

# Experimental whole-stream warming alters community size structure

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## Abstract

How ecological communities respond to predicted increases in temperature will determine the extent to which Earth's biodiversity and ecosystem functioning can be maintained into a warmer future. Warming is predicted to alter the structure of natural communities, but robust tests of such predictions require appropriate large-scale manipulations of intact, natural habitat that is open to dispersal processes via exchange with regional species pools. Here, we report results of a two-year whole-stream warming experiment that shifted invertebrate assemblage structure via unanticipated mechanisms, while still conforming to community-level metabolic theory. While warming by 3.8 °C decreased invertebrate abundance in the experimental stream by 60% relative to a reference stream, total invertebrate biomass was unchanged. Associated shifts in invertebrate assemblage structure were driven by the arrival of new taxa and a higher proportion of large, warm-adapted species (i.e., snails and predatory dipterans) relative to small-bodied, cold-adapted taxa (e.g., chironomids and oligochaetes). Experimental warming consequently shifted assemblage size spectra in ways that were unexpected, but consistent with thermal optima of taxa in the regional species pool. Higher temperatures increased community-level energy demand, which was presumably satisfied by higher primary production after warming. Our experiment demonstrates how warming reassembles communities within the constraints of energy supply via regional exchange of species that differ in thermal physiological traits. Similar responses will likely mediate impacts of anthropogenic warming on biodiversity and ecosystem function across all ecological communities.

**Keywords:** body size, community structure, energy demand, metabolic theory, stream warming, thermal preference

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## Introduction

Although the effects of climate warming on the phenology and distribution of species have received a great deal of recent attention, potential effects of warming on body-size distributions also have significant consequences for ecological pattern and process (Sheridan & Bickford, 2011; Ohlberger, 2013). Body size is a key trait that scales with many physiological and ecological processes (e.g., metabolism, abundance, range size; Peters, 1983; Brown *et al.*, 2004; Woodward *et al.*, 2005). Body size also plays an important role in community assembly and structure through its influence on competition, predation, and energy use (Brown *et al.*, 2004; Pawar, 2015). Understanding how taxa of different body sizes

respond to increasing temperature is thus crucial for predicting the effects of climate change on ecological communities. Progress on this front, however, has been hindered by the lack of a universal response across taxonomic groups or community types, as well as the need for a theoretical framework that links changes in body size and community structure with temperature (Dau-fresne, 2009; Gardner *et al.*, 2011; Sheridan & Bickford, 2011).

The metabolic theory of ecology (MTE) provides a framework for predicting community-level responses to environmental warming through its emphasis on interactions between temperature, body size, and metabolic rate (Brown *et al.*, 2004; Brown & Sibly, 2012). The MTE can inform predictions via manipulation of its organizing equation, which links metabolic rate ( $B$ ) of an individual to its body mass ( $M$ ) and temperature ( $T$ ):

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$$B = B_0 M^{0.75} e^{-E/kT}, \quad (1)$$

where  $B_0$  is a normalization constant independent of body size and temperature,  $E$  is the activation energy of cellular respiration,  $k$  is the Boltzmann constant, and  $T$  is absolute temperature in K (constrained to a temperature range of 0–40 °C). To predict how warming will affect the metabolism of whole communities (i.e., community energy demand) and potentially constrain community abundance or biomass, Eqn (1) can be expanded to the community level as follows:

$$\text{CED} = \sum (B_i \times N_i), \quad (2)$$

where CED is community energy demand,  $B_i$  is a categorical metabolic rate (e.g., the metabolic rate of an individual of a particular taxon or discrete size class within a community), and  $N_i$  is the abundance or density of that taxon or size class (Yvon-Durocher & Allen, 2012; Barneche *et al.*, 2014). When temperature increases, the metabolic rate ( $B$ ) of an individual should increase according to Eqn (1). Thus, assuming that (i) resource supply remained unchanged, (ii) all resource production was consumed, and (iii) the amount of energy that each taxon or size class uses per unit area is independent of body mass (i.e., the energetic equivalence rule [EER], where  $[B \propto M^{0.75}] \times [N \propto M^{-0.75}]$ , or  $\text{CED} \propto M^0$ ; Damuth, 1981), total community abundance and biomass would necessarily have to decrease with warming, as each individual used a larger proportion of the total energy available.

The MTE and related concepts such as the EER necessarily treat taxa as equivalent (i.e., differing only in body size). However, natural communities are comprised of diverse taxa with a broad range of body sizes and thermal preferences (Woodward *et al.*, 2010), allowing postwarming CED to be driven by many potential combinations of body sizes and abundances, posing a challenge to accurate prediction. Ectotherm performance metrics (e.g., growth, fecundity, population size) follow various unimodal responses to temperature gradients (Huey & Stevenson, 1979; Pörtner & Farrell, 2008). Some taxa occupy relatively narrow thermal windows (i.e., cold or warm stenotherms), while others are less sensitive to changes in temperature (i.e., eurytherms). Small shifts in temperature can consequently change the relative abundances of taxa within communities, as some taxa are eliminated and others added via dispersal from the regional species pool (Peterson *et al.*, 2002; Gibson-Reinemer *et al.*, 2015). Thus, while the response of CED to warming will ultimately depend on canonical relationships between summed metabolism and temperature, taxon-specific factors, including dispersal ability and thermal

preference, are likely to be important in controlling how postwarming CED is distributed among species and body sizes in natural ecosystems undergoing warming.

Here, we report results from a whole-stream warming experiment conducted at sufficient spatial and temporal scales to encompass a natural community open to exchange with a regional species pool that exhibits considerable diversity in thermal physiology and body size (Woodward *et al.*, 2010; O’Gorman *et al.*, 2012; Hanneadóttir *et al.*, 2013). After one year of sampling the macroinvertebrate communities of our experimental stream and a nearby reference stream, we used a novel geothermal heat exchanger to warm the experimental stream by 3.8 °C for two years. We predicted that warming would increase individual metabolism and hence CED. Assuming no change in resource supply and community body-size distribution, we expected that increased energy demand would lead to simple reductions in community abundance and biomass. Alternatively, if exchange of regional species and community turnover are important in structuring postwarming communities, we expected responses to deviate from predicted reductions in abundance and biomass, being driven instead by losses and gains of taxa that differ both in body size and thermal preference.

## Materials and methods

### Study sites and experimental design

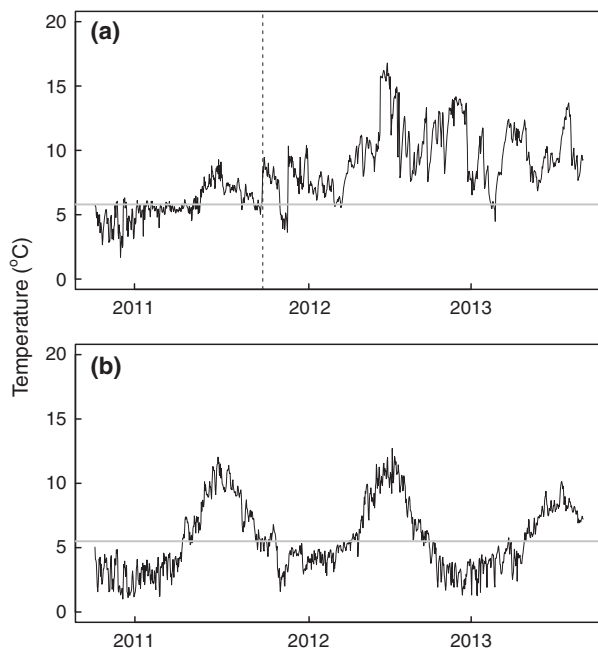
We conducted this study in two headwater streams in the Hengill region of southwestern Iceland. The experimental stream is within the Hengill geothermal field (64°03’N 021°18’W, 380 m a.s.l.), and the reference stream is in the Ölkelduháls geothermal field (64°03’N 021°12’W, 360 m a.s.l.), approximately 5 km from the experimental stream. Both areas have numerous groundwater-fed streams that differ in temperature due to degree of geothermal influence (Árnason *et al.*, 1969; Azimudin, 1995). Both streams are first order and groundwater-fed with little to no geothermal influence; they also have comparable physical and chemical characteristics (Table S1), including average annual temperatures and similar invertebrate communities (Ólafsson *et al.*, 2010).

The effects of experimental warming on stream assemblages were assessed using a before-after control-impact (BACI) design that evaluated the null hypothesis that the manipulation had no effect by comparing experimental responses to premanipulation trends (Stewart-Oaten *et al.*, 1986). The BACI framework accounts for environmental differences before and after the manipulation (e.g., changes in precipitation) by adjusting pre- and postmanipulation trends with data from a nearby reference system. In spite of the lack of replication, this manipulative approach has a successful history of addressing questions at the ecosystem scale (Carpenter *et al.*, 1995;

Schindler, 1998; Oksanen, 2001). Sampling was conducted during one prewarming year (YR1) and two years of warming (YR2 and YR3) in the experimental stream (warming = impact) and the reference stream (control). The two years of stream warming were treated separately because of the possibility of short- vs. mid-term effects of warming on invertebrates with varying life histories.

Study reaches were initially sampled during a 12-month prewarming period (YR1) beginning in October 2010. In October 2011, we began warming the 35-m reach of the experimental stream using a gravity-fed heat exchanger (Fig. S1). This warming was possible because the cold experimental stream (mean annual temperature 5.5 °C) runs parallel to a warm stream (mean annual temperature 22 °C), with just 2 m separating the two streams at their closest point. Water from the cold stream was diverted into the heat exchanger in the warm stream, warmed, and discharged back into the experimental stream, resulting in an average temperature increase of approximately 3.8 °C in the sampled reach during the two years of warming (Fig. 1; Table S1). This increase in temperature is consistent with potential levels of warming predicted over the next century by current climate models (IPCC 2013).

Water temperature and stage height were recorded every 15 min using Onset U20-001-01 water-level loggers (Onset Computer Corp., Pocasset, MA, USA). Discharge was estimated using stage–discharge relationships based on dilution gauging using NaCl slugs (experimental stream,  $n = 30$ ;



**Fig. 1** Time series of daily mean temperatures for the (a) experimental stream and (b) reference stream. The gray horizontal line indicates the mean annual temperature before warming (YR1; experimental stream = 5.8 °C, reference stream = 5.5 °C). The dashed vertical line indicates the onset of warming in the experimental stream.

reference stream,  $n = 21$ ). Triplicate water samples for  $\text{NH}_4^+$ -N,  $\text{NO}_3^-$ -N, and soluble reactive phosphorus (SRP) analyses were collected monthly at the lower end of each reach. Ammonium concentrations were measured using the orthophthalaldehyde fluorometric method (Holmes *et al.* 1999; Taylor *et al.*, 2007). Nitrate concentrations were measured using ion chromatography (Dionex ICS 2000 Ion Chromatograph, Dionex Corp., Sunnydale, CA, USA; APHA, 1989), and SRP concentrations were measured using the ascorbic acid method (Murphy & Riley, 1962).

### Benthic sampling

We sampled benthic invertebrates from the study reaches of both streams using a Surber sampler (250- $\mu\text{m}$  mesh, 0.0225  $\text{m}^2$  sampling area). Five samples were taken from each stream reach approximately monthly from October 2010 through September 2013. Mineral substrata were scrubbed with a stiff brush to dislodge organic matter. Organic matter retained on a 250- $\mu\text{m}$  sieve was collected and preserved in 5% formaldehyde in the field. In the laboratory, we split samples into coarse (>1 mm) and fine (<1 mm but >250  $\mu\text{m}$ ) fractions. We removed all invertebrates from coarse fractions, but occasionally subsampled fine fractions using a Folsom plankton splitter (minimum of 1/8 of the entire sample). Invertebrates were identified to the lowest practical taxonomic level (genus in most cases). The body length of each individual was measured to the nearest mm, except for Chironomidae, which were measured to the nearest 0.25 mm. Biomass was estimated using length–mass relationships (Benke *et al.*, 1999; Johnston & Cunjak, 1999; Miserendino, 2001).

To estimate potential resource supply, the biomass of organic matter from the Surber samples (e.g., fine benthic organic matter, coarse benthic organic matter, and filamentous algae) and epilithic biofilm biomass were quantified during each month of the study. Samples were split into fine benthic organic matter (FBOM, 0.25–1 mm) and coarse benthic organic matter fractions (CBOM, >1 mm) in the laboratory using nested sieves. The filamentous green alga *Ulva* was separated from the rest of the CBOM fraction. Organic matter was dried at 60 °C for at least 72 h, weighed, ashed at 500 °C for 24 h, and then reweighed to obtain ash-free dry mass (AFDM). To estimate algal biofilm biomass, we sampled known areas of biofilm from five rocks in each stream on the same days that invertebrates were sampled. The area within a 35-mm slide mount was scrubbed with a wire brush and rinsed with stream water into an amber Nalgene® bottle. We filtered subsamples of the slurry onto separate glass-fiber filters (Whatman GF/F, 0.7- $\mu\text{m}$ ) for chlorophyll *a* and AFDM. Chlorophyll *a* was extracted for 24 h in 90% acetone. We measured total chlorophyll with a Turner Designs AquaFluor fluorometer (Turner Designs, Sunnyvale, CA, USA). Biofilm AFDM samples were filtered onto precombusted and preweighed glass-fiber filters, dried at 60 °C for at least 72 h, allowed to cool overnight in a desiccator, and then reweighed. After the filters were reweighed, filters were combusted at 500 °C for at least 4 h, allowed to cool, and then reweighed to obtain AFDM.

### Community energy demand

To determine how warming affected community energy demand (CED), we estimated the amount of energy used by invertebrate communities in each stream during each month of sampling and over the entire year for all three years of the study. To estimate monthly energy demand, we used the size-specific abundance data and placed each individual into one of eight even  $\log_{10}$  body-mass bins regardless of taxon identity. The metabolic rate of an individual within a size bin was estimated based on Eqn (1) using mean monthly temperature and the midpoint of the size bin ( $\log_{10}$  scale) for mass. We used an activation energy ( $E$ ) of 0.65 eV and a normalization constant ( $B_0$ ) for invertebrates of  $19.75 \text{ W g}^{0.75}$  (Gillooly *et al.*, 2001; Brown *et al.*, 2004). Energy demand of each size bin was calculated as the density of individuals multiplied by the average metabolic rate of individuals in that bin. CED was calculated as the sum of all size bins (Eqn 2). We also calculated annual CED for each stream using the binned body-mass data as above and mean daily temperatures.

### Data analysis

We used generalized additive mixed models (GAMMs; Zuur *et al.*, 2007) to test for differences between streams and among years in the variables of interest (e.g., total invertebrate abundance and biomass, and CED). The models were fitted using the *gam4* function in the 'GAMM4' package (Wood, 2006) in the R platform (R Core Team, 2014). For each dependent variable, models included stream (experimental, reference), year (YR1, YR2, YR3), and the interaction term (stream  $\times$  year) as categorical fixed factors and month as a random factor. Coefficients for random effects were allowed to vary by stream. We used cubic regression smoothing to capture the seasonality in the data, and the interaction (stream  $\times$  year) was fitted using the 'by' command. The interaction (stream  $\times$  year) is of primary interest because it can be used to test the hypothesis that the temporal dynamics of the experimental stream diverged from those of the reference stream after warming. Data were  $\log_{10}$ -transformed prior to analysis when appropriate. We used the significance of the stream  $\times$  year interaction ( $P < 0.05$ ) to identify a significant effect of warming.

We used a combination of methods to detect changes in invertebrate assemblage structure and to identify which taxa contributed to dissimilarity among assemblages. Nonmetric multidimensional scaling (NMDS) of Bray–Curtis similarity matrices based on  $\log_{10}(x + 1)$  abundance and biomass data was used to describe temporal changes in invertebrate assemblage structure. Invertebrate assemblage structure data were further analyzed using permutational analysis of variance (PERMANOVA; Anderson, 2001) with three fixed factors: (i) stream (fixed: warmed and reference), (ii) year (fixed: YR1, YR2, and YR3), and (iii) month (fixed: month of sampling dates). Using this approach, any effect of the warming manipulation would be detected by a significant stream  $\times$  year interaction. Pairwise tests were performed to infer differences between the levels of each factor. The response variables chosen for PERMANOVA analysis were invertebrate abundance and invertebrate biomass. Based on  $\log_{10}(x + 1)$ -transformed data, species

dissimilarities were calculated using the Bray–Curtis dissimilarity coefficient. We used the similarity percentage routine (SIMPER) to indicate which taxa contributed most to the dissimilarities in abundance and biomass among years in the experimental stream. PERMANOVA and SIMPER analyses were performed using PRIMER v.6 with the PERMANOVA + add-on (Clarke & Gorley, 2006; Anderson *et al.*, 2008).

To estimate the magnitude of change in abundance or biomass between years, we calculated the relative percentage change (RPC) in the experimental stream relative to the reference stream for each taxon:

$$\text{RPC} = [(X_{BR}/X_{BE}) - (X_{AR}/X_{AE})]/(X_{AR}/X_{AE}) \times 100, \quad (3)$$

where  $X_{BR}$  = mean abundance or biomass in the reference stream before warming of the experimental stream;  $X_{BE}$  = mean abundance or biomass in the experimental stream before warming;  $X_{AR}$  = mean abundance or biomass in the reference stream after warming;  $X_{AE}$  = mean abundance or biomass in the experimental stream after warming.

We also examined whether changes in abundance or biomass were related to body size or thermal preferences ( $T_{\text{pref}}$ ). We attempted to estimate  $T_{\text{pref}}$  for 18 macroinvertebrate taxa commonly found in both the experimental and reference streams using macroinvertebrate abundance data from 54 sites across Iceland that ranged in average temperature from 6 to 46 °C (Ólafsson *et al.*, 2010). Sites were sampled during May–August 2002, and abundances were based on an average from five replicate samples. We fit Gaussian curves to  $\log_{10}(x + 1)$  abundance vs. temperature for each taxon. Gaussian curves were of the form  $y = (\text{amplitude} \times \exp(-0.5 \times ((x - \text{Mean})/\text{SD})^2))$ , where  $y = \log(x + 1)$  abundance,  $x = \text{temperature (°C)}$ , amplitude is the height of the center of the distribution, mean is the temperature at the center of the distribution ( $T_{\text{pref}}$ ), and SD is the measure of the width of the distribution. We plotted RPC vs. body size and  $T_{\text{pref}}$  and used least-squares regression to fit linear models to the plots. Variables were  $\log_{10}$ -transformed when appropriate.

## Results

### Temperature manipulation

The annual mean temperature in the experimental stream increased from 5.8 °C in YR1 to 9.1 and 10.1 °C in YR2 and YR3, respectively (Fig. 1; Table S1). Water temperature in the experimental stream was thus elevated by an average of 3.8 °C over two years of experimental warming. The annual mean temperature of the reference stream ranged from 5.3 to 6.3 °C during the three-year study (Fig. 1). Mean annual discharge ranged from 4 to 9  $\text{L s}^{-1}$  in the experimental stream and from 13 to 15  $\text{L s}^{-1}$  in the reference stream (Table S1). Dissolved nutrient concentrations were low in both streams (experimental stream ranges: 2–28  $\mu\text{g L}^{-1}$   $\text{NO}_3^- - \text{N}$ , <9  $\mu\text{g L}^{-1}$   $\text{NH}_4^+ - \text{N}$ , 16–42  $\mu\text{g L}^{-1}$  SRP; reference stream ranges: 2–7  $\mu\text{g L}^{-1}$   $\text{NO}_3^- - \text{N}$ , <9  $\mu\text{g L}^{-1}$   $\text{NH}_4^+ - \text{N}$ , 16–67  $\mu\text{g L}^{-1}$  SRP; Table S1).

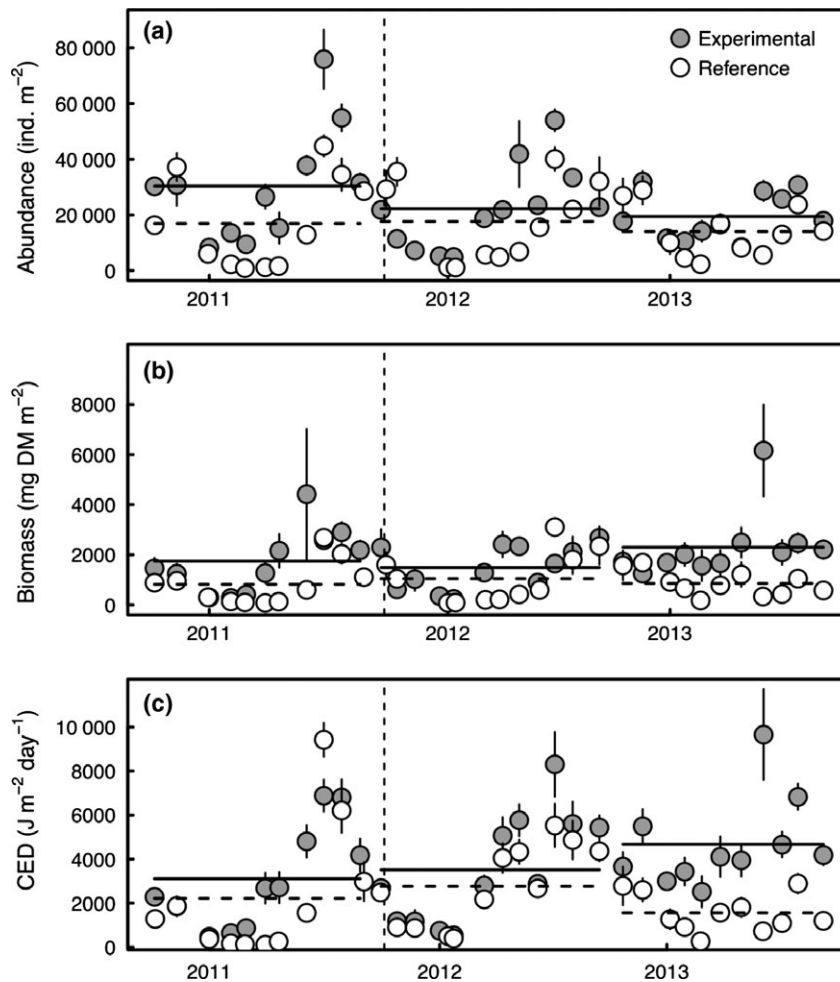
*Community abundance and biomass*

Two years of warming of the experimental stream by 3.8 °C decreased total invertebrate abundance significantly, but did not lead to significant changes in total invertebrate biomass (Fig. 2a, b, Tables 1 and S2). Total invertebrate abundance declined by 66% in the experimental stream relative to the reference stream (corresponding to a 27% decrease over time in the experimental stream) between YR1 and YR2 and by 60% between YR1 and YR3 (36% decrease in the experimental stream over time; Tables 1 and S2). Despite a significant decrease in invertebrate abundance, total invertebrate biomass in the experimental did not differ among years (Fig. 2b, Tables 1 and S2).

*Invertebrate assemblage structure*

Nonmetric multidimensional scaling (NMDS) plots of invertebrate abundance in the experimental stream

revealed clear shifts in seasonal cycles and assemblage structure among years (Fig. 3). In the experimental stream, YR2 and YR3 winter assemblages more closely resembled YR1 autumn assemblages than YR1 winter assemblages. Similarly, YR3 spring assemblages were more similar to summer assemblages in YR1 than they were to YR1 spring assemblages (Fig. 3). In the reference stream, there were no clear differences in assemblage structure among years and the separation between years based on abundance was weak (Fig. 3). Analyses of community structure based on invertebrate abundance using PERMANOVA revealed a significant difference in community structure between the experimental and reference stream (main effect of stream; Table S3). Interannual and monthly variation in community structure was also prevalent in both streams (main effects of month and year; Table S3). Warming led to significant stream  $\times$  year and stream  $\times$  month interactions, indicating temporal differences in



**Fig. 2** Time series of mean ( $\pm$  SE); a) abundance, b) biomass, and c) community energy demand (CED) in the experimental stream (grey circles) and reference stream (open circles). The dashed vertical lines indicate the onset of experimental warming. Horizontal lines indicate annual mean values (solid horizontal lines = experimental, dashed horizontal lines = reference).

community structure between streams (Table S3). There was also a significant year  $\times$  month interaction, suggesting that assemblage structure for a given month was different among years (Table S3).

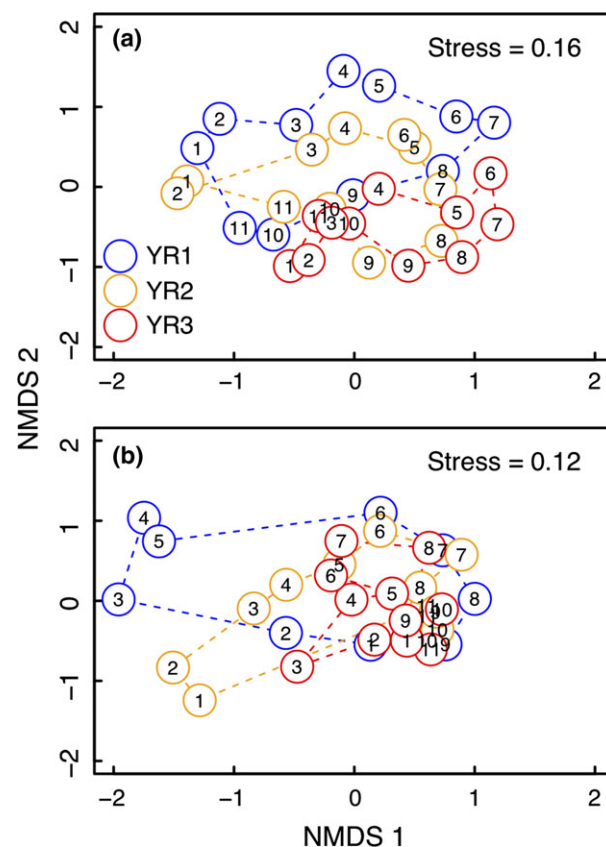
Experimental warming led to changes in the relative abundance and biomass of many taxa (Fig. 4, Tables S2, S4, and S5). A total of 42 invertebrate taxa were identified from both the experimental and reference stream over the course of the study. From YR1 to YR3, 31% of the taxa increased in abundance by at least 50%, while 26% decreased by at least 50%. Freshwater snails, in particular, showed dramatic increases in population size in response to warming (Fig. 4, Tables S2 and S4). Abundance of *Radix balthica*, for example, increased 30-fold from YR1 to YR3, while *Galba truncatula* increased in abundance from zero individuals in YR1 to 269 individuals  $m^{-2}$  by YR3 (Tables S2 and S4). The abundance of the filter-feeding blackfly *Simulium vittatum* increased fivefold from YR1 to YR3, while the abundance of the predatory dipteran *Limnophora riparia* increased approximately 14-fold over the same time period (Fig. 4, Tables S2 and S4). The predatory oligochaete *Chaetogaster diaphanous* also increased in abundance from zero in YR1 and YR2 to 397 individuals  $m^{-2}$  in YR3

**Table 1** Summary of generalized additive mixed modeling (GAMM) analyses to determine the effect of experimental warming on total invertebrate abundance, biomass, and community energy demand (CED). Significant stream  $\times$  year interactions indicate a significant effect of warming (significance: n.s.  $P > 0.10$ ; \* $P < 0.10$ ; \*\* $P < 0.05$ ; \*\*\* $P < 0.01$ )

	Estimate	SE	<i>t</i>	<i>P</i>
<b>Total abundance</b>				
Intercept	4.355	0.040	110.255	<0.001***
Stream (Ref)	-0.453	0.033	-13.536	<0.001***
YR2	-0.140	0.033	-4.214	<0.001***
YR3	-0.116	0.035	-3.354	<0.001***
Stream (Ref) $\times$ YR2	0.190	0.048	3.991	<0.001***
Stream (Ref) $\times$ YR3	0.254	0.048	5.349	<0.001***
<b>Total biomass</b>				
Intercept	3.017	0.041	74.190	<0.001***
Stream (Ref)	-0.432	0.058	-7.508	<0.001***
YR2	-0.040	0.057	-0.697	0.486n.s.
YR3	0.240	0.058	4.169	<0.001***
Stream (Ref) $\times$ YR2	0.077	0.082	0.941	0.348n.s.
Stream (Ref) $\times$ YR3	-0.027	0.082	-0.327	0.744n.s.
<b>CED</b>				
Intercept	3.304	0.042	78.609	<0.001***
Stream (Ref)	-0.410	0.047	-8.737	<0.001***
YR2	0.054	0.046	1.163	0.246n.s.
YR3	0.305	0.048	6.388	<0.001***
Stream (Ref) $\times$ YR2	0.283	0.065	4.333	<0.001***
Stream (Ref) $\times$ YR3	-0.119	0.066	-1.794	0.074*

in the experimental stream (Tables S2 and S4). Several taxa declined substantially in abundance. The abundance of the oligochaete *Nais communis* decreased by 73%, while the abundance of ostracods and nematodes decreased by 49% and 70%, respectively (Fig. 4, Tables S2 and S4). Of the 11 chironomid taxa recorded from both YR1 and YR3, eight declined in abundance from YR1 to YR3 in the experimental stream (Table S2). Although two novel species (*G. truncatula* and *C. diaphanous*) colonized the experimental stream during YR2 and YR3, no taxa were lost. Relative changes in biomass reflected the changes in abundance for most taxa (Fig. 4, Tables S2 and S5).

Changes in abundance and biomass were related to both thermal preference and body mass for taxa in the regional species pool (Figs 4 and 5a, b). We were able to estimate  $T_{pref}$  for 13 of the 18 taxa for which we had sufficient data (Fig. S2, Table S6). The temperature at

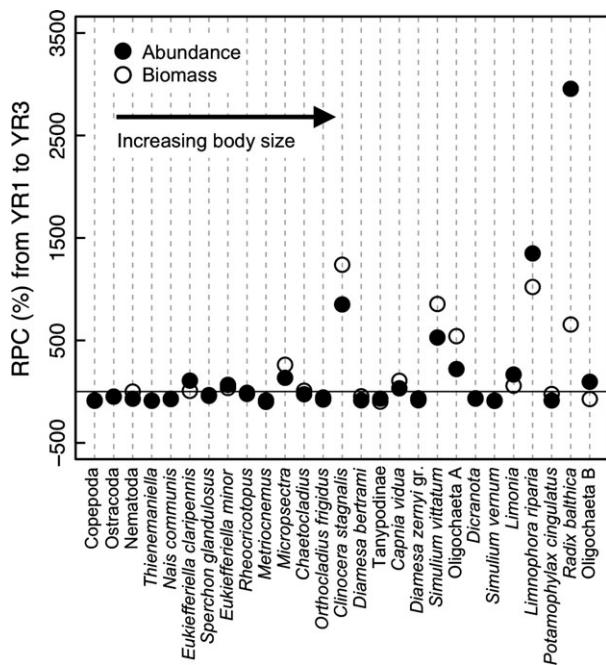


**Fig. 3** Nonmetric multidimensional scaling ordination plots based on Bray–Curtis similarities of  $\log(x + 1)$ -transformed invertebrate abundance data collected from the experimental stream (a) and reference stream (b). Symbol color indicates year (YR1 = blue, YR2 = orange, YR3 = red). Numbers inside the symbols correspond to the month during which samples were collected (1 = January, 2 = February, 3 = March, etc.).

which maximum abundance occurred ranged from 9.0 °C for the chironomid *Orthocladius frigidus* to 21.9 °C for the freshwater snail *R. balthica* (Table S6). The amplitude was found to be beyond the range in temperature data for several taxa; thus,  $T_{pref}$  could not be identified. However, Gaussian curves fit to the data indicated that abundance decreased with increasing temperature for those taxa (Fig. S2). Nevertheless, taxa with higher thermal preferences showed larger positive changes in both abundance and biomass in the experimental stream after warming (abundance  $P = 0.02$ ; biomass  $P = 0.03$ ; Fig. 5a). Furthermore, positive % changes in abundance between YR1 and YR3 were greater in larger taxa than smaller ones ( $P = 0.03$ ; Fig. 5b). Although % change in abundance increased with body mass, the relationship between % change in biomass and body mass was not significant ( $P = 0.10$ ; Fig. 5b).

### Community energy demand

Community energy demand (CED) followed seasonal patterns of biomass, with peaks during summer months in both streams (Fig. 2c). Despite a decrease in total abundance from YR1 to YR3, annual CED increased significantly in the experimental stream

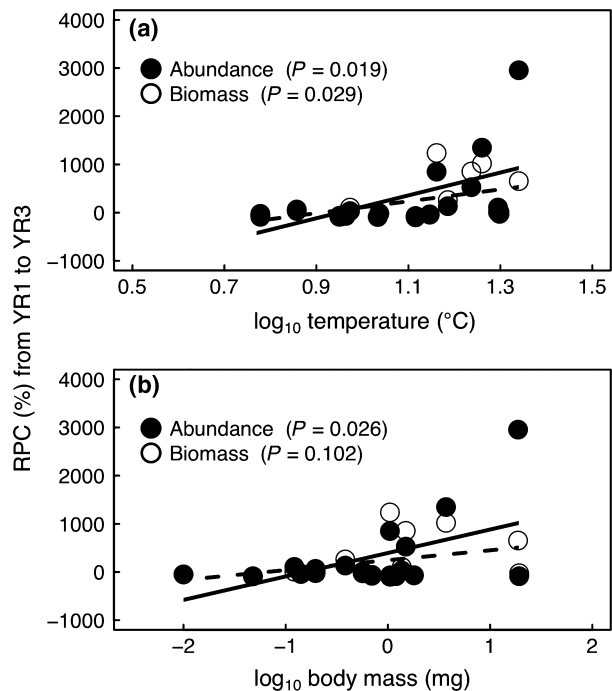


**Fig. 4** Relative percent change (RPC) in abundance (closed circles) and biomass (open circles) from YR1 to YR3 for 27 invertebrate taxa. Taxa are ordered by maximum mass attained during the study (smallest at the left to largest at the right). Only taxa that were present in both the experimental stream and the reference stream in YR1 and YR3 are shown.

relative to the reference stream from YR1 to YR3 (Fig. 6, Table 1). Annual CED increased 47% from YR1 to YR3 in the experimental stream, driven primarily by higher stream temperatures (Fig. 6). Annual CED declined by 32% from YR1 to YR3 in the reference stream, as a result of lower community abundance and mean annual temperature.

### Resource supply

Experimental warming had no effect on the standing crop of biofilm chlorophyll (Table S7). Mean annual standing crop of biofilm chlorophyll *a* in the reference stream ranged from 2.4 to 2.6  $\mu\text{g chl m}^{-2}$ , while in the experimental stream, it ranged from 5.6 to 5.8  $\mu\text{g chl m}^{-2}$ . Likewise, biofilm AFDM did not change as a result of warming (Table S7). The biomass of CBOM significantly increased in the experimental stream after warming (Table S7), but this was due to a large increase in biomass of the green filamentous alga *Ulva* (Fig. S3, Table S7). Mean annual biomass of *Ulva* increased approximately 20-fold in the experimental stream during warming (Fig. S3). Peak summer biomass of *Ulva*



**Fig. 5** Relationship between relative percent change (RPC) from YR1 to YR3 in abundance (black circles, solid regression line) and biomass (open circles, dashed regression line) and (a)  $\log_{10}(T_{pref})$  and (b)  $\log_{10}(\text{maximum body mass})$  in mg dry mass. Regression lines were fit using ordinary least-squares regression. In those taxa for which a mean temperature could not be calculated, the temperature at which peak abundance occurred was used.

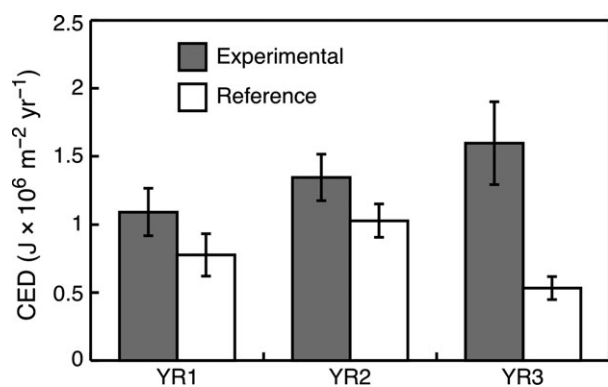


Fig. 6 Mean ( $\pm$  SE) annual community energy demand (CED) in the experimental and reference streams during the three years of the study.

increased from 7.2 g AFDM  $m^{-2}$  in YR1 to 79.7 g AFDM  $m^{-2}$  and 108.1 g AFDM  $m^{-2}$  in YR2 and YR3, respectively. In the reference stream, mean annual biomass of FBOM ranged from 21.8 to 28.7 g AFDM  $m^{-2}$  and from 17.9 to 20.2 g AFDM  $m^{-2}$  in the experimental stream. Warming had no effect on FBOM biomass (Table S7).

## Discussion

Our warming experiment resulted in both predicted and unanticipated community responses. While warming increased energy demand and reduced invertebrate abundance, population-level increases in warm-adapted taxa and declines in cold-water specialists together resulted in no effect on total biomass. This community-level response was largely driven by the diversity of thermal preferences among taxa in the regional species pool, which was related to body size. Higher stream temperatures also increased CED, which was presumably met by increased resource availability under warmed conditions (i.e., higher primary production).

The simplifying assumptions of the MTE framework predicts postwarming decreases in the abundance and total biomass of consumers because increased metabolic rates lead to greater *per capita* demands on resources. In essence, if resource supply remains constant and all resources are consumed, less consumer biomass can be supported (Brown *et al.*, 2004; Barneche *et al.*, 2014; Cross *et al.*, 2015). More specifically, community abundance and biomass should decline by  $\sim 9\%$  for every 1  $^{\circ}C$  increase in temperature, if community composition remains constant. Thus, the 3.8  $^{\circ}C$  increase in temperature in our study was predicted to decrease abundance and biomass by  $\sim 30\%$ . Consistent with this prediction, total invertebrate abundance decreased in the experimental stream by 36% (60% decrease relative to changes in the reference stream). However, relative

abundance of species changed with warming: many of the taxa that decreased in abundance following warming contributed little to community biomass (e.g., chironomids, oligochaetes, and microcrustaceans), while taxa that increased in abundance were mostly large-bodied (the freshwater snails *R. balthica* and *G. truncatula* and predatory dipterans *L. riparia* and *Clinocera stagnalis*). Together, these divergent responses resulted in no net change in community biomass.

Higher temperatures should result in higher metabolic demands by all organisms, regardless of size. If total abundance and the community size distribution had not changed, an increase in temperature by 4.3  $^{\circ}C$  (YR1 to YR3 in the experimental stream) would have increased CED by  $\sim 50\%$ . However, despite the 36% decline in abundance in the experimental stream, CED still increased 47% from YR1 to YR3. This increase in CED was partially driven by the increase in the relative abundances of larger taxa relative to smaller taxa during warming in the experimental stream. Larger taxa responded more positively to warming and had higher energy demands (Figs S4 and S5). Therefore, increases in CED were driven both by higher temperatures and increases in the absolute abundance of those warm-adapted taxa that occupied intermediate to large size classes.

Among the taxa that declined in abundance in the experimental stream, many had relatively narrow temperature ranges, with peak densities at cool temperatures ( $\leq 11^{\circ}C$ ). Declines of the small-bodied chironomids in particular were consistent with previous studies showing that taxa in the subfamilies Orthocladiinae and Diamesinae are cold-water stenotherms (Lindegaard, 1995; Woodward *et al.*, 2010). However, even some relatively large-bodied taxa were cold-adapted and subsequently declined in the experimental stream (e.g., the large caddisfly *Potamophylax cingulatus*). Postwarming increases in the abundance of other taxa were also related to thermal preferences. Many of the relatively large-bodied taxa in our streams were expected to be warm-adapted according to thermal preference data and other studies. For example, two taxa that increased in the experimental stream, the freshwater snail *R. balthica* and the blackfly *S. vittatum*, account for  $>83\%$  of total invertebrate abundance in three warm streams (summer temperatures  $>20^{\circ}C$ ) near our study sites (Woodward *et al.*, 2010). Overall, shifts in abundance with warming appeared more closely related to thermal preferences than to body size *per se*, although body size and thermal preference were positively linked (Fig. S6). Together, these relationships emphasize the importance of physiological traits in driving the population- and community-level responses to experimental warming in our study.



An important category of population-level responses to warming in the experimental stream was its invasion by new species (e.g., the snail *G. truncatula* and the predatory oligochaete *C. diaphanous*). Presumably, cool ambient temperatures had previously acted as a physiological filter, preventing these species from colonizing the experimental stream. Appearance of new, warm-adapted taxa therefore resulted from interactions among the relatively diverse thermal physiology of species in the regional species pool at our geothermally active study site, the close proximity of available colonists in nearby warm habitats, and dispersal processes that facilitated their exchange. Similar interactions are likely to operate at larger temporal and spatial scales as all natural ecosystems warm, making our geothermal study site and experimental manipulation a useful model for the proximate and ultimate drivers of community shifts under climate change (O’Gorman *et al.*, 2014).

Indirect responses to warming that are mediated by food-web interactions may also be important in driving community responses to warming. The basic MTE predictions that we tested assume no changes in resource supply (Brown *et al.*, 2004; Brown & Sibly, 2012; Cross *et al.*, 2015). Nevertheless, the increase in CED observed in the experimental stream would not have been possible without (i) increased resource supply or (ii) a situation in which all resources were not consumed prior to warming (i.e., resources were not limiting). Although there was no effect of warming on the biomass of the epilithic biofilm that formed the base of the grazing food web in the experimental stream, summer biomass of the filamentous green alga *Ulva* increased approximately 20-fold (Fig. S3) and gross primary production increased 170% (Hood *et al.*, unpublished manuscript), suggesting an overall increase in resource supply with experimental warming. Indirect effects at higher trophic levels within the food web are also likely. In our study, abundance of the predators *L. riparia* (Diptera: Muscidae) and *C. stagnalis* (Diptera: Empididae) increased markedly in the experimental stream following warming. The former species is a specialized predator of larval blackflies (Merritt & Wotton, 1988; Wotton & Merritt, 1988). Based on its dietary preference and thermal preference, increases in abundance of *L. riparia* may have been a direct result of warming or a numerical response to the increased abundance of its prey (Merritt & Wotton, 1988; Wotton & Merritt, 1988). However, it seems likely that a combination of direct and indirect factors is likely to drive most taxon-specific responses to warming.

Given the importance of body size in ecological networks (Peters, 1983; Woodward *et al.*, 2005), our results have implications for food-web stability and the routing of energy pathways. Aquatic food webs are often

highly size-structured (Sheldon *et al.*, 1972; Jennings & Mackinson, 2003), and any shifts in body-size distributions with warming are expected to influence trophic interactions (Woodward *et al.*, 2010). Previously, attention has focused on general trends toward smaller average body size with warming (Atkinson, 1995; Daufresne, 2009; Gardner *et al.*, 2011), but our results show that such reductions may not be universal because of the constraints of species composition, diversity of thermal preferences, and dispersal within regional species pools. Indeed, mean body size may even increase with warming (Chamailé-James *et al.*, 2006; *this study*), which is likely to have very different repercussions for food-web interactions. For instance, increased body size may be particularly important if larger taxa are also relatively invulnerable to predation, decoupling the production of predators and their prey (e.g., Power *et al.*, 2008; Davis *et al.*, 2010). At our fishless study site, the snails *R. balthica* and *G. truncatula* largely evade invertebrate predators; such taxa function as energy and nutrient sinks rather than resources for higher trophic levels.

In addition to increasing mean temperatures over much of the globe, climate warming will undoubtedly influence temperature variability as well (Thompson *et al.*, 2013; Wang & Dillon, 2014). While we successfully elevated the experimental stream’s temperature by an average of 3.8 °C during two years of warming, we also introduced some variation into the seasonal temperature cycle. Changes in mean temperatures and in annual temperature cycles could have profound effects on organism phenology, but any apparent responses were muted in our study. While the relatively weak temperature seasonality of the experimental stream did become more variable with warming, photoperiod and annual flow regime remained unaffected. Environmental factors such as current velocity and photoperiod have important influences on the timing and duration of insect development (Ward & Stanford, 1982). Thus, it is possible that factors other than temperature seasonality were more important in regulating invertebrate phenology in our study streams.

In summary, our experimental stream warming led to an unexpected increase in abundance of relatively large species at the expense of small taxa. Shifts in the abundance of these species appeared to be more related to thermal preferences than to body size *per se*. Declines in the abundance and biomass of small-bodied taxa with warming run counter to recently documented patterns, but are consistent with the particular set of traits in the regional species pool, their diversity in thermal preferences, and dispersal processes that operate at relatively large scales. Our findings highlight the importance of these factors as natural communities re-

assemble in response to warming. Such factors are often overlooked in tests of theory, the majority of which have used either population-based meta-analyses or small-scale mesocosm experiments and therefore could not incorporate all the processes that determine local community structure (Yvon-Durocher *et al.*, 2011; Dossena *et al.*, 2012). If climate warming leads to novel communities through losses and gains of species (Lurgi *et al.*, 2012) that are constrained by the dispersal and thermal physiology of regionally available species, prediction of community responses (e.g., changes in abundance or biomass), and how they relate to food web and ecosystem processes, may require combining general ecological theory with a functional understanding of regional species pools.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Table showing physical and chemical characteristics of the experimental and reference streams.

**Table S2.** Mean annual abundance and biomass of individual taxa.

**Table S3.** Table showing PERMANOVA results.

**Table S4.** Table showing results from SIMPER analysis on invertebrate abundance.

**Table S5.** Table showing results from SIMPER analysis on invertebrate biomass.

**Table S6.** Parameters and fit statistics for Gaussian curves fitted to abundance data across a range of temperatures for each taxon.

**Table S7.** Table showing summary of GAMM models to determine the effect of warming on basal resources.

**Figure S1.** Photograph of heat exchanger used to warm the experimental stream.

**Figure S2.** Gaussian distributions of thermal preferences for individual taxa.

**Figure S3.** Photographs and time series plot of *Ulva* biomass in the experimental stream.

**Figure S4.** Time series of energy demand by body size in the experimental stream.

**Figure S5.** Time series of energy demand by body size in the reference stream

**Figure S6.** Relationship between thermal preference and body size.