

Climate change links fate of glaciers and an endemic alpine invertebrate

A letter

Clint C. Muhlfeld · J. Joseph Giersch · F. Richard Hauer · Gregory T. Pederson · Gordon Luikart · Douglas P. Peterson · Christopher C. Downs · Daniel B. Fagre

Received: 11 January 2011 / Accepted: 6 March 2011
© U.S. Government 2011

Abstract Climate warming in the mid- to high-latitudes and high-elevation mountainous regions is occurring more rapidly than anywhere else on Earth, causing extensive loss of glaciers and snowpack. However, little is known about the effects of climate change on alpine stream biota, especially invertebrates. Here, we show a strong linkage between regional climate change and the fundamental niche of a rare aquatic invertebrate—the meltwater stonefly *Lednia tumana*—endemic to Waterton-Glacier International Peace Park, Canada and USA. *L. tumana* has been petitioned for listing under the U.S. Endangered Species Act due to climate-change-induced glacier loss, yet little is known on specifically how climate impacts may threaten this rare species and many other enigmatic alpine aquatic species worldwide. During 14 years of research, we documented that *L. tumana* inhabits a narrow distribution, restricted to short sections (~500 m) of cold, alpine streams directly below glaciers, permanent snowfields, and springs. Our simulation models suggest that climate change threatens the potential future distribution of these sensitive habitats and the

C. C. Muhlfeld (✉) · J. J. Giersch · D. B. Fagre
U.S. Geological Survey, Northern Rocky Mountain Science Center, Glacier National Park,
West Glacier, MT 59936, USA
e-mail: cmuhlfeld@usgs.gov

F. R. Hauer · G. Luikart
The University of Montana, Flathead Lake Biological Station, Polson, MT 59860, USA

G. T. Pederson
U.S. Geological Survey, Northern Rocky Mountain Science Center, Bozeman, MT 59715, USA

D. P. Peterson
U.S. Fish and Wildlife Service, Helena, MT 59601, USA

C. C. Downs
National Park Service, Glacier National Park, West Glacier, MT 59936, USA

persistence of *L. tumana* through the loss of glaciers and snowfields. Mountaintop aquatic invertebrates are ideal early warning indicators of climate warming in mountain ecosystems. Research on alpine invertebrates is urgently needed to avoid extinctions and ecosystem change.

1 Introduction

Climate change is rapidly altering physical and biological systems worldwide (Parmesan and Yohe 2003; Walther et al. 2002). Warming in the mid- to high-latitudes is occurring at two to three times the rate of the global average (Hansen et al. 2005; Pederson et al. 2010), and in mountainous regions, particularly at higher-elevations, recent data show increased magnitude and rate of warming with extensive loss of glaciers and snowpack (Rauscher et al. 2008; Hall and Fagre 2003). Climate warming and associated glacier loss is likely to shift patterns in distribution, abundance, and phenology of many species (Root et al. 2003; Parmesan and Yohe 2003; Walther et al. 2002). This is particularly true for range-restricted mountaintop aquatic species that show strong temperature and flow-related range contractions and thus are potentially the most threatened groups of species due to impeding climate change (Parmesan 2006; La Sorte and Jetz 2010; Brown et al. 2007; Milner et al. 2009). It is increasingly urgent to assess and monitor the status of species living in mountainous regions in order to fully understand their basic ecological requirements and the potential impacts of climate warming across spatial scales from local to global.

Cold-water stenothermic species inhabiting alpine stream environments are especially vulnerable to warming and snow loss (Brown et al. 2007), yet little is known about such species in glacier-fed streams in the Rocky Mountains of North America (Hauer et al. 2007). Aquatic invertebrates may be useful biological indicators of climate-induced changes in aquatic ecosystems because they are integral components of aquatic food webs and their distributions and abundances are strongly influenced by temperature and stream flow gradients (Milner et al. 2001; Hauer and Resh 2006; Jacobsen et al. 2009). One species that may be particularly vulnerable to climate change is the meltwater stonefly (*Lednia tumana*)—a species endemic to the Waterton-Glacier International Peace Park (WGIPP) area and previously reported to be limited to glacial and snowmelt-driven alpine streams (Ricker 1952; Gaufin et al. 1977; Baumann and Kondratieff 2010). The loss of glaciers in WGIPP is iconic of the combined impacts of global warming and reduced snowpack; 125 of the estimated 150 glaciers existing in 1850 have disappeared, and the remaining 25 are predicted to be gone by 2030 (Hall and Fagre 2003).

Although climate change threatens the persistence of many plant and animal species, few species have been listed as threatened or endangered due to climate change threats. For example, the only species currently listed under the US Endangered Species Act (ESA) due to threats from climate change is the polar bear (*Ursus maritimus*), but climate impacts may threaten more enigmatic organisms. *L. tumana* has been petitioned for ESA listing due to climate-change-induced glacier loss, yet little is known specifically about how climate impacts may threaten this rare species and many other alpine aquatic species worldwide.

2 Methods

From 1996 to 2010, we collected stream invertebrate samples at 74 sites to determine the presence or absence of *L. tumana* in WGIPP. Surveys were conducted by accessing each stream by foot and hiking upstream to permanent snowfields, glaciers, or cliffs, and then downstream to the point at which the invertebrate community changed to reflect lower elevation conditions (Lowe and Hauer 1999). Larval samples were collected by hand-picking rocks in the stream, while emerging adult insects were collected by vegetation sweeping and aspirating from rocks. Adult and/or larval *L. tumana* were identified in the field, preserved in 95% ethanol, and later verified in the laboratory. Locations were recorded using a GPS unit and overlaid on a hydrography layer to estimate site elevation, slope, and aspect using a 10-m digital elevation model. Stream distances to upslope permanent snow/ice were calculated in ArcView.

We estimated the density and longitudinal (thermal) distribution of larval *L. tumana* at eight sites in three drainages during the summer of 1998 (Fig. 1a, Table 1). Triplicate invertebrate samples were collected at each site with a 250- μ Surber sampler (Surber 1937) or a modified kick net (Hauer and Stanford 1981). Samples were field preserved in 95% ethanol, and later sub-sampled in the laboratory (Hauer and Resh 2006). Initially, the entire sample was picked for large and rare specimens. The sample was then poured into a 250- μ sieve and then divided into fractions, which were then picked in their entirety to attain a minimum of 500 invertebrate individuals. The total fraction of the sample was used to calculate the total portion sub-sampled. Total numbers were multiplied by the fractions picked and by the area sampled, yielding the number of individuals per area. Hourly stream temperatures were recorded at each site using electronic data loggers. August mean, minimum, maximum and daily ranges in temperature were summarized for each site.

We used the maximum entropy method (Maxent) to model the potential geographic distribution of *L. tumana* in WGIPP as a function of environmental variables (snow/ice, elevation, aspect) at sites of known occurrence (Phillips et al. 2006). Each occurrence locality was a latitude-longitude pair. Elevation and aspect were derived from 30-m digital elevation model, and snow/ice coverage was generated from 1999 imagery (Hop et al. 2007). The future distribution of *L. tumana* under a conservative climate warming scenario (A1B) was modeled using Maxent by applying the trained model to a new set of environmental conditions that did not include the presence of glaciers and permanent snowfields (Hall and Fagre 2003). There is a high likelihood of total glacier loss in WGIPP by 2030 since glacier mass balance of the Northern Rocky Mountains is strongly controlled by summer temperatures, which have increased dramatically (Pederson et al. 2010), and are expected to continue increasing throughout the twenty-first century (IPCC 2007). Furthermore, recent comparisons of modeled (Hall and Fagre 2003) versus observed glacial retreat suggest that the glaciers in WGIPP are a decade ahead of their predicted retreat (D. Fagre, personal communication), indicating the models of estimated glacier retreat are overly conservative. A recent model of glacier sensitivity to climate for Sperry glacier (Brown et al. 2010) suggests it will persist for a few decades more as a small remnant under a warming scenario because of snow avalanche inputs, wind redistribution of snow, and topographic shading. Regardless of uncertainty in timing, it is clear that glaciers will be too small in a matter of decades to provide suitable environments for *L. tumana*.

Fig. 1 Map of study area, occurrences, and predicted current and future distribution of *L. tumana* in Waterton-Glacier International Peace Park (WGIPP), Canada and USA. **a** *L. tumana* detections in relation to glaciers and permanent snow. **b** Predicted potential distribution (probability of occurrence); **c** Predicted potential distribution with the loss of glaciers and permanent snow (Hall and Fagre 2003). Scale bar is 5 km (**a**) and 10 km (**b**)

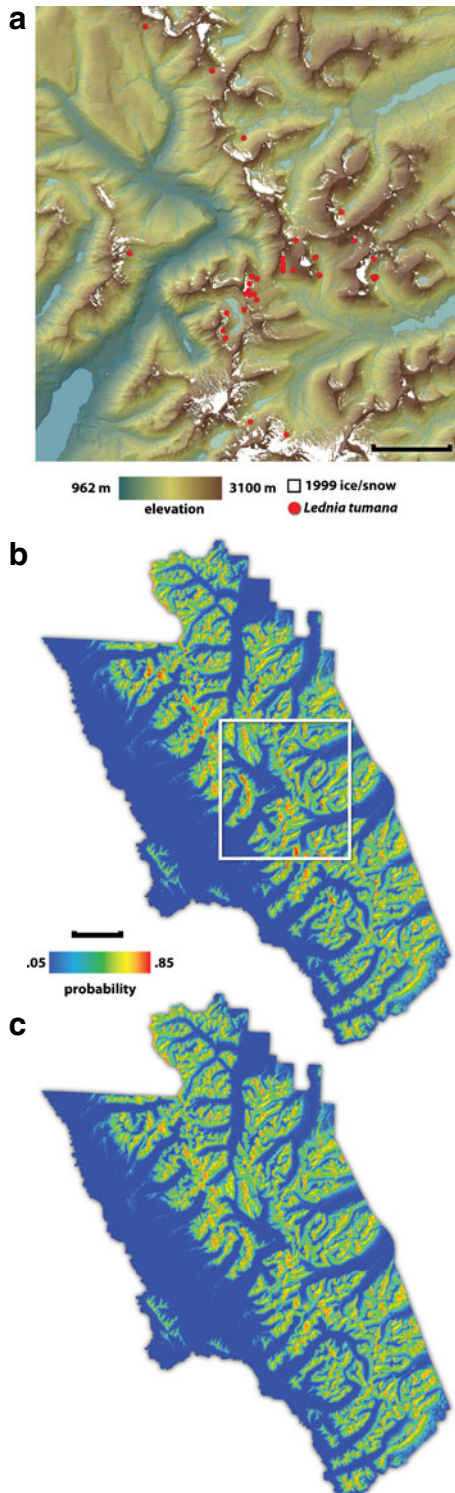


Table 1 Documented occurrence of the meltwater stonefly (*Lednia tumana*) from 1997 to 2010 in the Waterton-Glacier International Peace Park (WGIPP) area

Stream or drainage	Date	UTM X	UTM Y	Distance (m) to snow/ice	Source	Elevation (m)
Ahern	8/12/97	296429	5411065	524	Snow/ice	2038
Baring	7/7/98	307023	5398681	498	Snow/ice	2250
Baring	9/13/10	307193	5397480	856	Snow/ice	1770
Baring	9/13/10	307092	5397497	748	Snow/ice	1807
Baring	9/13/10	307038	5397496	691	Snow/ice	1821
Baring	9/13/10	307055	5397378	573	Snow/ice	1824
Baring	9/13/10	306981	5397480	630	Snow/ice	1842
Bullhead	8/5/00	298486	5406641	1532	Snow/ice	1610
Cataract	9/11/10	301920	5399895	135	Snow/ice	2222
Clements ^a	10/6/98	298830	5396609	41	Snow/ice	2168
Clements ^a	7/15/98	299186	5396357	509	Snow/ice	2043
Cracker	8/23/00	304915	5401753	511	Snow/ice	1891
Gunsight	7/19/97	298919	5387953	644	Snow/ice	2055
Hidden	7/28/98	298518	5395334	149	Snow/ice	2165
Hidden	8/21/10	297363	5395114	159	Snow/ice	2025
Hidden	9/7/10	297288	5393474	596	Snow/ice	2139
Hidden	9/7/10	297145	5393944	182	Snow/ice	2147
Logan ^a	9/29/98	299361	5397379	431	Spring	2051
Logan ^a	9/29/98	299031	5397529	19	Spring	2116
Lunch	8/27/10	301057	5398418	378	Snow/ice	2189
Lunch	8/27/10	301064	5397899	910	Snow/ice	2016
Lunch	8/27/10	301061	5398165	640	Snow/ice	2097
Lunch	8/27/10	301068	5398734	57	Snow/ice	2284
McDonald	9/3/10	290996	5399053	439	Snow/ice	1962
Mineral	8/8/97	292033	5413962	644	Spring	2009
Preston Park	8/14/05	305868	5399936	241	Snow/ice	2234
Reynolds ^a	10/16/97	298870	5397052	195	Snow/ice	2200
Reynolds	8/6/00	301753	5397923	50	Spring	2332
Reynolds ^a	9/18/97	298639	5396391	180	Snow/ice	2166
Reynolds ^a	7/13/98	298892	5396314	458	Snow/ice	2113
Reynolds ^a	7/29/98	299338	5395994	30	Spring	2074
Siyeh	8/25/10	303461	5397601	518	Snow/ice	1870
Siyeh	9/11/10	303215	5398795	538	Snow/ice	1948
Siyeh	9/11/10	303185	5398761	493	Snow/ice	1968
Tunnel	10/6/10	296837	5356535	360	Snow/ice	1825

The species was previously reported to occur in the Waterton River system in Alberta (Donald and Anderson 1977), although the exact location was not reported and has not been verified. UTM coordinates are for Zone 12. The sample in Tunnel Creek was collected below a glacier a few miles southwest of WGIPP in the Great Bear Wilderness

^aSites where densities and water temperatures were measured

3 Results

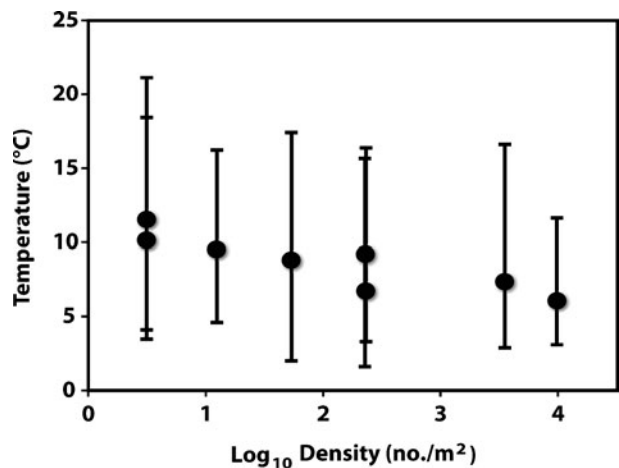
We documented *L. tumana* (larval and/or adult) in 35 locations in first-order alpine streams east and west of the Continental Divide at elevations ranging from 1,610 to 2,332 m (Fig. 1a, Table 1). Across all sites and years, 86% of occurrences were located in close proximity to glaciers or permanent snowfields (480 ± 305 m) and the remaining 14% were found immediately below alpine springs (235 ± 287 m; Fig. 1a).

L. tumana occupied short stream segments (507 ± 245 m) near these sources; mean larval densities sharply declined with increased distance downstream (Spearman's $\rho = -0.99$, $P < 0.001$). Densities also strongly correlated with summer (August) water temperatures (Fig. 2), rapidly declining with increasing mean (Spearman's $\rho = -0.95$, $P < 0.05$) and maximum temperatures (Spearman's $\rho = -0.76$, $P < 0.05$). Temperatures were also strongly associated with increasing distance from snow and ice fields (Spearman's $\rho = 0.95$ and 0.76 , respectively, $P < 0.05$), due to time of solar radiation exposure and warming as water flows down the stream length in the full sky exposure of the alpine. Indeed, *L. tumana* were not present at sites with mean and maximum temperatures exceeding 10°C and 18°C , respectively. Furthermore, densities correlated negatively with mean diel temperature range (Spearman's $\rho = -0.67$, $P < 0.10$), which varied by as much as 14.1°C (mean, 11.8°C) due to the daily cycle of solar heating and night time radiative losses. Water temperature, which is directly influenced by proximity to glacier or snowfield sources, clearly has direct effects on the distribution and abundance of *L. tumana* within streams.

We used a maximum entropy model (Maxent), which incorporates environmental variables (snow/ice, elevation, aspect) at sites of known occurrence (Phillips et al. 2006), to predict which areas within WGIPP satisfy *L. tumana*'s physical habitat requirements, as determined from this study, in order to better understand the species' distribution on the landscape and potential vulnerability to climate change impacts. We simulated a current probable geographic distribution and found that the highest probabilities of occurrence ($p > 0.75$) are associated with perennial snow and ice masses in upper-elevation areas (Fig. 1b). The full distribution (i.e., potential niche) of *L. tumana* may include these projected habitats in WGIPP, and areas extending north in Canada and south in Montana.

We then modeled the potential future distribution of *L. tumana* under the climate warming prediction that the glaciers and permanent snowfields will be gone in WGIPP (Hall and Fagre 2003; Fig. 1c). The areas with the highest probabilities of occurrence are drastically lower under the climate change prediction, with an overall 81% potential reduction in distribution; the total area potentially supporting *L. tumana* declines from 23.2074 km^2 (current) to 4.4784 km^2 (potential future).

Fig. 2 Mean densities ($\log_{10} + 0.5$) of *L. tumana* versus mean August (black circles) stream temperatures. Error bars indicate minimum and maximum temperatures



These data suggest that the loss of glaciers and perennial snowfields threatens the persistence of *L. tumana*.

4 Discussion

Understanding how species are likely to respond to climate change is critical for conservation and management strategies designed to enhance resiliency and adaptation. Our results show that *L. tumana* is a range-restricted endemic that may be particularly vulnerable to climate-change-induced snow and ice loss. The future projected distribution of *L. tumana* was shown to dramatically contract, with the species predicted to lose over 80% of its potential current range under future warming induced glacier and perennial snowfield loss (Hall and Fagre 2003). Generally, major habitat reductions imply one or a combination of the following: (1) greatly increased probability of extinction, (2) significant range contraction; (3) distributional shifts; and/or (4) dispersal to other suitable habitats (Parmesan 2006; Brown et al. 2007; Walther et al. 2002; Finn et al. 2010). However, we believe that in this case study the latter two outcomes are unlikely because *L. tumana* is (a) currently restricted to the upper limits of the alpine perennial stream system, thus an upstream distributional shift to higher-colder sites is not possible, and (b) adult Plecoptera have been shown to have poor dispersal abilities (Brown et al. 2009; Stewart and Stark 2002), thus dispersal to other suitable sites several hundred kilometers to the north along the Rocky Mountain cordilleran spine is likewise highly improbable. In short, we expect that the substantial reduction in suitable habitat, based on our projected habitat models, will result in population isolates to develop and increased probabilities of extinction. Research and development of conservation strategies for range-restricted, alpine aquatic species is urgently needed to avoid the high probability of future extinctions and aquatic ecosystem change.

Regional downscaled climate model simulations and trend data indicate that mountainous ecosystems in Western North America will likely continue to trend toward earlier and more rapid snowmelt in the spring, warmer drier summers, and increased late summer drought (Rauscher et al. 2008; Pederson et al. 2010). Glaciers and permanent snow sources will soon disappear in WGIPP (Hall and Fagre 2003). These changes in the hydrological cycle will warm perennial streams and some may transition to ephemeral flows (Hauer et al. 1997), thereby threatening the stability of sensitive alpine ecosystems that provide critical habitat for *L. tumana* and other alpine-restricted stream invertebrates, such as the rare caddisfly *Allomyia bifosa* (Hauer et al. 2007). In some cases, however, reduced meltwater from snow and ice masses may favor a more diverse suite of species adapted to warmer temperature regimes (Ward 1994), resulting in increased local (alpha) diversity (Brown et al. 2007). However, the loss of climate-sensitive species, such as the endemic alpine macroinvertebrate *L. tumana*, and decrease in stream habitat heterogeneity as alpine glaciers and snowpacks continue to shrink will likely lead to an overall reduction in regional (gamma) biodiversity (Brown et al. 2007).

A primary limitation to the use of global climate models (GCMs) in evaluating climate change impacts on species distribution and abundance is their coarse spatial resolution and poorly resolved physiography of mountainous regions. Consequently, most GCMs are less reliable in simulating regional to local spatial- and temporal-scale

features that are essential for climate change sensitivity assessments on biological communities, especially for species with small distributions and a narrow range of physical tolerances (Trivedi et al. 2008; Brown et al. 2009). Our results suggest that regional climate models and high-resolution bioclimatic assessments, as described herein, are needed in conjunction with the broader more general global assessments to understand the complexities of mountain ecosystems and comprehensively and reliably evaluate potential impacts on range-restricted species.

Alpine aquatic species are important to regional biodiversity in mountain ecosystems (Hauer et al. 2007; Pounds et al. 1999; Brown et al. 2009). Here we show compelling evidence that climate change links the fate of glaciers and a narrow endemic alpine stonefly. Mountaintop aquatic invertebrates exhibit severe climate-related range-restrictions are ideal early-warning indicators of thermal and hydrological modification that may be associated with climate warming in mountain ecosystems. Because relatively little is known about mountaintop invertebrates, yet they are increasingly threatened by climate change, more research and monitoring is urgently needed to avoid extinctions and to predict effects of extirpation on ecosystem integrity and function worldwide.

Acknowledgements We thank S. Hostetler, J. Stanford, P. Cross, J. Kershner, J. Potter, P. VanEimeren, and two anonymous reviewers for reviews of previous drafts. Funding was provided by the USGS Global Climate Change Program, Great Northern Landscape Conservation Cooperative (U.S. Department of Interior), National Park Service, National Science Foundation (DEB 1067129), and the Walton Family Foundation. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

- Baumann RW, Kondratieff BC (2010) The stonefly genus *Lednia* in North America (Plecoptera: Nemouridae). *Illiesia* 6(25):315–327
- Brown LE, Hannah DM, Milner AM (2007) Vulnerability of alpine stream biodiversity to shrinking glaciers and snowpacks. *Glob Change Biol* 13:958–966
- Brown J, Harper J, Humphrey N (2010) Cirque glacier sensitivity to 21st century warming: Sperry Glacier, Rocky Mountains, USA. *Glob Planet Change* 74:91–98
- Brown LE, Céréghino R, Compin A (2009) Endemic freshwater invertebrates from southern France: diversity, distribution and conservation implications. *Biol Conserv* 142:2613–2619
- Donald DB, Anderson RS (1977) Distribution of the stoneflies (Plecoptera) of the Waterton River Drainage, Alberta, Canada. *Syesis* 10:113–120
- Finn DS, Räsänen K, Robinson CT (2010) Physical and biological changes to a lengthening stream gradient following a decade of rapid glacial recession. *Glob Change Biol* 16:3314–3326
- Gaufin AR, Ricker WE, Miner M, Milam P, Hays RA (1977) The stoneflies (Plecoptera) of Montana. *Trans Am Entomol Soc* 98:31–32
- Hall MHP, Fagre DB (2003) Modeled climate-induced glacier change in Glacier National Park, 1850–2100. *Bioscience* 53(2):131–140
- 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 GA, Tausnev N (2005) Earth's energy imbalance: confirmation and implications. *Science* 308(5727):1431–1435. doi:10.1126/science.1110252
- Hauer FR, Resh VH (2006) Macroinvertebrates. *Methods in stream ecology* 2nd edn. Academic, New York
- Hauer FR, Stanford JA (1981) Larval specialization and phenotypic variation in *Arctopsyche grandis* (Trichoptera: Hydropsychidae). *Ecology* 62(3):645–653
- Hauer FR, Baron JS, Campbell DH, Fausch KD, Hostetler SW, Leavesley GH, Leavitt PR, Mcknight DM, Stanford JA (1997) Assessment of climate change and freshwater ecosystems of the Rocky Mountains, USA and Canada. *Hydrol Process* 11(8):903–924

- Hauer FR, Stanford JA, Lorang MS (2007) Pattern and process in northern Rocky Mountain headwaters: ecological linkages in the headwaters of the Crown of the Continent. *J Am Water Resour Assoc* 43 (1):104–117
- Hop K, Reid M, Dieck J, Lubinski S, Cooper S (2007) US Geological Survey-National Park service vegetation mapping program: Waterton-Glacier International Peace Park. US Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin
- IPCC (2007) Climate Change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge
- Jacobsen D, Dangles O, Andino P, Espinosa R, Hamerlík L, Cadier E (2009) Longitudinal zonation of macroinvertebrates in an Ecuadorian glacier-fed stream: do tropical glacial systems fit the temperate model? *Freshw Biol* 55:1234–1248
- La Sorte FA, Jetz W (2010) Projected range contractions of montane biodiversity under global warming. *Proc R Soc B* 277:3401–3410
- Lowé WH, Hauer FR (1999) Ecology of two large, net-spinning caddisfly species in a mountain stream: distribution, abundance and metabolic response to a thermal gradient. *Can J Zool* 77:1637–1644
- Milner AM, Brittain JE, Castella E, Petts GE (2001) Trends of macroinvertebrate community structure in glacier-fed rivers in relation to environmental conditions: a synthesis. *Freshw Biol* 46:1833–1847
- Milner AM, Brown LE, Hannah DM (2009) Hydroecological response of river systems to shrinking glaciers. *Hydrol Process* 23:62–77
- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Ann Rev Ecol Syst* 37:637–669. doi:[10.1146/annurev.ecolsys.37.091305.110100](https://doi.org/10.1146/annurev.ecolsys.37.091305.110100)
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421(6918):37–42
- Pederson GT, Graumlich LJ, Fagre DR, Kipfer T, Muhlfield CC (2010) A century of climate and ecosystem change in Western Montana: what do temperature trends portend? *Clim Change* 98(1):133–154
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecol Model* 190:231–259. doi:[10.1016/j.ecolmodel.2005.03.026](https://doi.org/10.1016/j.ecolmodel.2005.03.026)
- Pounds JA, Fogden MPL, Campbell JH (1999) Biological response to climate change on a tropical mountain. *Nature* 398:611–615
- Rauscher SA, Pal JS, Diffenbaugh NS, Benedetti MM (2008) Future changes in snowmelt-driven runoff timing over the western US. *Geophys Res Lett* 35(16):L16703. doi:[10.1029/2008gl034424](https://doi.org/10.1029/2008gl034424)
- Ricker WE (1952) Systematic studies of Plecoptera. Indiana University Publishing Science Services 18:1–200
- Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421(6918):57–60
- Stewart KW, Stark BP (2002) Nymphs of North American stonefly genera, vol xii, 2nd edn. Caddis, Columbus
- Surber EW (1937) Rainbow trout and bottom fauna production in one mile of stream. *Trans Am Fish Soc* 66:193–202
- Trivedi MR, Berry PM, Morecroft MD, Dawson TP (2008) Spatial scale affects bioclimate model projections of climate change impacts on mountain plants. *Glob Change Biol* 14:1089–1103. doi:[10.1111/j.1365-2486.2008.01553.x](https://doi.org/10.1111/j.1365-2486.2008.01553.x)
- Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416(6879):389–395
- Ward JV (1994) Ecology of alpine streams. *Freshw Biol* 32:277–294