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Macroinvertebrate richness is lower in high-elevation lakes vs nearby streams: evidence from Grand Teton National Park, Wyoming

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ABSTRACT

Mountain ecosystems will be strongly impacted by climate change, yet little is known of extant biodiversity in high-elevation lakes, particularly in North America. In this study, we sampled the littoral zone of six alpine and subalpine lakes in Grand Teton National Park (GRTE), Wyoming, to characterise invertebrate diversity and environmental variation in these climate change-threatened ecosystems. Overall, we collected 19 aquatic invertebrate taxa, and found that each lake harboured a unique assemblage of invertebrates despite close geographic proximity in some instances (e.g. less than 5 km). The results of this study complement previous efforts focused on macroinvertebrate diversity of streams in the Teton Range, highlighting much lower diversity in montane lakes vs nearby streams. Taken together, the two studies establish an important baseline understanding of mountain freshwater biodiversity in GRTE. With rapidly changing hydrologic inputs to mountain lakes driven primarily by the recession of alpine glaciers, these results may help target aquatic invertebrates to monitor as climate change affects the region. Moreover, these data clarify habitat factors, both biotic and abiotic, that influence high-elevation lake assemblages of the Teton Range.

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Teton Range; aquatic ecology; lentic; climate change; alpine; subalpine

Introduction

Climate change is dramatically altering habitats and shifting species distributions in mountain ecosystems (Parmesan and Yohe 2003; Hotaling et al. 2017a). At high altitudes and latitudes, climate change is proceeding at an elevated rate, potentially up to three times the global average (Malmqvist and Eriksson 1995; Hall and Fagre 2003; Brown et al. 2007). This is particularly concerning for freshwater lakes and streams where changes in hydrologic inputs through the melting of glaciers and permanent snowfields will greatly influence environmental conditions (Hall and Fagre 2003; Brown et al. 2007; Rauscher et al. 2008; Muhlfeld et al. 2011; Edmunds et al. 2012; Hotaling et al. 2017a). In mountainous regions, species move to higher elevations to compensate for rising

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temperatures, resulting in a long-term trend of habitat loss, increased fragmentation of species distributions (Parmesan and Yohe 2003; Chen et al. 2009), and the potential for reduced genetic variation (Jordan et al. 2016). Due to this 'Escalator Effect', and the implications for conservation efforts, species restricted to mountain ecosystems are indicator taxa for monitoring the impacts of climate change, effectively serving as sentinels of global threats to biodiversity (Giersch et al. 2016; Hotaling et al. 2017a).

To date, most discussion regarding climate change in mountain ecosystems has been focused on terrestrial species (e.g. the American pika, *Ochotona princeps*; Millar and Westfall 2010), stream taxa linked with rapidly receding glaciers (e.g. the meltwater stonefly, *Lednia tumana*; Muhlfeld et al. 2011), or glacier-associated microbiota (e.g. Hotaling et al. 2017b). Mountain lakes, and their inhabitants, are an additional component of alpine ecosystems that are equally relevant under global change scenarios (Slemmons et al. 2013). Much of the prior research into high-elevation lake ecology and ecosystem function was conducted in Europe (e.g. Fureder et al. 2006; De Mendoza and Catalan 2010), with comparatively little attention paid to North America. High-elevation lakes are often small and shallow, making them especially vulnerable to changes in climate (Thompson et al. 2009). Moreover, with significant hydrologic influence from receding glaciers and snowfields, mountain lakes are expected to rapidly change in the future (Slemmons et al. 2013). Together, mountain lakes and streams combine to create a heterogeneous landscape with unique and diverse habitats that support rare, often endemic, species that may be lost as climate change proceeds (Fureder et al. 2006; Clarke et al. 2008; De Mendoza and Catalan 2010; Muhlfeld et al. 2011; Giersch et al. 2015; Hotaling et al. 2017a, 2017b).

A warming climate will affect lakes in many ways; however, those at higher elevations are predicted to be acutely impacted through three primary mechanisms. First, the open water, ice-free season will become longer, thereby altering the date lakes turn over and nutrients are mixed throughout the water column (Catalán et al. 2009; Thompson et al. 2009). A change in the timing of lake turnover can cause a mismatch between invertebrates and their food, thereby decreasing invertebrate abundance (Winder and Schindler 2004). Second, invertebrate assemblages in high-elevation, aquatic ecosystems are likely to shift as warmer temperatures allow species from lower elevations to colonise and possibly outcompete resident taxa (Brown et al. 2007). As part of this process, invertebrate predators may become established in high-elevation lakes and alter food webs, both aquatic and terrestrial, in and around the lake (Hauer et al. 1997). Third, the hydrology of montane lakes will be altered as glaciers recede, changing biogeochemical fluxes and nutrient dynamics (Hauer et al. 1997; Slemmons et al. 2013; Hotaling et al. 2017a).

The overarching goal of this study was to collect baseline information on aquatic invertebrate assemblages and habitat conditions of alpine and subalpine lakes in the Teton Range of Grand Teton National Park (GRTE), Wyoming, USA. We define alpine and subalpine lakes as permanent bodies of standing water above or just below the permanent treeline, respectively. Specifically, we had three objectives: (1) to identify littoral invertebrates living in high-elevation lakes in the Teton Range, (2) to assess how species diversity and environmental variation vary among high-elevation lakes, and (3) to compare species assemblages in mountain lakes vs neighbouring stream ecosystems. To address these objectives, we visited seven lakes in the Teton Range and qualitatively sampled macroinvertebrates in lakes which contained water during our summer fieldwork. Working in GRTE was ideal as the land is protected and anthropogenic impacts are

minimised. Together with Tronstad et al. (2016), our study completes a first assessment of aquatic invertebrates from the Teton Range, provides vital baseline information of aquatic invertebrate assemblages in GRTE, and is an important resource for monitoring mountain species threatened by anthropogenic climate change.

Material and methods

Study area

GRTE is located in north-western Wyoming, and the Teton Range runs along the western side of the park (Grand Teton, 4197 m). For this study, we visited seven lakes in the Teton Range and assessed environmental and species diversity in the littoral zone for all lakes with water ($N = 6$; Figures 1 and S1; Table S1). Study lakes were distributed along the north–south line of the range and were selected to represent a diversity of lake habitats in terms of hydrologic influence and geology. In addition, sites were selected to complement a related study which characterised invertebrate assemblages of mountain streams in GRTE (Tronstad et al. 2016). The most northern lakes were two unnamed lakes in the Moose (2777 m) and Owl Creek (2804 m) watersheds – hereafter referred to as Unnamed Moose Lake and Unnamed Owl Lake, respectively. Both lakes are near the head of their respective drainages in north-western GRTE (Figure 1). This portion of the range is dominated by sedimentary rock and generally exhibits less extreme topography vs the higher peaks to the south. The lake in the Owl Creek drainage had no apparent inlet or outlet streams and was likely fed by snowmelt; however, the lake in the Moose Creek drainage likely received its water from snowmelt, glacier and groundwater inputs. Approximately 25 km south, Lake Solitude and Mica Lake are centrally located near the head of the North Fork of Cascade Creek and represented the lowest (2769 m) and highest (2912 m) lakes in our study, respectively. Both lakes have largely granite beds. Mica Lake is fed solely by meltwater from the Peterson Glacier whereas Lake Solitude is fed by a combination of snowmelt and rock glacier meltwater, and likely some groundwater. Holly Lake (2807 m) is to the east of Mica Lake and Lake Solitude in a cirque near the head of Paintbrush Canyon, and flows into Paintbrush Creek. The geology of Holly Lake is dominated by granite and its hydrologic inputs likely stem from snowfields and groundwater. Pass Lake (2874 m) and Marion Lake (2835 m) sit at the southern end of GRTE, approximately 15 km south of Lake Solitude. The bedrock of both lakes is a combination of granite and sedimentary rock. At just ~0.3 hectares, Pass Lake was the smallest lake in our study and is also a closed lake, meaning it lacks both an inlet and an outlet stream, and likely receives all of its hydrologic input from snowmelt and groundwater. Marion Lake is south-west of Pass Lake at the head of the Granite Creek drainage (Figure 1). The lake likely receives hydrologic input from rock glaciers, snowmelt and groundwater.

Sampling and analysis

To estimate the degree to which invertebrate relative abundance and richness varied with environmental conditions at each lake, we measured water temperature, dissolved oxygen concentration and saturation, specific conductivity (SPC), pH and oxidation-reduction potential (ORP) with a YSI Professional Plus Multiprobe. The dissolved oxygen probe was calibrated at each site, and probes for specific conductivity, pH and ORP were calibrated at

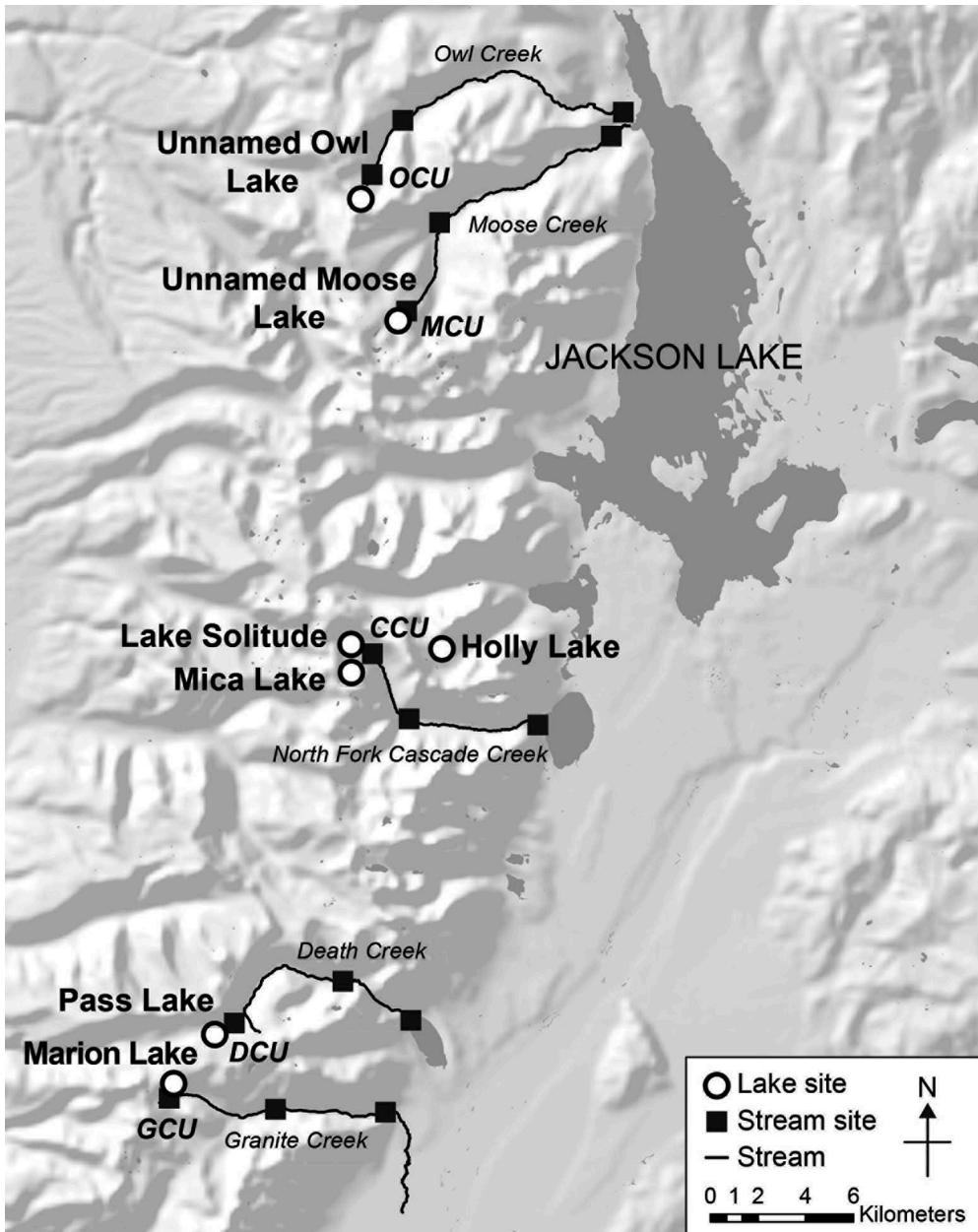


Figure 1. Lakes (white circles) in Grand Teton National Park, Wyoming, USA, sampled for this study. Black squares indicate nearby stream sites described in Tronstad et al. (2016).

the trailhead before each sampling trip. We measured aspect (the direction the stream reach was flowing) using a compass in degrees from magnetic north, mean particle size (MPS) with a gravelometer (Wildlife Supply Company), and slope with a clinometer. Biofilm cover was ranked as 1 (little growth), 2 (intermediate growth) or 3 (high growth) on the substrate (Finn and Poff 2005). The dominant riparian and landscape vegetation at each site were recorded. Elevation and location were measured with a global positioning system (GPS) unit

(datum NAD83). In addition, the visual presence or absence of fish was noted. Invertebrates were sampled using a D-frame dipnet and hand-collection in wadeable areas of the lakes. All sampling was performed during July or August when the sites are most accessible and snow-free. Insects were identified to genus when mature larvae were collected, using Merritt et al. (2008), and non-insect invertebrates were generally identified to higher taxonomic levels, although the lowest we could determine, using Thorp and Covich (2009).

To compare the similarity of invertebrate assemblages among lakes, we used non-metric multidimensional scaling (NMDS) implemented in the 'vegan' (Oksanen et al. 2007) package of the R statistical environment (R Core Development Team 2013). NMDS provides an ordination-based approach to rank distances between objects, and has been shown to perform well with non-normally distributed species data (Legendre and Legendre 1998). All NMDS analyses were performed on relative taxonomic abundance using default setting. Analyses converged on a locally minimum stress and a two-dimensional solution was used to simplify interpretation. We also used NMDS to compare the diversity of lake invertebrate assemblages to streams (shown in Figure 1, with stream sites described in detail in Tronstad et al. 2016) near our focal lakes. This was an apt comparison as the highest elevation sampling site of all nearby streams was < 1 km away from our study lakes. To limit any influence of season, streams and lakes were sampled on the same backcountry trips in July or August, 2012 (Table 1). Lake-to-stream comparisons were made in three ways: first, comparing the six lakes to all 15 sites along five streams included in Tronstad et al. (2016); second, comparing the six lakes to only the five highest-elevation stream sites (and those closest to the lakes); and finally, comparing the species richness of our six study lakes with the five highest-elevation sites from Tronstad et al. (2016) using a nonparametric, independent two-group Mann-Whitney test.

To address the degree to which environmental variation differed across high-elevation lakes and streams in the Teton Range, we used principal component analysis (PCA) performed in the standard R package 'prclust'. For PCA analyses, we made two comparisons: first, we compared our six study lakes to one another for the full suite of variables in Table 1. Next, we compared our six study lakes to the five highest-elevation stream sites included in Tronstad et al. (2016) for eight overlapping variables between the two habitats (Table S2).

Table 1. Water quality and habitat characteristics of six lakes in Grand Teton National Park, Wyoming, USA, sampled in July or August, 2012.

	Unit	Holly	Mica	Solitude	Unnamed	Pass	Marion
Date		21 July	23 July	23 July	29 July	14 Aug	14 Aug
Elevation	m	2817	2912	2769	2777	2874	2820
Temp	°C	16.5	3.2	11.7	16.1	16.6	17.9
DO	% sat.	109	113	122	133	119	118
DO	mg O ₂ /L	9.3	13.1	11.8	11.6	10.2	9.9
SPC	µS/cm	10.2	9.3	9.3	7.8	70	136.4
pH		7.8	8.8	7.6	8.3	10.2	9.0
ORP	mV	180.1	99.9	174.2	281.2	155	188.5
MPS	mm	22	258	286	165	82	100
Biofilm rank	1 to 3	1	1	2	2	3	3
Aspect	Degrees	106	19	100	34	n/a	131
Area	~Hectares	2.6	3.8	14.9	6	0.3	2.3

Abbreviations: DO = dissolved oxygen, Temp = water temperature, ORP = oxidation-reduction potential, MPS = mean particle size, and SPC = specific conductivity. 'Unnamed' refers to Unnamed Moose Lake. The unnamed lake in the Owl Creek basin was dry at the time of sampling. Aspect measures the direction a stream reach is flowing, using a compass in degrees from magnetic north (e.g. 45° = north-east).

Results

Most high-elevation lakes in the Teton Range are glacially formed cirques fed by streams, snowfields, glaciers or groundwater. All lakes held water during the study period, except for Unnamed Owl Lake and therefore no results are presented for it. Mica Lake was both the highest elevation and coldest lake sampled (Table 1). Water in all lakes was supersaturated with oxygen, with the highest concentration observed for Mica Lake. All lakes had low concentrations of dissolved ions and were uniformly basic. Water in most lakes favoured reducing conditions (< 200 mV) and lakes tended to have large substrate in the littoral zone (Table 1). Rocks had the most visible biofilm in Pass and Marion Lakes. Lake Solitude was the largest lake sampled. Trout were observed in two lakes, Holly Lake and Lake Solitude.

At least 19 benthic invertebrate taxa reside in the littoral zone of high-elevation lakes in GRTE (Table 2; Figure S2), with an average of 5.33 taxa in each lake. Moose and Holly Lakes contained the most unique taxa, and Mica Lake had the fewest. Chironomidae were the most commonly collected invertebrates. *Agabus* (Coleoptera) was collected in half of the study lakes. Trichoptera, primarily belonging to the case-making family Limnephilidae, were the most diverse group observed. In several lakes, limnephilid caddisflies were observed pupating in preparation to emerge as adults.

Table 2. The relative abundance of each taxon sampled in high-elevation lakes of Grand Teton National Park, Wyoming, USA. 'Unnamed' refers to Unnamed Moose Lake. The unnamed lake in the Owl Creek basin was dry at the time of sampling.

Taxa	Holly	Mica	Solitude	Unnamed	Pass	Marion
Coleoptera						
<i>Agabus</i>	1	0	0	0	5	2
<i>Hygrotus</i>	4	0	0	1	0	0
Diptera						
Chironomidae	1	0	3	2	1	0
Non-Tanypodinae						
Tanypodinae	0	1	1	0	0	0
Ephemeroptera						
<i>Parameletus</i>	0	0	0	1	0	0
<i>Procladius</i>	4	4	0	0	0	0
Hemiptera						
Corixidae	0	0	0	0	2	0
<i>Notonecta</i>	0	0	0	1	0	0
Trichoptera						
<i>Apatania</i>	0	0	0	8	0	0
<i>Desmona mono</i>	1	0	0	0	0	0
<i>Hesperophylax</i>	0	0	4	0	0	0
Limnephilidae (pupae)	1	0	6	3	0	0
<i>Limnephilus</i>	0	0	0	0	0	11
<i>Psychoglypha</i>	0	0	0	1	0	0
Non-insects						
Acari	0	0	0	0	12	0
<i>Gammarus</i>	0	0	0	0	0	2
<i>Helobdella stagnalis</i>	0	0	0	0	0	1
Oligochaeta	2	0	0	0	0	0
Sphaeriidae	0	0	0	8	0	12
Turbellaria	3	3	0	0	0	0
Total taxa	8	3	4	8	4	5

NMDS analyses revealed that lakes differed in species assemblages, with seemingly no influence of distance between sites (i.e. sites close together geographically appeared equally dissimilar vs those far apart; Figure 2). When environmental variation was considered, sampled lakes were still different, though more overlap was present than for species diversity comparisons (Figure 3). However, NMDS distance between the lake vs stream clusters was reduced when only the highest elevation stream sites were considered, indicating that high-elevation lakes and streams are more similar in terms of species assemblages than the same lakes are to lower elevation sites along the same streams. High-elevation lakes also contained fewer taxa on average than nearby high-elevation stream sites did (means, lakes = 5.33, streams = 26.2; Mann-Whitney, $P = 0.008$). From an environmental perspective, lakes and nearby high-elevation stream sites differed primarily according to three variables: ORP, SPC and elevation (Figure 3(b)). Moreover, environmental variation among our study lakes and the highest elevation stream sites was much less pronounced than species assemblage differences (Figure 3(b)), though two loose grouping of lakes and streams were present.

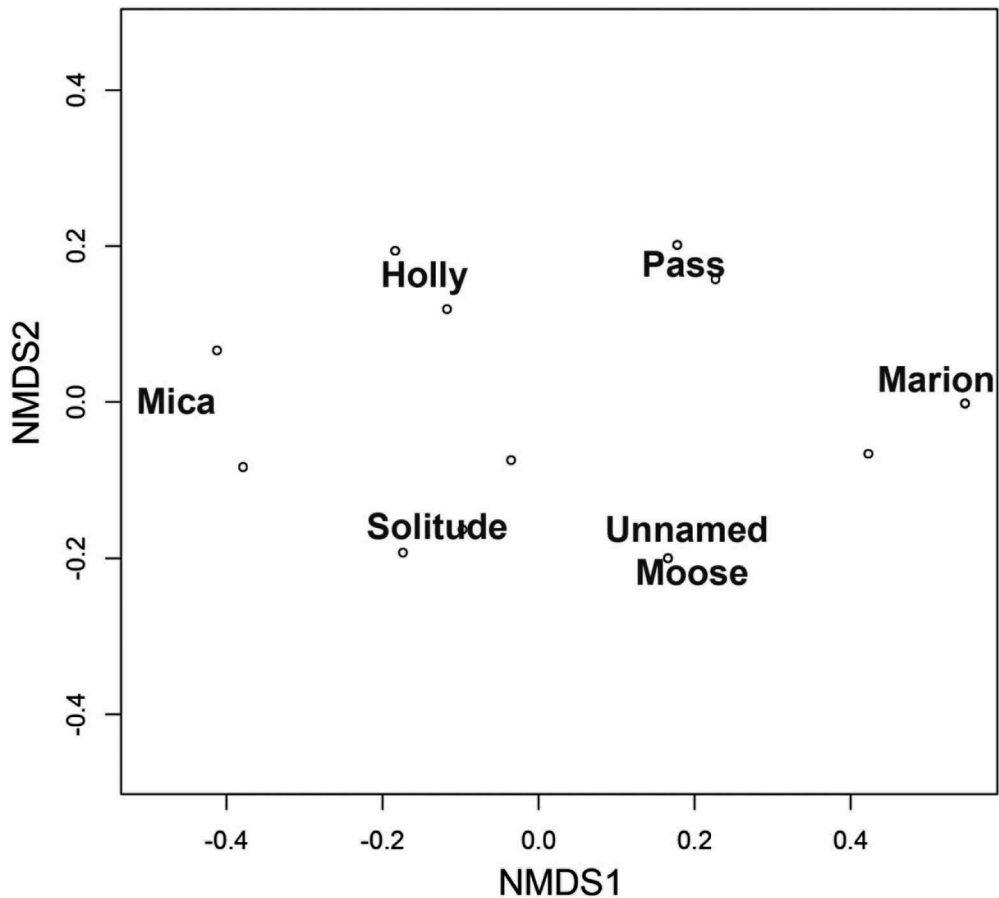


Figure 2. A two-dimensional non-metric multidimensional scaling (NMDS) plot of taxon occurrence and abundance in six mountain lakes of Grand Teton National Park, Wyoming. Circles indicate individual taxa. Ordinations were calculated using Bray-Curtis dissimilarities. Unnamed Owl Lake was dry at the time of sampling.

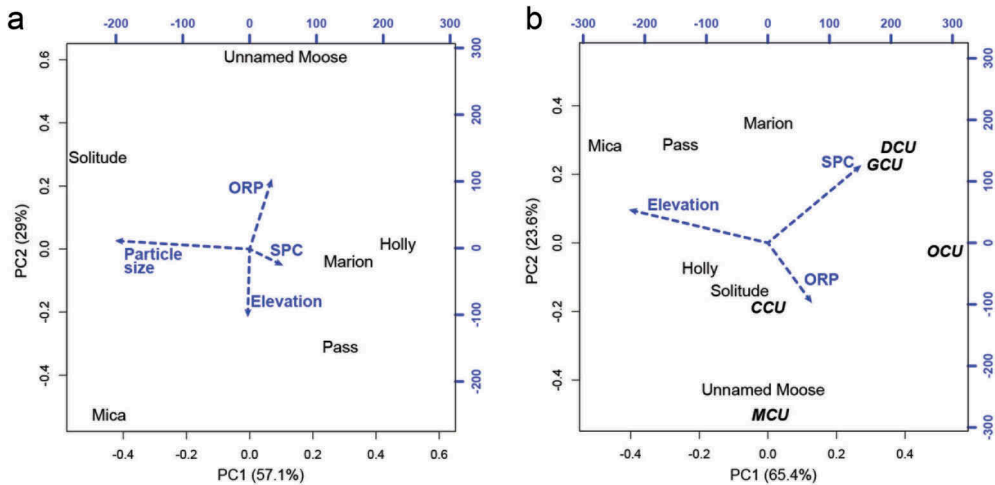


Figure 3. Principal component (PC) analyses comparing (a) six lakes in Grand Teton National Park for 11 environmental variables (excluding date; Table 1) and (b) for the same six lakes and the five highest elevation stream sites included in Tronstad et al. (2016). Stream sites are in bold and italics (Death Creek, DCU; Granite Creek, GCU; Cascade Creek, CCU; Owl Creek, OCU; and Moose Creek, MCU). Environmental variables used for the stream vs lake comparison are included in Supplementary Table 2. Abbreviations: ORP, oxidation-reduction potential; SPC, specific conductivity.

Discussion

As climate change proceeds, glaciers and permanent snowfields recede, and mountain freshwater habitats change, the species assemblages residing within them will be fundamentally altered (Slemmons et al. 2013; Hotaling et al. 2017a). Though mountain lakes and streams have historically been understudied vs their lower elevation counterparts, these ecosystems, along with their high-latitude counterparts, are receiving increased attention as rates of warming are predicted to be higher in these habitats than anywhere else on Earth (Hall and Fagre 2003; Wang et al. 2016). As an ecosystem that is relatively free of human influence and federally protected, GRTE, and the Teton Range specifically, provides an ideal setting for extending our understanding of how biodiversity is structured in North American alpine freshwaters. To date, only Tronstad et al. (2016) have investigated montane invertebrate communities in the Teton Range; however, that study was focused on streams.

Invertebrate assemblages and habitat characteristics (e.g. flowing vs standing water; Bushnell et al. 1987) differ dramatically between lakes and streams. The results of our study support these general expectations. We documented 19 taxa inhabiting six high-elevation lakes in the Teton Range, compared to 67 taxa observed by Tronstad et al. (2016) in five adjacent streams. When compared, only a few taxa were observed in both lakes and streams (e.g. freshwater clams of the Family Sphaeriidae were observed in the Moose Creek drainage; Tronstad et al. 2016). Even when only lakes and the nearest high-elevation sites were considered, we still observed many more taxa in streams than lakes in terms of both gamma (total) and alpha (per-site) diversity. Moreover, we documented greater, and more distinctive, species assemblage diversity in lakes vs nearby streams (Figure 4).

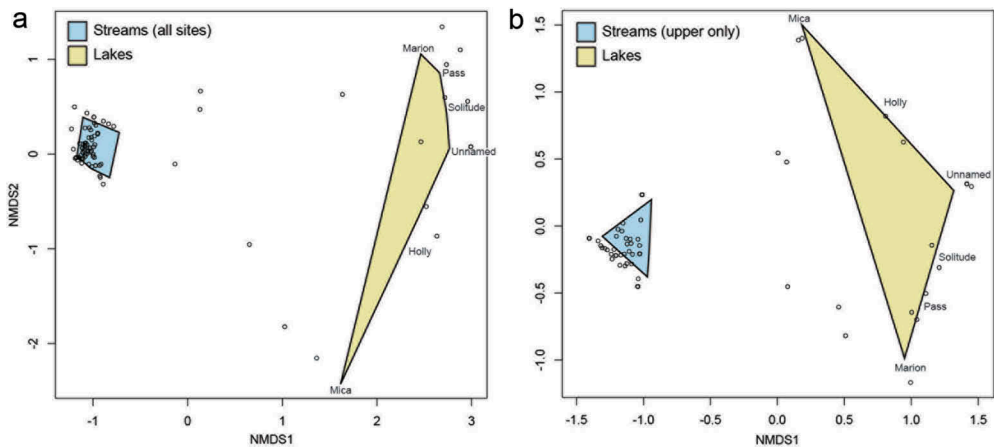


Figure 4. Two-dimensional non-metric multidimensional scaling (NMDS) plots comparing mountain lakes and stream invertebrate assemblages in Grand Teton National Park, Wyoming. (a) NMDS comparison of the six lake sites included in this study and 15 sites along five nearby streams included in Tronstad et al. (2016). (b) NMDS comparison of the same six lakes and only the five highest elevation stream sites from Tronstad et al. (2016). Circles indicate individual taxa. Ordinations were calculated using Bray-Curtis dissimilarities.

However, these direct comparisons should be interpreted with some degree of caution due to differences in sampling methods. Specifically, Tronstad et al. (2016) sampled streams quantitatively with a Surber sampler, whereas in this study, macroinvertebrates were sampled via hand-picking and dipnets. Also, with fewer taxa observed, it is likely the wide breadth of variation observed in lakes vs streams is magnified in our NMDS analyses by the many instances of taxa observed in a single lake and nowhere else. Still, this type of comparison and our conclusions are not novel. Bushnell et al. (1987) used the same sampling methods to compare alpine lakes and streams, and found more taxa in streams (24–40) compared to lakes (9–19). Similarly, Guareschi et al. (2012) also observed both higher diversity and tighter NMDS clustering of species assemblages in lotic vs lentic habitats, speculating that this variation may stem from the greater heterogeneity in flowing vs standing waters. While we would have observed more taxa if we had also sampled the open-water and profundal zones, these habitats tend to contain limited taxonomic richness and therefore likely would not have significantly influenced our results. While our study lakes differed substantially for the environmental variables measured, this variation did not extend to observed species assemblage patterning. This suggests that additional factors – perhaps related to colonisation or other environmental variables – dictate how species assemblages accumulate and are maintained in high-elevation ecosystems of the Teton Range.

Sampling lakes and streams together clearly identifies higher, and more representative, diversity than sampling either habitat exclusively. For example, Bushnell et al. (1987) collected 111 taxa from alpine lakes and streams in the Green Lakes Valley, Colorado over two summers. Fifty-eight percent of invertebrates were only collected in streams and 16% of taxa resided exclusively in lakes. Aquatic ecologists tend to specialise in either lake or stream ecosystems; however, we urge future researchers to consider how these ecosystems interact, to investigate biodiversity in a more comprehensive framework and to cultivate collaborations when necessary. Identifying species

living in high-elevation lakes or streams will also help target species at risk of climate change-induced extirpation or extinction. Some aquatic invertebrates are endemic, high-elevation specialists with clear conservation threats. For instance, the stonefly *Lednia tetonica* is only known from a single location in the Teton Range, Wind Cave at the head of Darby Canyon, a stream fed by subterranean ice meltwater (Baumann and Call 2012). However, *L. tetonica* adults have been observed along the margins of the Mica Lake outlet stream (J. Giersch, personal communication). This observation suggests that Mica Lake and its glacial influence may be an important habitat source for an endemic alpine stonefly. Unfortunately, to date, no study has characterised the benthic community of the Mica Lake outlet stream.

Aquatic ecosystems in mountainous regions are predicted to be dramatically altered by climate change through shifts in hydrology (e.g. receding glaciers and altered precipitation patterns), rising atmospheric temperatures and increased nutrient deposition. These changes may drive the decline or extinction of alpine and subalpine biodiversity. Similar to streams (e.g. Kubo et al. 2013; Tronstad et al. 2016), mountain lakes of GRTE exhibit unique species assemblages despite limited geographic isolation (i.e. < 1 km between lakes) and/or environmental similarity (e.g. Pass and Marion Lakes are environmentally similar but equally different in terms of species assemblages). Headwater lakes and streams receive hydrological input from a variety of sources – glacier meltwater, snowmelt runoff, groundwater or rain (Ward 1994) – and in the Teton Range, these standard inputs also include a high amount of rock glacier meltwater (Fegel et al. 2016). However, as climate change proceeds, lakes and streams will likely be differentially affected. For instance, rising air temperatures will increase lake water temperatures and melt ice cover earlier (Catalan et al. 2009; Slemmons et al. 2013). Earlier ice-off can cause a mismatch between phytoplankton blooms and zooplankton densities (Winder and Schindler 2004), with potential implications throughout the food web. Furthermore, the ‘Escalator Effect’ of climate change in mountain ecosystems may be particularly acute for high-elevation lakes. Unlike their terrestrial or stream counterparts that likely have some, albeit an increasingly small amount of, habitat to disperse to as temperatures rise, lake residents inhabit an even narrower band of habitat with little potential for upward dispersal. Non-insect invertebrates in particular may be at even greater risk given their lack of a terrestrial stage and therefore highly limited opportunities for migration. Even for species that can disperse among lakes as winged adults, their dispersal ability is still often limited (Finn and Poff 2008). Dispersal potential aside, it is clear that the collective effects of glacier loss will have serious implications for entire communities if all alpine glaciers in the region disappear.

Collecting baseline information is a vital step in monitoring ecosystem responses to climate change. With the greatest risk of extinction associated with taxa restricted to (or most abundant at) high-elevation sites, repeat sampling at regular intervals will provide crucial information regarding how habitats are changing, both taxonomically and environmentally. Lake and stream ecosystems differ in many environmental characteristics as well as in the invertebrates that inhabit them. More than ever before, we are refining our collective understanding of what controls the distribution of lentic invertebrates in mountain lakes, with location, size, water chemistry, elevation and food web configuration clearly driving species variation (Catalan et al. 2009; Kernan et al. 2009; Catalan and Rondón 2016). However, many geographic regions have not been sampled and a

significant portion of variance among localities remains unexplained. In the Teton Range, combined lake and stream perspectives highlighted that despite their close proximity, unique invertebrate assemblages still inhabit each habitat. Therefore, monitoring biodiversity in both mountain lakes and streams is crucial to preserving not only species but total biodiversity in mountain ecosystems. Going forward, future monitoring efforts should incorporate both lakes and streams, and, if possible, include an array of sampling methods to characterise invertebrate assemblages of these imperiled ecosystems.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Geolocation information

Our research took place in the Teton Range of Grand Teton National Park (43.7411°N, -110.7975°W).

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