perturbations of global (40, 41, 42) and regional (18) biogeochemical cycles. Glaciers receive and accumulate dissolved organic carbon (DOC) and inorganic nutrients from both wet and dry deposition. Red-colored green algae growing on the glacier surface can reduce the albedo, thereby increasing melting – a phenomenon known as the 'bio-albedo' effect (43). These species are frequently derived from remote sources (e.g., 44, 45, 46, 47). A wide variety of microorganisms, including algae, assimilate inorganic nutrients within the snow and ice (48), and in meltwater flowing down crevasses and entering sedimentary habitats at the glacier bed (49). Microorganisms transform labile inorganic nutrients, such as ammonium and phosphate, into organic forms (50) that ultimately contribute to the pool of ice-locked organic matter. At a global scale, ice-locked organic matter is substantial and represents a hitherto poorly understood reservoir of carbon (42). The biogeochemical diversity of this organic matter is also unexpectedly high, with many constituents containing proteinaceous molecules, lignins and tannins (45, 47, 51).

Studies on Alaskan (46) and alpine (47) glaciers have shown that ice-locked DOC is highly bioavailable (up to 80%) to microbial heterotrophs, and that upon release this DOC can stimulate riverine carbon cycling (47) and sustain aquatic food webs (52) in glacier-fed rivers. Bioreactive proteinaceous molecules have a near global distribution within glacial meltwaters (53) and changes to the export of this labile substrate to downstream ecosystems will occur with glacial recession. DOC, dissolved inorganic (DIN) and dissolved organic nitrogen (DON) concentrations in runoff increase as glacier coverage in the catchment decreases (Figures 1b and 3a-c), although overall DOC bioavailability decreases (Figure 1b) (46). Despite the low DOC concentrations found in glacier runoff, the lability of glacier-derived DOC may mean it is ecologically important in receiving ecosystems given the relatively high specific discharge and thus the DOC flux associated with glacierized watersheds. A significant flux of reactive N, equivalent to the sum of the dissolved nitrogen, may be associated with NH_4 adsorption onto suspended sediments, as shown for the Leverett Glacier, an outlet of the Greenland Ice Sheet (18). Glacial sediments also appear to promote nitrification, thereby making glacier basins net exporters of nitrate to downstream ecosystems (54, 55, 56).

The concentration of soluble reactive phosphorus (SRP) is predicted to decrease with declining glacier coverage in the watershed (Figure 1b,) as shown by Hood and Berner (57 – Figure 3d) and a large proportion of that reactive P flux can also be bound loosely to suspended sediment (18). Similar studies are needed for other glacierized catchments with variable glacial coverage so that these conclusions can be made with greater certainty. However, with increasing glacier retreat, DOC, DIN and DON concentrations are likely to increase, while SRP concentrations will decrease (Figure 1b). In the short term, dependent on factors such as the flux of glacier meltwater and the concentration of glacial suspended sediment, elevated fluxes of potentially bioavailable NH_4^+ and P may mitigate declines in dissolved N and P.

An unexpected impact of glacier shrinkage is the liberation of contaminants from the early industrial revolution and onwards (58). These contaminants include emission products from industrial activity, such as black carbon and associated compounds, mercury, pesticides and other persistent organic pollutants (59, 60). A recent concern relates to the uncertainty in how climate change is moving these contaminants from glacial sinks to glacial sources and their potential impact on downstream ecosystems (61). Importantly, glaciers now represent the most unstable stores of the so-called legacy pollutants, such as dichlorodiphenyltrichloroethane (DDT) in European and other mountain areas flanking large urban centers. Their accumulation in lake ecosystems downstream from glacierized mountains has been modeled using climate-driven mass balance change to alpine glaciers in Europe (58). This type of modeling needs to be extended to other mountain environments, such as the Himalaya, where meltwater supplies rivers that provide drinking and irrigation water to billions of people.

Biodiversity

Rich ecological communities have adapted over evolutionary timescales to the harsh environmental conditions in glacier-fed streams and rivers. Benthic invertebrate communities play important roles in the flux of biomass and nutrients (C, N & P) from lower (algal, microbial, detrital resources) to upper trophic levels (fish, birds, amphibians). Shifts in the hydrological regime will alter the physical and chemical template to which these communities have adapted, ultimately leading to overall loss of biodiversity, ranging from algae to fish (61). The scale of these effects on biodiversity remains poorly quantified (62) with studies to date focusing primarily on community-level changes. Here, we focus on differences among species (including functional trait responses) regarding their ability to withstand changing conditions, and the role of phenotypic plasticity and genetic adaptations in response to climate.

Microbial and algal communities**.** Microbial life in glacier-fed streams is dominated by biofilms that extensively colonize the sediment surface (63). Encapsulated in a polymeric matrix, species from all three domains of life (Archaea, Bacteria and Eukarya) co-exist in these biofilms, where they are protected against harsh environmental conditions including pronounced variability in flow, high ultraviolet radiation and low availability of organic carbon (63). Benthic biofilms in mid-high latitude glacier-fed streams can flourish during optimal environmental windows in spring, when channels unfreeze, flow is low and the water is clear, and in fall, when similar conditions exist (64, 65). Similarly, benthic biofilms can develop markedly where channels remain open during winter due to upwelling groundwater.

Biofilms drive most of the ecosystem respiration and gross primary production, and are therefore critical to the carbon cycle in glacier-fed streams and rivers. The extension of the temporal period of clear water may cause sites of increased primary production (66) dominated by diatoms and the gold filamentous alga (*Hydrurus foetidus* Villars) (67). Channels become more stable as glacial inputs diminish, analogous to non-glacial Arctic streams (68), and bryophytes may become more abundant and replace benthic algae in glacier-fed streams.

Next generation sequencing has recently highlighted surprisingly high bacterial richness in biofilms in glacier-fed streams (69) due to turnover between putatively active and dormant taxa continuously recruited from upstream sources in the catchment (e.g., from soils, rocks, groundwater, which maintains high bacterial richness (70). This is advantageous for biofilms to react rapidly to an environment that is continuously subject to physical disturbance and environmental fluctuations. In fact, it has been suggested that community assembly of microbial biofilms is largely deterministic involving a series of environmental filters (71, 69). However, with ongoing glacier shrinkage, increasingly unpredictable flows during the spring window when glacier cover is low (Figure 1a) will likely reduce the optimal period for biofilm growth in glacier-fed streams. In addition, as glacial runoff further decreases, bacterial communities in biofilms will become more similar to those in streams fed predominantly by groundwater, snowmelt and rain (69, 72). Ultimately, this is will lead to a homogenisation of microbial diversity at the landscape level because of increasing similarity (i.e. loss of beta diversity) and decreasing regional diversity (gamma diversity) (69, 72).

Macroinvertebrates. This group has been well studied in freshwaters globally. As such their environmental requirements are relatively well known, and macroinvertebrates are therefore often considered as a `model' group for tracking environmental change. Glacially dominated rivers are characterized typically by the deterministic nature of their benthic macroinvertebrate communities, due to the overriding conditions of low water temperature and low channel stability (73, 74). Substantial changes in macroinvertebrate diversity and distribution patterns are likely as glacial cover and meltwater runoff decline in catchments and the hydrological regime in glacier-fed rivers becomes more stochastic (28, 75) (Figure 1c). In general, local diversity (alpha) is expected to increase at the reach level as environmental conditions ameliorate with lower summer discharge and turbidity, and higher channel stability and water temperature, with communities migrating upstream tracking preferred or optimal water temperature (76).

A longitudinal displacement of species composition with changes in runoff is intriguing because during the initial phase of loss of larger glacial masses, increased glacial runoff may cause stream communities to migrate downstream, thereby reducing alpha diversity (76). However, although in the longer term alpha diversity will increase, beta and gamma diversity are expected to decrease at the stream and catchment level (15, 28, 75, 77) – Figure 1c and genetic diversity at the regional level (77). Stream reaches will become gradually more homogenous and unique glacial river specialist species will become extinct with water temperature increases and competition for food and space with newly colonizing species (78) and predator range shifts (79). This is similar to the response for biofilm microbial communities described above. Nevertheless, even as riverine conditions become more favorable to colonization by new, often more ubiquitous, species, other factors may restrict establishment, for example weak dispersal ability, mountain barriers, lack of suitable microhabitats, scarcity of food or other possible environmental conditions (61, 80).

Rivers with high glacial influence typically support communities with low taxonomic diversity dominated by highly adapted taxa, which display a convergence of functional traits. Analysis of a unique 27-year record of community assembly following a reduction in glacier cover in southeast Alaska, demonstrated that niche-filtering processes were dominant with high glacier cover (74). However, significant shifts in the trait composition of stream invertebrate communities occur as catchment glacial cover decreases (74, 81, 82) with stochastic and deterministic assembly processes co-occurring. Specialist taxa are replaced by more generalist taxa with a greater diversity and width of biological traits. The size spectra of aquatic biota typically increases with warmer thermal regimes and higher productivity, and larger sized predators (e.g. fish, amphibians, large invertebrates) colonize rivers or move upstream in greater abundance as glaciers retreat (Figure 1c; 76). Functional diversity and functional redundancy increase rapidly (74, 82) as new colonizers possess many similar traits to taxa already present. This redundancy may contribute to the functional resilience of ecological communities to further ecosystem change.

The adaptive potential (evolutionary and phenotypic) of aquatic biota to projected changes in glacial runoff is not well known (83), but dispersion and phenotypical plasticity generally provide a possibility for some threatened taxa to respond to climate and environmental changes in the short term (84, 85). Dispersal propensity and the level of specialization and capacity to exploit refugia are important considerations. Some traits (e.g., long-lived, light bodies and good adult fliers, eurythermy, generalist feeders) are typically associated with high dispersal capacity. A possible mechanism for some species to avoid extinction is to survive as a glacial relict in groundwater systems. An intriguing example is the cold stenothermal stygobiotic crustacean *Niphargus strouhali alpinus* found in sediments (30 cm deep) in the Italian Alps where it had been trapped for at least 150 years following the Little Ice Age (86).

Salmonids. Both Atlantic and Pacific species of salmon and trout provide important sources of proteins to millions of people worldwide and sustain major commercial and sport fisheries. Rising water temperature may threaten the persistence of these important fishes and has been linked to increased mortality of juvenile chinook salmon, raising concerns over the future viability of this important species (87). Population models indicate that, based on average warming predictions, there is a 17% chance of catastrophic loss in the chinook salmon population by 2100 (87). However, where glacier cover is both intermediate and high, increased glacial melt with climate change will have a cooling effect on monthly mean stream temperature during the summer. For each 10% increase in glacier cover in a catchment, mean stream summer temperature can decrease by > 1°C (88), which will potentially reduce the growth of fish. Conversely, future reductions in glacier run-off may actually improve the thermal suitability of glacially dominated streams for salmon. One intriguing aspect of glacial recession in coastal Alaska has been the creation of new streams which potentially can support salmonids. An extensive amount of salmon habitat has been created with > 500 systems documented along the coast of southeast Alaska alone (89). However, climate change may expose these systems to more extreme weather events which conversely can significantly reduce salmonid population sizes (90), so much more work is needed to understand the implications of these interacting phenomena.

Glacier-fed rivers conserve a greater proportion of their annual flow budget for late summer and through winter than streams and rivers fed by snowmelt (91). Increased summer flows in glacier-fed rivers enhance and facilitate the migration of anadromous salmon through river corridors to spawning grounds at a time when summer flows fed by other sources are typically low (91). Some of the largest runs of anadromous salmon in south-central Alaska that support commercial fishing occur in glacially influenced rivers (92). As glaciers shrink and meltwater inputs into these rivers recede, summer discharge will diminish, thereby restricting the number of adult salmon spawners migrating upstream. This may impact commercial and sport fisheries in these regions (Figure 1d). Sockeye salmon have also been shown to prefer the turbid glacial meltwaters for spawning (93) and turbidity can provide cover for rearing fish from predators (94). In addition, a more stochastic flow regime in summer (Figure 1a) will have a negative effect on stream juvenile rearing salmonids and other fish species. However, the potentially higher flows in winter and early spring may be of benefit to reduce overwintering mortality, particularly for rearing salmonids, a time period when mortality is typically at its highest. Climatic change will likely have widely divergent impacts on the timing of salmon migration, but evidence exists that the amount of glacier cover within a watershed does not influence long-term shifts in the phenology of migration timing (95).

Thresholds and Tipping Points

The concept of ecological thresholds is particularly relevant for glacier-fed streams with their environment changing at a rapid pace because of glacier shrinkage (96). Thus, it is increasingly important to identify transition or tipping points between alternate ecosystem states to aid conservation and mitigation efforts (97). Here we present a threshold analysis conducted on three comprehensive datasets of macroinvertebrate abundance from equatorial (E; Ecuador), temperate (T; Italian Alps) and sub-Arctic (A, Iceland) glacierized river systems. For each region quantitative benthic macroinvertebrate samples were collected along a gradient of glacier influence (quantified as % glacier cover in the catchment; GCC) We used Threshold Indicator Taxa ANalysis (TITAN; Baker & King (2010)), a non-parametric technique that orders and partitions observations along environmental gradients using IndVal scores (Dufrene and Legendre, 1997), to define ecological thresholds. Multiple candidate change points were identified (250 permutations) and IndVal scores calculated for each taxa then standardized (Z-scores). Declining (*z*-) and increasing (*z+*) taxa were used to identify community-level change points and uncertainty estimated via bootstrapping (500 replicates). For all systems, a distinct peak in the *z*- taxa, taxa that decrease in abundance across an increasing glacial gradient, was observed (T 31.8%; E 20.4%; A 19%). This suggests non-linear responses of alpine aquatic assemblages to changes in glacier influence (Figure 4) consistent with global patterns of macroinvertebrate alpha diversity in glacier-fed rivers (75), and illustrates a phenomenon that is increasingly recognized across differing levels of biological organization in glacier-fed rivers (75, 76, 98).

It should be noted, however, that the change point confidence intervals were relatively broad (See Extended Data Table 1), indicative of a gradual decrease/increase in taxa along the gradient. This type of response is often associated with invasive or weedy species (99), and, in the case of glacier-fed rivers, represents the replacement of specialist stress tolerant species (e.g., the non-biting midge *Diamesa* spp.) by generalist species, such as the mayfly *Baetis alpinus* (77). Interestingly, few taxa displayed increases across the gradient and no distinct peak in *z+* was apparent (Figure 4), possibly due to the patchy distribution of stress tolerant, specialists in glacier-fed streams (75, 77).

Food-web complexity and ecosystem functioning

The consequences of species extinction on trophic interactions and related matter fluxes in glacier-fed rivers following glacier shrinkage currently remain elusive (61). We know that food webs in glacier-fed rivers can be sustained in part by ancient DOC released from glaciers, which can be transferred to higher trophic levels, including invertebrates and fish after incorporation into bacterial biomass in biofilms (52). This glacial source of organic carbon will decrease long-term with ongoing glacier shrinkage and will likely be replaced by organic carbon from in-stream and terrestrial primary production. Species turnover in glacier-fed rivers is linked strongly to glacier shrinkage, where colonizing species likely compete for resources with native species. These changes can be ‘bottom up’ (e.g., from biofilm) (101) or ’top down’ (e.g., colonization by predatory invertebrates) (79). Both mechanisms will potentially influence food web structure and trophic interactions as glaciers vanish (102). This is supported by a four-year experimental flow manipulation in the Ecuadorian Andes, diverting one-third of natural discharge from a glacier-fed stream (66). This experiment showed that meltwater reduction led to increased biomass of benthic algal and invertebrate herbivores and, furthermore, altered the invertebrate community composition within only a few weeks (66).

Ecosystem services

The seasonal predictability of glacial melt facilitates a range of important socio-economic ecosystem services, spanning provisioning, regulating and cultural services (Figure 5).

Provisioning ecosystem services associated with glacier and snowpack storage of water are perhaps the most prominent of the three associated with glacier-fed rivers. The seasonally predictable peak flow regimes of glacier-fed rivers enable navigation on larger rivers, provide water for hydropower, human consumption and irrigation for agriculture, and in some regions support significant freshwater and inshore fisheries. This is particularly important in semi-arid and arid regions where other water source contributions are limited (5, 103, Pritchard 2017). In addition, glacial meltwater during the dry season dilutes possible anthropogenic pollutants and can mitigate effects of river regulation (28). These ecosystem services will be perturbed markedly by the expected shifts of the hydrological regime owing to glacier shrinkage, causing significant economic ramifications.

In Wyoming, the production of barley and hay to support an $800 million cattle industry is dependent upon glacial meltwater to supply a stable source of stream flow during the critical late summer and early autumn growing season. However, over a 21-year period (1985 to 2005), glacier surface area decreased on average by 32%, resulting in 10% less stream flow during this critical period (104). Agriculture in Alberta is also dependent upon meltwater from the Peyto Glacier and proximal glaciers in the Canadian Rockies, which are estimated to lose 90% of their present volume by 2100 (105). As an example of potential future changes in some regions of the world, the Tien Shan region of China is relatively arid, but was once known as the ‘Green Labyrinth’ due to glacial runoff being a significant source of water for agriculture. However, a 20% reduction in volume of 446 glaciers within the region over a 40-year period (1964-2004) is already impacting the sustainability of the region’s water sources (106).

There is considerable concern about the likely impacts of glacier retreat on agriculture in the Andean region of South America, where many smaller low lying glaciers have already vanished, or will disappear within a few decades, significantly affecting the availability of water downstream due to a lack of a glacial buffer during the dry season (107). This is of particular concern for many large cities in the Andean region, which depend heavily on these glacial sources during this season, not only for agriculture but also for drinking water. For example, 27 % of La Paz’s water consumption is glacial meltwater from the Cordillera Real (108), which is projected to decrease annually by 12% (109). During the dry season 40% of the discharge of the Rio Santa, which drains the Cordillera Blanca in Peru, is from glacial runoff (110), providing extensive irrigated areas along the dry Atacama coast as well as 5 % of Peru´s electricity and (108). Estimated glacial retreat within the upper Rio Santa could lead to a decrease in the dry season average flow by 30% (111) further impacting the provisioning of water with significant implications for associated provision of agricultural crops.

Glacial runoff can be a significant contributor to hydropower generation, for example accounting for 50% of Switzerland's and 15-20% of Norway’s electricity supply. More significantly, Austria generates 70% of its electricity from hydropower, with many of the larger facilities being glacier-fed and the glacier-fed Rhone River has 19 hydropower plants supplying 25% of France’s hydropower. The effects of glacier retreat on hydropower revenue are uncertain as a consequence both of predictions in meltwater runoff in future as well as market fluctuations (112). For glacier-fed rivers, ecosystem service valuations are best developed for this sector. For example, the Mauvoisin power plant in Switzerland gathers runoff from nine glaciers, and revenue is expected to increase initially from between USD87.5 – 104.3M (1981-2010), to USD87.5 – 108.6M in 2021-2050 as a result of increasing rates of glacier retreat and thus extra runoff generation potential. However, revenue is estimated to fall to USD74.0 – 91.3M by 2071-2100 as glacier runoff declines. However, a number of South American countries and associated cities are also highly dependent upon glaciers and glacial runoff for energy production. For example, La Paz, Boliva, depends heavily on hydropower for its electricity powered by glacier meltwater (11) but estimates of revenue shifts are needed from this and other regions to develop a more coherent picture of the economic issues associated with glacier retreat.

One possible issue with increasing summer melt from larger alpine glaciers is that current reservoir capacities may be unable to store the additional available water, leading to only marginal electricity generation gains but increased numbers of overspill events and associated hazards (113). On the other hand, there will be new opportunities for hydropower opening up as glaciers recede. In the short term, hydropower may benefit from higher hydrological yields in summer (113), but this will decrease as glaciers shrink further or disappear (Figure 1d). Glacier shrinkage also may open up new terrain for the construction of new dams and reservoirs in valleys not previously suitable for hydropower and now fed from other water sources (114, 115). In addition shifting of the timing of peak melt compared to peak electricity demand may require society to invest more in storage reservoirs. Although typically holding less ice, rock glaciers may prove to be an important alternative source of water (117, 118). For example, in the Chilean Andes the water equivalent of rock glaciers is an order of magnitude higher than that found in the Swiss Alps (117). Research into rock glaciers and their importance is relatively new in the South American Andes and a wider inventory and understanding of these water sources is critical to ensure their future protection under a changing climate.

River fisheries provide important sources of food in many regions, but there is currently relatively little information available in scientific publications considering the implications of glacier retreat. There is though the potential for significant local-regional scale economic perturbations if glacier-fed river fisheries change dramatically. For example, in the glacial Kenai River in Alaska, sport and commercial fisheries generate as much as USD 70M to the State’s economy, but increased flow variability and flooding due to enhanced glacier melting and glacial outburst floods can significantly affect these important fisheries in this and other Alaskan glacier-fed rivers (Dorava and Milner 2000). Interestingly the diversion of headwaters of one river into another driven by glacier retreat as documented for the Kaskawulsh Glacier, one of Canada’s largest glaciers in Yukon Territories, may increase sediment transport and bank erosion into the receiving river. Associated large-scale changes in basin geometry and re-routing of meltwater may significantly affect salmonid habitat (Shugar et al. 2017). However as outlined earlier, glacial recession can be beneficial for creating new salmon habitat, as documented along the Pacific northwest coast and be of considerable benefit to fisheries (38).

Glaciers and their downstream river systems provide important regulating services, most notably related to water quality, hazard generation/mitigation and climate feedbacks via carbon cycles. Glacial meltwater during the dry season can dilute possible anthropogenic pollutants and mitigate water quality modifications associated with river regulation such as river thermal regimes (28). However, enhanced glacier retreat may lead to the liberation of historically deposited pollutants, which could significantly reduce water quality of downstream rivers. Changes in sediment loads are also likely, although these could be beneficial if suspended load is reduced due to glacier retreat leading to decreases in erosional processes. An alternative possibility is the potential for river networks to reorganize themselves as shown for the Kuskawulsh Glacier outflow in Canada, where rerouting of sediments and water to one valley have created far lower flows in valleys with previously abundant river flow [Shugar et al.2017]. Glacier shrinkage is furthermore creating thousands of new lakes worldwide (34), where outburst floods are increasingly threatening hydropower facilities and downstream settlements (116) therewith only a handful of detailed studies available at present to underpin our understanding of current and future regulating services of glacier-fed rivers, there is a pressing need for further detailed studies that integrate the range of scenarios.

Amongst the cultural services provided by glacierized mountain landscapes, tourism makes a particularly important contribution to the economy of many regions. For example, the glaciers of Banff National Park, Canada, attract >3 million visitors each year (119), in Austria the Pasterze glacier attracts an estimated 800,000 people annually, whilst Glacier Bay National Park, Alaska USA typically attracts in excess of 400,000 people per year, many visiting on cruise ships. In New Zealand, glacier tourism is estimated to contribute USD 84 million annually to the economy. Tourism numbers are likely to be affected by glacier retreat and loss in the long-term, although counter-intuitively there may be increases in visitor numbers in some areas if access improves or there is a desire to learn about climate change and see glaciers before they are lost (120; Figure 1d). This is true in South America where glacier tourism represents an important economic factor. However, till late 2007 the Pastoruri glacier became the first tourism destination in Peru to be closed because of the adverse effect of too abundant visitors degrading the glacial surface (121) with similar problems reported in China (120).

In addition to sightseeing, glaciers can provide important tourism and recreation opportunities for year-round skiing. However, in parts of the Austrian and Swiss Alps there are already reports suggesting that rising numbers of visitors noted during the 1980s and 1990s are stagnating (122), although these trends are only partly related to glacier snowpack cover with leisure costs versus disposable income also serving as important drivers of change. In Italy at the Vedretta Piana where the glacier area has shrink by approximately 2/3 since 1965, the threat of glacier retreat to the ski industry has prompted the redistribution of snow from accumulation zone to fill in crevasses and cover debris (123). Other adaptation measures that have been attempted include extension of ski areas to higher elevations, and investments in artificial snow making machinery although these carry heavy costs (e.g. snow machinery installation cost of > USD 400M in 2006-07 alone (124). In contrast in Bolivia, the loss of glaciers has already prompted the closure of the world's highest ski resort (Chacaltaya) in 2009, six years earlier than predicted (11), whilst in parts of the Alps summer glacier skiing has been abandoned because conditions are now too dangerous. On the other hand a decrease in skiing activities and the number of visitors could be beneficial for the environment leading to more sustainable use of water resources associated with snow and ice and also allow for ecological recovery.

Cultural services associated with glaciers incorporate religious beliefs and/or landscape character. Glacierized mountain peaks are considered as spiritual to some indigenous peoples and thus accorded high cultural significance (Xiao et al. 2015). For example, thousands of pilgrims annually traverse the Gangotri Glacier in India considering it a sacred spot (Wang and Qin, 2015) and in Peru and the Yukon Territory of Canada indigenous people consider glaciers as gods. In Peru the loss of ice and snow from mountain peaks is thus associated with the god's departure and the end of the world (Steinberg, 2008). On the Tibetan Plateau, residents consider the glacierized Mount Yulong Snow their spiritual home but already > 65% have recognized the necessity to potentially migrate to adapt to climate change and achieve a sustainable livelihood (Shijin & Dahe 2015). These social upheavals would clearly lead to implications across the wider array of services that human populations utilize from glacier-fed rivers. In addition conflicts may occur in the future between neighbouring countries as water resources become more scarce due to lower glacial runoff as highlighted for certain regions in Asia (Pritchard 2017).

Our conceptual synthesis of the multiple ecosystem services associated with glacial rivers, but which will be altered by the retreat or loss of ice masses, reveals the potential for several interlinked effects (Figure 5, Table 1). For example, these may be considered as unidirectional effects such as new water storage reservoirs (provisioning) altering landscape character (cultural). Alternatively, more complex bidirectional effects occur with meltwater reductions leading to more extreme droughts, with a counter response being the development of more storage facilities to mitigate these effects thereby further altering river flows. However, it is more likely that society will be faced with more complex trade-offs (Bennett 2009) and suitable management strategies must be developed and adopted to mitigate these societal impacts of profound changes in glacial runoff. In the Andes, for example, glacier retreat may necessitate a shift to a less water-intensive agriculture to reduce demand but there is still likely to be a need to create new highland reservoirs to supply water during the dry season, leading to knock on changes amongst regulating services currently provided by downstream river systems. This could necessitate a shift from hydropower electricity generation to other sources (109) to retain water for food. Other solutions could be behavioral, for example reductions in water use and waste, and managerial in terms of water source management (11). The development of new storage facilities would in turn lead to alteration to landscape character, which for some groups may be seen as a negative for cultural tourism related services. In 2010, Argentina became the first country to adopt a Glacier Protection Act that aims to preserve glaciers as "strategic reserves of water for human consumption, for agriculture and as suppliers of water to recharge basins, for the protection of biodiversity; and as a source of scientific and tourist attraction". This kind of solution may become more common to prevent modifications within glacierized watersheds, but is unlikely to be useful in the face of global climate change unless adopted internationally as an additional driver of emissions mitigation policies.

Table 1. Examples of unidirectional (→) and bidirectional (←→) linkages that are likely to arise as a consequence of glacier retreat (cf. Figure 5). These linkages will not be mutually exclusive, leading to the prospect of complex adaptive trade-offs having to be negotiated amongst human populations that are affected by glacier retreat.

Ecosystem service linkages	**Implications**
Changing water sources ←→ *Artificial snow*	Retreating glaciers and snowpacks leads to a need for artificial snow to maintain the winter sports industry adding further pressure on rivers with reduced flow
Changing water sources → *Landscape*	Development of new storage facilities further alters landscape character
Changing water sources ←→ *C cycle*	New reservoirs may release more CO2/CH4, adding further to water source changes due to climate change
Changing water sources ←→ *Hazards*	Receding glaciers may lead to more extreme droughts, with a response being the development of more storage facilities to mitigate against the effects
Changing water sources → *Agriculture/Fisheries*	Altered river flows lead to changes in water supply for irrigation and fisheries
Changing water sources ←→	Pollutant release from glacier stores may degrade water

Water quality	sources for drinking/irrigation users; reservoirs can alter river thermal and sediment regimes
Food supply ←→ Cultural	Loss of water for agriculture could mean a need for populations to migrate, leading to a reduced need for food supply services from these rivers
Water quality → Fisheries	Warmer thermal regimes may be detrimental to some fish species
Water quality → C cycle	Elevated nutrient loads may enhance carbon cycling leading to positive or negative feedbacks that alter thermal regimes or nutrient loads
Hazards → Water Quality	Droughts can lead to excessive water temperature; landslides often deposit large amounts of sediments in rivers
Hazards → Landscape/Social	Landslides and/or outburst floods will alter existing landscape character or make some areas unsafe for habitation
Hazards → Amenity/Tourism	Droughts reduce ability for artificial snow generation; landslides may make some areas dangerous for tourism

Summary

The area of land occupied by glaciers will decrease significantly by the end of the present century, particularly in the European Alps and the South American Andes where many alpine glaciers are projected to disappear. Although the impact of melting glaciers on sea levels has received much attention to date, our synthesis clearly outlines multiple other downstream effects that will alter riverine ecosystems with significant societal implications. There will be major changes to flow regimes in glacierized watersheds, with a shift to greater stochasticity as glacial runoff decreases and flow becomes more dependent on unpredictable precipitation events and snow melt. Among the major impacts are profound changes to ecosystem functions and services, via altered provision of water resources to human society, reorganization of the regulatory processes that shape water quality and geohazards, and cultural changes associated with tourism, landscape character and religion. Clearly, the breadth and complexity of interactions amongst the various impacts will underpin calls for a global research agenda involving interdisciplinary research to meet the following research priorities which need urgent attention to inform effective societal adaptation:

- High-resolution (space and time) mapping of glacier mass loss based on new imagery and technologies.
- Global census and continuous monitoring of key environmental variables and biodiversity in glacier-fed rivers using a network of sites with a wide geographical coverage and adopting standard techniques of sampling so as to make findings comparable. This will allow detection of early warning and regime shifts based on temporal and spatial analyses.
- Earth observatories focusing on relevant biogeochemical fluxes in major glacier systems.
- A better understanding of the effect of glacial recession on salmon habitat linking to commercial and sport fisheries
- Valuation of provisioning, regulating and cultural ecosystem services associated with glacier-fed systems
- Critical adaptive management decisions in the most sensitive areas to mitigate ecosystem service effects that will have major ramifications for billions of people, with international legislation to protect these strategic water resources.

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List of Figures;

Figure 1. Conceptual response curves for (a) river flow and hydrohazards, (b) nutrients, (c) ecological communities and (d) ecosystem services for large and small glaciers with decreasing glacial cover. Note that for each panel the y axis is relative to the system type (i.e., low discharge for a large valley glacier in (a) will be greater than low discharge for a small alpine glacier).

Figure 2. (a) Conceptual representation of the changing hydrograph for alpine glacier-fed rivers. For the *low glacier cover* scenario, a change in climate is also anticipated; in particular, an increase in the magnitude and frequency of extreme events and a decrease in the fraction of precipitation falling as snow. (b) Hypothesized sensitivity of river flow to extreme events (droughts and high intensity storms) and short-term flow variability (i.e., variability in the weekly mean discharge), (c) discharge for the Rhone River with high glacial cover, and (d) discharge of the Taillon River in the French Pyrenees with low glacial cover, indicating stochastic discharge events due to rainfall or rain on snow events.

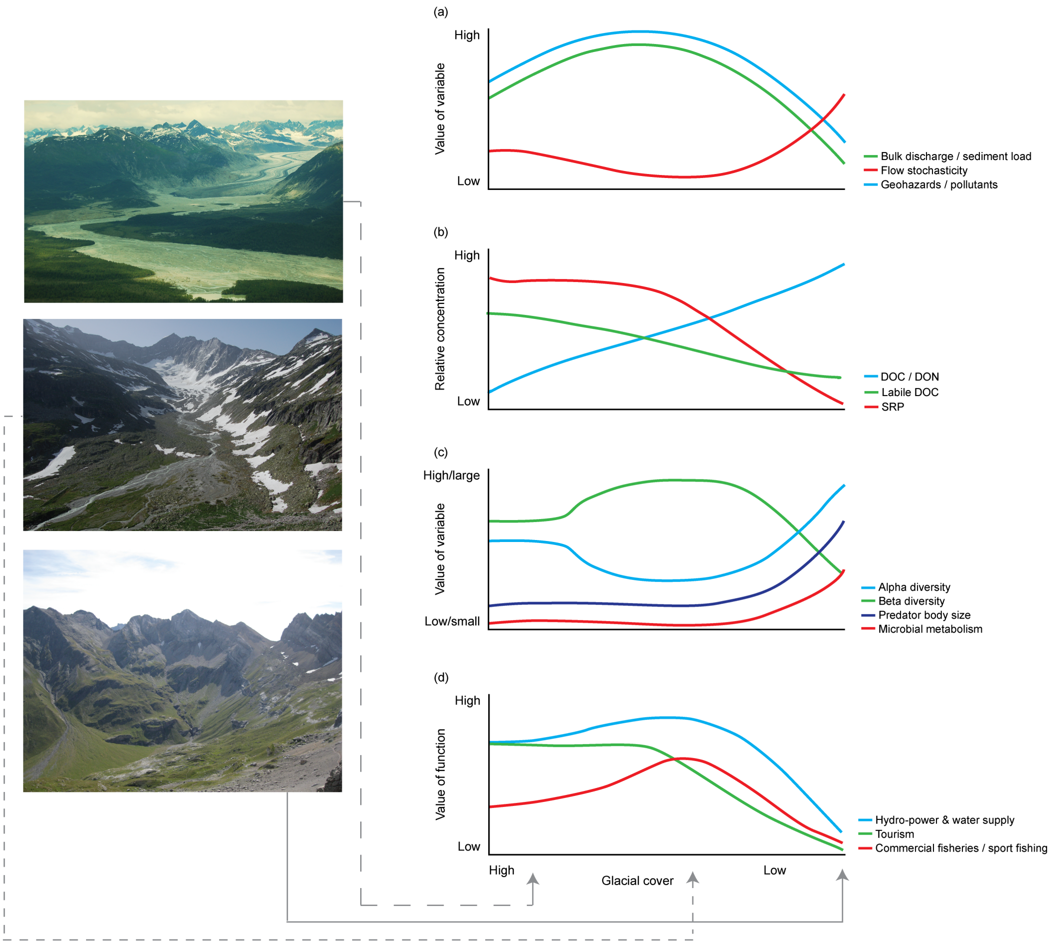
Figure 3. Variations in (a) DIN (b) DOC, (c) DON and (d) SRP as a function of glacier coverage in the catchment (GCC) (57).

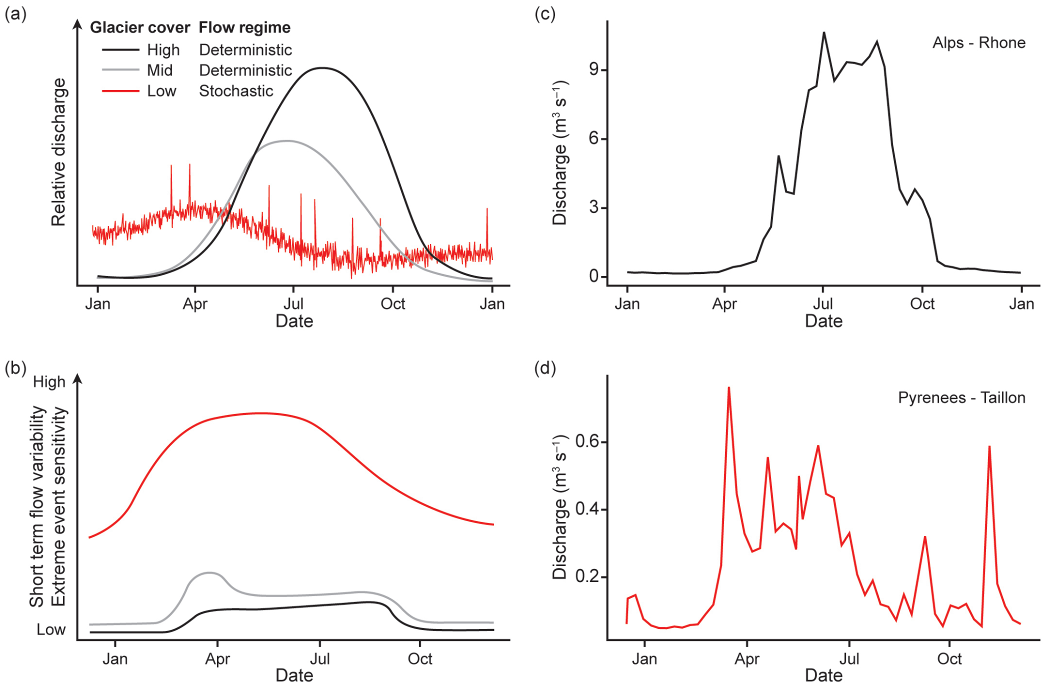
Figure 4. Community change points identified across glacier influence gradients (glacier cover in catchment; GCC) for equatorial (Ecuador), temperate (Italian Alps) and Arctic (Iceland) systems. Change points were estimated using Threshold Indicator Taxa ANalysis (TITAN; 99), a non-parametric technique that orders and partitions observations along the gradient using IndVal scores (100) to define groupings. Multiple candidate change points are identified and IndVal scores are calculated for each taxon (250 permutations) then standardised (Z-scores). Declining (z-) and increasing (z+) taxa are used to identify community-level change points and uncertainty is estimated via bootstrapping (500 replicates).

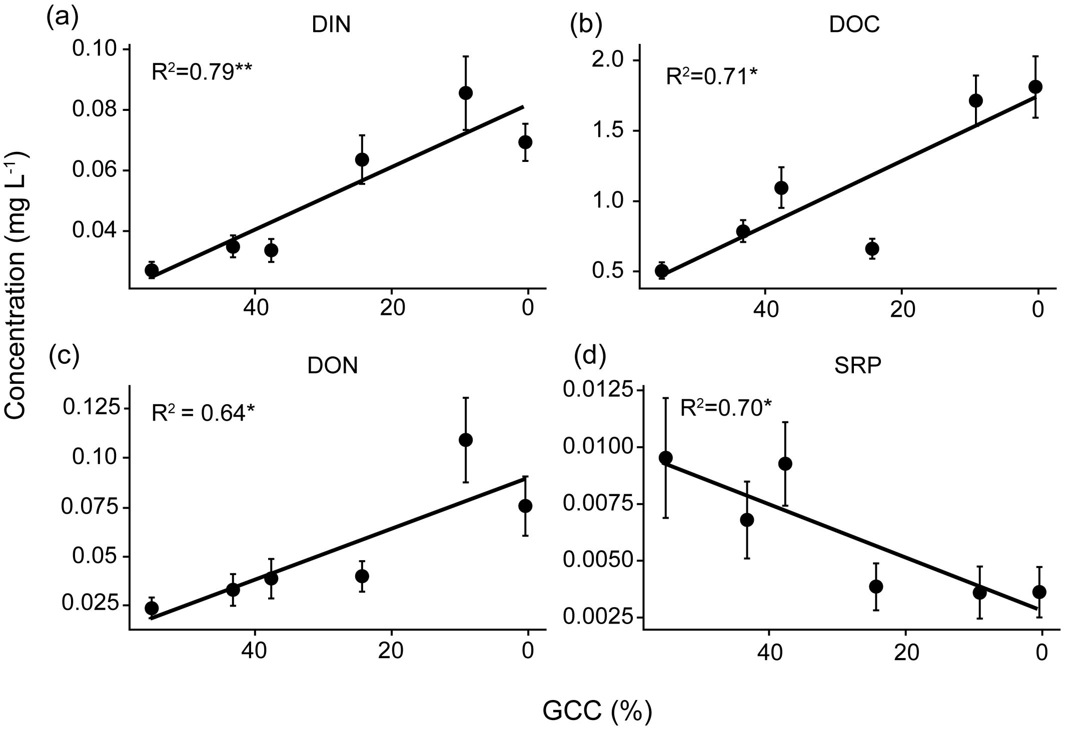
Figure 5. Conceptual framework integrating the effects of glacier shrinkage on provisioning, regulating and cultural ecosystem services. The outer ring highlights broad groups of ecosystem services provided by glacier fed river catchments. The inner ring highlights the specific ecosystem services that are expected to be altered by glacier retreat and disappearance, as detailed in the main text. The centre highlights the complexity of interactions amongst the various ecosystem services, which will necessitate trade-offs as society adapts to cryospheric environmental change.

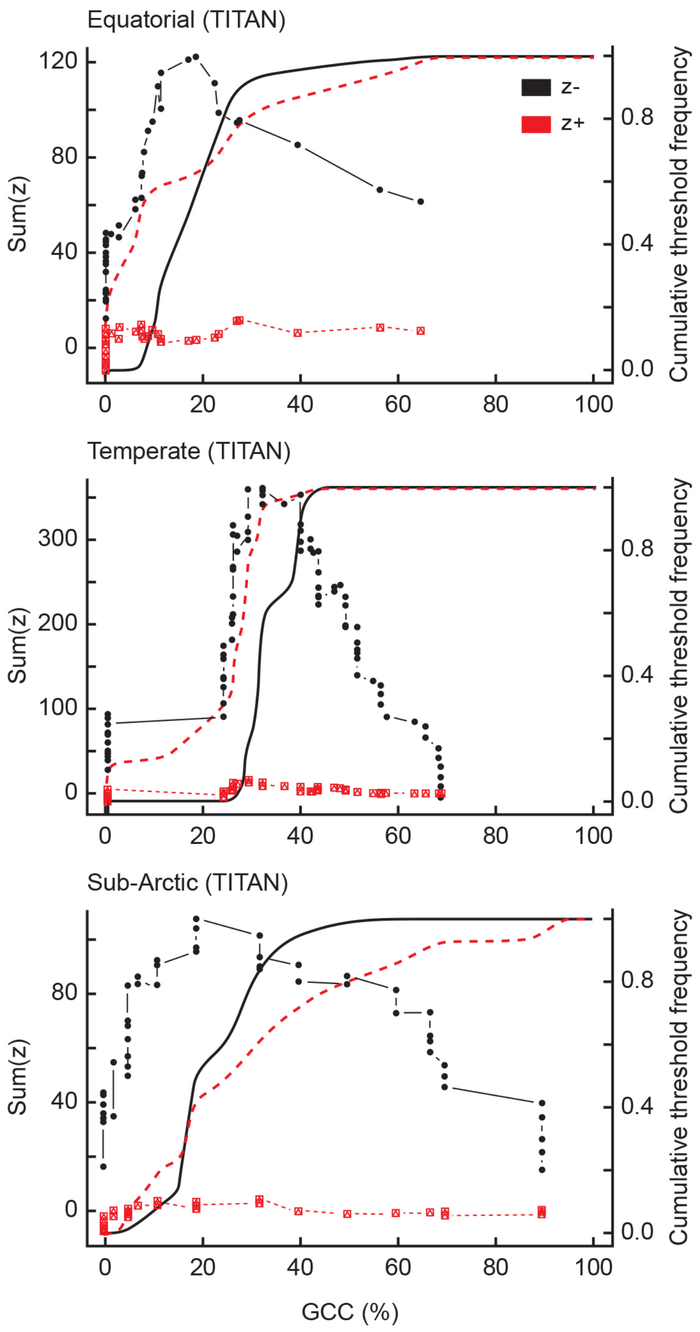
	Iceland				Ecuador				Italy			
Method	Obs.	0.05	0.5	0.95	Obs.	0.05	0.5	0.95	Obs.	0.05	0.5	0.95
sumz-	25.5	11.0	19.0	45.0	17.7	8.2	15.9	27.2	31.8	26.6	31.8	41.6
sumz+	36.0	5.0	32.0	90.0	33.4	0.0	7.3	68.5	11.9	0.0	23.8	31.8
ncpa.bc	25.5	11.0	32.0	68.5	17.7	7.7	17.7	33.4	30.3	27.8	31.8	41.9

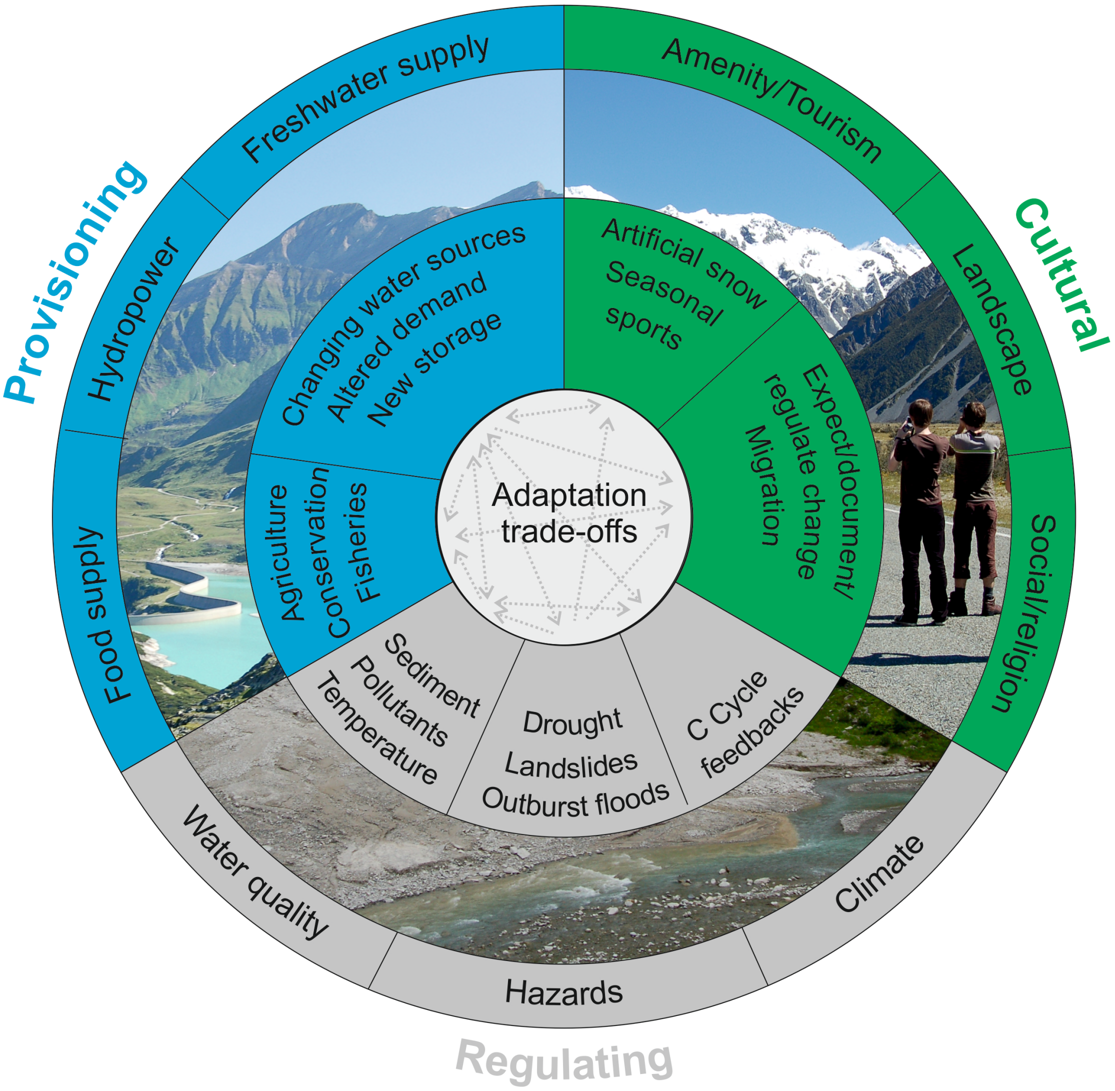
Extended Data Table 1. Threshold indicator taxa analysis results for the three regions. Observed change points (Obs), 5th, 50th and 95th quantiles of bootstrapped change points correspond to the value resulting in the largest sum of indicator value (IndVal) z scores for z− and z + taxa. T or nCPA thresholds correspond to the maximum deviance reduction calculated using Bray–Curtis distance.


(a)
High
Value of variable
Low
Bulk discharge / sediment load
Flow stochasticity
Geohazards / pollutants
(b)
High
Relative concentration
Low
DOC / DON
Labile DOC
SRP
(c)
High/large
Value of variable
Low/small
Alpha diversity
Beta diversity
Predator body size
Microbial metabolism
(d)
High
Value of function
Low
Hydro-power & water supply
Tourism
Commercial fisheries / sport fishing
High
Glacial cover
Low


(a)
Glacier cover
Flow regime
High
Deterministic
Mid
Deterministic
Low
Stochastic
Relative discharge
Jan
Apr
Jul
Oct
Jan
Date
(b)
High
Low
Short term flow variability
Extreme event sensitivity
Jan
Apr
Jul
Oct
Date
(c)
Alps - Rhone
Discharge (m³ s⁻¹)
0
3
6
9
Jan
Apr
Jul
Oct
Jan
Date
(d)
Pyrenees - Taillon
Discharge (m³ s⁻¹)
0.2
0.4
0.6
Jan
Apr
Jul
Oct
Date


(a)
DIN
R²=0.79**
(b)
DOC
R²=0.71*
(c)
DON
R² = 0.64*
(d)
SRP
R²=0.70*
Concentration (mg L⁻¹)
GCC (%)
0.10
0.08
0.06
0.04
2.0
1.5
1.0
0.5
0.125
0.10
0.075
0.05
0.025
0.0125
0.0100
0.0075
0.0050
0.0025
40
20
0


Equatorial (TITAN)
Temperate (TITAN)
Sub-Arctic (TITAN)
Sum(z)
Cumulative threshold frequency
GCC (%)
z-
z+
0
20
40
60
80
100
120
200
300
0.0
0.4
0.8


Provisioning
Cultural
Regulating
Freshwater supply
Hydropower
Food supply
Amenity/Tourism
Landscape
Social/religion
Water quality
Hazards
Climate
Changing water sources
Altered demand
New storage
Agriculture
Conservation
Fisheries
Artificial snow
Seasonal
sports
Expect/document/
regulate change
Migration
Sediment
Pollutants
Temperature
Drought
Landslides
Outburst floods
C Cycle
feedbacks
Adaptation
trade-offs