REVIEW ARTICLE

Forecasting extinction risk of ectotherms under climate warming: an evolutionary perspective

Richard J. Walters*[1,2], Wolf U. Blanckenhorn[1] and David Berger[1,3]

[1]*Institute of Evolutionary Biology and Environmental Studies, University of Zürich, Winterthurerstrasse 190, CH-8057, Zürich, Switzerland;* [2]*Environmental Biology, School of Biological Sciences, University of Reading, Reading, RG6 6BX UK; and* [3]*Evolutionary Biology Centre, Uppsala University, Norbyvägen 14-18, 75236, Uppsala, Sweden*

Summary

1. It has been postulated that climate warming may pose the greatest threat species in the tropics, where ectotherms have evolved more thermal specialist physiologies. Although species could rapidly respond to environmental change through adaptation, little is known about the potential for thermal adaptation, especially in tropical species.

2. In the light of the limited empirical evidence available and predictions from mutation-selection theory, we might expect tropical ectotherms to have limited genetic variance to enable adaptation. However, as a consequence of thermodynamic constraints, we might expect this disadvantage to be at least partially offset by a fitness advantage, that is, the 'hotter-is-better' hypothesis.

3. Using an established quantitative genetics model and metabolic scaling relationships, we integrate the consequences of the opposing forces of thermal specialization and thermodynamic constraints on adaptive potential by evaluating extinction risk under climate warming. We conclude that the potential advantage of a higher maximal development rate can in theory more than offset the potential disadvantage of lower genetic variance associated with a thermal specialist strategy.

4. Quantitative estimates of extinction risk are fundamentally very sensitive to estimates of generation time and genetic variance. However, our qualitative conclusion that the *relative* risk of extinction is likely to be lower for tropical species than for temperate species is robust to assumptions regarding the effects of effective population size, mutation rate and birth rate per capita.

5. With a view to improving ecological forecasts, we use this modelling framework to review the sensitivity of our predictions to the model's underpinning theoretical assumptions and the empirical basis of macroecological patterns that suggest thermal specialization and fitness increase towards the tropics. We conclude by suggesting priority areas for further empirical research.

Key-words: adaptation, ecological forecasting, extinction, hotter is better, metabolic scaling, temperature, thermal specialization

Vulnerability of tropical species to climate warming

A diverse range of ecological responses to recent climate warming have been widely documented (Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003), notably at mid- to high latitudes where the rate of warming has been fastest, and the extent of monitoring has been the greatest (Parmesan 2007). Although increases in temperature are predicted to be greatest at higher latitudes (IPCC 2007), it has been suggested that climate warming may pose a greater threat to species living in the biodiversity-rich tropics. This is because tropical (ectotherm) species are likely to have evolved a thermal specialist physiology

*Correspondence author. E-mail: r.j.walters@reading.ac.uk

that lowers tolerance to temperature change, an adaptation to the more stable climatic conditions typically experienced at lower latitudes (Tewksbury, Huey & Deutsch 2008). By operating at body temperatures close to their critical thermal maximum, thermal specialists are vulnerable to even modest increases in regional temperature, whereas temperate species may benefit from climate warming because many typically experience environmental temperatures below their thermal optimum (Deutsch *et al.* 2008; Huey *et al.* 2009). Although organisms are likely to avoid the lethal effects of hot temperatures through avoidance strategies such as thermoregulatory behaviour and physiological acclimation (Angilletta 2009; Huey & Tewksbury 2009; Kearney, Shine & Porter 2009), costs are likely incurred by changes to foraging behaviour and/or reduced opportunities for reproduction (Huey, Losos & Mortiz 2010). If tropical species cannot migrate to cooler areas quickly, enough populations will have to effectively track climate change through adaptation to maintain positive population growth rate and avoid extirpation (Hewitt & Nichols 2005; Visser 2008; Hoffmann & Sgrò 2011).

Evolutionary responses to climate warming are already evident (see Parmesan 2006 for a review), but it is debateable whether the rate of adaptation will be sufficient to avoid extinction (Skelly *et al.* 2007; Huey, Losos & Mortiz 2010), especially in the species-rich tropics where local extirpations are already apparent (Sinervo *et al.* 2010). Two important macroecological patterns are predicted to influence the relative evolutionary potential of tropical species. Firstly, the increase in thermal specialization towards the tropics (Tewksbury, Huey & Deutsch 2008; Sunday, Bates & Dulvy 2011) is predicted to reduce genetic variance via stronger stabilizing selection (Huey & Kingsolver 1993; Bürger & Lynch 1995; Angilletta 2009). The resultantly low trait heritabilities will reduce the capacity of the mean phenotype of a population to closely track environmental change reducing fitness and increasing the likelihood of extinction (Huey & Kingsolver 1993; Lynch & Lande 1993). Secondly, because of what is believed to be a thermodynamic constraint, adaptation to high temperatures is associated with a higher maximum population growth rate (r_{max}) (Huey & Kingsolver 1989; Frazier, Huey & Berrigan 2006; Kingsolver & Huey 2008; Knies, Kingsolver & Burch 2009; Angilletta, Huey & Frazier 2010). A high r_{max} is predicted to lower the risk of extinction by minimizing the costs of selection (Lynch & Lande 1993) and demographic stochasticity (Gomulkiewicz & Holt 1995).

In this paper, we demonstrate the relative importance of these opposing forces on extinction risk using an established modelling framework (Lynch & Lande 1993; reviewed by Huey & Kingsolver 1993; Angilletta 2009; Kingsolver 2009; Hoffmann & Sgrò 2011) and metabolic scaling relationships (Brown *et al.* 2004). Our primary prediction is that tropical species are at no greater risk of extinction than temperate species, a conclusion robust to assumptions regarding population size, mutation rate and birth rate. The extent of this potential evolutionary advan-

tage is greatest for species with life histories that already maximize r_{max}, that is, small and fecund organisms. In the light of these theoretical findings, we review and critically discuss the empirical basis for these macroecological patterns and the theoretical assumptions underpinning these predictions with the view to improving ecological forecasts.

A theoretical framework for thermal adaptation

Consider the performance curve of an ectotherm adapted to local thermal conditions. Fitness can be approximated as a concave quadratic function of temperature, or a simple transformation thereof (Lynch & Gabriel 1987; Angilletta 2006), where the maximum defines the thermal optimum, T_{opt}, and the breadth defines the thermal tolerance of the organism (Huey & Kingsolver 1989). Thermal tolerance is defined at the lower limit by the critical minimum temperature, CT_{min}, and at the higher limit by the critical maximum temperature, CT_{max}. In reality, the T_{opt} is often higher than the mean environmental temperature, a strategy that can help to maximize geometric mean fitness under variable conditions (Martin & Huey 2008). Because here we only consider a change in mean temperature, the effects of selection on the breadth of the thermal reaction norm can be ignored under all but the most abrupt of environmental changes (Lande 2009). For simplicity, we also assume the organism is a thermoconformer, that is, body temperature is equal to ambient environmental temperature. Without loss of generality, body temperature can be used instead of environmental temperature to accommodate complexities of thermoregulation (Gilchrist 1995; Angilletta 2009).

Under climate change, the more closely the mean T_{opt} of a population can continue to *evolutionarily* track changes in mean environmental temperature the more likely it is that the population can maintain positive growth rate and avoid extirpation. A suite of models have been developed to quantify such phenotypic changes for a range of life histories to predict persistence time under directional selection (Lynch, Gabriel & Wood 1991; Lynch & Lande 1993; Bürger & Lynch 1995; see Box 1). Factors that are expected to promote the rate of adaptation include high levels of genetic variance, a high population growth rate and a short generation time. Huey & Kingsolver (1993) applied this general framework specifically to thermal adaptation to yield further insights into the role of performance breadth and the consequences of specialist–generalist trade-offs (reviewed by Angilletta 2009; Kingsolver 2009). One clear consequence of being a thermal specialist is that a narrow performance breadth subjects the ectotherm to a stronger intensity of selection for a given rate of temperature change. By implication, tropical species, as thermal specialists, are predicted to elicit a greater response to climate warming. But because strong stabilizing selection is also predicted to erode away genetic variance, the resultantly lower heritabilities may ultimately limit any response to selection. The scale of the predicted heritability advantage

for thermal generalists increases asymptotically with population size because of an increase in mutational input (Box 2; Fig. 1a). For effective population sizes exceeding ca. 500, this heritability advantage is sufficient to offset a lower selection intensity (Fig. 1b). Although tropical species have the potential to avoid or delay time to extinction under slow rates of warming (Fig. 2), temperate species are predicted to have a lower risk of extinction overall (Fig. 3). Here, we demonstrate how other factors hereto unconsidered, namely an increase in maximal fitness, might influence the extinction risk of tropical thermal specialist species.

Box 1: Modelling adaptation and extinction risk under environmental change

To estimate mean time to extinction under directional selection, it is necessary to model the dynamics of the distribution of phenotypes over time. The expected mean phenotype ($E[\bar{p}]$) and expected variance in mean phenotype ($V[\bar{p}]$) can be obtained by recursion using the following difference equations (Bürger & Lynch 1995; see original equations 6a and b).

$$E[\bar{p}_{t+1}] = E[\bar{p}_t] + s(kt - E[\bar{p}_t]),\qquad \text{eqn1}$$

$$V[\bar{p}_{t+1}] = \frac{V_A}{N_e} + (1-s)^2 V[\bar{p}_t] + s^2 V_\theta,\qquad \text{eqn2}$$

where t is time in generations, k is the rate of environmental change per unit time, V_θ is a measure of environmental stochasticity and N_e is effective population size. s is a measure of the strength of directional selection, equal to $V_A/(V_P + \omega^2)$, where V_P is phenotypic variance and ω^2 is an inverse measure of environmental specialisation. If direct estimates of additive genetic variance are unavailable, V_A can be estimated theoretically as a function of mutation–selection–drift balance (see Box 2).

Under directional selection, the mean phenotype is predicted to eventually evolve at rate k, but lag behind the mean environment θ by k/s. If the lag between the mean phenotype and the environment becomes too large, population growth rate becomes negative, at which point the population rapidly goes extinct. The expected population growth rate at time t is given as:

$$r_t = r_{\max,t} - \frac{(\bar{p}_t - \theta)^2}{2V_{\lambda,t}}\qquad \text{eqn3}$$

where the maximal population growth rate can be given as, $r_{\max,t} = \ln(B\omega/\sqrt{V_{\lambda,t}})$, where B offspring per capita when the mean phenotype is equal to its environment, that is, $E[\bar{p}] = \theta$, and where $V_{\lambda,t}$ is equal to the sum: $\omega^2 + V_P + V[\bar{p}_t] + V_\theta$. In the simplest case of density dependence, for a population size of N breeding adults limited by a carrying capacity K, of the $N \exp^r$ offspring produced per generation only a maximum of K will survive; when $N \exp^r < K$, all

offspring are assumed to survive to the next generation. Extinction is assumed to occur once the population reaches a minimum threshold (e.g. $N < 2$ for sexually reproducing organisms). To evaluate the relative contribution of adaptation to reducing extinction risk, mean time to extinction of an adapting population can be compared with that of a population where the mean phenotype is otherwise held constant, that is, $E[\bar{p}_{t+1}] = E[\bar{p}_0]$.

An alternative measure of extinction risk that can be derived analytically is the theoretical maximum rate of environmental change at which a population could continue to just replace itself (i.e. $r_{\max} = 0$) under directional selection. This measure of extinction risk is referred to as the critical rate of environmental change, k_c (Lynch & Lande 1993). Beyond this rate, population growth rate becomes negative leading to rapid extinction. Bürger & Lynch (1995) derive the critical rate of change as:

$$k_c = \frac{V_A}{V_P + \omega^2}\sqrt{2V_\lambda r_{\max}}.\qquad \text{eqn4}$$

where $V_\lambda = V_{\lambda,\infty}$ and $r_{\max} = \ln(B\omega/\sqrt{V_\lambda})$.

Obviously, no trait can be expected to evolve indefinitely. But on the basis that long-term selection experiments on small populations have shown responses of ten or more phenotypic standard deviations, a low critical rate of change could sustain an adaptive response to selection for hundreds, perhaps even thousands of generations before pleiotropic constraints are encountered (Lynch & Lande 1993; Bürger & Lynch 1995). Note that while these solutions can provide good estimates of *mean* time to extinction, they fail to account for the skewed distributions of extinction times expected to occur at rates of environmental change close to the critical rate. Caution should be taken therefore when interpreting the risk of extinction.

Huey & Kingsolver (1993) showed that if fitness is subject to a specialist-generalist trade-off then thermal specialists should have a lower risk of extinction, all else being equal. Evidence that trade-offs observable at the enzyme-kinetic level (Hochachka & Somero 2002) scale up to that of the whole organism remains equivocal (Gilchrist 1995; Angilletta *et al.* 2009); nonetheless, there is strong evidence that tropical species do possess a fitness advantage, if only because they are warm-adapted (Savage *et al.* 2004; Angilletta *et al.* 2010). This apparent thermodynamic constraint on maximum population growth rate (Savage *et al.* 2004) is attributed to the fundamental role of enthalpy in driving metabolic processes (Gillooly *et al.* 2001) and is otherwise known as the 'hotter is better' hypothesis (Frazier *et al.* 2006; Kingsolver & Huey 2008; Knies *et al.* 2009; Angilletta *et al.* 2010). This fitness advantage could be mediated
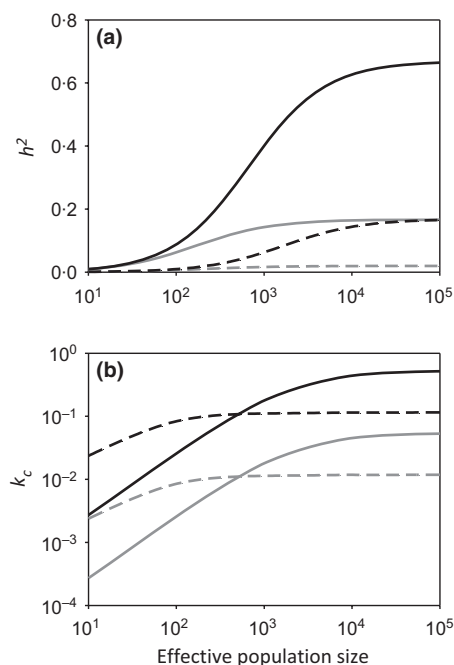
Fig. 1. (a) Theoretical estimates of heritability at mutation–selection–drift equilibrium and (b) the respective predicted critical rates of change calculated for thermal specialists (dashed lines; $\omega = 3$) and thermal generalists (solid lines; $\omega = 10$). Black lines are predictions based on the lower estimate of mean observed mutational variance ($V_m = 10^{-3}V_E$), and grey lines are predictions based on expected proportion of mutations that are quasineutral in their effects, thereby taking account of Lande's discount factor ($V_m = 10^{-4}V_E$). Other parameters: $B = 2$; $\alpha^2 = 0.05$.
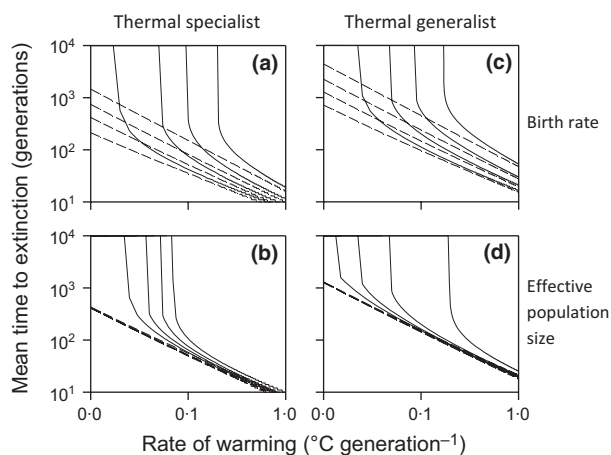

Fig. 2. Mean time to extinction calculated for (a, b) a thermal specialist ($\omega = 3$) and (c, d) a thermal generalist ($\omega = 10$) as a function of (a and c) birth rate per capita (bottom left to top right: $B = 1.2, 2, 10, 10000$; $N_e = 500$) and (b and d) effective population size (bottom left to top right: $N_e = 100, 200, 500, 10000$; $B = 2$). Solid lines represent the adaptive genetic response to temperature change, and dashed lines represent the null hypothesis of no adaptive change. Note the log-scale of both axes. Other parameters: $V_m/V_e = 5 \times 10^{-4}/1$; $\alpha^2 = 0.05$; $V_\theta = 1$.

either by a shorter generation time or an increase in potential fecundity (Kingsolver & Huey 2008). Thermodynamic constraints are also known to affect other biological rates potentially important in promoting adaptation, such as

mutation rate (Gillooly *et al.* 2005; Gillooly, McCoy & Allen 2007), but since all these temporal rates appear to share the same dependence upon temperature and body size (Brown *et al.* 2004) they are not expected to have an additive influence on evolutionary potential. Moreover, because these temporal rates share the same temperature dependence as development rate (Gillooly *et al.* 2002) and lifespan (Munch & Salinas 2009), the temperature and body size dependence of evolutionary potential can be modelled solely as a function of generation time.

> **Box 2: Maintenance of genetic variance under stabilizing selection**
>
> The amount of genetic variance, V_G, that can be maintained within a finite population is dependent upon a balance between mutation, selection and drift processes. At equilibrium, this can be modelled using the stochastic house-of-cards approximation (SHC) (Bürger, Wagner & Stettinger 1989; Bürger & Lynch 1995):
>
> $$V_G(\text{SHC}) = \frac{4n\mu\alpha^2 N_e}{1 + ((\alpha^2 N_e)/V_s)}, \qquad \text{eqn5}$$
>
> where mutational input is determined as the product of the effective number of additively contributing loci, n, mutation rate per generation, μ, mutational effect, α^2, and effective population size, N_e. The loss of alleles by selection is governed by V_s, an inverse measure of the strength of stabilizing selection, which is equal to the sum of the squared width of the fitness function, ω^2, and V_E, the environmental component of phenotypic variance, V_P.
>
> This particular formulation (Eqn 5) applies to a sexual organism (see Lynch & Lande 1993 for an approximation for asexual organisms). The model assumes there is no dominance or epistasis, thus additive genetic variance is equal to the total genetic variance ($V_G = V_A$) and narrow-sense heritability is given by $h^2 = V_G/V_P$. Because quantitative traits are mainly determined by additive genes (Hill, Goddard & Visscher 2008), the exclusion of nonadditive genetic interactions from such models has little to no negative effect on the efficacy of predictions (Crow 2010). The SHC approximation provides the best estimate of mean genetic variance maintained at mutation–selection–drift equilibrium (Bürger, Wagner & Stettinger 1989; Bürger & Lynch 1995). However, populations are rarely at equilibrium, especially those with a low effective population size (Willi, Van Buskirk & Hoffmann 2006). Consequently, levels of genetic variance among populations will be more variable but this should not affect mean time to extinction unless the mean population size is very small. We expect therefore greater variance in extinction times.
>
> To parameterize the breadth of the fitness curve, we draw on reviews of common-garden studies, which

measured the thermal sensitivity of maximal population growth rate on a range of ectothermic taxa from a range of latitudes (Frazier, Huey & Berrigan 2006; Deutsch *et al.* 2008). These studies reveal a trend in thermal specialization towards the tropics. The potential increase in the strength of stabilizing selection from weak ($\omega \approx 10$) to moderate ($\omega \approx 3$) is within the range tested by theoretical models (Bürger & Krall 2004; Johnson & Barton 2005). The parameterization of genetic variables is more problematic as estimates tend to vary substantially. Nevertheless, values for mutational heritability (V_m/V_E), a standardized composite measure of the input of mutational variance per generation, are remarkably consistent among traits and taxa, varying between 10^{-3} and 10^{-2} (Lynch & Walsh 1998, pp. 335–340). Accordingly, we follow Bürger & Lynch (1995) in assuming that $V_m = 2n\mu\alpha^2 = 0\cdot001$ and standardize parameter values to $V_E = 1$. On the conservative basis that genomic mutation rate ($2n\mu$) equals $0\cdot02$, α^2 is determined to be $0\cdot05$. To assess the sensitivity of our predictions of extinction risk to genetic input, we also tested the effect of a lower mutational variance: $V_m = 10^{-4}V_E$ to account for the observation that up to 90% of mutations could be unconditionally deleterious (Lande 1995). The combined effects of thermal specialization, effective population size and mutational variance on estimates of heritability are illustrated in Fig. 1a.

Gillooly *et al.* (2002) present a universal model for development time based on the principles of metabolic theory, which they validate with data drawn on a range of taxa from insects to birds. Empirical relationships for mean embryonic and mean post-embryonic development times have been determined as: $\ln(t/m_0^{1/4}) = -0\cdot12T + 6\cdot0$ and $\ln(t/M^{1/4}) = -0\cdot11T + 7\cdot2$, respectively, where t is development time in days, T is body temperature in °C and m_0 and M are body mass in grams measured at hatching and at final asymptotic size. Here, we use the sum of these relationships to estimate generation time as a function of temperature and body size. Because the above-mentioned empirical relationship for postembryonic development time is only based on data for zooplankton, we calculate generation time using the most conservative theoretical estimate of the intercept value for taxa in general (Gillooly *et al.* 2002), accordingly generation time $t = m_0^{1/4}e^{-0\cdot12T+6\cdot0} + M^{1/4}e^{-0\cdot11T+7\cdot32}$. We further assume that $m_0/M = 0\cdot01$, which is equal to the upper limit observed among ectothermic taxa (reptilia: Hendriks & Mulder 2008).

Using this estimate of generation time, the critical rate of change k_c can be calibrated in respect of absolute time (i.e. °C year^{-1}) to directly compare the increased risk of extinction associated with lower additive genetic variance (owing to thermal specialization in the tropics) against the
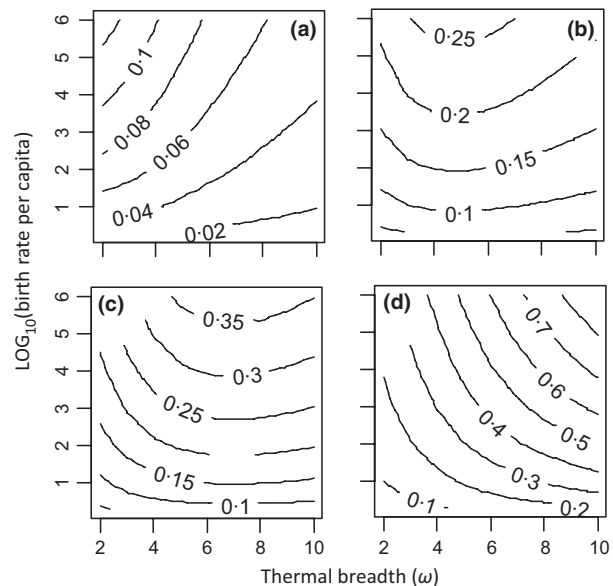

Fig. 3. The predicted critical rate of change k_c (°C gen^{-1}) plotted against the breadth of the thermal reaction norm and per capita birth rate for an effective population size of (a) 100, (b) 500, (c) 1000 and (d) 10 000. At low effective population sizes, thermal specialists have a lower relative risk of extinction but at high effective population sizes thermal generalists have a lower relative risk of extinction. Other parameters: $V_m/V_e = 5 \times 10^{-4}/1$; $\alpha^2 = 0\cdot05$; $V_\theta = 1$.

lowered risk of extinction associated with a shorter generation time, as predicted by the 'hotter-is-better' hypothesis. Figure 4 illustrates how extinction risk is predicted to vary for three hypothetical scenarios of thermal adaptation, in which the thermal optima for an extreme thermal specialist and an extreme thermal generalist differ by an arbitrary 0, 10 or 20 °C. This analysis suggests that tropical species can offset any predicted disadvantage of thermal specialization providing their body temperatures are 10+ °C higher on average than those of equivalent temperate species (Fig. 4e). This is before differential rates of temperature change and seasonal constraints between the tropics and temperate areas are taken into account.

To further determine the role of generation time on extinction risk in different regions, we ran simulations to determine the largest body mass likely to survive respective predicted rates of temperature change. We refer to this extinction risk measure as the 'critical body size' (M_c). If we can assume (as in Fig. 4b) that (i) the body temperatures of tropical species are 10+ °C higher than equivalently sized temperate species and that (ii) those temperate species are likely to experience double the rate of temperature change relative to tropical species, that is, up to 0·06 vs. 0·03 °C year^{-1} (reflecting emissions scenario A2; IPCC 2007), then we can confidently expect extinction risk to decrease towards the tropics. This is evident as an increase in the critical body size with increased thermal specialization (from right to left in Fig. 4g–i).

In all scenarios, those organisms with the highest potential fecundity (per capita birth rate) have the lowest risk of extinction but show the highest sensitivity to a change in
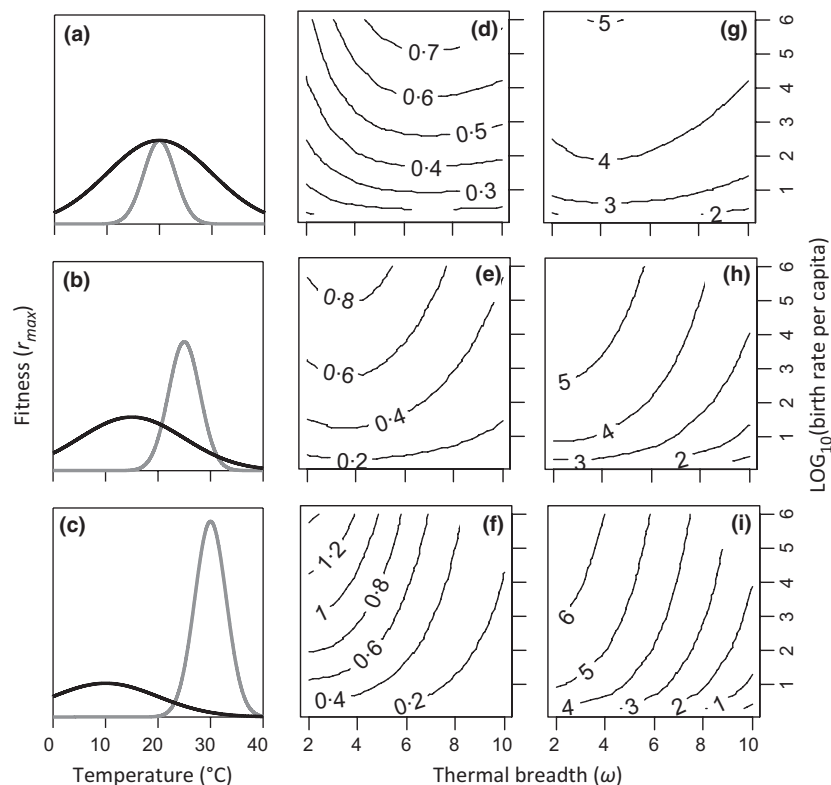
Fig. 4. The effects of temperature-dependent fitness, as mediated by development rate, on predicted extinction risk. Hypothetical scenarios depict the consequences of a thermodynamic constraint ($-E = 0.65$) on the relative performance of an extreme thermal specialist (grey lines; $\omega = 3$) and an extreme thermal generalist (black lines; $\omega = 10$). In (a) species share the same thermal optima (temperate T_{opt} = tropical $T_{opt} = 20$ °C), in (b) the T_{opt} differs by 10 °C (temperate $T_{opt} = 15$ °C; tropical $T_{opt} = 25$ °C) and in (c) the T_{opt} differs by a 20 °C (temperate $T_{opt} = 10$ °C; tropical $T_{opt} = 30$ °C). Panels d–f illustrate the respective consequences for the critical rate of change k_c (contours indicate equivalent rates in °C year^{-1}) for the full range of thermal specializations and birth rates (body mass = 1 g). In panels g–i, contours indicate an equivalent critical body mass [log$_{10}$ (grams)] based on the calculations including the assumption that 'temperate' thermal generalist ($\omega = 10$) species are exposed to double the rate of temperature change of 'tropical' thermal specialist ($\omega = 3$) species (0.06 vs. 0.03 °C year^{-1}). Other parameters: $N_e = 1000$; $V_m/V_e = 5 \times 10^{-4}/1$; $\alpha^2 = 0.05$; $V_0 = 1$.

thermal specialization. While this qualitative result is robust, quantitative estimates of critical body mass itself are extremely sensitive to assumptions relating to mutational variance and the possibility of seasonal constraints on the number of generations that can be completed within a given year (Fig. 5). Specifically, a one order of magnitude reduction in mutational input has the effect of reducing the critical mass by four orders of magnitude, while restricting development to one quarter of the year, that is, a single season, has the effect of reducing the critical mass by 2·4 orders of magnitude. This sensitivity of critical body mass to underlying assumptions can be generalized as $M_c \propto ak_c^{1/b}$, where a is a constant that has a proportionate scaling effect on the critical rate of change and b is the scaling exponent of development time on body mass (i.e. ¼). The critical body mass, therefore, responds as a power to the fourth function to any proportional change in the critical rate of change. Because this is a power law, the combined impact of n factors can be derived simply as $\log(M_c) = \sum_{i=1}^{n}(1/b)\log(a_i)$. For example, the combination of development constrained to a single season per year (0·25) and a one order of magnitude reduction (0·1) in genetic variance leads to a 6·4 magnitude reduction in the critical body mass (Fig. 5).

In summary, the combination of shorter generation times and slower predicted rates of temperature change in the tropics should enable tropical species to overcome any *relative* evolutionary disadvantage associated with lower genetic variance arising from increased thermal specialization. This qualitative theoretical result appears to be robust to the parameterization of variables, although it must be stressed that quantitative predictions, particularly of critical body mass, are extremely sensitive to actual generation time (i.e. number of generations per year vs. age at maturity), mutational input and estimates of how much of this genetic variance is actually adaptive. It should be noted also that the use of a common intercept and slope value effectively models the response of the 'average' species. It is well known that the intercept value of metabolic scaling relationships can differ substantially between taxonomic groups (Brown *et al.* 2004); however, the results of recent empirical analyses also question the supposed universality of the predicted allometric and exponential exponents. The greatest deviations from Kleiber's ¾ power scaling law appear to occur at the deepest evolutionary transitions between the prokaryotes and eukaryotes and between unicellular and multicellular organisms (DeLong *et al.* 2010), but they are also
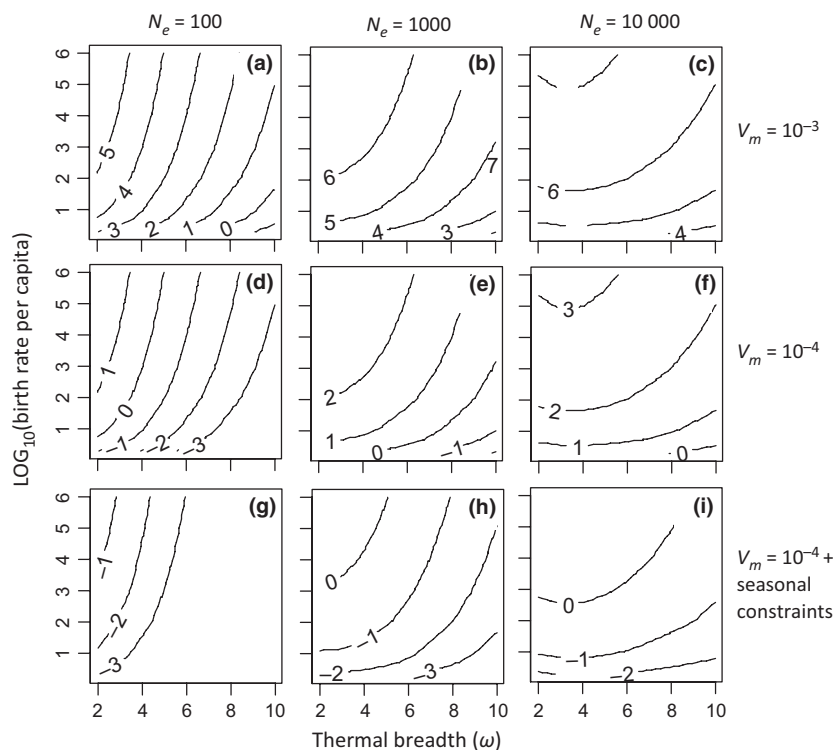
Fig. 5. The predicted critical body mass [$\log_{10}$ (grams)] of ectotherms with respect to effective population size, mutational variance and seasonal constraints (where development is restricted to a single season, that is, ¼ of the year). Calculations are based on the assumption that 'temperate' thermal generalist species (T_{opt} = 15 °C; ω = 10) are exposed to a higher rate of temperature change than tropical thermal specialist species (T_{opt} = 25 °C; ω = 3): 0·06 vs. 0·03 °C year^{-1} (see scenarios in Fig. 4b). Contours depict equivalent values of the critical body mass calculated for various combinations of variables. Other parameters: $-E$ = 0·65; V_E = 1; α^2 = 0·05; V_θ = 1.

evident at lower taxonomic levels (e.g. Capellini, Venditti & Barton 2010). If the mass scaling relationships of metabolic rate map onto development time as predicted, that is, $I \propto M^b \Rightarrow t \propto M^{1-b}$, we would predict the allometric exponent of mammal orders alone to range in value between 0·18 and 0·41 (cf. theoretical value of b = 0·25). A similar range of exponent values is predicted among classes of terrestrial invertebrates that also show substantial variation in their exponential exponent (0·38 < E < 0·80 eV), which determines sensitivity to temperature (Ehnes, Rall & Brose 2011). Much of this variation is expected to reflect differences in body architecture (constraints) and ecological lifestyles and habitats (adaptations). Where such taxonomic data are available, the resolution of ecological forecasts should be parameterized accordingly.

Our discussion hereafter will focus on the macroecological patterns and theoretical assumptions underpinning our projections of latitudinal extinction risk in an effort to identify areas where future empirical research can best contribute to improving evo-ecological forecasts.

Macroecological patterns

ARE TROPICAL SPECIES THERMAL SPECIALISTS?

Analyses of global data sets demonstrate that in general the thermal tolerance range of ectotherms increases with latitude, especially in the northern hemisphere (Addo-Bediako, Chown & Gaston 2000; Ghalambor *et al.* 2006; Sunday, Bates & Dulvy 2011). This pattern is most pronounced for terrestrial organisms, which show a 50% increase in thermal breadth due higher tolerance to cold temperatures. Marine organisms, however, appear to show little change in thermal breadth because of concomitant reductions in both the upper and lower tolerance limits (Sunday, Bates & Dulvy 2011). The close association between these critical/lethal limits and climatic variation in these respective habitats suggests that the increase in thermal specialization in terrestrial ectotherms towards the tropics is an adaptive response to temperature *per se*, an assertion supported by further analyses of thermotolerance replicated at smaller spatial scales, for example, with respect to altitude (Brattstrom 1968). However, the increase in the strength of stabilizing selection associated with this increase in thermal specialization towards the tropics would appear to be modest.

In a separate study conducted on a smaller data set of 38 insect species (data collated by Frazier, Huey & Berrigan 2006), other measures of thermal tolerance were found to more strongly decrease towards the tropics. On the basis of this latter analysis, the 'warming tolerance' (defined as the difference between the CT_{max} and mean environmental temperature of the habitat, T_{hab}) of tropical species is only

one-third that of temperate species; the respective figure for the 'thermal safety margin' (TSM; defined as the difference between the T_{opt} and T_{hab}) is just one-fifth (Deutsch *et al.* 2008; Fig. 2). A reanalysis of the supplementary data for this article reveals that these various potential surrogate measures of thermal specialization are poorly correlated with thermal tolerance ($CT_{max} - CT_{min}$) (linear and nonlinear regression, whether hemispheres pooled or analysed separately: all *P* values >0·20). Although there is a trend for increasing thermal tolerance with latitude in this data set, it amounts to <21% over the whole range (3·0–52·4°; hemispheres pooled). Consequently, the decrease in both 'warming tolerance' and 'TSM' towards the tropics is almost entirely attributable to variation in the environmental temperature (mean annual temperature) rather than to evolved differences in thermal physiology. However, this conclusion is based on critical thermal limits that were determined by the statistical fitting of a function rather than by direct measurement.

Although these various measures of thermotolerance are correlated with performance breadth, they do not provide adequate measures of the strength of stabilizing selection. Ideally, we require estimates of the intrinsic rate of increase *r* (under nonlimiting conditions) for multiple temperatures. The strength of stabilizing selection can then be estimated by fitting a Gaussian distribution of the form: $r = r_{max} \exp[-0{\cdot}5 \, (|T - T_{opt}|/\omega)^2]$, where *T* is temperature, ω is performance breadth and r_{max} is *r* at T_{opt} (Angilletta 2009). By reanalysing the data collated by Frazier, Huey & Berrigan (2006), we estimate ω varies between ≈3 (extreme thermal specialist) and ≈10 (extreme thermal generalist), respectively. Assuming $V_E \approx 1$, these values fall within the range typically used by theoretical models (Bürger & Krall 2004) although they might be considered relatively weak compared with the median value of stabilizing selection strength reported from empirical studies more generally (Johnson & Barton 2005). Nevertheless, if thermal specialisation were to increase from temperate to tropical regions by this full extent it could have a substantial impact upon genetic variance for T_{opt} (Fig. 1a), and consequently extinction risk (Fig. 1b).

While the fitting of a Gaussian distribution to thermal performance curves provides a practicable means of parameterizing the existing theoretical models of adaptation and extinction risk (Angilletta 2009), the accuracy of estimates strongly depends upon the number and range of temperatures at which performance was measured (see Angilletta 2006; Knies & Kingsolver 2010). The mean number of temperatures at which *r* was measured in the empirical studies collated by Frazier, Huey & Berrigan (2006) is 5·2 (range: 4–8) while the range of temperatures in some cases was limited to those where *r* was >0·64 of that achieved at the T_{opt} (e.g. *Cotesia flavipes*; Mbapila & Overholt 2001). The fitting of curves to restricted data sets such as these is expected to yield poor estimates of ω, a limitation that would also apply to the most comprehensive data set most recently compiled by Dell, Pawar &

Savage (2011) on 1072 thermal responses for 309 species (Huey & Kingsolver 2011). In the light of the constraints posed by these studies, the wide variation in thermal responses (Huey & Kingsolver 2011) and the inherent difficulties of characterizing fitness landscapes using the ordinary least squares approach in general (Shaw & Geyer 2010; Kingsolver & Diamond 2011), predictions that use mutation–selection balance theory to estimate how genetic variance will vary with thermal specialization are likely to remain effectively qualitative. A more practical approach will be to estimate genetic variance for relevant traits directly.

IS HERITABILITY FOR T_{OPT} LOWER AMONG TROPICAL SPECIES?

We know of no study that has specifically tested whether tropical species possess less genetic variance for T_{opt} or other measures of heat tolerance. However, a survey conducted on *Drosophila* species distributed along a latitudinal gradient has revealed that genetic variance for two other ecological traits, cold tolerance and desiccation resistance, is substantially lower among tropical species (Kellermann *et al.* 2009). These tropical species were also found to have narrow geographical distributions. If a restricted range size reflects environmental specialization then strong stabilizing selection could provide an explanation for why genetic variance is lower in these species. Unfortunately, auxiliary data to test this hypothesis are not available. However, alternative explanations for this erosion of genetic variance, including the roles of directional selection, phylogenetic constraints, inbreeding and drift, could all be ruled out in this study. The favoured explanation by Kellermann *et al.* was DNA decay – the process by which gene function is degraded under relaxed selection due to the accumulation of neutral and conditionally deleterious mutations (Whitlock 1996; Lahti *et al.* 2009; Hoffmann 2010). DNA decay can eventually lead to the complete and irreversible loss of complex traits (Ostrowski, Ofria & Lenski 2007; Collin & Miglietta 2008). If this explanation is correct, it would imply that tropical species are derived and that past populations must have been small enough for long enough to allow mutations to reach fixation (Hoffmann 2010).

Similar surveys of heritabilities for T_{opt} are required, a nontrivial task given that the estimation of T_{opt} itself requires the rearing of organisms at multiple temperatures. Nevertheless, the alternative, that is, to estimate heritabilities for related or surrogate traits such as heat knock-down resistance, the critical thermal maximum (CT_{max}) or the LT_{50} (the temperature at which 50% of individuals die), is not without difficulties. This is exemplified by the dependency of CT_{max}, and the heritability of CT_{max}, on the experimental protocol used to measure it. Both traits are found to be markedly lower if temperatures are elevated ('ramped up') slowly. It was postulated therefore that under 'natural' field conditions species would have less

capacity to adapt to high temperatures experienced under 'natural' field conditions (Chown *et al.* 2009; Mitchell & Hoffmann 2010). However, this curious result could merely reflect an artefact of the experimental design, in which the physiological condition of flies tested under the more lengthy ramping up regime deteriorates due to dessication to a further extent (Rezende, Tejedo & Santos 2011). If we exclude studies based on ramping temperatures, then estimates of heritabilities for upper thermal limits, including CT_{max} ($h^2 = 0 \cdot 12$–$0 \cdot 22$ in *Drosophila*: Gilchrist & Huey 1999; Mitchell & Hoffmann 2010) and LT_{50} ($h^2 = 0 \cdot 32$ in fish; Meffe *et al.* 1995), appear to fall within the general range for physiological traits (Mousseau & Roff 1987). How these estimates might vary with latitude has not been systematically investigated; although it is interesting to note that in one study conducted by Mitchell & Hoffmann (2010) on *Drosophila melanogaster*, a simple comparison between two populations revealed that, contrary to our predictions, narrow-sense heritability ($h^2 \pm 1$ SE: $0 \cdot 22 \pm 0 \cdot 07$ vs. $0 \cdot 14 \pm 0 \cdot 05$) and additive genetic variance ($h^2 \pm 1$ SE: $24 \cdot 32 \pm 7 \cdot 84$ vs. $14 \cdot 40 \pm 6 \cdot 51$) for heat knockdown time were markedly higher for the tropical population.

DO TROPICAL SPECIES HAVE HIGHER FITNESS? IS HOTTER REALLY BETTER?

Higher temperatures reflect greater enthalpy or kinetic energy available for work – this basic thermodynamic principle underpins the 'hotter-is-better' hypothesis proposed to explain why the maximum rate of population (r_{max}) increases with body temperature in a range of organisms, from bacteriophages to mammals (Savage *et al.* 2004; Angilletta, Huey & Frazier 2010). According to the metabolic theory of ecology (MTE), if r_{max} is fundamentally constrained by metabolic rate, then we would predict r_{max} to scale with the average activation energy of rate-limiting biochemical metabolic reactions ($E \approx 0 \cdot 6$–$0 \cdot 7$) (Savage *et al.* 2004). On a plot of log-transformed r_{max} against the inverse of mean body temperature ($1/kT$; where k is the Boltzmann's constant and T is absolute temperature), this value is represented as the negative slope of the linear relationship (Gillooly *et al.* 2001). The common slope observed among taxonomic groups is attributed to a universal temperature dependence, that is, a constraint. Nonetheless, there is considerable variation in slope values evident at the intra- and interspecific level, which suggests there is substantial genetic variance for this trait (Clarke 2004, 2006; Gillooly *et al.* 2006; Terblanche, Janion & Chown 2007). Given the potential for local adaptation, it remains unclear why lower optimal temperatures should be associated with a lower maximal performance.

To evaluate the extent to which local adaptation or 'temperature compensation' (Clarke 2003) has occurred Frazier, Huey & Berrigan (2006) collated a detailed data set on the temperature dependence of maximal r_{max} in insect species living at a range of latitudes to test whether the slope of temperature dependence significantly differs to theoretical predictions. If perfect temperature compensation were possible, we would predict no resulting relationship between log maximal r_{max} and the inverse of thermal optima ($1/kT_{opt}$), that is, $E = 0$. In other words, all species should achieve the same level of maximal performance irrespective of the temperature they are locally adapted to. However, if maximal performance is ultimately constrained by metabolic rate, and the thermodynamic constraints it is subject to, we would predict maximal fitness to increase with the thermal optima. Specifically, in MTE terms, maximal fitness should decrease with the inverse of the thermal optima ($1/kT_{opt}$) with a slope approximately equal to $-0 \cdot 65$. Activation energies lying between these two extreme values would provide evidence of partial compensation. The results of Frazier *et al.*'s meta-analysis revealed that maximal r_{max} decreased on average by between 8% and 12% for every 1 °C drop in the optimal body temperature of taxa. This is strong evidence for a thermodynamic constraint , however, the level of temperature dependence ($-E = 0 \cdot 97$) i much greater than predicted.

If it can be assumed that maximal performance is subject to a specialist–generalist trade-off then this stronger-than-expected temperature dependence could simply reflect the parallel trend for increased thermal specialization towards the tropics. Using a structural equation modelling approach, Frazier, Huey & Berrigan (2006) attempted to control for thermal specialization in their analysis indirectly via (a presumed adaptation to) seasonal variation. The addition of this surrogate measure failed to improve their model, although it is debatable whether the use of path analysis with its demanding statistical methods (Petraitis, Dunham & Niewiarowski 1996) was completely suitable given the size of this data set. Further comparative studies that aim to address the influence of taxonomic level (e.g. among vs. within species), life history (e.g. nocturnal vs. diurnal) and environment (e.g. terrestrial vs. aquatic organisms) could help to further clarify the nature of the thermodynamic constraint by decoupling the relationship between thermal specialization and maximal performance. However, only a systematic approach to the study of thermal reaction norm evolution is expected to establish the respective roles of phylogenetic constraints and adaptation to climate variability in shaping the temperature dependence of fitness (Dell, Pawar & Savage 2011; Huey & Kingsolver 2011).

The results of experimental evolution experiments undertaken in different thermal environments have so far failed to support the basis of a thermodynamic constraint (Knies *et al.* 2006; reviewed in Angilletta, Huey & Frazier 2010). This might simply be attributed to a lack of statistical power, or it may reflect the lack of suitable control for thermal specialization (J. Kingsolver, personal communication). In the latter case, it is interesting to note that small-scale comparative studies of thermal reaction norms

suggest that thermal specialization alone could underpin the 'hotter-is-better' response (Latimer, Wilson & Chenoweth 2011). In the theoretical analysis presented here, it is important to bear in mind that we have considered temperature only as a proxy for predicting how (a constant) evolutionary potential varies with latitude. In other words, we have not assumed a 'universal thermodynamic constraint' (Clarke 2004, 2006; Clarke & Fraser 2004; Gillooly *et al.* 2006) that would give rise to a positive feedback between adaptation to warmer temperatures and increased adaptive potential (i.e. a higher maximum development rate).Our forecasts of extinction risk therefore can be considered conservative in this regard.

Theoretical assumptions of quantitative genetic models

DO HERITABILITY ESTIMATES OVERESTIMATE LONG-TERM EVOLUTIONARY POTENTIAL?

Although mutational heritability provides a reliable measure of total genetic input, it is likely to substantially overestimate the generation of potentially beneficial mutations required to maintain a long-term adaptive response to environmental change (Lynch & Walsh 1998). This is because standing genetic variance for fitness includes contributions from unconditionally deleterious mutations. Lande (1995) estimates that up to 90% of new mutations could be deleterious, and on this basis recommended a revised-down figure of $V_m = 10^{-4} V_E$ when calculating the minimum effective population size necessary for maintaining evolutionary potential (Fig. 5d–f). Recent molecular analyses confirm that only around 10% of mutations are shown to be adaptive (Eyre-Walker & Keightley 2007). Nonetheless, this figure is likely to exclude mutations that may influence fitness through genotype–environment interactions and which may improve fitness in another environment. For this and other reasons, Franklin & Frankham (1998) disputed Lande's correction factor as being too high. Accordingly, the range of mutational heritabilities that we have evaluated here ($10^{-4} < V_m/V_E < 10^{-3}$) is likely to represent the lower and upper limit. Note that even on the basis of this restricted parameter range, the predicted critical body mass, the largest ectotherm body size assured of survival under predicted rates of climate change, can vary enormously, for example, by between 100 g and 1 metric tonne for an organism of intermediate thermal specialization, a per capita birth rate of 10 and with an effective population size of 1000 (Fig. 5).

HOW RELIABLE ARE HERITABILITY ESTIMATES UNDER ENVIRONMENTAL CHANGE?

Estimates of heritability are by definition specific to the environment in which they were measured. Although estimates of heritability measured in the laboratory are not found to substantially differ on average to those measured in the field (Roff 2002), in general, 'unfavourable' growth conditions tend to lower heritability estimates by inflating environmental variance while novel conditions tend to increase heritability estimates by revealing hidden additive genetic variance maintained by genotype–environment interactions (Charmantier & Garant 2005). It is unclear whether these factors are likely to systematically bias quantitative forecasts of extinction risk but one factor that could influence our qualitative conclusion regarding regional extinction risk is the tendency for additive genetic variance, and therefore heritability, to increase under stressfully high temperatures (Agrawal & Whitlock 2010).

Heat stress under climate warming will be felt most strongly by tropical species, which operate at body temperatures closer to their upper thermal limits (Deutsch *et al.* 2008; Tewksbury, Huey & Deutsch 2008). Whether this additional heat stress will enhance the adaptive potential of tropical species relative to that of temperate species will depend upon the underlying mechanism generating increases in genetic variance with temperature. For example, any increase because of higher rates of recombination and/or mutation (Hoffmann & Parsons 1997) is likely to consist largely of nondirected and generally deleterious genetic changes (Eyre-Walker & Keightley 2007). These are likely to impose a demographic cost on fitness that could potentially outweigh any advantage of producing rare beneficial alleles under directional selection. Under mild heat stress, these deleterious effects may in part be offset by an elevated production of heat shock proteins responsible for molecular chaperoning (Casanueva, Burga & Lehner 2012), although under moderate-to-severe heat stress this reservoir of heat shock proteins may become depleted to reveal cryptic genetic variance (Rutherford 2003; Jarosz & Lindquist 2010). In the latter case, it has been argued, heat stress could promote the evolvability of the species by exposing 'preadaptations' to selection (Eshel & Matessi 1998; Masel & Trotter 2010; Rajakumar *et al.* 2012).

The relative roles that heat-induced mutations and molecular chaperoning will have the risk of extinction will depend upon the rate of temperature change for the organism. At slow rates of change, that is, $k \leq k_c$, when the selection intensity is weak and heat stress is mild the demographic cost of producing deleterious mutations is likely to be minimized and also partially offset by molecular chaperoning. At fast rates of change, that is, those exceeding the critical rate k_c, when the selection intensity is strong and heat stress is moderate to severe, the likelihood of adaptive rescue under a finite temperature change will be primarily dependent upon the existing and cryptic genetic variance rather than novel mutations. Accordingly, heat stress could in theory favour the adaptive potential of tropical species irrespective of the rate of change, strengthening our qualitative conclusion that extinction risk will be lower towards the tropics. Nonetheless, whether this

increase in additive genetic variance revealed at high temperatures will contribute to an adaptive response remains to be tested.

CAN A LOW HERITABILITY POSE AN ABSOLUTE GENETIC CONSTRAINT?

Low heritability imposes a quantitative genetic constraint on trait responses to selection. In cases where demographic stochasticity is high, such as in small populations, it can in effect pose an absolute constraint to adaptation (Gomulkiewicz & Houle 2009). Although there is little utility in forecasting the evolutionary trajectory of small populations, there are other circumstances in which a low heritability could impose an absolute constraint irrespective of population size. It has been shown, for example, that in some populations of *Drosophila*, low heritability for ecological traits such as desiccation resistance is associated with a lack of response to artificial selection (Hoffmann *et al.* 2003). If, as has been proposed (Hoffmann 2010), this lack of genetic variance is a result of DNA decay, it will be difficult, if not impossible (e.g. Wiens 2011), for new beneficial mutations to arise. The finding that heritabilities for both desiccation and cold resistance are very low in tropical vs. temperate populations that otherwise show an abundance of neutral genetic variance (Kellermann *et al.* 2009) is therefore a cause for concern. Nonetheless, it is also the case that low heritability estimates can often underestimate potential for adaptation. For instance, it appears that the grayling, a freshwater fish, has undergone rapid physiological adaptation to differences in stream temperature between closely situated sites despite showing low levels of genetic variance for thermal tolerance and a lack of gene flow among populations (Kavanagh *et al.* 2010; Skelly 2010). Ultimately, the only way to determine whether genetic limits really do exist for particular traits or trait combinations is to conduct resource-intensive selection experiments on the trait in question (Hoffmann *et al.* 2003).

The primary method to infer the potential role of genetic constraints is to evaluate phylogenetic inertia among closely related species (Huey & Bennett 1987; Somero 2011). A prerequisite for this comparative approach is the ability to disentangle the influence of a common evolutionary history from a common selective environment (Losos 2011), often a difficult task in the case of thermal adaptation (Angilletta 2009). Consider, for example, the apparent lack of variability in the critical thermal maximum among reptiles (Huey & Bennett 1987). A lack of genetic variation in this trait among terrestrial species has been interpreted as evidence of a genetic constraint (Huey & Kingsolver 1989); alternatively, it might simply reflect adaptation to a weak latitudinal trend in maximum temperatures (Addo-Bediako, Chown & Gaston 2000).

The situation is more complicated if one considers the thermal optimum. A substantial mismatch between the optimal or preferred body temperature and the mean environmental temperature might appear mal-adaptive at first sight, but it can serve to maximize geometric mean fitness in a variable environment (Gilchrist 1995; Martin & Huey 2008). This is true whether we consider the asymmetry of the thermal reaction norm to be a constraint imposed at the enzyme kinetic level (Knies & Kingsolver 2010) or an adaptation to thermodynamic constraints imposed upon maximal performance, that is, 'hotter is better' (Asbury & Angilletta 2010). These alternative scenarios serve to underscore our poor understanding of thermodynamic constraints and the resulting difficulty to quantitatively define a null model for thermal adaptation.

GENETIC COVARIANCE

The rate at which a trait can respond to selection is also influenced by genetic correlations between multiple traits (Walsh & Blows 2009). A negative genetic covariance is indicative of antagonistic pleiotropy or trade-offs, which can severely constrain the rate of adaptation (Etterson & Shaw 2001). Genetic variance–covariance matrices (G) can be used to quantify the strength and direction of these correlations to more accurately predict the fate of individual populations (Blows & Hoffmann 2005). But because positive genetic correlations, which can otherwise promote a response to selection (Agrawal & Stinchcombe 2009), appear to be as common as negative correlations, predictions of mean extinction risk at the macroecological level are not expected to be systematically biased. Moreover, although G-matrixes can be used to predict short-term responses to environmental change, they are themselves moulded by selection. Theoretical simulations suggest that the evolutionary dynamics of G is highly dependent on its dimensionality and its alignment with the selection gradient but that directional selection may contribute to its stability (Jones, Arnold & Bürger 2004). On the other hand, the breaking down of genetic constraints can occur extremely quickly. For instance, in a recent study on the annual plant *Brassica rapa*, five generations were sufficient to overcome the constraints predicted by genetic correlations and enable the rapid adaptive evolution of multiple traits in response to drought selection (Franks & Weis 2008).

MUTATIONS OF LARGE EFFECT

Mutational effects for individual traits are often leptokurtic, not normally distributed as often assumed by theory (Eyre-Walker & Keightley 2007). Although such traits are still influenced by many genes, responses to selection are dominated by a very few genes of large effect, which tends to increase genetic stochasticity and lower mean time to extinction (Bürger & Lynch 1995). This is because the disproportionate influence of a limited number of genes necessarily limits the number of evolutionary trajectories towards a new adaptive peak evolution (Kopp & Hermisson 2007). The potential cost to population fitness in producing less than optimal phenotypes is expected to

increase with the strength of selection (e.g. abrupt climate warming) and the rarity and size of the mutational effect (Collins, de Meaux & Acquisti 2007; Collins & de Meaux 2009). While estimates of genetic variance can be adjusted where distributions deviate from normality, such corrections tend to be unnecessary for complex traits such as fitness where the influence of individual loci are ameliorated by the averaging effects of multiple additive loci (Lynch & Lande 1993). This apparent robustness of predicted changes in fitness and population persistence under directional selection to the uncertainties associated with genetic architecture further supports the general use of quantitative genetic models in global change biology.

SUMMARY

Quantitative genetics continues to provide researchers with a practical and general tool for modelling phenotypic evolution under directional selection (see Stockwell, Hendry & Kinnison 2003; Skelly *et al.* 2007; Visscher, Hill & Wray 2008; Hoffmann & Sgrò 2011 for recent reviews and commentaries), especially thermal adaptation under climate change (Huey & Kingsolver 1993; Angilletta 2009; Kingsolver 2009; Chevin, Lande & Mace 2010). Here, we used the modelling framework developed by Lynch & Lande (1993) and Bürger & Lynch (1995) to consider the potential role of adaptation and a temperature-dependent rate of evolution on the extinction risk of ectotherms with latitude. Contrary to previous ecological forecasts based solely upon macroecological patterns in ecophysiology, that is, thermal specialization (Deutsch *et al.* 2008), we found that tropical species should be as, if not more, resilient to climate change than temperate species.

The principle evolutionary advantage tropical species are predicted to possess is a shorter development time at their respective thermal optima. We showed here that the combination of a shorter generation time and a lower predicted rate of regional temperature change can more than offset the disadvantage of low genetic variance associated with thermal specialization. This qualitative theoretical prediction is robust to assumptions regarding population size, birth rate and mutation rate. Moreover, this prediction can be considered conservative for a number of reasons. Firstly, we assumed an extreme trend in thermal specialization, and therefore genetic variance, with latitude although it remains to be established whether tropical species do have lower genetic variance for heat tolerance. Secondly, because we neither assumed a 'universal thermodynamic constraint' (and therefore a feedback between higher thermal optima and adaptive potential) nor a generalist–specialist trade-off in performance, we have in effect restricted our analysis to the impacts of an existing trend in fitness with latitude. Nonetheless, if it is the case that tropical species have very low genetic variance and that this low level poses an absolute rather than merely a quantitative genetic constraint to adaptation, our analysis will inevitably prove to be overly optimistic.

IMPROVING ECOLOGICAL FORECASTS

There appear to be three key areas where further empirical research could greatly improve the accuracy and therefore value of evolutionary forecasts not just to climate warming but to environmental change in general. Firstly, and arguably most importantly, it remains to be established whether tropical species possess lower heritabilities in general for ecological traits as a result of ecological specialization and whether this limited adaptive potential represents an absolute vs. merely a quantitative genetic constraint. Few large-scale studies have been undertaken to investigate such patterns but because these questions are intrinsically linked to the wider question of what determines the evolution of range size, further insights could be drawn from studies conducted with respect to other traits, organisms and other geographical regions. Secondly, although a number of mechanisms are known to increase genetic variance under heat stress, to what extent this release of novel genotypes can contribute to the rate of adaptation remains to be tested. Interestingly, this potential to accelerate adaptation could apply to any new environments as a general consequence of low genetic quality manifested as poor phenotypic condition (Sharp & Agrawal 2012). Thirdly, if the 'hotter-is-better' response is caused by a thermodynamic constraint, then we would predict potential rates of adaptation to accelerate under climate warming and decelerate under climate cooling. Manipulative experiments are therefore necessary to test whether thermodynamic constraints shape the evolution of thermal reaction norms as predicted (Angilletta 2009). Although we have only explicitly considered the potential for the 'hotter-is-better' response to contribute to the thermal adaptation of tropical species under climate warming, the benefits of a faster generation time apply to any trait under selection.

Acknowledgements

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