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Temperature-driven selection on metabolic traits increases the strength of an algal–grazer interaction in naturally warmed streams

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Abstract

Trophic interactions are important determinants of the structure and functioning of ecosystems. Because the metabolism and consumption rates of ectotherms increase sharply with temperature, there are major concerns that global warming will increase the strength of trophic interactions, destabilizing food webs, and altering ecosystem structure and function. We used geothermally warmed streams that span an 11°C temperature gradient to investigate the interplay between temperature-driven selection on traits related to metabolism and resource acquisition, and the interaction strength between the keystone gastropod grazer, *Radix balthica*, and a common algal resource. Populations from a warm stream (~28°C) had higher maximal metabolic rates and optimal temperatures than their counterparts from a cold stream (~17°C). We found that metabolic rates of the population originating from the warmer stream were higher across all measurement temperatures. A reciprocal transplant experiment demonstrated that the interaction strengths between the grazer and its algal resource were highest for both populations when transplanted into the warm stream. In line with the thermal dependence of respiration, interaction strengths involving grazers from the warm stream were always higher than those with grazers from the cold stream. These results imply that increases in metabolism and resource consumption mediated by the direct, thermodynamic effects of higher temperatures on physiological rates are not mitigated by metabolic compensation in the long term, and suggest that warming could increase the strength of algal–grazer interactions with likely knock-on effects for the biodiversity and productivity of aquatic ecosystems.

KEYWORDS

consumer–resource interactions, global warming, interaction strength, metabolism, thermal adaptation

1 | INTRODUCTION

The strength of consumer–resource interactions (e.g. the effect of a consumer on the population density of its prey) plays a critical role

#Student Research Team members are present in the Appendix.

in shaping the stability of food webs (May, 1973; McCann, Hastings, & Huxel, 1998; Otto, Rall, & Brose, 2007; Paine, 1980). Grazing is an important class of consumer–resource interaction, determining the flux of energy and materials from autotrophs to heterotrophs. There are currently major concerns that global warming will increase the impact of grazers on algal or plant communities because the ingestion and respiration rates of heterotrophs tend to increase more rapidly with rising temperatures than rates of photosynthesis and growth in autotrophs (Gilbert et al., 2014; O'Connor, 2009; West & Post, 2016). Stronger interactions have the potential to destabilize food webs and consequently, warming induced increases in interaction strengths could have fundamental implications for ecosystem structure and function. For example, elevated grazing rates in aquatic ecosystems, driven by the mismatch in thermal sensitivity between autotrophs and heterotrophs, are hypothesized as a key driver of projected declines in aquatic primary production over the 21st century in models of ocean biogeochemistry (Laufkötter et al., 2015).

The effects of temperature on metabolic rates and traits associated with consumer–resource interactions (e.g. attack rates, handling times) often follow characteristic unimodal thermal response curves, where rates increase exponentially to an optimum and decline rapidly thereafter (Dell, Pawar, & Savage, 2011, 2014; Englund, Öhlund, Hein, & Diehl, 2011; Gilbert et al., 2014; Rall et al., 2012). Integrating thermal responses for metabolism and interaction traits with dynamical models of consumer–resource interactions offers a promising framework for predicting food web responses to global warming (Binzer, Guill, Rall, & Brose, 2015; Shurin, Clasen, Greig, Kratina, & Thompson, 2012; Vasseur & McCann, 2005). However, thermal response curves are often flexible, and can shift when organisms are exposed to novel thermal environments, both via phenotypic plasticity, where organisms change phenotypic characteristics rapidly and with no underlying *heritable* genetic change (West-Eberhard, 2003), and adaptive evolution, where organisms respond to changes in the environment through heritable genetic change over many generations, resulting in better adapted phenotypes (Angilletta, Wilson, Navas, & James, 2003; Deutsch et al., 2008; Kingsolver & Huey, 2008; Kingsolver, Ragland, & Shlichta, 2004). Consequently, plasticity and evolution have the potential to modulate the effects of rising temperatures on the strength of species interactions (Sentis, Morisson, & Boukal, 2015). For example, if metabolic rates are down-regulated after long-term exposure to higher temperatures (Addo-Bediako, Chown, & Gaston, 2000), then compensatory metabolic responses to warming (e.g. Padfield et al., 2017) could mitigate predicted increases in consumer–resource interaction strength. How these long-term responses to warming affect rates of metabolism and in turn, the strength of consumer–resource interactions, are largely unknown, limiting our ability to predict how trophic interactions will change in response to warming in the long term.

There is evidence from studies across naturally occurring thermal gradients over large spatial scales, that local thermal adaptation can play an important role in shaping the strength of species interactions (Barton, 2011; De Block, Pauwels, Van Den Broeck, De Meester, & Stoks, 2012). While these studies provide important insights into how consumer–resource interactions are shaped by evolution across thermal gradients (Fukami & Wardle, 2005), their usefulness for understanding responses to rapid climate warming might be limited because other factors, such as day length, light intensity and precipitation, tend to be confounded with temperature along such broad scale spatial gradients. Furthermore, the timescales over which local adaptation has occurred in such broad scale studies could be much longer than the rapid evolutionary change required to keep pace with climate warming (Hoffmann & Sgrò, 2011; Loarie et al., 2009). Here, we investigate how temperature-driven selection on traits that determine the thermal responses of metabolism and resource acquisition affect the strength of a keystone grazing interaction (the gastropod *Radix balthica*, which grazes algal biofilms in streams) in naturally warmed Icelandic geothermal streams spanning a gradient of 11°C. Critically, temperature is the main abiotic factor that varies among streams in the catchment and is not correlated with pH, conductivity or inorganic nutrient concentrations (see Table 1, also Padfield et al., 2017). These streams are thought to have been subject to geothermal heating for at least the last century (O'Gorman et al., 2012). This system therefore provides the opportunity to investigate how long-term differences in temperature between otherwise similar sites shape the expression of metabolic traits and the subsequent impact of any temperature-driven selection on species interactions in a natural system. Specifically, we test the hypothesis that long-term differences in temperature drive selection for metabolic traits that dampen the direct effects of warming on metabolic rates and the strength of consumer–resource interactions. We predict that (i) snails from warm streams will have down-regulated rates of metabolism when normalized to a reference temperature, and (ii) consequently, the effects of warming on algal–grazer interaction strengths involving snails from warm streams will be attenuated relative to expectations based on the direct effects of rising temperature alone.

TABLE 1 Physical and chemical characteristics of the streams. Temperature data were collected over a 3-day period. All other parameters were collected on the first day of the experiment. Temperature data are displayed as means ±1 *SD*.

Parameter	Stream 5	Stream 11
Average temperature (°C, 5 days)	17.5 ± 4.5	28.3 ± 1.3
pH	7.63	7.17
Conductivity (μS)	273.6	235.7
NO_2 (μmol/L)	0.22	0.24
NO_3 (μmol/L)	0.57	0.29
NH_4 (μmol/L)	0.17	0.19
PO_4 (μmol/L)	0.27	0.35
Velocity (m/s)	0.10	0.15
Stream depth (m)	0.041	0.042

2 | MATERIALS AND METHODS

2.1 | Study site

The streams are located North of the Hveragerði valley, in the south east of the Hengil high temperature geothermal field, Iceland (N64° 0′ 2.944″ W21° 11′ 17.451″) and consist of a catchment of 11 streams spanning a temperature gradient of approximately 20°C (see Figures 1 and S1). Two streams, stream 5 (17.5°C ± 4.5°C, hereafter "cold stream") and stream 11A (28.3°C ± 1.3°C, hereafter "warm stream," see Table 1 for a comparison of other chemical and physical parameters), were chosen for experiments due to their close proximity, the large temperature differential and similar abundances of the keystone grazer, *R. balthica*. The grazer plays an important functional role in geothermal stream ecosystems, where grazer biomass as well as grazing rates are strongly influenced by temperature (O'Gorman et al., 2012). The two streams are similar in all other measured physical and chemical characteristics, including stream velocity at the sampling location, but differ in average temperature by 11°C (see Table 1), and hence present an opportunity to investigate how the effects of long-term differences in temperature shape consumer–resource interactions. The experiment was carried out from 26 May 2016 to 2 June 2016, with a pilot study testing the general experimental set-up conducted from 1 June 2015 to 7 June 2015.

2.2 | Grazer metabolism

To quantify whether the different thermal regimes in the two adjacent streams resulted in divergence in metabolic traits of mature *R. balthica* (based on mass and shell length), we measured the adult responses of respiration to a broad gradient in temperature. For the metabolic measurements, we collected 33 individuals of similar mass and length (average mass of snails from cold stream 0.087 ± 0.014 g, average mass of snails from warm stream 0.098 ± 0.016, both ±1 SEM, ANOVA: $F_{1,61}$, p = 2.15, see Table S1 and also compare Figure S2 for mass of another 205 randomly collected snails) from each stream, which were cleaned from any algal debris to avoid carry-over of a food source into the tank or

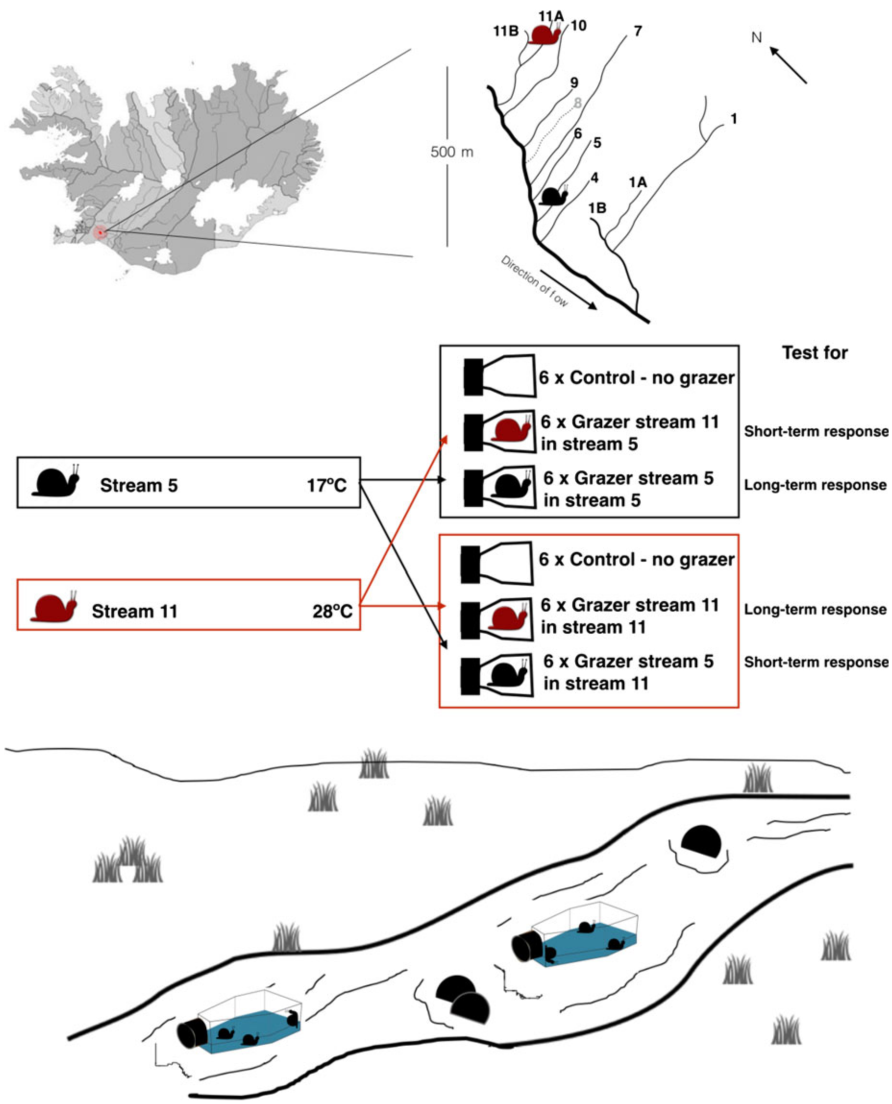

FIGURE 1 Map and experimental set-up. Top panel: The catchment area, with streams used in this experiment indicated by black (for the colder stream 5 with 17.5°C ± 4.5°C) and grey (for the warmer stream 11A with 28.3°C ± 1.3°C) snail icons. Middle panel: Schematic overview of experimental set-up for the grazing experiment. Lower panel: Schematic overview of microcosms in stream. Tent pegs and cable ties used for fixing the microcosms in place have been omitted from the schematic. See Figure S1 for a photograph [Colour figure can be viewed at wileyonlinelibrary.com]

subsequent respiratory measurements on the oxygen electrode. The snails were kept for 48 hr in aerated tanks at the average stream temperature of origin and in the absence of a food source to minimize any potential effects of differences in food quantity or quality between streams. Respiration was quantified as the rate of oxygen consumption in a Clark-Type oxygen electrode (Oxylab, Hansatech™), measured between 4 and 44°C in 4°C increments (11 temperatures in total) within a day. At each temperature, respiration was measured for three individuals, and a different set of individuals was measured at each temperature (i.e. each animal was only subjected to a single assay). Individuals were allowed 15 min at the assay temperature prior to the measurements. The subsequent thermal responses of respiration were quantified using a modification of the Sharpe–Schoolfield equation (see Schoolfield, Sharpe, & Magnuson, 1981 and Sharpe & DeMichele, 1977 for the original equation):

$$\ln(b(T)) = E_a\left(\frac{1}{kT_c} - \frac{1}{kT}\right) + \ln(b(T_c)) + \alpha \ln(M_i) - \ln\left(1 + e^{E_h\left(\frac{1}{kT_h} - \frac{1}{kT}\right)}\right) \quad (1)$$

where $b(T)$ is the *per capita* metabolic rate (μmol O_2 L^{-1} hr^{-1}) at temperature T in Kelvin (K), k is Boltzmann's constant (8.62×10^{-5} eV/K), E_a is an apparent activation energy (in eV) for the metabolic process, ln ($b(T_c)$) is the rate of metabolism normalized to an arbitrary reference temperature, T_c = 18°C, where no low or high temperature inactivation is experienced. M_i is the mass (g) of an individual i, α is the allometric scaling exponent that characterizes the power-law relation of mass and metabolic rate (Brown, Gillooly, Allen, Savage, & West, 2004). E_h characterizes temperature-induced inactivation of enzyme kinetics above T_h where half the enzymes are rendered non-functional. Differentiating Equation (1) and solving for the global maxima yields an expression for the optimum temperature

$$T_{opt} = \frac{E_h T_h}{E_h + kT_h \ln\left(\frac{E_h}{E_a - 1}\right)} \quad (2)$$

Equation (1) differs from the Sharpe–Schoolfield equation (Schoolfield et al., 1981; Sharpe & DeMichele, 1977) in a number of ways. First, we account for the power-law relation between body mass and metabolic rate, M^{α} (Brown et al., 2004). Second, we exclude parameters from Equation (1) used to characterize low-temperature inactivation due to insufficient data to quantify this phenomenon in our analysis. Third, rather than characterize temperature effects below T_{opt} using the Eyring (1935) relation, $\left(\frac{T}{T_c}\right)e^{E_a\left(\frac{1}{kT_c} - \frac{1}{kT}\right)}$, we instead use the simpler Boltzmann factor, $e^{E_a\left(\frac{1}{kT_c} - \frac{1}{kT}\right)}$. This simplification enables an explicit solution for T_{opt} (Equation 2) and facilitates more direct comparison with previous work on the temperature dependence of metabolism using metabolic theory (e.g. Allen, Gillooly, & Brown,2005; Brown et al., 2004; Gillooly, 2001; Savage, Gillooly, Brown, West, & Charnov, 2015).

The parameters, ln $b(T_c)$, α, E_a, E_h, T_h, and T_{opt}, in Equations (1) and (2) represent traits characterizing the metabolic thermal response that we expect to be under selection in *R. balthica* inhabiting the hot and cold streams. We tested for differences in each of the parameters between the populations of *R. balthica* by fitting the respiration data to Equation (1) using generalized non-linear least squares regression (within the "gnls" function in the "nlme" package for R, package version 3.1-128) and including "origin" as a two-level factor (i.e. "cold" and "warm" stream). We tested for differences between populations for each parameter by sequentially removing the effect of "origin" on each parameter and comparing the Akaike Information Criterion for small sample sizes (AICc) for all possible models (see Tables S1 and S3) using the "aictab" and "modavg" functions from the AICcmodavg package (package version 2.1-0). The model chosen for further exploration was that with the lowest (AICc) value. Model averaging was carried out when models fell within 2 AICc units of each other, and the conditional averages of the parameters were used for curve fitting and interpretation (see also Table 2). The relative importance of the fixed factors in the averaged model was determined using the sum of their relative weights.

2.3 | Reciprocal transplant experiment

We carried out a reciprocal transplant experiment to determine how long-term differences in temperature and the resultant impacts on metabolic traits affect the strength of algal–grazer interactions. We achieved this by placing adult snails from each population in microcosms consisting of a tissue culture flask on which diatom biofilms had been established. There was no significant difference in size or mass of the snails chosen for the reciprocal transplant experiment. Snails from the cold stream weighed approximately 0.83 ± 0.08 g, and snails from the warm stream, 0.89 ± 0.07 g (with no significant difference between streams, see also Table S4, ANOVA $F_{1,65}$ = 0.81, p = 0.76). Diatoms of the genera, *Acnanthes*, *Nitzschia*, *Navicula* and *Gomphonema* are common in streams across the Hengill volcanic

TABLE 2 Parameter estimates and output from the best fitting gnls model to the thermal response curves of respiration rates. Where differences in parameters between streams where detected, values for both the warm (W) and the cold (C) stream are given. Parameter estimates are taken from the averaged generalised linear models along with their standard errors (±1 *SEM*). C, cold stream; W, warm stream. See supporting information for details on model selection and information on AICc scores for all possible models. Here, the model average of the conditional average output for the four best models (within 2 AICc units of each other) are displayed

Non-linear mixed model output for respiration rates (*R*)		
Treatment effect on	Estimate	±1 *SEM*
E_a	C: 0.96	0.05
ln $R(T_c)$	**C: 1.77** **W: 2.04**	**0.15** **0.12**
E_h	**C: 5.01** **W: 3.16**	**0.97** **0.96**
T_h [K] **(°C)**	**C: 307.16 (34.01)** **W: 314.15 (41.00)**	**0.94** **1.69** **0.78**
α	0.36	0.03

area (Gudmundsdottir et al., 2013) and were ordered from culture collections (Culture collection of algae and protozoa and Sciento) and grown in the laboratory in mixed assemblages to yield common resource for testing the effects of temperature and local adaptation on grazing. The diatom assemblages were inoculated into Corning plastic translucent flasks (maximum volume 1 L) with 20 mL COMBO medium (Kilham, Kreeger, Lynn, Goulden, & Herrera, 1998), and brought to a salinity of 5–10 (equivalent to approximately 5–10 g salts/kg water) to match the slightly elevated salinity and conductivity found in these thermal stream environments (Gudmundsdottir et al., 2013). The flasks were turned onto their sides to allow for a larger area of biofilm growth on the base (~60 cm^2 in total per flask) and the algal communities were left to grow for 14 days prior to the experiment. After 14 days, all flasks had substantial biofilm development on the base and were used as microcosms for the in situ reciprocal transplant experiment. Analysis of control flasks (no grazer) showed that growth of the diatom lawn *per se* did not differ significantly for flasks placed in hot or cold streams (Figure S3, one-way ANOVA $F_{1,10} = 1.28$, $p = 0.26$). Thus, any changes to the biofilm biomass in the experiment can be attributed to the per capita effects of the grazer.

The experiment consisted of three treatments (each with six replicate microcosms placed in each of the two streams): (i) a control microcosm in which a biofilm was present and no *R. balthica* were added, (ii) an "origin" treatment in which *R. balthica* that were resident in the stream were added to microcosms and (iii) a "transplanted" treatment in which *R. balthica* that were from the adjacent stream were added to microcosms. *Radix balthica* individuals used for the reciprocal transplant experiment were collected from the two streams prior to the experiment and were starved for 48 hr in the laboratory in aerated tanks at the average temperature of the stream of origin. Microcosms were assembled by adding three snails of similar body dimensions (0.35 ± 0.03 g of *R. balthica* mass reported as blotted fresh weight throughout) and 100 mL of 0.4 μm filtered water from the stream in which the microcosm was to be placed. This resulted in a grazer density of 5 individuals/m^2, which was comparable to the average in situ density in the streams (see Figure S4, no significant difference in in situ density between the two streams: one-way ANOVA: $F_{1,66,}$ $p = 0.54$). This design was preferred to a set-up with each microcosm holding a single grazer, which attempt to exclude the effects of mutual interference on feeding behaviour (e.g. Lang, Rall, & Brose, 2011; Rall, Vucic-Pestic, Ehnes, Emmerson, & Brose, 2010; Skalski & Gilliam, 2001; Vucic-Pestic, Ehnes, & Rall, 2011) because (i) the experimental densities are representative of natural conditions; and (ii) the consumption rates of a single individual were insufficient to detect a significant change in algal biomass. The microcosms were submerged in each stream facing downstream so that the stream water controlled the ambient temperature of the microcosms but did not fill the flasks further with water or organic matter (see Figure 1 for conceptual graphic). The snails were left to graze for 48 hr. We observed no grazer mortality over the experimental period. Sampling of another 206 snails from each stream confirmed no significant difference in average snail size in the cold and warm stream at this time of the year (see Figure S2, one-way ANOVA: $F_{1,408} = 0.15$, $p = 0.7$).

2.4 | Interaction strength

At the end of the experiment, algal biomass in each of the microcosms was quantified via methanol chlorophyll extraction modified from Holm-Hansen and Riemann (1978). Here, the walls of the microcosms were scrubbed until all biofilm particles were in suspension. The solution was filtered onto a 0.4 μm GF/F filter, which was then ground in methanol for 5 min. The samples were centrifuged at 6,800 *g* for 15 min and the absorbance of the supernatant was measured at 632, 665 and 750 nm. Total chlorophyll content in μg/mL was then calculated as described in Holm-Hansen and Riemann (1978). The *per capita* interaction strength in each microcosm was then estimated by calculating the dynamic index (DI, see also (Berlow et al., 2004) for a technically similar set-up): Note that in Berlow et al. 2004, *N* is for the grazed, and *D* for the ungrazed habitats. We chose to invert this ratio for a more intuitive comparison of metabolic rate and grazing data.

$$\mathrm{DI} = \frac{\ln\left(\frac{N}{D}\right)}{Yt} \tag{3}$$

here DI is the dynamic index (gChl gC^{-1} hr^{-1}), *N* is the total chlorophyll (sum of Chl *a* + Chl *c*) content of control, *D* is the total chlorophyll in the grazed microcosm, *Y* is the grazer biomass (g C), and *t* is time in hours. Snail blotted wet weight was converted to carbon mass (in grams) using conversion factors that assume dry weight to be 7.5% of the blotted wet weight (Ricciardi & Bourget, 1998) and a carbon content of 22% dry weight (Burgmer, Reiss, Wickham, & Hillebrand, 2010).

We carried out two analyses using the data from the reciprocal transplant experiment. The first analysis used a generalized linear model (GLM), with "interaction strength" as the response variable and "origin" ("cold" or "warm" stream) and "transplant temperature" (17.5 and 28.3°C) as potentially interacting factors. We used this analysis to determine (i) whether interaction strengths differed between snails that originated from the warm or cold streams (e.g. a main effect of "origin"); (ii) whether interaction strengths were temperature-dependent (e.g. a main effect of "temperature") and (iii) whether the temperature dependence of interaction strength differed between the snails from the cold and warm streams (e.g. interaction between "origin" and "temperature").

We examined the relative contributions of short- and long-term responses to warming: The design of the reciprocal transplant experiment enabled us to disentangle short-term temperature responses attributable to acclimation (e.g. responses to the temperature in the "transplanted" stream) from those reflecting processes operating over longer, timescales (e.g. adaptation to the stream of "origin"). Note that these "long-term" effects, which we call "adaptation," could reflect strict genetic microevolution (e.g. resulting in divergent genotypes among populations) or they could represent non-genetic effects of the different temperature regimes that manifest over ontogenetic development, but are nevertheless adaptive (Bonduriansky, Crean, & Day, 2011). In the second GLM, we included "interaction strength" as the response variable and "timescale" ("short" or "long") and "transplant temperature" (17.5 and 28.3°C) as potentially interacting factors. Here, "short-term" temperature responses were characterized as the change in interaction strength between the stream of origin and the transplant stream. By contrast, the "long-term" temperature response was characterized as the change in interaction strength comparing measurements made only when the snails were in their stream of origin. For better comparison of the steepness of the respiration reaction norms, we re-express the transplant temperature data as Boltzmann temperatures $\left(\frac{1}{kT_c} - \frac{1}{kT}\right)$ so that the coefficients of the model yield activation energies in units of eV (see Equation 1). In this analysis, a significant interaction between "transplant temperature" and "timescale" would demonstrate that the temperature dependence of interaction strength differs between the "short term" (E_{short}, change in interaction strength between the stream of origin and the transplant stream, see also Figure 3), and "long term" (E_{long}, i.e. change in interaction strength comparing measurements made only when the snails were in their stream of origin, see also Figure 3). We assume that E_{short} captures rapid physiological plasticity (e.g. acclimation) in interaction strength in response to a change in temperature and E_{long} captures processes operating over longer timescales—for example, genetic microevolution and non-genetic developmental effects. Consequently, the component of the temperature sensitivity attributable to "adaptation" (recognizing that this might be genetically and/or developmentally determined) is given by $E_{adapt} = E_{long} - E_{short}$.

3 | RESULTS

3.1 | Metabolic thermal response curves

The allometric scaling coefficient, α, and the apparent activation energy, E_a, were consistent between the populations of *R. balthica* from the cold and warm streams (see Table 2 for model comparison and estimated parameter values). The temperature normalized rate of respiration, ln $b(T_c)$, and T_h (the temperature at which respiration was 50% inactivated) were both higher in the population of *R. balthica* from the warm stream. Because the optimum temperature, T_{opt}, depends strongly on T_h (see Equation 2), T_{opt} was higher in *R. balthica* from the warmer stream (T_{opt} warm = 38.25 ± 0.6°C; T_{opt} cold = 33.05 ± 1.5°C). As ln $b(T_c)$ and T_{opt} were both higher, the warm populations of *R. balthica* had elevated metabolic rates across the full range of measurement temperatures (Figure 2).

3.2 | Local adaptation of interaction strength

Interaction strength increased with elevated transplant temperature for the populations of *R. balthica* from both the warm and the cold streams (Figure 3; main effect of "transplant temperature" GLM $t_{1,21} = 2.56$; $p < 0.01$). Furthermore, interaction strengths were consistently higher for the populations of *R. balthica* from the warm stream in both transplant temperatures (Figure 3; GLM main effect of "origin" $t_{1,121} = 2.92$; $p < 0.005$). These findings are consistent with the higher respiration rates observed in the warm population (Figure 2) and highlight the association between metabolism and interaction strength.

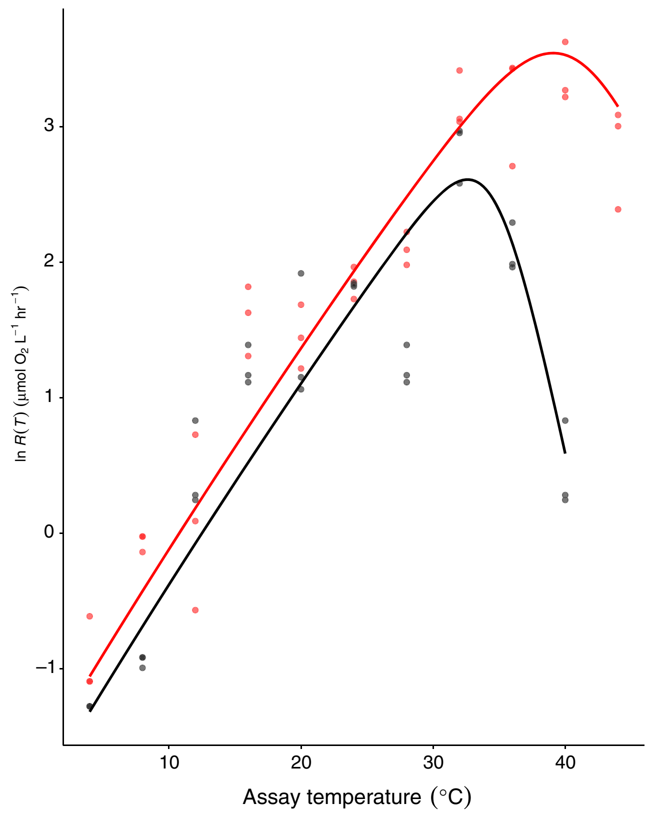

FIGURE 2 Thermal response curves for respiration. Thermal response curves of respiration rates in μmol O_2 L^{-1} hr^{-1} as a function of increasing temperature for populations of the snail *Radix balthica* from the cold (black, solid line, circles) and warm (grey, dotted line) stream. Lines are derived from fitting a modified Sharpe–Schoolfield equation (see Methods) to the rate data. Snails from the warm stream have higher temperature normalised metabolic rates (ln $R(T_c)$, with T_c = 18°C) and have higher optimal temperatures (T_{opt}), than snails from the cold stream. The inactivation energy (E_h) is lower in snails from the warm stream, resulting in a curve that is both broader and elevated in comparison to the thermal response curve of respiration for snails from the cold stream [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Disentangling the short- and long-term effects of warming on interaction strengths

Our experimental design enabled us to compare temperature sensitivities that capture short-term thermal acclimation (e.g. changes in interaction strength in response to the reciprocal transplant) as well as the long-term temperature sensitivity, which also includes effects of local adaptation (e.g. changes in rates between warm and cold populations quantified in the stream of origin). We found that interaction strength increased with temperature in both the short term

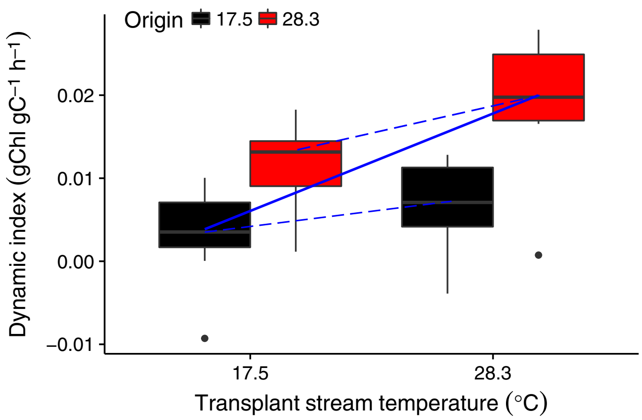

FIGURE 3 Long-term and short-term effects of stream temperature on interaction strength. Long-term and short-term effects of temperature in interaction strength measured via the dynamic index in units of chlorophyll consumed per hour. Populations originating from the warm stream (grey) have stronger interaction strength indices than snails from the colder stream (black) in all environments and the highest dynamic index overall was found for snails from the warm stream in their original environment. Interaction strength increased with temperature both in the short term (E_{short}, dashed lines) and in the long term (E_{long}, solid line, comparing dynamic indexes of snails in their temperatures of origin), with E_{long} significantly greater than E_{short} [Colour figure can be viewed at wileyonlinelibrary.com]

and the long term (Figure 3). However, the magnitude of the temperature response was significantly larger in the long term (Figure 3; interaction between "transplant temperature" and "timescale" on interaction strength; $GLM_{1,18} = -2.91$; $p < 0.05$), where the average E_{short} was 0.46 eV, while E_{long} was significantly higher at 0.99 eV. This divergence between the short- and long-term temperature sensitivities implies a non-trivial contribution of adaptation in amplifying the effects of temperature on interaction strength in situ, with the contribution of E_{adapt} of 0.51 and 0.53 eV in the cold and warm adapted populations, respectively.

4 | DISCUSSION

Understanding how global warming will affect the strength of consumer–resource interactions and the stability of aquatic food webs is a fundamental challenge in ecology. Tackling this challenge requires insight on the short-term effects of temperature on metabolism and interaction traits and on how they are modulated by evolutionary and developmental processes over longer timescales. There is evidence from terrestrial (Barton, 2011; Brose et al., 2012; Rall et al., 2010; Vucic-Pestic et al., 2011), freshwater (Kratina, Greig, & Thompson, 2012) and marine ecosystems (Sanford, 1999), that warming is likely to increase the strength of consumer–resource interactions, at least in the short term, owing to the exponential effects of temperature on the consumption rates of mobile ectothermic consumers (Dell et al., 2014; Gilbert et al., 2014). What is less clear, however, is how long-term responses to rising temperatures will modulate the direct effects of warming on species interactions. Space-for-time substitutions across broad spatial scales indicate that local adaptation to different thermal regimes can play an important role in shaping species interactions, often compensating for the direct effects of temperature on interaction traits (Barton, 2011; De Block et al., 2012). Here, we build on this work by investigating the effects of temperature and local adaptation on the interaction between the gastropod grazer, *R. balthica*, and its algal resource. Our study contributes novel insights in a number of ways. First, we explore patterns of local adaptation over a relatively small spatial scale (m as opposed to km). The two streams in our experiment are separated by approximately 500 m but differ in temperature by 11°C. Dispersal, gene flow and genetic divergence among populations in this species are strongly related to geographic distance (Johansson, Quintela, & Laurila, 2016), and *R. balthica* are known to disperse slowly, but regularly over short distances (Hoffman et al., 2006; Kappes & Haase, 2012), but rarely over long distances, where such events are usually associated with passive dispersal, for example, via association with vertebrates (Bolotov et al., 2017; Hansson & Akesson, 2014). Thus, our study, over a relatively small spatial scale (500 m), provides insight into how metabolic and resource acquisition traits in closely related natural populations have diverged in response to warming and is therefore directly relevant for understanding the effects of rapid climate change (Keller, Alexander, Holderegger, & Edwards, 2013; Merilä & Hendry, 2014; Richter-Boix, Teplitsky, Rogell, & Laurila, 2010). Second, we quantified the effects of temperature on both metabolic and consumption rates to determine how temperature-driven selection on key traits shape the effects of long-term warming on the strength of consumer–resource interactions.

We found significant variation in the thermal response curves for respiration between the populations of *R. balthica* from the warm and cold streams. The optimum temperature (T_{opt}) for respiration was higher in the warm population (i.e. metabolic rates peaked at higher temperatures). Furthermore, the inactivation energy (E_h) was lower in the warm population, indicating that declines in the rate of respiration after the optimum (i.e. at high temperatures) were less pronounced than in grazers from the cold stream, where metabolic rates peaked at lower temperatures and declined markedly at temperatures above T_{opt}. These divergences indicate that the different thermal regimes in these streams have selected for different metabolic traits in warm and cold populations of *R. balthica*. Whilst the higher T_{opt} and lower E_h in the warm population were in line with expectations assuming local thermal adaptation, we found no evidence that metabolic performance at high temperature was traded-off against performance at low temperature. Instead, metabolic rates were higher for *R. balthica* from the warm stream across all measurement temperatures. These results are in broad agreement with the "hotter is better" hypothesis, which proposes that maximal performance of organisms with higher optimal temperatures should be greater than those with lower optimum temperatures because of the thermodynamic constraints imposed by high temperatures on enzyme kinetics (Angilletta, Huey, & Frazier, 2010; Huey &

Kingsolver, 1993; Kingsolver et al., 2004; Knies, Kingsolver, & Burch, 2009). Indeed, maximal respiration rates in the population from the warm stream were greater than those from the cool (ln(R) warm stream: 3.39 ± 0.14 μmol O_2 L^{-1} hr^{-1}, and cool stream: 2.54 ± 0.26 μmol O_2 L^{-1} hr^{-1}, both ±1 *SEM*). The lower E_h (i.e. the steepness of the decline of the thermal reaction norm past the optimum), and higher ln $b(T_c)$, that is, the rate of respiration normalized to 18°C, in the warm population also meant that the thermal response curve for *R. balthica* from the warm stream was broader. In agreement with previous work (e.g. on bacteriophages Knies et al., 2009), our data for the gastropod *R. balthica* indicate that adaptation to higher temperatures resulted in both greater maximal metabolic performance and a broader metabolic thermal reaction norm.

The general patterns observed in the metabolic traits were also reflected in the effects of temperature on interaction strength. Interaction strength was higher for individuals placed in the warm stream, irrespective of their stream of origin. These findings suggest that elevated temperatures increase consumption rates though the effects of temperature on respiratory physiology, but local adaptation to warmer environments also results in a correlated increase in metabolism and interaction strength at low temperature. This may have important wider implications for the effects of warming on the structure, functioning and stability of aquatic food webs (Dell et al., 2014; Fussmann, Schwarzmüller, Brose, Jousset, & Rall, 2014; Gilbert et al., 2014; O'Connor, Gilbert, & Brown, 2011; Rall et al., 2010; Vucic-Pestic et al., 2011). If long-term responses to increasing temperature give rise to higher maximal rates of metabolism and consumption as well as elevating rates at lower temperatures, then the effects of warming on the strength of consumer–resource interactions in the long term could be greater than previously anticipated (Gilbert et al., 2014). Indeed, work on experimental warming of aquatic ecosystems has shown that increases in the strength of top-down control can have profound effects on community structure and ecosystem processes (Burgmer & Hillebrand, 2011; Kratina et al., 2012; Yvon-Durocher et al., 2015). Elevated grazing rates at warmer temperatures can have a wide range of impacts in aquatic systems, with evidence for both increases (Yvon-Durocher et al., 2015) and decreases (Burgmer & Hillebrand, 2011) in algal species richness, biomass and productivity.

In our experiments, the thermal sensitivities of metabolic rates were much larger than those of interaction strengths in the short term (e.g. 0.96 and 0.45 eV, respectively), in line with findings in other invertebrate systems (Fussmann et al., 2014; Rall et al., 2010; Vucic-Pestic et al., 2011). These findings suggest that rates of grazing and metabolism were clearly linked, but became decoupled when individuals experience rapid changes in temperature that depart substantially from those in their local environment. In the short term, if increases in metabolic demands with temperature are greater than those of consumption rates (as found here), then less energy will be transferred from the resource to the consumer, that is, more is lost through respiration (see also Rall et al., 2010). If such imbalances are maintained over long periods of time, then starvation of the consumer can ultimately result in a decline in top-down control on the resource (Binzer et al., 2015; Fussmann et al., 2014; Rall et al., 2010). However, when consumers' feeding rates are more sensitive to temperature than metabolic rates, interaction strengths can become amplified in warmer environments, leading to faster resource depletion and eventually driving either the resource or the consumer to local extinction (Vasseur & McCann, 2005). Long-term effects of temperature on interaction strengths have so far only been explored using food web models, parameterized using temperature sensitivities derived from short-term experiments (Fussmann et al., 2014; Rall et al., 2012; Vasseur & McCann, 2005). Consequently, such analyses do not capture the evolutionary and developmental effects which can modulate the short-term effects of temperature on *per capita* rates. Our results highlight substantial differences between the short- and long-term effects of temperature on interaction strength, implying that local adaptation can play an important role in modulating the balance between metabolic and consumption rates.

We quantified the short- and long-term effects of temperature in the reciprocal transplant experiment. The short-term temperature response (E_{short}) captures the effects of physiological plasticity over the 48-hr experiment. Conversely, the long-term response (E_{long}) also accounts for processes operating over longer timescales, including genetic micro-evolution and non-genetic developmental effects of temperature. In our experiment, E_{long} was higher than E_{short}, implying a significant role for adaptation in shaping the effects of temperature on in situ interaction strengths. Notably, the higher E_{long} was driven both by elevated grazing rates in the warm populations in the warm stream and lower rates in the cold populations in the cold stream. These results diverge from our expectations based on the metabolic cold adaptation hypothesis (Addo-Bediako et al., 2000) which would predict populations from warmer environments should dampen the acute effects of temperature on metabolic rates. On the contrary, our results suggest that adaptation to warming amplified the effects of temperature on metabolic as well as grazing rates. The lower interaction strengths in the population of *R. balthica* from the colder stream highlight unexpected long-term effects of temperature on species interactions. For example, maintenance of low grazing rates in the cold stream could arise via differences in consumer and/or resource stoichiometry between warmed and cold streams, such that lower consumption rates are required in the cold stream to achieve stoichiometric homeostasis (Cross, Benstead, Frost, & Thomas, 2005; Cross, Hood, Benstead, Huryn, & Nelson, 2014) under the prevailing temperature regime. Thus, understanding the impacts of environmental change on the strength of consumer–resource interactions over timescales that are relevant to the rate of climate change (e.g. gradual warming over decades) will require an appreciation both of the direct effects of rising temperatures on species interactions and the reciprocal feedback between ecological and evolutionary dynamics (Barraclough, 2015; Fussmann, Loreau, & Abrams, 2007; Gravel et al., 2010; Loeuille, 2010; Urban, 2013).

We used a natural geothermal temperature gradient to investigate how warming influences the strength of algal–grazer interactions via the direct effects of temperature on metabolism and consumption, and indirect feedbacks through adaptation. Metabolic rates and interaction strength increased with temperature in the same way for both the warm and cold populations of *R. balthica*, suggesting that rapid changes in temperature have a consistent effect on interactions between mobile consumers and sessile resources, mediated by the effects of temperature on consumer metabolic rates (Dell et al., 2014). However, the warm populations had higher metabolic and grazing rates across all measurement temperatures compared to their colder counterparts. These findings are consistent with the "hotter is better and broader" hypothesis (Angilletta et al., 2010; Huey & Kingsolver, 1993; Knies et al., 2009) (e.g. adaptation to warming gives rise to higher maximal metabolic rates and broader thermal reaction norms). In consequence, our results suggest that warming could increase the strength of algal–grazer interactions, which are often "keystone" interactions in aquatic systems, both via the thermodynamic effects of higher temperatures on enzyme kinetics and through correlated increases in *per capita* metabolism and consumption as organisms adapt to warmer temperatures.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

GYD conceived the experiment. GYD and ES supervised the experiment, analysed data and wrote the manuscript. All authors contributed to later versions of the manuscript.

DATA ACCESSIBILITY

All data will be made available as supporting information should the manuscript be accepted. R-Code for analysis will be available from the authors on request.

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REFERENCES

Addo-Bediako, A., Chown, S. L., & Gaston, K. J. (2000). Thermal tolerance, climatic variability, and latitude. *Proceedings of the Royal Society B: Biological Sciences*, *267*, 739–745. https://doi.org/10.1098/rspb.2000.1065

Allen, A. P., Gillooly, J. F., & Brown, J. H. (2005). Linking the global carbon cycle to individual metabolism. *Functional Ecology*, *19*, 202–213. https://doi.org/10.1111/j.1365-2435.2005.00952.x

Angilletta, Jr, M. J., Huey, R. B., & Frazier, M. R. (2010). Thermodynamic effects on organismal performance: Is hotter better? *Physiological and Biochemical Zoology*, *83*, 197–206. https://doi.org/10.1086/648567

Angilletta, Jr, M. J., Wilson, R. S., Navas, C. A., & James, R. S. (2003). Tradeoffs and the evolution of thermal reaction norms. *Trends in Ecology & Evolution*, *18*, 234–240. https://doi.org/10.1016/s0169-5347(03)00087-9

Barraclough, T. G. (2015). How do species interactions affect evolutionary dynamics across whole communities? *Annual Review of Ecology, Evolution, and Systematics*, *46*, 25–48. https://doi.org/10.1146/annurev-ecolsys-112414-054030

Barton, B. T. (2011). Local adaptation to temperature conserves top-down control in a grassland food web. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 3102–3107. https://doi.org/10.1098/rspb.2011.0030

Berlow, E. L., Neutel, A. M., Cohen, J. E., de Ruiter, P. C., Ebenman, B., Emmerson, M., ... Petchey, O. (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, *73*, 585–598. https://doi.org/10.1111/j.0021-8790.2004.00833.x

Binzer, A., Guill, C., Rall, B. C., & Brose, U. (2015). Interactive effects of warming, eutrophication and size structure: Impacts on biodiversity and food-web structure. *Global Change Biology*, *22*, 220–227.

Bolotov, I. N., Kondakov, A. V., Vikhrev, I. V., Aksenova, O. V., Bespalaya, Y. V., Gofarov, M. Y., ... Tumpeesuwan, S. (2017). Ancient river inference explains exceptional freshwater mussel radiations. *Scientific Reports*, *7*, 2135. https://doi.org/10.1038/s41598-017-02312-z

Bonduriansky, R., Crean, A. J., & Day, T. (2011). The implications of nongenetic inheritance for evolution in changing environments. *Evolutionary Applications*, *5*, 192–201.

Brose, U., Dunne, J. A., Montoya, J. M., Petchey, O. L., Schneider, F. D., & Jacob, U. (2012). Climate change in size-structured ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 2903–2912. https://doi.org/10.1098/rstb.2012.0232

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*, 1771–1789. https://doi.org/10.1890/03-9000

Burgmer, T., & Hillebrand, H. (2011). Temperature mean and variance alter phytoplankton biomass and biodiversity in a long-term microcosm experiment. *Oikos*, *120*, 922–933. https://doi.org/10.1111/j.1600-0706.2010.19301.x

Burgmer, T., Reiss, J., Wickham, S. A., & Hillebrand, H. (2010). Effects of snail grazers and light on the benthic microbial food web in periphyton communities. *Aquatic Microbial Ecology*, *61*, 163–178. https://doi.org/10.3354/ame01449

Cross, W. F., Benstead, J. P., Frost, P. C., & Thomas, S. A. (2005). Ecological stoichiometry in freshwater benthic systems: Recent progress and perspectives. *Freshwater Biology*, *50*, 1895–1912. https://doi.org/10.1111/j.1365-2427.2005.01458.x

Cross, W. F., Hood, J. M., Benstead, J. P., Huryn, A. D., & Nelson, D. (2014). Interactions between temperature and nutrients across levels of ecological organization. *Global Change Biology*, *21*, 1025–1040.

De Block, M., Pauwels, K., Van Den Broeck, M., De Meester, L., & Stoks, R. (2012). Local genetic adaptation generates latitude-specific effects of warming on predator–prey interactions. *Global Change Biology*, *19*, 689–696.

Dell, A. I., Pawar, S., & Savage, V. M. (2011). Systematic variation in the temperature dependence of physiological and ecological traits. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 10591–10596. https://doi.org/10.1073/pnas.1015178108

Dell, A. I., Pawar, S., & Savage, V. M. (2014). Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *Journal of Animal Ecology*, *83*, 70–84. https://doi.org/10.1111/1365-2656.12081

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 6668–6672. https://doi.org/10.1073/pnas.0709472105

Englund, G., Öhlund, G., Hein, C. L., & Diehl, S. (2011). Temperature dependence of the functional response. *Ecology Letters*, *14*, 914–921. https://doi.org/10.1111/j.1461-0248.2011.01661.x

Eyring, H. (1935). The activated complex in chemical reactions. *The Journal of Chemical Physics*, *3*, 107–115.

Fukami, T., & Wardle, D. A. (2005). Long-term ecological dynamics: Reciprocal insights from natural and anthropogenic gradients. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 2105–2115. https://doi.org/10.1098/rspb.2005.3277

Fussmann, G. F., Loreau, M., & Abrams, P. A. (2007). Eco-evolutionary dynamics of communities and ecosystems. *Functional Ecology*, *21*, 465–477. https://doi.org/10.1111/j.1365-2435.2007.01275.x

Fussmann, K. E., Schwarzmüller, F., Brose, U., Jousset, A., & Rall, B. C. (2014). Ecological stability in response to warming. *Nature Climate Change*, *4*, 206–210. https://doi.org/10.1038/nclimate2134

Gilbert, B., Tunney, T. D., McCann, K. S., DeLong, J. P., Vasseur, D. A., Savage, V., … O'Connor, M. I. (2014). A bioenergetic framework for the temperature dependence of trophic interactions (ed Wootton T). *Ecology Letters*, *17*, 902–914. https://doi.org/10.1111/ele.12307

Gillooly, J. F. (2001). Effects of size and temperature on metabolic rate. *Science*, *293*, 2248–2251. https://doi.org/10.1126/science.1061967

Gravel, D., Bell, T., Barbera, C., Bouvier, T., Pommier, T., Venail, P., & Mouquet, N. (2010). Experimental niche evolution alters the strength of the diversity–productivity relationship. *Nature*, *469*, 89–92.

Gudmundsdottir, R., Palsson, S., Hannesdottir, E. R., Olafsson, J. S., Gislason, G. M., & Moss, B. (2013). Diatoms as indicators: The influences of experimental nitrogen enrichment on diatom assemblages in sub-Arctic streams. *Ecological Indicators*, *32*, 74–81. https://doi.org/10.1016/j.ecolind.2013.03.015

Hansson, L. A., & Akesson, S. (Eds.). (2014). *Animal movement across scales*. Oxford, UK: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199677184.001.0001

Hoffman, A. L., Olden, J. D., Monroe, J. B., LeRoy Poff, N., Wellnitz, T., & Wiens, J. A. (2006). Current velocity and habitat patchiness shape stream herbivore movement. *Oikos*, *115*, 358–368. https://doi.org/10.1111/j.2006.0030-1299.14675.x

Hoffmann, A. A., & Sgrò, C. M. (2011). Climate change and evolutionary adaptation. *Nature*, *470*, 479–485. https://doi.org/10.1038/nature09670

Holm-Hansen, O., & Riemann, B. (1978). Chlorophyll *a* determination: Improvements in methodology. *Oikos*, *30*, 438. https://doi.org/10.2307/3543338

Huey, R. B., & Kingsolver, J. G. (1993). Evolution of resistance to high temperature in ectotherms. *The American Naturalist*, *142*, S21–S46. https://doi.org/10.1086/285521

Johansson, M. P., Quintela, M., & Laurila, A. (2016). Genetic divergence and isolation by thermal environment in geothermal populations of an aquatic invertebrate. *Journal of Evolutionary Biology*, *29*(9), 1701–1712. https://doi.org/10.1111/jeb.12902

Kappes, H., & Haase, P. (2012). Slow, but steady: Dispersal of freshwater molluscs. *Aquatic Sciences*, *74*(1), 1–14. https://doi.org/10.1007/s00027-011-0187-6

Keller, I., Alexander, J. M., Holderegger, R., & Edwards, P. J. (2013). Widespread phenotypic and genetic divergence along altitudinal gradients in animals. *Journal of Evolutionary Biology*, *26*, 2527–2543. https://doi.org/10.1111/jeb.12255

Kilham, S. S., Kreeger, D. A., Lynn, S. G., Goulden, C. E., & Herrera, L. (1998). COMBO: A defined freshwater culture medium for algae and zooplankton. *Hydrobiologia*, *377*, 147–159. https://doi.org/10.1023/a:1003231628456

Kingsolver, J. G., & Huey, R. B. (2008). Size, temperature, and fitness: Three rules. *Evolutionary Ecology Research*, *10*, 251–268.

Kingsolver, J. G., Ragland, G. J., & Shlichta, J. G. (2004). Quantitative genetics of continuous reaction norms: Thermal sensitivity of caterpillar growth rates. *Evolution*, *58*(7), 1521–1529. https://doi.org/10.1111/j.0014-3820.2004.tb01732.x

Knies, J. L., Kingsolver, J. G., & Burch, C. L. (2009). Hotter is better and broader: Thermal sensitivity of fitness in a population of bacteriophages. *The American Naturalist*, *173*, 419–430. https://doi.org/10.1086/597224

Kratina, P., Greig, H. S., & Thompson, P. L. (2012). Warming modifies trophic cascades and eutrophication in experimental freshwater communities. *Ecology*, *93*, 1421–1430. https://doi.org/10.1890/11-1595.1

Lang, B., Rall, B. C., & Brose, U. (2011). Warming effects on consumption and intraspecific interference competition depend on predator metabolism. *Journal of Animal Ecology*, *81*, 516–523.

Laufkötter, C., Vogt, M., Gruber, N., Aita-Noguchi, M., Aumont, O., Bopp, L., … Völker, C. (2015). Drivers and uncertainties of future global marine primary production in marine ecosystem models. *Biogeosciences*, *12*, 6955–6984. https://doi.org/10.5194/bg-12-6955-2015

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*, 1052–1055. https://doi.org/10.1038/nature08649

Loeuille, N. (2010). Influence of evolution on the stability of ecological communities. *Ecology Letters*, *13*, 1536–1545. https://doi.org/10.1111/j.1461-0248.2010.01545.x

May, R. M. (1973). Qualitative stability in model ecosystems. *Ecology*, *54*, 638–641. https://doi.org/10.2307/1935352

McCann, K., Hastings, A., & Huxel, G. R. (1998). Weak trophic interactions and the balance of nature. *Nature*, *395*, 794–798. https://doi.org/10.1038/27427

Merilä, J., & Hendry, A. P. (2014). Climate change, adaptation, and phenotypic plasticity: The problem and the evidence. *Evolutionary Applications*, *7*, 1–14. https://doi.org/10.1111/eva.12137

O'Connor, M. I. (2009). Warming strengthens an herbivore–plant interaction. *Ecology*, *90*, 388–398. https://doi.org/10.1890/08-0034.1

O'Connor, M. I., Gilbert, B., & Brown, C. J. (2011). Theoretical predictions for how temperature affects the dynamics of interacting herbivores and plants. *The American Naturalist*, *178*, 626–638. https://doi.org/10.1086/662171

O'Gorman, E. J., Pichler, D. E., Adams, G., Benstead, J. P., Cohen, H., Craig, N., … Woodward, G. (2012). *Impacts of warming on the structure and functioning of aquatic communities: Individual- to ecosystem-level responses* (1st ed., Vol. 47). Burlington, MA: Elsevier Ltd. 96 pp.

Otto, S. B., Rall, B. C., & Brose, U. (2007). Allometric degree distributions facilitate food-web stability. *Nature*, *450*, 1226–1229. https://doi.org/10.1038/nature06359

Padfield, D., Lowe, C., Buckling, A., ffrench-Constant, R., Jennings, A., Shelley, F., … Yvon-Durocher, G. (2017). Metabolic compensation constrains the temperature dependence of gross primary production. *Ecology Letters*, *20*, 1250–1260. https://doi.org/10.1111/ele.12820

Paine, R. T. (1980). Food webs: Linkage, interaction strength and community infrastructure. *Journal of Animal Ecology*, *49*, 666. https://doi.org/10.2307/4220

Rall, B. C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmuller, F., Vucic-Pestic, O., & Petchey, O. L. (2012). Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 2923–2934. https://doi.org/10.1098/rstb.2012.0242

Rall, B. C., Vucic-Pestic, O., Ehnes, R. B., Emmerson, M., & Brose, U. (2010). Temperature, predator–prey interaction strength and population stability. *Global Change Biology*, *16*, 2145–2157.

Ricciardi, A., & Bourget, E. (1998). Weight-to-weight conversion factors for marine benthic macroinvertebrates. *Marine Ecology Progress Series*, *171*, 245–251. https://doi.org/10.3354/meps163245

Richter-Boix, A., Teplitsky, C., Rogell, B., & Laurila, A. (2010). Local selection modifies phenotypic divergence among Rana temporariapopulations in the presence of gene flow. *Molecular Ecology*, *19*, 716–731. https://doi.org/10.1111/j.1365-294x.2009.04502.x

Sanford, E. (1999). Regulation of keystone predation by small changes in ocean temperature. *Science*, *283*, 2095–2097. https://doi.org/10.1126/science.283.5410.2095

Savage, V. M., Gillooly, J. F., Brown, J. H., West, G. B., & Charnov, E. L. (2015). Effects of body size and temperature on population growth. *The American Naturalist*, *163*, 429–441.

Schoolfield, R. M., Sharpe, P. J. H., & Magnuson, C. E. (1981). Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. *Journal of Theoretical Biology*, *88*, 719–731. https://doi.org/10.1016/0022-5193(81)90246-0

Sentis, A., Morisson, J., & Boukal, D. S. (2015). Thermal acclimation modulates the impacts of temperature and enrichment on trophic interaction strengths and population dynamics. *Global Change Biology*, *21*, 3290–3298. https://doi.org/10.1111/gcb.12931

Sharpe, P. J., & DeMichele, D. W. (1977). Reaction kinetics of poikilotherm development. *Journal of Theoretical Biology*, *64*, 649–670. https://doi.org/10.1016/0022-5193(77)90265-x

Shurin, J. B., Clasen, J. L., Greig, H. S., Kratina, P., & Thompson, P. L. (2012). Warming shifts top-down and bottom-up control of pond food web structure and function. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 3008–3017. https://doi.org/10.1098/rstb.2012.0243

Skalski, G. T., & Gilliam, J. F. (2001). Functional responses with predator interference: Viable alternatives to the Holling type II model. *Ecology*, *82*, 3083. https://doi.org/10.1890/0012-9658(2001)082[3083:frwpiv]2.0.co;2

Urban, M. C. (2013). Evolution mediates the effects of apex predation on aquatic food webs. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20130859–20130869. https://doi.org/10.1098/rspb.2013.0859

Vasseur, D. A., & McCann, K. S. (2005). A mechanistic approach for modeling temperature-dependent consumer-resource dynamics. *The American Naturalist*, *166*, 184–198. https://doi.org/10.1086/431285

Vucic-Pestic, O., Ehnes, R. B., & Rall, B. C. (2011). Warming up the system: Higher predator feeding rates but lower energetic efficiencies. *Global Change Biology*, *17*, 1301–1310. https://doi.org/10.1111/j.1365-2486.2010.02329.x

West, D. C., & Post, D. M. (2016). Impacts of warming revealed by linking resource growth rates with consumer functional responses (ed Behmer S). *Journal of Animal Ecology*, *85*, 671–680. https://doi.org/10.1111/1365-2656.12491

West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. New York, NY: Oxford University Press.

Yvon-Durocher, G., Allen, A. P., Cellamare, M., Dossena, M., Gaston, K. J., Leitao, M., ... Trimmer, M. (2015). Five years of experimental warming increases the biodiversity and productivity of phytoplankton (ed Levin SA). *PLoS Biology*, *13*, e1002324. https://doi.org/10.1371/journal.pbio.1002324

SUPPORTING INFORMATION

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APPENDIX

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