



Longitudinal changes in stream invertebrate assemblages of Grand Teton National Park, Wyoming

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Abstract. 1. High elevation ecosystems are predicted to be strongly impacted by climate change; however, little is known of extant biodiversity in mountain streams. For this study, five streams in Grand Teton National Park, Wyoming were sampled along a longitudinal gradient to establish a baseline of invertebrate assemblages and environmental conditions. Five Surber samples were collected from low, middle and high elevation sites along each stream.

2. Nearly 10 000 ind m⁻² lived in these streams on average, but the density (mixed effects model, $P = 0.54$) and richness ($P = 0.18$) of invertebrates did not vary significantly by elevation. Total density of invertebrates was positively related to the amount of visible biofilm (ANOVA, $P = 0.03$) and oxidation-reduction potential ($P = 0.05$) and taxa richness was negatively related to specific conductivity ($P = 0.009$).

3. Invertebrate assemblages and environmental conditions were more similar at low versus high sites when compared using non-metric multidimensional scaling and tests of multivariate dispersion indicating that higher elevation sites harboured more environmental and species diversity.

4. These results can help target which aquatic invertebrates to monitor as stream temperatures rise, and highlight the biotic and abiotic factors that structure aquatic ecosystems in the Teton Range of Grand Teton National Park.

Key words. Alpine, benthic, biodiversity, climate change, community ecology.

Introduction

Climate change is dramatically altering ecosystems worldwide (Parmesan & Yohe, 2003). At high altitudes and latitudes, this change is magnified by an elevated rate of warming, potentially up to three times the global average (Malmqvist & Eriksson, 1995; Brown *et al.*, 2007; Hannah *et al.*, 2007; Brown *et al.*, 2009). This warming trend is causing massive loss of glacial and permanent snowfield volume, and significantly changing the hydrologic dynamics of aquatic ecosystems (Rauscher *et al.*, 2008; Hall & Fagre, 2003; Brown *et al.*, 2007; Finn *et al.*, 2010). Globally, warmer temperatures cause species to shift their

range to higher latitudes, elevations, or both (Parmesan & Yohe, 2003). In mountainous regions, species move higher to compensate for rising temperatures resulting in a long-term trend of habitat loss and fragmentation (Parmesan & Yohe, 2003; Chen *et al.*, 2009). For instance moths have moved between 10 and 16 m decade⁻¹ upward in elevation on Mount Kinabalu in Borneo (Chen *et al.*, 2009). Due to this 'escalator effect', mountain ecosystems and especially those species restricted to high elevation habitat are important foci for monitoring the effects of climate change. Nevertheless, for monitoring to be possible, baseline information about high elevation assemblages, distribution of putatively threatened species and associated environmental variables must be collected.

Streams in mountainous environments are predicted to be strongly affected by a warming climate (Hall & Fagre, 2003). Headwater streams can form $\geq 75\%$ of the stream

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length in a basin (Leopold *et al.*, 1964; Benda *et al.*, 2004), and collectively, these streams account for a large fraction of the biodiversity in a given watershed (Clarke *et al.*, 2008; Finn *et al.*, 2011). Headwater streams are sensitive to changes in adjacent riparian areas because many small streams rely on terrestrial litter as a carbon source (e.g. Bilby & Likens, 1980), though for streams originating above treeline, riparian input is of lesser concern. Mountain lakes and streams combine to create a heterogeneous landscape with unique and diverse habitats that can support rare or endemic species that may be lost if climate continues to warm (Gomi *et al.*, 2002; Meyer *et al.*, 2007; Clarke *et al.*, 2008; Muhlfield *et al.*, 2011; Giersch *et al.*, 2015).

Warmer water temperatures and changes in flow regime likely threaten the biodiversity of invertebrates in high elevation aquatic ecosystems. In addition to affecting species distributions, rising water temperatures may increase the metabolism, growth (Sweeney *et al.*, 1992) and size structure of invertebrates (Dossena *et al.*, 2012), resulting in higher biomass (Greig *et al.*, 2012) or earlier emergence of adult insects (Harper & Peckarsky, 2006). Increased temperatures also reduce oxygen solubility in water. For instance a 4 °C increase in water temperature results in a 10% decrease in dissolved oxygen (Sweeney *et al.*, 1992). Rising temperatures may shift the flow regime of streams resulting in earlier runoff, and disturbances becoming more frequent and unpredictable (Vitousek, 1994; Milly *et al.*, 2005). Models predict that stream flow will decrease in the western United States under most climate change scenarios (Milly *et al.*, 2005). The subsequent drought conditions may stress organisms living in headwater streams by increasing water temperatures (Harper & Peckarsky, 2006), decreasing dissolved oxygen concentrations and decreasing available habitat resulting in lower fitness, reproduction and growth of invertebrates (Sweeney *et al.*, 1992; Jacobsen, 2008).

The goal of this study was to collect baseline information on aquatic invertebrate assemblages in the Teton Range of Grand Teton National Park, Wyoming, USA, a mountainous area likely to be strongly affected by climate-change-induced warming. Specifically, this centred upon four primary objectives: (i) To assess how the density and richness of aquatic invertebrates varied by elevation, (ii) identify aquatic invertebrates that are restricted to high elevation sites, (iii) to estimate what biotic and abiotic factors most influence the structure of aquatic invertebrate communities across elevations and (iv) to compare the relative similarity of invertebrate assemblages among sites. To address these objectives, five streams and three sites per stream were sampled across the Teton Range. Study sites were distributed broadly along the north-south line of the range and were selected to represent a diversity of stream habitats in terms of both hydrologic influence and local geology. Working in Grand Teton National Park was ideal because the land is protected to minimise anthropogenic impacts. This study represents the first assessment of aquatic invertebrates from

the Teton Range. The results presented here provide vital baseline information of aquatic invertebrate assemblages in Grand Teton National Park, an important resource for monitoring global change in mountain ecosystems, and also add to a growing literature investigating biodiversity in mountain streams worldwide.

Materials and methods

Study area

Grand Teton National Park sits in the Snake River valley in northwestern Wyoming. The Teton Range (Grand Teton, 4197 m) looms over Jackson, Leigh, Jenny and Phelps Lakes on the eastern side of the range. Ecosystems change dramatically from the sagebrush dominated valley floor to the forested mountainsides to the barren peaks. Canopy cover at the high elevation sites tended to have sparse or lack coniferous trees and deciduous shrubs. Middle and low elevation sites were usually located in dense conifer forests with shrubs. Samples were collected from Moose, Owl, Cascade, Death and Granite Creeks (Fig. 1).

Moose and Owl Creeks are located in the northwestern area of the park and range from ~3050 m (Moose Creek) and ~2800 m (Owl Creek) down to 2064 m where they flow into Jackson Lake. The geology of both streams is dominated by sedimentary rock. Much of Owl Creek meanders through a wide valley with only a few tributary streams and one intermittent lake (dry during our visit) based upon a 1:80 000 scale map. Conversely, Moose Creek has many tributary streams in remote areas of Grand Teton National Park and ~10 backcountry lakes in its watershed. The lower section of Moose Creek flows through a tight canyon with many falls.

Cascade Creek is centrally located in the range and its bedrock is dominated by granite. The North Fork of Cascade Creek flows below Paintbrush Divide from five lakes and six tributary streams. Several tributaries flow from snowfields including one that begins at ~3353 m. The South Fork of Cascade Creek has five tributaries of which two begin in cirque lakes that are highly influenced by snowfields. The streams join at ~2362 m and flow down canyon into Jenny Lake (2067 m).

Death and Granite Creeks are located in the southwestern portion of the park. The geology of the drainages is primarily granite with some sedimentary areas. Death Creek has ~24 tributary streams of which several originate from springs on Death Shelf and two tributaries originate from lakes. Death Creek flows through dense forest for much of its length and enters a tight canyon approximately one mile before flowing into Phelps Lake (2022 m). Granite Creek has three branches (North, Middle and South Forks) and 18 tributary streams, of which three originate from lakes. Granite Creek flows through a densely forested canyon and eventually drains into the Snake River.

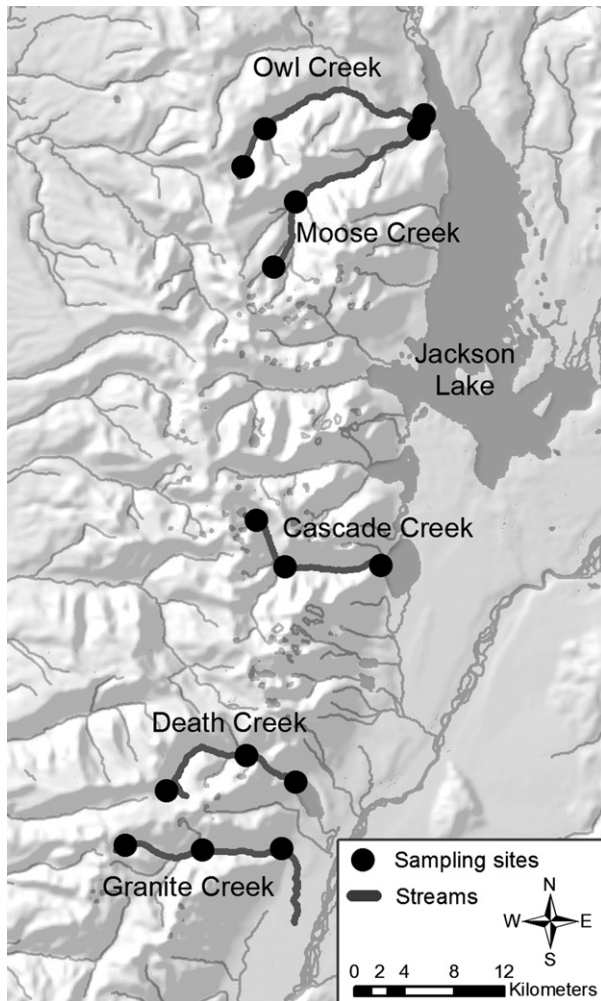


Fig. 1. Locations of sampling sites in Grand Teton National Park, Wyoming, USA.

Field sampling

For each stream, five replicate Surber samples (Wildco, 243 μm mesh size; 0.093 m^2) were collected at each elevation (low, middle and high) in riffles and runs along a longitudinal gradient. For dates of sampling events and specific locations, see Table S1. High elevation sites were sampled as close to the headwaters as possible where the stream was wide enough to sample. Low elevation sites were sampled near the valley floor or before flowing into a lake. Middle elevation sites were identified by calculating the mean elevation between high and low sites. All benthic samples were preserved in 80% ethanol and returned to the laboratory for sorting, identifying and counting. Invertebrates were identified to genus when mature specimens were captured using a dissecting microscope and identification keys (Merritt *et al.*, 2008; Thorp & Covich, 2010).

Environmental variables were measured to estimate the degree to which invertebrate density and richness varied

with biotic and abiotic conditions. Mean stream width and depth were measured at three different locations per site. Water temperature, dissolved oxygen concentration, specific conductivity, pH and oxidation-reduction potential were measured using a YSI Professional Plus Multiprobe. Dissolved oxygen was calibrated at each site and specific conductivity, pH and oxidation-reduction potential were calibrated at the trailhead before each trip. Biofilm cover was ranked as either 1 (little growth), 2 (intermediate growth) or 3 (high growth) on the substrate (Finn & Poff, 2005). Mean particle size of stream substrate was measured by recording the diameter of 20 haphazardly selected rocks. The dominant riparian and landscape vegetation at each site was recorded as viewed from the stream bank. Slope and aspect were measured in the field using a clinometer. For analysis, aspect (A') was transformed according to Beers *et al.* (1966) using $A' = \cos(45^\circ - A) + 1$ where A is the measured aspect in degrees. Elevation and location were measured with a GPS unit (datum NAD83).

Statistical analyses

The density of invertebrates were analysed using mixed effects models using stream as a random effect to investigate the degree to which elevation affected these animals. All environmental variables and invertebrate metrics were compared among sites using separate one-way analysis of variance (ANOVA). Mean invertebrate densities calculated from five samples collected at each site were used for analyses ($n = 75$; Surber samples). Taxa richness was calculated as cumulative richness among replicate samples at each site (electronically composited all five Surber samples from each site). Shannon diversity was calculated for each site as an additional metric to describe species diversity. All multivariate analyses were performed in the 'vegan' (Oksanen *et al.*, 2011) community ecology package of the R statistical environment (R Core Development Team, 2008). For indicator species analyses, the library 'indicpecies' (De Cáceres & Jansen, 2014) was used to calculate IndVal.g, a statistic of indicator values given species combinations. Samples were grouped according to elevation or stream, with the same analyses performed for both.

To compare similarity of aquatic insect community assemblages among streams and elevations, non-metric multidimensional scaling (NMDS) was used in conjunction with permutational multivariate analyses of variance (analogous to a 'permutational MANOVA', Anderson, 2001) and analyses of multivariate homogeneity of groups dispersions (analogous to PERMDISP2, Anderson, 2006). 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 & Legendre, 1998). NMDS was performed on the mean density of taxa across five replicate samples per site. NMDS iterations were run 100 times to ensure conver-

gence on locally minimum stress and a 2D solution was used to simplify interpretation. A goodness-of-fit of the NMDS results was assessed through a regression of the observed Bray–Curtis dissimilarities and NMDS ordination distances. A series of permutational multivariate analyses of variance implemented using the function ‘adonis’ were used to test the influence of environmental variables on community assemblages given the groupings (strata) of our sampling design (streams or elevation). The homogeneity of group dispersions was assessed for both environmental and species assemblages as well as streams and elevations in a multivariate framework using the function ‘betadisper’, a sister function to ‘adonis’ that allows for the assessment in dispersion in the same geometric framework. Significance of dispersion was assessed using a permutation test which permutes model residuals to generate a distribution of F under the null hypothesis of no dispersion between groups. When applicable, 999 permutations were used for all multivariate analyses and results were considered significant if $P < 0.05$.

For model selection, the AICcmoavg package in R (Mazerolle, 2013) was used to describe total density, density of Ephemeroptera, Plecoptera, and Trichoptera (EPT), total richness and EPT richness using the environmental data collected at each site. Models were ranked according to second-order Akaike information criterion (AICc). AICc is appropriate for datasets with a small sample size such as this one with data summarised for each site ($n = 15$; Table 1; analysis done on mean invertebrate measures calculated from five Surber samples). For any highly correlated (>0.8) pair of environmental variables, one was excluded in candidate models. Models were developed using information from correlation tables (Pearson’s correlation), Random Forest models (Liaw & Wiener, 2002) and best subsets (regsubsets; Lumley & Miller, 2009) in R (R Core Development Team, 2008). In addition, knowledge of aquatic invertebrates, field sites and ecological insight were included whenever possible.

Results

Stream characteristics

All sites were cool mountain streams with cobble bottoms. Water temperature generally decreased with elevation; however, some of the highest temperatures were observed below lakes at high sites (e.g. Moose and Cascade; Table 1). Dissolved oxygen was supersaturated ($>100\%$) at most sites, and its concentration was inversely related to elevation. Specific conductivity was lowest in Moose and Cascade Creeks, and stream pH was basic. Oxidation-reduction potential indicated that oxidising conditions occurred in most streams (>200 mV). As expected, streams were wider and deeper at lower elevations. Mean particle size in Granite (172 mm) and Cascade Creeks (180 mm) was larger than in Death, Owl and

Moose Creeks (~ 107 mm). Rocks had more visible biofilm (i.e. the greenest rocks) at high sites and Moose Creek had the highest biofilm rank compared to the other streams. All streams were flowing in an easterly direction (mean aspect = 72°) and stream slope was generally steepest at the high sites.

Invertebrate assemblages

Streams in the Teton Range are home to many aquatic invertebrates; an average of nearly 10 000 individuals m^{-2} were recorded across sampling sites (Fig. 2). At least 68 taxa were collected representing five phyla and eight classes (Table S2). Of the sampled taxa, 86% were insects in 24 families and 6 orders, and insects accounted for approximately 80% of the individuals collected. Diptera was the most abundant insect order followed by Ephemeroptera, Plecoptera and Trichoptera. Sphaeriidae was the most abundant non-insect invertebrate followed by Acari, Oligochaeta and Crustacea.

Aquatic invertebrate assemblages differed among streams and elevations. The mean density of invertebrates in Moose Creek (17 550 ind m^{-2} ; Fig. 2a) was higher than Owl (7500 ind m^{-2} ; Fig. 2b), Cascade (5170 ind m^{-2} ; Fig. 2c) and Death Creeks (5140 ind m^{-2} ; Fig. 2d; ANOVA, Tukey’s $P < 0.05$; Table 1). The most taxa were observed in Moose Creek (50) and the fewest in Granite and Death Creeks (34 and 35 respectively; ANOVA, $P = 0.15$). The density (6240 ind m^{-2} ; Fig. 2) and richness (49 taxa) of invertebrates was lowest at the low elevation. EPT taxa were least dense (1075 ind m^{-2}) and made up the smallest proportion of taxa at the high elevation (11%), but EPT richness was similar among elevations (10 taxa).

Total density (mixed effects model, $F = 0.66$, $P = 0.54$, d.f. = 2/8), density of EPT taxa ($F = 1.65$, $P = 0.25$, d.f. = 2/8), total richness ($F = 2.13$, $P = 0.18$, d.f. = 2/8) and richness of EPT taxa ($F = 0.83$, $P = 0.47$, d.f. = 2/8) were not related to elevation. Nevertheless, elevation was correlated with other measured parameters. Dissolved oxygen ($\rho = -0.56$), width ($\rho = -0.70$) and depth ($\rho = -0.70$) negatively correlated with elevation, and stream slope ($\rho = 0.61$) positively correlated with elevation.

Between four and 16 insect taxa (7–30%) were collected at all sites along a stream, and five were only collected at high elevation sites: *Ampumixis* (Coleoptera, Elmidae), *Tipula* (Diptera, Tipulidae), *Isoperla* (Plecoptera, Perlodidae), *Perlinodes* (Perlodidae) and *Dicosmoecus* (Trichoptera, Limnephilidae). *Clinocera*, *Hemerodromia*, *Oreogeton* (Diptera, Empididae), Tanypodinae (Diptera, Chironomidae), *Kogotus* (Plecoptera, Perlodidae) and *Perlomyia* (Plecoptera, Leuctridae) were most abundant at the high sites. Of the 54 insect taxa collected (excluding Chironomidae), 37% were captured in only one stream. Approximately one-fourth of taxa were collected in two streams, and half of those were in adjacent drainages. Furthermore, 7.5% of taxa were found in three streams,

Table 1. Biotic and abiotic factors at low (L), middle (M) and high (H) elevation sites from five streams in Grand Teton National Park, Wyoming. Dissolved oxygen (DO), specific conductivity (SPC), oxidation-reduction potential (ORP), mean particle size (MPS) of the substrate, Ephemeroptera, Plecoptera, and Tricoptera (EPT) density and richness and Shannon's diversity index (SI) were measured at each site. Density is in thousands of individuals per m².

Stream Variable	Cascade			Death			Granite			Moose			Owl		
	L	M	H	L	M	H	L	M	H	L	M	H	L	M	H
Elevation (m)	2003	2391	2726	2038	2470	2697	2032	2389	2703	2083	2379	2764	2082	2356	2586
Temp. (°C)	11	7.5	11	12.3	12.1	10.6	9.5	6.3	10.2	10.1	10.1	17.8	13.2	9	5.1
DO (%)	121	114	115	123	124	109	134	124	130	129	109	126	133	96	106
DO (mg l ⁻¹)	12.6	12.5	11.3	12.4	12.2	10.8	14.4	14	13	13.7	11.3	10.6	13.1	10.2	12.1
SPC (µS cm ⁻¹)	25.5	44.8	9.3	103.5	123.1	190.8	169.7	176.2	174.3	99	50	7.8	185.4	160.5	147.5
pH	8.0	8.2	7.9	8.3	8.3	8.6	8.6	8.6	8.7	8.2	8.3	7.1	8.6	8.6	8.5
ORP (mV)	224.5	177.9	169.2	195.4	172.5	217.8	209.2	208.7	216.2	276.3	299	300.9	257.7	192.2	211.4
Width (m)	17	6	6	8	5	2	8	5	1	7	10	4	8	3	1
Depth (cm)	60	33	28	28	24	14	29	38	10	30	27	15	51	16	7
MPS (mm)	202	165	174	152	73	103	282	160	74	44	128	152	110	97	105
Biofilm (1–3)	3	1	1	1	1	2	1	2	2	2	3	3	1	1	2
Slope (%)	2	2	8	2	1.5	4	2	3	2	1	2	4	1	3	8
Density (ind m ⁻²)	6.6	3.5	5.3	5.3	6.9	3.2	6.9	24.9	7.6	5.5	13.3	33.8	7.0	3.7	11.8
EPT den. (ind m ⁻²)	0.5	1.2	0.3	3.9	4.5	1.1	4.7	2.4	0.8	1.5	2.4	3.4	3.5	1.7	0.8
Richness	31	36	31	26	25	27	28	27	26	29	33	28	24	23	19
EPT richness	19	22	16	18	18	16	17	18	14	17	23	18	17	14	9
SI	1.5	2.4	1.6	2.4	2.2	2.1	2.4	1.3	1.2	1.4	1.7	1.7	1.9	2.0	1.0

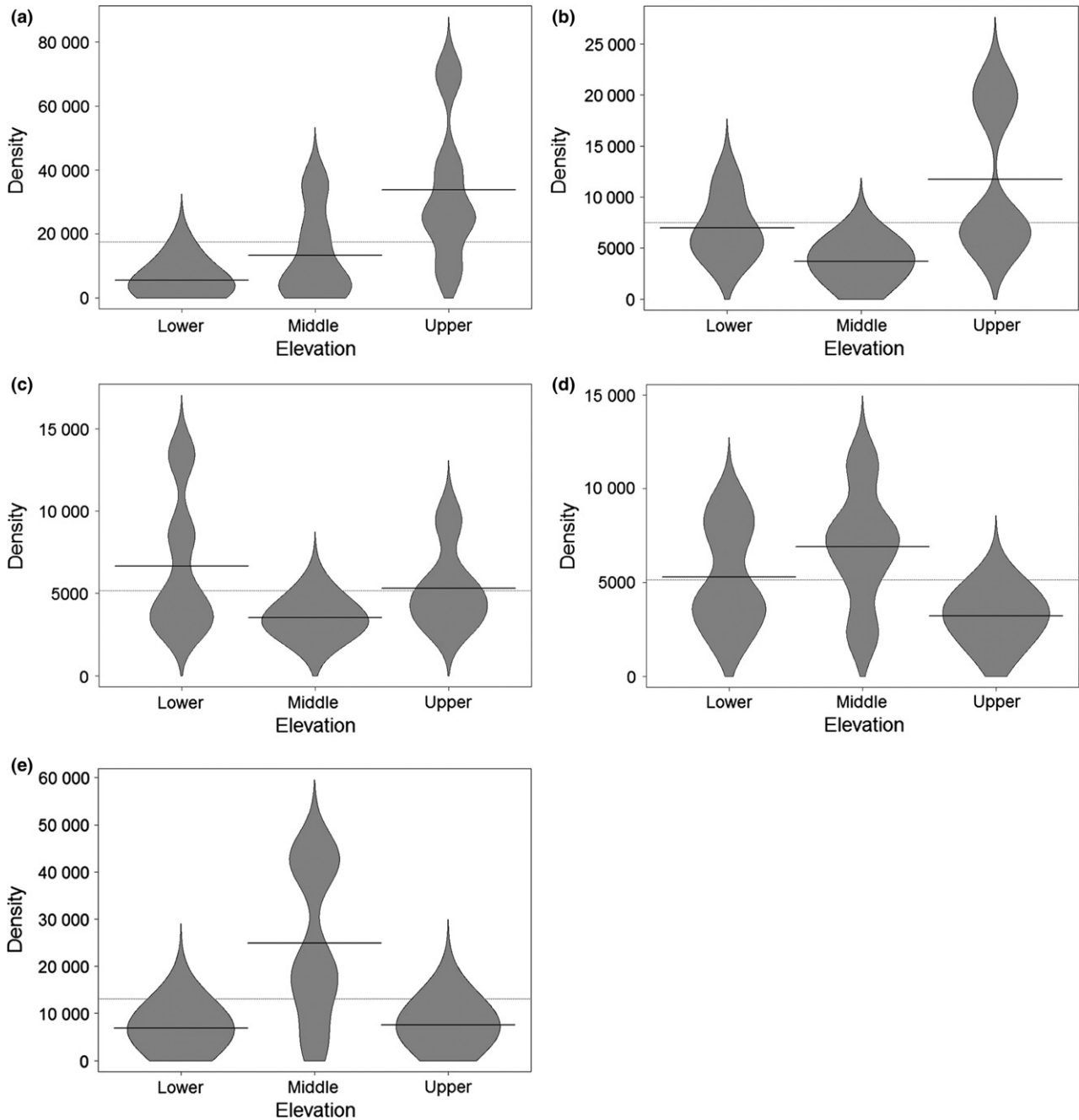


Fig. 2. The density (ind m^{-2}) of aquatic invertebrates at three elevations (low, middle and high) along (a) Moose, (b) Owl, (c) Cascade, (d) Death and (e) Granite Creeks in Grand Teton National Park. The bold lines are the mean densities for each site and the dotted line is the average density for each stream.

11% in four streams and 20.5% of taxa were collected in all five streams. Eight taxa (excluding Chironomidae) were collected in all low elevation sites, yet only two taxa were found at all high elevation sites (*Sweltsa* and *Zapada*).

Different variables explained the density of the entire invertebrate assemblage and the density of EPT taxa. Total density of aquatic invertebrates was best explained

by two models (Table S3). Biofilm rank ($t = 2.4$, $P = 0.03$) explained the most variance in density ($Density = -784 + 6042 \times Biofilm$, $AICc = 315.9$, $AICc$ weight = 0.58). In addition, oxidation-reduction potential ($Density = -13135 + 103 \times ORP$; $t = 2.1$, $P = 0.05$, $AICc = 317.0$, $AICc$ weight = 0.33) also ranked highly. EPT taxa composed 28% of the individuals collected

and their densities appeared to be regulated by different variables compared to the entire assemblage. The highest ranked model for EPT density ($Density_{EPT}$) indicated that higher densities were associated with higher saturation of dissolved oxygen (SDO ; $t = 2.0$, $P = 0.06$) and reaches flowing in a northeasterly direction (transformed aspect; $t = 2.0$, $P = 0.07$; $Density_{EPT} = -6160 + 61 \times SDO + 994 \times Aspect$; $AICc = 264.5$, $AICc$ weight = 0.36). Much of the variation in density of EPT taxa was explained by the saturation of dissolved oxygen alone ($Density_{EPT} = -5563 + 65 \times SDO$; $t = 2.0$, $P = 0.07$; $AICc = 265.1$, $AICc$ weight = 0.27).

Richness of the entire assemblage and EPT taxa were best explained by specific conductivity (Table S3). Specific conductivity (SPC ; $t = -3.1$, $P = 0.009$) explained the most variation in total taxa richness ($Richness = 32 - 0.04 \times SPC$, $AICc = 84.5$, $AICc$ weight = 0.76). Approximately 36% of taxa collected were EPT taxa. Similarly, specific conductivity explained ($t = -2.0$, $P < 0.069$) the most variation in EPT richness ($Richness_{EPT} = 19.7 - 0.024 \times SPC$; $AICc = 81.6$, $AICc$ weight = 0.38). The model that included elevation ($t = -2.1$, $P = 0.06$), specific conductivity ($t = 3.0$, $P = 0.01$) and transformed aspect ($t = 2.1$, $P = 0.06$) also ranked highly ($Richness_{EPT} = 31 - 0.0054 \times Elevation - 0.033 \times SPC + 2.3 \times Aspect$; $AICc = 82.8$, $AICc$ weight = 0.21). These models indicate that the richness of EPT taxa is higher at sites with lower SPC, at lower elevations and in stream reaches flowing in a northeasterly direction.

Analysis of indicator taxa by stream and elevation revealed 12 taxa (10 for streams, two for elevations) with significant associations to one or more groupings. Among streams, *Simulium* was an indicator of Death Creek (Indval.g = 0.98, $P = 0.04$). *Hemerodromia*, *Rhyacophila hyalinata* (Banks) and *Pericoma/Telmatoscopus* (Indval.g = 1, $P = 0.01$; Indval.g = 0.96, $P = 0.03$; Indval.g = 0.85, $P = 0.04$ respectively) were indicators of Granite Creek and Nematomorpha (Indval.g = 0.97, $P = 0.02$) was an indicator of Moose Creek. Across elevations, *Epeorus* (Indval.g = 0.98, $P = 0.004$) and *Drunella coloradensis* (Dodds; Indval.g = 0.95, $P = 0.01$) were indicators of a combined grouping of lower and middle elevation. But, our analyses revealed no species that represented specific indicators of high elevation sites.

Two-dimensional NMDS ordinations revealed that invertebrate assemblages were more tightly grouped when analysed by stream than elevation (Fig. 3). When organised by stream (Fig. 3a), groupings were discrete and had no overlap (stress = 0.055). Conversely, when samples were analysed according to elevation (Fig. 3b), significant overlap existed with low elevations clustering most tightly and high elevations most broadly (stress = 0.363). Only NMDS of taxa assemblages (Fig. 3a) was significant (P , species <0.001; P , environment = 0.75) and goodness-of-fit analyses indicated that Bray–Curtis dissimilarities were accurately depicted in ordination space (R^2 , environment = 0.89 and R^2 , species = 0.98).

No clear patterns emerged when comparing environmental diversity among streams via NMDS although Cascade Creek did appear to be disjunct from the other streams (Fig. 3c). Although, when samples were grouped according to elevation, low and middle elevations clustered together and high elevation sites formed a clear, more environmentally diverse grouping (Fig. 3d). Specific conductivity was the only environmental variable driving taxa assemblages (SPC ; $r^2 = 0.61$, $P = 0.003$); however, biofilm ($r^2 = 0.35$, $P = 0.075$) was nearly significant (Table 2).

Results of permutational multivariate analyses of variance for both stream and elevation groupings are presented in Table S4. For stream groupings, only two variables significantly contributed to variance after groupings (strata) were accounted for: elevation ($P = 0.029$) and biofilm ($P = 0.016$). For elevation groupings, biofilm ($P = 0.005$) again contributed significantly to variance after grouping were accounted for. For assessments of the homogeneity of group dispersions among streams and elevations, only two comparisons were significant: (i) for environmental variation among elevations, the comparison of lower-middle ($P = 0.007$) and (ii) for species assemblages among streams, the comparison of Cascade Creek-Owl Creek ($P = 0.043$). One of the most informative ways to visualise group mean dispersions is by plotting the two most informative principal coordinates in 2D space (Figure S1) and calculating mean distance to the centre of the resulting dispersion centroid (Figure S2). When taking this approach, the highest distances to the centre for each comparison were: streams and species assemblages, Owl Creek (0.448); streams and environmental variation, Moose Creek (0.254); elevations and species assemblages, Lower (0.407); elevations and environmental variation, Middle (0.236). Conversely, the lowest distances for each comparison were as follows: streams and species assemblages, Cascade Creek (0.198); streams and environmental variation, Cascade Creek (0.100); elevations and species assemblages, upper (0.307); elevations and environmental variation, lower (0.090).

Discussion

The Teton Range in Grand Teton National Park rises steeply from the Snake River floodplain and provides an ideal location to investigate longitudinal changes in mountain streams. Gradients in aquatic invertebrates across elevations are often obscured by anthropogenic factors (Rundle *et al.*, 1993), but the streams in Grand Teton National Park have minimal human impacts. Few studies have investigated the aquatic invertebrate diversity of Grand Teton National Park, and none have focused on the Teton Range specifically. Within the park, lower elevation streams in the eastern portion have been sampled for aquatic invertebrates including Kelly Warm Springs (Hotchkiss & Hall, 2010), Two Ocean Lake Creek (Marshall & Hall, 2004), the Snake River (Kroger, 1970) and

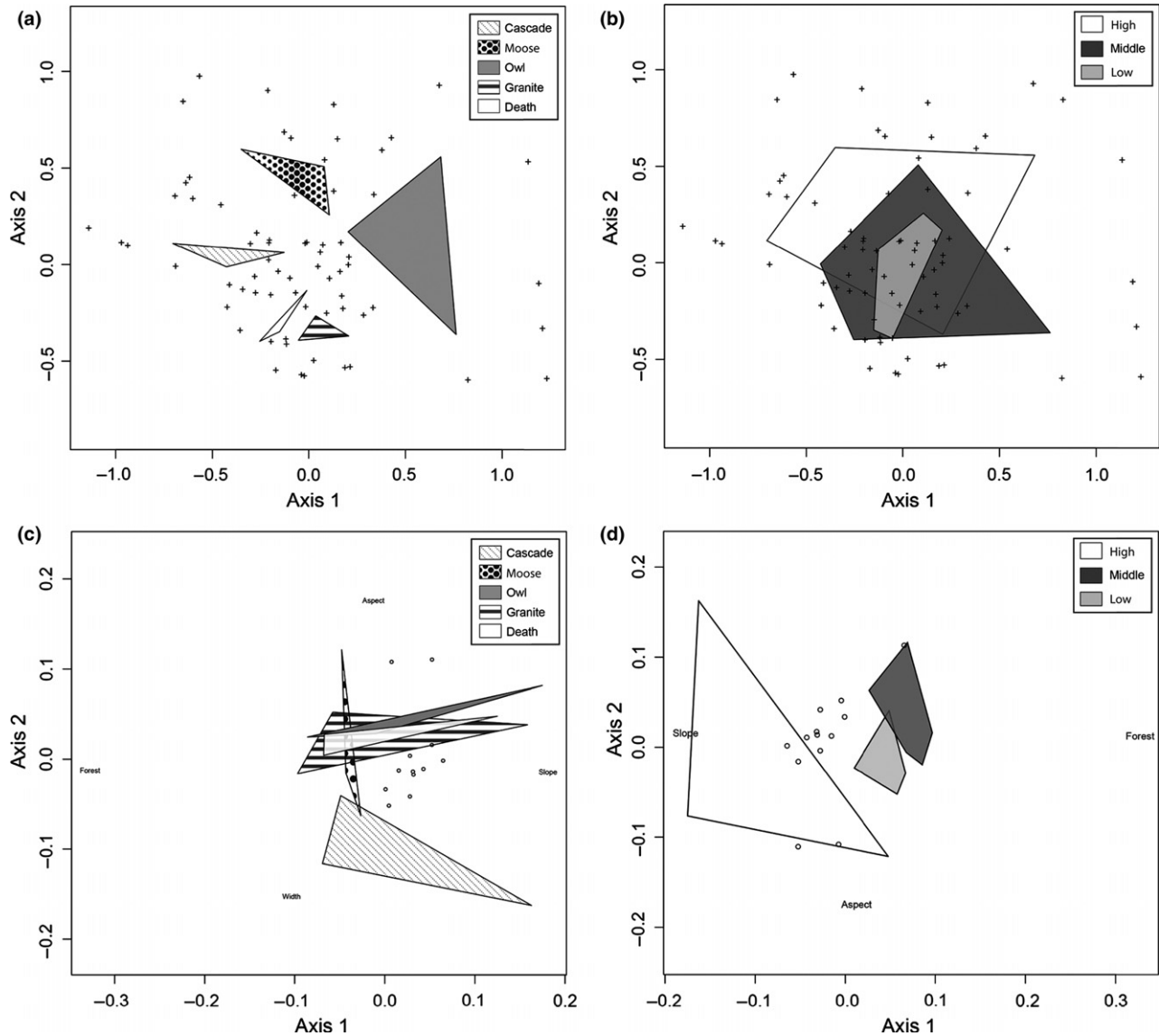


Fig. 3. Two-dimensional non-metric multidimensional scaling (NMDS) ordination plots of aquatic invertebrate density grouped by stream (a) and elevation (b). Hash marks indicate individual taxa. NMDS was also used to group environmental diversity across streams (c) and elevations (d). Outlier environmental variables were labelled with text. Ordinations were calculated using Bray–Curtis dissimilarities.

Pacific Creek (Freilich, 1991). The results presented here establish a baseline of biodiversity and habitat variability across the Teton Range, and are especially important given the inclusion of high elevation sites that may be most at risk due to anthropogenic climate change.

Many biotic and abiotic parameters structure streams from headwaters to the valley floor and studies suggest that elevation strongly influences aquatic invertebrate assemblages (Ward, 1986; Rundle *et al.*, 1993; Suren, 1994; Finn & Poff, 2005). Suren (1994) noted that taxa richness was inversely related to elevation in Nepalese streams and this pattern has been observed around the world (Jacobsen *et al.*, 1997; Jacobsen, 2004). Jacobsen

(2004) found that 50% of invertebrate families lived at 4000 m compared to sea level in the Andes Mountains, and the loss of most families occurred at greater than 1800 m. But elevation does not influence biota directly. Rather, elevation was a proximal measure correlated with several biotic and abiotic factors (e.g. temperature, slope, specific conductivity, dissolved oxygen and biofilm) that more directly affect organisms. The results presented here support this as elevation was not correlated with stream invertebrate assemblages but abiotic and biotic parameters were.

Fewer aquatic invertebrate taxa at higher elevations were thought to be driven by lower dissolved oxygen con-

Table 2. Correlations (r^2) of environmental attributes with stream invertebrate assemblage axis scores in non-metric multidimensional scaling (NMDS) ordination space. Significance is based upon 9999 permutations. Abbreviated environmental variables were dissolved oxygen (DO), specific conductivity (SPC) and mean particle size (MPS) of stream substrate.

Attribute	Axis 1	Axis 2	r^2	P-value
Elevation	-0.51	0.86	0.06	0.683
Temperature	-0.93	0.38	0.21	0.246
DO	-0.10	-0.99	0.08	0.614
SPC	0.69	-0.73	0.61	0.003
MPS	-0.96	-0.29	0.17	0.326
Biofilm	0.08	1.00	0.35	0.075
Slope	-0.05	1.00	0.14	0.421
Aspect	-0.72	-0.70	0.00	0.986
Forest	-0.68	-0.73	0.01	0.941

centrations resulting from lower atmospheric pressure (Jacobsen, 2008). Water can hold more oxygen at cooler temperatures, and streams are generally colder at the headwaters. Jacobsen (2008) argued that the decrease in oxygen concentration due to atmospheric pressure negates any increase in oxygen due to temperature. The results presented here support this hypothesis. Both the concentration of oxygen and % saturation of oxygen were negatively correlated with elevation. In addition, % saturation of dissolved oxygen best explained the density of EPT taxa. EPT taxa, and specifically Plecoptera, are notoriously sensitive to oxygen concentrations, while other aquatic invertebrates (e.g. blood midges) are adapted to survive with low oxygen availability. Over time, lower oxygen concentrations may reduce the metabolism, feeding, growth, emergence and fecundity of sensitive aquatic invertebrates (Jacobsen, 2008). Oxygen was probably not limiting in our study because most dissolved oxygen concentrations were supersaturated. Still, dissolved oxygen concentration may capture a range of habitat variables (e.g. gradient, turbulence, primary production) that may drive the patterns observed in this study.

Model selection results suggest that specific conductivity, elevation and aspect best explained the richness of aquatic invertebrates in Teton Mountain streams. These results also indicate that more invertebrates are present at sites with greener rocks and higher oxidation-reduction potential. Specific conductivity was the only environmental variable that showed a significant correlation with invertebrate assemblages. Sampled streams differed in geology, with northern watersheds primarily composed of sedimentary bedrock and the central and southern watersheds composed mostly of granite. As a result, specific conductivity varied among watersheds with Cascade Creek (granite bedrock) having the lowest values. Specific conductivity varied less within streams (SE = 2–26) than across elevations (e.g. all high elevation sites; SE = 27–40, data not shown). These findings differed from Himalayan streams where conductivity was inversely related to eleva-

tion (Rundle *et al.*, 1993), likely because specific conductivity depends more on local geology than elevation.

Streams flowing to the northeast had higher densities and richness of EPT taxa in the Teton Range. Southwest facing slopes are generally warmest and driest with sparser forest cover, and northeast facing slopes are coolest and wettest with denser forest cover (Stage, 1976). Streams flowing southeast or northwest may have dense forest growing on the south side (northeast facing slope). The dense forest would contribute terrestrial organic matter to the stream and shade the channel (more heterotrophic). Conversely, streams flowing to the northeast or southwest have sparser forest growing on the southern side (northwest facing slope) and may have less terrestrial organic matter inputs and more light reaching the stream (more autotrophic). Few studies have described how streams and their associated invertebrate communities, change depending upon aspect. Perdrial *et al.* (2014) measured higher soil carbon in streams with north-facing watersheds compared to south-facing watershed due to higher soil flushing rates. Much more effort is needed to understand how stream aspect may affect the structure and function of streams.

High elevation sites in the Teton Range harbour significant species and environmental diversity, especially when compared with their lower elevation counterparts. This result is similar to other studies in North America (e.g. Finn & Poff, 2005; Brown *et al.*, 2009; Kubo *et al.*, 2013), and fits in with a broader hypothesis that greater environmental diversity in headwater basins contributes to more diverse invertebrate assemblages (Finn *et al.*, 2013). Among streams, variation in dispersion was present but when categorised by elevation, the greatest dispersion was clearly seen among middle and high elevation sites, with the least dispersion at low elevation sites. These results indicated that middle and high elevation sites were more environmentally diverse and supported a broader swath of invertebrate diversity in the Teton Range.

Headwater streams have been increasingly identified as hotspots for diversity, both in terms of β (richness among streams) and α (site specific richness) diversity (Clarke *et al.*, 2008; Finn *et al.*, 2011). River ecosystems have traditionally been viewed as longitudinal continuums from small headwaters streams to large order rivers. The river continuum concept has been used to describe streams along their length (Vannote *et al.*, 1980) and this model has been referenced extensively in stream ecology. In this context, many studies report that high elevation streams have the lowest invertebrate diversity (Ward & Dufford, 1979; Ward, 1986; Suren, 1994; Jacobsen, 2004; Finn & Poff, 2005; Jacobsen, 2008) and here, three of the five streams had the lowest diversity of invertebrates at the high elevation sites. When streams are viewed from a basin-wide perspective their dendritic nature is evident; >75% of stream length in a given basin can be in the headwaters (1st or 2nd order streams; Leopold *et al.*, 1964; Benda *et al.*, 2004). Comparing headwater streams collectively to larger order rivers downstream suggests

that headwater streams have higher α and β diversity (Clarke *et al.*, 2008; Finn *et al.*, 2011). That is, the diversity of invertebrates and habitats in all headwater streams within a basin is higher compared to larger rivers downstream. Here, high elevation sites exhibited the broadest assemblage profile (α diversity) when analysed in ordination space indicating that Grand Teton National Park would be an ideal place to investigate diversity in headwater streams further.

Invertebrate assemblages in high elevation streams can vary greatly from one stream to another, even within the same watershed. Water sources (lake, snowmelt, spring, etc.) in headwater streams may cause much of the observed variation (Kubo *et al.*, 2013). Non-insect invertebrates do not have an aerial stage and their predominant mode of dispersal is likely within the stream channel. Conversely, aquatic insects emerge as winged adults and move across the terrestrial landscape. The distance that adults disperse depends on both topography and suitability of the surrounding landscape for dispersal as well as species-specific flight ability (Macneale *et al.*, 2005). Relatively few studies have investigated winged dispersal in aquatic insects but results suggest that dispersal ability varies considerably across taxa and habitat (Finn & Poff, 2008; Macneale *et al.*, 2005). In the alpine, mayflies and stoneflies may be poor dispersers as less than 50% of adults were captured ≥ 10 m from a stream in the Colorado Rocky Mountains (Finn & Poff, 2008). But caddisflies may fare better as 30–100% of adults were captured ≥ 10 m from a stream, with some up to 30 m away. At lower elevation, a stable isotope study revealed that most stoneflies disperse upstream but evidence for cross-watershed dispersal was also found (Macneale *et al.*, 2005). Molecular work has supported the idea that populations of aquatic invertebrates are increasingly isolated at higher elevations (Finn & Poff, 2011). Metacommunity analysis also supports the idea that dispersal ability and network topology regulate the aquatic invertebrates colonising reaches (Campbell *et al.*, 2015; Brown *et al.*, 2011). Benthic invertebrates can be limited by their dispersal ability (Astorga *et al.*, 2012) and assemblages typically share fewer similarities when sites are farther apart (Altermatt *et al.*, 2013). The degree to which aquatic invertebrates are isolated at high elevations in the Teton Range has not been investigated; however, results of the NMDS analyses indicate that the high elevation sites had the widest environmental profile, shared few similar taxa and had the most diverse invertebrate assemblages, all of which support a greater degree of isolation than at other elevations.

Collecting baseline information is a critical step in monitoring how ecosystems are changing and identifying what species may be most at risk of local extirpation or extinction. Climate change poses the greatest risk to taxa restricted to or most abundant at high elevation sites. Eleven taxa identified in this study meet these criteria; five were only collected at the high elevation sites (*Ampumixis*, *Tipula*, *Isoperla*, *Perlinodes* and *Dicosmoecus*) and six were most abundant there (*Clinocera*, *Hemerodromia*, *Oreoge-*

ton, Tanypodinae, *Kogotus* and *Perlomyia*). Regular benthic sampling of high elevation streams (e.g. every 5–10 years) and comparisons to previous results is a crucial component in monitoring how climate change may affect headwater streams. Streams at the highest elevations in Grand Teton National Park (i.e. above 3000 m) were not sampled in this study, but these streams may show even more pronounced effects of climate change, especially those below glaciers or snowfields. Species that are restricted to this habitat, such as the recently described stonefly *Lednia tetonica* (Baumann & Call, 2012), are at even greater risk as temperatures rise.

Acknowledgements

We thank Kyle Hack, Morgan Ford, Oliver Wilmot and Phil Branigan for sorting samples and Mark Andersen for help making the map of sampling sites. Bryan Tronstad was instrumental in data entry. Don and Lusha Alzner graciously provided meals and lodging between backpacking trips. Grand Teton National Park funded the project. In addition, we thank two anonymous reviewers for valuable comments that strengthened this manuscript.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12169:

Figure S1. Two-dimensional plots of dispersion (variance) for stream and species diversity (a), elevations and species diversity (b), streams and environmental diversity (c) and elevations and environmental diversity (d). Multivariate dispersions were calculated using Bray–Curtis dissimilarities. The first two letters of each abbreviation correspond to a stream (CC = Cascade Creek, DC = Death Creek, GC = Granite Creek, MC = Moose Creek, OC = Owl Creek) and the third letter corresponds to an elevation (L = low, M = middle, U = upper).

Figure S2. Boxplots of the distance to the centre of dispersion centroids for stream and species diversity (a), elevations and species diversity (b), streams and environmental diversity (c) and elevations and environmental diversity (d). The first two letters of each abbreviation correspond to a stream (CC = Cascade Creek, DC = Death Creek, GC = Granite Creek, MC = Moose Creek, OC = Owl Creek) and the third letter corresponds to an elevation (L = low, M = middle, U = upper). Dark lines indicate the dispersal median for each comparison. Upper and lower bounds of boxes indicate the upper and lower quartile limits respectively. Whiskers indicate the highest and lowest values observed. Multivariate dispersions were calculated using Bray–Curtis dissimilarities.

Table S1. Location (NAD83), date visited and elevation (m) of all sampled sites in Grand Teton National Park, Wyoming.

Table S2. The mean density (ind. m⁻²) of aquatic invertebrates at three elevations for each of five streams sampled in Grand Teton National Park, Wyoming.

Table S3. The top five models ranked using AICc scores that explained total invertebrates density, Ephemeroptera, Plecoptera and Trichoptera (EPT) density, invertebrate richness and EPT richness. Dissolved oxygen (DO), percent saturation of DO (%DO), oxidation-reduction potential (ORP), specific conductivity (SPC) and mean particle size (MPS) were some of the variables used to explain invertebrate metrics.

Table S4. Significance of permutational multivariate analyses of variance using distance matrices for two strata: streams and elevations. Abbreviated environmental variables are dissolved oxygen (DO), specific conductivity (SPC) and mean particle size (MPS) of stream substrate. Significance is based upon 999 permutations.

Table S5. Mean distance to the centre of dispersal centroids for four comparisons: streams-species diversity, streams-environmental variation, elevations-species diversity and elevations-environmental diversity. Stream abbreviations are as follows: CC = Cascade Creek, DC = Death Creek, GC = Granite Creek, MC = Moose Creek, OC = Owl Creek.

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Accepted 8 March 2016
First published online 9 April 2016

Editor: Simon R. Leather
Associate editor: Göran Sahlen