









PRIMARY RESEARCH ARTICLE

Thermal acclimation increases the stability of a predator–prey interaction in warmer environments

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Abstract

Global warming over the next century is likely to alter the energy demands of consumers and thus the strengths of their interactions with their resources. The subsequent cascading effects on population biomasses could have profound effects on food web stability. One key mechanism by which organisms can cope with a changing environment is phenotypic plasticity, such as acclimation to warmer conditions through reversible changes in their physiology. Here, we measured metabolic rates and functional responses in laboratory experiments for a widespread predator–prey pair of freshwater invertebrates, sampled from across a natural stream temperature gradient in Iceland (4–18°C). This enabled us to parameterize a Rosenzweig–MacArthur population dynamical model to study the effect of thermal acclimation on the persistence of the predator–prey pairs in response to warming. Acclimation to higher temperatures either had neutral effects or reduced the thermal sensitivity of both metabolic and feeding rates for the predator, increasing its energetic efficiency. This resulted in greater stability of population dynamics, as acclimation to higher temperatures increased the biomass of both predator and prey populations with warming. These findings indicate that phenotypic plasticity can act as a buffer against the impacts of environmental warming. As a consequence, predator–prey interactions between

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ectotherms may be less sensitive to future warming than previously expected, but this requires further investigation across a broader range of interacting species.

KEYWORDS

climate change, functional response, interaction strength, metabolic rate, phenotypic plasticity, population stability, thermal adaptation, trophic interaction

1 | INTRODUCTION

The average global surface temperature is on course to rise by at least 1.5°C above pre-industrial levels in the coming decades (Masson-Delmotte et al., 2018). Warming will not be evenly distributed across the globe, however, with the Arctic likely to experience more pronounced increases in temperature than other regions. Furthermore, the impacts of climate change will differ among ecosystem types, with marine environments expected to be more buffered against climate change than terrestrial or freshwater ecosystems (Woodward, Perkins, et al., 2010). Warming should alter the physiology of individuals, with the rate of energy and material uptake, transformation, and expenditure (i.e. metabolic rate) shown to increase exponentially up to the thermal optimum of the organism (Brown et al., 2004; Kordas et al., 2011). This could have direct effects on population biomasses but also indirect effects through changes in the strength of predator–prey interactions, with consequences for community structure and food web stability (Emmerson et al., 2004; Fussmann et al., 2014; Rall et al., 2010).

Differences in the acute temperature dependence (thermal sensitivity) of metabolic and feeding rates could either stabilize or destabilize population dynamics. For example, if energy intake by the predator outpaces its energy demand, and prey growth rate offsets predation pressure, then predator–prey dynamics should be stable (Vasseur & McCann, 2005). Alternatively, if predator feeding rates become too high in warmer environments, the stronger top-down control could lead to prey extinction (Vasseur & McCann, 2005). Similarly, if warming elevates metabolic rates more than feeding rates, then the reduction in energetic efficiency may lead to extinction of the predator due to starvation (Fussmann et al., 2014; Rall et al., 2010; Vucic-Pestic et al., 2011). It is thus crucial to understand how warming alters both metabolic demand and the strength of interactions between consumers and resources, to predict how future warming might alter community structure and food web stability.

A widely used method to quantify the strength of trophic interactions is the functional response, which describes the per capita feeding rate of a predator as a function of prey density (Holling, 1959). Functional response parameters include the following: attack rate, which describes the initial increase in feeding rate; handling time, which is the time taken to ingest and digest the prey and therefore limits the maximum feeding rate; and Hill exponent, which characterizes the shape of the functional response (e.g. linear, saturating, or sigmoidal). The effects of temperature on the functional

response have received increasing attention in climate change research (Archer et al., 2019; Englund et al., 2011; Rall et al., 2012; Uiterwaal & DeLong, 2020; Vucic-Pestic et al., 2011). In general, higher temperatures are associated with an increase in attack rates and a decrease in handling times (Rall et al., 2012); however, attack rates have also been shown to follow sigmoidal, dome-shaped, or power-law relationships with increasing temperature (Bailey, 1989; Englund et al., 2011; Gresens et al., 1982; Thompson, 1978; Uiterwaal & DeLong, 2020). Such changes in functional response parameters can have dramatic effects on population dynamics (Rall et al., 2008). Small modifications to the Hill exponent have also been demonstrated to stabilize chaotic dynamics and eliminate extinctions (Rall et al., 2008; Williams & Martinez, 2004). Yet, despite the potentially important effects on predator–prey interaction strengths, the temperature dependence of the Hill exponent has received surprisingly little attention (Daugaard et al., 2019; Uszko et al., 2017). Studies of temperature effects on functional response parameters are thus pivotal to understanding how population dynamics may change with warming.

Organisms are limited in the environments they can inhabit by both their physiological requirements and the degree to which they can moderate their physiology (Pörtner & Farrell, 2008). Ectotherms are particularly susceptible to environmental temperature, which directly affects their metabolism and behaviour (Bale, 2002; Deutsch et al., 2008). The range between minimum and maximum temperature that an organism can tolerate is called its thermal window, which determines whether it can persist in a given habitat or not (Dixon et al., 2009). If the thermal limits of an organism are exceeded through environmental warming, persistence of the species can be achieved through (1) dispersal into new habitats that match its thermal requirements; (2) evolutionary adaptation to the warmer environment through genetic shifts; or (3) phenotypic plasticity, which is the ability of an organism to modulate morphological, behavioural, or physiological traits (Abram et al., 2017; Leroi et al., 1994; Seebacher et al., 2015).

Acclimation is one particular type of phenotypic plasticity, which includes reversible changes in physiological phenotypes as a result of chronic exposure to a distinct environmental factor (Schulte et al., 2011; Wilson & Franklin, 2002). Thermal acclimation consists of a shift in the thermal window through exposure to higher temperatures (Hofmann & Todgham, 2010; Schulte et al., 2011), which may maintain the physiological performance of an organism in a warmer environment (although see Leroi et al., 1994; Wilson & Franklin, 2002). Recent studies have demonstrated compensatory effects of thermal acclimation on organismal responses to warming, with

a reduced thermal sensitivity of metabolic rates (Seebacher et al., 2015; Semsar-Kazerouni & Verberk, 2018), and even altered functional response parameters, with a decrease in attack rates and handling times following acclimation to higher temperatures (Sentis et al., 2015). Not all biological rates respond consistently to thermal acclimation (Sentis et al., 2015), however, and the topic requires more extensive investigation. There is also no clear understanding of the underlying energetics of predators and their prey, or the implications for population stability.

Here, our goal was to examine how environmental warming and thermal acclimation influence predator–prey dynamics using a model system: freshwater invertebrates collected from streams of different temperature in a single catchment. We hypothesized that acclimation to warmer environments would dampen the thermal sensitivity of (1) metabolic and (2) feeding rates (Seebacher et al., 2015; Semsar-Kazerouni & Verberk, 2018; Sentis et al., 2015), resulting in (3) higher energetic efficiencies and (4) more stable predator–prey dynamics at higher temperatures (Rall et al., 2010; Vasseur & McCann, 2005; Vucic-Pestic et al., 2011).

2 | METHODS

2.1 | Study system

Organisms were collected from the Hengill geothermal valley in Iceland, which has been extensively studied over the past decade (Friberg et al., 2009; O’Gorman et al., 2017, 2019; Woodward, Dybkjaer, et al., 2010). The system includes the river Hengladalsá and several of its tributaries, which are groundwater fed (Friberg et al., 2009). Due to geothermal activity in the Hengill region, the streams experience a temperature gradient from around 4–25°C, driven by indirect heating of bedrock, rather than direct upwelling of chemically altered water (O’Gorman et al., 2017). As a result, the streams are very similar in all other physiochemical characteristics (Friberg et al., 2009; O’Gorman et al., 2017), facilitating the study of temperature effects on organisms and communities without other confounding factors. Note that while dissolved oxygen concentration declines with temperature (a physical law that applies to all systems), the percentage saturation is independent of temperature across the gradient (Friberg et al., 2009) and never approaches the hypoxic conditions that could lead to interactive effects with temperature (Verberk et al., 2016).

Previous research in the system has shown that the dipteran larva *Limnophora riparia* is the most abundant invertebrate predator, while blackfly larvae from the Simuliidae family are the most abundant prey (O’Gorman et al., 2017). Both predator and prey are distributed across the entire temperature gradient in the system, although they are least common in the coldest streams and their population abundances increase log-linearly with temperature up to 25°C (Archer et al., 2019). *Limnophora riparia* is found in streams throughout the Palearctic region (Skidmore, 1985) and is an active suctional predator with a preferred diet of blackfly larvae (Merritt

& Wotton, 1988). Simuliidae larvae are largely sedentary filter feeding organisms, which are usually found securely attached to stone surfaces or vegetation in flowing waters (Werner & Pont, 2003). They often reach very high abundances and therefore play a key role in fuelling freshwater food webs (Malmqvist et al., 2004). Both predator and prey are highly likely to spend their larval life-stages in their natal freshwater stream (i.e. exposed to a single temperature regime), but have the potential to disperse throughout the landscape during their aerial adult stage (i.e. they are less likely to experience genetic selection for the environmental conditions of their natal stream over multiple generations). Thus, they are ideal organisms for studying the impacts of thermal acclimation in a natural setting on physiological and trophic responses to warming.

The sedentary nature of Simuliidae means that they do not exhibit a strong escape mechanism from the predator and are unlikely to be strongly influenced by thermal acclimation. Thus, we only aimed to manipulate the thermal acclimation of the predator in our feeding experiments to restrict our experimental design to a logistically feasible number of treatment combinations. Simuliidae prey (7.09 ± 1.39 mm; mean \pm SD body length) were hand-collected from the river Hengladalsá ($7.7 \pm 1.9^\circ\text{C}$) as a single source common to all experiments, whereas *L. riparia* predators (10.43 ± 1.39 mm; mean \pm SD body length) were hand-collected from three streams of different temperature between May and July 2015. We collected only third instar larvae of a similar size from all three streams to standardize the predator size as much as possible in the experiments (Figure S1). The streams were categorized as cold (IS11; $4.5 \pm 1.5^\circ\text{C}$), tepid (IS5; $13.8 \pm 0.9^\circ\text{C}$), and warm (IS8; $18.0 \pm 1.0^\circ\text{C}$) using Maxim Integrated DS1921G Thermochron iButtons, which logged temperature every 4 h from 1st May to 3rd July. Note that the warmest stream (IS8) only reached a maximum temperature of 20°C as the field expedition took place in early summer in a particularly cold year, although it can reach up to 25°C by late summer in hotter years (O’Gorman et al., 2019). All organisms were immediately transported to temperature-controlled facilities at the University of Iceland, which were set to the same temperatures as their ‘home streams’. The organisms were maintained in aquaria filled with water from the river Hengladalsá, which was continuously aerated using air pumps.

2.2 | Metabolic rate experiments

To quantify the effect of thermal acclimation on the temperature dependence of the predator’s metabolic rate, we measured the oxygen consumption rate of individual *L. riparia* from the cold, tepid, and warm streams at 5, 10, 15, 20, and 25°C. Before each experiment, individuals were confined in glass chambers immersed in a water bath to allow them to adjust to the experimental temperature for 15 min. The glass chambers were completely filled (i.e. no headspace) with water from the river Hengladalsá, which was filtered through a 0.45 µm Whatman membrane filter and bubbled to reach 100%

oxygen saturation. Note that by using stream water from a common source, the starting concentration of oxygen in the experiments was always approximately the same. A magnetic stir bar was placed at the bottom of each chamber but separated from the organism by a mesh screen. In each trial, one individual *L. riparia* was placed in each of seven chambers and the eighth chamber was used as an animal-free control to account for sensor drift and any background microbial respiration (which was minimal throughout).

Oxygen consumption was measured with an oxygen microelectrode (MicroResp, Unisense) fitted through a capillary in the gas-tight stopper of each chamber. Three measurement periods were recorded for each individual predator (10–15 s each, where oxygen concentration was measured every second). Oxygen concentrations were not allowed to drop below 70% of the starting value to avoid stressing the predators, measuring anaerobic metabolism, or quantifying non-linear oxygen depletion. Metabolic rates [$\mu\text{mol O}_2 \text{ h}^{-1}$] were calculated as the best-fitting line through all the data points measured in each chamber, corrected for background rates in the animal-free control chamber, then converted to energetic equivalents [J h^{-1}] using atomic weight (1 mol $\text{O}_2 = 31.9988 \text{ g}$), density (1.429 g L^{-1}), and a standard conversion (1 ml $\text{O}_2 = 20.1 \text{ J}$; Peters, 1983). Metabolic rate was measured for 5–10 individuals of the cold, tepid, and warm populations of *L. riparia* at each experimental temperature, with a new individual used in every trial. The body length of *L. riparia* was measured after each trial to estimate individual dry mass, M_L [mg], from length–weight relationships established for the system (Archer et al., 2019).

The temperature dependence of metabolic rate was estimated using an Arrhenius temperature term, as in the Metabolic Theory of Ecology (Brown et al., 2004; Rall et al., 2012):

$$I = I_0 M_L^{b_I} e^{E_I \frac{T - T_0}{kT_0}}, \quad (1)$$

where I_0 is the metabolic rate at T_0 , b_I is an allometric exponent, E_I [eV] is the activation energy (or slope of the ln-linear scaling with Arrhenius temperature), k [$8.618 \times 10^{-5} \text{ eV K}^{-1}$] is the Boltzmann constant, T [K] is the absolute experimental temperature, and T_0 [283.15 K] is the normalization temperature. We additionally modelled the acclimation temperature of the predator as a categorical predictor:

$$I = I_{0A} M_L^{b_I} e^{E_{IA} \frac{T - T_0}{kT_0}}. \quad (2)$$

This means that for each level of acclimation temperature (A = cold, tepid, or warm), we allowed individual intercepts and/or slopes in the ln-linear scaling of the continuous predictor experimental temperature.

We examined four versions of Equation (2): (a) individual intercepts and slopes for acclimation temperature; (b) individual intercepts only for acclimation temperature; (c) no effect of acclimation temperature; and (d) no effect of acclimation or experimental temperature (see Figure S2 for a conceptualization of each model). We used Bayesian parameter estimation and the leave-one-out cross-validation information criterion (LOOIC) to determine the most parsimonious model (see Section 2.4 below).

2.3 | Functional response experiments

Functional response experiments were conducted in a climate chamber (GRAM K400LE, type 3011-1F4B) at the University of Iceland. Plastic cylindrical containers (7.3 cm diameter, 11.5 cm height) filled with 100 ml water collected from the river Hengladalsá served as experimental arenas. Each experimental unit encompassed one predator individual and prey individuals varying in their initial densities (1, 2, 3, 4, 8, 16, 32, or 48 individuals). Note that these densities are representative of the natural environment, where Simuliidae can reach up to 8500 individuals m^{-2} (or 36 individuals per unit area of our experimental arenas; Archer et al., 2019). Predators were starved for at least 24 h prior to the beginning of each experiment. All prey individuals were placed in the arenas first to help them become accustomed to the new environment before predators were added. Experimental arenas were placed randomly in the climate chamber so there was no systematic pattern in the treatment combinations. Experiments were run at four temperatures (4, 6, 10, and 18°C, which was the maximum temperature of the climate chamber) for precisely 24 h, during which time aeration was not provided to avoid any physical disturbance during the experiment. At the end of each experiment, predators were removed, and the remaining living prey were counted. Predator and prey larvae occasionally pupated during the experiments, which prevents the predator from feeding, but leaves the prey vulnerable to predation. As such, experimental units where the predator had pupated were discounted, but pupated prey individuals were still counted as living prey. To assess natural mortality of the prey, one predator-free control was added for every prey density in each experimental block. The experiments consisted of all possible combinations of the three predator populations (i.e. cold, tepid, and warm acclimation), eight prey densities, four experimental temperatures, and at least three replicates, resulting in 297 experimental units and 58 predator-free controls.

To account for natural mortality of the prey, we numerically integrated prey decline in the predator-free controls over the experimental duration ($t = 1 \text{ day}$), as per Rosenbaum and Rall (2018):

$$\frac{dN}{dt} = -mN, \quad (3)$$

where m is the natural mortality rate [individuals day^{-1}] and N is the initial prey density [individuals arena^{-1}]. Temperature dependence was incorporated into Equation (3) as for Equation (1), that is, scaling m by an Arrhenius temperature term:

$$m = m_0 e^{E_m \frac{T - T_0}{kT_0}}. \quad (4)$$

We used Bayesian parameter estimation and LOOIC to determine the density dependence of natural mortality and any associated temperature dependence (see Tables S1 and S2; Figure S3).

Saturation for feeding was not reached in the experimental data, making it difficult to estimate handling time (Rosenbaum & Rall, 2018). Therefore, large initial prey densities (i.e. 32 and 48) were

excluded from the dataset in order to fit a non-saturating generalized functional response:

$$F(N) = aN^h, \quad (5)$$

where a is the attack coefficient describing the linear increase in attack rate, N is the prey abundance, and h is the Hill exponent. There was no replacement of consumed or dead prey during the experiments, hence prey density declined over time. Thus, the change in prey abundance over time [individuals day⁻¹], accounting for both predation and natural mortality, was expressed as the ordinary differential equation:

$$\frac{dN}{dt} = -aN^hP - mN, \quad (6)$$

where P is the abundance of the predator [1 individual arena⁻¹]. All functional response models were fitted using the mean parameter values from the best-fitting model for natural mortality as fixed values in Equation (6; Table S2). The temperature dependences of a and h were incorporated into Equation (6) by scaling each parameter by an Arrhenius temperature term, as for m in Equation (4). We additionally modelled the acclimation temperature of the predator as a categorical predictor, as in Equation (2). This resulted in 16 different models, that is, four models for $a \times$ four models for h , where each functional response parameter can have (a) individual intercepts and slopes for acclimation temperature; (b) individual intercepts only for acclimation temperature; (c) no effect of acclimation temperature; and (d) no effect of acclimation or experimental temperature (see Figure S2). We again used Bayesian parameter estimation and LOOIC model selection to determine the most parsimonious functional response model.

2.4 | Model fitting and comparison

All data and statistical analyses were conducted in R 4.0.2. We combined numerical simulations of Equation (6) (including the temperature dependence of a , h , and m , as indicated in Equation 4) with Bayesian parameter estimation by drawing samples from the posterior probability distribution $p(\theta|z)$ of the free parameters θ given the data z , based on the likelihood function $p(z|\theta)$ and a prior distribution $p(\theta)$. We used Hamiltonian Monte Carlo sampling in Stan via the R-package 'rstan'. The software includes a backward differentiation algorithm for numerical simulation of ordinary differential equations. In each iteration of the Monte Carlo sampling (for a given parameter combination θ), the numerical solution for the predicted prey density at the end of the experiment, \hat{N}_{end} , was calculated for each given initial prey density, N_{start} . The likelihood was calculated assuming binomial distributions of the observed numbers of dead prey, N_{dead} with $n = N_{\text{start}}$ trials and $p = \frac{N_{\text{start}} - N_{\text{end}}}{N_{\text{start}}}$ success probabilities. We used a normal distribution with a mean of zero and a standard deviation of 2 as weakly informative priors for all free parameters (note

that all scalings are on the ln-linear scale). We used LOOIC for model comparison, which is computed from the log-likelihood values of the posterior samples in the R-package 'loo'. We fitted all models by running four individual MCMC chains with an adaptation phase of 1000 iterations and a sampling phase of 10,000 iterations each, summing up to 40,000 samples of the posterior distribution. Visual inspection of the trace plots and density plots showed a good mixture of the chains. Gelman–Rubin statistics of $\hat{R} < 1.01$ and an adequate effective sampling size (i.e. the estimated number of independent samples) verified convergence (Gelman & Hill, 2006).

2.5 | Predicted effects on energetic efficiency

To determine the potential impact of thermal acclimation on the energetic constraints of the predator, we calculated a dimensionless energetic efficiency, y , at each acclimation temperature, A , as the ratio of feeding rate to metabolic rate:

$$y_A = \frac{\omega_A F_A}{I_A}. \quad (7)$$

Here, I_A is the model-predicted metabolic rate (and associated model uncertainty) at each level of acclimation temperature (A = cold, tepid, or warm), with values of T in Equation (2) corresponding to the temperature of each stream (i.e. 4.5, 13.8, and 18.0°C, respectively). Note that this is equivalent to measuring metabolic rate in situ, that is, with an experimental temperature that matches the environment the organism is acclimated to. F_A is the model-predicted feeding rate (and associated model uncertainty) at each level of acclimation temperature, with values of N in Equation (5) corresponding to average summer densities of Simuliidae in each stream measured over an 8-year period (Archer et al., 2019). Feeding rates [individuals day⁻¹] were converted to energetic equivalents [J h⁻¹] using the average ash-free dry mass of Simuliidae used in the experiments (0.546 mg) and an established conversion factor of 23.1 J mg⁻¹ (Cummins, 1967). Finally, ω_A is the assimilation efficiency, which was estimated at each level of acclimation temperature using an established temperature dependence (Lang et al., 2017):

$$\omega = \frac{\omega_0 e^{\frac{E_w}{RT_0^*} - \frac{E_w}{RT^*}}}{1 + \omega_0 e^{\frac{E_w}{RT_0^*} - \frac{E_w}{RT^*}}}. \quad (8)$$

Here, ω_0 [e^{2.266}] is the intercept of the linearized version of Equation (8) at T_0^* [293.15 K] and E_w [0.164 eV] is the activation energy for carnivorous invertebrates (Lang et al., 2017). Note that values of $y \geq 1$ in Equation (7) indicate that the feeding rate of the predator is sufficient to meet its metabolic demands while values of $y < 1$ suggest that the predator is energetically constrained.

2.6 | Stability analysis

To determine the consequences of thermal acclimation for population stability, we set up the following Rosenzweig–MacArthur population dynamical model (Rosenzweig & MacArthur, 1963; Williams et al., 2007):

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) - aN^h P, \quad (9)$$

$$\frac{dP}{dt} = \omega c a N^h P - IP. \quad (10)$$

Equation (9) models the change in prey abundance through time [individuals arena⁻¹ day⁻¹] using a logistic growth term with growth rate r and carrying capacity K , and a loss term based on the functional response defined in Equation (5; note that r is a population growth rate which implicitly includes natural mortality). Equation (10) models the change in predator abundance through time [individuals arena⁻¹ day⁻¹] using a growth term based on the same functional response with assimilation efficiency ω and a body mass conversion factor c , and a loss term based on the metabolic rate defined in Equation (2).

The system was parameterized using an established intrinsic rate of prey population growth, r , for invertebrates (Savage et al., 2004; Sentis et al., 2015):

$$r = r_0 M_S^{b_r} e^{\frac{E_r}{kT}}. \quad (11)$$

Here, r_0 is a normalization constant independent of body size and temperature [1.166×10^{14} individuals day⁻¹], M_S is the body mass of Simuliidae prey [μg], b_r is an allometric exponent [-0.25], and E_r is the activation energy for invertebrates [-0.84 eV]. We used ln-linear temperature scaling of Simuliidae abundance in the Hengill system [individuals arena⁻¹] as a proxy for prey carrying capacity (Archer et al., 2019):

$$K = 10e^{2.2295 \frac{T-T_0}{kT_0}}. \quad (12)$$

Note that we chose an intercept that scaled carrying capacity in line with field abundances of Simuliidae, but an exploration of different intercept values indicated no qualitative change in the results (see Figure S4).

The scaling of the functional response parameters a and h with experimental and acclimation temperature was determined from the functional response experiments, and assimilation efficiency was estimated using Equation (8). The conversion factor c was defined as prey body mass, M_S , divided by predator body mass, M_L , where individual body masses of the predator and prey [mg] scale ln-linearly with experimental temperature, as observed in the Hengill system:

$$M_S = -4.9230e^{1.9987 \frac{T-T_0}{kT_0}}, \quad (13)$$

$$M_L = -2.2473e^{0.3944 \frac{T-T_0}{kT_0}}. \quad (14)$$

Finally, the scaling of the predator's metabolic rate with body mass and experimental and acclimation temperature was determined from the oxygen consumption experiments.

Equilibrium densities of the system [individuals arena⁻¹] were calculated using isoclines from Equations (9) and (10; $\frac{dN}{dt} = 0$, $\frac{dP}{dt} = 0$):

$$P^* = \frac{-r(K-N)N^{1-h}}{aK}, \quad (15)$$

$$N^* = \left(\frac{I}{a\omega c} \right)^{\frac{1}{h}}. \quad (16)$$

For $h \geq 1$, P^* is a monotonically decreasing function of N . This means that if $N^* < K$, the intersection (N^*, P^*) is a stable equilibrium (Rosenzweig & MacArthur, 1963). For $0 < h < 1$, P^* is a hump-shaped function of N . The maximum of $P^*(N)$ is located at $N_{\text{hump}} = \frac{K(h-1)}{h-2}$ (solving for $\frac{dP^*}{dN} = 0$). Right of the maximum, $P^*(N)$ is declining. Again, this means that (N^*, P^*) is a stable equilibrium, if $\frac{K(h-1)}{h-2} < N^* < K$. Left of the maximum, the equilibrium is unstable, and the system exhibits cyclic dynamics that lead to the extinction of both predator and prey for $0 < N^* < \frac{K(h-1)}{h-2}$. This scenario did not occur in the investigated temperature range. If $N^* > K$, the predator will go extinct and a stable equilibrium is found at $(K, 0)$. The resulting equilibrium biomasses [mg arena⁻¹] were calculated by multiplying equilibrium abundances by individual body masses of the predator and prey (see Figure S5 for examples of predator prey dynamics).

3 | RESULTS

3.1 | Metabolic rate

According to LOOIC (Table S3), the temperature dependence of metabolic rate for *L. riparia* was best described by the ln-linear model that included individual intercepts and slopes for acclimation temperature (Table 1; Figure S2a). The slope of the temperature scaling for tepid-acclimated *L. riparia* was significantly smaller than for both

TABLE 1 Mean, standard deviation (SD), and 95% credible intervals of the posterior distribution of parameters describing the best-fitting model for metabolic rate in *Limnophora riparia* ($n = 132$)

Parameter	Mean	SD	2.5%	97.5%
$\ln(I_{0,\text{cold}})$	-0.805	0.072	-0.853	-0.664
$\ln(I_{0,\text{tepid}})$	-0.350	0.099	-0.416	-0.156
$\ln(I_{0,\text{warm}})$	-0.953	0.080	-1.007	-0.794
b_1	0.451	0.074	0.402	0.597
$E_{\text{I,cold}}$	0.442	0.060	0.402	0.558
$E_{\text{I,tepid}}$	0.270	0.059	0.230	0.387
$E_{\text{I,warm}}$	0.690	0.057	0.652	0.802

the cold- and warm-acclimated populations (posterior probabilities: $p = 0.028$ and $p < 0.001$, respectively; Figure 1), partially supporting our first hypothesis. Predicted metabolic rates for cold- and warm-acclimated populations showed a wide overlap over the whole range of experimental temperatures (Figure 1), and were generally lower than the predicted rates for tepid acclimation. This indicates a hump-shaped relationship of metabolic rates with acclimation temperature, that is, cold < tepid > warm when measured at temperatures < 20°C.

3.2 | Functional response

According to LOOIC (Table S4), the best-fitting functional response model included individual intercepts and slopes for the effect of acclimation temperature on the experimental temperature dependence of the attack coefficient, and a single slope for the experimental temperature dependence of (i.e. no effect of acclimation temperature on) the Hill exponent (Table 2). Both the attack coefficient and Hill exponent increased with experimental temperature (Figure 2), leading to higher overall feeding rates in warmer environments (Figure S6). The slope of the temperature scaling for the attack coefficient of cold-acclimated *L. riparia* was higher than for both the tepid- and warm-acclimated populations (posterior probabilities: $p < 0.001$ and $p = 0.009$, respectively; Figure 3). No strong evidence was found for a difference in slopes ($p = 0.158$) or intercepts ($p = 0.083$) between tepid and warm acclimation. This implies that there was no significant

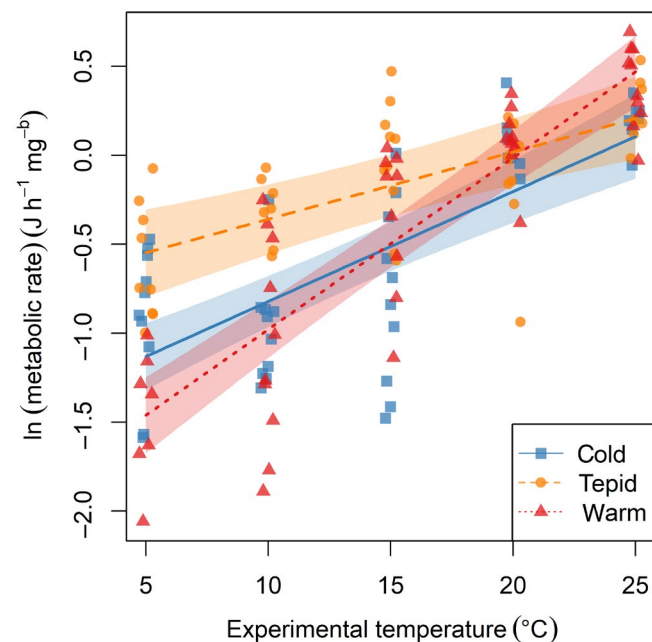


FIGURE 1 Temperature dependence of per-unit-biomass metabolic rate in the predatory dipteran *Limnophora riparia* for populations acclimated to cold, tepid, and warm streams. Solid lines and shaded areas represent the median and 95% credible intervals of the predictions, respectively. Note that we present mass-corrected metabolic rates in the figure after dividing the raw rates by body mass raised to the allometric exponent b_1 (see Table 1)

difference in the temperature dependence of attack coefficient between the tepid- and warm-acclimated populations of *L. riparia*, but there was a significantly stronger temperature dependence of attack

TABLE 2 Mean, standard deviation, and 95% credible intervals of the posterior distribution of parameters describing the best-fitting functional response model ($n = 255$)

Parameter	Mean	SD	2.5%	97.5%
$\ln(a_{0,cold})$	-0.816	0.203	-1.210	-0.445
$\ln(a_{0,tepid})$	-1.514	0.256	-2.067	-1.057
$\ln(a_{0,warm})$	-1.216	0.256	-1.759	-0.761
$E_{a,cold}$	0.815	0.269	0.255	1.310
$E_{a,tepid}$	-0.263	0.370	-1.039	0.409
$E_{a,warm}$	0.067	0.414	-0.816	0.811
$\ln(h_0)$	0.030	0.103	-0.174	0.228
E_h	0.322	0.156	0.024	0.627

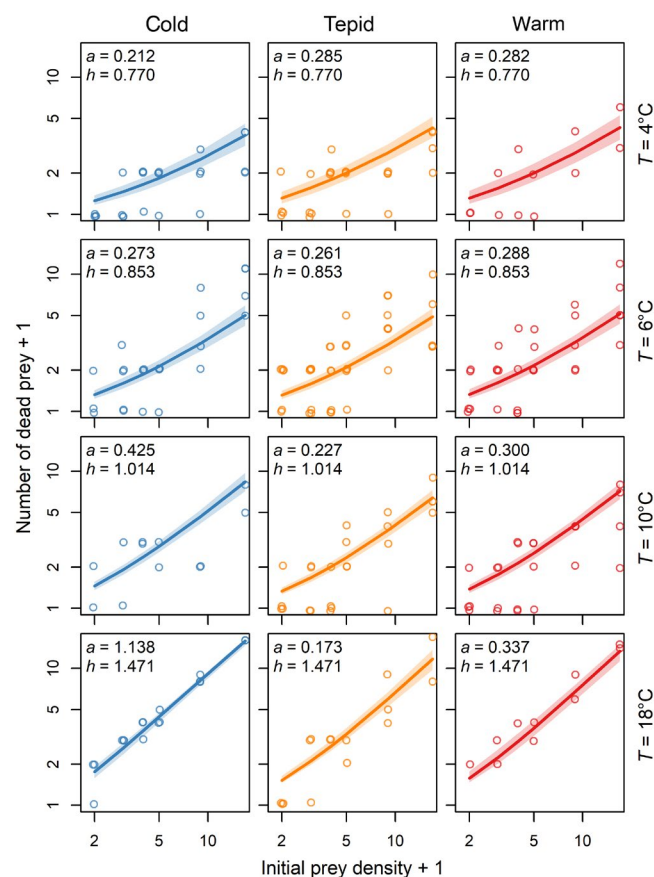


FIGURE 2 Number of dead prey (Simuliidae) that were observed (circles) and predicted (lines) in the functional response experiments, depending on initial prey density, following exposure to individuals of the predatory *Limnophora riparia* acclimated to cold, tepid, and warm streams. Solid lines and shaded areas depict the median and 95% credible intervals of the predictions, respectively. We added an offset of 1 to all values to plot the axes on a log scale. Values for a and h in each panel represent the median estimated values of the posterior according to the best-fitting model

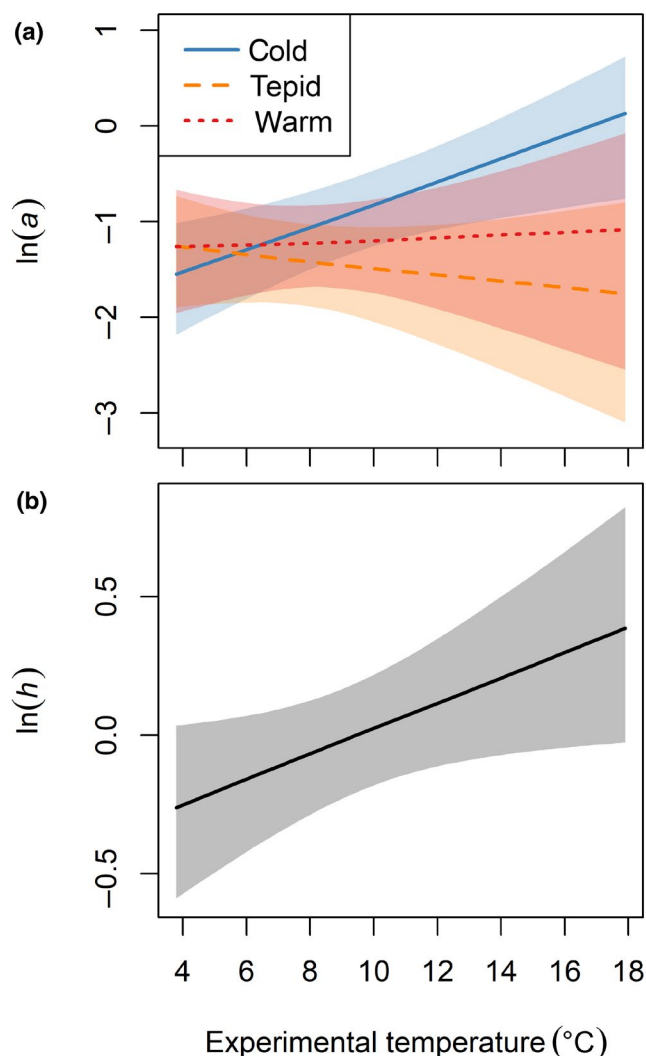


FIGURE 3 Effect of experimental temperature on the functional response parameters (a) attack coefficient, a and (b) Hill exponent, h . The best-fitting model indicated an additional effect of the categorical predictor acclimation temperature (populations of the predatory dipteran *Limnophora riparia* acclimated to cold, tepid, and warm streams) on the temperature dependence of the attack coefficient. Solid lines and shaded areas depict the median and 95% credible intervals of the predictions, respectively

coefficient in the cold-acclimated population (Figure 3), in support of our second hypothesis.

3.3 | Predicted effects on energetic efficiency

Model-predicted metabolic rates for the cold-acclimated population of *L. riparia* were lower than for both the tepid- and warm-acclimated populations at their home-stream temperatures (posterior probabilities: $p < 0.001$), with no difference between the latter two populations ($p = 0.063$; Figure 4a). Model-predicted feeding rates for the cold-acclimated population of *L. riparia* at its home-stream temperature were lower than the tepid-acclimated

population ($p < 0.001$), which was, in turn, lower than the warm-acclimated population ($p < 0.001$; Figure 4b). The energetic efficiency of the cold-acclimated population was below the threshold value of 1 (Figure 4c), indicating that it should struggle to meet its energetic demands at its home-stream temperature. Its energetic efficiency was also lower than the tepid-acclimated population ($p < 0.001$), which was, in turn, lower than the warm-acclimated population ($p < 0.001$; Figure 4c), supporting our third hypothesis. These changes in energetic efficiency were largely driven by acclimation effects on the attack coefficient, rather than metabolic rate or the Hill exponent (Figure S7). The increasing density of prey with increasing temperature in the natural system also had some influence on the changes in energetic efficiency, with minimal effect of predator body mass or assimilation efficiency (Figure S8).

3.4 | Stability analysis

Population dynamical modelling indicated that the prey population should persist across the full range of experimental temperatures (Figure 5a). Prey biomass was predicted to be higher in the warmer streams if the predator was acclimated to higher temperatures (i.e. warm or tepid streams). The predator population was only predicted to persist at experimental temperatures above 9°C (Figure 5b), but predator biomass was predicted to be higher in the warmer streams if the predator was acclimated to higher temperatures (i.e. tepid or warm streams). This offers widespread support for our fourth hypothesis that acclimation of the predator to warmer environments should lead to more stable predator-prey dynamics at higher temperatures. Interestingly, the highest predator and prey biomasses were predicted to occur if the predator was acclimated to the tepid stream, suggesting a hump-shaped response to acclimation temperature. Cold-acclimated predators persisted in the system at lower temperatures than the tepid- and warm-acclimated predators, however, suggesting that predators performed worse at stream temperatures below their acclimation temperature.

4 | DISCUSSION

We have shown that acclimation to warmer environments either dampened or had neutral effects on the thermal sensitivity of metabolic rate for the predatory invertebrate, *L. riparia*. We also found that thermal acclimation reduced the attack coefficient of *L. riparia* feeding on Simuliidae prey, leading to lower feeding rates in warmer environments, but still greatly exceeding the predator's metabolic demand. Thus, thermal acclimation increased the predator's energetic efficiency at higher temperatures, promoting a greater population biomass of both the predator and the prey. These results indicate that increased energetic efficiency following acclimation to warmer conditions could be an important physiological mechanism

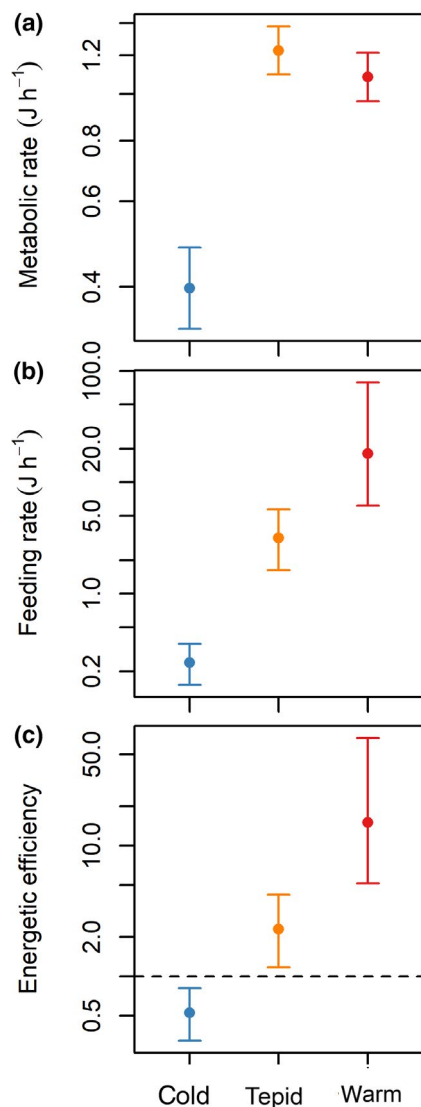


FIGURE 4 Model-predicted (a) metabolic rates and (b) feeding rates measured at the home-stream temperature of *Limnophora riparia* populations acclimated to cold, tepid, and warm streams. Rates are expressed in standardized energetic equivalents [J h^{-1}]. (c) Energetic efficiency of the cold-, tepid-, and warm-acclimated *L. riparia* populations, expressed as the dimensionless ratio of feeding to metabolism. All axes are shown on a log scale. Mean values \pm 95% credible intervals are shown. Values above or below the horizontal dashed line indicate that the predator's feeding rate is sufficient or insufficient to meet its metabolic demand, respectively

for increasing the stability of predator–prey interactions in the face of climate change.

4.1 | Thermal sensitivity of metabolic and feeding rates

Species interactions that involve ectotherms strongly depend on environmental temperature, as their physiology is directly influenced

by warming (Huey & Stevenson, 1979). As a result, factors that determine interaction strength such as metabolic rates and attack coefficients have been shown to scale predictably with environmental temperature (Brown et al., 2004; Englund et al., 2011; Rall et al., 2012; Vucic-Pestic et al., 2011). Consistent with these expectations, we found that the metabolic rate, attack coefficient, and overall feeding rate of the predatory *L. riparia* increased with experimental warming. The relative thermal sensitivity of metabolism (energy demand) and feeding (energy intake) determines population persistence, however, whereby a reduction in the ratio of feeding to metabolism (energetic efficiency) with warming may lead to local

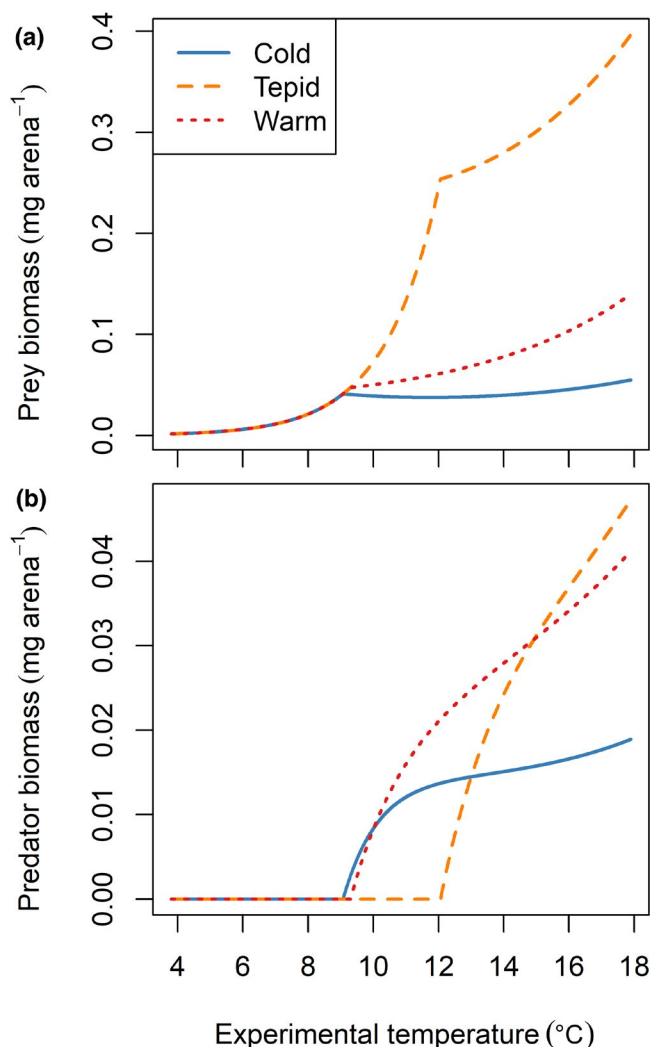


FIGURE 5 Stability analysis of the trophic interaction between *Limnophora riparia* (predator) and Simuliidae (prey). Equilibrium biomasses of (a) prey and (b) predator are plotted against experimental temperature for predator populations acclimated to cold, tepid, and warm streams. The system either features a stable equilibrium with persistence of prey and predator ($N^* > 0$, $P^* > 0$) or the predator goes extinct and prey persists in a stable equilibrium ($N^* > 0$, $P^* = 0$). Acclimation to higher temperatures increases both predator and prey biomasses in warmer environments, although the temperature at which the predator begins to persist in the system is higher

extinction of predator populations (Archer et al., 2019; Vucic-Pestic et al., 2011). Thus, strategies that help to minimize the increase in energy demand with warming should maximize the persistence of predator populations while minimizing the increase in energy intake can contribute to long-term population stability of predators and their prey.

We found that the Hill exponent increased with experimental temperature (Figure 3b), which to the best of our knowledge, has not previously been shown in functional response experiments. The only other experiments we are aware of that examined temperature effects on the Hill exponent found contrasting U-shaped and hump-shaped responses (Daugaard et al., 2019; Uszko et al., 2017), indicating the potentially species-specific nature of this effect. The Hill exponent has been highlighted as an important parameter for stabilizing predator–prey interactions (Brose, 2010; Williams & Martinez, 2004). An increasing Hill exponent can reduce feeding at low prey densities, and accelerate feeding at higher prey densities (Brose, 2010; Crawley, 1992). Thus, a higher Hill exponent in warmer environments should help to inhibit over-exploitation of declining prey populations and maximize the energy gained by the predator from abundant resources, which could stabilize predator–prey interactions. Temperature effects on the Hill exponent should be investigated more broadly to determine the prevalence of stabilizing *versus* destabilizing responses, and to identify the underlying mechanisms.

4.2 | Thermal acclimation of metabolic and feeding rates

Thermal acclimation has received increasing attention as a key mechanism by which organisms can cope with the impacts of environmental warming (Seebacher et al., 2015). We found that attack coefficient decreased with acclimation to warmer environments, whereby both tepid- and warm-acclimated predators attacked prey to a lesser extent than cold-acclimated predators. This matches the results of a previous functional response experiment, where the attack coefficient of dragonfly larvae feeding on water fleas declined following acclimation to higher temperatures (Sentis et al., 2015). These results suggest that predators can compensate for warming by matching their physiological phenotypes to their habitat (Seebacher et al., 2015). Thus, if thermal acclimation acts as a buffer against warming, trophic interactions involving ectotherms may be less sensitive to environmental warming than some predictions suggest (Fussmann et al., 2014; Rall et al., 2010). The ingestion rate of suspension-feeding echinoderm larvae has been shown to decline with lifetime exposure to higher temperatures (Podolsky, 1994), although grazing on biofilms was greater for snails collected from warmer streams (Schaum et al., 2018), suggesting that thermal acclimation does not universally induce a weaker feeding response. Indeed, when feeding rates were considered at the home-stream temperature of each predator population here, tepid- and warm-acclimated *L. riparia* were found to have stronger interactions than their cold-acclimated counterparts (Figure 4b). This indicates that

thermal acclimation may dampen, though not entirely offset the impacts of acute warming, that is, feeding rates of predators in the tepid and warm streams were lower than they would have been without thermal acclimation, but still higher than in the coldest environment.

We also found that acclimation to a warmer environment over the course of the predator's lifetime reduced the temperature dependence of metabolic rate, which has been demonstrated for other aquatic organisms (Seebacher et al., 2015; Semsar-Kazerouni & Verberk, 2018). Neutral or opposite effects have also been shown (Cloyed et al., 2019; Schaum et al., 2018; Sentis et al., 2015), however, which may be because the degree of thermal acclimation depends on species traits and the magnitude or intensity of thermal stress (Schulte et al., 2011). Note that the metabolism experiments did not contain any prey, so the observed acclimation effects must be entirely due to the environmental conditions of the predator's home stream. Here, the greatest deviation from the cold-acclimated population occurred in the tepid-acclimated *L. riparia*, with a subsequent drop-off in the warm-acclimated population, indicating a potential threshold for the moderating effects of thermal acclimation. One possible explanation for this may be a reduction in acclimation potential as organisms get closer to their thermal limits in the warmest environments (Stillman, 2003). Alternatively, the benefits of acclimation may be exceeded by the costs as thermal limits are approached, that is, there is a trade-off in lowering metabolic rate and reducing the capacity to fuel other metabolically expensive traits such as locomotion and foraging (Norin & Metcalfe, 2019). Hump-shaped responses to acclimation temperature have also been demonstrated in experiments with *Drosophila* flies (Salachan et al., 2019), highlighting the importance of avoiding linear assumptions about the effects of thermal acclimation in predictive modelling of climate change impacts on natural populations.

While the tepid-acclimated population of *L. riparia* had the weakest temperature scaling of metabolism, their metabolic rate was greater than the rates of the other two populations at temperatures below their normal thermal environment and converged on the rate of the other two populations at higher temperatures (Figure 1). This highlights the trade-offs involved in thermal acclimation, whereby metabolism may be dampened by acclimating to a warmer environment, but the organism's metabolic requirements could subsequently be much higher than they would be without acclimation if temperature declines again. It should be noted, however, that the link between metabolism and performance is unclear, with the higher energy demands of an elevated metabolism offset by the potential gains in activity and speed (Cloyed et al., 2019; Dell et al., 2011), contributing to a higher probability of foraging success. Nevertheless, attack coefficients of the tepid-acclimated *L. riparia* were lower than the cold-acclimated population and actually decreased with increasing temperature, albeit with confidence intervals that included zero (Figure 3a). This is in contrast to the general expectation of increasing attack rates with warming, up to the thermal optimum of a species (Rall et al., 2012), and suggests that thermal acclimation may not just alter the strength, but even the sign of the response.

4.3 | Predicted effects on population dynamics

Our population dynamical modelling indicated that both the tepid- and warm-acclimated predators should achieve a higher biomass in the warmer streams. In contrast, larger predatory organisms are often shown to decline with warming (Fussmann et al., 2014; Petchey et al., 1999; Yvon-Durocher et al., 2011). Thus, thermal acclimation may be one factor explaining the surprising success of larger consumers in warmer streams in the Hengill system (O'Gorman et al., 2017), although the relative position of predatory organisms within their thermal performance curves should also be considered (Schulte et al., 2011). Perhaps this is best explained by the far greater predicted energetic efficiency of *L. riparia* as stream temperature increases (Figure 4c), enabling them to expend much less energy in obtaining sufficient resources to meet their metabolic requirements. Prey populations were also predicted to benefit from this response, achieving a higher biomass when the predator was acclimated to the warmer environment (Figure 5a). This illustrates how the stabilizing effect of thermal acclimation by a single population can percolate through the food web, emphasizing the importance of trophic interactions for anticipating ecological surprises in climate change research (Woodward, Perkins, et al., 2010).

The trade-off in the predator's acclimation response was again apparent from its inability to persist in the modelled system at the lowest temperatures. Thus, thermal acclimation was only stabilizing in this predator-prey motif for temperatures close to or greater than the predator's home-stream environment. Note that our model failed to predict the persistence of the cold-acclimated population at its home-stream temperature, which may be due to the absence of thermal acclimation effects on the prey in our experiments. Future research should examine the impacts of thermal acclimation on both predators and prey, particularly for highly mobile prey where thermal acclimation may improve their escape response. Alternatively, the weaker predictive power of our model for the cold-acclimated population at its home-stream temperature may be a consequence of microhabitat variability in prey density and predator foraging success, or only considering a single prey population (Simuliidae) in determining energetic constraints of the predator. While Simuliidae are the preferred prey of *L. riparia*, the predator readily supplements its diet by feeding on oligochaete worms and midge fly larvae (Merritt & Wotton, 1988), which are the dominant invertebrate groups in the coldest streams in the Hengill system (O'Gorman et al., 2017). Thus, future population dynamical modelling needs to incorporate greater food web complexity to increase the predictive power of temperature effects on population persistence, and the findings should be validated with long-term monitoring of population dynamics from natural environments.

Finally, it should be acknowledged that the studied populations were collected from the field, rather than cultured under controlled conditions in the laboratory. This increases the potential relevance of the findings for real systems, but limits the level of control over the experimental conditions (O'Gorman et al., 2014). Thus, factors other than acclimation by the predators to their home-stream

temperatures could be influencing our results, for example, local food web effects on their feeding preferences. Due to their aerial adult stage, we assume that the predators do not exhibit natal site fidelity, and thus any effects of acclimation are within- rather than trans-generational. This should preclude differences in juvenile survival/recruitment that would favour offspring of successive thermally acclimated generations reproducing in the same stream. Nonetheless, we cannot exclude epigenetic or maternal effects that could alter offspring performance, for example, via differences in F1 offspring size (Burton & Metcalfe, 2014). Further laboratory studies are needed to tease apart these potential contributing factors.

5 | CONCLUSION

Understanding how temperature may alter predator-prey interactions and identifying mechanisms by which species can acclimate to new thermal regimes is vital for predicting the consequences of environmental warming for ecological communities. The results of this study suggest that feeding interactions should intensify with warming, but that predators may be able to moderate these impacts through phenotypic plasticity. Importantly, we demonstrate these effects in natural populations outside of the laboratory setting. Moreover, we highlight an underlying physiological mechanism by which acclimation can modulate the effects of climate warming on predator-prey interactions and population dynamics—increased energetic efficiency in predators. Acclimation to higher temperatures reduced the thermal sensitivity of both metabolic demand and consumption rates at low prey densities. This shifted predator-prey interactions towards more stabilizing dynamics by increasing the persistence of both species in warmer environments. Thermal acclimation could thus buffer ecological communities against the impacts of warming on ectothermic organisms. It is now important to study how thermal acclimation can alter the impacts of warming across a broader range of species interactions and under more realistic conditions to improve applicability of these findings for natural communities.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the University of Essex Research Data Repository at <https://dx.doi.org/10.5526/ERDR-00000137>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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