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

Running head: Linking metabolism and trophic interactions

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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, metabolism, thermal adaptation, interaction strength

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 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 (Laufko€tter 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, O€hlund, 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

94 organisms are exposed to novel thermal environments, both via phenotypic plasticity, where
95 organisms change phenotypic characteristics rapidly and with no underlying heritable genetic
96 change (West-Eberhard, 2003), and adaptive evolution, where organisms respond to changes
97 in the environment through heritable genetic change over many generations, resulting in
98 better adapted phenotypes (Angilletta, Wilson, Navas, & James, 2003; Deutsch et al., 2008;
99 Kingsolver & Huey, 2008; Kingsolver, Ragland, & Shlichta, 2004). Consequently, plasticity
100 and evolution have the potential to modulate the effects of rising temperatures on the strength
101 of species interactions (Sentis, Morisson, & Boukal, 2015). For example, if metabolic rates
102 are down-regulated after long-term exposure to higher temperatures (Addo-Bediako, Chown,
103 & Gaston, 2000), then compensatory metabolic responses to warming (e.g. Padfield et al.,
104 2017) could mitigate predicted increases in consumer–resource interaction strength. How
105 these long-term responses to warming affect rates of metabolism and in turn, the strength of
106 consumer– resource interactions, are largely unknown, limiting our ability to predict how
107 trophic interactions will change in response to warming in the long term.
108 There is evidence from studies across naturally occurring thermal gradients over large spatial
109 scales, that local thermal adaptation can play an important role in shaping the strength of
110 species in shaping the stability of food webs (May, 1973; McCann, Hastings, & Huxel, 1998;
111 Otto, Rall, & Brose, 2007; Paine, 1980). Grazing is an important class of consumer–resource
112 interaction, determining the flux of energy and materials from autotrophs to heterotrophs.
113 There are currently major concerns that global warming will increase the impact of grazers
114 on algal or plant communities because the ingestion and respiration rates of heterotrophs tend
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116 autotrophs (Gilbert et al., 2014; O'Connor, 2009; West & Post, 2016). Stronger interactions
117 have the potential to destabilize food webs and consequently, warming induced increases in
118 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 (Laufko€tter 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, O€hlund, 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

144 consumer– resource interactions, are largely unknown, limiting our ability to predict how
145 trophic interactions will change in response to warming in the long term.
146 There is evidence from studies across naturally occurring thermal gradients over large spatial
147 scales, that local thermal adaptation can play an important role in shaping the strength of
148 species interactions (Barton, 2011; De Block, Pauwels, Van Den Broeck, De Meester, &
149 Stoks, 2012). While these studies provide important insights into how consumer–resource
150 interactions are shaped by evolution across thermal gradients (Fukami & Wardle, 2005), their
151 usefulness for understanding responses to rapid climate warming might be limited because
152 other factors, such as day length, light intensity and precipitation, tend to be confounded with
153 temperature along such broad scale spatial gradients. Furthermore, the timescales over which
154 local adaptation has occurred in such broad scale studies could be much longer than the rapid
155 evolutionary change required to keep pace with climate warming (Hoffmann & Sgro , 2011;
156 Loarie et al., 2009). Here, we investigate how temperature-driven selection on traits that
157 determine the thermal responses of metabolism and resource acquisition affect the strength of
158 a keystone grazing interaction (the gastropod Radix balthica, which grazes algal biofilms in
159 streams) in naturally warmed Icelandic geothermal streams spanning a gradient of 11°C.
160 Critically, temperature is the main abiotic factor that varies among streams in the catchment
161 and is not correlated with pH, conductivity or inorganic nutrient concentrations (see Table 1,
162 also Padfield et al., 2017). These streams are thought to have been subject to geothermal
163 heating for at least the last century (O'Gorman et al., 2012). This system therefore provides
164 the opportunity to investigate how long-term differences in temperature between otherwise
165 similar sites shape the expression of metabolic traits and the subsequent impact of any
166 temperature-driven selection on species interactions in a natural system. Specifically, we test
167 the hypothesis that long-term differences in temperature drive selection for metabolic traits
168 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.

MATERIALS AND METHODS

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 ºC (see Figure 1 and Figure S1). Two streams, stream 5 (17.5 ºC ± 4.5 ºC, hereafter 'cold stream') and stream 11A (28.3 ºC ± 1.3 ºC, hereafter 'warm stream', see Table 1 for a comparison of other chemical and physical parameters), were chosen for experiments due to their close proximity to each other, the large temperature differential and similar abundances of the keystone grazer, *Radix 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 (OGorman *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 ºC (see Table 1), and hence present an opportunity to investigate how the effects long-term differences in temperature shape consumer-resource interactions. The experiment was carried out from 26.05.2016 to 02.06. 2016, with a pilot study testing the general experimental set-up conducted from 01.06.2015 to 07.06. 2015.

Grazer metabolism

196 To quantify whether the different thermal regimes in the two adjacent streams resulted in
197 divergence in metabolic traits of mature *R. balthica* (based on mass and shell length) we
198 measured the acute responses of respiration to a broad gradient in temperature. For the
199 metabolic measurements, we collected 33 individuals of similar mass and length (average
200 mass of snails from cold stream 0.087 g ± 0.014g, average mass of snails from warm stream
201 0.098 ± 0.016, both ± 1 SEM, ANOVA: $F_{1,61}$, P = 2.15, see Table S1 and also compare
202 Figure S2 for mass of another 205 randomly collected snails) from each stream, which were
203 cleaned from any algal debris to avoid carry-over of a food source into the tank or subsequent
204 respiratory measurements on the oxygen electrode. The snails were kept for 24hrs in aerated
205 tanks at the average stream temperature of origin and in the absence of a food source to
206 minimise any potential effects of differences in food quantity or quality between streams.
207 Respiration was quantified as the rate of oxygen consumption in a Clark-Type oxygen
208 electrode, measured between 4 – 44 ºC in 4 ºC increments (11 temperatures in total) within a
209 day. At each temperature, respiration was measured for 3 individuals, and a different set of
210 individuals was measured at each temperature (i.e. each animal was only subjected to a single
211 assay). Individuals were allowed 15 minutes at the assay temperature prior to the
212 measurements. The subsequent thermal responses of respiration were quantified using a
213 modification of the Sharpe-Schoolfield equation (see (Schoolfield *et al.*, 1981) and (Sharpe &
214 DeMichele, 1977)for the original equation):

215 $$\ln\big(b(T)\big) = E_a\left(\frac{1}{kT_c} - \frac{1}{kT}\right) + \ln\big(b(T_c)\big) + \alpha\ln(M_i) - \ln\left(1 + e^{E_h\left(\frac{1}{kT_h} - \frac{1}{kT}\right)}\right) \qquad (1)$$

216 where $b(T)$, is the *per capita* metabolic rate (µmol O_2 L^{-1} h^{-1}) at temperature T in Kelvin (K),
217 k is Boltzmann's constant (8.62×10^{-5} eV K^{-1}), E_a is an apparent activation energy (in eV) for
218 the metabolic process, ln ($b(T_c)$) is the rate of metabolism normalised to an arbitrary
219 reference temperature, T_c = 18 ºC, where no low or high temperature inactivation is
220 experienced. M_i is the mass (g) of an individual i, α is the allometric scaling exponent that

characterises the power-law relation of mass and metabolic rate (Brown *et al.*, 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 (Sharpe & DeMichele, 1977; Schoolfield *et al.*, 1981) 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 Eq. (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} (Eq. 2) and facilitates more direct comparison with previous work on the temperature dependence of metabolism using metabolic theory e.g. (Allen *et al.*,2005, Gillooly, 2001; Brown *et al.*, 2004; Van M Savage *et al.*, 2015).

The parameters, ln $b(T_c)$, α, E_a, E_h, T_h, and T_{opt}, in Eqs. (1) & (2) represent traits characterising 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 Eq. (1) using generalised 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 Table S1 and

Table 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.

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 ± 0.08g, and snails from the warm stream, 0.89g ± 0.07g (no significant difference, 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 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 1L) with 20 mL COMBO medium (Kilham *et al.*, 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 3 treatments (each with 6 replicate microcosms placed in each of the 2 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. *R. balthica* individuals used for the reciprocal transfer experiment were collected from the 2 streams prior to the experiment and were starved for 48h in the laboratory in aerated tanks at the average temperature of the stream of origin. Microcosms were assembled by adding 3 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. (Skalski & Gilliam, 2001; Rall *et al.*, 2010; Lang *et al.*, 2011; Vucic-Pestic *et al.*, 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

295 microcosms were submerged in each stream facing downstream, so that the stream water
296 controlled the ambient temperature of the microcosms but did not fill the flasks further with
297 water or organic matter (see Figure 1 for conceptual graphic). The snails were left to graze
298 for 48 hours. We observed no grazer mortality over the experimental period. Sampling of
299 another 206 snails from each stream confirmed no significant difference in average snail size
300 in the cold and warm stream at this time of the year (see Figure S2, one-way ANOVA: $F_{1,408}$
301 = 0.15, P = 0.7).

302

303

304

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 & Riemann, 1978). Here, the walls of the microcosms were scrubbed until all biofilm particles were in suspension. The solution was filtered onto a 0.4µm GF/F filter, which was then ground in methanol for 5 minutes. The samples were centrifuged at 3500 rpm for 15 minutes and the absorbance of the supernatant was measured at 632nm, 665nm, and 750nm. Total chlorophyll content in µg mL^{-1} was then calculated as described in Holm-Hansen & 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.

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

where DI is the dynamic index (g Chl gC^{-1} h^{-1}), *N* is total chlorophyll (sum of Chl *a* + Chl *c*) content of control, *D* 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 *et al.*, 2010).

We carried out two analyses using the data from the reciprocal transplant experiment. The first analysis, used a generalised linear model (GLM), with 'interaction strength' as the response variable and 'origin' ('cold' or 'warm' stream) and 'transplant temperature' (17.5 and 28.3 ºC) 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

330 (e.g. a main effect of 'origin'); (ii) whether interaction strengths were temperature dependent
331 (e.g. a main effect of 'temperature'); and (iii) whether the temperature dependence of
332 interaction strength differed between the snails from the cold and warm streams (e.g.
333 interaction between 'origin' and 'temperature').

334 We examined the relative contributions of short - and long-term responses to
335 warming: The design of the reciprocal transplant experiment enabled us to disentangle short-
336 term temperature responses attributable to acclimation (e.g. responses to the temperature in
337 the 'transplanted' stream) from those reflecting processes operating over longer, time scales
338 (e.g. adaptation to the stream of 'origin'). Note that these 'long-term' effects, which we call
339 'adaptation', could reflect strict genetic microevolution (e.g. resulting in divergent genotypes
340 among populations) or they could represent non-genetic effects of the different temperature
341 regimes that manifest over ontogenetic development, but are nevertheless adaptive
342 (Bonduriansky *et al.*, 2011). In the second GLM we included 'interaction strength' as the
343 response variable and 'timescale' ('short' or 'long') and 'transplant temperature' (17.5 and
344 28.3 ºC) as potentially interacting factors. Here, 'short-term' temperature responses were
345 characterised as the change in interaction strength between the stream of origin and the
346 transplant stream. By contrast, the 'long-term' temperature response was characterised as the
347 change in interaction strength comparing measurements made only when the snails were in
348 their stream of origin. For better comparison of the steepness of the respiration reaction
349 norms, we re-express the transplant temperature data as Boltzmann temperatures $\left(\frac{1}{kT_c} - \frac{1}{kT}\right)$
350 so that the coefficients of the model yield activation energies in units of eV (see Eq. (1)). In
351 this analysis, a significant interaction between 'transplant temperature' and 'timescale' would
352 demonstrate that the temperature dependence of interaction strength differs between the
353 'short-term' (E_{short}, change in interaction strength between the stream of origin and the
354 transplant stream, see also Fig. 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 Fig. 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 – e.g. genetic microevolution and non-genetic developmental effects. Consequently, the component of the temperature sensitivity attributable to 'adaptation' (recognising that this might be genetically and/or developmentally determined) is given by $E_{adapt} = E_{long}\, E_{short}$.

RESULTS

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 normalised 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 Eq. (2)), T_{opt} was higher in *R. balthica* from the warmer stream (T_{opt} warm = 38.25 ± 0.6 ºC; T_{opt} cold = 33.05 ± 1.5 ºC). 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 (Fig. 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 (Fig. 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 (Fig. 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 (Fig. 2) and highlight the association between metabolism and interaction strength.

Disentangling the shortand 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 shortand the long-term (Fig. 3). However, the magnitude of the temperature response was significantly larger in the long-term (Fig. 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 shortand 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.

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 evolutionary 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 time scales. There is evidence from terrestrial (Rall *et al.*, 2010; Barton, 2011; Vucic-Pestic *et al.*, 2011; Brose *et al.*, 2012), freshwater (Kratina *et al.*, 2012) and marine ecosystems (Sanford, 1999), that warming is likely to increase the

406 strength of consumer-resource interactions, at least in the short-term, owing to the
407 exponential effects of temperature on the consumption rates of mobile ectothermic consumers
408 (Dell *et al.*, 2014; Gilbert *et al.*, 2014). What is less clear however, is how long-term
409 responses to rising temperatures will modulate the direct effects of warming on species
410 interactions. Space-for-time substitutions across broad spatial scales indicate that local
411 adaptation to different thermal regimes can play an important role in shaping species
412 interactions, often compensating for the direct effects of temperature on interaction traits
413 (Barton, 2011; De Block *et al.*, 2012). Here, we build on this work by investigating the
414 effects of temperature and local adaptation on the interaction between the gastropod grazer,
415 *R. balthica*, and its algal resource. Our study contributes novel insights in a number of ways.
416 First, we explore patterns of local adaptation over a relatively small spatial scale (m as
417 opposed to km). The two streams in our experiment are separated by approximately 500 m
418 but differ in temperature by 11 ºC. Dispersal, gene flow and genetic divergence among
419 populations in this species are strongly related to geographic distance (Johansson *et al.*,
420 2016), and *R. balthica* are known to disperse slowly, but regularly over short distances
421 (Kappes & Haase 2012, Hoffman *et al.* 2006), but rarely over long distances, where such
422 events are usually associated with passive dispersal, e.g. via association with vertebrates
423 (Bolotov *et al.,* 2017, Hansson & Akesson*.,* 2014). Thus, our study over a relatively small
424 spatial scale (500m), provides insight into how metabolic and resource acquisition traits in
425 closely related natural populations have diverged in response to warming and is therefore
426 directly relevant for understanding the effects of rapid climate change (Richter-Boix *et al.*,
427 2010; Keller *et al.*, 2013; Merilä & Hendry, 2014). Second, we quantified the effects of
428 temperature on both metabolic and consumption rates to determine how temperature-driven
429 selection on key traits shape the effects of long-term warming on the strength of consumer-
430 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 (Knies *et al.*, 2009, Huey & Kingsolver, 1993; Kingsolver *et al.*, 2004; Angilletta *et al.*, 2010). 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} h^{-1}, and cool stream: 2.54 ± 0.26 μmol O_2 L^{-1} h^{-1}, both ± 1.s.e.m.). The lower $E_{h,}$ (i.e. the steepness of the decline of the thermal reaction norm past the optimum), and higher ln $b(T_c)$, i.e. the rate of respiration normalised to 18 ºC, 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, Huey & Kingsolver, 1993; Kingsolver *et al.*, 2004; Angilletta *et al.*, 2010), our data for the gastropod *R. balthica*

456 indicate that adaptation to higher temperatures resulted in both greater maximal metabolic
457 performance and a broader metabolic thermal reaction norm.
458 The general patterns observed in the metabolic traits were also reflected in the effects
459 of temperature on interaction strength. Interaction strength was higher for individuals placed
460 in the warm stream, irrespective of their stream of origin. These findings suggest that
461 elevated temperatures increase consumption rates though the effects of temperature on
462 respiratory physiology, but local adaptation to warmer environments also results in a
463 correlated increase in metabolism and interaction strength at low temperature. This may have
464 important wider implications for the effects of warming on the structure, functioning and
465 stability of aquatic food webs (Rall *et al.*, 2010; O'Connor *et al.*, 2011; Vucic-Pestic *et al.*,
466 2011; Dell *et al.*, 2014; Fussmann *et al.*, 2014; Gilbert *et al.*, 2014). If long-term responses to
467 increasing temperature give rise to higher maximal rates of metabolism and consumption as
468 well as elevating rates at lower temperatures, then the effects of warming on the strength of
469 consumer-resource interactions in the long-term could be greater than previously anticipated
470 (Gilbert *et al.*, 2014). Indeed, work on experimental warming of aquatic ecosystems has
471 shown that increases in the strength of top-down control can have profound effects on
472 community structure and ecosystem processes (Burgmer & Hillebrand, 2011; Kratina *et al.*,
473 2012; Yvon-Durocher *et al.*, 2015). Elevated grazing rates at warmer temperatures can have a
474 wide range of impacts in aquatic systems, with evidence for both increases (Yvon-Durocher
475 *et al.*, 2015) and decreases (Burgmer & Hillebrand, 2011) in algal species richness, biomass
476 and productivity.
477 In our experiments, the thermal sensitivities of metabolic rates were much larger than
478 those of interaction strengths in the short-term (e.g. 0.96 and 0.45 eV respectively), in line
479 with findings in other invertebrate systems (Rall *et al.*, 2010; Vucic-Pestic *et al.*, 2011;
480 Fussmann *et al.*, 2014). 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, i.e. 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 (Rall *et al.* 2010, Fussmann *et al.*, 2014; Binzer *et al.*, 2015). 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, parameterised using temperature sensitivities derived from short-term experiments (Vasseur & McCann, 2005; Rall *et al.*, 2012; Fussmann *et al.*, 2014). 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 shortand 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 shortand 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 48h 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 long-term processes in shaping the effects of

506 temperature on *in situ* interaction strengths. Notably, the higher E_{long} was driven both by
507 elevated grazing rates in the warm populations in the warm stream and lower rates in the cold
508 populations in the cold stream. These results diverge from our expectations based on the
509 metabolic cold adaptation hypothesis (Addo-Bediako *et al.*, 2000) which would predict
510 populations from warmer environments should dampen the acute effects of temperature on
511 metabolic rates. On the contrary, our results suggest that adaptation to warming amplified the
512 effects of temperature on metabolic as well as grazing rates. The lower interaction strengths
513 in the population of *R. balthica* from the colder stream highlight unexpected long-term
514 effects of temperature on species interactions. For example, maintenance of low grazing rates
515 in the cold stream could arise via differences in consumer and/or resource stoichiometry
516 between warmed and cold streams, such that lower consumption rates are required in the cold
517 stream in order to achieve stoichiometric homeostasis (Cross *et al.*, 2005; 2015) under the
518 prevailing temperature regime. Thus, understanding the impacts of environmental change on
519 the strength of consumer-resource interactions over timescales that are relevant to the rate of
520 climate change (e.g. gradual warming over decades) will require an appreciation both of the
521 direct effects of rising temperatures on species interactions and the reciprocal feedback
522 between ecological and evolutionary dynamics (Fussmann *et al.*, 2007; Gravel *et al.*, 2010;
523 Loeuille, 2010; Urban, 2013; Barraclough, 2015)
524
525 We used a natural geothermal temperature gradient to investigate how warming influences
526 the strength of algal-grazer interactions via the direct effects of temperature on metabolism
527 and consumption, and indirect feedbacks through adaptation. Metabolic rates and interaction
528 strength increased with temperature in the same way for both the warm and cold populations
529 of *R. balthica*, suggesting that rapid changes in temperature have a consistent effect on
530 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 (Huey & Kingsolver, 1993; Knies *et al.*, 2009; Angilletta *et al.*, 2010) (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.

Conflict of interest

The authors declare no conflict of interest

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721

722

Tables and Table captions:

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 day of the experiment. Temperature data are displayed as means ± 1SD. All other data were originally collected for correlation with temperature across the catchment area (all 11 streams), so that replication for these parameters was on the level of stream identity.

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^{-1})	0.22	0.24
NO_3 (µmol L^{-1})	0.57	0.29
NH_4 (µmol L^{-1})	0.17	0.19
PO_4 (µmol L^{-1})	0.27	0.35
Velocity (m s^{-1})	0.10	0.15
Stream depth (m)	0.041	0.042

Table 2. Parameter estimates and output from the best fitting gnls model to the thermal response curves of respiration rates. Differences in treatments are given in **bold.** Parameter estimates are taken from the averaged generalised linear models along with their standard errors (± 1 s.e.m). 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) is displayed.

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

Figure Captions online

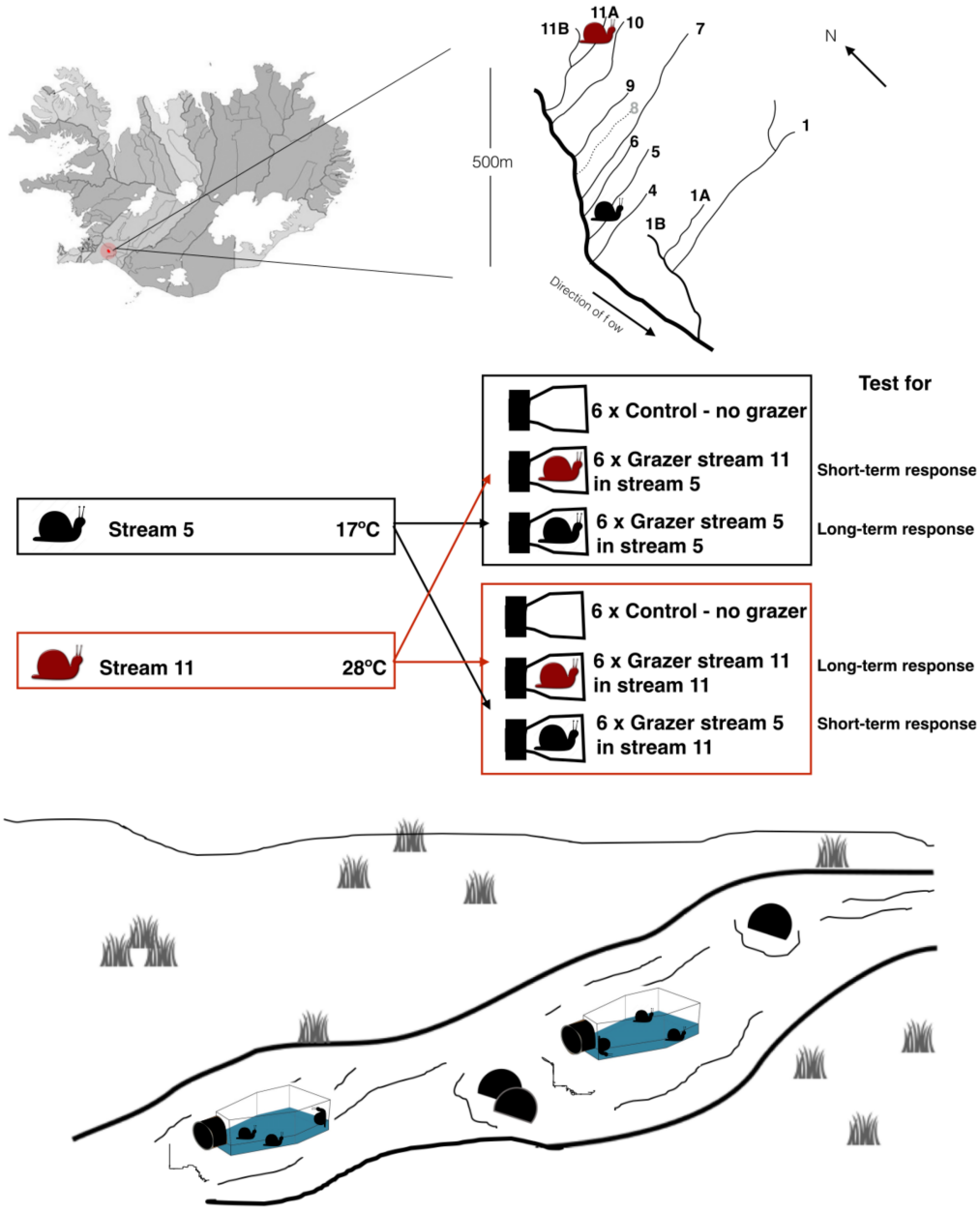

FIGURE 1 Map and experimental set-up. Top panel: The catchment area, with streams used in this experiment indicated by black (for the colder stream 5 with 17.5 ºC ± 4.5 ºC) and red (for the warmer stream 11A with 28.3 ºC ± 1.3 ºC) snail icons. **Middle panel**: Schematic overview of experimental set-up 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.

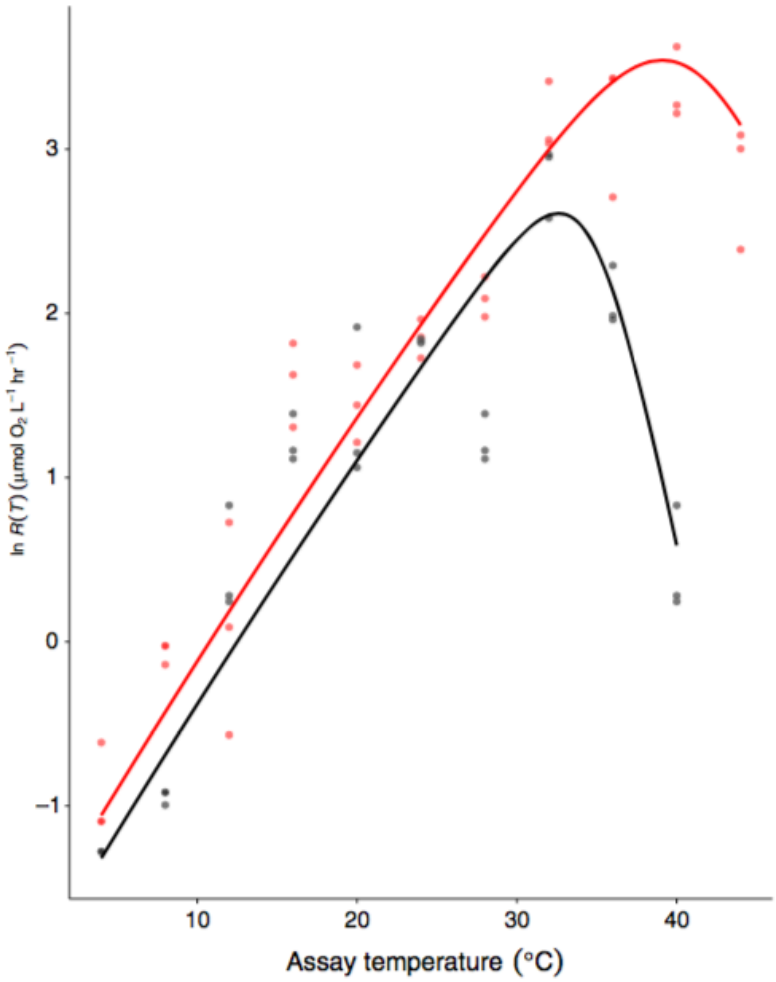

FIGURE 2 Thermal response curves for respiration. Thermal response curves of respiration rates in µmol O_2 L^{-1} h^{-1} as a function of increasing temperature for populations of the snail *Radix balthica* from the cold (black) and warm (red) stream. Lines are derived from fitting a modified Sharpe-Schoolfied 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=18ºC) at all measurement temperatures 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.

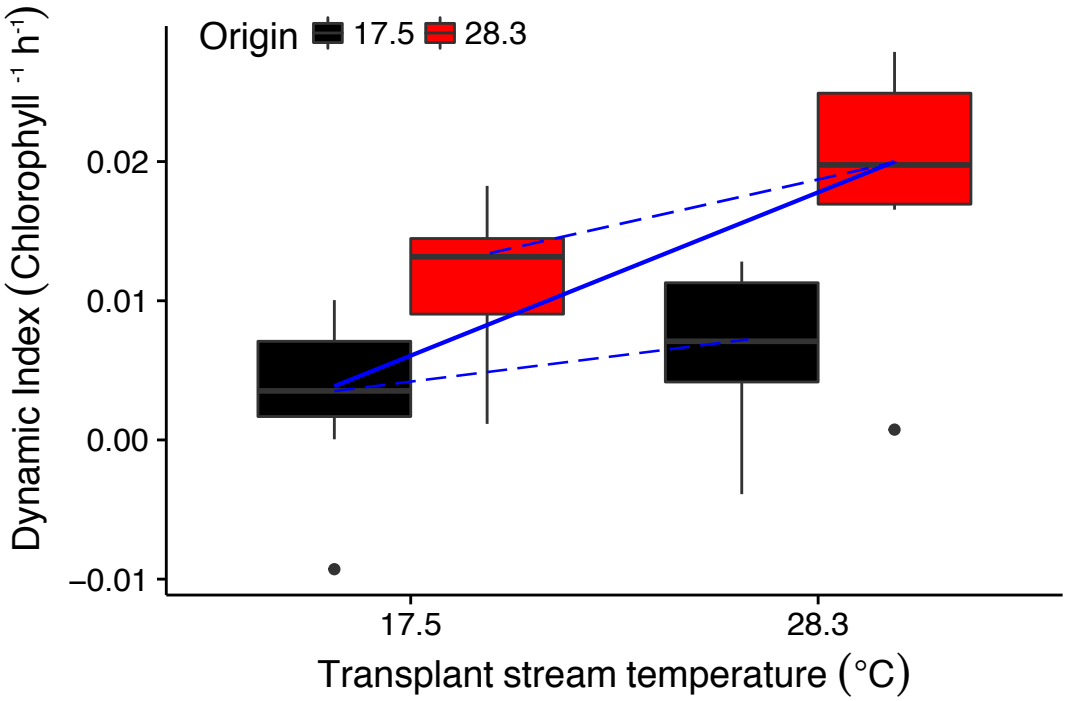

FIGURE 3 Long-term and short-term effects of stream temperature on interaction strength Long-term and short-term effects of temperature in interaction strength measured via the dynamic index in units of chlorophyll consumed per hour. Populations originating from the warm stream have stronger interaction strength indices 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 blue lines) and in the long-term (E_{long}, solid blue line, comparing dynamic indexes of snails in their temperatures of origin), with E_{long} significantly greater than E_{short}.

Figure Captions print (greyscale)

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 ºC ± 4.5 ºC) and grey (for the warmer stream 11A with 28.3 ºC ± 1.3 ºC) 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.

FIGURE 2 Thermal response curves for respiration. Thermal response curves of respiration rates in µmol O_2 L^{-1} h^{-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, triangles) stream. Lines are derived from fitting a modified Sharpe-Schoolfied 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=18ºC) at all measurement temperatures 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.

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}.