Adaptation to warming increases the strength of an algal-grazer interaction in naturally heated streams

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GYD conceived the experiment. GYD and ES supervised the experiment, analysed data, and all authors wrote the manuscript.

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Keywords: Consumer-resource interactions, global warming, metabolism, thermal adaptation, interaction strength

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ABSTRACT

Trophic interactions are important determinants of the structure and functioning of ecosystems. As the metabolism and consumption rates of ectotherms increase sharply with rising temperature, there are currently 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 a ~10 ºC temperature gradient to investigate the interplay between the thermal response of respiration, local adaptation, and the interaction strength between the keystone gastropod grazer, the wandering snail *Radix balthica*, and a common algal resource. Populations from a warm stream (~28ºC) had higher maximal metabolic rates and optimal temperatures across all measurement temperatures than those from a colder stream (~17ºC), suggesting local adaptation of metabolic rates. A reciprocal transplant experiment demonstrated that the interaction strength between the grazer and its resource were highest for both populations when transplanted into the warm stream. In line with the thermal response curves for respiration, interaction strengths of the warm-adapted grazers were higher than their cold-adapted counterparts in both the warm and the cold stream. These findings suggest that warming can increase the strength of algal-grazer interactions both through the thermodynamic effects of higher temperatures on physiological rates and through correlated increases in *per capita* metabolism and consumption as organisms adapt to warmer temperatures.

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INTRODUCTION

59 The strength of consumer-resource interactions (e.g. the effect of a consumer on the
60 population density of its prey) play a critical role in shaping the stability of food webs (May
61 1973; Paine 1980; McCann *et al.* 1998; Otto *et al.* 2007). Grazing is an important class of
62 consumer-resource interaction, determining the flux of energy and materials from autotrophs
63 to heterotrophs. There are currently major concerns that global warming will increase the
64 impact of grazers on algal or plant communities because the ingestion and respiration rates of
65 heterotrophs tend to be more sensitive to rising temperatures than rates of photosynthesis and
66 growth in autotrophs (O'Connor 2009; Gilbert et al. 2014; West and Post 2016). Stronger
67 interactions have the potential to destabilise food webs and consequently, warming induced
68 increases in interaction strengths could have fundamental implications for ecosystem
69 structure and function. For example, elevated grazing rates in aquatic ecosystems, driven by
70 the mismatch in thermal sensitivity between autotrophs and heterotrophs, are a key driver of
71 projected declines in aquatic primary production over the 21st century in models of ocean
72 biogeochemistry (Laufkötter *et al.* 2015).
73 The effects of temperature on metabolic rates and traits associated with consumer-
74 resource interactions (e.g. consumption rates, handling times) often follow characteristic
75 unimodal thermal response curves, in which rates increase exponentially to an optimum and
76 decline rapidly thereafter (Dell *et al.* 2011, 2014; Englund *et al.* 2011; Rall *et al.* 2012;
77 Gilbert *et al.* 2014). Integrating thermal responses for metabolism and interaction-traits with
78 dynamical models of consumer-resource interactions offers a promising framework for
79 predicting food web responses to global warming (Vasseur and McCann 2005; Shurin et al.
80 2012; Binzer et al. 2016). However, thermal response curves are often evolutionarily flexible
81 (Angilletta *et al.* 2003; Kingsolver *et al.* 2004; Deutsch *et al.* 2008; Kingsolver and Huey
82 2008) and can shift as organisms adapt to novel thermal environments, meaning that rapid
83 evolution could modulate the effects of rising temperatures on the strength of species

84 interactions. For example, if thermal adaptation serves to down-regulate metabolic rates at
85 higher temperatures (Addo-Bediako *et al.* 2002), then rapid evolutionary responses to
86 warming could mitigate predicted increases in consumer-resource interaction strength. How
87 adaptation to warming affects rates of metabolism and in turn, the strength of consumer-
88 resource interactions, is largely unknown, limiting our ability to predict how trophic
89 interactions will change in response to warming in the long-term.

90 There is evidence from studies across naturally occurring thermal gradients over large
91 spatial scales, that local thermal adaptation can play an important role in shaping the strength
92 of species interactions (Barton 2011; De Block *et al*. 2012). While these studies provide
93 important insights into how consumer-resource interactions are shaped by evolution across
94 thermal gradients (Fukami and Wardle 2005), their usefulness for understanding the
95 mechanisms underlying responses to rapid climate warming might be limited, because other
96 factors, such as day length, light intensity and precipitation, tend to be confounded with
97 temperature along such broad scale spatial gradients. Furthermore, the timescales over which
98 local adaptation has occurred in such broad scale studies could be much longer than the rapid
99 evolutionary change required to keep pace with climate warming (Loarie *et al.* 2009;
100 Hoffmann and Sgrò 2011). Here, we focus on the *interplay* between the effects of local
101 thermal adaptation on metabolism and the strength of a keystone grazing interaction (the
102 gastropod *Radix balthica,* which grazes algal biofilms in streams) in naturally warmed
103 Icelandic geothermal streams spanning a gradient of 11ºC. Critically, temperature is the main
104 abiotic factor that varies among streams in the catchment and is not correlated with pH,
105 conductivity or inorganic nutrient concentrations (see Table 1), and the streams are thought to
106 have been subject to geothermal heating for at least the last century (O'Gorman *et al.* 2012).
107 This system therefore provides the opportunity to investigate the mechanisms that shape how
108 temperature and local adaptation influence species interactions in a natural system, where the

effects of confounding factors are minimised. Specifically, we ask (i) can the underlying responses of metabolism to temperature explain the magnitude of the effects of warming on the strength of algal-grazer interactions? (ii) Can local thermal adaptation dampen the direct effects of warming on the strength of consumer-resource interactions?

METHODS

Study site

The streams are located North of the Icelandic Hveragerði valley, in the south east of the Hengil high temperature geothermal field (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 SI Figure 1). 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'), were chosen for experiments due to their close proximity, large temperature difference and the abundance of the keystone grazer, *Radix balthica*. The grazer plays an important functional role 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 but differ in average temperature by 11 ºC (see Table 1), and hence present an opportunity to investigate how the effects of warming and local adaptation interact to shape the thermal dependence of consumer-resource interactions.

Grazer metabolism

To quantify whether local adaptation to the different thermal regimes in the two adjacent streams resulted in divergence in metabolic traits of *R. balthica* we measured the acute responses of respiration to a broad gradient in temperature. We collected 33 individuals of similar weight and length from each stream, which were cleaned from any algal debris to avoid carry-over of a food source into the tank or subsequent respiratory measurements on

136 the oxygen electrode. The snails were kept overnight in aerated tanks at the average stream
137 temperature of origin and in the absence of a food source to minimise any potential effects of
138 differences in food quantity or quality between streams. Respiration was quantified as the
139 rate of oxygen consumption in a Clark-Type oxygen electrode, measured between 4 – 44 ºC
140 in 4 ºC increments (11 temperatures in total). At each temperature, respiration was measured
141 for 3 individuals, and a different set of individuals was measured at each temperature (i.e.
142 each animal was only subjected to a single assay). Individuals were allowed 15 minutes at the
143 assay temperature prior to the measurements. The subsequent thermal responses of
144 respiration were quantified using a modification of the Sharpe-Schoolfield equation (see
145 Schoolfield *et al.* (1981) for the original equation):

146 $$\ln\big(b(T)\big) = E_a\left(\frac{1}{kT_c} - \frac{1}{kT}\right) + \ln\big(b(T_c)\big) + \alpha\ln(M_i) - \ln\left(1 + e^{E_h\left(\frac{1}{kT_h} - \frac{1}{kT}\right)}\right) \quad (1)$$

147 where $b(T)$, is the *per capita* metabolic rate (µmol O_2 L^{-1} h^{-1}) at temperature T in Kelvin (K),
148 k is Boltzmann's constant (8.62×10^{-5} eV K^{-1}), E_a is an apparent activation energy (in eV) for
149 the metabolic process, ln ($b(T_c)$) is the rate of metabolism normalised to an arbitrary
150 reference temperature, T_c = 18 ºC, where no low or high temperature inactivation is
151 experienced. M_i is the mass (g) of an individual i, α is the allometric scaling exponent that
152 characterises the power-law relation of mass and metabolic rate (Brown *et al.* 2004). E_h
153 characterizes temperature-induced inactivation of enzyme kinetics above T_h where half the
154 enzymes are rendered non-functional. Differentiating equation (1) and solving for the global
155 maxima yields an expression for the optimum temperature

156 $$T_{opt} = \frac{E_h T_h}{E_h + kT_h \ln\left(\frac{E_h}{E_a} - 1\right)} \quad (2)$$

157 Equation (1) differs from the Sharpe-Schoolfield equation (Sharpe & DeMichele 1977;
158 Schoolfield *et al.* 1981) in a number of ways. First, we account for the power law relation
159 between body mass and metabolic rate, M^{α} (Brown *et al.* 2004). Second, we exclude

160 parameters from Eq. (1) used to characterize low-temperature inactivation due to insufficient
161 data to quantify this phenomenon in our analysis. Second, rather than characterize
162 temperature effects below T_{opt} using the Eyring (1935) relation, $\left(\frac{T}{T_c}\right) e^{E_a(\frac{1}{kT_c}-\frac{1}{kT})}$, we instead
163 use the simpler Boltzmann factor, $e^{E_a(\frac{1}{kT_c}-\frac{1}{kT})}$. This simplification enables an explicit solution
164 for T_{opt} (Eq. 2) and facilitates more direct comparison with previous work on the temperature
165 dependence of metabolism using metabolic theory (e.g. Gillooly *et al* 2001; Savage *et al*
166 2004; Brown *et al* 2004; Allen *et al.* 2005).
167 The parameters, ln $b(T_c)$, α, E_a, E_h, T_h, and T_{opt}, in Eqs. (1) & (2) represent traits
168 characterising the metabolic thermal response that we expect to be under selection in *R.*
169 *balthica* inhabiting the hot and cold streams. We tested for differences in each of the
170 parameters between the populations of *R. balthica* by fitting the respiration data to Eq. (1)
171 using generalised non-linear least squares regression (within the 'gnls' function in the 'nlme'
172 package for R, package version 3.1-128) and including 'origin' as a two level factor (i.e.
173 'cold' and 'warm' stream). We tested for differences between populations for each parameter
174 by sequentially removing the effect of 'origin' on each parameter and comparing the Akaike
175 information criterion for small sample sizes (AICc) for all possible models (see SI Table 1
176 and SI Table 2) using the 'aictab' and 'modavg' functions from the AICcmodavg package
177 (package version 2.1-0). The model chosen for further exploration was that with the lowest
178 (AICc) value. Model averaging was carried out when models fell within 2 AICc units of each
179 other, and the conditional averages of the parameters were used for curve fitting and
180 interpretation (see also Table 2). The relative importance of the fixed factors in the averaged
181 model was determined using the sum of their relative weights.
182
183
184 **Reciprocal transplant experiment**

185 The reciprocal transplant experiments to assess the effects of temperature and local
186 adaptation on algal-grazer interactions were carried out by placing snails in microcosms
187 consisting of a tissue culture flask on which diatom biofilms had been established. Diatoms
188 of the genera*, Acnanthes, Nitzschia, Navicula*, and *Gomphonema* are common in streams
189 across the Hengill volcanic area (Guðmundsdóttir *et al.* 2012) were ordered from culture
190 collections (Culture collection of algae and protozoa and Sciento) and grown in the
191 laboratory in mixed assemblages to yield common resource for testing the effects of
192 temperature and local adaptation on grazing . The diatom assemblages were inoculated into
193 Corning plastic translucent flasks (maximum volume 1L) with 20 mL COMBO medium
194 (Kilham *et al.* 1998), and brought to a salinity of 5-10 (equivalent to approximately 5-10 g
195 salts/kg water) to match the slightly elevated salinity and conductivity found in these thermal
196 stream environments (Guðmundsdóttir *et al.* 2012). The flasks were turned onto their sides to
197 allow for a larger area of biofilm growth on the base (~ 60 cm^2 in total per flask) and
198 communities were left to grow for 14 days prior to the experiment. After 14 days all flasks
199 had substantial biofilm development on the base and were used as microcosms for the *in situ*
200 reciprocal transplant experiment. Analysis of control flasks (no grazer) showed that growth of
201 the diatom lawn *per se* did not differ significantly for flasks placed in hot or cold streams (SI
202 Figure 2). Thus, any changes to the biofilm biomass in the experiment can be attributed to the
203 per capita effects of the grazer.
204 The experiment consisted of 3 treatments (each with 6 replicate microcosms placed in
205 each of the 2 streams): (i) a control microcosm in which a biofilm was present and no *R.*
206 *balthica* were added, (ii) an 'origin' treatment in which *R. balthica* that were resident in the
207 stream were added to microcosms, and (iii) a 'transplanted' treatment in which *R. balthica*
208 that were from the adjacent stream were added to microcosms. *R. balthica* individuals were
209 collected from the 2 streams the day before the experiment and were starved for 24h in the

210 laboratory in aerated tanks at the average temperature of the stream of origin. There was no
211 significant difference in average snail weight between the two streams (see SI Figure 3).
212 Microcosms were assembled by adding 3 snails of similar body dimensions (0.35 ± 0.03 g of
213 *R. balthica* weight reported as blotted fresh weight throughout) and 100 mL of 0.4 µm
214 filtered water from the stream in which the microcosm was to be placed. This resulted in a
215 grazer density of 5 individuals m^{-2}, which was comparable to the average *in situ* density in
216 the streams (see SI Figure 4). This design was preferred to a set-up with each microcosm
217 holding a single grazer, which attempt to exclude the effects of mutual interference on
218 feeding behaviour (e.g. Lang et al. (2011), Skalski and Gilliam (2001),Rall *et al.* (2010);
219 Vucic-Pestic *et al*. (2011)), because (i) the experimental densities are representative of
220 natural conditions; and (ii) the consumption rates of a single individual were insufficient to
221 detect a significant change in algal biomass. The microcosms were submerged in each stream
222 and the snails were left to graze for 48 hours. We observed no grazer mortality over the
223 experimental period.
224
225 **Interaction strength**
226 At the end of the experiment, algal biomass in each of the microcosms was quantified via
227 methanol chlorophyll extraction (modified from Holm-Hansen & Riemann (1978)). Here, the
228 walls of the microcosms were scrubbed until all biofilm particles were in suspension. The
229 solution was filtered onto a 0.4µm GF/F filter, which was then ground in methanol for 5
230 minutes. The samples were centrifuged at 3500 rpm for 15 minutes and the absorbance of the
231 supernatant was measured at 632nm, 665nm, and 750nm. Total chlorophyll content in µg
232 mL^{-1} was then calculated as described in Holm-Hansen & Riemann (1978). The *per capita*
233 interaction strength in each microcosm was then estimated by calculating the dynamic index
234 (DI, see also Berlow *et al.* (1999; 2004) for a technically similar set-up):

235 $$DI = \frac{\ln\left(\frac{N}{D}\right)}{Yt} \quad (3)$$

236 where N is total chlorophyll (sum of Chl *a* + Chl *c*) content of control, D total chlorophyll in
237 the grazed microcosm, Y is the grazer biomass (g C), and t is time in hours. Snail blotted wet
238 weight was converted to carbon mass (in grams) using conversion factors that assume dry
239 weight to be 7.5% of the blotted wet weight (Ricciardi & Bourget 1998) and a carbon content
240 of 22% dry weight (Burgmer *et al.* 2010).

241 We carried out two analyses using the data from the reciprocal transplant experiment.
242 The first analysis, used a generalised linear model (GLM), with 'interaction strength' as the
243 response variable and 'origin' ('cold' or 'warm' stream) and 'transplant temperature' (17.5
244 and 28.3 ºC) as potentially interacting factors. We used this analysis to determine (i) whether
245 interaction strengths differed between snails that originated from the warm or cold streams
246 (e.g. a main effect of 'origin'); (ii) whether interaction strengths were temperature dependent
247 (e.g. a main effect of 'temperature'); and (iii) whether the temperature dependence of
248 interaction strength differed between the snails from the cold and warm streams (e.g.
249 interaction between 'origin' and 'temperature'). The design of the reciprocal transplant
250 experiment also enabled us to disentangle short-term temperature responses attributable to
251 acclimation (e.g. responses to the temperature in the 'transplanted' stream) from those
252 reflecting processes operating over longer, evolutionary time scales (e.g. adaptation to the
253 temperature in the stream of 'origin'). The second GLM included 'interaction strength' as the
254 response variable and 'timescale' ('short' or 'long') and 'transplant temperature' (17.5 and
255 28.3 ºC) as potentially interacting factors. Here, 'short-term' temperature responses were
256 characterised as the change in interaction strength between the stream of origin and the
257 transplant stream. By contrast, the 'long-term' temperature response was characterised as the
258 change in interaction strength comparing measurements made only when the snails were in
259 their stream of origin. We re-express the transplant temperature data as Boltzmann

260 temperatures $\left(\frac{1}{kT_c} - \frac{1}{kT}\right)$ so that the coefficients of the model yield activation energies in units

261 of eV (see E. (1)). In this analysis, a significant interaction between 'transplant temperature'

262 and 'timescale' would demonstrate that the temperature dependence of interaction strength

263 differs between the 'short-term' (E_{short}), and 'long-term' (E_{long}). We assume that E_{short}

264 captures rapid physiological plasticity (e.g. acclimation) in interaction strength in response to

265 a change in temperature and E_{long} captures both acclimation and adaptation (evolution).

266 Consequently, the component of the temperature sensitivity attributable to evolution is given

267 by $E_{\text{evol}} = E_{\text{long}} - E_{\text{short}}$.

268

269 **RESULTS**

270 **Metabolic thermal response curves**

271 The allometric scaling coefficient, α, and the apparent activation energy, E_a, were consistent

272 between the populations of *R. balthica* from the cold and warm streams (see Table 2 for

273 model comparison and estimated parameter values). The temperature normalised rate of

274 respiration, ln $b(T_c)$, and T_h (the temperature at which respiration was 50% inactivated) were

275 both higher in the population of *R. balthica* from the warm stream. Because the optimum

276 temperature, T_{opt}, depends strongly on T_h (see Eq. (2)), T_{opt} was higher in *R. balthica* from

277 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

278 T_{opt} were both higher, the warm populations of *R. balthica* had elevated *per capita* metabolic

279 rates across the full range of measurement temperatures (Fig. 2).

280

281

282

283 **Local adaptation of interaction strength**

284 Interaction strength increased with elevated transplant temperature for the populations of *R.*
285 *balthica* from both the warm and the cold streams (Fig. 3; main effect of 'transplant
286 temperature' (GLM, $t_{1,21}$=2.56; $p<0.01$). Furthermore, interaction strengths were consistently
287 higher for the populations of *R. balthica* from the warm stream in both transplant
288 temperatures (Fig. 3; GLM main effect of 'origin' $t_{1,21} = 2.90$; $p < 0.005$). These findings are
289 consistent with the higher respiration rates observed in the warm population (Fig. 2) and
290 highlight the association between metabolism and interaction strength.
291
292 **Disentangling the effects of acclimation and adaptation on interaction strength**
293 Our experimental design enabled us to compare temperature sensitivities that capture short-
294 term thermal acclimation (e.g. changes in interaction strength in response to the reciprocal
295 transplant) as well as the long-term temperature sensitivity, which also includes effects of
296 local adaptation (e.g. changes in rates between warm and cold populations quantified in the
297 stream of origin). We found that interaction strength increased with temperature in both the
298 short- and the long-term (Fig. 3). However, the magnitude of the temperature response was
299 significantly larger in the long-term (Fig. 3; interaction between 'transplant temperature' and
300 'timescale' on interaction strength; GLM $t_{1,18}$= -2.19; $p < 0.05$), where, the average E_{short} was
301 0.46 eV, while E_{long} was significantly higher at 0.99 eV. This divergence between the short-
302 and long-term temperature sensitivities implies a non-trivial contribution of evolution in
303 amplifying the effects of temperature on interaction strength *in situ*, with the contribution of
304 E_{evol} of 0.51 and 0.53 eV in the cold and warm adapted populations respectively.
305
306 **DISCUSSION**
307 Understanding how global warming will affect the strength of consumer-resource interactions
308 and the stability of aquatic food webs is a fundamental challenge in evolutionary ecology that

309 requires insight on the short-term effects of temperature on metabolism and interaction traits
310 as well as how these processes are modulated by evolution over longer time scales. There is
311 evidence from terrestrial (Rall *et al.* 2010; Vucic-Pestic *et al.* 2011; Barton 2011; Brose *et al.*
312 2012), freshwater (Kratina *et al.* 2012) and marine ecosystems (Sanford 1999), that warming
313 is likely to increase the strength of consumer-resource interactions, at least in the short-term,
314 owing to the exponential effects of temperature on the consumption rates of mobile
315 ectothermic consumers (Dell *et al.* 2014; Gilbert *et al.* 2014). What is less clear however, is
316 how rapid evolutionary adaptation to rising temperatures will modulate the direct effects of
317 warming on species interactions. Space-for-time substitutions across broad spatial scales
318 indicate that local adaptation to different thermal regimes can play an important role in
319 shaping species interactions, often compensating for the direct effects of temperature on
320 interaction traits (Barton 2011; De Block *et al.* 2012). Here, we build on this work by
321 investigating the effects of temperature and local adaptation on the interaction between the
322 gastropod grazer, *R. balthica*, and its algal resource. Our study contributes novel insights in a
323 number of ways. First, we explore patterns of local adaptation over a relatively small spatial
324 scale (m as opposed to km). The two streams in our experiment are separated by
325 approximately 500 m but differ in temperature by 11 ºC. Because dispersal, gene flow and
326 genetic divergence among populations in this species are strongly related to geographic
327 distance (Johansson *et al.* 2016), our study over a relatively small spatial scale, provides
328 insight into how closely related natural populations evolve in response to warming and is
329 therefore directly relevant for understanding adaptation to climate change (Richter-Boix *et al.*
330 2010; Keller *et al.* 2013; Merilä and Hendry 2014). Second, we quantified the effects of
331 temperature on both metabolic and consumption rates to determine the mechanisms
332 underpinning patterns of thermal adaptation and their influence on the strength of consumer-
333 resource interactions.

334 We found significant variation in the thermal response curves for respiration between
335 the populations of *R. balthica* from the warm and cold streams. The optimum temperature
336 (T_{opt}) for respiration was higher in the warm population (i.e. metabolic rates peaked at higher
337 temperatures). Furthermore, the inactivation energy (E_h) was lower in the warm population,
338 indicating that declines in the rate of respiration after the optimum (i.e. at high temperatures)
339 were less pronounced than in grazers from the cold stream, where metabolic rates peaked at
340 lower temperatures and declined markedly at temperatures above T_{opt}. These divergences in
341 metabolic traits suggest that the metabolism of the warm and cold populations of *R. balthica*
342 reflect local adaptation to the different thermal regimes in these streams. Whilst the higher
343 T_{opt} and lower E_h in the warm population were in line with expectations assuming local
344 thermal adaptation, we found no evidence that metabolic performance at high temperature
345 was traded-off against performance at low temperature. Instead, metabolic rates were higher
346 for *R. balthica* from the warm stream across all measurement temperatures. These results are
347 in broad agreement with the "hotter is better" hypothesis, which proposes that maximal
348 performance of organisms with higher optimal temperatures should be greater than those with
349 lower optimum temperatures because of the thermodynamic constraints imposed by high
350 temperatures on enzyme kinetics (Huey and Kingsolver 1993; Kingsolver *et al.* 2004;
351 Angilletta *et al.* 2010). Indeed maximal respiration rates in the population from the warm
352 stream were greater than those from the cool (warm stream: 8.26 ± 0.41 μmol O_2 L^{-1} h^{-1}, cool
353 stream: 7.3 ± 0.22 μmol O_2 L^{-1} h^{-1}). The lower E_h, (i.e. the steepness of the decline of the
354 thermal reaction norm past the optimum), and higher ln $b(T_c)$, i.e. the rate of respiration
355 normalised to 18 ºC, in the warm population also meant that the thermal response curve for *R.*
356 *balthica* from the warm stream was broader. In agreement with previous work (e.g. on
357 bacteriophages, Knies *et al.(* 2009)), our data for the gastropod *R. balthica* indicate that
358 adaptation to higher temperatures resulted in both greater maximal metabolic performance

359 and a broader metabolic thermal reaction norm.

360 The general patterns observed in the metabolic traits were also reflected in the effects
361 of temperature on interaction strength. Interaction strength was higher for individuals placed
362 in the warm stream, irrespective of their stream of origin. These findings suggest that
363 elevated temperatures increase consumption rates though the effects of temperature on
364 respiratory physiology, but local adaptation to warmer environments also results in a
365 correlated increase in metabolism and interaction strength at low temperature. This may have
366 important wider implications for the effects of warming on the structure, functioning and
367 stability of aquatic food webs (Rall *et al.* 2010; O'Connor *et al.* 2011; Vucic-Pestic *et al.*
368 2011; Dell *et al.* 2014; Fussmann *et al.* 2014; Gilbert *et al.* 2014, Fussmann *et al.* 2017). If
369 adaptive responses to increasing temperature give rise to higher maximal rates of metabolism
370 and consumption as well as elevating rates at lower temperatures, then the effects of warming
371 on the strength of consumer-resource interactions in the long-term could be greater than
372 previously anticipated (Gilbert *et al.* 2014). Indeed, work on experimental warming of
373 aquatic ecosystems has shown that increases in the strength of top-down control can have
374 profound effects on community structure and ecosystem processes (Burgmer and Hillebrand
375 2011; Kratina *et al*. 2012; Yvon-Durocher *et al*. 2015). Elevated grazing rates at warmer
376 temperatures can have a wide range of impacts in aquatic systems, with evidence for both
377 increases (Yvon-Durocher *et al.* 2015) and decreases (Burgmer and Hillebrand 2011) in algal
378 species richness, biomass and productivity.

379 In our experiments, the thermal sensitivities of metabolic rates were much larger than
380 those of interaction strengths in the short-term (e.g. 0.96 and 0.45 eV respectively), in line
381 with findings in other invertebrate systems (Rall *et al.* 2010; Vucic-Pestic et al. 2011;
382 Fussmann et al. 2014). These findings suggest that rates of grazing and metabolism were
383 clearly linked, but became decoupled when individuals experience rapid changes in

384 temperature that depart substantially from those in their local environment. In the short-term,
385 if increases in metabolic demands with temperature are greater than those of consumption
386 rates (as found here), then less energy will be transferred from the resource to the consumer
387 (i.e. more is lost through respiration, see also Rall *et al.* 2010). If such imbalances are
388 maintained over long periods of time then starvation of the consumer can ultimately result in
389 a decline in top-down control on the resource (Fussman *et al.* 2014, Binzer *et al* .2016).
390 However, when consumers' feeding rates are more sensitive to temperature than metabolic
391 rates, interaction strengths can become amplified in warmer environemnts, leading to faster
392 resource depletion and eventually driving either the resource or the consumer to extinction
393 (Vasseur &McCann 2005). Long-term effects of temperature on interaction strengths have so
394 far only been explored using food web models, parameterised using temperature sensitivities
395 derived from short-term experiments (Vasseur &McCann 2005; Rall *et al.* 2010; Fussman *et*
396 *al.* 2014). Consequently, such analyses don't capture the capacity for thermal adaptation to
397 modulate *per capita* rates. Our results highlight substantial differences between the short- and
398 long-term effects of temperature on interaction strength; implying that thermal adaptation
399 plays an important role in maintaining the balance between metabolic and consumption rates
400 over the long-term.
401 We quantified the effects of local adaptation (evolution) on interaction strength by
402 comparing the short-and long-term effects of temperature in the reciprocal transplant
403 experiment. The short-term temperature response (E_{short}) captures the effects of physiological
404 plasticity over the 48h experiment. Conversely, the long-term response (E_{long}) also accounts
405 for processes operating over longer, evolutionary timescales. The E_{long} value was higher than
406 E_{short}, implying a significant role for evolution in shaping the effects of temperature on *in situ*
407 interaction strengths. Notably, the higher E_{long} was driven both by elevated grazing rates in
408 the warm populations in the warm stream and lower rates in the cold populations in the cold

409 stream. These results diverge from expectations based on the metabolic cold adaptation
410 hypothesis (Addo-Bediako *et al.* 2002) which would predict adaptation to higher
411 temperatures should dampen the acute effects of temperature on metabolic rates. On the
412 contrary, our results suggest that adaptation to warming amplified the effects of temperature
413 on metabolic as well as grazing rates. The lower interaction strengths in the population of *R.*
414 *balthica* locally adapted to the colder stream highlight that evolution can have unexpected
415 effects on species interactions. The evolutionary maintenance of lower than anticipated
416 grazing rates in the cold stream could be selected for since lower grazing rates might result in
417 greater food chain stability and/or stoichiometric homeostasis (Sterner & Elser 2002, Cross et
418 al. 2005; 2015) under the prevailing temperature regime. Thus, understanding the impacts of
419 environmental change on the strength of consumer-resource interactions over timescales that
420 are relevant to the rate of climate change (e.g. gradual warming over decades) will require an
421 appreciation both of the direct effects of rising temperatures on species interactions and the
422 reciprocal feedback between ecological and evolutionary dynamics (Fussmann *et al.* 2007;
423 Gravel *et al.* 2010; Loeuille 2010; Urban 2013; Barraclough 2015)
424
425 **Conclusions**
426 We used a natural geothermal temperature gradient to investigate how warming influences
427 the strength of algal-grazer interactions via the direct effects of temperature on metabolism
428 and consumption, and indirect feedbacks through evolutionary adaptation. Metabolic rates
429 and interaction strength increased with temperature in the same way for both the warm- and
430 cold-adapted populations of *R. balthica*, suggesting that rapid changes in temperature have a
431 consistent effect on interactions between mobile consumers and sessile resources, mediated
432 by the effects of temperature on consumer metabolic rates (Dell *et al.* 2014). However, the
433 warm-adapted populations had higher metabolic and grazing rates across all measurement

temperatures compared to their cold-adapted counterparts. These findings are consistent with the 'hotter is better and broader' hypothesis (Huey and 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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626 **Tables**

627 **Table 1. Physical and chemical characteristics of the streams**. Temperature data were
628 collected over a 3-day period. All other parameters were collected on the first day of the day
629 of the experiment. Temperature displayed as means ± 1SD. All other data were collected for
630 correlation with temperature across the entire catchment area (all 11 streams), i.e. replication
631 was on the level of stream identity.

Parameter	Stream 5	Stream 11 A
Average Temperature (5 days)	17.5 ± 4.5	28.3 ± 1.3
pH	7.63	7.17
Conductivity	273.6	235.7
NO_2	0.22	0.24
NO_3	0.57	0.29
NH_4	0.17	0.19
PO_4	0.27	0.35

632

633

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 model along with their standard deviations (± 1SD). C = cold stream. W = warm stream. See Supporting Information for details on model selection and information on AICsc 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	± 1SD
E_a	C: 0.96	0.06
ln $R(T_c)$	**C: 6.833**	**0.18**
	W: 7.06	**0.13**
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 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. **Lower panel**: Schematic overview of experimental set-up for the grazing experiment.

Figure 2 Thermal response curves for respiration. Thermal response curves of respiration rates 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 $R(T_c)$) 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 and metabolic rates. Long-term and short-term effects of temperature in interaction strength measured via the dynamic index. 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), with E_{long} significantly greater than E_{short}. Black boxplots for snails from the colder stream, while red denotes snails from the warmer stream.

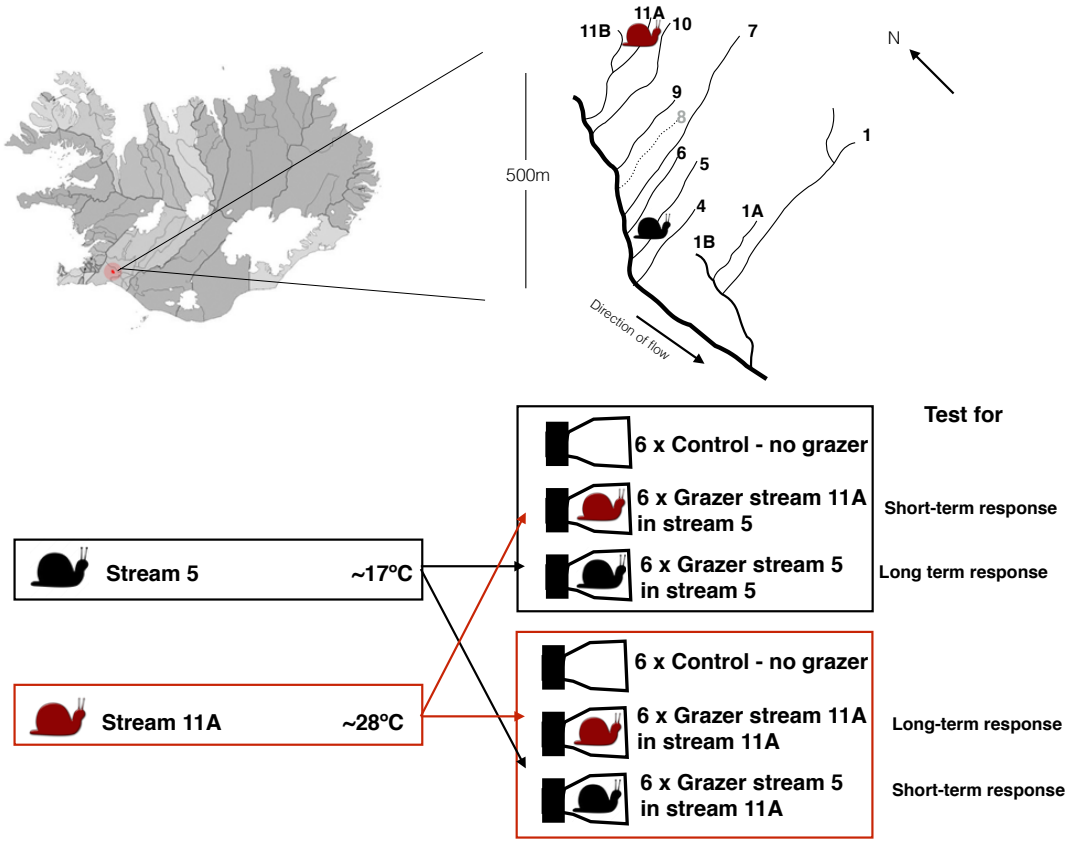
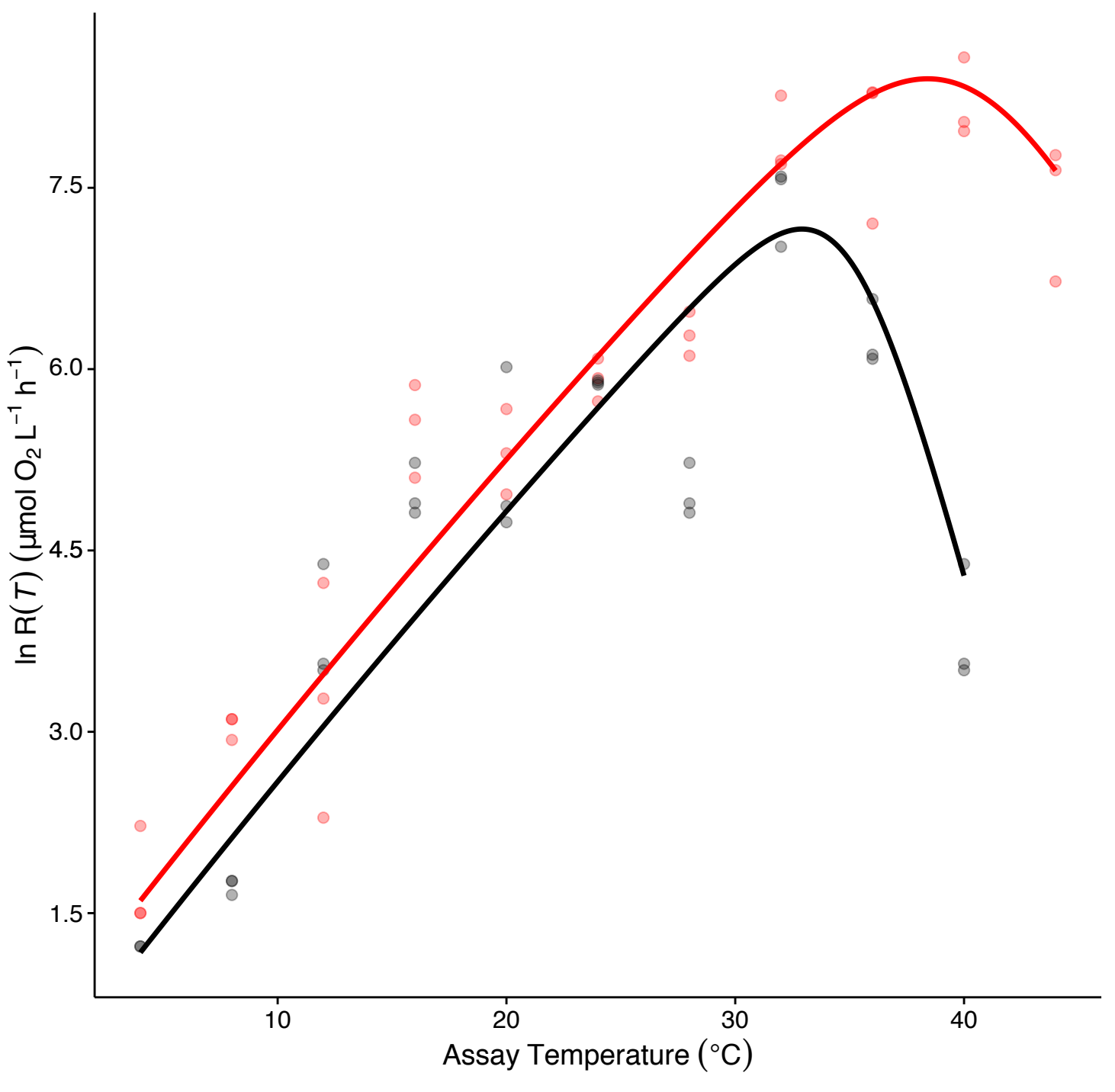
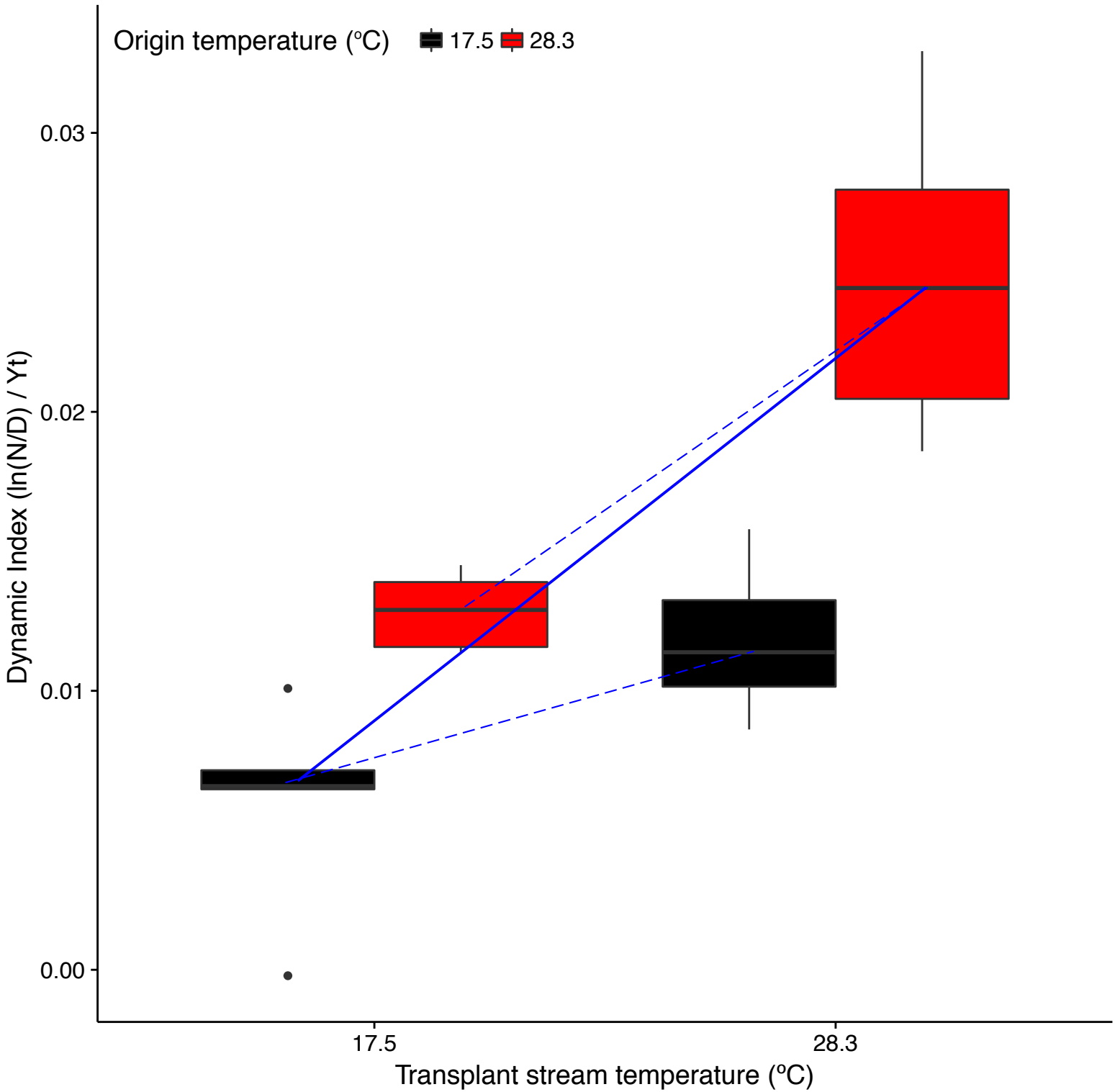


Figure 1: Map and experimental set-up. Top panel: The catchment area, with streams used in this experiment indicated by black (for the colder stream 5 with 17.5 ºC ± 4.5 ºC) and red (for the warmer stream 11A with 28.3 ºC ± 1.3 ºC) snail icons. **Lower panel**: Schematic overview of experimental set-up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


7.5
6.0
4.5
3.0
1.5
ln R(T) (μmol O2 L−1 h−1)
10
20
30
40
Assay Temperature (°C)


Origin temperature (°C)
17.5
28.3
0.03
0.02
0.01
0.00
Dynamic Index (ln(N/D) / Yt)
17.5
28.3
Transplant stream temperature (°C)