LETTER

Temperature-size responses alter food chain persistence across environmental gradients

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Abstract

Body-size reduction is a ubiquitous response to global warming alongside changes in species phenology and distributions. However, ecological consequences of temperature-size (TS) responses for community persistence under environmental change remain largely unexplored. Here, we investigated the interactive effects of warming, enrichment, community size structure and TS responses on a three-species food chain using a temperature-dependent model with empirical parameterisation. We found that TS responses often increase community persistence, mainly by modifying consumer-resource size ratios and thereby altering interaction strengths and energetic efficiencies. However, the sign and magnitude of these effects vary with warming and enrichment levels, TS responses of constituent species, and community size structure. We predict that the consequences of TS responses are stronger in aquatic than in terrestrial ecosystems, especially when species show different TS responses. We conclude that considering the links between phenotypic plasticity, environmental drivers and species interactions is crucial to better predict global change impacts on ecosystem diversity and stability.

Keywords

Body size, climate change, food web, interaction strength, paradox of enrichment, phenotypic plasticity, temperature-size rule.

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INTRODUCTION

Human activities impact the diversity, structure and function of ecological communities on a global scale (Pereira *et al.* 2010; Harley 2011). However, understanding how global change effects on individual species influence stability and persistence of natural communities is still challenging. Recent studies revealed three main types of species responses to climate change: shifts in geographical ranges, changes in seasonal and phenological patterns and changes in body sizes (Parmesan 2006; Gardner *et al.* 2011). While the first two responses have been studied extensively (Walther *et al.* 2002; Parmesan 2006), the third has received less attention. Previous studies focused mainly on proximal causes of body-size changes (Atkinson & Sibly 1997; Walters & Hassall 2006; Karl & Fischer 2008; Zuo *et al.* 2012) and their variability among species and habitats (Atkinson 1994; Forster *et al.* 2012; Horne *et al.* 2015). However, the consequences of temperature-size (TS) responses for the stability and persistence of ecological communities remain largely unexplored. This is puzzling since body size is a master trait that determines many ecological properties including fecundity, behaviour, population growth rate, trophic position, species interactions and community stability (Peters 1983; Brose *et al.* 2006b; White

et al. 2007). Thus, knowledge of how TS responses modulate the impact of global change drivers (including temperature) on species interactions and community persistence is crucial for understanding and predicting global change impacts on ecological systems.

Ectotherms usually mature at smaller size when developing under warmer conditions (Atkinson 1994; Forster *et al.* 2012; Horne *et al.* 2015). This response, called the "temperature-size rule" (Atkinson 1994), is one of the most widespread patterns in organismal biology (Angilletta *et al.* 2004; Kingsolver & Huey 2008) and is found in taxa as diverse as bacteria, protists, invertebrates, plants and ectothermic vertebrates (Horne *et al.* 2015). Different theories have been proposed to explain this ubiquitous response. The theory of differential sensitivities of development and growth rates to temperature posits that at warmer temperatures, organisms develop faster than they grow and hence reach smaller body sizes (Forster *et al.* 2011; Zuo *et al.* 2012). The oxygen supply hypothesis assumes that growing to a smaller size facilitates the maintenance of aerobic scope when oxygen concentrations decline with temperature (Atkinson *et al.* 2006; Forster *et al.* 2012). Finally, various mechanisms under the umbrella of size-dependent population feedback hypothesis (density-dependent growth, size-dependent survival, asymmetric competition between

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size-classes and size-selective predation) affect the relative abundances of different age classes or life stages, leading to a shift in mean body size in the population (Ohlberger *et al.* 2011; DeLong 2012; Ohlberger 2013; DeLong *et al.* 2017).

However, none of these theories can fully explain why the magnitude and direction of TS responses (i.e. percentage change in body mass per °C, hereafter PCM after Forster *et al.* 2012) is not equal for all species and differs systematically among habitats (Forster *et al.* 2012; Horne *et al.* 2015). Indeed, body size declines faster with warming in aquatic multicellular ectotherms than in terrestrial ones. Moreover, aquatic species conform to the temperature-size rule in over 90% of cases, whereas terrestrial species have more variable responses, including more frequent opposite ones known as "converse" or "reverse" temperature-size rule (Forster *et al.* 2012). Finally, the magnitude of TS responses is also size-dependent with opposite trends in terrestrial and aquatic habitats: larger aquatic species shrink more with warming than smaller species and vice and versa for terrestrial species (Forster *et al.* 2012; Horne *et al.* 2015). Variations in the sign and strength of TS responses suggest that we should consider habitat differences and heterogeneity in species responses to better understand (1) mechanisms by which TS responses influence community dynamics, (2) conditions for which these phenotypic changes increase species survival.

In addition to TS responses, temperature directly affects biological rates, species interactions and population dynamics. Ectotherm predators search for and handle prey faster in warmer environments (Rall *et al.* 2012; Dell *et al.* 2013), although temperatures exceeding the optimal temperature at which search and handling rates are maximal may lead to the opposite pattern (Englund *et al.* 2011; Sentis *et al.* 2012). Mild warming thus typically increases short-term interaction strengths (i.e. feeding rates) and destabilizes community dynamics. However, many consumers become less energetically efficient at higher temperatures because metabolic rates increase faster with temperature than feeding rates (Vucic-Pestic *et al.* 2011; Fussmann *et al.* 2014). This reduces energy flow between trophic levels and hence stabilizes food-web dynamics in the long run (Rip & McCann 2011; Binzer *et al.* 2012; Gilbert *et al.* 2014). Additionally, empirical studies demonstrated that elevated temperature increases consumer extinction risk when metabolic demands exceed ingestion rates, leading to consumer starvation (Petchey *et al.* 1999; Rall *et al.* 2010; Fussmann *et al.* 2014).

Increased eutrophication is another widespread consequence of human activities (Sala *et al.* 2000) affecting the composition, structure and stability of food webs together with temperature (O'Connor *et al.* 2009; Binzer *et al.* 2012, 2016; Kratina *et al.* 2012; Sentis *et al.* 2014). Enrichment increases energy flux from resources to higher trophic levels, which increases population fluctuations and extinction risks when population minima are close to or below extinction boundaries (Rosenzweig 1971; Boukal *et al.* 2007; Rip & McCann 2011; Gilbert *et al.* 2014). This predicted pattern has been observed in both laboratory and field experiments (McCauley *et al.* 1999). For instance, eutrophication increases variation in phytoplankton community biomass and significantly reduces taxonomic richness in experimental freshwater pond mesocosms (Kratina *et al.* 2012). Interestingly, theory predicts that moderate warming and increasing consumer-resource body mass ratios can alleviate this paradox of enrichment by decreasing trophic interaction strength and thereby stabilising population dynamics (see Binzer *et al.* 2012; Binzer *et al.* 2016 for more details). Consistent with theoretical models, empirical studies reported that warming strengthens top-down and weakens bottom-up control, which decreases eutrophication impact on mean population biomasses and their temporal variations (O'Connor *et al.* 2009; Hoekman 2010; Kratina *et al.* 2012).

Can phenotypic plasticity, such as temperature-induced body-size changes, alter these effects of temperature and enrichment on food webs? Surprisingly, consequences of TS responses for the dynamics of communities facing environmental changes are largely unexplored. Temperature effects on trophic interaction strengths and consumer energetic efficiency critically depend on both the absolute and relative body masses of consumers and their resources (Rip & McCann 2011; Binzer *et al.* 2012; Gibert & DeLong 2014) because consumer-resource body-mass ratios underlie food-web persistence, and ratios that lead to highly unstable population dynamics are rarely observed in natural food webs (Otto *et al.* 2007). TS responses can thus modulate the effects of warming and eutrophication on communities directly by modifying body masses of the constituent species and indirectly by changing consumer-resource body-mass ratios as suggested by Gibert & DeLong (2014).

Here, we investigated long-term consequences of TS responses for population persistence. We extended a temperature- and mass-dependent model of population dynamics of a three-species food chain (Yodzis & Innes 1992; Binzer *et al.* 2012) by adding the temperature dependence of body size based on empirical estimates of TS response slopes in Forster *et al.* (2012) and studied the effects of enrichment and warming on population persistence. We were particularly interested in the following questions: (1) How do TS responses modulate the effects of enrichment and warming on species persistence? (2) How does community size structure influence these effects? and (3) Does heterogeneity in TS responses among species exacerbate or diminish the effects of temperature and enrichment on species persistence?

METHODS

We use a three-species extension of the classical Yodzis & Innes (1992) consumer–resource model with added body size and temperature dependencies of the biological rates (Binzer *et al.* 2012):

$$\dot{A} = e_{AI} f_{AI} B_A - x_A B_A \qquad (1)$$
$$\dot{I} = e_{IB} f_{IB} B_I - B_A f_{AI} - x_I B_I \qquad (2)$$
$$\dot{B} = r B_B \left(1 - \frac{B_B}{K}\right) - f_{IB} B_I \qquad (3)$$

Rates of change of the basal, intermediate and apical species biomass densities $\dot{B}$, $\dot{I}$ and $\dot{A}$ depend on their respective biomass densities B_B, B_I and B_A (g m^{-2}), the carrying capacity of the basal species K (g m^{-2}), its maximum growth rate r (s^{-1}), the metabolic rates of the intermediate and apical

species x_I and x_A (s^{-1}) and feeding efficiencies e_{IB} and e_{AI} that denote the fraction of resource biomass converted into consumer biomass (unitless, set to 0.85 since all feeding interactions in our model are carnivorous, following Yodzis & Innes 1992). Feeding rate f_{ji} of consumer j depends on the density of its resource i and follows a type II functional response, with consumer-resource specific attack rates a_{ji} (m^2 s^{-1}) and handling times h_{ji} (s):

$$f_{ji} = \frac{a_{ji}B_i}{1 + a_{ji}h_{ji}B_i} \tag{4}$$

Following the metabolic theory of ecology (Brown *et al.* 2004), the maximum growth rate r_i, carrying capacity K_i, attack rate a_{ji}, handling time h_{ji} and metabolic rate x_i of species i scale with its body mass M_i (g) and the environmental temperature T (K):

$$Q_i = f_Q(M_i, T) = d_Q M_i^{b_Q} e^{E_Q \frac{T_0 - T}{kTT_0}} \tag{5}$$

where Q stands for r, K, a, h or χ, d_Q is a parameter-specific constant calculated for a body mass of 1 g and temperature of 20 °C (= 293.15 K), and b_Q is the exponent of the respective body-mass scaling relationship. The temperature dependence is characterised by the respective activation energy E_Q (eV), normalisation temperature $T_0 = 20$ °C and the Boltzmann constant $k = 8.62 \times 10^{-5}$ eVK^{-1}. We parameterised eqns 1–5 with empirically derived scaling relationships for the size and temperature scaling of the biological rates (Table S1). Moreover, size and temperature dependences of functional response parameters are often unimodal rather than allometric or exponential (Englund *et al.* 2011; Rall *et al.* 2012). We thus included additional temperature and mass scaling in our model. Following Binzer *et al.* (2012), attack rates and maximum ingestion rates scale additionally with consumer body mass M_j and show a hump-shaped dependence on the body-mass ratio between the consumer and its resource. In addition, handling times also display a U-shaped relationship with temperature (see Data S1, Fig. S1, and Tables S1 and S2 for details).

Body masses of all species are temperature-dependent using empirical estimates of TS response slopes in Forster *et al.* (2012):

$$M = cm_{20}e^{s(T-20)} \tag{6}$$

Here, c converts dry mass into wet mass 6.5 (Peters 1983), m_{20} is the dry mass of the species at 20 °C (set to 1 mg), and s quantifies the sign and magnitude of the TS response. Following Forster *et al.* (2012), we calculate PCM (i.e. percentage change in body mass per °C) as $(e^s - 1) \times 100$. Negative PCM values indicate a warming-induced body-size reduction, while positive PCM values correspond to larger body sizes. Under this notation, the reference body masses are measured at 20 °C, and body mass reduction at temperatures above 20 °C (negative PCM) implies larger body size at temperatures below 20 °C.

As the TS response slope (i.e. PCM) varies among taxonomic groups and ecosystem types and can even become positive, we selected four different TS response slopes from Forster *et al.* (2012) to investigate how variability in TS responses may affect our results:

(1) Maximum TS response: $PCM = -8$, the strongest negative TS response.
(2) Reverse TS response: $PCM = 4$, the strongest positive TS response.
(3) Mean aquatic TS response: $PCM = -3.90 - 0.53$ $\log_{10}(m_{20})$, the average TS response for aquatic Metazoa.
(4) Mean terrestrial TS response: $PCM = -1.72 + 0.54$ $\log_{10}(m_{20})$, the average TS response for terrestrial Metazoa.

For each selected TS response slope, we simulated four scenarios: (1) all species follow the same TS response slope, (2) only the basal, (3) intermediate or (4) top species follows a TS response while the other two species do not (i.e. their body masses do not change with temperature; PCM = 0). Additionally, we simulated a baseline scenario with no TS response in either species.

To investigate the individual and combined effects of enrichment, warming, community size structure [i.e. the consumer-resource Body-Mass Ratios (BMR)] and TS responses, we varied the temperature (401 values ranging from 0 to 40 °C by 0.1 °C) and the resource carrying capacity intercept (parameter d_K in eqn 5; 200 values ranging from 0.1 to 20 g m^{-2} by 0.1 g m^{-2}, overlapping with reported mean annual population biomass estimates; Cyr *et al.* 1997) and simulated the dynamics given by eqns 1–3 for 100 000 years to enable the system to reach an attractor (either a steady state or a stable limit cycle) before we assessed the final state. Therefore, each TS-response scenario involved simulating 80 200 combinations of environmental conditions (401 temperatures by 200 enrichment levels). We assessed each TS-response scenario at four different consumer-resource body-mass ratios (BMR; set to 1, 2, 5 and 10 with a basal species dry mass of 1 mg) within the range of observed BMR values (Brose *et al.* 2006a; Forster *et al.* 2012). Initial biomass density of each species was set to 1.02 times its equilibrium density in the three-species system (calculated by solving eqns 1–6; Data S2) to avoid extinctions caused solely by transient dynamics. Any population falling below the extinction threshold of 10^{-12} g m^{-2} during the simulation was deemed extinct and its biomass set to zero to exclude ecologically unrealistic limit cycles.

For each TS-response scenario, we calculated system persistence as the percentage of simulations with all three species remaining extant at the end of the simulations. For each scenario, system persistence (%) is thus calculated as (number of simulations with all three species present at the end)/(total number of simulations = 80 200) × 100.

To disentangle environmental effects on system persistence, we divided the temperature gradient into high and low temperature (above and below 20 °C, respectively) and the enrichment gradient into high and low enrichment (above and below 10 g m^{-2}, respectively). This yielded four environmental regimes: low enrichment–low temperature; low enrichment–high temperature; high enrichment–low temperature and high enrichment–high temperature. For each combination of community structure and environmental regime, we calculated system persistence as mentioned above (see Figs S4 and S5 for detailed underlying results).

Finally, we investigated the effects of TS responses on species interaction strengths and consumer energetic efficiencies for both pairwise interactions to better understand the mechanisms driving the changes in systems persistence across the temperature-enrichment and BMR gradients. Long-term *per capita* interaction strengths (*IS*) was characterised using the dynamic index (Berlow *et al.* 1999), $IS = \left| \frac{\ln(R^+/R^-)}{C^+} \right|$, where C^+ is the consumer equilibrium density and R^+ and R^- respectively denote resource equilibrium density with and without consumer (details not shown). The dimensionless energetic efficiency of the apical species, defined as the rate of mass-specific biomass gain over biomass loss, was calculated as $Y_A = e_{AI} f_{AI}(B_I) x_A^{-1}$ (Rall *et al.* 2010; Vucic-Pestic *et al.* 2011). We exemplify the results by identifying the temperature $T_{\max}$ at which $Y_A = 1$ for a carrying capacity intercept of 5 g m^{-2} (i.e. the mean value of the low enrichment regimes) and intermediate consumer at equilibrium density B_I. This indicates the critical upper thermal limit for the apical species in the ecological context of the entire food chain. Above this limit, the metabolic rate of the apical species exceeds assimilation (i.e., $Y_A < 1$) and causes its extinction due to lack of food (i.e. upper border between the dark orange and orange areas in Fig. 1). We have also calculated the level of enrichment $K_{\min}$ at which $Y_A = 1$ at 30 °C (i.e. the mean value of the high temperature regimes). This identifies the minimum resource requirements below which the apical species goes extinct at this temperature. These two values were chosen to characterise the extinction threshold of the apical species under the low enrichment–high temperature environmental regime (Data S2 and Figs S4–S5).
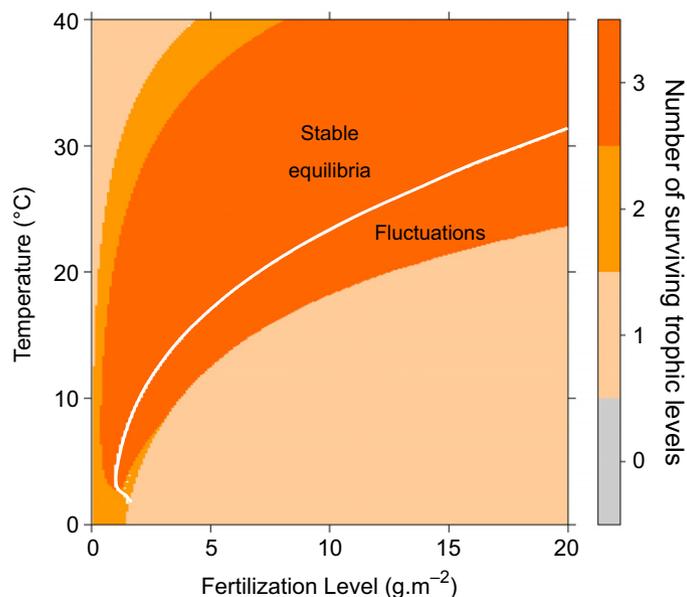

Figure 1 Interactive effects of temperature and enrichment (i.e. resource carrying capacity intercept d_K) on species survival for a tri-trophic food chain without size structure (i.e. body-mass ratio = 1) and without temperature-size response (PCM = 0). The complete food chain (dark orange area) is in a stable equilibrium above the white curve and exhibits limit cycles below it.

RESULTS

Effects of temperature and enrichment on system persistence without TS responses (PCM = 0)

Species survival and extinctions in our model are driven by two food- and temperature-dependent mechanisms. The food chain is in a steady state when temperatures are relatively high or system productivity relatively low (i.e. above the white line marking the transition to limit cycles in Fig. 1). In this case, we observe progressive shortening of the food chain with increasing temperature for any level of system productivity, because the energetic efficiency of the apical and then of intermediate species fall below unity and the populations go extinct because they cannot cover their metabolic demands at high temperatures. When the system oscillates (below white line marking the Hopf bifurcation curve of the three-species equilibrium in Fig. 1), increasing fertilisation levels at low temperatures cause extinctions of the intermediate and top species due to increased energy fluxes and population fluctuations caused by the paradox of enrichment. The range of temperatures and fertilisation levels leading to population cycles shrinks and can become vanishingly small at larger BMR values (Figs S4–S7). These overall qualitative patterns remain unchanged when TS responses are introduced, and we thus report only on the quantitative changes caused by shifts of both types of extinction thresholds.

Effects of TS responses on system persistence across enrichment and temperature gradients

TS responses systematically alter system persistence relative to the baseline no-response scenario. Differences from the baseline scenario scale with the strength of body-size changes (i.e. magnitude of PCM), indicating mostly stronger effects of TS responses on community persistence for aquatic than for terrestrial systems (Fig. 2). Increased size structure (i.e. higher BMR values) within the food chain typically amplifies the relative differences among TS response effects, which are weak in non-structured food chains (i.e. BMR = 1) and enhanced when consumer-resource body-mass ratio increases (Fig. 2).

Our simulations revealed that body-size reductions with warming (i.e. PCM < 0) may lead to both substantial decrease and increase in the overall system persistence. We observed decreased persistence when only the body size of the basal species (Fig. 2b) or body sizes of the basal and one additional species at the higher trophic levels (Fig. S2c and S2d) decline with warming. On the other hand, reductions in body size with warming lead to increased persistence when all species (Fig. 2a) or all but the basal species (Fig. S3b) showed the TS response. The observed changes in persistence were substantial in these scenarios, with up to *c.* 15% for the maximum TS response (PCM = –8). Body-size reductions with warming in the remaining two scenarios (TS response in only the intermediate or only the apical species) led to smaller changes in overall system persistence. These two scenarios were the only ones in which body sizes increases with warming (i.e. PCM > 0) had a much larger, negative effect on system persistence (Fig. 2c and d).
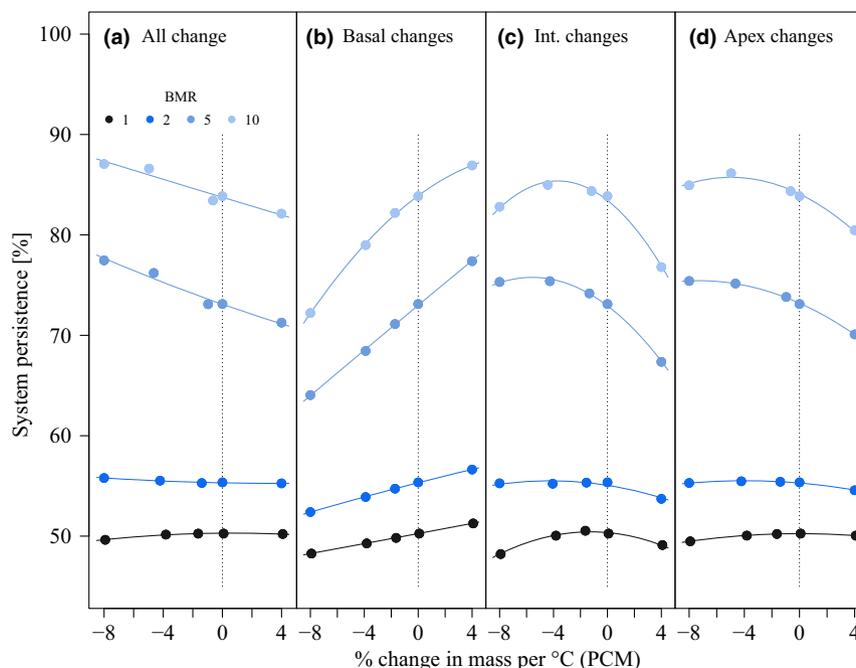
Figure 2 System persistence (%) as a function of TS response slope (PCM) of the changing species and consumer-resource body-mass ratio (BMR, colour coded) when (a) all species have the same TS response and when the body mass of only the (b) basal, (c) intermediate or (d) apical species changes with temperature. The dotted line indicates the baseline scenario with constant body size in all species. Quadratic linear models (solid coloured lines) were fitted to the data to represent the relationship between system persistence and PCM (See Table S3 for coefficients and *P*-values).

TS response effects on system persistence: different environmental regimes

TS response effects on system persistence differed markedly among the four temperature–enrichment regimes (Fig. 3). Overall, system persistence increases with body-mass ratio except in the low enrichment–high temperature regime (Fig. 3a–d). In this regime, consumers are threatened by starvation and body-size reduction with warming leads to lower system persistence except for when only the apical species' body-size changes with temperature (Fig. 3d) as it decreases the body-mass ratio of the apical and intermediate species. TS responses have weak effects in the high enrichment–high temperature regime, in which system persistence is generally highest (Fig. 3e–h). In the low enrichment–low temperature regime (Fig. 3g–i), the impact of TS responses on persistence is context-dependent: when only the basal species or only the apical species follows a TS response, system persistence decreases with positive TS responses (i.e. PCM > 0), whereas it increases when the size of all three species or only that of the intermediate species changes with temperature (Fig. 3i–l). In the high enrichment–low temperature regime (Fig. 3m–p), the food chain rarely or never persists when size differences are small (BMR ≤ 2). This contrasts with a moderate to high proportion of persisting systems with larger size differences (BMR ≥ 5). Here, increasing the relative body mass of the basal species decreases system persistence (Fig. 3n), while increasing the relative body mass of all three species or the intermediate or the apical species increases system persistence (Fig 3m and o–p).

Energetic efficiency of apical species at high temperatures

Upper thermal and minimum resource thresholds for the apical species, indicative of its ability to cope with high temperatures and low system productivity, depend strongly on the magnitude of TS responses and identity of the species showing the response. The apical species is more susceptible to warming and goes extinct at lower temperatures if body sizes decline with warming (i.e. PCM < 0) at all three trophic levels or at the lower trophic levels (Fig. 4a–c). When body sizes decline with warming at all three trophic levels, or only at the intermediate trophic level, the apical species also requires higher system productivity to persist compared to the baseline scenario without TS responses (Fig 4e and f). Interestingly, when only the size of the apical species declines with warming (Figs. 4d and h), the species has a higher thermal threshold and lower minimum resource requirements, indicating increased energetic efficiency. Finally, increasing predator–prey body-mass ratios (BMRs) does not affect the sign or magnitude of these effects, but generally lowers the thermal threshold while having no effect on minimum resource requirements.

Mechanisms underlying system persistence

Our analyses indicate that the direct and indirect effects of TS responses in each species jointly determine both species survival and system persistence. The direct effect modifies species body size, which influences consumer energetic efficiency and species interaction strength (Fig. 5). Energetic efficiency of consumers increases with their body size (Fig. 4a and e, PCM = 4). This explains why, when all species have the same
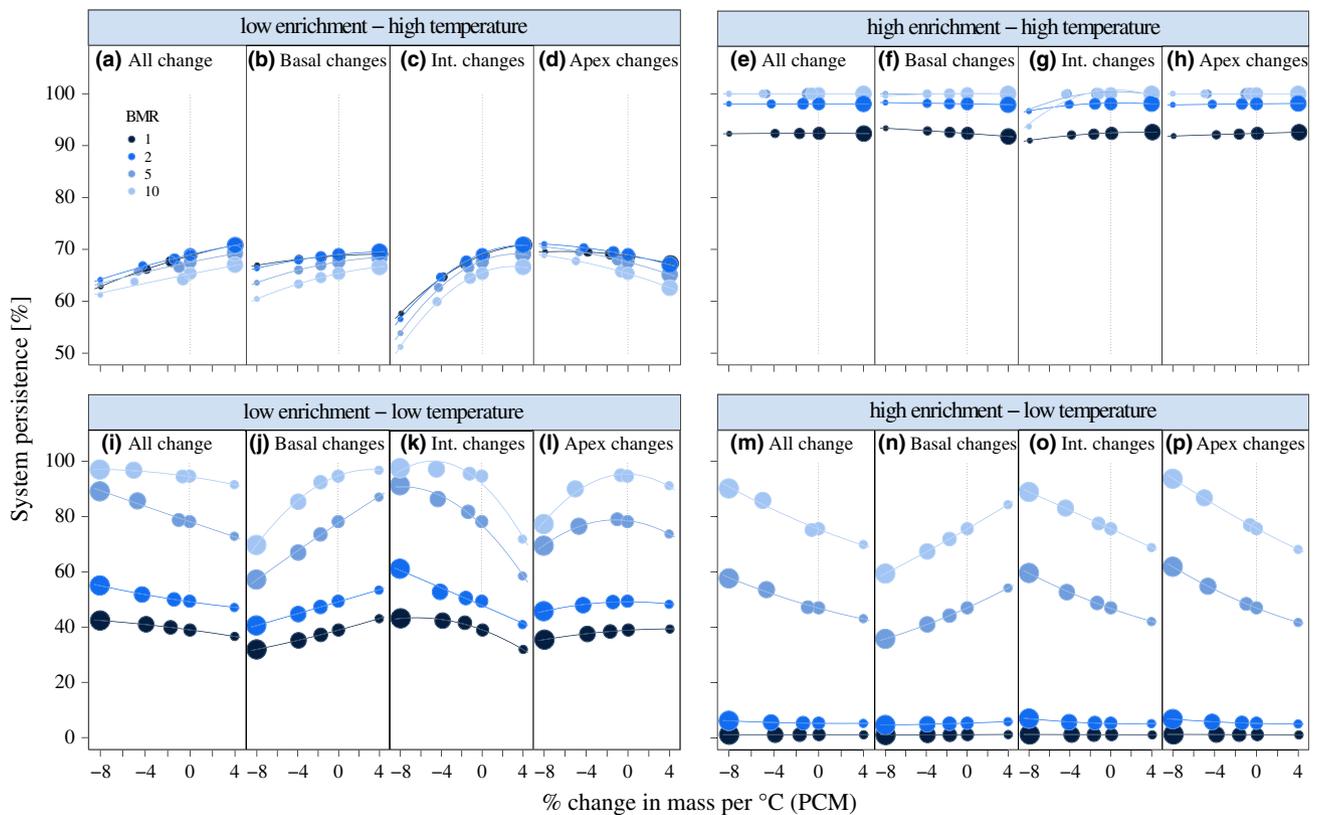
Figure 3 System persistence (%) as a function of TS response slope (PCM) of the changing species and consumer-resource body-mass ratio (BMR, colour coded) at low enrichment–high temperature (a–d), high enrichment–high temperature (e–h), low enrichment–low temperature (i–l), high enrichment–low temperature (m–p), when the body mass of (i) all the species, (ii) only the basal, (iii) intermediate or (iv) apical species changes with temperature. All three species change their body-mass with temperature (i.e. follow the same TS response slope). Circle diameters scale with body sizes of the body-mass responsive species relative to the baseline scenario with no TS response (indicated by dotted lines). Solid lines as in Fig. 2 (See Table S4 for coefficients and *P*-values).

response to temperature (i.e. same PCM), declining body sizes with warming have negative consequences for consumer energetic efficiency and survival at higher temperatures (Fig. 5).

The indirect effect of TS responses arises from modifications of consumer-resource body-size ratios (Fig. 5). Increasing body-size ratios decrease the relative rates of consumption per unit of consumer biomass (details not shown), which decreases trophic interaction strengths and stabilises the food chain. Hence, heterogeneous TS responses across trophic levels can either stabilise or destabilise the food chain (Fig. 5). Moreover, increasing body-size ratios decrease consumer energetic efficiency below a critical threshold at high temperatures (Fig. 4a) and thus decrease system persistence (Fig. 5). These indirect effects of altered consumer-resource body-mass ratios also explain why TS responses are more important in food chains with large size differences across trophic levels. Altogether, our results indicate that the indirect effect of TS responses is probably more important for system persistence than the direct effect.

DISCUSSION

Phenotypic responses of individuals to environmental changes are ubiquitous and play a crucial role in the ability of species to adapt to rapidly changing environments (Chevin *et al.* 2010; Donelson *et al.* 2011; Huey *et al.* 2012; Sentis *et al.*

2015). Individuals of many species are becoming smaller as a result of climate warming (Daufresne *et al.* 2009; Sheridan & Bickford 2011; Horne *et al.* 2015). However, the ecological consequences of phenotypically plastic size changes for the dynamics and stability of ecological communities remain largely unexplored. This is surprising given that absolute and relative consumer-resource body sizes are key determinants of trophic interaction strengths and food web structure (Brose *et al.* 2006b; Petchey *et al.* 2008). Here, we found that body-size reductions with warming influence the effects of temperature, enrichment and body-size ratios on the dynamics of a tri-trophic food chain and often (but not always) increase its persistence under global change. Our results highlight the importance of considering the links between phenotypic responses to temperature and species interactions to improve our ability to predict the impacts of global change on ecosystem diversity and stability.

Effects of TS responses on system persistence across enrichment and temperature gradients

Our main finding is that TS responses modulate the effects of temperature, enrichment and body-size ratios on system persistence. Most importantly, we show for the first time that the direction and magnitude of TS response effects on system persistence largely depends on the heterogeneity in TS responses
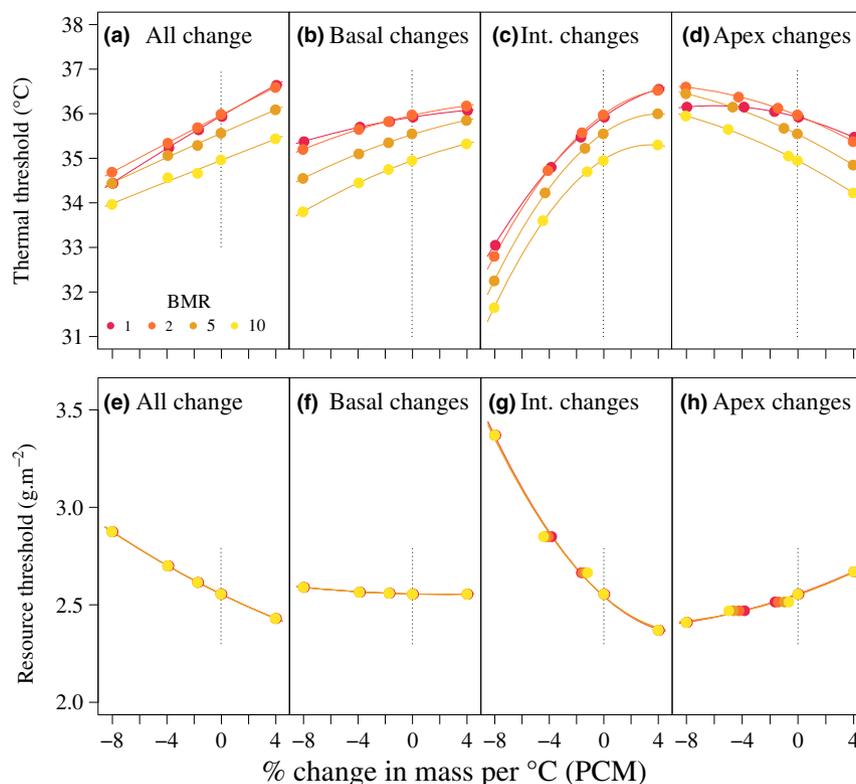
Figure 4 (a–d) Upper thermal threshold T_{max} (°C) for the apical species as a function of TS response slope (PCM) and body-mass ratio (BMR) when (a) all species follow the same TS response and when the body mass of only the (b) basal, (c) intermediate or (d) apical species changes with temperature. In all simulations, the carrying capacity intercept d_K was set at 5 g m^{-2}. (e-h) Lower resource threshold K_{min} (g m^{-2}) for the apical species as a function of TS response slope (PCM) and body-mass ratio (BMR) when (e) all species follow the same TS response and when the body mass of only the (f) basal, (g) intermediate or (h) apical species changes with temperature. In all simulations, the temperature was set at 30 °C. Solid lines as in Fig. 2 (See Table S5 for coefficients and *P*-values). Apical species persists at temperatures below the thermal threshold in panels a–d and at resource levels above the resource threshold in panels e-h.

across trophic levels (Fig. 2). Body mass reductions, which are likely to occur in many taxa under climate change (Gardner *et al.* 2011), increase community persistence when all three species or all but the basal species show this TS response. On the other hand, body mass reductions in the basal species alone or jointly with one species at the higher trophic levels lead to decreased community persistence. We also predict that, with a few exceptions, more pronounced body mass changes with temperature (i.e. PCM >> 0 or << 0) lead to stronger effects on food-chain persistence. As the sign and strength of the body-size responses vary substantially among species and ecosystems (Forster *et al.* 2012; Horne *et al.* 2015), TS response effects on community persistence are likely to be important in nature and require more attention.

According to our model, mismatches in TS responses across trophic levels can decrease or increase food-web stability and persistence depending on which species responds to warming. Interestingly, the decrease in system persistence is most pronounced when only the basal species body mass reduces with warming. This accelerates the loss of apical consumers and releases lower trophic levels from predation; a pattern often observed in microcosm experiments (Petchey *et al.* 1999; Yvon-Durocher *et al.* 2011; McElroy *et al.* 2015). Recent studies reported that species at lower trophic levels show strong reductions in body size with warming, whereas

evidence for body-size change are weaker for higher trophic levels (Teplitsky & Millien 2014; Garzke *et al.* 2015). In such a case, our model predicts decreased resilience of communities to climate change and accelerated losses of apical consumers, which may contribute to the observed shifts in communities size structure towards smaller species with warming (Yvon-Durocher *et al.* 2011; Gibert & DeLong 2014).

Second, our results imply that long-term consequences of thermal plasticity in body size will be more important in aquatic than in terrestrial ecosystems. Average consumer-resource body-size ratios are more pronounced in freshwater than in marine or terrestrial habitats (Brose *et al.* 2006a) and aquatic species experience a stronger size reduction than terrestrial species at higher temperatures (Forster *et al.* 2012; Horne *et al.* 2015). We found that large consumer-resource body-mass ratios exacerbate the effects of TS responses. For example, when all species show the same TS response, decreasing body masses with warming markedly increases community persistence only if consumer-resource size ratios are large. Our prediction is supported by recent studies indicating strong effects of temperature on aquatic communities, frequently associated with changes in species body size (Daufresne *et al.* 2009; Winder *et al.* 2009; Yvon-Durocher *et al.* 2011; Dossena *et al.* 2012), whereas these effects are weak in terrestrial systems (Gardner *et al.* 2011). We thus call for
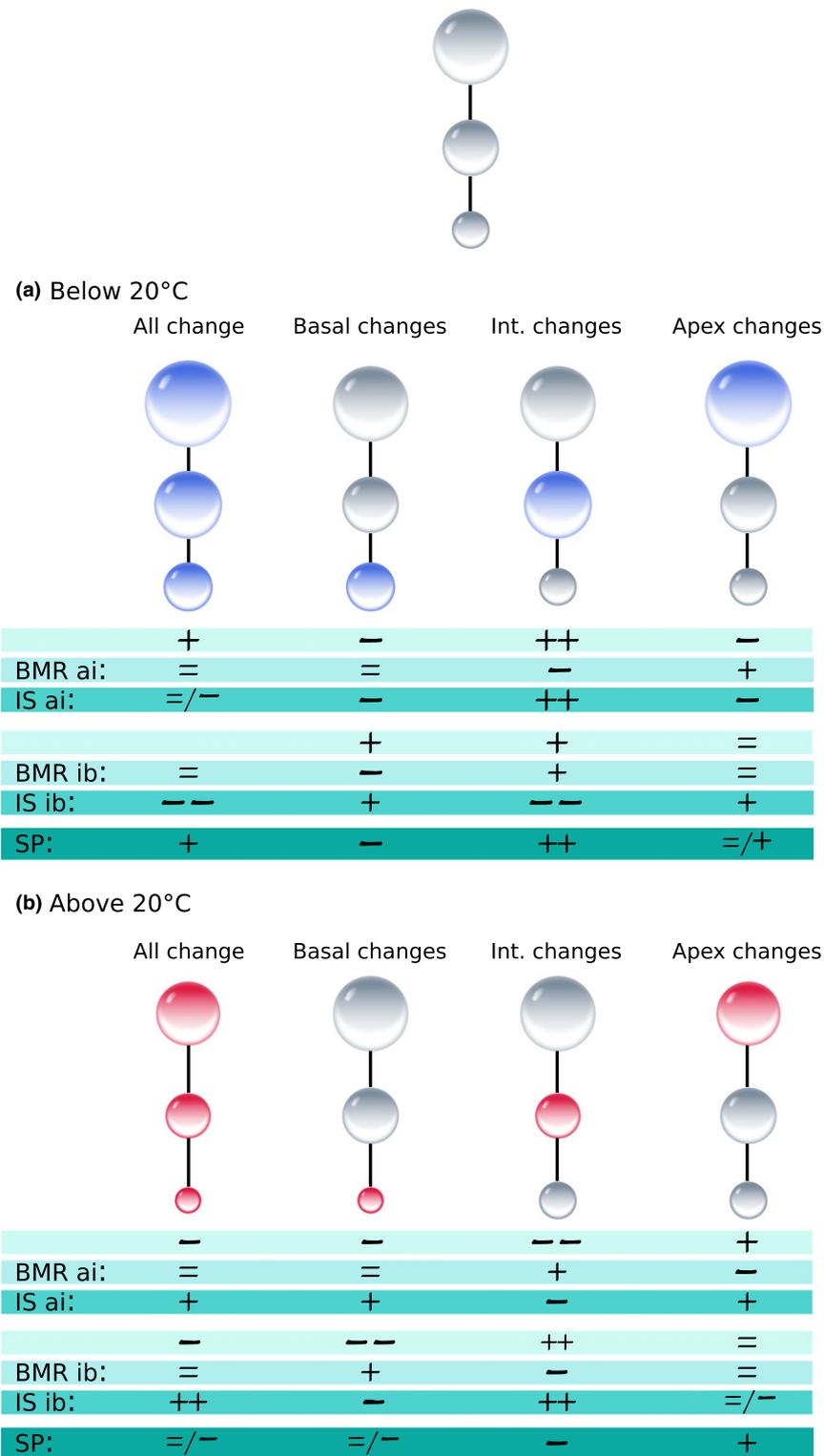
Figure 5 Qualitative effects of negative TS response slopes (a) below and (b) above 20 °C on the consumer-resource body-mass ratios (BMR), interaction strength (IS), energetic efficiency (EE) and system persistence (SP) for four response scenarios (all species change or only the basal, intermediate or apical species changes) in the tri-trophic food chain. Body size is proportional to symbol size: warming decreases body mass (red circles) and cooling increases it (blue circles) relative to the baseline scenario without TS responses (grey circles). At 20 °C, each consumer species is twice as large as its resource (BMR = 2). Symbols and abbreviations: a: apical species, i: intermediate species, ai: link between the apical and intermediate species, ib: link between the intermediate and basal species, =: no effect of TS response (relative changes <5% compared to the baseline scenario without TS response), +: TS response increases the value by >5% and <20% relative to the baseline scenario, −: TS response decreases the relative value by >5% and <20%, ++: TS response increases the relative value by >20%, -- TS response decreases the relative value by >20%.

further studies comparing the ecological consequences of body-size change in aquatic and terrestrial communities.

Effects on system persistence: different environmental regimes

Our simulations revealed that TS response effects on food chain persistence are not even across environmental gradients, but depend both qualitatively and quantitatively on the combination of warming and enrichment levels. We found that the impact of TS responses on system persistence is substantial (either positive or negative) at low temperatures, where they modulate extinctions due to resource limitation and paradox of enrichment, and at high temperatures accompanied by low enrichment levels, where they modulate extinctions due to resource limitation. On the other hand, their impacts on system persistence at high temperature and enrichment levels are negligible. This suggests that TS responses play at most a minor role in productive systems at low altitudes/latitudes but may have important consequences elsewhere.

In summary, TS response effects on system persistence likely depend on environmental conditions (temperature and enrichment), consumer-resource body-size ratios, and the TS responses of other species within the community. Although we did not test the effects of TS responses on individual fitness, population responses (i.e. persistence) observed in our model means that TS responses can be maladaptive. We conclude that the adaptive value of TS responses for a given species is likely context-dependent, which could partly explain (1) why previous studies had difficulties in assessing the adaptive value of TS responses (Atkinson & Sibly 1997; Angilletta & Dunham 2003; Walters & Hassall 2006; Karl & Fischer 2008; Kingsolver & Huey 2008), (2) why TS response strength is so variable among species (Forster *et al.* 2012; Horne *et al.* 2015) and (3) why no single theory embraces the generality of TS relationships in ectotherms (Atkinson & Sibly 1997; Angilletta & Dunham 2003; Walters & Hassall 2006; Karl & Fischer 2008; Kingsolver & Huey 2008). Our model provides the first step in the exploration of the consequences of TS responses for food web persistence. It paves way for further extensions required to fully understand the causes and consequences of body-size changes. For instance, we did not account for migration, evolutionary change or size-dependent population feedbacks (e.g. asymmetric competition between size-classes and size-selective predation) that can also influence body-size distributions and lead to the emergence of TS responses (Ohlberger *et al.* 2011; DeLong 2012; Ohlberger 2013). Additionally, it would be interesting to investigate how the shape of functional responses modulates TS response effects on system persistence.

CONCLUSION

Warming-induced reductions in mean body sizes are common and have been termed a "third universal response to global warming" (Gardner *et al.* 2011). However, the long-term community consequences of this phenomenon remain poorly understood. We show that body-size reductions often increase community persistence, but the sign and magnitude of these effects strongly depend on (1) the degree and combination of

warming and enrichment, (2) the TS response of each individual species and (3) the community size structure. Our model indicates that TS response effects on species survival can be explained by alterations of species interaction strengths and consumer energetic efficiency. We predict that the consequences of size reduction are more important in systems where species show heterogeneous TS responses, and in strongly size-structured communities such as aquatic ones. We conclude that considering the links between resource gradients, species interactions and variability in species phenotypic responses is crucial to improve our ability to predict the impacts of size changes on community stability and persistence in a rapidly changing world.

AUTHOR CONTRIBUTIONS

A.S., A.B. and D.S.B. conceived and developed the models. A.B. and A.S. wrote the first draft of the manuscript, and A.B., A.S. and D.S.B. contributed substantially to revisions.

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