

Climate change and alpine stream biology: progress, challenges, and opportunities for the future

Scott Hotaling^{1,*†}, Debra S. Finn^{2,3,†}, J. Joseph Giersch⁴, David W. Weisrock¹ and Dean Jacobsen⁵

¹*Department of Biology, University of Kentucky, Lexington, KY 40506, U.S.A.*

²*Department of Integrative Biology, Oregon State University, Corvallis, OR 97331, U.S.A.*

³*Departamento de Recursos Hídricos y Ciencias Ambientales, Universidad de Cuenca, Cuenca, Ecuador*

⁴*U.S. Geological Survey, Northern Rocky Mountain Science Center, West Glacier, MT 59936, U.S.A.*

⁵*Freshwater Biological Laboratory, Department of Biology, University of Copenhagen, DK-2100, Copenhagen, Denmark*

ABSTRACT

In alpine regions worldwide, climate change is dramatically altering ecosystems and affecting biodiversity in many ways. For streams, receding alpine glaciers and snowfields, paired with altered precipitation regimes, are driving shifts in hydrology, species distributions, basal resources, and threatening the very existence of some habitats and biota. Alpine streams harbour substantial species and genetic diversity due to significant habitat insularity and environmental heterogeneity. Climate change is expected to affect alpine stream biodiversity across many levels of biological resolution from micro- to macroscopic organisms and genes to communities. Herein, we describe the current state of alpine stream biology from an organism-focused perspective. We begin by reviewing seven standard and emerging approaches that combine to form the current state of the discipline. We follow with a call for increased synthesis across existing approaches to improve understanding of how these imperiled ecosystems are responding to rapid environmental change. We then take a forward-looking viewpoint on how alpine stream biologists can make better use of existing data sets through temporal comparisons, integrate remote sensing and geographic information system (GIS) technologies, and apply genomic tools to refine knowledge of underlying evolutionary processes. We conclude with comments about the future of biodiversity conservation in alpine streams to confront the daunting challenge of mitigating the effects of rapid environmental change in these sentinel ecosystems.

Key words: lotic, ecology, glacier recession, global change, biodiversity, macroinvertebrate, benthic, mountain, microbial ecology, conservation biology.

CONTENTS

I. Introduction	2
II. Current approaches	3
(1) Linking organisms to environment	3
(2) Tracking and modelling temporal change	4
(3) Characterizing microbial diversity and function	6
(4) Life-history response to changing environments	6
(5) Population genetics	8
(6) Characterizing functional traits	10
(7) Field experimentation	11
III. Integrating multiple approaches	12

* Address for correspondence (Tel: 828 507 9950; Fax: 859 2571717; E-mail: srho224@g.uky.edu).

† Authors contributed equally to this work.

IV. Global perspectives, standardized methods, and emerging technologies	13
(1) Making the most of repeat sampling	14
(2) Incorporating new and improved remote sensing and GIS	14
(3) Applying genome-wide perspectives to understand evolutionary processes better	15
V. Conservation	15
VI. Conclusions	16
VII. Acknowledgements	16
VIII. References	16

I. INTRODUCTION

Alpine streams are often remote and represent some of the world's most pristine freshwater ecosystems, primarily due to limited anthropogenic impacts. Nevertheless, the highest rates of climate change are occurring above the permanent treeline in alpine and arctic ecosystems (Bradley *et al.*, 2006; Prowse *et al.*, 2006). Alpine biota are particularly vulnerable to rapid environmental warming due to the combined effects of high mountaintop insularity and upslope shifts of distributional ranges into increasingly smaller areas of suitable habitat (e.g. Walther, Beissner & Burga, 2005; Galbreath, Hafner & Zamudio, 2009; Rubidge *et al.*, 2012). Climate change is also substantially shrinking alpine glacier and snowfield mass (Hall & Fagre, 2003; Hansen *et al.*, 2005; Rauscher *et al.*, 2008; Pederson *et al.*, 2010), resulting in hydrologic shifts in existing streams (Milner, Brown & Hannah, 2009; Jacobsen *et al.*, 2014b) and new freshwater habitat taking the place of once-perennial ice (e.g. Finn, Räsänen & Robinson, 2010). Furthermore, the upslope advance of treeline into previously alpine habitat is likely to significantly affect the basal resources of aquatic food webs (Hauer *et al.*, 1997; Hood *et al.*, 2015). Alpine streams are important strongholds for biodiversity and production of food web subsidies versus the comparatively harsh terrestrial environment. However, global alpine stream biodiversity is being negatively impacted across multiple levels of taxonomic resolution (Jacobsen *et al.*, 2012; Wilhelm *et al.*, 2013; Finn *et al.*, 2014).

Alpine streams are highly environmentally heterogeneous, even across small spatial extents (<1 km), primarily due to variation in hydrologic source contributions, including glacier melt, snowmelt and rain run-off, groundwater springs, and others. Each source type results in a unique signature of stream flow, temperature, sediment load, and chemistry (Ward, 1994), although individual sources rarely act in isolation, especially when seasonal melting is occurring (Füreder *et al.*, 2001; Smith *et al.*, 2001; Brown, Hannah & Milner, 2003). Therefore, alpine stream networks are habitat mosaics harbouring significant beta diversity (differentiation among sites) both in terms of species diversity (e.g. Finn & Poff, 2005; Brown, Hannah & Milner, 2007b; Jacobsen *et al.*, 2012; Kubo *et al.*, 2012) and genetic diversity (Finn, Khamis & Milner, 2013; Finn *et al.*, 2014; Leys *et al.*, 2016). Many alpine stream species are uniquely adapted to cold, harsh conditions (Füreder, 1999; Lencioni, Boschini & Rebecchi, 2009; Lencioni *et al.*, 2015) and often

endemic (e.g. Finn & Poff, 2008; Muhlfeld *et al.*, 2011; Giersch *et al.*, 2015, 2016).

Diminishing hydrologic influence of glaciers and permanent snowfields is expected to ultimately result in environmental homogenization of alpine streams. Predicted biological effects at the regional scale include increased local (α) diversity as more-diverse assemblages shift upstream, but decreased among-stream (β) diversity as meltwater-specific assemblages are lost (Jacobsen *et al.*, 2012; Cauvy-Fraunié *et al.*, 2015a). The predicted erosion of regional-scale (γ) biodiversity associated with the homogenization of alpine stream habitat conditions includes both eukaryotes and prokaryotes (Wilhelm *et al.*, 2013), with associated negative implications for microbially mediated ecosystem function. And, although accelerated melting of the alpine cryosphere may initially benefit cold-adapted stream organisms as increased meltwater volume pushes harsh conditions farther downstream (Jacobsen *et al.*, 2014b), these conditions will be short-lived as meltwater sources eventually dwindle (Jacobsen *et al.*, 2012).

Generally, species at risk of extirpation under changing environmental conditions have three options to persist: migrate to more suitable habitat, leverage a plastic response to the changing environment, or adapt (Hoffman & Sgrö, 2011; Pauls *et al.*, 2013). For dispersal-limited alpine taxa, migration is an unlikely solution as species become caught in 'summit traps' at the upper, isolated end of available habitat (Pertoldi & Bach, 2007; Phillipsen & Lytle, 2012; Sheldon, 2012). As life history responses tend to be plastic in stream insects, an *in situ* plastic response to environmental change may be the most likely mechanism for population and species persistence, relative to long-distance migration or adaptation, at least in the short term (Treanor *et al.*, 2013; Lencioni & Bernabó, 2015; Madsen *et al.*, 2015). Furthermore, the potential for adaptation of alpine populations to changing conditions will depend upon standing genetic variation in genes that are relevant to the specific environmental changes occurring (Barrett, Roger & Schluter, 2008; Hohenlohe *et al.*, 2010). Ultimately, local extinctions at the scale of individual streams can be expected for dispersal-limited taxa that are restricted to cold, meltwater-influenced alpine streams (Giersch *et al.*, 2015). However, with better understanding of both species' adaptive potential and the distribution of stream types (and associated environmental characteristics) that are expected to be more resistant to the effects of climate change, management strategies aimed at preventing extinctions may be possible.

A rich early history in alpine stream biology spanned multiple continents and emphasized the relationship between species assemblages and environmental conditions (Steinmann, 1907; Thienemann, 1912; Dodds & Hisaw, 1925; Steinböck, 1934; Dorier, 1937; Léger, 1937; Mathews, 1951; Martinelli, 1959). The field began to develop substantially following reviews by Ward (1994) on the environmental and biological heterogeneity of alpine streams, and Milner & Petts (1994), who developed a conceptual model of the influence of glacier meltwater on stream biology at both high altitudes and latitudes. Because the field has continued to grow rapidly – potentially exceeded in pace only by the rate of climate change itself – specific topical reviews have appeared relatively regularly in the intervening two decades. These include a review of the sensitivity of alpine streams to various human impacts (McGregor *et al.*, 1995), revisits of the Milner & Petts (1994) model of glacier-melt influence (Brittain & Milner, 2001; Milner, 2016), a review of our understanding of biological responses to hydrologic change in glacier-influenced streams (Milner *et al.*, 2009), and a summary of primarily biogeochemical effects of meltwater hydrology in alpine lakes and streams (Slemmons, Saros & Simon, 2013).

Given the exceptionally high natural biodiversity contributed by flowing water habitat to alpine regions and the vulnerability of these systems to rapid environmental change, episodic reviews of the state of the science are essential. Here, for the first time since Ward (1994), we review the current state and future promise of organism-focused research in alpine streams, including all high-altitude lotic systems both with and without the presence of glaciers. We define ‘organism-focused’ as any research where the taxonomic identity of individual specimens is essential, including intraspecific genetic diversity, microbial community diversity, ecological responses of single species, and various ways of measuring eukaryotic community diversity. We build significantly on previous reviews that have emphasized glacier-influenced hydrology and macroinvertebrate species assemblages (e.g. Milner & Petts, 1994; Brittain & Milner, 2001; Milner *et al.*, 2009). Our organism-focused review also complements the recent ecosystem-focused review of Slemmons *et al.* (2013). We begin with a summary of seven major approaches historically and currently applied to organism-focused ecology of alpine streams, including both long-standing, standard approaches and emerging approaches based on either newly developed methodological tools or novel concepts. We then take a forward-looking perspective on how alpine stream research could be bolstered through the thoughtful integration of long-standing approaches with emerging concepts and technologies, improved and more-standardized monitoring of alpine stream ecosystems on a global scale, and increased collaboration across disciplines (e.g. remote sensing and organismal biology). Ultimately, our aim is to provide a unified front to aid alpine stream biologists in overcoming conceptual and methodological hurdles in the field, while also confronting the pressing challenge of understanding

the implications of rapid global change on sensitive alpine stream ecosystems in real time.

II. CURRENT APPROACHES

(1) Linking organisms to environment

Alpine streams are biologically diverse due to their significant environmental heterogeneity and relative isolation, which limits the distribution of specialized taxa and promotes endemism (Brown *et al.*, 2007b; Füreder, 2007). Early research provided valuable descriptions of the spatial heterogeneity of alpine streams and their species assemblages (e.g. Tynen, 1970; Lavandier & Décamps, 1983; Ward, 1986), and this observational foundation linking organisms to environment has continued to expand in recent years (Muhlfeld *et al.*, 2011; Kubo *et al.*, 2012; Thompson *et al.*, 2013; Cauvy-Fraunié *et al.*, 2014b; Khamis *et al.*, 2014a; Laursen *et al.*, 2015; Lencioni & Spitale, 2015; Giersch *et al.*, 2016; Tronstad, Hotaling & Bish, 2016). Generally, these studies integrate taxonomy and environmental parameters to describe patterns of species diversity with habitat. This approach has resulted in a global perspective on the environmental drivers of alpine stream biodiversity – as influenced both by local environmental filtering across the variety of alpine stream types and by limited dispersal among isolated alpine areas – and provided a plethora of snapshots to which future observational data can be compared (see approach 2). Much of the historical effort applying this standard, observational approach was focused in Europe, but alpine stream research on other continents has also been represented to varying degrees with North and South America receiving considerable recent attention (Fig. 1). Still, many alpine regions – including mountain ranges within comparatively well-studied continents – have been understudied or overlooked.

Inferences about the effects of rapid environmental change on alpine stream biodiversity within this observational approach rely on a space-for-time framework, in which a gradient of spatial conditions is expected to represent the temporal trajectory of environmental change. Because a significant impact of climate change in alpine streams is the ongoing decline of glacier and snowfield mass (Oerlemans, 2005; Jacob *et al.*, 2012), many studies have emphasized biological responses to spatial gradients of hydrologic conditions, typically from glacier-fed to groundwater-dominated stream reaches (Milner *et al.*, 2008, 2009; Finn *et al.*, 2010, 2013, 2014; Jacobsen *et al.*, 2012; Cauvy-Fraunié *et al.*, 2014b, 2015a). Various indices have been developed to quantify the proportional influence of glacier meltwater on local stream environments and biota (e.g. Ilg & Castella, 2006; Brown, Hannah & Milner, 2007a; Jacobsen & Dangles, 2012; reviewed by La Frenierre & Mark, 2014), and implementations of the space-for-time approach in different alpine regions often support a general conclusion: that decline in meltwater conditions will likely decrease regional biodiversity (Jacobsen *et al.*, 2012; Fig. 2).

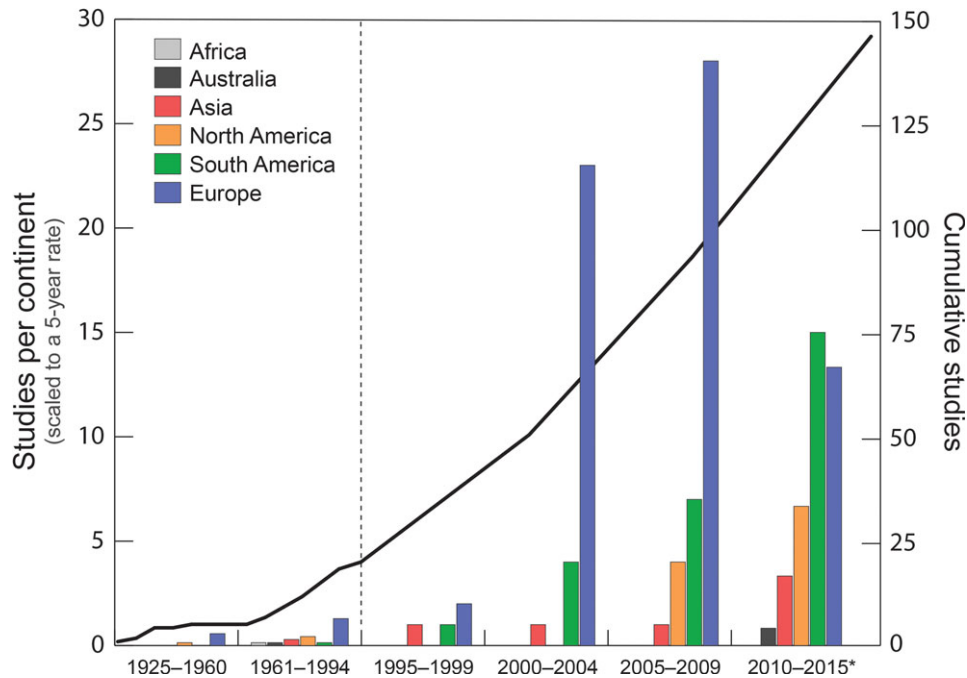


Fig. 1. Continental distribution of alpine stream biology research published before and after seminal publications by Ward (1994) and Milner & Petts (1994), denoted by the vertical dashed line. The left y-axis and histogram bars are studies per continent across 5-year intervals for the period 1995–2015 and ~35-year intervals for 1925–1994 (the asterisk indicates a 6-year interval where data are scaled by a factor of 0.833 to be equivalent to the other modern 5-year periods). The right y-axis and black line reflect the cumulative number of studies on all continents through time. To generate a literature database, we first added known citations to a combined database. Next, this database was supplemented through two *Web of Science* searches: (a) for “alpine stream* ecology” OR “alpine stream* biology and (b) for “alpine” AND “stream” AND “gene*”. Searches were conducted for the years 1925–2015. The references included as data for this figure are marked with an asterisk in the References list.

Space-for-time studies also provide important starting points for identifying regions, stream types, or taxa most at risk from climate change, but correlations between extant biological diversity and current environmental conditions have limitations particularly when projecting future changes to single localities. They do not consider: changes in assemblage structure that could alter biotic interactions through time (Brown & Milner, 2012; Clitherow, Carrivick & Brown, 2013; Khamis *et al.*, 2015); the adaptive potential of resident species to changing conditions (e.g. Barrett *et al.*, 2008; Hohenlohe *et al.*, 2010); or how changes in specific environmental factors might differentially influence altitudinal distributions of individual species (Jacobsen, 2008; Loayza-Muro *et al.*, 2013a; Giersch *et al.*, 2015; Leys *et al.*, 2016). Furthermore, many space-for-time predictions are based on comparisons between extant meltwater-fed and non-meltwater-fed (e.g. groundwater) streams. As such, they tend to not consider the potential for meltwater streams to become seasonally intermittent, a possibly fatal flaw considering that little is known about how dwindling meltwater sources influence groundwater aquifers in alpine regions (Haldorsen & Heim, 1999). Certainly, a complete disappearance of permanent stream habitat can be expected to have substantially greater impacts on biodiversity than, for example, a meltwater habitat transitioning to groundwater-fed habitat.

(2) Tracking and modelling temporal change

Studies that resample the same locations through time or use historical occurrence data can demonstrate explicit biotic responses to environmental change and provide empirical data for testing model-based predictions of species occurrences and range shifts. For example, Sheldon (2012) collected two species of stoneflies along an elevation and stream-size gradient in the Great Smoky Mountains in both 1977–1978 and 2006 to assess the magnitude of upstream range shifts in response to climate change in the region. With known rates of warming for the area ($\sim 0.72^\circ\text{C}$ over the study period), these data provided an empirical assessment of a general model-based prediction ($+11\text{ m/decade}$) of upslope shifts for biotic assemblages (Chen *et al.*, 2011). Results revealed differential responses of the two study species, with evidence for an uphill shift in one but not the other, suggesting that factors other than water temperature influence elevational distributions of stream-dwelling species in the Great Smoky Mountains (Sheldon, 2012). In a similar example from alpine streams, Giersch *et al.* (2015) combined contemporary sampling of an alpine stonefly, *Zapada glacier*, with historical records and a known temperature increase in Glacier National Park ($0.67\text{--}1^\circ\text{C}$) over a 52-year study period (1960–2012). The results pointed to a climate-change-induced range contraction of *Z. glacier* into

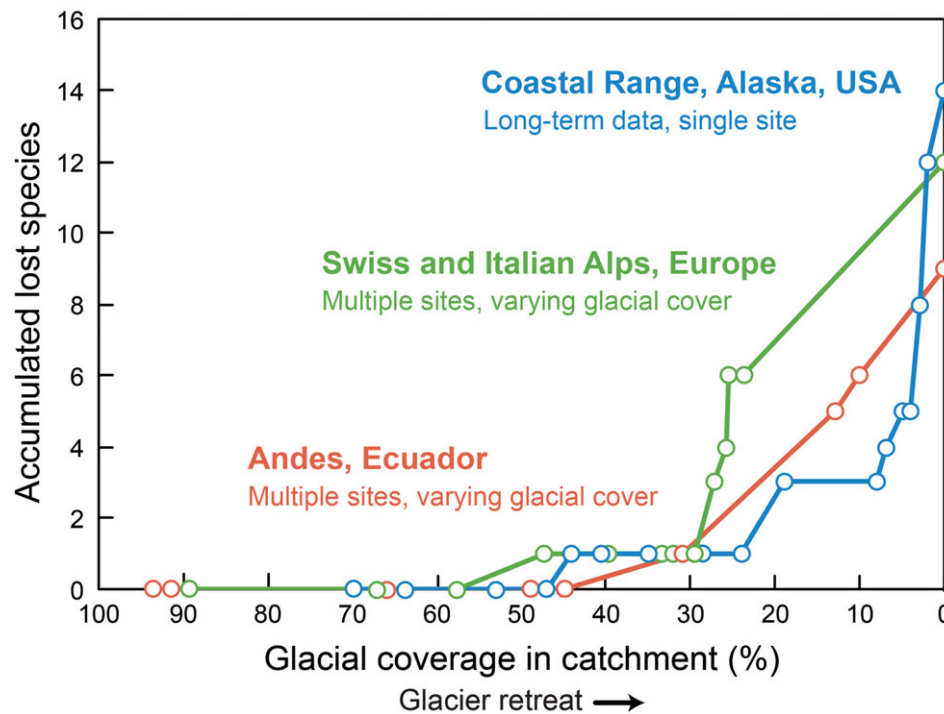


Fig. 2. Cumulative decrease of regional species richness (γ diversity) as a function of glacial cover. Glacier-obligate macroinvertebrates begin disappearing when glacial cover drops below approximately 50%. Each data point represents a river site. Figure modified with permission from Jacobsen *et al.* (2012).

the uppermost limits of the streams where it historically occurred. With alpine stream monitoring efforts becoming more common, exciting opportunities exist for resampling prior snapshots (approach 1) to analyse the rate and nature of single-site temporal change.

Glacier recession can also unveil virgin stream channels, providing an opportunity for temporal studies of colonization and succession in glacier-fed stream environments. Milner *et al.* (2008) monitored colonization and succession of an Alaskan stream community over nearly three decades, and Finn *et al.* (2010) assessed the impact of rapid glacial recession over a 10-year period on macroinvertebrates and environmental features along an alpine stream gradient in the Swiss Alps. Both studies generally corroborated inferences from space-for-time research, showing that newly exposed and early successional glacier-fed stream habitats supported assemblages of cold-hardy species that likely colonized these habitats from downstream reaches with recently reduced meltwater influence. However, Finn *et al.* (2010) also demonstrated that the rate of temperature increase with stream distance below a glacial source had significantly steepened over a single decade, an observation that would not have been predicted in a space-for-time framework.

Beyond retrospective empirical studies, species distribution models (SDMs) predict future distributions by integrating occurrence data and associated environmental factors, and projecting these into the future under specific scenarios (e.g. climate change models). SDMs have become essential tools in conservation biology (Elith & Leathwick, 2009) but

are currently underrepresented in alpine streams [but see Bálint *et al.* (2011); Muhlfeld *et al.* (2011) and Giersch *et al.* (2016)]. Although limited, these studies predict significant threats to alpine biodiversity due to loss of glaciers (Muhlfeld *et al.*, 2011; Giersch *et al.*, 2016) or more general mountaintop habitat decline (Bálint *et al.*, 2011). Alpine stream biology is poised for increased application of SDMs to assess future threats to biodiversity, perhaps with a focus on developing implementations that account for more alpine-specific changes (e.g. shifts in meltwater influence and/or new stream habitat being uncovered as glaciers recede).

Predictive modelling has also been used to identify ecological tipping points in glacial streams that represent a point at which cold, stenothermic species assemblages may be extirpated. For instance, a Threshold Indicator of Taxa Analysis (TITAN; Baker & King, 2010) identified thresholds of < 5.1% glacier cover and < 66.6% meltwater contribution as tipping points where more generalist macroinvertebrates would begin to replace cold-adapted specialists in Pyrenean alpine stream communities (Khamis *et al.*, 2014a). When viewed in isolation, it is impossible to make predictions about how strongly these results apply to other glaciated alpine regions, but this type of region-specific predictive modelling provides a valuable glimpse into potential points-of-no-return for alpine stream diversity. Future assessments carried out with the same methodology in additional regions hold the potential for clarifying alpine stream ecological tipping points from a global perspective.

(3) Characterizing microbial diversity and function

Alpine glaciers and snowfields, and the extreme cryophilic habitat they represent, provide habitat for diverse microbial communities, including on the surface of glaciers (Anesio & Laybourn-Perry, 2012), below glaciers (Hamilton *et al.*, 2013), in meltwater streams (Wilhelm *et al.*, 2013), and stream sediments (Fegel *et al.*, 2016). Until recently, microbial biodiversity and function in alpine headwaters had been largely unexplored. This disconnect is particularly noteworthy considering that stream microbial communities have been widely recognized for their general importance to biodiversity, ecosystem processes, and biogeochemistry (Zeglin, 2015; Battin *et al.*, 2016). Microbial biofilms in particular alter physical and chemical microhabitats, acting as living zones of transient organic molecule storage. Moreover, because local-scale diversity of multicellular organisms is often relatively low in alpine streams, diverse microbial communities could play a disproportionate role in the ecology of alpine streams.

Structure and function of alpine stream microbial communities vary depending upon hydrology (Freimann *et al.*, 2013, 2014; Wilhelm *et al.*, 2013, 2014) and local habitat, whether streamwater, biofilm, sediments, or glacial snow and ice (Wilhelm *et al.*, 2013, 2014; Fegel *et al.*, 2016). In Swiss alpine floodplains, microbial community structure and enzymatic function are influenced by sediment pH, conductivity, and other physicochemical conditions affected by the presence of glacial meltwater (Freimann *et al.*, 2013, 2014). To understand the connection between glacial ice and downstream microbial diversity better, Wilhelm *et al.* (2013) characterized 16S rDNA diversity of microorganisms in streamwater, biofilm, and source glacial ice for 26 glacier-fed streams in the Austrian Alps (Fig. 3). This approach revealed that glacier retreat is likely to increase within-stream microbial α diversity while reducing among-stream β diversity, a pattern similar to that predicted for alpine macroinvertebrates as local environmental conditions become less harsh but more homogeneous (Jacobsen & Dangles, 2012; Jacobsen *et al.*, 2012). In a subsequent study, Wilhelm *et al.* (2014) used an RNA sequencing approach to compare the abundances of RNA (the product of cellular processes) to DNA for microbiota in the same Austrian streams. Their findings revealed that rare taxa (from a total DNA perspective; Wilhelm *et al.*, 2013) play a disproportionate role in microbial community dynamics of alpine glacier-fed streams (Wilhelm *et al.*, 2014). By comparing abundance of RNA *versus* DNA, it is possible to move beyond descriptions of biodiversity patterns to understand the activity of microbial life in alpine streams better and identify which taxa are most important under a given set of sampling conditions (e.g. time of day, season, flow, etc.). Given the role of microbial life in dictating biogeochemical processes [e.g. carbon fixation (Singer *et al.*, 2012) or nitrogen cycling (Dodds & Smith, 2016)], any clarification of microbial diversity and activity, as well as the environmental conditions both are linked to, will greatly improve understanding of how alpine stream ecosystems function.

A warming climate is also expected to affect basal resources (and microbial dynamics) in alpine streams, particularly in terms of organic carbon (OC), as glaciers recede, treelines rise, and stream energy inputs shift (Hood *et al.*, 2015; Wilhelm *et al.*, 2015). Mountain glaciers store considerable OC, primarily within englacial (the glacial core where light does not penetrate) and basal ice (Hood *et al.*, 2015). However, the implications of the accelerated release of this glacially derived OC on downstream ecosystems remain unclear (Hood *et al.*, 2015), although links between glacially derived OC, microorganisms, macroinvertebrates, and fish have been made in Alaskan streams (Fellman *et al.*, 2015). This is particularly important for heterotrophic microbial communities as glacial OC is significantly more biologically available than dissolved OC from other inputs (e.g. vascular plants; Singer *et al.*, 2012). A slowly climbing treeline is also relevant to the availability of OC in alpine streams primarily because trees add an additional input of allochthonous dissolved OC. Below treeline, specialization by biofilm bacteria in response to more diverse allochthonous and autochthonous dissolved OC has been hypothesized to drive shifts from more-generalist biofilm communities (in terms of functional traits related to the utilization of resources) above treeline to specialist-rich communities below. In a study of three alpine streams in the Swiss Alps, this hypothesis was partially supported with generalist microbiota dominating biofilm communities along an altitudinal gradient (including above and below treeline), and specialists gaining importance with increasing distance downstream of the treeline (Wilhelm *et al.*, 2015). Furthermore, questions of treeline shifts, energy inputs, and available OC may be further complicated in alpine streams by seasonality as energy inputs vary with magnitude of glacial discharge (Fenoglio *et al.*, 2015).

(4) Life-history response to changing environments

Like many aspects of alpine stream biology, life histories of alpine macroinvertebrates are poorly understood. In the context of environmental change, population persistence could depend on the potential for life-history traits (e.g. development rate, emergence timing, size at maturity, and other reproductive traits) to respond rapidly to abiotic change. For aquatic insects, most life-history traits are highly plastic, at least within certain bounds (e.g. Vannote & Sweeney, 1980; Newbold, Sweeney & Vannote, 1994). Or, if adaptive, such traits may respond quickly to natural selection (Poff *et al.*, 2006). Hence, if selection pressures in alpine streams naturally vary spatially and/or temporally, resident insects could have a strong capacity to respond through phenotypic plasticity (e.g. Vannote & Sweeney, 1980; Stearns, 1989), adaptation (e.g. Hynes, 1976; Gray, 1981; Lytle, 2001; Lytle & Poff, 2004; Lytle, Bogan & Finn, 2008), or a combination of the two.

Diversity in life-history traits may provide the raw material for selection, adaptation, and persistence of species in the face of rapid environmental change (*cf.* Schindler *et al.*, 2010), particularly if the characteristic environmental heterogeneity of alpine streams across small spatial extents translates

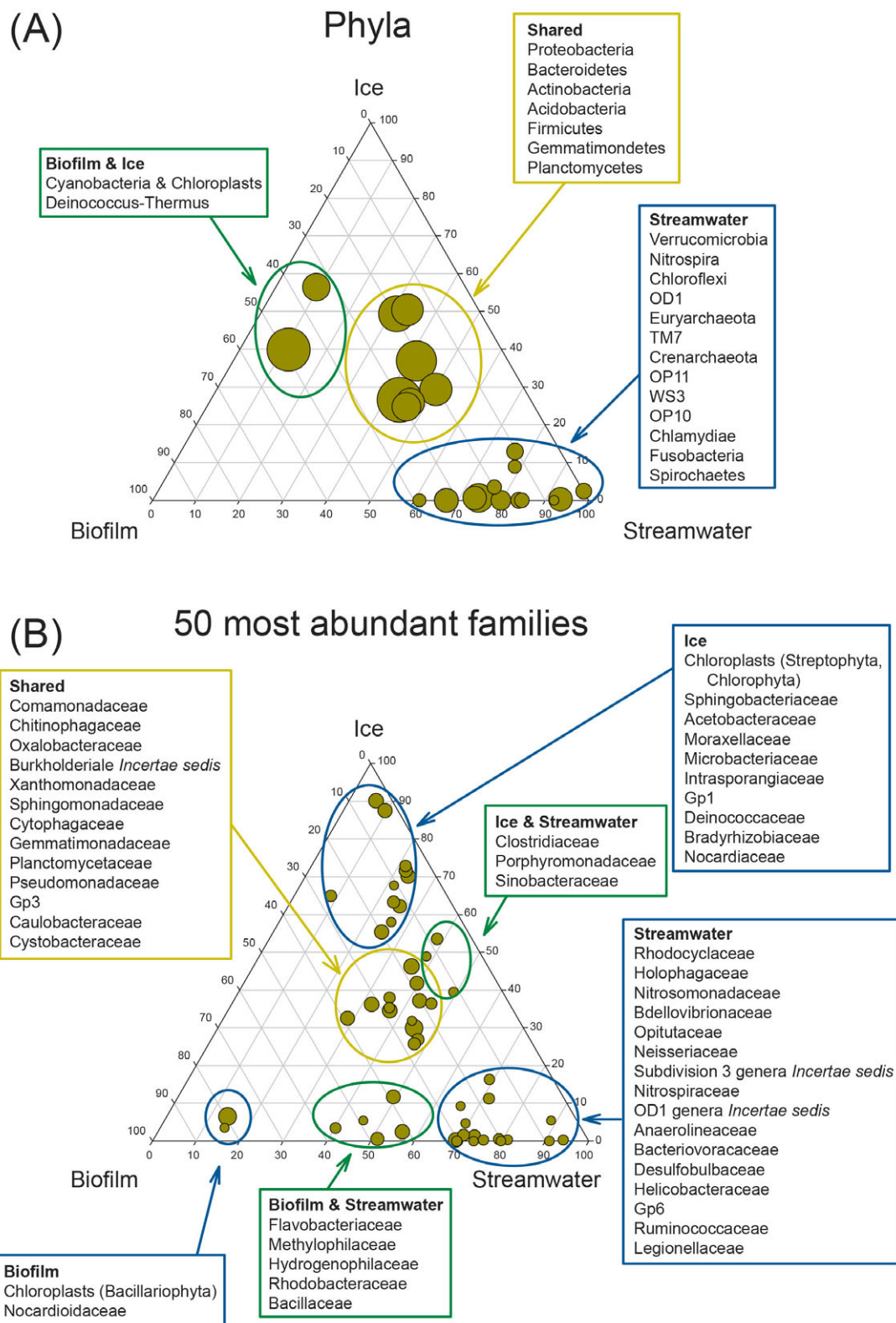


Fig. 3. Distribution of microbial taxonomic groups in glacial ice, streamwater, and biofilm. The percentage of (A) phyla and (B) the 50 most abundant families associated with each habitat are visualized in ternary plots. Position within each triangle indicates the relative abundance of each taxon among the three habitats. Circle size represents the relative abundance of taxa overall. Figure modified with permission from Wilhelm *et al.* (2013).

to intraspecific diversity in life histories. Indeed, many aquatic insects inhabiting steep temperature gradients (as is common in alpine streams) exhibit life-history variation along the gradient. For example, *Rhyacophila evoluta*, an alpine caddisfly, can enter diapause at any instar, which translates to a 1-, 2-, or 3-year life cycle depending upon thermal conditions (Décamps, 1967). At high elevations, the alpine mayfly *Baetis alpinus* is semivoltine (2-year life cycle), larger at maturity, and females produce more eggs, while at low elevations, it is univoltine (1-year life cycle), smaller at maturity, and females produce on average approximately 25% fewer eggs (Lavandier & Décamps, 1984). Interestingly, *Allogamus uncatatus*, another alpine caddisfly, showed life-history patterns more-or-less opposite of expectations in stream reaches 0.9–1.7 km downstream of a glacier (Shama & Robinson, 2009). Individuals closest to the glacier tended to reach pupation more rapidly and be smaller at maturity than those furthest away (Fig. 4A). However, the study reaches were part of a complex alpine floodplain, and upstream–downstream patterns of environmental variation did not vary as expected with distance from the glacier, likely due to patchy groundwater inputs (Uehlinger, Malard & Ward, 2003; Ward & Uehlinger, 2003) and minimal elevation difference (Shama & Robinson, 2009). These results highlight that spatial heterogeneity among alpine streams even over a very small spatial extent can significantly amplify intraspecific life-history variation.

Life-history traits of alpine stream insects might also respond quickly to temporal environmental variation. In a 2-year study of insect emergence in a Rocky Mountain alpine stream, Finn & Poff (2008) found that emergence timing of four common species (a caddisfly, a stonefly, and two mayflies) was significantly later in a year following an above-average winter snowpack, compared to one preceded by a below-average snowpack (Fig. 4B). Documentation of these temporal differences in the same location suggests phenotypic plasticity, likely in response to degree-day accumulation, which depends heavily on duration of snowpack covering streams. Although largely unexplored, changes in snow accumulation and melt timing likely impact insect emergence, and therefore could affect connectivity among populations. Questions concerning life-history diversity and physiological limits on plasticity and adaptive potential in obligate alpine stream species remain underexplored but should be important foci in future studies addressing the potential for species persistence under rapidly changing conditions.

(5) Population genetics

Population genetics has a rich history informing many aspects of evolutionary and conservation biology, but has been under-represented in alpine streams. To date, genetic studies on alpine stream organisms have focused on estimating population structure, demography, gene flow, and the impacts of glacier recession on intraspecific genetic variation (Monaghan *et al.*, 2001, 2002; Finn & Adler, 2006; Finn *et al.*, 2006, 2014; Li *et al.*, 2009; Bálint *et al.*, 2011; Elbrecht *et al.*,

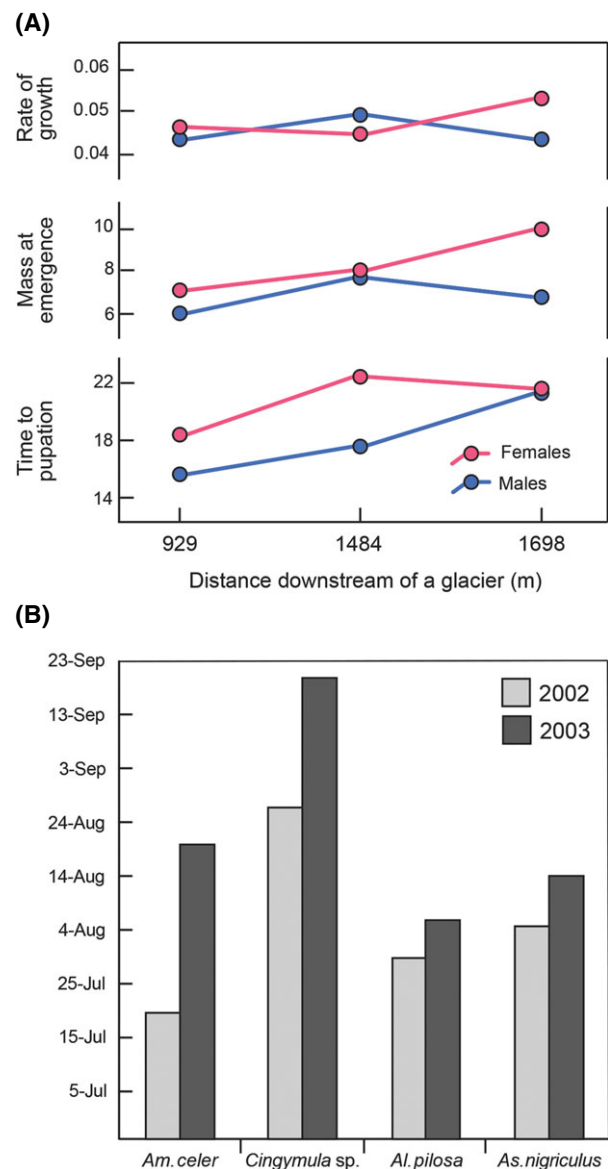


Fig. 4. (A) Examples of fine-scale spatial variation in life-history traits of alpine stream insects. Plots indicate population-level differences in rate of growth [$\ln(\text{mg}) \text{ day}^{-1}$], mass at emergence (mg), and time to pupation (measured from third-instar larvae to the onset of pupation; days) for permanent stream populations of the alpine caddisfly, *Allogamus uncatatus*, with increasing distance from glaciers in the Val Roseg floodplain of the Swiss Alps. Results were averaged across treatments in a common garden experiment. (B) An example of temporal variation in life-history traits. Histograms indicate the date at which 25% of the cumulative abundance of emerging adults was reached for four common alpine stream species (Ephemeroptera: *Ameletus celer* and *Cinygmula* sp., Plecoptera: *Alloperla pilosa*, and Trichoptera: *Asynarchus nigriculus*) along an alpine stream in the Rocky Mountains, USA. Samples were collected in 2 years: 2002, which followed an exceptionally dry winter, and 2003, which followed a winter with an above-average snowpack. Emergence timing was significantly earlier for all species in 2002. Data for (A) were redrawn (and approximated) from Fig. 5 in Shama & Robinson (2009). Data for (B) are from Finn & Poff (2008).

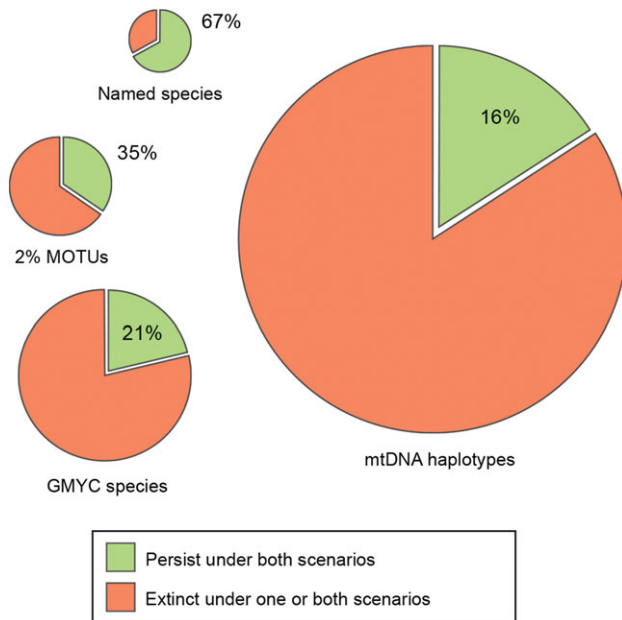


Fig. 5. Projected loss or extinctions of morphologically diagnosed species, molecular operational taxonomic units (MOTUs) identified as having <2% sequence divergence, general mixed Yule-coalescent (GMYC; Monaghan *et al.*, 2009) species delimited using a model-based approach, and mitochondrial DNA (mtDNA) haplotypes for nine montane stream insects in Europe under 2 IPCC 2080 CO₂ emission scenarios as inferred from future species distribution modelling. Green slices indicate units predicted to persist under both future emission scenarios and red slices indicate units predicted to go extinct under one or both scenarios. Circles are scaled proportionally by total units for each classification. Figure modified with permission from Bálint *et al.* (2011).

2014; Geismar *et al.*, 2015; Giersch *et al.*, 2015, 2016; Jordan *et al.*, 2016). These studies have identified a general trend among alpine stream taxa of relatively high levels of genetic differentiation among populations, indicative of spatial isolation and limited gene flow (e.g. Finn *et al.*, 2006), as well as taxon-specific patterns including putative sex-biased dispersal (e.g. Elbrecht *et al.*, 2014) and variation in the influence of landscape features on population connectivity (e.g. Geismar *et al.*, 2015). These molecular studies have tended to focus on single species, but some comparisons have been made across related or co-occurring species. For example, a multi-species comparison revealed that differences among species in dispersal behaviour appear to be both order-specific (e.g. caddisflies were found to be better dispersers than mayflies) and dependent upon spatial scale (Monaghan *et al.*, 2002). In a study combining population genetics and SDM for nine montane macroinvertebrates, results indicated that loss of genetic diversity under future warming scenarios is predicted to greatly exceed that of more traditional biodiversity metrics (e.g. morphologically defined species, Fig. 5; Bálint *et al.*, 2011).

An emerging genetic focus is understanding how decreasing habitat heterogeneity associated with glacial

recession will impact intraspecific genetic variation. Using a space-for-time approach, Finn *et al.* (2013) classified 18 alpine stream reaches in the French Pyrénées as high-, mid-, or low-'glaciation', according to physicochemical variables linked to meltwater influence (Ilg & Castella, 2006). Population structure of *B. alpinus* was significantly greater among high-glaciation streams (Fig. 6), indicating that decreasing habitat heterogeneity associated with shrinking glacial influence could lead to reduced regional-scale genetic variation. Furthermore, *B. alpinus* sampled from two recently deglaciated mountain ranges south of the Pyrénées had significantly lower regional-scale genetic diversity than at a similar spatial scale in the still-glaciated Pyrénées (Finn *et al.*, 2014). In another *B. alpinus* study, evidence from both mitochondrial DNA (mtDNA) and microsatellites revealed two distinct cryptic lineages that occurred in sympatry with differentiation between the two seemingly driven by elevation and habitat (one lineage was more abundant in groundwater-fed tributaries *versus* glacier-fed streams; Leys *et al.*, 2016). It will be important to monitor and understand how climate-induced environmental homogenization of alpine streams might also erode existing patterns of genetic diversity, particularly given the role of genetic diversity as the template for natural selection.

Moving forward, significant opportunity exists to take advantage of next-generation sequencing (NGS) to address fundamental questions in alpine stream biology through the analysis of genome-scale data. While NGS inquiry is becoming commonplace within biological research, it is still under-represented in freshwater science at large (Pauls *et al.*, 2014), and particularly in the context of alpine streams. NGS data sets allow researchers to investigate the same questions described above but at finer scales and higher resolution while also providing the statistical power to address more complex questions (e.g. selecting models of demographic history, testing for signatures of natural selection). The potential of NGS in alpine stream biology is evidenced by two recent studies. A phylogeographic study of the montane caddisfly *Thremma gallicum* employed thousands of restriction-site-associated DNA sequencing (RADseq; Miller *et al.*, 2007; Baird *et al.*, 2008; Andrews *et al.*, 2016) markers to assess models of demographic history and compare results to those inferred using mtDNA data (Macher *et al.*, 2015). The RADseq data had much greater statistical power than the mtDNA data to estimate genetic diversity, and to discern among alternative phylogeographic hypotheses. The second example used genotyping-by-sequencing (another restriction-site-associated method for generating large numbers of anonymous markers, see Elshire, Glaubitz & Sun, 2011) to take a genome-wide perspective on genetic differentiation among co-occurring winged and wingless stonefly species of the genus *Zelandoperla* (Dussex, Chuah & Waters, 2015). The results provided fine-scale evidence of the implications of flight loss on genetic differentiation as wingless populations of *Z. fenestrata* exhibited distinct genetic structure whereas populations of winged *Z. decorata* did not (Dussex *et al.*, 2015). Furthermore, signatures of low

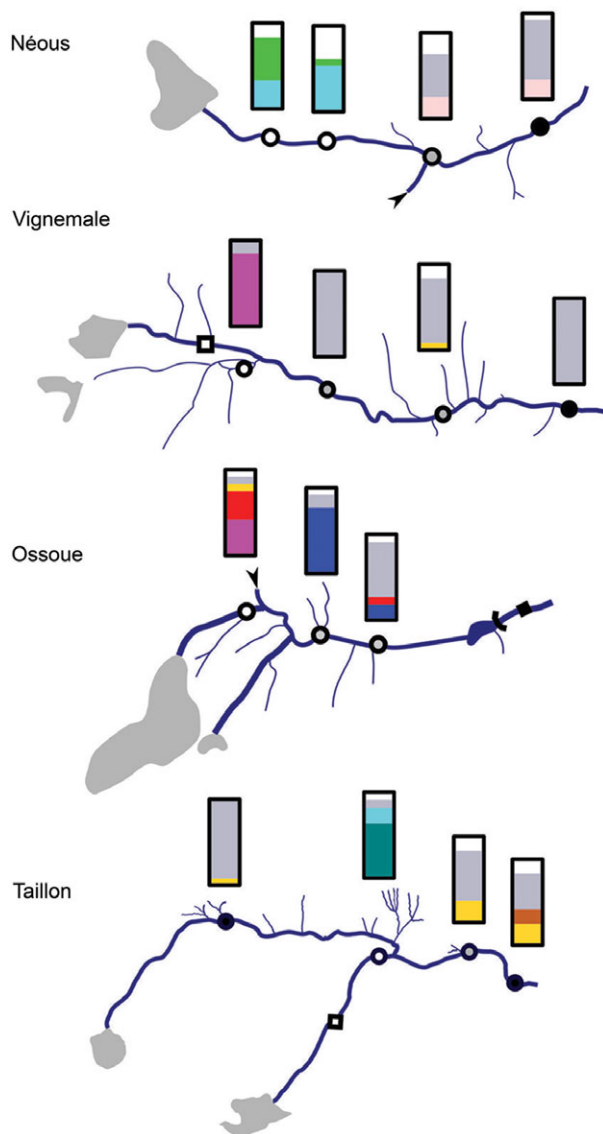


Fig. 6. Distribution of common *Baetis alpinus* mitochondrial DNA (mtDNA) haplotypes along four streams of the French Pyrénées National Park. Stream drawings are approximations and are reoriented such that glaciers (grey) are to the left, and downstream-most sample reaches are to the right. Maximum downstream distance of a sample reach is 4.5 km (Vignemale basin). Coloured bars indicate haplotype abundance (total $N = 11–13$ per reach as indicated by height of bars). Sample reaches along streams are coded white for high-glaciality, grey for mid-glaciality, and black for low-glaciality. Squares indicate sites without *B. alpinus* populations. Figure modified with permission from Finn *et al.* (2013). Copyright © 1999–2016, John Wiley & Sons, Inc.

levels of hybridization between *Z. fenestrata* and *Z. decorata* were recovered raising questions regarding the fluidity of sympatric species and the possibility of dispersal-related phenotypes introgressing between taxonomically distinct taxa (Dusseix *et al.*, 2015). Beyond extensions to both the power and diversity of analyses, NGS data sets also alleviate

many limitations of mtDNA markers (e.g. matrilineal inheritance, no recombination), and application of these methods does not depend on previous genomic knowledge of the focal species. For these combined reasons, NGS data sets hold great promise for alpine stream biologists to describe existing genetic patterns better, address evolutionary questions in the field, and refine predictions of how climate change will affect alpine stream taxa.

(6) Characterizing functional traits

Describing biological communities according to functional traits can provide a mechanistic understanding of the relationships between communities and their environment. This approach is used widely in stream ecology (Poff, 1997; Usseglio-Polatera *et al.*, 2000; Poff *et al.*, 2006) and has clear application to the heterogeneous environments of alpine streams. Rather than taxonomic descriptions, species are assigned traits related to habitat characteristics and environmental response (Lamouroux, Dolédec & Bayraud, 2004; Statzner, Dolédec & Hugué, 2004). One requirement for a traits-based approach is that the ecology of the taxa under consideration is relatively well understood. This is a challenge for rare, understudied alpine stream species that also tend to face atypical environmental filters compared to other stream types (Füreder, 1999; Lencioni, 2004).

In glacier-influenced streams, resilience and resistance traits (e.g. streamlined bodies, high adult mobility, habitat and feeding generalism, clinging behaviour, short life cycles) are common among macroinvertebrates (e.g. Snook & Milner, 2002) and provide advantages for coping with harsh conditions (Füreder, 2007). Along gradients of decreasing glacial influence in streams, such coping traits tend to decrease in relative abundance, while others increase (Fig. 7), with overall trait diversity rising in parallel with taxonomic diversity (Ilg & Castella, 2006; Milner *et al.*, 2009; Brown & Milner, 2012). To this end, the harsh conditions of glacier-fed streams may act as an environmental filter for both taxonomic and functional diversity, but strength of response to changes in glacial run-off appears to be highly taxon-specific (Jacobsen *et al.*, 2014a). These differential responses are likely driven by varying types of coping traits among taxa (Füreder, 2007), with some species possessing traits better suited to one change (e.g. decreased suspended sediments), and others possessing traits better suited to a different change (e.g. increased water temperature). Certain ecophysiological traits [e.g. cold hardiness, metabolic performance, tolerance to ultraviolet (UV) radiation] are also likely drivers of species distributions in harsh alpine stream environments; however, the adaptive roles (and related physiology) of these traits have rarely been addressed. For macroinvertebrates in high-Andean streams for example, range shifts to higher elevation in response to warming temperature will likely be accompanied by a decrease in metabolic rate as a result of oxygen limitation (Jacobsen & Brodersen, 2008), or upstream range expansion might be limited by the negative effects of increasing UV (Loayza-Muro *et al.*, 2013a). These types of perspectives linking possible physiological limitations

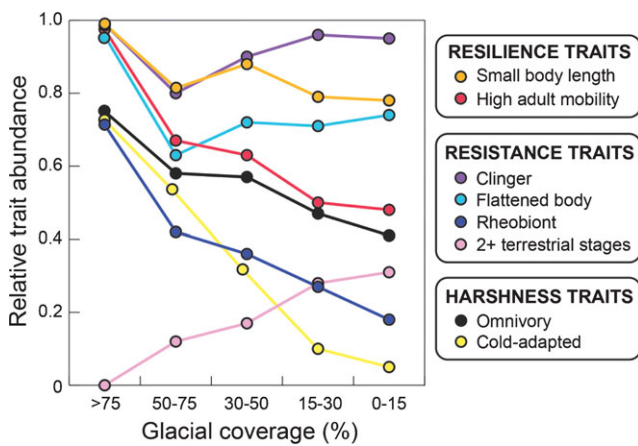


Fig. 7. Mean relative abundance of eight species traits defined as either resilience, resistance or harshness traits for 297 aquatic invertebrate taxa collected from 60 sites along 37 different rivers representing a gradient of glacial cover in Hohe Tauern National Park, Austria. Resilience traits aid in rapid return to pre-disturbance population densities following a hydrologic disturbance. Resistance traits are linked to the capacity of organisms to withstand a hydrologic disturbance without significant loss of individuals. Harshness traits are linked to the capacity of individuals to survive cold temperatures or periods of low food availability. See Füreder (2007) for original data and additional discussion of specific traits.

with scenarios of climate-change-induced range shifts can provide the foundation for hypothesis-driven experiments to assess the future viability of populations.

Two prominent selective agents in alpine streams are constant cold temperature and seasonal formation of ice (Lencioni, 2004; Danks, 2007). While water acts as a thermal buffer minimizing extreme temperature fluctuation and stream flow limits the formation of ice crystals (Danks, 1971; Füreder, 1999), aquatic insects still experience long periods of sustained cold during development which almost always takes place under snow or ice (Lencioni, 2004). For freeze-tolerant aquatic insects, one adaptive theme is the repeated evolution of elevated concentrations of glycerol and/or ice-binding factors (or anti-freeze proteins) in larval haemolymph (Walters *et al.*, 1998; Füreder, 1999; Lencioni, 2004; Danks, 2007; Lencioni *et al.*, 2008, 2009, 2015; Lencioni & Bernabó, 2015). For instance, Lencioni *et al.* (2008, 2015) and Lencioni & Bernabó (2015) comprehensively studied respiratory performance and thermal limits of the midge *Pseudodiamesa branickii* which inhabits glacier-fed streams in the Italian Alps. Larvae of this species are tolerant to freezing to temperatures as low as -16°C and although the upper lethal temperature of *P. branickii* may be as high as $\sim 32^{\circ}\text{C}$, specimens appeared stressed above 12°C . These results suggest an adaptive strategy by *P. branickii* to thrive in extremely cold glacier-fed stream environments at the expense of effective competitive abilities for persisting in warmer downstream habitats. With increases in water temperature and associated decreases in dissolved oxygen availability, specialists such as *P. branickii* could lose their advantage in inhabiting glacier-fed streams

and be replaced by more generalist taxa with greater competitive ability. Species turnover dictated by competition in glacier-fed streams has been described previously for other midges, including those of the genus *Diamesa* (see Saether, 1968; Nolte, 1991), and may represent a general mechanism applicable to cold-tolerant macroinvertebrate communities on a global scale (Flory & Milner, 2000). Furthermore, the extreme conditions associated with glacier-fed streams and the unique suite of traits required to withstand them likely exacerbate trade-offs between competitive (e.g. temperature generalism) and specialist traits (e.g. freeze-tolerant larvae).

Evaluation and monitoring of trophic (feeding) traits is also relevant to alpine stream biology as climates warm and basal food resources shift from predominantly autochthonous to allochthonous (Hauer *et al.*, 1997). Trophic traits in macroinvertebrates, including those driving specialization by consumers on either algae or leaves, tend to be phylogenetically constrained and therefore less likely to respond to natural selection than other, more evolutionarily labile traits (Poff *et al.*, 2006). As such, strong shifts in food resources might translate to relatively rapid changes in the functional and taxonomic structure of alpine stream assemblages and associated ecosystem-level processes (e.g. Robinson & Gessner, 2000; Cauvy-Fraunié *et al.*, 2016).

(7) Field experimentation

Experimentation under natural conditions is a powerful tool for understanding the mechanisms of observed pattern and process and for predicting ecological responses to climate change. However, *in situ* experimentation in alpine streams is rare, likely due to the logistical constraints of carrying out field experiments in remote, harsh environments. Furthermore, experiments in which natural conditions are manipulated for long time periods (>1 year) are particularly rare, and even short-term (single season or less) studies are uncommon. Nonetheless, alpine streams offer useful opportunities for field-based ecological experiments given their small size, limited taxonomic diversity and ecological complexity, minimal human impact, and natural habitat variation over small spatial extents. These advantages also ought to attract a broader swathe of ecologists looking for suitable ecological systems for experimentation.

In perhaps the only long-term ecological field experiment in alpine streams, Cauvy-Fraunié *et al.* (2016) conducted a 4-year experimental flow manipulation in the Ecuadorian Andes, diverting one-third of natural discharge from a glacier-fed stream to assess how decreased run-off affects ecological pattern and process. Meltwater reduction increased benthic algal and macroinvertebrate herbivore biomass and changed macroinvertebrate community composition within a few weeks. After the diversion was terminated and the stream was returned to natural flow levels, the system did not return to its pre-perturbation state for over a year. From a climate change perspective, the rapid response to flow diversion suggests that as meltwater influence is reduced,

impacts to alpine stream ecosystems will occur rapidly across a variety of biological metrics (Fig. 8).

Short-term field experiments have evaluated biological drivers of organic matter decomposition rates in alpine streams. For instance, experimentally increased nutrient concentrations in an alpine groundwater-fed stream spurred an increase in shredder (detritus-feeding macroinvertebrates) abundance and faster breakdown of detritus in leaf packs (Robinson & Gessner, 2000). The authors speculated that microbial assemblages colonizing leaves in these streams are nutrient-limited, such that when nutrients were supplemented, the microbially mediated quality of the leaf litter increased, leading to the observed increase in shredder abundance and feeding activity. In another alpine leaf-pack experiment focused on the relationship between shredder diversity and ecosystem function (i.e. decomposition rates), an interaction between shredder species richness and abundance had the strongest impact on decomposition rates in high-Andean streams (Dangles *et al.*, 2011). In this study, the three most-abundant shredder species produced the greatest decomposition rates when co-occurring, a result that implies some degree of complementary resource use and/or facilitation among species (Dangles *et al.*, 2011). These findings suggest that differential climate-mediated range shifts (of both macroinvertebrates and terrestrially derived organic matter) could decouple important biological interactions in alpine stream ecosystems.

Experimental transplantation of species into novel communities and/or environments can help researchers understand how range shifts of alpine stream species might impact biotic interactions and ecosystem processes. In an Alaskan glacier-fed stream, transplanting stones colonized by midges of the genus *Diamesa* between reaches at different elevations demonstrated that the natural absence of this species from lower elevation sites was due to competitive exclusion rather than inability to tolerate the local environmental conditions (Flory & Milner, 2000). Similarly, Madsen *et al.* (2015) transplanted larvae of selected macroinvertebrates upstream of their natural altitudinal limit in a high-Andean glacier-fed stream to test the short-term (two weeks) effect on survival. This treatment reduced survival by varying degrees among taxa, but the stonefly *Claudioperla* sp. survived well at a site where it did not naturally occur, suggesting that altitudinal limits are not always directly related to the abiotic environment, at least not in the short term. Khamis *et al.* (2015) tested the potential impacts of an introduced predator on natural species densities using side channels constructed next to an alpine stream in the French Pyrénées. By manipulating densities of the predacious stonefly *Perla grandis*, which occurs in the same streams but at slightly lower elevations, they simulated an upstream range expansion of *P. grandis* and found that some (but not all) prey species were reduced. The authors concluded that the extinction risk of range-restricted prey taxa could increase with upstream predator range shifts. From a broader perspective, transplant studies demonstrate the utility of

short-term field experiments in alpine streams, particularly in addressing the influence of rapid environmental change on species interactions and ecosystem processes.

III. INTEGRATING MULTIPLE APPROACHES

The seven approaches for organism-focused research in alpine stream biology described in Section II are not mutually exclusive, and here, we argue that thoughtful integration of multiple approaches will lead to more robust understanding of these rapidly changing systems (e.g. Pauls *et al.*, 2014). Even in our discussion of each approach independently, it is clear that many examples bridged multiple approaches. For example, Shama & Robinson (2009) used common garden experiments (approach 7) to understand life-history variation (approach 4) of alpine caddisflies across a complex environment; Snook & Milner (2002) and others evaluated species traits (approach 6) to understand associations of species with environmental conditions (approach 1); and population genetic analysis of common species (approach 5) can be combined with the more traditional approach of evaluating spatial patterns of assemblage diversity (approach 1) to generate a more thorough understanding of the biological effects of environmental heterogeneity in alpine streams (Finn *et al.*, 2013). Future biological research in alpine streams should emphasize continued integration, with a particular emphasis on multiple levels of biological organization (genes to assemblages, and prokaryotes to eukaryotes) and a merging of the more traditional ‘snapshot’ observational approaches with experimentation and/or emerging technologies (e.g. NGS).

Recent studies showcase the power and promise of highly integrative research in alpine streams. For instance, Bálint *et al.* (2011) evaluated the contemporary spatial distributions of nine alpine/arctic macroinvertebrate morphospecies (approach 1) and three levels of cryptic biodiversity determined with population genetic methods (approach 5) for the same morphospecies. The authors then applied SDM (approach 2) according to two climate models based on future CO₂ emissions scenarios to each of the four levels of biodiversity independently. The results of their integrative analysis suggested that biodiversity loss under either climate model would be proportionally much greater in terms of genetic variation than morphospecies diversity (Fig. 5). This outcome supports a broader hypothesis that rates of climate-related biodiversity loss (in fresh waters and otherwise) will be significantly underestimated if measured as impacts to morphological species diversity alone (e.g. Dudgeon *et al.*, 2006; Strayer & Dudgeon, 2010) without consideration of intraspecific genetic diversity (Bálint *et al.*, 2011; Pauls *et al.*, 2013).

Another promising example of integrating approaches is the resampling of the same systems and species through time (approach 2) and applying increasingly powerful population genetic tools (approach 5) to understand specific biological effects of rapid environmental change, including biodiversity,

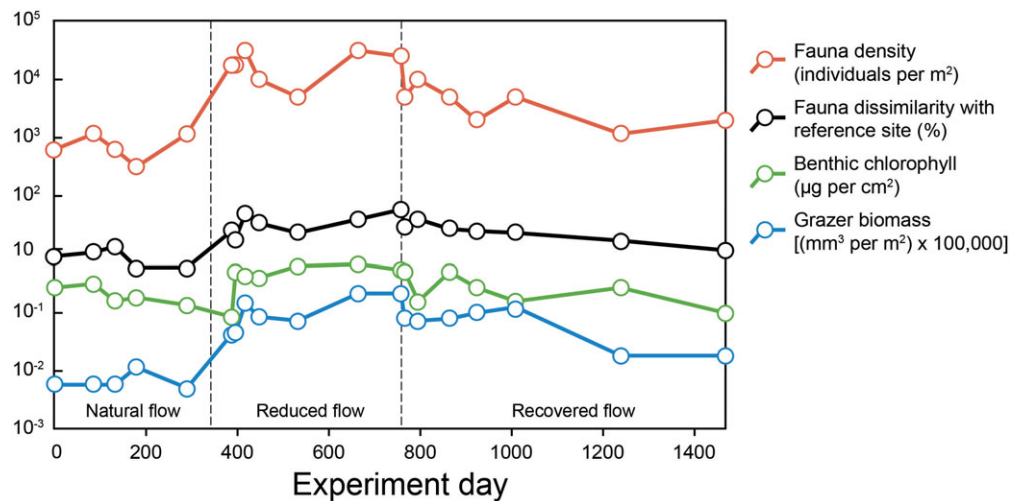


Fig. 8. Results from a flow-reduction experiment in an Ecuadorian glacier-fed stream where benthic samples were collected at irregular intervals over a 4-year study period. The experimental reach was sampled for approximately 1 year prior to flow manipulation ('natural flow'). After this initial period, approximately one-third of the discharge was diverted away from the reach for ~1 year ('reduced flow'). Natural flow then was re-established and the reach was monitored for another 2 years ('recovered flow'). Data shown include density of benthic macroinvertebrates (red), fauna dissimilarity (Bray-Curtis; black) *versus* an unmanipulated upstream reference site, benthic chlorophyll (green), and total biomass of macroinvertebrate grazers (blue). Figure modified with permission from Cauvy-Fraunié *et al.* (2016).

population structure, and demography. To our knowledge, there have been just two published temporal comparisons of genetic variation in alpine streams. In the first, Shama *et al.* (2011) assessed genetic diversity both spatially and temporally for the caddisfly, *A. uncatatus*, before and after an extreme drought in the Swiss Alps, revealing a significant decrease in overall genetic diversity but an increase in differentiation among populations over just two generations. In the second, Jordan *et al.* (2016) compared genetic diversity and patterns of population structure between historic (>10 years old) and modern (2010) samples of an endemic stonefly, *Lednia tumana*, threatened by climate change in Glacier National Park, USA. The results indicated decreased genetic diversity and increased subdivision among populations in just 10 years, an alarming finding given the near-term decline of the extremely cold glacier meltwater that comprises much of *L. tumana*'s habitat in the region. In the terrestrial alpine environment, a 90-year study of two alpine chipmunk species in Yosemite National Park revealed different population genetic responses to warming. One species maintained connectivity and gene flow through a largely unaffected range size over the study period, while the second species underwent significant fragmentation and genetic differentiation among populations likely as a result of a 500 m upslope range contraction (Rubidge *et al.*, 2012). In alpine streams, a related question remains to be addressed: will a changing climate affect population genetic structure across communities in a synchronous way or will changes be taxon-specific?

There are a number of other opportunities for novel integrative research to address pressing questions in alpine systems facing rapid change, particularly within the context

of whether plastic or adaptive responses in life-history traits (approach 4) could have biological repercussions beyond local population persistence. For example, differences in emergence timing influenced by snowpack duration appear to affect flight activity of insect species (Finn & Poff, 2008), likely due to late-season colder air temperatures discouraging adult flight activity. Differential dispersal through time can affect regional-scale population persistence (approach 2) and genetic diversity (approach 5), and potential responses of both can be measured or modelled with molecular methods (e.g. Bálint *et al.*, 2011; Shama *et al.*, 2011; Jordan *et al.*, 2016). Furthermore, spatial variation in development rates and emergence timing between streams with different temperature and flow regimes (e.g. a glacier-fed stream *versus* a groundwater-fed spring) has been hypothesized as a potential driver of reproductive isolation among stream insect populations (Finn *et al.*, 2013, 2014). As alpine streams become more environmentally homogenous at the regional scale, these life-history traits will likely follow suit. Future research integrating the monitoring of temporal change in environmental variation, life-history traits, population structure, and genetic variation will improve understanding of how these aspects of population biology are interconnected in alpine streams.

IV. GLOBAL PERSPECTIVES, STANDARDIZED METHODS, AND EMERGING TECHNOLOGIES

Beyond integration across the 'standard seven' approaches, we also see fruitful opportunity associated with recent and emerging technological advances. Examples of these

include database management for long-term and universally accessible storage of samples and data, high-resolution remote sensing, and population genomics and associated analytical tools (NGS, approach 5). We elaborate here on methods and applications for seizing these opportunities in alpine stream biology.

(1) Making the most of repeat sampling

Given the rapid pace of environmental change in alpine streams, temporal monitoring of environmental parameters and biota will be important to developing greater understanding of the degree of vulnerability of these systems to climate warming. To make the most of observational data henceforth, alpine stream researchers should ideally apply universally standard collection methods and proper storage of samples to serve as temporal comparisons for future studies. With the continued rise of powerful genomic tools (e.g. RADseq; Andrews *et al.*, 2016) and development of advanced morphometric approaches (e.g. micro-computed tomography; Verdú, Alba-Tercedor & Jiménez-Manrique, 2012; Friedrich *et al.*, 2014), properly stored and annotated biological specimens will no doubt provide useful genotypic and phenotypic reference points for understanding rates and mechanisms of evolutionary change as well as better understanding of existing variation. Furthermore, standardized monitoring of environmental parameters and biological assemblages will be essential for linking habitat change to biological change at a global scale.

In alpine stream biology, internationally accessible database(s) and associated collaborative networks have been proposed (e.g. Füreder & Schöner, 2013), but the idea has yet to be realized. The spatially limited temporal data sets discussed above (e.g. Milner *et al.*, 2008; Finn *et al.*, 2010; Shama *et al.*, 2011) provide useful precedents to justify a unified effort towards the development of such a network. Indeed, there are now international networks and databases set up to monitor long-term change in other ecological systems that alpine stream scientists can look to for guidance. These include the Global Observation Research Initiative in Alpine Environments (GLORIA), which emphasizes the monitoring of terrestrial alpine plants (Grabherr, Gottfried & Pauli, 2000), and the Global Lake Ecological Observatory Network (GLEON), an international program with standardized protocols for documenting environmental change in lakes (Weathers *et al.*, 2013; Read *et al.*, 2016). As with any integrated monitoring effort, a networked alpine stream ecology database should provide explicit guidelines on standardized protocols for measuring and storing (if applicable) the unique suite of physicochemical, hydrologic, and biological variables relevant to the system. Discussions and previous large-scale research projects in the past [e.g. Arctic and Alpine Stream Ecosystem Research (AASER); Brittain & Milner, 2001] have emphasized a set of appropriate environmental variables (with a focus on hydrology) and collection methods for macroinvertebrate assemblage data. We suggest adding standardized protocols

for storing and vouchering specimens for subsequent genetic and/or morphometric analyses. Furthermore, it will be important to recommend balanced spatial sampling strategies within each alpine region added to an international network (e.g. Füreder & Schöner, 2013), including multiple drainage basins and hydrologically defined stream types to address questions about landscape-scale connectivity, population genetic structure, and the interacting influences of local environment and spatial distance on biological responses. By putting these goals in a standardized global network, the field is poised to move beyond the story of one range or species that may be an anomaly of local variation, to the story of many species and ranges with the power to portend more significant trends.

(2) Incorporating new and improved remote sensing and GIS

Opportunity also exists for alpine stream biologists to incorporate remote sensing technology and geographic information system (GIS)-based approaches into future research (e.g. Carbonneau & Piégay, 2012). Through these tools, baseline measurements of landscape features specific to alpine stream structure and function can be assessed and serve as reference points for future research. Recent developments in remote sensing technology for spatial mapping (e.g. Light Detection and Ranging, LiDAR) as well as aerial infrared sensing provide more accurate (and more efficient) collection of stream and watershed attributes than previously possible. Example applications include, but are not limited to, monitoring of succession at the watershed scale in recently deglaciated basins (Klaar *et al.*, 2015), remote measurements of stream temperature (Handcock *et al.*, 2012), and remote characterization of watershed attributes (Hopkinson, Hayashi & Peddle, 2009). Glacial and snowfield margins, as well as corresponding stream networks, can also be digitized in GIS, quantified, and compared with other time periods or localities (e.g. del Rio *et al.*, 2014; Hall *et al.*, 2015) or linked with existing biodiversity to assess ties between glaciers and species occurrences more clearly (e.g. Giersch *et al.*, 2016). From the perspective of modelling threats to biodiversity, finer-scale resolution of geologic and environmental change can directly bolster predictions about future distributions or environmental pressures. For all remote sensing projects in alpine streams, it is important that imagery be captured during later parts of the season to minimize ice coverage and maximize stream resolution. Monitoring of glaciers and the alpine environment – whether *via* remote sensing or other methods – is not new (e.g. Francou *et al.*, 2000; Hall & Fagre, 2003; Rabatel *et al.*, 2013). Rather, our take-home message is the potential for alpine stream biologists to cultivate collaborations with researchers carrying out existing spatial monitoring and remote sensing efforts to inform links between abiotic (e.g. glacier size, water temperature) and biotic (e.g. algal growth) characteristics of alpine headwater ecosystems.

(3) Applying genome-wide perspectives to understand evolutionary processes better

NGS and associated approaches (e.g. RADseq) for generating large genomic data sets can significantly improve our understanding of biological responses to rapid environmental change in alpine streams, specifically in an evolutionary context. Until recently, questions that required information from a genome-wide perspective (e.g. identifying genes under selection) were difficult even for model organisms and out of reach for all other taxa. This is no longer an issue for most species, thanks to the falling cost and rising efficiency of NGS data collection. Genome-scale data sets overcome many limitations of single- or few-marker studies (e.g. an overemphasis on the unique evolutionary history of the mitochondrial genome) that have been widely applied in alpine stream biology. However, with orders of magnitude more data and computationally intensive analytical methodologies, implementing NGS approaches requires specific laboratory and bioinformatic training. While a full review of NGS applications is beyond the scope of this review [but see Manel & Holderegger (2013) and Andrews *et al.* (2016)], we discuss specific topics below where an NGS toolkit could be particularly valuable for studying alpine stream biota from a climate change perspective.

A standing question in alpine stream biology is whether population connectivity will be substantially altered with the decline of cold meltwater habitat. Genome-scale data sets are well suited to this challenge as they provide the necessary power to resolve fine-scale variation in migration among genetic clusters (e.g. Beerli, 2006) or can be used to characterize migration as a subset of parameters in an overarching demographic modelling framework (e.g. Gutenkunst *et al.*, 2009; Excoffier *et al.*, 2013). Indeed, this latter approach is particularly useful because, in addition to estimating parameters like migration, it also provides a means for simultaneous estimation of other aspects of population biology and history (e.g. divergence times among lineages, temporal changes in effective population sizes). For instance, given the important role that fragmented habitat plays in shaping genetic diversity (see approach 5), constructing a timeline of population divergence provides an outlet for linking divergence events with past landscape-level processes (e.g. recession of glaciers after the Last Glacial Maximum).

NGS data sets also represent a promising avenue for identifying ecologically relevant genetic diversity, a virtually unexplored realm in alpine stream biology. Using predominantly neutral, genome-wide markers to reconstruct the demographic history of populations provides a null model for identifying outlier markers that are either portions of genes responding to natural selection or are at least in linkage with them (Nielsen *et al.*, 2005). For example, across a heterogeneous alpine stream network, if there is strong enough selection to drive adaptive divergence between populations in different habitats and enough time has passed for signatures of this selection to accumulate, divergent

adaptation in outlier genes (e.g. a heat shock gene involved in chaperoning cellular processes under cold stress; Matz *et al.*, 1995) may be observed. The potential for using genomic tools to link genotype to phenotype holds particular relevance for addressing questions of ecophysiology in a changing climate (see approach 6). Specifically, understanding the genomic mechanisms through which species have adapted to harsh conditions (e.g. the evolution of anti-freeze proteins) can also inform the degree to which those mechanisms may be flexible as conditions change, especially if closely related species or ecological gradients are available for comparison. A combined approach integrating analysis of population connectivity, demographic history, and detection of outlier loci that may be under selection all in the context of future distribution modelling, represents a framework for investigating how focal species may respond at the genomic level to changing environmental conditions. For instance, if many populations in a single mountain range are locally adapted to different thermal regimes then the rate and direction of migration (i.e. the potential for the spread of adaptive genetic diversity) among populations is a critical component of any species-wide adaptive response.

V. CONSERVATION

Despite the documented importance of alpine headwaters to biodiversity at the scale of whole stream networks (e.g. Finn *et al.*, 2013), there has been little emphasis on developing management strategies for biodiversity conservation in these systems (Khamis *et al.*, 2014b). Unlike in lowland rivers where climate change is proceeding more slowly and conservation management and restoration practices typically emphasize returning systems back to some historical steady state from other types of anthropogenic impacts, rapid climate change is the single greatest threat to the integrity of otherwise pristine alpine streams (Hannah *et al.*, 2007). As such, conservation management in alpine streams is a daunting prospect, often perceived to be insurmountable due to the limited potential to reverse the environmental effects of climate change (Khamis *et al.*, 2014b). Therefore, the common conservation strategy of protecting individual, range-restricted or rare species and intraspecific genetic diversity (e.g. Allendorf & Luikart, 2007) may have minimal benefit in alpine streams. Instead, Khamis *et al.* (2014b) call for a shift in focus from single species of concern to conserving ecosystem processes when possible, including maintaining or enhancing biological connectivity among alpine basins and limiting additional anthropogenic stressors.

However, even under this promising, more holistic conservation framework of maintaining ecosystem processes and broad swathes of heterogeneous habitat (e.g. Linke, Turak & Nel, 2011), we can still expect a systematic disappearance of many headwater streams fed by the melting of ice or snow under future warming scenarios, along with the unique species and genetic variation they harbour. In terms of biodiversity conservation in alpine streams, then, a

worthwhile goal is to identify and prioritize the protection of robust local populations of cold stenothermic species associated with meltwater habitat (e.g. Finn & Adler, 2006), as well as meltwater-associated habitats that are likely to be most resistant to climate change. As part of this process, robust assessments of species boundaries from multi-locus genetic data will be an important component of conservation strategies (e.g. Grummer, Bryson & Reeder, 2014; Hime *et al.*, 2016; Hotaling *et al.*, 2016). Although many alpine glaciers and associated meltwater habitats are expected to disappear in the near future (Hall & Fagre, 2003; Edmunds *et al.*, 2012), it is becoming increasingly apparent that there are other types of extremely cold meltwater habitat (not previously recognized in the alpine stream ecology literature) that might be more resistant to change and could serve as climate refugia for cold-adapted biota. Specifically, rock glaciers – subsurface masses of ice and rock debris – act as hydrologic sources for some alpine streams and are likely more resistant to atmospheric warming due to the overlying layers of insulating debris (Millar & Westfall, 2008; Fegel *et al.*, 2016). Streams primarily fed by rock glacier meltwater might contain robust populations of cold stenothermic species of concern (e.g. Muhlfield *et al.*, 2011; Giersch *et al.*, 2015, 2016) and would therefore be ideal sites to prioritize for biodiversity conservation (as per Finn, Bogan & Lytle, 2009). We advocate an integration of the approaches described above, including remote sensing for locating rock-glacier-fed streams and other potentially resistant alpine stream types, genetic methods for determining recent population demographics and species boundaries, and temporal sampling to evaluate population stability through time, as an effective toolkit for making conservation decisions for alpine stream biodiversity.

VI. CONCLUSIONS

(1) Alpine stream ecosystems contain disproportionately high biodiversity at multiple levels of taxonomic resolution, from genes to communities. This biodiversity, along with extensive environmental heterogeneity, natural geographic isolation, generally low anthropogenic impact, and rapid warming at high altitudes combine to make alpine streams sentinels of environmental change on a global scale. Increasing environmental homogenization of alpine streams with climate change, and potential ramifications from both biodiversity conservation and ecosystem function perspectives, are of major concern. It is timely and important to increase our understanding of the processes affecting alpine stream biodiversity and to make scientifically defensible conservation decisions for protecting the evolutionary legacy of these imperiled ecosystems.

(2) We identify and summarize seven major, organism-focused research approaches that have been applied in alpine stream research both historically and more recently. These approaches vary from basic observational

research of environmental conditions and macroscopic organisms to approaches emphasizing newly developed methods. Through awareness of existing methods and tools, future researchers are better suited to address research questions in an integrated, collaborative framework.

(3) To develop a more robust understanding of the processes affecting alpine stream biodiversity under climate change, we advocate the following: (i) thoughtful integration of the seven approaches, with a specific focus on combinations of traditional and emerging approaches, to address complex hypotheses spanning multiple levels of biological organization; (ii) increased multidisciplinary collaboration, specifically to integrate useful tools outside of biology (e.g. remote sensing); (iii) systematic development and expansion of international research networks and the establishment of agreed-upon standards for sample collection, database management, and communication; and (iv) application of high-resolution genomic methods to address evolutionary, systematic, and conservation questions for alpine stream species.

(4) Because the single greatest threat to alpine stream organisms is climate change, biodiversity conservation is a daunting challenge, and to date, minimal emphasis has been placed on this aspect of alpine stream biology. We suggest the best way forward for conserving threatened species is to identify and prioritize demographically stable, genetically diverse populations occupying stream sites with the maximum possible resistance to changing environmental conditions.

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VIII. REFERENCES

- References marked with * were used in the construction of Fig. 1.
- ACOSTA, R. & PRAT, N. (2010). Chironomid assemblages in high altitude streams of the Andean region of Peru. *Fundamental and Applied Limnology* **177**, 57–79.*
- ALLAN, J. D. (1975). Faunal replacement and longitudinal zonation in an alpine stream. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* **19**, 1646–1652.*

- ALLENDORF, F. & LUIKART, G. (2007). *Conservation and the Genetics of Populations*. Blackwell Publishing, Oxford.
- ANDREWS, K. R., GOOD, J. M., MILLER, M. R., LUIKART, G. & HOHENLOHE, P. A. (2016). Harnessing the power of RADseq for ecological and evolutionary genomics. *Nature Reviews Genetics* **17**, 81–92.
- ANESIO, A. M. & LAYBOURN-PERRY, J. (2012). Glaciers and ice sheets as a biome. *Trends in Ecology & Evolution* **27**, 219–225.
- BAIRD, N. A., ETTER, P. D., ATWOOD, T. S., CURREY, M. C., SHIVER, A. L., LEWIS, Z. A., SELKER, E. U., CRESKO, W. A. & JOHNSON, E. A. (2008). Rapid SNP discovery and genetic mapping using sequenced RAD markers. *PLoS Genetics* **3**, e3376.
- BAKER, M. E. & KING, R. S. (2010). A new method for detecting and interpreting biodiversity and ecological community thresholds. *Methods in Ecology and Evolution* **1**, 25–37.
- BÁLINT, M., DOMISCH, S., ENGELHARDT, C. H. M., HAASE, P., LEHRMAN, S., SAUER, J., THEISSINGER, K., PAULS, S. U. & NOWAK, C. (2011). Cryptic biodiversity loss linked to global climate change. *Nature Climate Change* **1**, 313–318.
- BARIC, S., RIEDL, A., MERANER, A., MEDGYESY, N., LACKNER, R., PELSTER, B. & DALLA VIA, J. (2010). Alpine headwater streams as reservoirs of remnant populations of the Danubian clade of brown trout. *Freshwater Biology* **55**, 866–880.*
- BARRETT, R. D. H., ROGER, S. M. & SCHLUTER, D. (2008). Natural selection on a major armor gene in threespine stickleback. *Science* **322**, 255–257.
- BASCHEN, C., MANZ, W., NEU, T. R., MARVANOVÁ, L. & SZEWZYK, U. (2008). In situ detection of freshwater fungi in an alpine stream by new taxon-specific fluorescence in situ hybridization probes. *Applied and Environmental Microbiology* **74**, 6427–6436.*
- BATTIN, T. J., BESEMER, K., BENGTSSON, M. M., ROMANI, A. M. & PACKMAN, A. I. (2016). The ecology and biogeochemistry of stream biofilms. *Nature Reviews Microbiology* **14**, 251–263.
- BATTIN, T. J., WILLE, A., PSENNER, R. & RICHTER, A. (2004). Large-scale environmental controls on microbial biofilms in high-alpine streams. *Biogeosciences* **1**, 159–171.*
- BEERLI, P. (2006). Comparison of Bayesian and maximum likelihood inference of population genetic parameters. *Bioinformatics* **22**, 341–345.
- BRADLEY, R. S., VUILLE, M., DIAZ, H. F. & VERGARA, W. (2006). Threats to water supplies in the tropical Andes. *Science* **312**, 1755–1756.
- BREWIN, P. A., NEWMAN, T. M. L. & ORMEROD, S. J. (1995). Patterns of macroinvertebrate distribution in relation to altitude, habitat structure and land use in streams of the Nepalese Himalaya. *Archiv für Hydrobiologie* **135**, 79–100.*
- BRINCK, P. & WINGSTRAND, K. G. (1949). The mountain fauna of the Virihaure area in Swedish Lapland. I. General account. *Lunds Universitets Årsskrift N.F.* **2**, 1–69.*
- BRITTAIN, J. E. & MILNER, A. M. (2001). Ecology of glacier-fed rivers: current status and concepts. *Freshwater Biology* **46**, 1571–1578.
- BROWN, L. E., HANNAH, D. M. & MILNER, A. M. (2003). Alpine stream habitat classification: an alternative approach incorporating the role of dynamic water source contributions. *Arctic, Antarctic, and Alpine Research* **35**, 313–322.*
- BROWN, L. E., HANNAH, D. M. & MILNER, A. M. (2005). Spatial and temporal water column and streambed temperature dynamics within an alpine catchment: implications for benthic communities. *Hydrological Processes* **19**, 1585–1610.*
- BROWN, L. E., HANNAH, D. M. & MILNER, A. M. (2007a). ARISE: a classification tool for Alpine River and Stream Ecosystems. *Freshwater Biology* **54**, 1357–1369.
- BROWN, L. E., HANNAH, D. M. & MILNER, A. M. (2007b). Vulnerability of alpine stream biodiversity to shrinking glaciers and snowpacks. *Global Change Biology* **13**, 958–966.*
- BROWN, L. E., MILNER, A. M. & HANNAH, D. M. (2007c). Groundwater influence on alpine stream ecosystems. *Freshwater Biology* **52**, 878–890.*
- BROWN, L. E. & MILNER, A. M. (2012). Rapid loss of glacial ice reveals stream community assembly processes. *Global Change Biology* **18**, 2195–2204.
- BROWN, L. E., MILNER, A. M. & HANNAH, D. M. (2006). Stability and persistence of alpine stream macroinvertebrate communities and the role of physicochemical habitat variables. *Hydrobiologia* **560**, 159–173.*
- BRUNO, M. C., MAIOLINI, B., CAROLLI, M. & SILVERI, L. (2009). Impact of hydropeaking on hyporheic invertebrates in an Alpine stream (Trentino, Italy). *Annales De Limnologie - International Journal of Limnology* **45**, 157–170.*
- BRUNO, M. C., MAIOLINI, B., CAROLLI, M. & SILVERI, L. (2010). Short time-scale impacts of hydropeaking on benthic invertebrates in an Alpine stream (Trentino, Italy). *Limnologia* **40**, 281–290.*
- CADBURY, S. L., MILNER, A. M. & HANNAH, D. M. (2011). Hydroecology of a New Zealand glacier-fed river: linking longitudinal zonation of physical habitat and macroinvertebrate communities. *Ecology* **92**, 520–531.*
- CARBONNEAU, P. E. & PIÉGAY, H. (2012). *Fluvial Remote Sensing for Science and Management*. John Wiley & Sons, Ltd., Chichester.
- CAUVY-FRAUNTIÉ, S., ANDINO, P., ESPINOSA, R., CALVEZ, R., ANTHELME, F., JACOBSEN, D. & DANGLES, O. (2014a). Glacial flood pulse effects on benthic fauna in equatorial high-Andean streams. *Hydrological Processes* **28**, 3008–3017.*
- CAUVY-FRAUNTIÉ, S., ESPINOSA, R., ANDINO, P., DANGLES, O. & JACOBSEN, D. (2014b). Relationships between stream macroinvertebrate communities and new flood-based indices of glacial influence. *Freshwater Biology* **59**, 1916–1925.*
- CAUVY-FRAUNTIÉ, S., ANDINO, P., ESPINOSA, R., JACOBSEN, D. & DANGLES, O. (2016). Ecological responses to experimental glacier-runoff reduction in alpine rivers. *Nature Communications* **7**, 12025.
- CAUVY-FRAUNTIÉ, S., ANDINO, P., ESPINOSA, R., JACOBSEN, D. & DANGLES, O. (2015a). Temporal scaling of high flow effects on benthic fauna: insights from equatorial glacier-fed streams. *Limnology and Oceanography* **60**, 1836–1847.*
- CAUVY-FRAUNTIÉ, S., ESPINOSA, R., ANDINO, P., JACOBSEN, D. & DANGLES, O. (2015b). Invertebrate metacommunity structure and dynamics in an Andean glacial stream network facing climate change. *PLoS One* **10**, e0136793.
- CHAVES, M. L., RIERADEVALL, M., CHAINHO, P., COSTA, J. L., COSTA, M. J. & PRAT, N. (2008). Macroinvertebrate communities of non-glacial high altitude intermittent streams. *Freshwater Biology* **53**, 55–76.*
- CHEN, L. C., HILL, J. K., OHLEMULLER, R., ROY, D. B. & THOMAS, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026.
- CLITHEROW, L. R., CARRIVICK, J. L. & BROWN, L. E. (2013). Food web structure in a harsh glacier-fed river. *PLoS One* **8**, 1–11.
- CROSA, G., CASTELLI, E., GENTILI, G. & ESPA, P. (2010). Effects of suspended sediments from reservoir flushing on fish and macroinvertebrates in an alpine stream. *Aquatic Sciences* **72**, 85–95.*
- DANGLES, O., CRESPO-PÉREZ, V., ANDINO, P., ESPINOSA, R., CALVEZ, R. & JACOBSEN, D. (2011). Predicting richness effects on ecosystem function in natural communities: insights from high-elevation streams. *Ecology* **92**, 733–743.*
- DANKS, H. V. (1971). Overwintering of some north temperate and arctic Chironomidae. II. Chironomid biology. *The Canadian Entomologist* **103**, 589–604.
- DANKS, H. V. (2007). How aquatic insects live in cold climates. *The Canadian Entomologist* **139**, 443–471.
- DÉCAMPS, H. (1967). Écologie des Trichoptères de la vallée d'Aure. (Hautes-Pyrénées). *Annales de Limnologie* **3**, 399–577.*
- DEL *****RIO, M., RICO, I., SERRANO, E. & TEJADO, J. J. (2014). Applying GPR and laser scanner techniques to monitor the Ossoue Glacier. (Pyrenees). *Journal of Environmental and Engineering Geophysics* **19**, 239–248.
- DI LORENZO, T., STOCH, F. & GALASSI, D. M. P. (2013). Incorporating the hyporheic zone within the river discontinuum: longitudinal patterns of subsurface copepod assemblages in an Alpine stream. *Limnologia* **43**, 288–296.*
- DODDS, G. S. & HISAW, F. L. (1925). Ecological studies on aquatic insects. IV. Altitudinal range and zonation of mayflies, stoneflies and caddisflies in the Colorado Rockies. *Ecology* **6**, 380–390.*
- DODDS, W. K. & SMITH, V. H. (2016). Nitrogen, phosphorous, and eutrophication in streams. *Inland Waters* **6**, 155–164.
- DORIER, A. (1937). La faune des eaux courantes alpines. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* **8**, 33–41.
- DUBEY, O. P. & KAUL, B. K. (1971). Torrenticole insects of the Himalaya. IV. Some observations on the ecology and the character-insect communities of the R. Alhni. *Oriental Insects* **5**, 47–71.*
- DUDGEON, D., ARTHINGTON, A. H., GESSNER, M. O., KAWABATA, Z., KNOWLER, D. J., LÉVÊQUE, C., NAIMAN, R. J., PRIEUR-RICHARD, A. H., SOTO, D., STIASNY, M. L. & SULLIVAN, C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* **81**, 163–182.
- DUSSEX, N., CHUAH, A. & WATERS, J. M. (2015). Genome-wide SNPs reveal fine-scale differentiation among wingless alpine stonefly populations and introgression between winged and wingless forms. *Evolution* **70**, 38–47.
- EDMUNDS, J., TOOTLE, G., KERR, G., SIVANPILLAI, R. & POCHOP, L. (2012). Glacier variability (1967–2006) in the Teton Range, Wyoming, United States. *Journal of the American Water Resources Association* **48**, 187–196.
- ELBRECHT, V., FELD, C. K., GIES, M. & HERING, D. (2014). Genetic diversity and dispersal potential of the stonefly *Dinocras cephalotes* in a central European low mountain range. *Freshwater Science* **33**, 181–192.
- ELGMORK, K. & SAETHER, O. A. (1971). Distribution of invertebrates in a high mountain brook in the Colorado Rocky Mountains. *University of Colorado Studies, Series in Biology* **45**, 1–55.*
- ELITH, J. & LEATHWICK, J. R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* **40**, 677–697.
- ELSHIRE, R. J., GLAUBITZ, J. C. & SUN, Q. (2011). A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. *PLoS One* **6**, e19379.
- EXCOFFIER, L., DUPANLOUP, I., HUERTA-SÁNCHEZ, E., SOUSA, V. C. & FOLL, M. (2013). Robust demographic inference from genomics and SNP data. *PLoS Genetics* **9**, e1003905.
- FEGL, T. S., BARON, J. S., ANDREW, F. G., JOHNSON, G. F. & HALL, E. K. (2016). The differing biogeochemical and microbial signatures of glaciers and rock glaciers. *Journal of Geophysical Research: Biogeosciences* **121**, 919–932.
- FELLMAN, J. B., HOOD, E., RAYMOND, P. A., HUDSON, J., BOZEMAN, M. & ARIMITSU, M. (2015). Evidence for the assimilation of ancient glacier organic carbon in a proglacial stream food web. *Limnology and Oceanography* **60**, 1118–1128.

- FENOGLIO, S., BO, T., CAMMARATA, M., LÓPEZ-RODRÍGUEZ, M. J. & TIerno DE FIGUEROA, J. M. (2015). Seasonal variation of allochthonous and autochthonous energy inputs in an Alpine stream. *Journal of Limnology* **74**, 272–277.
- FINN, D. S. & ADLER, P. H. (2006). Population genetic structure of a rare high-elevation black fly, *Metacnephia coloradensis*, occupying Colorado lake outlet streams. *Freshwater Biology* **51**, 2240–2251.*
- FINN, D. S., KHAMIS, K. & MILNER, A. M. (2013). Loss of small glaciers will diminish beta diversity in Pyrenean streams at two levels of biological organization. *Global Ecology and Biogeography* **22**, 40–51.*
- FINN, D. S. & POFF, N. L. (2005). Variability and convergence in benthic communities along the longitudinal gradients of four physically similar Rocky Mountain streams. *Freshwater Biology* **50**, 243–261.*
- FINN, D. S. & POFF, N. L. (2008). Emergence and flight activity of alpine stream insects in two years with contrasting winter snowpacks. *Arctic, Antarctic, and Alpine Research* **40**, 636–646.*
- FINN, D. S. & POFF, N. L. (2011). Examining spatial concordance of genetic and species diversity patterns to evaluate the role of dispersal limitation in structuring headwater metacommunities. *Journal of the North American Benthological Society* **30**, 273–283.*
- FINN, D. S., BOGAN, M. T. & LYTLE, D. A. (2009). Demographic stability metrics for conservation prioritization of isolated populations. *Conservation Biology* **23**, 1185–1194.
- FINN, D. S., RÄSÄNEN, K. & ROBINSON, C. T. (2010). Physical and biological changes to a lengthening stream gradient following a decade of rapid glacial recession. *Global Change Biology* **16**, 3314–3326.
- FINN, D. S., THEOBALD, D. M., BLACK, W. C. & POFF, N. L. (2006). Spatial population genetic structure and limited dispersal in a Rocky Mountain alpine stream insect. *Molecular Ecology* **15**, 3553–3566.*
- FINN, D. S., ZAMORA-MUÑOZ, C., MÚRRIA, C., SÁINZ-BARIÁIN, M. & ALBA-TERCEDOR, J. (2014). Evidence from recently deglaciated mountain ranges that *Baetis alpinus* (Ephemeroptera). Could lose significant genetic diversity as alpine glaciers disappear. *Freshwater Science* **33**, 207–216.*
- FISCHER, S. & KUMMER, H. (2000). Effects of residual flow and habitat fragmentation on distribution and movement of bullhead (*Cottus gobio* L.) in an alpine stream. *Hydrobiologia* **422**, 305–317.*
- FLORY, E. A. & MILNER, A. M. (2000). The role of competition in invertebrate community development in a recently formed stream in Glacier Bay National Park, Alaska. *Aquatic Ecology* **33**, 175–184.
- FONTANETO, D., MELONE, G. & RICCI, C. (2004). Structure of bdelloid rotifer metacommunities in two alpine streams in northern Italy. *Studi Trentini di Scienze Naturali Acta Biologica* **80**, 23–26.*
- FRANCOU, B., RAMIREZ, E., CACERES, B. & MENDOZA, J. (2000). Glacier evolution in the tropical Andes during the last decades of the 20th century: Chacaltaya, Bolivia, and Antizana, Ecuador. *AMBIO* **29**, 416–422.
- FREIMANN, R., BÜRGEMANN, H., FINDLAY, S. E. G. & ROBINSON, C. T. (2013). Bacterial structures and ecosystem functions in glaciated floodplains: contemporary states and potential future shifts. *The ISME Journal* **7**, 2361–2373.
- FREIMANN, R., BÜRGEMANN, H., FINDLAY, S. E. G. & ROBINSON, C. T. (2014). Spatio-temporal patterns of major bacterial groups in alpine waters. *PLoS One* **9**, e113524.
- FRIEDRICH, F., MATSUMARA, Y., POHL, H., BAL, M., HÖRNSCHEMEYER, T. & BEUTEL, R. G. (2014). Insect morphology in the age of phylogenomics: innovative techniques and its future role in systematics. *Entomological Science* **17**, 1–24.
- FUGÈRE, V., ANDINO, P., ESPINOSA, R., ANTHELME, F., JACOBSEN, D. & DANGLES, O. (2012). Testing the stress-gradient hypothesis with aquatic detritivorous invertebrates: insights for biodiversity-ecosystem functioning research. *Journal of Animal Ecology* **81**, 1259–1267.*
- FÜREDER, L. (1999). High-alpine streams: cold habitats for insect larvae. In *Cold-Adapted Organisms* (eds R. Margesin and F. Schinner), pp.181–196. Springer, Berlin, Heidelberg.
- FÜREDER, L. (2007). Life at the edge: habitat condition and bottom fauna of alpine running waters. *International Review of Hydrobiology* **92**, 491–513.*
- FÜREDER, L. & SCHÖNER, W. (2013). Framework for long-term ecological research in alpine river systems. In *5th Symposium for Research in Protected Areas*, 10–12 June 2013, Vol. 5, pp. 197–204. Mittersill, Austria.
- FÜREDER, L., SCHÜTZ, C., WALLINGER, M. & BURGER, R. (2001). Physio-chemistry and aquatic insects of a glacier-fed and a spring-fed alpine stream. *Freshwater Biology* **46**, 1673–1690.*
- FÜREDER, L., WALLINGER, M. & BURGER, R. (2005). Longitudinal and seasonal pattern of insect emergence in alpine streams. *Aquatic Ecology* **39**, 67–78.*
- FÜREDER, L., WELTER, C. & JACKSON, J. K. (2003). Dietary and stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) analyses in alpine stream insects. *International Review of Hydrobiology* **88**, 314–331.*
- GALBREATH, K. E., HAFNER, D. J. & ZAMUDIO, K. R. (2009). When cold is better: climate-driven elevation shifts yield complex patterns of diversification and demography in an alpine specialist. (American pika, *Ochotona princeps*). *Evolution* **63**, 2848–2863.
- GAY, C. (1982). La faune benthique d'un torrent glaciaire des Alpes françaises: la Romanche au Plan de l'Alpe (Hautes-Alpes). *Travaux du Laboratoire d'Hydrobiologie et de Pisciculture de l'Université de Grenoble* **71**, 33–44.*
- GEISSNER, M. O., ROBINSON, C. T. & WARD, J. V. (1998). Leaf breakdown in streams of an alpine glacial floodplain: dynamics of fungi and nutrients. *Journal of the North American Benthological Society* **17**, 403–419.*
- GEISMAR, J., HAASE, P., NOWAK, C., SAUER, J. & PAULS, S. U. (2015). Local population genetic structure of the montane caddisfly *Drusus discolor* is driven by overland dispersal and spatial scaling. *Freshwater Biology* **60**, 209–221.
- GIERSCH, J. J., HOTALING, S., KOVACH, R. P., JONES, L. A. & MUHLFELD, C. C. (2016). Climate-induced glacier and snow loss imperils alpine stream insects. *Global Change Biology* (doi: 10.1111/gcb.13565).
- GIERSCH, J. J., JORDAN, S., LUIKART, G., JONES, L. A., HAUER, F. R. & MUHLFELD, C. C. (2015). Climate-induced range contraction of a rare alpine aquatic invertebrate. *Freshwater Science* **34**, 53–65.*
- GILL, B. A., HARRINGTON, R. A., KONDRATIEFF, B. C., ZAMUDIO, K. R., POFF, N. L. & FUNK, W. C. (2014). Morphological taxonomy, DNA barcoding, and species diversity in Southern Rocky Mountain headwater streams. *Freshwater Science* **33**, 288–301.*
- GRABHERR, G., GOTTFRIED, M. & PAULI, H. (2000). GLORIA: a global observation research initiative in Alpine environments. *Mountain Research and Development* **20**, 190–191.
- GRAY, L. J. (1981). Species composition and life histories of aquatic insects in a lowland Sonoran Desert stream. *The American Midland Naturalist* **106**, 229–242.
- GUTENKUNST, R. N., HERNANDEZ, R. D., WILLIAMSON, S. H. & BUSTAMANTE, C. D. (2009). Inferring the joint demographic history of multiple populations from multidimensional SNP frequency data. *PLoS Genetics* **5**, e1000695.
- GRUMMER, J. A., BRYSON, R. W. JR. & REEDER, T. W. (2014). Species delimitation using Bayes factors: simulations and application to the *Sceloporus scalaris* species group (Suamata: Phrynosomatidae). *Systematic Biology* **63**, 119–133.
- HALDORSEN, S. & HEIM, M. (1999). An arctic groundwater system and its dependence upon climatic change. *Pernafrost and Periglacial Processes* **10**, 137–149.
- HALL, D. K., CRAWFORD, C. J., DIGIROLAMO, N. E., RIGGS, G. A. & FOSTER, J. L. (2015). Detection of earlier snowmelt in the Wind River Range, Wyoming, using Landsat imagery, 1972–2013. *Remote Sensing of Environment* **162**, 45–54.
- HALL, M. H. P. & FAGRE, D. B. (2003). Modeled climate-induced glacier change in Glacier National Park, 1850–2100. *BioScience* **53**, 131–140.
- HAMERLIK, L. & JACOBSEN, D. (2012). Chironomid (Diptera) distribution and diversity in Tibetan streams with different glacial influence. *Insect Conservation and Diversity* **5**, 319–326.*
- HAMILTON, T. L., PETERS, J. W., SKIDMORE, M. L. & BOYD, E. S. (2013). Molecular evidence for an active endogenous microbiome beneath glacial ice. *The ISME Journal* **7**, 1402–1412.
- HANDCOCK, R. N., TORGENSEN, C. E., CHERKAUER, K. A., GILLESPIE, A. R., TOCKNER, K., FAUX, R. N. & TAN, J. (2012). Thermal infrared remote sensing of water temperature in riverine landscapes. In *Fluvial Remote Sensing for Science and Management* (eds P. E. CARBONNEAU and H. PIÉGAY), pp. 85–113. John Wiley & Sons, Ltd., Chichester.
- HANNAH, D. M., BROWN, L. E., MILNER, A. M., GURNELL, A. M., MCGREGOR, G. R., PETTS, G. E., SMITH, B. P. G. & SNOOK, D. L. (2007). Integrating climate–hydrology–ecology for alpine river systems. *Aquatic Conservation: Marine and Freshwater Ecosystems* **17**, 636–656.*
- HANSEN, J., NAZARENKO, L., RUEDY, R., SATO, M., WILLIS, J., DEL GENIO, A., KOCH, D., LACIS, A., LO, K., MENON, S., NOVAKOV, T., PERLWITZ, J., RUSSELL, G., SCHMIDT, G. A. & TAUSNEV, N. (2005). Earth's energy imbalance: confirmation and implications. *Science* **308**, 1431–1435.
- HARI, R. E., LIVINGSTONE, D. M., SIBER, R., BURKHARDT-HOLM, P. & GUTTINGER, H. (2006). Consequences of climatic change for water temperature and brown trout populations in Alpine rivers and streams. *Global Change Biology* **12**, 10–26.*
- HAUER, F. R., BARON, J. S., CAMPBELL, D. H., FAUSCH, K. D., HOSTETLER, S. W., LEAVESLEY, G. H., LEAVITT, P. R., MCKNIGHT, D. M. & STANFORD, J. A. (1997). Assessment of climate change and freshwater ecosystems of the Rocky Mountains, USA and Canada. *Hydrological Processes* **11**, 903–924.
- HIEBER, M., ROBINSON, C. T., RUSHFORTH, S. R. & UEHLINGER, U. (2001). Algal communities associated with different alpine stream types. *Arctic, Antarctic, and Alpine Research* **33**, 447–456.*
- HIEBER, M., ROBINSON, C. T. & UEHLINGER, U. (2003). Seasonal and diel patterns of invertebrate drift in different alpine stream types. *Freshwater Biology* **48**, 1078–1092.*
- HIEBER, M., ROBINSON, C. T., UEHLINGER, U. & WARD, J. (2005). A comparison of benthic macroinvertebrate assemblages among different types of alpine streams. *Freshwater Biology* **50**, 2087–2100.*
- HIME, P. M., HOTALING, S., GREWELLE, R. E., O'NEILL, E. M., VOSS, S. R., SHAFFER, H. B. & WEISROCK, D. W. (2016). The influence of locus number and information content on species delimitation: an empirical test case in an endangered Mexican salamander. *Molecular Ecology* **23**, 5959–5974.
- HOFFMAN, A. A. & SGRÖ, C. M. (2011). Climate change and evolutionary adaptation. *Nature* **470**, 479–485.

- HOHENLOHE, P. A., BASSHAM, S., ETTER, P. D., STIFFLER, N., JOHNSON, E. A. & CRESKO, W. A. (2010). Population genomics of parallel adaptation in threespine stickleback using sequenced RAD tags. *PLoS Genetics* **6**, e1000862.
- HOOD, E., BATTIN, T. J., FELLMAN, J., O'NEEL, S. & SPENCER, R. G. M. (2015). Storage and release of organic carbon from glaciers and ice sheets. *Nature Geoscience* **8**, 91–96.
- HOPKINSON, C., HAYASHI, M. & PEDDLE, D. (2009). Comparing alpine watershed attributes from LiDAR, photogrammetric, and contour-based digital elevation models. *Hydrological Processes* **23**, 451–463.
- HOTALING, S., FOLEY, M. E., LAWRENCE, N. M., BOCANEGRAS, J., BLANCO, M. B., RASOLOARISON, R., KAPPELER, P. M., BARRETT, M. A., YODER, A. D. & WEISROCK, D. W. (2016). Species discovery and validation in a cryptic radiation of endangered primates: coalescent-based species delimitation in Madagascar's mouse lemurs. *Molecular Ecology* **25**, 2029–2045.
- HYNES, H. B. N. (1976). Biology of Plecoptera. *Annual Review of Entomology* **21**, 135–153.
- ILG, C. & CASTELLA, E. (2006). Patterns of macroinvertebrate traits along three glacial stream continuums. *Freshwater Biology* **51**, 840–853.*
- JACOB, T., WAHR, J., PFEFFER, W. T. & SWENSON, S. (2012). Recent contributions of glaciers and ice caps to sea level rise. *Nature* **482**, 514–518.
- JACOBSEN, D. (2003). Altitudinal changes in diversity of macroinvertebrates from small streams in the Ecuadorian Andes. *Archiv für Hydrobiologie* **158**, 145–167.*
- JACOBSEN, D. (2004). Contrasting patterns in local and zonal family richness of stream invertebrates along an Andean altitudinal gradient. *Freshwater Biology* **49**, 1293–1305.*
- JACOBSEN, D. (2008). Low oxygen pressure as a driving factor for the altitudinal decline in taxon richness of stream macroinvertebrates. *Oecologia* **154**, 795–807.*
- JACOBSEN, D. (2009). Classical alpine stream types on the equator: are they different? *International Association of Theoretical and Applied Limnology* **8**, 1245–1250.*
- JACOBSEN, D., ANDINO, P., CALVEZ, R., CAUVY-FRAUNIE, S., ESPINOSA, R. & DANGLES, O. (2014a). Temporal variability in discharge and benthic macroinvertebrate assemblages in a tropical glacier-fed stream. *Freshwater Science* **33**, 32–45.*
- JACOBSEN, D., CAUVY-FRAUNIE, S., ANDINO, P., ESPINOSA, R., CUEVA, D. & DANGLES, O. (2014b). Runoff and the longitudinal distribution of macroinvertebrates in a glacier-fed stream: implications for the effects of global warming. *Freshwater Biology* **59**, 2038–2050.*
- JACOBSEN, D. & BRODERSEN, K. P. (2008). Are altitudinal limits of equatorial stream insects reflected in their respiratory performance? *Freshwater Biology* **53**, 2295–2308.
- JACOBSEN, D. & DANGLES, O. (2012). Environmental harshness and global richness patterns in glacier-fed systems. *Global Ecology and Biogeography* **21**, 647–656.*
- JACOBSEN, D., DANGLES, O., ANDINO, P., ESPINOSA, R., HAMERLIK, L. & CADIER, E. (2010). Longitudinal zonation of macroinvertebrates in an Ecuadorian glacier-fed stream: do tropical glacial systems fit the temperate model? *Freshwater Biology* **55**, 1234–1248.*
- JACOBSEN, D. & MARIN, R. (2008). Bolivian Altiplano streams with low richness of macroinvertebrates and large diel fluctuations in temperature and dissolved oxygen. *Aquatic Ecology* **42**, 643–656.*
- JACOBSEN, D., MILNER, A. M., BROWN, L. E. & DANGLES, O. (2012). Biodiversity under threat in glacier-fed river systems. *Nature Climate Change* **2**, 361–364.*
- JACOBSEN, D., ROSTGAARD, S. & VASCONEZ, J. J. (2003). Are macroinvertebrates in high altitude streams affected by oxygen deficiency? *Freshwater Biology* **48**, 2025–2032.*
- JACOBSEN, D., SCHULTZ, R. & ENCALADA, A. (1997). Structure and diversity of stream invertebrate assemblages: the influence of temperature with altitude and latitude. *Freshwater Biology* **38**, 247–261.*
- JACOBSEN, D. & TERNEUS, E. (2001). Aquatic macrophytes in cool aseasonal and seasonal streams: a comparison between Ecuadorian highland and Danish lowland streams. *Aquatic Botany* **71**, 281–295.*
- JIANG, X., XIE, Z. & CHEN, Y. (2013). Longitudinal patterns of macroinvertebrate communities in relation to environmental factors in a Tibetan-Plateau river system. *Quaternary International* **304**, 107–114.*
- JORDAN, S., GIERSCHE, J. J., MUHLFELD, C. C., HOTALING, S., FANNING, L. & LUIKART, G. (2016). Low genetic diversity and strong subdivision in an endemic alpine stonefly threatened by climate change. *PLoS One* **11**, e0157386.
- KAWECKA, B. & ROBINSON, C. (2008). Diatom communities of lake/stream networks in the Tatra Mountains, Poland, and the Swiss Alps. *Oceanological and Hydrobiological Studies* **37**, 21–35.*
- KHAMIS, K., BROWN, D. E., HANNAH, D. M. & MILNER, A. M. (2015). Experimental evidence that predator range expansion modifies alpine stream community structure. *Freshwater Science* **34**, 66–80.*
- KHAMIS, K., HANNAH, D. M., BROWN, L. E., TIBERTI, R. & MILNER, A. M. (2014a). The use of invertebrates as indicators of environmental change in alpine rivers and lakes. *Science of the Total Environment* **93**, 1242–1254.
- KHAMIS, K., HANNAH, D. M., MILNER, A. M., CALVIS, M. H., BROWN, L. E. & CASTELLA, E. (2014b). Alpine aquatic ecosystem conservation policy in a changing climate. *Environmental Science and Policy* **43**, 39–55.
- KLAAR, M. J., KIDD, C., MALONE, E., BARTLETT, R., PINAY, G., CHAPIN, F. S. & MILNER, A. (2015). Vegetation succession in deglaciated landscapes: implications for sediment and landscape stability. *Earth Surface Processes and Landforms* **40**, 1088–1100.
- KOHSHIMA, S. (1984). A novel cold-tolerant insect found in a Himalayan glacier. *Nature* **310**, 225–227.*
- KONNO, Y., NISHIMOTO, H., MARUYAMA, H., TORII, T. & ISHIWATA, S. (2003). Lotic aquatic insects in the alpine zone of Daisetsuzan National Park, Hokkaido. *Japanese Journal of Limnology* **64**, 141–144.*
- KOWNACKA, M. & KOWNACKI, A. (1972). Vertical distribution of zoocenoses in the streams of the Tatra, Caucasus and Balkans Mts. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* **18**, 742–750.*
- KOWNACKA, M. & KOWNACKI, A. (1975). Gletscherbach-Zuckmücken der Ötztal Alpen in Tirol (Diptera: Chironomidae: Diamesinae). *Entomologica Germanica* **2**, 35–43.*
- KOWNACKI, A. (1985). Effect of droughts on the invertebrate communities of high mountain streams. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* **22**, 2069–2072.*
- KOWNACKI, A. (1987). Benthic invertebrate fauna of high mountain streams in the Caucasus. *Acta Universitatis Lodzianensis* **2**, 89–99.*
- KOWNACKI, A. (1991). Zonal distribution and classification of the invertebrate communities in high mountain streams in South Tyrol (Italy). *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* **24**, 2010–2014.*
- KUBO, J. S., TORGENSEN, C. E., BOLTON, S. M., WEEKES, A. A. & GARA, R. I. (2012). Aquatic insect assemblages associated with subalpine stream segment types in relict glaciated headwaters. *Insect Conservation and Diversity* **6**, 422–434.*
- KUBOW, K. B., ROBINSON, C. T., SHAMA, L. N. S. & JOKELA, J. (2010). Spatial scaling in the phylogeography of an alpine caddisfly, *Allogamus uncutus*, within the central European Alps. *Journal of the North American Benthological Society* **29**, 1089–1099.*
- KUHN, J., ANDINO, P., CALVEZ, R., ESPINOSA, R., HAMERLIK, L., VIE, S., DANGLES, O. & JACOBSEN, D. (2011). Spatial variability in macroinvertebrate assemblages along and among neighbouring equatorial glacier-fed streams. *Freshwater Biology* **56**, 2226–2244.*
- LA FRENIERRE, J. & MARK, B. G. (2014). A review of methods for estimating the contribution of glacial meltwater to total watershed discharge. *Progress in Physical Geography* **38**, 173–200.
- LAMOUROUX, N., DOLÉDEC, S. & BAYRAUD, S. (2004). Biological traits of stream macroinvertebrate communities: effects of microhabitat, reach, and basin filters. *Journal of the North American Benthological Society* **23**, 449–466.
- LAURSEN, S. K., HAMERLIK, L., MOLTESSEN, K., CHRISTOFFERSEN, K. S. & JACOBSEN, D. (2015). Diversity and composition of macroinvertebrate assemblages in high-altitude Tibetan streams. *Inland Waters* **5**, 263–274.*
- LAVANDIER, P. & DÉCAMPS, H. (1983). Un torrent d'altitude dans les Pyrénées. *l'Estaragne*. In *Ecosystèmes Limniques* (eds M. Lamotte and P. Bourlière), pp. 81–111. Masson, Paris.
- LAVANDIER, P. & DÉCAMPS, H. (1984). Estaragne. In *Ecology of European Rivers* (ed. B. A. WHITTON), pp. 237–264. Blackwell, Oxford.
- LÉGER, M. L. (1937). *Economie biologique générale des cours d'eau alpins*. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* **8**, 5–14.
- LENCIONI, V. (2004). Survival strategies of freshwater insects in cold environments. *Journal of Limnology* **63**, 45–55.
- LENCIONI, V. & BERNABÓ, P. (2015). Thermal survival limits of young and mature larvae of a cold stenothermal chironomid from the Alps (Diamesinae: *Pseudodiamesa branickii* [Nowicki, 1873]). *Insect Science* (doi: 10.1111/1744-7917.12278).
- LENCIONI, V., BERNABÓ, P., VANIN, S., DI MURO, P. & BELTRAMINI, M. (2008). Respiratory rate and oxy-regulatory capacity in cold stenothermal chironomids. *Journal of Insect Physiology* **54**, 1337–1342.
- LENCIONI, V., BOSCHINI, D. & REBECCHI, L. (2009). Expression of the 70 kDa Heat shock protein family in Alpine freshwater chironomids (Diptera, Chironomidae) under natural conditions. *Journal of Limnology* **68**, 251–256.*
- LENCIONI, V., JOUSSON, O., GUELLA, G. & BERNABÓ, P. (2015). Cold adaptive potential of chironomids overwintering in a glacial stream. *Physiological Entomology* **40**, 43–52.
- LENCIONI, V., MAIOLINI, B., FOCHETTI, R., GRASSO, M., BOSCAINI, A. & DUMNICKA, E. (2006). Artificial substrate colonization by invertebrates in two high altitude alpine streams. *Verhandlungen des Internationalen Verein Limnologie* **29**, 1866–1870.*
- LENCIONI, V. & ROSSARO, B. (2005). Microdistribution of chironomids (Diptera: Chironomidae) in Alpine streams: an autoecological perspective. *Hydrobiologia* **533**, 61–76.*
- LENCIONI, V. & SPITALE, D. (2015). Diversity and distribution of benthic and hyporheic fauna in different stream types on an alpine glacial floodplain. *Hydrobiologia* **751**, 73–87.*
- LEPORI, F., BARBIERI, A. & ORMEROD, S. J. (2003). Effects of episodic acidification on macroinvertebrate assemblages in Swiss Alpine streams. *Freshwater Biology* **48**, 1873.*
- LEYS, M., KELLER, I., RÄSÄNEN, K., GATTOLLIAT, J. & ROBINSON, C. T. (2016). Distribution and population genetic variation of cryptic species of the Alpine mayfly

- Baetis alpinus* (Ephemeroptera: Baetidae) in the Central Alps. *BMC Evolutionary Biology* **16**, 77.
- LI, R., CHEN, W., TU, L. & FU, J. (2009). Rivers as barriers for high elevation amphibians: a phylogeographic analysis of the alpine stream frog of the Hengduan Mountains. *Journal of Zoology* **277**, 309–316.*
- LINKE, S., TURAK, E. & NEL, J. (2011). Freshwater conservation planning: the case for systematic approaches. *Freshwater Biology* **56**, 6–20.
- LOAYZA-MURO, R. A., ELÍAS-LETTES, R., MARTICORENA-RUIZ, J. K., PALOMINO, E. J., DUIVENVOORDEN, J. F., KRAAK, M. H. & ADMIRAAL, W. (2010). Metal-induced shifts in benthic macroinvertebrate community composition in Andean high altitude streams. *Environmental Toxicology and Chemistry* **29**, 2761–2768.*
- LOAYZA-MURO, R. A., MARTICORENA-RUIZ, J. K., PALOMINO, E. J., MERRITT, C., BREEUWER, J. A. J., KUPERUS, P., KRAAK, M. H. S. & ADMIRAAL, W. (2013a). Ultraviolet-B-driven pigmentation and genetic diversity of benthic macroinvertebrates from high-altitude Andean streams. *Freshwater Biology* **58**, 1710–1719.*
- LOAYZA-MURO, R. A., MARTICORENA-RUIZ, J. K., PALOMINO, E. J., MERRITT, C., DE BAAT, M. L., VAN GEMERT, M., VERWEIJ, R. A., KRAAK, M. H. S. & ADMIRAAL, W. (2013b). Persistence of chironomids in metal polluted Andean high altitude streams: does melanin play a role? *Environmental Science & Technology* **47**, 601–607.*
- LODS-CROZET, B., LENCIONI, V., OLAFSSON, J. S., SNOOK, D. L., VELLE, G., BRITTAIN, J. E., CASTELLA, E. & ROSSARO, B. (2001). Chironomid (Diptera: Chironomidae) communities in six European glacier-fed streams. *Freshwater Biology* **46**, 1791–1809.*
- LUJAN, N. K., ROACH, K. A., JACOBSEN, D., WINEMILLER, K. O., VARGAS, V. M., CHING, V. R. & MAESTRE, J. A. (2013). Aquatic community structure across an Andes-to-Amazon fluvial gradient. *Journal of Biogeography* **40**, 1715–1728.*
- LYTLE, D. A. (2001). Disturbance regimes and life history evolution. *American Naturalist* **157**, 525–536.
- LYTLE, D. A., BOGAN, M. T. & FINN, D. S. (2008). Evolution of aquatic insect behaviors across a gradient of disturbance predictability. *Proceedings of the Royal Society B* **275**, 453–462.
- LYTLE, D. A. & POFF, N. L. (2004). Adaptation to natural flow regimes. *Trends in Ecology & Evolution* **19**, 94–100.
- MACHER, J., ROZENBERG, A., PAULS, S. U., TOLLRIAN, R., WAGNER, R. & LEESE, F. (2015). Assessing the phylogeography history of the montane caddisfly *Thremma gallicum* using mitochondrial and restriction-site-associated DNA (RAD) markers. *Ecology and Evolution* **5**, 648–662.
- MADSEN, P. B., MORABOWEN, A., ANDINO, P., ESPINOSA, R., CAUVY-FRAUNIE, S., DANGLES, O. & JACOBSEN, D. (2015). Altitudinal distribution limits of aquatic macroinvertebrates: an experimental test in a tropical alpine stream. *Ecological Entomology* **40**, 629–638.*
- MAIOLINI, B., LENCIONI, V., BERERA, R. & COTTARELLI, V. (2005). Effects of flood pulse on the hyporheic harpacticoids (Crustacea, Copepoda) in two high altitude alpine streams. *Meiofauna Marina* **14**, 105–108.*
- MAIOLINI, B., LENCIONI, V., BOGGERO, A., THALER, B., LOTTER, A. F. & ROSSARO, B. (2006). Zoobenthic communities of inlets and outlets of high altitude Alpine lakes. *Hydrobiologia* **562**, 217–229.*
- MANEL, S. & HOLDEREGGER, R. (2013). Ten years of landscape genetics. *Trends in Ecology & Evolution* **28**, 614–621.
- MARGONI, S. & MAIOLINI, B. (2004). Distribuzione altitudinale di Simuliidi in torrenti alpini d'alta quota (Trentino, Italia). *Studi Trentini di Scienze Naturali, Acta Biologica* **80**, 63–64.*
- MARTINELLI, M. JR. (1959). Some hydrologic aspects of Alpine snowfields under summer conditions. *Journal of Geophysical Research* **64**, 451–455.
- MATHEWS, W. H. (1951). Historic and prehistoric fluctuations of alpine glaciers in the Mount Garibaldi map-area, southwestern British Columbia. *The Journal of Geology* **4**, 357–380.
- MATZ, J. M., BLAKE, M. J., LAVOI, K. P. & HOLBROOK, N. J. (1995). Characterization and regulation of cold-induced heat shock protein expression in mouse brown adipose tissue. *American Journal of Physiology* **269**, R38–R47.
- MCCLENTIC, A. S., CASAMATTA, D. A. & VIS, M. L. (2003). A survey of algae from montane cloud forest and alpine streams in Bolivia: macroalgae and associated microalgae. *Nova Hedwigia* **76**, 363–379.*
- MCGREGOR, G., PETTS, G. E., GURNELL, A. M. & MILNER, A. M. (1995). Sensitivity of alpine stream ecosystems to climate change and human impacts. *Aquatic Conservation: Marine and Freshwater Ecosystems* **5**, 233–247.
- MILLAR, C. I. & WESTFALL, R. D. (2008). Rock glaciers and related periglacial landforms in the Sierra Nevada, CA, USA; inventory, distribution and climatic relationships. *Quaternary International* **188**, 90–104.
- MILLER, M. R., DUNHAM, J. P., AMORES, A., CRESKO, W. A. & JOHNSON, E. A. (2007). Rapid and cost-effective polymorphism identification and genotyping using restriction site associate DNA (RAD) markers. *Genome Research* **17**, 240–248.
- MILNER, A. M. (2016). The Milner & Petts (1994) conceptual model of community structure within glacier-fed rivers: 20 years on. In *River Science: Research and Management for the 21st Century* (eds D. J. GILVEAR, M. T. GREENWOOD, M. C. THOMS and P. J. WOOD), pp. 156–170. John Wiley & Sons, Ltd., Chichester.
- MILNER, A. M., BROWN, L. E. & HANNAH, D. M. (2009). Hydroecological response of river systems to shrinking glaciers. *Hydrological Processes* **23**, 62–77.
- MILNER, A. M. & PETTS, G. E. (1994). Glacial rivers: physical habitat and ecology. *Freshwater Biology* **32**, 295–307.
- MILNER, A. M., ROBERTSON, A. L., MONAGHAN, K. A., VEAL, A. J. & FLORY, E. A. (2008). Colonization and development of an Alaskan stream community over 28 years. *Frontiers in Ecology and Environmental Research* **6**, 413–419.
- MONAGHAN, M. T., HIEBER, M., ROBINSON, C. T., SPAAK, P. & WARD, J. V. (2003). Spatial patterns of Ephemeroptera, Plecoptera and Trichoptera diversity in fragmented alpine streams. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* **28**, 1429–1435.*
- MONAGHAN, M. T., ROBINSON, C. T., SPAAK, P. & WARD, J. V. (2005). Macroinvertebrate diversity in fragmented Alpine streams: implications for freshwater conservation. *Aquatic Sciences* **67**, 454–464.*
- MONAGHAN, M. T., SPAAK, P., ROBINSON, C. T. & WARD, J. V. (2001). Genetic differentiation of *Baetis alpinus* Pictet (Ephemeroptera: Baetidae) in fragmented alpine streams. *Heredity* **86**, 395–403.*
- MONAGHAN, M. T., SPAAK, P., ROBINSON, C. T. & WARD, J. V. (2002). Population genetic structure of 3 alpine stream insects: influences of gene flow, demographics, and habitat fragmentation. *Journal of the North American Benthological Society* **21**, 114–131.*
- MONAGHAN, M. T., WILD, R., ELLIOT, M., FUJISAWA, T., BALKE, M., INWARD, D. J., LEES, D. C., RANAIVOSOLO, R., EGGLETON, P., BARRACLOUGH, T. G. & VOGLER, A. P. (2009). Accelerated species inventory on Madagascar using coalescent-based models of species delineation. *Systematic Biology* **58**, 298–311.
- MORALES, E. A. & VIS, M. L. (2007). Epilithic diatoms (Bacillariophyceae) from cloud forest and alpine streams in Bolivia, South America. *Proceedings of the Academy of Natural Sciences of Philadelphia* **156**, 123–155.*
- MUHLFELD, C. C., GERSCH, J. J., HAUER, F. R., PEDERSON, G. T., LUIKART, G., PETERSON, D. P., DOWNS, C. C. & FAGRE, D. B. (2011). Climate change links fate of glaciers and an endemic alpine invertebrate. *Climatic Change* **106**, 337–345.*
- MURAKAMI, T., HAYASHI, Y., MINAMI, M., WANG, J. B., TORII, T., FUJITANI, T., YOSHINARI, G., ZHU, L. P. & NISHIMURA, M. (2012). Limnological features of glacier-fed rivers in the Southern Tibetan Plateau, China. *Limnology* **13**, 301–307.*
- NEUBOLD, J. D., SWEENEY, B. W. & VANNOTE, R. L. (1994). A model for seasonal synchrony in stream mayflies. *Journal of the North American Benthological Society* **13**, 3–18.
- NIELSEN, R., WILLIAMSON, S., KIM, Y., HUBISZ, M. J., CLARK, A. G. & BUSTAMANTE, C. (2005). Genomic scans for selective sweeps using SNP data. *Genome Research* **15**, 1566–1575.
- NOLTE, U. (1991). Seasonal dynamics of moss-dwelling chironomid communities. *Hydrobiologia* **222**, 197–211.
- OERLEMANS, J. (2005). Extracting a climate signal from 169 glacial records. *Science* **308**, 675–677.
- PAULS, S. U., ALP, M., BÁLINT, M., BERNABÒ, P., ČIAMPOR, F. JR., ČIAMPOROVÁ-ZATOVIČOVÁ, Z., FINN, D. S., KOHOUT, J., LEESE, F., LENCIONI, V., PAZ-VINAS, I. & MONAGHAN, M. T. (2014). Integrating molecular tools into freshwater ecology: developments and opportunities. *Freshwater Biology* **59**, 1559–1576.
- PAULS, S. U., NOWAK, C., BÁLINT, M. & PFENNINGER, M. (2013). The impact of global climate change on genetic diversity within populations and species. *Molecular Ecology* **22**, 925–946.
- PEDERSON, G. T., GRAUMLICH, L. J., FAGRE, D. R., KIPFER, T. & MUHLFELD, C. C. (2010). A century of climate and ecosystem change in Western Montana: what do temperature trends portend? *Climatic Change* **98**, 133–154.
- PERIC, M. S., JOLIDON, C., UEHLINGER, U. & ROBINSON, C. T. (2015). Long-term ecological patterns of alpine streams: an imprint of glacial legacies. *Limnology and Oceanography* **60**, 992–1007.*
- PERIC, M. S. & ROBINSON, C. T. (2015). Spatio-temporal shifts of macroinvertebrate drift and benthos in headwaters of a retreating glacier. *Hydrobiologia* **751**, 25–41.*
- PETROLDI, C. & BACH, L. A. (2007). Evolutionary aspects of climate-induced changes and the need for multidisciplinary. *Journal of Thermal Biology* **32**, 118–124.
- PHILLIPSEN, I. C. & LYTLE, D. A. (2012). Aquatic insects in a sea of desert: population genetic structure is shaped by limited dispersal in a naturally fragmented landscape. *Ecography* **35**, 1–13.
- PIZZUL, E., BERTOLI, M., BASSET, A., VIGNES, F., CALLIGARIS, M. & TIBALDI, E. (2009). Energy densities of Brown Trout (*Salmo trutta*) and its main prey items in an alpine stream of the Slizza Basin (Northwest Italy). *Journal of Freshwater Ecology* **24**, 403–410.*
- POFF, N. L. (1997). Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* **16**, 391–409.
- POFF, N. L., OLDEN, J. D., VEIRA, N. K. M., FINN, D. S., SIMMONS, M. P. & KONDRATIEFF, B. C. (2006). Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society* **25**, 730–755.

- PROWSE, T. D., WRONA, F. J., REIST, J. D., GIBSON, J. J., HOBBIE, J. E., LÉVESQUE, L. M. & VINCENT, W. F. (2006). Climate change effects on hydroecology of arctic freshwater ecosystems. *AMBIO* **35**, 347–358.
- RABATEL, A., FRANCOU, B., SORUCO, A., GOMEZ, J., CÁCERES, B., CEBALLOS, J. L., BASANTES, R., VUILLE, M., SICART, J.-E., HUGGEL, C., SCHEEL, M., LEJEUNE, Y., ARNAUD, Y., COLLET, M., CONDOM, T., CONSOLI, G., FAVIER, V., JOMELLI, V., GALARRAGA, R., GINOT, P., MAISINCHO, L., MENDOZA, J., MÉNÉGOZ, M., RAMIREZ, M., RIBSTEIN, P., SUAREZ, W., VILLACIS, M. & WAGNON, P. (2013). Current state of glaciers in the tropical Andes: a multi-century perspective on glacier evolution and climate change. *The Cryosphere* **7**, 81–102.
- RAUSCHER, S. A., PAL, J. S., DIFFENBAUGH, N. S. & BENEDETTI, M. M. (2008). Future changes in snowmelt-driven runoff timing over the western US. *Geophysical Research Letters* **35**, L16703.
- READ, E. K., O'ROURKE, M., HONG, G. S., HANSON, P. C., WINSLOW, L. A., CROWLEY, S., BREWER, C. A. & WEATHERS, K. C. (2016). Building the team for team science. *Ecosphere* **7**, 3.
- ROBINSON, C. T. & GESSNER, M. O. (2000). Nutrient addition accelerates leaf breakdown in an alpine springbrook. *Oecologia* **122**, 258–263.*
- ROBINSON, C. T., GESSNER, M. O. & WARD, J. V. (1998). Leaf breakdown and associated macroinvertebrates in alpine glacial streams. *Freshwater Biology* **40**, 215–228.*
- ROBINSON, C. T. & KAWECKA, B. (2005). Benthic diatoms of an Alpine stream/lake network in Switzerland. *Aquatic Sciences* **67**, 492–506.*
- ROBINSON, C. T., TOCKNER, K. & BURGHERR, P. (2002). Seasonal patterns in macroinvertebrate drift and seston transport in streams of an alpine glacial flood plain. *Freshwater Biology* **47**, 985–993.*
- ROSSARO, B., MONTAGNA, M. & LENCIONI, V. (2016). Environmental traits affect chironomid communities in glacial areas of the Southern Alps: evidence from a long-lasting case study. *Insect Conservation and Diversity* **9**, 192–201.*
- ROSTGAARD, S. & JACOBSEN, D. (2005). Respiration rate of stream insects measured in situ along a large altitude range. *Hydrobiologia* **549**, 79–98.*
- ROTT, E., CANTONATI, M., FÜREDER, L. & PFISTER, P. (2006). Benthic algae in high altitude streams of the Alps – a neglected component of the aquatic biota. *Hydrobiologia* **562**, 195–216.*
- RUBIDGE, E. M., PATTON, J. L., LIM, M., BURTON, A. C., BRASHARES, J. S. & MORITZ, C. (2012). Climate-induced range contraction drives genetic erosion in an alpine mammal. *Nature Climate Change* **2**, 285–288.
- RUEGG, J. & ROBINSON, C. T. (2004). Comparison of macroinvertebrate assemblages of permanent and temporary streams in an Alpine flood plain, Switzerland. *Archiv für Hydrobiologie* **161**, 489–510.*
- SAETHER, O. A. (1968). Chironomids of the Finse Area, Norway, with special reference to their distribution in a glacial brook. *Archiv für Hydrobiologie* **64**, 426–483.*
- SANDIN, L., DAHL, J. & JOHNSON, R. (2004). Assessing acid stress in Swedish boreal and alpine streams using benthic macroinvertebrates. *Hydrobiologia* **516**, 129–148.*
- SCHINDLER, D. E., HILBORN, R., CHASCO, B., BOATRIGHT, C. P., QUINN, T. P., ROGERS, L. A. & WEBSTER, M. S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature* **465**, 609–612.
- SCHÜTZ, C., BURGER, R., WALLINGER, M. & FÜREDER, L. (2001). Resilience of faunistic communities in two high alpine streams with different disturbance regimes. *International Association of Theoretical and Applied Limnology* **27**, 1626–1630.*
- SHAMA, L. N., KUBOW, K. B., JOKELA, J. & ROBINSON, C. T. (2011). Bottlenecks drive temporal and spatial genetic changes in alpine caddisfly metapopulations. *BMC Evolutionary Biology* **11**, 278.*
- SHAMA, L. N. & ROBINSON, C. T. (2009). Microgeographic life history variation in an alpine caddisfly: plasticity in response to seasonal time constraints. *Freshwater Biology* **54**, 150–164.
- SHELDON, A. (2012). Possible climate-induced shift of stoneflies in a southern Appalachian catchment. *Freshwater Science* **31**, 765–774.
- SILVERI, L., TIerno DE FIGUEROA, J. M. & MAIOLINI, B. (2008a). Feeding habits of Perlodidae (Plecoptera) in the hyporheic habitats of alpine streams (Trentino-NE Italy). *Entomologica Fennica* **19**, 176–183.*
- SILVERI, L., TIerno DE FIGUEROA, J. M. & MAIOLINI, B. (2008b). Notes on the nymphal biology of *Nemoura mortoni* Ris 1902 (Plecoptera, Nemouridae) in a high altitude stream (Trentino, Italian Alps). *Zoologica Baetica* **19**, 51–56.*
- SINGER, G. A., FASCHING, C., WILHELM, L., NIGGEMANN, J., STEIR, P., DITTMAR, T. & BATTIN, T. J. (2012). Biogeochemically diverse organic matter in Alpine glaciers and its downstream fate. *Nature Geoscience* **5**, 710–714.
- SLACK, K. V., NAUMAN, J. W. & TILLEY, L. J. (1979). Benthic invertebrates in a north-flowing stream and a south flowing stream. Brooks Range, Alaska. *Water Resources Bulletin* **15**, 108–135.*
- SLEMMONS, K. E. H., SAROS, J. E. & SIMON, K. (2013). The influence of glacial meltwater on alpine aquatic ecosystems. *Environmental Science: Processes & Impacts* **15**, 1794–1806.
- SMITH, B. P. G., HANNAH, D. M., GURNELL, A. M. & PETTS, G. E. (2001). A hydromorphological context for ecological research on alpine glacial rivers. *Freshwater Biology* **46**, 1579–1596.*
- SNOOK, D. L. & MILNER, A. M. (2001). The influence of glacial runoff on stream macroinvertebrate communities in the Taillon catchment, French Pyrénées. *Freshwater Biology* **46**, 1609–1623.*
- SNOOK, D. L. & MILNER, A. M. (2002). Biological traits of macroinvertebrates and hydraulic conditions in a glacier-fed catchment. (French Pyrénées). *Archiv für Hydrobiologie* **153**, 245–271.*
- STATZNER, B., DOLÉDEC, S. & HUGUENY, B. (2004). Biological trait composition of European stream invertebrate communities: assessing the effects of various trait filter types. *Ecography* **27**, 470–488.
- STEARNS, S. C. (1989). The evolutionary significance of phenotypic plasticity. *BioScience* **39**, 436–445.
- STEINBÖCK, O. (1934). Die Tierwelt der Gletschergewässer. *Zeitschrift Deutsch-Oesterreich. Alpenvereins* **65**, 263–275.*
- STEINMANN, P. (1907). Die Tierwelt der Gebirgsbäche. Eine faunistisch-biologische Studie. *Annales de Biologie Lacustre* **2**, 30–150.
- STRAYER, D. L. & DUDGEON, D. (2010). Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society* **29**, 344–358.
- SUREN, A. M. (1991). Bryophytes as invertebrate habitat in two New Zealand alpine streams. *Freshwater Biology* **26**, 399–418.*
- THIENEMANN, A. (1912). Der Bergbach des Sauerland. *Internationale Revue gesamten Hydrobiologie Supplement* **4**, 1–125.
- THOMPSON, C., DAVID, E., FREESTONE, M. & ROBINSON, C. T. (2013). Ecological patterns along two alpine glacial streams in the Fitzpatrick Wilderness, Wind River Range, USA. *Western North American Naturalist* **73**, 1–11.*
- TREANOR, H. B., GIERSCHE, J. J., KAPPENMAN, K. M., MUHLFELD, C. C. & WEBB, M. A. H. (2013). Thermal tolerance of meltwater stonefly *Lednia tumana* nymphs from an alpine stream in Waterton-Glacier International Peace Park, Montana, USA. *Freshwater Science* **32**, 597–605.*
- TRONSTAD, L. M., HOTALING, S. & BISH, J. C. (2016). Longitudinal changes in stream invertebrate assemblages of Grand Teton National Park, Wyoming. *Insect Conservation and Diversity* **9**, 320–331.
- TURCOTTE, P. & HARPER, P. P. (1982). The macro-invertebrate fauna of a small Andean stream. *Freshwater Biology* **12**, 411–419.*
- TYNEN, M. J. (1970). The geographical distribution of ice worms (Oligochaeta: Enchytraeidae). *Canadian Journal of Zoology* **48**, 1363–1367.
- UEHLINGER, U., MALARD, F. & WARD, J. V. (2003). Thermal patterns in the surface waters of a glacial river corridor. (Val Roseg, Switzerland). *Freshwater Biology* **48**, 284–300.
- USSEGLIO-POLATERA, P., BOURNARD, M., RICHOUX, P. & TACHET, H. (2000). Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. *Freshwater Biology* **43**, 175–205.
- VAN DAMME, P. A., HAMEL, C., AYALA, A. & BEROVETS, L. (2008). Macroinvertebrate community response to acid mine drainage in rivers of the High Andes (Bolivia). *Environmental Pollution* **156**, 1061–1068.*
- VANNOTE, R. L. & SWEENEY, B. L. (1980). Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *The American Naturalist* **115**, 667–695.
- VERDÚ, J. R., ALBA-TERCEDOR, J. & JIMÉNEZ-MANRIQUE, M. (2012). Evidence of different thermoregulatory mechanisms between two sympatric *Scarabeus* species using infrared thermography and micro-computer tomography. *PLoS One* **7**, e33914.
- VEZZA, P., PARASIEWICZ, P., CALLES, O., SPAIRANI, M. & COMOGLIO, C. (2014). Modelling habitat requirements of bullhead (*Cottus gobio*) in Alpine streams. *Aquatic Sciences* **76**, 1–15.*
- VILLAMARÍN, C., RIERADEVALL, M., PAUL, M. J., BARBOUR, M. T. & PRAT, N. (2013). A tool to assess the ecological condition of tropical high Andean streams in Ecuador and Peru: the IMEERA index. *Ecological Indicators* **29**, 79–92.*
- VINÇON, G. (1987). Etude hydrobiologique de la vallée d'Ossau (Pyrénées-Atlantiques). II. Le milieu et la structure du peuplement benthique. *Annals of Limnology* **23**, 225–243.*
- WALTERS, K. R. JR., SFORMO, T., BARNES, B. M. & DUMAN, J. G. (1998). Freeze tolerance in an arctic Alaska stonefly. *The Journal of Experimental Biology* **212**, 305–312.
- WALTHER, G., BEISSNER, S. & BURGA, C. (2005). Trends in the upward shift of alpine plants. *Journal of Vegetation Science* **16**, 541–548.
- WARD, J. V. (1982). Altitudinal zonation of Plecoptera in a Rocky Mountain stream. *Aquatic Insects* **4**, 105–110.*
- WARD, J. V. (1986). Altitudinal zonation in a Rocky Mountain stream. *Archiv für Hydrobiologie, Supplement* **74**, 133–199.
- WARD, J. V. (1994). Ecology of alpine streams. *Freshwater Biology* **32**, 277–294.
- WARD, J. V. & UEHLINGER, U. (2003). *Ecology of a Glacial Floodplain*. Kluwer Academic, Dordrecht.
- WEATHERS, K. C., HANSON, P. C., ARZBERGER, P., BRENTUP, J., BROOKES, J., CAREY, C. C., GAISER, E., HAMILTON, D. P., HONG, G. S., IBELINES, B., ISTVÁNOVICS, V., JENNINGS, E., KIM, B., KRATZ, T., LIN, F., MURAOKA, K.,

- O'REILLY, C., PICCOLO, C., ROSE, K. C., RYDER, E. & ZHU, G. (2013). The Global Lake Ecological Observatory Network (GLEON): the evolution of grassroots network science. *Limnology and Oceanography Bulletin* **22**, 71–73.
- WELLNITZ, T. A. & WARD, J. V. (2000). Herbivory and irradiance shape periphytic architecture in a Swiss alpine stream. *Limnology and Oceanography* **45**, 64–75.*
- WILHELM, L., BESEMER, K., FASCHING, C., URICH, T., SINGER, G. A., QUINCE, C. & BATTIN, T. J. (2014). Rare but active taxa contribute to community dynamics of benthic biofilms in glacier-fed streams. *Environmental Microbiology* **16**, 2514–2524.
- WILHELM, L., BESEMER, K., FRAGNER, L., HANNES, P., WECKWERTH, W. & BATTIN, T. J. (2015). Altitudinal patterns of diversity and functional traits of metabolically active microorganisms in stream biofilms. *The ISME Journal* **9**, 2454–2464.
- WILHELM, L., SINGER, G. A., FASCHLING, C., BATTIN, T. J. & BESEMER, K. (2013). Microbial biodiversity in glacier-fed streams. *The ISME Journal* **7**, 1651–1660.*
- WILLASSEN, E. & CRANSTON, P. S. (1986). Afrotropical montane midges (Diptera, Chironomidae, Diamesa). *Zoological Journal of the Linnean Society* **87**, 91–123.*
- ZEGLIN, L. Z. (2015). Stream microbial diversity in response to environmental changes: review and synthesis of existing research. *Frontiers in Microbiology* **6**, 454.

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