Evolutionary responses to climate change in parasitic systems

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Abstract

Species may respond to climate change in many ecological and evolutionary ways. In this simulation study, we focus on the concurrent evolution of three traits in response to climate change, namely dispersal probability, temperature tolerance (or niche width), and temperature preference (optimal habitat). More specifically, we consider evolutionary responses in host species involved in different types of interaction, that is, parasitism or commensalism, and for low or high costs of a temperature tolerance–fertility trade-off (cost of generalization). We find that host species potentially evolve all three traits simultaneously in response to increasing temperature but that the evolutionary response interacts and may be compensatory depending on the conditions. The evolutionary adjustment of temperature preference is slower in the parasitism than in commensalism scenario. Parasitism, in turn, selects for higher temperature tolerance and increased dispersal. High costs for temperature tolerance (i.e. generalization) restrict evolution of tolerance and thus lead to a faster response in temperature preference than that observed under low costs. These results emphasize the possible role of biotic interactions and the importance of ‘multidimensional’ evolutionary responses to climate change.

Keywords: climate change, commensalism, dispersal, parasitism, temperature preference, temperature tolerance, trade-off

Received 26 December 2014 and accepted 10 March 2015

Introduction

It is predicted that by the next century mean global temperature will raise 1.5–4.5°C (IPCC, 2013). Many scientific reports show that current climate changes have already affected the behaviour, biodiversity, and distribution of many species (reviewed in IPCC, 2014). Increasing temperature, for example, leads to earlier first flight in butterflies (Roy & Sparks, 2000; Forister & Shapiro, 2003). Moreover, climate change promotes shifting, expansion, or contraction of range in many insects (Parmesan et al., 1999; Battisti et al., 2005; Hickling et al., 2006; Menéndez, 2007) and small mammal species (Moritz et al., 2008). Such changes can result in changing community composition and biodiversity (Daufresne et al., 2004; Menéndez et al., 2006; Moritz et al., 2008; Urban et al., 2012). Indeed, it is speculated that for species currently interacting closely with other species, climate change might disrupt the spatial and/or temporal synchrony of partner species (Visser & Both, 2005; Parmesan, 2006; Schweiger et al., 2008; Berg et al., 2010; Kiers et al., 2010; Pelini et al., 2010).

‘Bioclimatic envelope models’ (also ‘ecological niche models’, ‘habitat suitability models’, or ‘species distribution models’) are widely used to explore possible species response to future climate by utilizing the association between current climatic conditions and occurrences of species to define the regions where a species is likely to maintain or establish viable populations in the future (Pearson & Dawson, 2003; Thomas et al., 2004; Araújo & Townsend Peterson, 2012). Such models assume that species would disperse to track climate change and move along with their optimal habitat (Hill et al., 1999; Parmesan et al., 1999; Thomas et al., 2001; Parmesan & Yohe, 2003; Thuiller et al., 2005, 2011; Hickling et al., 2006; Moritz et al., 2008). These models may predict that species would go extinct due to climate change because they fail to track suitable habitat; species’ ranges should consequently contract and ultimately collapse (Pounds et al., 1999, 2006; Thuiller et al., 2005, 2011; Franco et al., 2006; Thomas et al., 2006).

There are two important problems in using such models for exploring the potential responses of species to climate change. (i) They often assume that species are unchangeable entities lacking genetic variability to adjust to new conditions and that the only response of species to climate change would be tracking such change by movement. However, other ecological and evolutionary responses are also conceivable (Davis et al., 2005; Parmesan, 2006; Urban et al., 2012); for...
example, species might persist climate change in situ or adapt by evolving new temperature preference (Levitan, 2003; Balanyà et al., 2006) and/or increased temperature tolerance (niche width; Skelly et al., 2007; Oliver & Palumbi, 2011). (ii) The above-mentioned models focus mostly on abiotic conditions, such as climate (e.g. annual, winter and summer precipitation, mean annual temperature and minimum temperature of the coldest month, growing degree days, and humidity), geo-morphological characters (e.g. terrain types), or topographical characters (e.g. slope, altitude, and convexity) (Thuiller, 2003; Bedia et al., 2011; Booth et al., 2014), but typically do not consider biotic interactions. A few exceptions exist, however. For example, the models of Acevedo et al. (2012) and Boulangeat et al. (2012) account for competition and facilitation. (Giannini et al., 2013) included biotic interactions into species distribution model and found that this information can improve the accuracy of species distribution models and forecast distribution change. Yet, theoretical and empirical studies show that species interactions such as parasitism can be main factors affecting the evolution of traits that are important for coping with the effects of climate change, such as dispersal or specialization (Weisser et al., 1999; Lill et al., 2002; Sloggett & Weisser, 2002; Kunert & Weisser, 2003; Mondor et al., 2005; Green, 2009; Diamond & Kingsolver, 2010; Poethke et al., 2010; Choutt et al., 2011; Chaianunporn & Hovestadt, 2012a,b).

In this study, we investigate the potential effects of climate change in a system that includes host–parasite interspecific interactions and allows for evolutionary responses of species. We utilize a spatially explicit individual-based model with landscape heterogeneity in temperature similar to that of Chaianunporn & Hovestadt (2012b). We assume that a host species may principally respond in three different and nonexclusive ways, that is (i) by modifying its dispersal probability, (ii) by adjusting its optimum temperature (or habitat preference), or (iii) by changing its temperature tolerance (or niche width). We further consider how the type of species interaction (commensalism and parasitism) and trade-off associated with niche widening affect the evolutionary response in host species. As commensals in our model do not affect the host’s fitness in any way, the commensalism simulations produce identical results for the host populations as would simulations without guests, that is a ‘single-species version’ of the model. However, the results for guests are not identical to those for hosts in these scenarios due to the dependence of guests on hosts. We compare the parasitism and commensalism scenarios because we have previously demonstrated that – in contrast to commensalism – strong parasitism generates population fluctuation that promotes the evolution of dispersal and niche widening (Chaianunporn & Hovestadt, 2012a,b). A cost for niche widening constitutes an obvious constraint on niche widening that may indirectly also affect dispersal evolution (see Chaianunporn & Hovestadt, 2012b).

Materials and methods

Simulation landscape and climate change

We utilize a spatially explicit, individual-based two-species model previously presented by Chaianunporn & Hovestadt (2012a,b). We create spatially explicit lattice landscapes of dimension 32 × 32 grid patches. The grid of the landscapes is wrapped into a torus in both dimensions (a typical step taken is such simulations) to avoid edge effects.

Each patch m is characterized by a continuous number indicating a habitat attribute that represents mean temperature (Hm). Even though we assume here that the habitat attribute is temperature (or an attribute directly correlated with it), it could also be interpreted as another abiotic factor with continuous variation, such as salinity or pH. Mean temperature in each patch fluctuates annually by adding or subtracting a random number from a Gaussian distribution with mean = 0 and standard deviation σ = 0.4 in all scenarios – that is, in c. 99% of years, actual temperature Hm,t falls within a range of ±1°C around Hm. This variation is applied independently to each patch. This variability reflects natural annual variability in climate and promotes the selection of a certain ‘temperature tolerance’ (see ‘Host species’) as a means to cope with unpredictable variability.

We first carry out simulations over 2000 generations without climate change to allow evolution of populations that are well adapted to the initial conditions in each scenario. After this period, we store all host and guest individuals with their (evolved) traits in each patch. These populations are then exposed to alternative ‘climate change scenarios’ (X): (i) no change in mean temperature (as control) X = 0°C, (ii) an increase of X = 2.0°C, and (iii) an increase of X = 4.0°C over 100 years (generations), thus covering the prediction range of global circulation models (IPCC, 2013). Accordingly, mean habitat temperature of every patch (Hm) increases annually by 2/100 (X = 2.0°C) and 4/100 (X = 4.0°C) degrees between years 101 and 200. Thereafter, temperature increase stops and mean temperature stays at its new value. During the whole phase of climate change, the annual variability in habitat temperature is still applied. We continue simulations for another 800 generations to investigate the evolutionary response after climate change has ceased and the system settles into a new equilibrium.

Species community

Throughout we simulate population dynamics and evolution in a community of two interacting species. We assume two types of interaction in separate simulations: commensalism and parasitism. From now on, we use the term ‘guest’ as a collective term for a species that always benefits from the interaction and completely depends on the presence of the ‘host’.

species for survival and reproduction. A host can survive and reproduce in the absence of guests. The reproduction of an infected host individual is reduced to zero when the interaction is ‘parasitism’, whereas fitness of hosts is unaffected if the interaction is ‘commensalism’. According to this definition, our ‘parasitism’ scenario resembles a host-parasitoid interaction. Each habitat patch can in principle support a community of both species. We assume that hosts and guests have a synchronized annual life cycle with discrete generations. Hosts and guests are both haploid organisms reproducing asexually. The order of the life cycle of both species is as follows: (i) after births of hosts and guests, both species perform either natal dispersal to a new target patch or stay in their natal patch; (ii) species interaction occurs after dispersal; (iii) hosts and guests reproduce with fertilities determined according to the interaction; and (iv) after reproduction, all adult host and guest individuals die – newborn individuals again perform dispersal (i).

**Host species**

Host fitness (reproduction) generally depends on habitat temperature and competition. Each host individual $j$ is characterized by the heritable and evolvable traits $h_j$ and $g_j$ where $h_j$ defines the individual’s ‘temperature preference’ and $g_j$ its ‘temperature tolerance’. The fertility of host individual $j$ in habitat $m$ and year $t$ $(\lambda_{mjt})$ is estimated according to a Gaussian distribution as:

$$\lambda_{mjt} = T_j \varphi e^{-\frac{(u_{mjt} - u_j)^2}{2\sigma^2}},$$

with $T = e^{\frac{u_j}{\sigma}}$, where $\lambda_0$ is the maximum fertility in optimal temperature (habitat). The fertility of any host individual is thus controlled by the match between the actual temperature of the patch at year $t$ ($u_{mjt}$) and the host’s temperature preference ($u_j$), and the host’s temperature tolerance ($g_j$) that controls the width of the Gaussian distribution. With the term $T_j$ we introduce a ‘fertility sanction’ for increasing temperature tolerance (niche widening), that is for individuals that evolve a wider acceptable temperature range – otherwise, selection would obviously favour complete temperature generalists. In the following, we call this the ‘tolerance–fertility trade-off’. The principle existence of such trade-offs is a fundamentally accepted idea in evolutionary ecology (e.g. Caley & Munday, 2003; Koricheva et al., 2004; Palaima, 2007), well captured in the Gaussian distribution as:

$$\lambda_{mjt} = T_j \varphi e^{-\frac{(u_{mjt} - u_j)^2}{2\sigma^2}},$$

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The expected number of offspring surviving to reproduction for each host individual $(O_{njt})$ is affected by species interaction and local competition between host individuals and is estimated according to the Beverton–Holt model (Beverton & Holt, 1981):

$$O_{njt} = \lambda_{njt} w$$

with survival probability $w = \frac{1}{1 + \frac{(N_{njt})}{C_0}}$.

Here, $K$ defines patch capacity for hosts and $N_{njt}$ is the number of hosts in patch $m$ at year $t$. Under commensalism, guests do not affect host reproduction ($I = 1$). In parasitism scenario ($I = 0$), infected hosts do not reproduce, but we assume that they are only killed at the end of their development. They thus still compete with other individuals for, for example, food resources, as is the case in many host species infected by parasites. For this reason, $N_{njt}$ is not discounted by the number of infected hosts.

In our stochastic simulations, a nonparasitized host individual $j$ in patch $m$ at year $t$ thus produces a Poisson-distributed number of surviving offspring with mean $O_{njt}$. Accordingly, realized equilibrium density depends on how well individuals are adapted to the habitat temperature, and their temperature tolerance – generalists cannot reach the same densities than specialists even in optimal habitat.

**Host–guest interaction**

We assume that the probability $p_{mjt}$, that a host encounters and interacts with at least one guest individual within any habitat patch $m$ at year $t$ follows the Nicholson–Bailey equation (Nicholson & Bailey, 1935) with Holling’s type II functional response (Holling, 1959a,b), that is

$$p_{mjt} = 1 - e^{-\frac{N_{njt}}{p_{mjt}}}.$$  

where $N_{G,njt}$ and $N_{H,njt}$ are the number of guests and hosts within patch $m$ at year $t$, respectively, and $a$ is the per capita search efficiency of guests. We implicitly assume that guests’ handling time is one, which implies that a guest individual interacts at most with a single host in its lifetime. Note that the exponential term of Eqn 3 provides the probability of a host to not interact with parasites.

As no individual attributes of hosts or guests affect encounter probability, we use Eqn 3 to first estimate the total number of encounters in the population and then randomly select the corresponding number of guests and hosts, respectively, from the total population as being involved in an encounter. Guests that encounter hosts always reproduce successfully with number of offspring drawn from a Poisson distribution with mean $\psi$. As a consequence, the guest population is implicitly density-regulated by the number of available hosts. Change in fertility of a host interacting with guests depends on the interaction type as mentioned above.

**Dispersion**

All adult hosts and guests die after reproduction. Newborn hosts and guests decide to disperse or stay in their natal patch. For each individual, this decision is determined by an inherited and evolvable trait called ‘dispersal probability’ ($d_h$ and $d_g$ for hosts and guests, respectively) that determines the
individual’s probability to emigrate; \(d_h\) and \(d_g\) always take values between 0 and 1. Each individual draws a random number from the interval \([0 \ldots 1]\). If this number is lower than the dispersal probability, the individual disperses; otherwise, it stays in its natal patch. If an individual decides to disperse, it moves randomly to one of the eight neighbouring patches (Moore neighbourhood; Gray, 2003) irrespective of the habitat type of the target patches. After dispersal, the life cycle continues as explained above.

Evolution

We assume three evolving traits of hosts and one of guests, namely temperature preference of hosts \((b)\), temperature tolerance of hosts \((c)\), and the dispersal probability of hosts and guests \((d_h\) and \(d_g\)). These traits are typically inherited from the parent, but occasionally mutate with rate \(\mu_b\) and \(\mu_c\) for hosts and guests, respectively (both fixed at 0.01); such high mutation rate should maintain genetic diversity in case of small population size during climate change (more on reasons for choosing such a high mutation probability in the discussion). Mutations of traits occur independently. The mutation process of three traits is similar; that is, a random value from the uniform interval \([-0.05, 0.05]\) is added to the trait value. Whereas temperature preference is allowed to evolve any value between \([-\infty, \infty]\), we limit allowable values for dispersal probability to the interval \([0, 1]\) and for temperature tolerance to the interval \([0.05, \infty]\); temperature tolerance always evolved towards larger values than the minimum, however, as in annually variable habitats a minimum temperature tolerance is mandatory for long-term survival.

Simulation scenarios

We focus on the evolutionary response of hosts under gradually increasing mean habitat temperature (climate change). We assume that the host species may respond to this change by evolution of all three traits, that is temperature preference \((b)\), temperature tolerance \((c)\), and dispersal probability \((d_h\) or \(d_g\)). Guests’ fitness is as such independent of habitat and guests can only adjust their dispersal probability \((d_g)\). Based on our previous studies (Chaianunporn & Hovestadt, 2012a,b), we hypothesize that hosts evolutionary response to climate change will be modulated by the kind of interaction and the trade-off associated with temperature tolerance.

In our scenarios, we compare the influence of two types of interaction, that is commensalism and parasitism as described above. We fix the search efficiency of guests \((a)\) in both scenarios at 0.04. We also carried out parasitism scenarios with a lower search efficiency \((a = 0.01)\), but in this case, results resemble those for commensalism (see Chaianunporn & Hovestadt, 2012a; for further explanation); we thus do not provide corresponding results here. Secondly, we compare the effects of two different values for the tolerance-fertility trade-off that defines the disadvantage associated with evolving a high temperature tolerance (high cost: \(T_1, c = 1\); low cost: \(T_2, c = 4\), see Eqn 1). In all scenarios, we use a noncorrelated, random ‘heterogeneous landscape’ generated in the same way as the random landscapes described in Chaianunporn & Hovestadt (2012d) with mean zero and standard deviation of landscapes \(s_x = 2s_t\) (the range of habitat temperatures is approximately \([-2, 2]\)). Note that a mean temperature assigned to grid patch \(m\) \((H_{\text{loc}})\) remains unchanged throughout a simulation run except for the systematic increase imposed during climate change.

Initialization and analyses

Patches are initialized with \(K = 1000\) host individuals and a small number of guests \((10\) individuals\) to avoid the collapse of host population at the beginning of the simulation in parasitism scenarios. With such high \(K\) values, effects of demographic stochasticity are reduced (see Chaianunporn & Hovestadt, 2012a). Dispersal probabilities of hosts and guests are initialized by drawing random values from the uniform interval \([0, 1]\) for each individual. Temperature preference of hosts is initialized with random values from the uniform interval \([-2.5, 2.5]\), and temperature tolerance is initialized with random values from uniform interval \([0.05, 2.05]\). A summary of all model and simulation parameters and their standard values can be found in Table 1.

For each parameter combination, we carry out ten simulation replicates on 10 different landscapes. For graphical presentation, we calculate averages of means and standard deviations estimated for each of the ten replicates and for each of the three evolving host traits (dispersal, temperature preference, and temperature tolerance) after 2000 generations but before the onset of climate change \((t = 100)\) and at \(t = 200\) (at the end of climate change). Due to the large population sizes, means and standard deviations of trait values were calculated only from a set of randomly selected individuals (one individual from each local population, i.e. \(32 \times 32 = 1024\) individuals). We mainly present results from the scenarios with an increase of 4.0°C because in 2.0°C scenarios, hosts show principally similar but obviously weaker responses. In figures, we show moving time averages (moving window = 20) of host population size for visualization because in parasitism scenarios (Appendix S1), host populations may fluctuate intensively. To present the evolutionary response in the three traits, we plot their mean and standard deviation before and after climate change in arrow plots. On these plots, we rescale the mean for temperature preference by dividing by the temperature increase (4°C) – resulting values thus fall into the range between 0 and 1.

Results

Generally, our simulations show that climate change could lead to a concurrent evolutionary response in all three host traits. In Fig. 1, we show one exemplary set of trajectories for simulations of the commensalism scenario with low cost of tolerance-fertility trade-off (for other sets of trajectories, see Appendix S1). The increase in habitat mean temperature leads to a reduction of total population size by about 1/3 over the 100 years.
Climate change induces a substantial increase in dispersal probabilities in the commensalism scenario, while under parasitism, only slight evolutionary changes in dispersal can be observed. Interestingly, the dispersal probabilities of guests tend to change so that they match to dispersal probabilities of hosts (Fig. 2a and c, arrowheads at column d). The population-wide variability in the dispersal trait is little affected by climate change in all scenarios (Fig. 2b,d).

**Responses in temperature preference**

After 2000 generations of evolution but before the onset of climate change, mean temperature preferences of hosts expectedly and perfectly match the prevailing mean habitat temperature in all scenarios. Climate change obviously mandates an adjustment of this trait to new conditions. In none of the scenarios, however, evolution can fully track climatic conditions during the period of change, but under commensalism habitat preference traces climate change more closely than under parasitism (Fig. 2a, c); the discrepancy is especially large in scenarios with a low trade-off cost for temperature tolerance (\(c = 4\)). The response is always more rapid if the trade-off costs for temperature tolerance are high (\(c = 1\)). Besides the change in trait mean, we observe a considerable effect of climate change on variance in temperature preference (Fig. 2b, d). Under commensalism, the trait’s variance considerably declines during climate change. In parasitism scenario, host populations generally develop a lower variance in temperature preference than in commensalism scenarios, but if the cost for temperature tolerance is low (\(c = 4\)), the variance in temperature preference increases under parasitism during the phase of climate change (more on this in discussion).

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**Table 1** Summary of model parameter definitions and ranges of values used

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>(H_m)</td>
<td>habitat temperature of patch (m)</td>
<td>depending on landscape arrangement</td>
</tr>
<tr>
<td>(s_t)</td>
<td>temporal variability in habitat temperature</td>
<td>(s_t = 0.4)</td>
</tr>
<tr>
<td>(K)</td>
<td>patch capacity for hosts</td>
<td>(K = 1000)</td>
</tr>
<tr>
<td>(\lambda_0)</td>
<td>intrinsic host growth rate per capita</td>
<td>(\lambda_0 = 5)</td>
</tr>
<tr>
<td>(a)</td>
<td>mean number of offspring for a guest</td>
<td>(a = 0.04)</td>
</tr>
<tr>
<td>(\psi)</td>
<td>per host search efficiency</td>
<td>(\psi = 2)</td>
</tr>
<tr>
<td>(\mu_h) and (\mu_g)</td>
<td>mutation rate of hosts and guests, respectively</td>
<td>(\mu_h = 0.01)</td>
</tr>
<tr>
<td>(h)</td>
<td>temperature preference of hosts</td>
<td>evolving</td>
</tr>
<tr>
<td>(g)</td>
<td>temperature tolerance of hosts</td>
<td>evolving</td>
</tr>
<tr>
<td>(d_h)</td>
<td>dispersal probability of hosts</td>
<td>evolving</td>
</tr>
<tr>
<td>(d_g)</td>
<td>dispersal probability of guests</td>
<td>evolving</td>
</tr>
</tbody>
</table>

**Simulation scenario parameters**

- \(X\): climate change over 100 generations, \(X = 0^\circ C, 2.0^\circ C, 4.0^\circ C\)
- \(s_s\): spatial variability in temperature, \(s_s = 0.8\)
- \(c\): cost of tolerance–fertility trade-off; see Eqn (1), high cost: \(c = 1\); low cost: \(c = 4\)
- \(l\): interaction type; see Eqn (2), parasitism: \(l = 0\); commensalism: \(l = 1\)
Responses in temperature tolerance

The initial temperature tolerance (before climate change) is higher in the parasitism than in the commensalism scenarios. The cost of tolerance–fertility trade-off is the most important factor determining evolution of temperature tolerance (Fig. 2a and c): the higher the cost, the lower the temperature tolerance that evolves. Climate change only induces noticeable generalization if trade-off costs are low ($c = 4$) in any scenario, and generally induces a slight increase of variance in this trait.

Effects of interspecific interaction

We find that differences in response between the two types of interaction are most pronounced under low costs for the tolerance–fertility trade-off (compare Fig. 2 – square symbols). Before climate change, parasitism selects for higher dispersal probabilities and temperature tolerance than commensalism. However, parasitism is also associated with the establishment of much lower variance in temperature preference. Under climate change, dispersal probabilities massively increase in the commensalism scenario (from a very low level), whereas dispersal hardly changes (from a very high value) in the parasitism scenario. Host temperature preference adjusts slower to climate change under parasitism than under commensalism so that after 100 generations, at the end of climate change, an ‘adaptation gap’ (discrepancy between mean preferred temperature and mean ambient habitat temperature) of c. 2.4°C has formed in this scenario, whereas the gap is only c. 1.3°C in the commensalism scenario. Interestingly, climate change induces an opposing effect on trait variance of temperature preference in the two scenarios – in commensalism, it substantially falls from a high value, while trait variance increases under parasitism (Figs 2 and 3). Finally, temperature tolerance expands under both

Fig. 1 An example of host’s responses to climate change over time. Results from the commensalism scenario ($I = 1$) with low cost of tolerance–fertility trade-off ($c = 4$). Lines in each panel represent results from three different climate change scenarios: no change (solid line), $X = 2.0°C$ (dashed line), and $X = 4.0°C$ scenario (dotted line) over 100 generations. The two vertical, dashed grey lines show the time step at the beginning of climate change (101st) and the end (200th) of climate change: (a) moving average (20 generations) of host population size; (b) mean host dispersal probability ($d_h$); (c) mean host temperature tolerance ($g$); and (d) mean host temperature preference ($h$).
types of interaction, but the tolerance is and remains higher under parasitism.

**Discussion**

In our simulations, we allow for the evolution of three traits in hosts (and only one trait in guests) that may play an important role in response to climate change, namely temperature preference (optimal habitat), temperature tolerance (or niche width), and dispersal probability; note that for simplicity, we assume that temperature preference is not only related to temperature *per se*, but the trait could also represent adaptation to other attributes that correlate with habitat temperature, for example vegetation height or habitat dryness (Allen *et al.*, 2010; Elmendorf *et al.*, 2012).

Changes in dispersal induced by climate change have previously been reported (e.g. Hill *et al.*, 1999; Parmesan *et al.*, 1999; Thomas *et al.*, 2001; Parmesan & Yohé, 2003; Hickling *et al.*, 2006; Moritz *et al.*, 2008). However, to our knowledge, an evolutionary adjustment in temperature preference and tolerance as a potential response has drawn less attention in the context of climate change, even though they are obvious ‘strategies’ to deal with climate change (Skelly *et al.*, 2007; Dawson *et al.*, 2011) – especially if the latter also results in an increase in climatic variability as is suggested by current climate models (Moss *et al.*, 2010). Here, we test...

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**Fig. 2** Effects of species interaction and tolerance–fertility trade-off on the host’s and guest’s evolutionary responses to climate change (*X* = 4°C). Arrow base represents mean or standard deviation (SD) of traits before climate change (generation 100), and arrow heads represent means or SD at the end of climate change [generation 200; symbols at arrow base indicate results for different cost of tolerance–fertility trade-off (squares for low cost, *c* = 4, circles for high cost, *c* = 1)]. Results for evolving dispersal probabilities in hosts and guests (*d*; closed symbol for hosts and open symbol for guests), temperature preference (*h*), and temperature tolerance (*g*) are indicated on x-axis. The scale for temperature tolerance is shown on the axis on the right side. (a) Mean and (b) standard deviation of trait values for commensalism scenarios (*I* = 1). (c) Mean and (d) standard deviation of trait values for parasitism scenarios (*I* = 0) (for more detail, see Model and simulation).
effects of different parameters/attributes potentially affecting the evolutionary response in any of the three traits, that is the impact of parasitism and the tolerance–fertility trade-off (or some other relevant trade-off) associated with the evolution of temperature tolerance.

Compared to commensalism, parasitism has two effects on the system provided that the interaction is strong enough: it affects the evolution of dispersal in hosts and guests due to the strong spatio-temporal dynamics in host population size induced by the interaction (for more details, see Chaianunporn & Hovestadt, 2012a). As a consequence, parasitism also limits the emergence of diversity in temperature preference in heterogeneous landscapes as hosts continuously on the move have to follow a ‘generalist’ strategy with a high tolerance and a preference for the ‘landscapewide’ average temperature; Fig. 3 contrasts the distribution of host temperature preference under commensalism and parasitism. Before climate change, this distribution (Fig. 3c) is very narrow under parasitism compared to the corresponding distribution under commensalism (Fig. 3a): this lack of genetic diversity in temperature preference slows down the response to climate change under parasitism. Indeed, it must be noted that the lacking diversity in temperature preference already prevents the colonization of the more extreme habitats before climate change sets in, contributing – in addition to the direct effects of parasitism – to a reduction in effective host population size. Yet lower population size, in turn, reduces the frequency at which new (and favourable) mutations may appear in the population. Nonetheless, at the end of climate change, the shape of the distribution of habitat preferences in the parasitism scenario is actually more similar to that in the commensalism scenario, but in comparison lags further behind the ambient temperature (Fig. 3b,d); that is, maladaptation becomes larger.

The lack in variance and adaptability with respect to temperature preference can, to a certain degree, be compensated by an increase in temperature tolerance. More tolerance is generally favoured under parasitism for the reasons already provided above. We do not observe a difference in the increase in tolerance

Fig. 3 Histograms of hosts’ temperature preference distribution before (generation 100) and after climate change (generation 200; \( X = 4^\circ C \)) for commensalism and parasitism scenarios (low cost of tolerance-fertility trade-off, \( c = 4 \)). The y-axis presents the proportion of traits falling into specified categories. The dashed lines indicate mean habitat temperature at corresponding time step (0°C for before and 4°C after climate change). (a) Commensalism before and (b) after climate change. (c) Parasitism before and (d) after climate change.

induced by climate change between commensalism and parasitism (which only occurs if trade-off costs are low), but nonetheless, the standing larger tolerance in the parasitism scenario in part mitigates the effects of climate change providing a larger temporal ‘buffer’ for adjustment in temperature preference.

To express it in another way – the modification of the trade-off cost indicates that a more rapid adjustment of temperature preference could, to a certain degree, compensate an existing limitation in temperature tolerance – we recognize that the adjustment in temperature preference is faster (c. 80% vs. 60% by the end of climate change phase) when the evolution of temperature tolerance is prevented by a costly tolerance–fertility trade-off; such a relationship has already been predicted by Whitlock (1996).

Even though evolution in three traits is allowed for in our simulations, we do not necessarily see responses in all three traits in every scenario. For example, temperature tolerance does only increase under climate change if the trade-off associated with such an increase is not too severe. Dispersal propensity shows a strong (especially proportionally strong) response only where it is initially very low (i.e. in commensalism scenario). Our results thus indicate that the evolutionary response of species to climate change may be different depending on the conditions (such as the presence or absence of parasites or cost of tolerance–fertility trade-off). We also want to point out that further ecological and evolutionary responses to climate change might exist that we did not explore in this study, for example shifts in phenology (Visser & Both, 2005; Parmesan, 2006) or change of interaction partners (Kiers et al., 2010). Estimating the (additional) role of such responses and how they might interact with the responses considered here requires even further investigation.

We emphasize that the range of temperature values provided in our scenarios should not be taken too literally. The important point is that the evolutionary responses to climate change should critically depend on how the magnitude of temporal climatic variability scales to the cost of tolerance–fertility trade-off. In our model, this depends on three key parameters, namely the unpredictable interannual variability in climatic conditions ($s_a$), the spatial heterogeneity in ambient habitat temperature ($s_h$), and the trade-off cost ($c$) that results in fertility reduction as tolerance increases (the trade-off could also affect other fitness components). It may indeed be a challenging task to quantify these parameters for a real system, and matters may further be complicated if costs (fertility reduction at nonoptimum temperature) associated with trade-off were nonlinear or would even show a threshold behaviour.

The role of spatial and temporal heterogeneity may at a first glance seem similar, but the important difference is that individuals cannot avoid temporal variability according to our model assumption. The only evolutionary response to this ‘problem’ is thus the evolution of a sufficient temperature tolerance with the latter determined by the underlying trade-off. Spatial heterogeneity, in contrast, may be mostly irrelevant for the evolution of temperature tolerance as long as individuals do not need to disperse much. Under scenarios promoting low dispersal, we thus see the evolution of a wide spectrum of locally adapted individuals with different temperature preference (Fig. 3a) whereas temperature tolerance is not different from that evolving in homogeneous landscapes despite the fact that spatial heterogeneity ($s_h$) is twice as large as temporal heterogeneity ($s_t$). In reality, organisms might, however, be able to avoid temporal variability also by, for example, active choice of suitable microclimatic conditions (Hof et al., 2011).

In this study, we assume seemingly unrealistically high mutation rates ($\mu_h$ and $\mu_p = 0.01$) that may be rare in nature (Lynch, 2010). Technically, such high mutation rates allow a quick evolutionary response leading to higher survival chances of populations exposed to climate change. The strong changes in distribution of temperature preference presented in Fig. 3 indicate that mutations were indeed the ultimate source of genotypes that were not originally present in the population when climate change started. It is difficult, though, to directly compare ‘mutation events’ in our model and those in nature, because the mutation process behind complex behavioural traits such as dispersal, temperature preference, or temperature tolerance is not well understood and certainly more complicated than implemented in our model of haploid organisms. In fact, sexual reproduction plays an important role in adaptation to continual environmental change and is presumably especially valuable in host–parasite interaction (reviewed in Lively & Morran, 2014). Adding sexual reproduction and recombination in the model might improve our understanding on how organisms can adapt to rapid environmental change. For example, if traits were determined by many loci, selection could operate much more with the standing variance by just recombining alleles without a need for ‘de novo’ mutations – a mechanism that would be similar in effect to the high mutation rate assumed in our model. Several studies suggest that changes in, for example, thermal tolerance or thermal preference can indeed occur rapidly within few generations (Good, 1993; Skelly & Freidenburg, 2000; Balanyá et al., 2006; Skelly et al., 2007). This makes our assumption of rapid evolutionary response to climate change more credible.
Further note that in our simulations, we consider a limited regional dimension only; that is, we do not assume a large-scale gradient in temperature conditions. Real systems are typically not closed, however, and a likely resource – especially if species are dispersive – of genetic innovation may thus be immigrants from other regions, where conditions are, for example, already warmer (Kubisch & Poethke, 2011); such immigrants would basically take the same role as a new favourable mutant.

To avoid dealing with even further issues, we focus here only on the responses of host species to climate change, but do not investigate the potential direct effects of climate change on guests, that is the survival and reproduction of guest species does not depend on any habitat attributes; this simplifying assumption may be justified because parasites typically live within and from their guest and are thus not exposed to such additional direct effects. We also want to mention that in our system, guests are fundamentally more sensitive as they cannot survive and reproduce without their hosts. This explains why the evolutionary change in dispersal probability of guests induced by climate change corresponds to that in hosts’ even though the guests are not directly affected by that change. Without such changes, guests might mismatch hosts after dispersal. Additional simulations (results not shown) indicate that under more extreme conditions (e.g. faster climatic change, higher trade-off costs), guests might even go extinct, whereas hosts survive. This warrants further investigation, especially as guest species are often targets of conservation efforts, such as Maculinea butterflies that are closely associated with specific host ants (Settele & Kuehn, 2009; Thomas et al., 2009). A possible and highly interesting topic for future research is whether virulence or comparable attributes in guests might also change under the influence of climate change.

Many studies predict the potential impacts of climate change on species distribution and biodiversity using ‘bioclimatic envelope models’ according to in which organisms respond to climate change primarily by ‘tracking’ (dispersing to) suitable climatic areas (e.g. Thuiller, 2003; Thomas et al., 2004; Thuiller, 2003; Thuiller et al., 2005, 2011; Lawler et al., 2009). This approach has been criticized because it ignores many factors that could potentially affect the prediction such as biotic interactions, potential evolutionary response, or interindividual variation in dispersal abilities (Pearson & Dawson, 2003; Hampe, 2004). Various studies indeed evidence that evolutionary responses to climate change can occur in brief periods (Good, 1993; Skelly & Freudenburg, 2000; Balanyá et al., 2006; Skelly et al., 2007). We show here that mitigating evolutionary responses might even be ‘multidimensional’ including several traits and that selection on different attributes can be interactive and compensatory. Moreover, our results emphasize that the effect on interspecific interactions (in our case, parasitic interaction; see Kubisch et al., 2013 for inter-specific competition) may possibly play a very important role for correctly predicting the responses to climate change. We suggest that considering different types of responses of organisms should help improving the accuracy of predictions concerning future species distributions and especially want to point out that evolutionary response might be compensatory (e.g. if dispersal is too costly, local adaptation may proceed faster).

The simulations presented here constitute only a ‘conceptual approach’ to explore what kind of ‘multidimensional’ evolutionary responses to climate change might be possible and how the nature of responses may depend on external conditions. Our simplistic approach should only be taken as an outline towards developing evolutionary models that relate to real-world systems. Clearly, a more detailed evaluation of the critical assumptions and model parameters would be necessary, before such application-orientated models and predictions could be generated. The challenge may especially be demanding to quantify the potential to ‘generate’ evolutionary innovations (e.g. by immigration, mutation, recombination) and the possible role of trade-offs associated with selection on tolerance or other changes in life-history attributes associated with climate change.

Acknowledgements

We thank H. J. Poethke, J. A. Thomas, and K. Schönrogge for valuable discussion and improvement of the manuscript. TC is grateful for financial support by DPST project by the Royal Thai Government. TH has been supported by the EU project CLIMIT funded by the ANR through the FP6 BiodivERsA Eranet. TH further acknowledges support by the SBF 1047 ‘Insect Timing’ supported by the ‘Deutsche Forschungsgemeinschaft’ (DFG).

References


Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Host’s responses to climate change over time from different scenarios.