

REVIEW AND SYNTHESIS

Heat freezes niche evolution

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Abstract

Climate change is altering phenology and distributions of many species and further changes are projected. Can species physiologically adapt to climate warming? We analyse thermal tolerances of a large number of terrestrial ectotherm ($n = 697$), endotherm ($n = 227$) and plant ($n = 1816$) species worldwide, and show that tolerance to heat is largely conserved across lineages, while tolerance to cold varies between and within species. This pattern, previously documented for ectotherms, is apparent for this group and for endotherms and plants, challenging the longstanding view that physiological tolerances of species change continuously across climatic gradients. An alternative view is proposed in which the thermal component of climatic niches would overlap across species more than expected. We argue that hard physiological boundaries exist that constrain evolution of tolerances of terrestrial organisms to high temperatures. In contrast, evolution of tolerances to cold should be more frequent. One consequence of conservatism of upper thermal tolerances is that estimated niches for cold-adapted species will tend to underestimate their upper thermal limits, thereby potentially inflating assessments of risk from climate change. In contrast, species whose climatic preferences are close to their upper thermal limits will unlikely evolve physiological tolerances to increased heat, thereby being predictably more affected by warming.

Keywords

Bioclimatic envelope models, biological invasions, climate change, CTmax, CTmin, evolutionary rates, lower thermal tolerance, niche conservatism, species distributions, thermal adaptation, upper thermal tolerance.

Ecology Letters (2013) 16: 1206–1219

INTRODUCTION

There is a general expectation that climate, both at present and historically, governs the broadest outlines of species distributions. The degree to which climatic preferences of species and climatic tolerances are conserved across lineages is still a matter of debate, as rates of niche evolution and the mechanisms underlying them remain poorly known (e.g. Losos 2008). The assumption is that some significant degree of conservatism exists in the fundamental niche – the set of environmental states that permits species to persist (for recent review of niche concepts see Peterson *et al.* 2011) – which provides predictability across taxa, environmental dimensions and time frames, when species responses to abiotic variables are investigated from evolutionary and ecological perspectives (e.g. Jablonski *et al.* 2006; Romdal *et al.* 2013). Nonetheless, a growing number of analyses suggest that key traits affecting physiological tolerances, which contribute to setting the fundamental niche, show much variation in the extent of their conservatism. Compelling examples include little systematic environmental variation in the sum of effective temperatures for insect development, compared with much rainfall-related variation in desiccation resistance for the same group (e.g. Addo-Bediako *et al.* 2001), and, in *Drosophila*,

differences among various traits in the scope of their variation (e.g. Kellermann *et al.* 2012a,b).

In keeping with the finding that some traits show much variation, adaptations to recent climate change have been reported in several taxa, mostly involving phenological adaptation to shifts in the timing of seasonal events (e.g. Visser 2008), but also involving changes in the geographical distribution of genetic polymorphisms (e.g. Umina *et al.* 2005). Recorded differences among climatic niches in the native and non-native ranges of invasive species have also led to the suggestion that niches might have evolved during the invasion process (e.g. Broennimann *et al.* 2007; Fitzpatrick *et al.* 2007). Notwithstanding, tests of niche conservatism (sensu Losos 2008; i.e. whether niches change more slowly than expected from Brownian motion evolution) with measures of overlap between climatic niches inferred using methods that relate geographical distributions of species to aspects of climate have one important limitation: the theoretical expectation of conservatism is justified for fundamental (abiotic) niches rather than for realized niches (Araújo & Peterson 2012).

Realized niches are a subset of the fundamental niche reduced by the effects of dispersal, biotic interactions, and, with animals, by aspects of behaviour that affect resource utilization (e.g. Peterson

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et al. 2011). Although these factors are constrained by traits that, themselves, are expected to be conserved over long periods of time, the realized niches emerging from interactions between traits and the environment are not expected to be conserved. For example, non-physiological mechanisms of adaptation, such as thermoregulatory behaviour used by ectotherms to regulate physiological performance (and allow survival beyond species thermal tolerance limits), are often labile. Simulations have shown that such behavioural adaptations can even constrain rather than drive evolution (Huey *et al.* 2003), thereby reinforcing conservatism of the fundamental niches; an outcome being borne out by empirical work (e.g. Marais & Chown 2008). Another extreme case of lability in factors influencing realized niches are changes in diet. Adélie penguins in Antarctica, e.g. were able to switch in <200 year from a diet mainly composed of fish to one predominantly based on krill (Emslie & Patterson 2007). Although several of the factors determining realized niches of species are unlikely to remain stable through time, tests of conservatism are typically based on measurements of the realized niche (e.g. Hof *et al.* 2010; Kozak & Wiens 2010). It follows that since realized niches generally represent subsets of the fundamental niche, and ecological conditions in different times or regions can lead to different occupation of the fundamental niche (e.g. Jackson & Overpeck 2000), shifts in realized niches are often likely to indicate that different portions of the fundamental niche are being occupied rather than that evolutionary changes in the fundamental niche have taken place.

The significant question thus remains of whether physiological adaptation to ongoing climate warming or conservatism of climatic tolerances is more likely. Answers to this question are important for several reasons. First, several studies have suggested that a suite of tropical to subtropical ectotherms may be close to their thermal safety margins, which, if exceeded, could lead to the extinction of several species (Deutsch *et al.* 2008; Huey *et al.* 2009; Clusella-Trullas *et al.* 2011). Population-level assessments of reptiles suggest that climate change-driven extinctions may already be occurring (Sinervo *et al.* 2010), while some studies suggest that tropical endotherms may be similarly at risk (Cooper *et al.* 2011). Meta-analysis for many different terrestrial organisms is also showing that distributions of species have recently shifted to higher elevations at a rate of 11 metres per decade, and to higher latitudes at a rate of 16.9 km per decade, thus compromising the ability of several species to adapt to ongoing climate change by tracking shifting climate suitability (Chen *et al.* 2011). Second, understanding the scope for niche evolution is critical because the assumption of little evolutionary change underlies many projections of climate change effects on species distributions, both in the past (e.g. Nogués-Bravo *et al.* 2008) and future (e.g. Garcia *et al.* 2012). Third, the extent to which niche evolution takes place is a fundamental question in biogeography and evolution, with strong implications for understanding the origin, diversification and distribution of life on earth, and fundamental differences therein between marine and terrestrial systems (e.g. Wiens & Donoghue 2004; Sunday *et al.* 2012; Romdal *et al.* 2013).

IS EVOLUTION OF CLIMATIC NICHES ASYMMETRIC?

Questions regarding the evolution of the fundamental niches are difficult to address for at least three reasons. First, measuring the fundamental niche of a species is challenging because the full set of dimensions that constitute a species' niche is unknown and is likely

to vary from one species to another. Furthermore, interactions between dimensions of the niche, e.g. temperature and water, can modify the tolerance of species to individual niche dimensions in ways that are not always easily predicted (e.g. Crimmins *et al.* 2011). Second, experiments measuring aspects of the fundamental niche are expensive and time consuming, thus being typically limited to small numbers of species. Third, demonstrating changes in one aspect of the niche of a species might provide little information about potential evolutionary changes in other aspects thereof (e.g. Angilletta *et al.* 2003). Nonetheless, biophysical approaches are demonstrating that a limited suite of traits can readily characterize important aspects of the fundamental niche, and that many of these have to do with thermal biology (Porter & Kearney 2009; Kearney *et al.* 2010). Indeed, suggestions have recently been made that the stage on which ecological and evolutionary interactions play out should be termed the 'thermodynamic niche' (Kearney *et al.* 2013). In consequence, investigations of differential variation in traits underpinning thermal biology are starting to provide important insights into the extent to which fundamental niches might evolve, and what the consequences thereof are for species distribution modelling and for predicting species responses to climate change, especially in environments as different as those found in marine and terrestrial systems (e.g. Sunday *et al.* 2012).

For many terrestrial animals and plants, the upper and lower thermal limits to performance are significant components of the thermal niche (e.g. Larcher 1995; Pörtner 2001; Hoffmann 2010). Specifically, for a number of terrestrial animal ectotherms, it has been shown that upper and lower thermal tolerance limits covary to only a limited extent or do not do so at all (Addo-Bediako *et al.* 2000; Hoffmann *et al.* 2013). However, in others, stronger covariation exists (e.g. Calosi *et al.* 2010). In marine groups, such covariation is especially pronounced (Sunday *et al.* 2011), perhaps owing to oxygen limitation of thermal tolerance (Pörtner 2010). In consequence, while evidence of general patterns is emerging for ectotherm animals (e.g. Addo-Bediako *et al.* 2000; Sunday *et al.* 2011; Kellermann *et al.* 2012b; Grigg & Buckley 2013; Hoffmann *et al.* 2013), how extensive the asymmetry in variability of upper and lower tolerances is among terrestrial organisms, and what its implications are for niche evolution in particular have not been comprehensively explored across a wide range of terrestrial plants and animals.

VARIATION IN CRITICAL THERMAL LIMITS ACROSS TAXA

Here, we explore the extent of the asymmetry in upper and lower tolerances by examining standardized metrics of thermal tolerance for 2740 terrestrial ectotherm, endotherm, and plant species with data spanning distributions across the world (Fig. 1; for full description of the data see Tables S1–S6 and references provided in the supporting information). Because thermal tolerance metrics are not fully comparable across studies (both within and between biological groupings), data were subdivided and analysed separately for each metric.

For ectotherms, the first group (A) includes critical minimum temperatures (CT_{\min}) and critical maximum temperatures (CT_{\max}) matched for 129 reptile species, minimum lethal temperatures (LT_{\min}) and CT_{\max} matched for 26 amphibians, and CT_{\min} and CT_{\max} matched for 12 spiders and 40 insects (Sunday *et al.* 2011; Hoffmann *et al.* 2013). The second group (B) includes estimates of CT_{\min} and CT_{\max} matched for 38 insect species (from Deutsch *et al.*

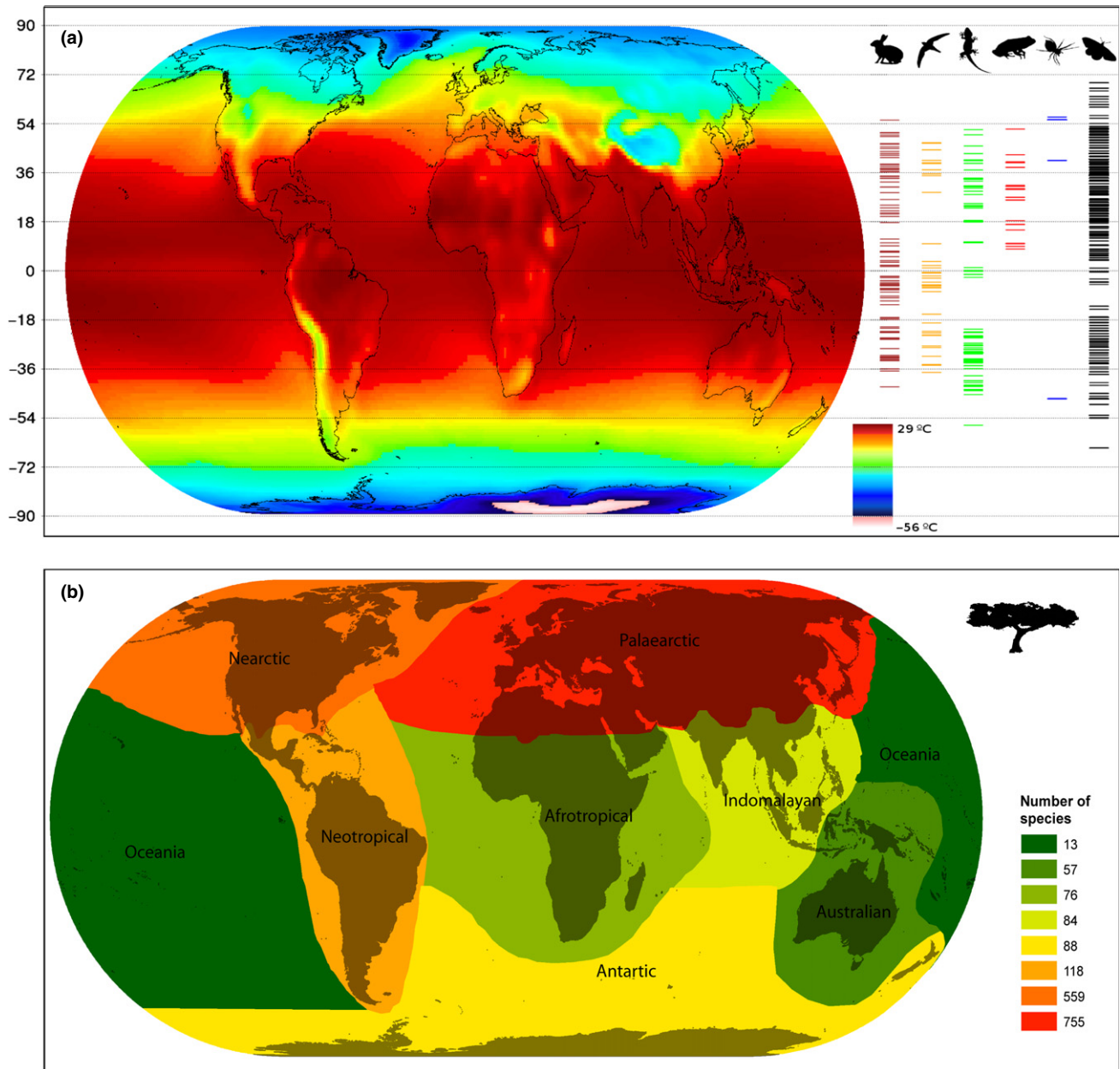


Figure 1 Distribution of the thermal tolerance data utilized in this study. (a) Colours depict annual mean temperature and bars on the right represent the centroids of species ranges calculated with data provided by Holt *et al.* (2013). Black bars are centroids of the range of insect species, spiders are represented with blue bars, amphibians are represented with red bars, reptiles are represented with green bars, birds are represented with orange bars and mammals are represented with brown bars. (b) Udvardy's plant Biogeographical Provinces of the World. Since maps of distributions of the plant species were not available for us, we assigned species to their native realms so that colours represent the number of species with thermal data per realm.

2008). Notice that the latter metrics are estimated from performance curves of the rate of development of organisms at different temperatures, so they are not directly comparable with other critical thermal measurements. The third group (C) includes a mix of metrics (CT_{min} and CT_{max} , lethal maximum and minimum temperatures in which 50% of the individuals die (LT_{min50} and LT_{max50}), and lethal maximum and minimum temperatures in which 100% die (LT_{min100} and LT_{max100}) for 704 insects (Kellermann *et al.* 2012b; Hoffmann *et al.* 2013). While the data sets A and B include upper and lower tolerances matched for each individual species, the third data set includes unmatched upper and lower thermal tolerances across species. These unmatched data provide a less powerful com-

parison, but due to the substantial sample size we elected to analyse them, while distinguishing these data from those where lower and upper tolerance metrics were matched for every species.

For endotherms, we reviewed 84 studies determining thermal neutral zone (TNZ) boundaries for birds and mammals, i.e. the range of external ambient temperatures in which the resting metabolic rate is constant and minimum (McNab 2012), and constructed a database of paired lower critical temperatures (LCT) and upper critical temperatures (UCT) for 227 species (see supporting information).

For plants, we reviewed 35 physiological studies using photosystem II (PSII), a protein complex that is related with the performance and survival of plants under extreme temperatures (e.g.

Valladares & Pearcy 1997). Non-destructive measurements of chlorophyll fluorescence, determining the maximal efficiency of PSII photochemistry (F_v/F_m) of the leaves, are recorded as temperatures are raised or lowered under controlled laboratory conditions (e.g. Gimeno *et al.* 2009). The critical temperature promoting a reduction of 50% of the initial F_v/F_m values (LT_{50}) is then obtained after fitting the corresponding response curves. This metric has been shown to correlate with other physiological estimates of thermal tolerance, such as membrane breakage and electrolyte leakage (Sierra-Almeida & Cavieres 2010), although lower performance limits may be set more by constraints on growth than on photosynthesis, at least for elevation tree lines (e.g. Hoch & Körner 2012). When data on LT_{50} were not provided in the papers reviewed, whenever possible we estimated it from alternative measures such as T_c , the critical temperature, defined as the intersection of the lines extrapolated from the slow and fast rise portion of the temperature basal fluorescence response curve, which is highly correlated with LT_{50} (e.g. Zhang *et al.* 2012). Regression lines obtained from studies simultaneously reporting various parameters were used to estimate LT_{50} values from studies only providing values for these alternative parameters. Overall, LT_{50} values were obtained for 520 plant species, 64% of them for cold tolerance, 36% for heat tolerance, with paired data representing only 4% of the total ($n = 19$). Estimates of cold tolerance were also available for a large number

of plant species, specifically cold hardiness ($n = 1190$) and frost tolerance ($n = 106$), but no analogue measurements were found for heat tolerance. The latter is typically expressed as number of days above 30 °C that a species is able to tolerate, but not as absolute temperature. Thus, results regarding these tolerance measures are provided in the supporting information.

Regarding ectotherms, more specifically reptile species from group A, we found that CT_{max} averaged 42.2 °C with variance 8.3, whereas CT_{min} was 7.8 °C with variance of 13.5 (Fig. 2a). Similar differences between CT_{max} and LT_{min} were found for amphibians, with twofold increases in the variance of tolerance to heat vs. cold (11.3 vs. 20.7), and for spiders with sixfold increases of variance (2.6 vs. 16.7) (Fig. 2a). For insects, we recorded almost twofold increases of variance (29.0 vs. 41.1) with data from group A (Fig. 2a), and roughly the same with group B (13.8 vs. 30.6) (Fig. 2b). With the unmatched lower and upper tolerance values with data from group C (Fig. 2c) the same general pattern emerged (variance of lower tolerance = 142.2 with $N = 254$, and variance of upper tolerance = 37.9 with $N = 371$), with lethal minimum temperature values extending far below any CT_{min} measurement for ectotherms (Fig. 2a and b) and below LT_{min} values reported for amphibians (Fig. 2a).

To explore the prediction that intraspecific niche variation is also lower near the critical thermal maximum than near the thermal critical minimum, we analysed data from 29 species of South American

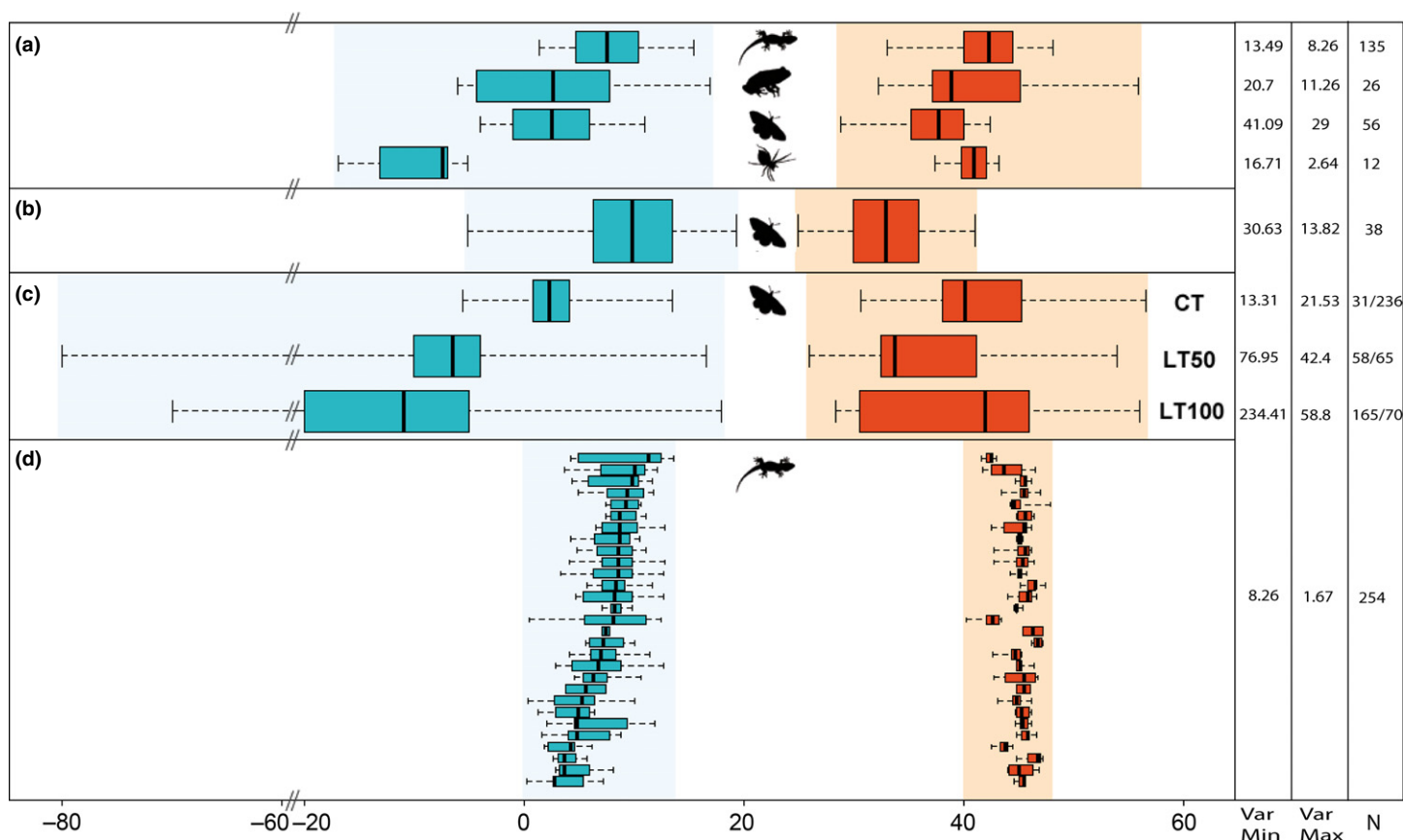


Figure 2 Variance of cold tolerance (green plots, left) vs. heat tolerance (red plots, right) among terrestrial ectotherms. (a) Box plots of CT_{min} and CT_{max} for 135 species of reptiles and LT_{min} and CT_{max} for 26 species of amphibians, and CT_{min} and CT_{max} for 12 spiders and 56 insects (Sunday *et al.* 2011; Hoffmann *et al.* 2013); (b) Box plots of CT_{min} and CT_{max} for 38 species of insects (data from Deutsch *et al.* 2008); (c) Box plots of a mix of unmatched lower and upper CT and LT values for 459 insects (Kellermann *et al.* 2012b; Hoffmann *et al.* 2013); (d) Box plots of CT_{min} and CT_{max} for 29 *Liolaemus* lizard species (each one of the 29 boxes represents intraspecific variation among individuals of the same species) in Chile (F. Ferri-Yáñez, unpublished data).

Liolaemus lizards from Chile for which several individual replicates exist for different species (mean number of individuals per species 9 ± 4.2 , unpublished data from F. Ferri-Yáñez, see details on the methods for data collection in the supplementary material). Results of intraspecific variation of thermal niche traits for the Chilean lizards were consistent with interspecific variability found among other ectotherms, i.e. lower for intraspecific CT_{max} than for CT_{min} (Fig. 2d). Critical maximum temperatures (CT_{max}) among *Liolaemus* species averaged $45.0\text{ }^{\circ}\text{C}$ (Variance = 1.7) and critical minimum temperatures (CT_{min}) averaged $7.4\text{ }^{\circ}\text{C}$ (Variance = 8.3) (Fig. 2d).

The same pattern of asymmetric variation in lower and upper thermal tolerances for ectotherms was recorded for endotherms and plants. Mean L_{CT} and U_{CT} for birds were 24 and $35\text{ }^{\circ}\text{C}$, respectively, with estimates of cold tolerance being more than four times as variable as heat tolerance (Fig. 3a). For mammals, average L_{CT} and U_{CT} were 26 and $34\text{ }^{\circ}\text{C}$, respectively, and variances of L_{CT} were more than seven times larger than variances of U_{CT} (Fig. 3b).

For plants, the differences in variance were even more striking. For the subset of species with paired measurements of cold and heat tolerance (Fig. 4a), mean critical values were -20 and $46\text{ }^{\circ}\text{C}$ for cold vs. heat tolerance and variances were almost 24 times greater for cold tolerance than for heat tolerance. For the species with unpaired measurements, mean critical values were -12 and $47\text{ }^{\circ}\text{C}$, and variances were five times greater for critical tolerances to cold than to heat (Fig. 4b). Even greater variances existed for measurement of frost tolerance and cold hardiness (Fig. S2), but no analogue metrics were available for upper limits.

VARIATION IN CRITICAL THERMAL LIMITS ACROSS ENVIRONMENTAL GRADIENTS

Given the asymmetry in variation of lower and upper thermal limits found in previous analyses (e.g. Addo-Bediako *et al.* 2000), and stronger relationships between lower limits and latitude than

between upper limits and latitude (e.g. Sunday *et al.* 2011), we expected that a positive correlation should exist between lower thermal limits and ambient temperature. Likewise, a much weaker relationship should be expected for upper thermal limits and ambient temperature. In other words, if tolerances to low temperatures are highly labile and lability is driven by natural selection, species exposed to low temperatures should have a tendency for greater tolerance to cold, while species not exposed to low temperatures should have a tendency for reduced tolerance to cold. In contrast, if tolerances to high temperatures are highly conserved across clades, natural selection might not be expected to be acting as strongly on this trait, resulting in a weak relationship. We examined these expectations by plotting physiological metrics of critical tolerance (CT_{max} and CT_{min} for ectotherms and U_{CT} and L_{CT} for endotherms) against metrics of ambient temperature averaged across species ranges. Plotting biological patterns against measured environmental gradients is generally preferable to plotting them as general geographical clines (i.e. as a function of latitude or altitude), as the latter are usually only indirectly, and often differently, related to the various environmental measures that are of biological significance (see for discussion Hawkins & Diniz-Filho 2004; Korner 2007). We also compensated for the allometric relation between L_{CT} and mass (McNab 2012), by fitting a linear model of L_{CT} with the log-transformed body weight in mass and using the residuals to assess the relationship with ambient temperatures.

The ambient temperature metrics we selected are commonly used in modelling studies of species distributions (e.g. Peterson *et al.* 2011) and include the following: minimum temperature of the coldest month (T_{min}), maximum temperature of the warmest month (T_{max}) and mean annual temperatures (T_{mean}). The analysis comparing upper and lower thermal limits against ambient temperatures was only possible for a subset of the species in our database with both physiological data and geographical distributional data, i.e. 64 reptiles (geographical data from www.iucnredlist.org), 38 insects

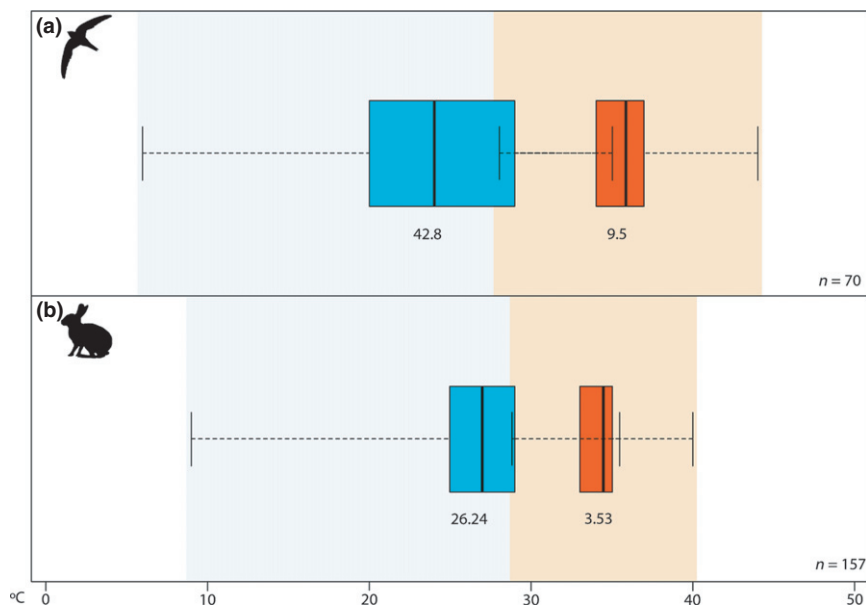


Figure 3 Variance of cold tolerance (green plots, left) vs. heat tolerance (red plots, right) for endotherms. Variances are depicted below every boxplot, number of species (n) is on the lower right section of the graph.

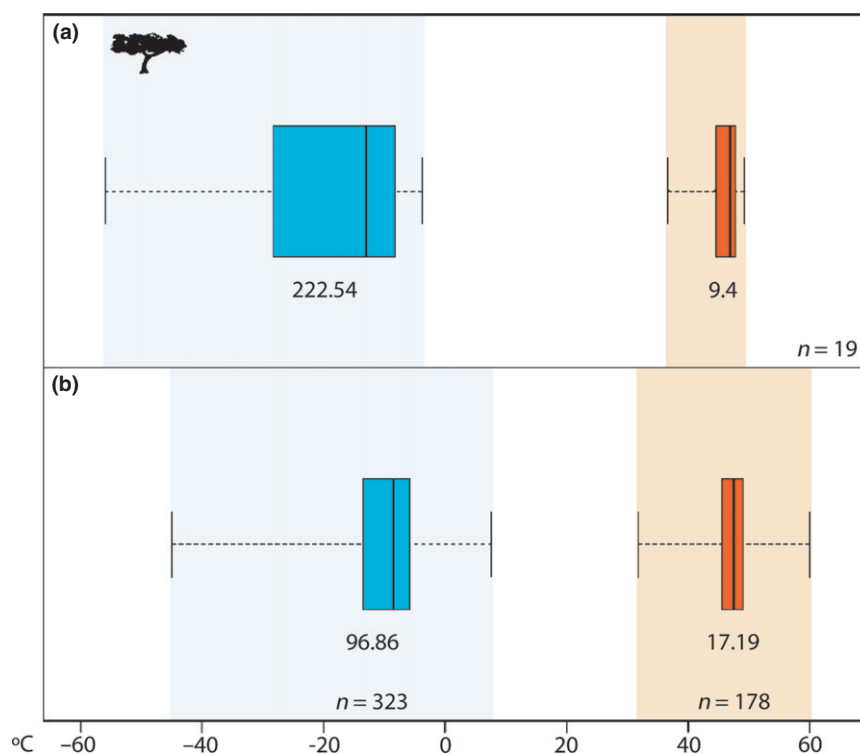


Figure 4 Variance of cold tolerance (green plots, left) vs. heat tolerance (red plots, right) among terrestrial plants. Physiological estimates of plant cold tolerance and heat tolerance (LT_{50}) are provided for (a) paired data and (b) unpaired data.

(from Deutsch *et al.* 2008) and 24 amphibians, 43 birds and 137 mammals (from Holt *et al.* 2013).

As expected, for ectotherms, we found that positive correlations exist between CT_{min} and averaged ambient temperatures (Fig. 5a, for correlations and P -values see Table S5). Although the strength of the correlations varies with taxonomic group, the relationship is positive for all. In contrast and consistent with our expectations, we found no clear pattern of correlation between CT_{max} and ambient temperatures (Fig. 5a). For example, for reptiles the correlation between CT_{max} and metrics of ambient temperature is markedly negative leading to the suggestion that adaptation to heat among these species might be driven by more complex relationships with a variety of climate variables (see discussion in Clusella-Trullas *et al.* 2011; Grigg & Buckley 2013). Indeed, most species have similar tolerances to heat (42 °C) and this is independent of the environments they are exposed to (e.g. *Zootoca vivipara* is exposed to T_{min} across the range of -20 °C and the species has as CT_{max} of 43.9 °C, whereas *Sphaerodactylus klauberi* is exposed to T_{min} of 16 °C and has CT_{max} of 36.3 °C). For amphibians, the correlation is either close to zero (with T_{mean}), clearly positive (for T_{max}), or slightly negative (for T_{mean}). For insects the correlation is positive but weak for all three metrics (i.e. always below $\rho = 0.35$).

For endotherms, there is an apparent lack of correlation between thermal limits and ambient temperature (Fig. 5b, for correlations and P -values see Table S6). The exception is T_{max} for which positive correlations with L_{CT} and U_{CT} were found for birds. A weak positive correlation was also found for U_{CT} in mammals ($\rho = 0.25$). However, when compensating for body mass (residuals L_{CT} in Fig. 5b) there is a significant correlation between cold tolerance and temperature, which is stronger for T_{max} ($\rho = 0.414$). For birds, T_{max}

also correlates with residuals of cold tolerance ($\rho = 0.380$). In other words, we found partial support for the prediction that natural selection might be driving physiological responses of mammals and birds to changes in ambient temperature (evidence for birds is restricted to T_{max}). In contrast, limited evidence supports that the physiological adaptation to heat is constrained by the environment with the exception of T_{max} for which a weak signal of adaptation was detected.

The most prominent feature of the above analysis is that, as expected, CT_{min} and L_{CT} tend to have a positive relationship with ambient temperature. By and large, ectotherm and endotherm species living in cold environments tend to be more tolerant to cold than ectotherm and endotherm species living in warm environments. Also, as predicted, species with greater tolerances to heat are not necessarily restricted to warmer environments. Correlations of CT_{max} and U_{CT} with ambient temperature were either close to zero, weakly positive or negative. Nonetheless, a consistent tendency for a positive correlation between T_{max} and upper thermal limits among ectotherms (except for reptiles) and endotherms was found. This is because some of the species with greater tolerances to high temperatures do live in the warmest environments (but species with great tolerances to heat are also found in colder zones). If this tendency were to be broadly confirmed it would indicate that some degree of selection, even if weak, might be occurring for upper thermal limits in warmer environments (but always below 50 °C, see following discussion on 'hard' physiological limits). Further exploration of this idea, and the general tendencies we have confirmed here building on previous work (Addo-Bediako *et al.* 2000; Clusella-Trullas *et al.* 2011; Sunday *et al.* 2011), is clearly required, especially taking more explicit account of phylogenetic correlation. Although we did not

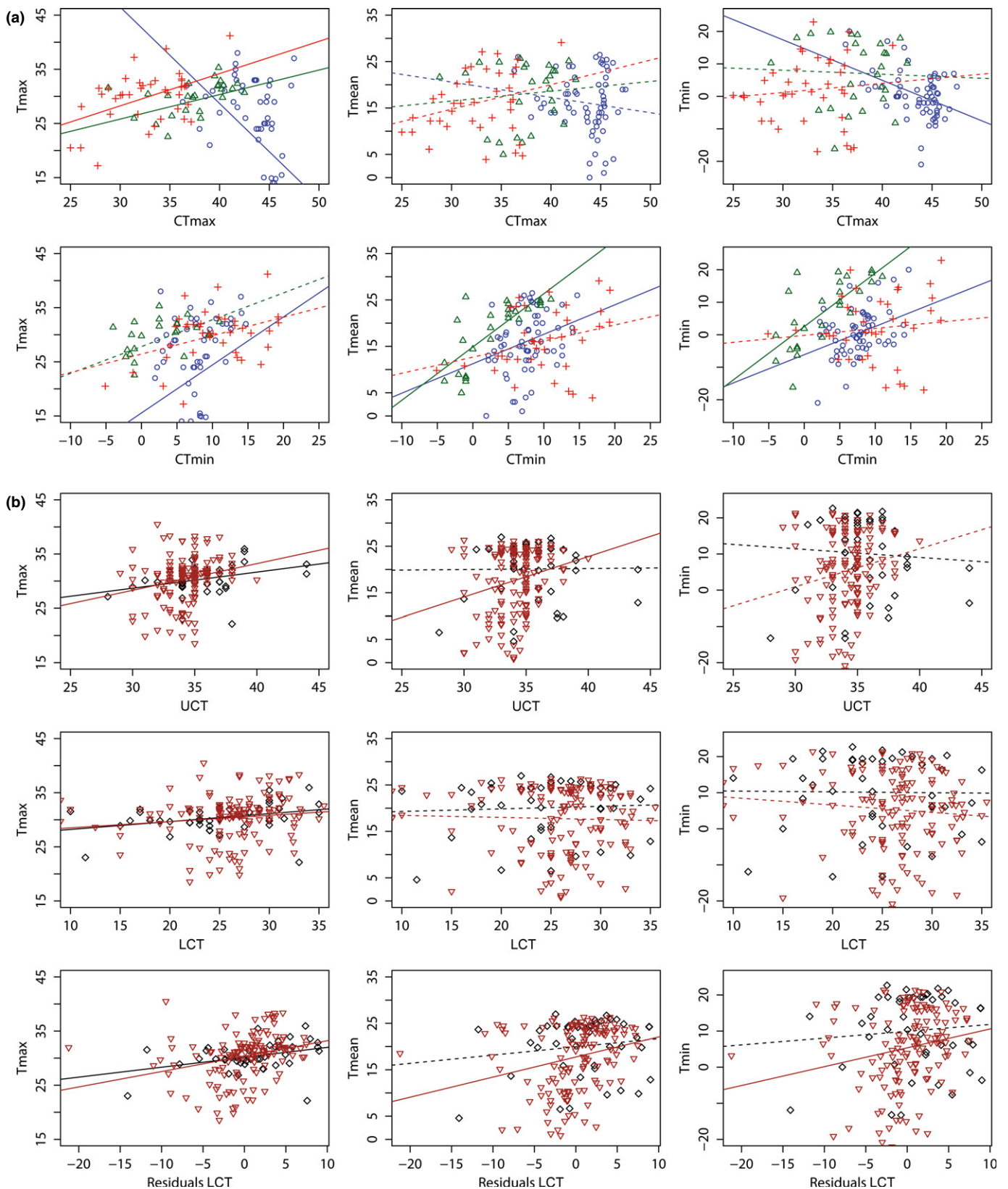


Figure 5 Scatter plots and regression lines between thermal tolerances and ambient temperatures for 64 species of reptiles (Blue circles), 26 species of amphibians (green triangles), 38 species of insects (from Deutsch *et al.* 2008; red crosses), 43 species of Birds (black squares) and 137 species of mammals (brown inverse triangles). T_{mean} : yearly mean temperature, T_{max} : Maximum temperature of warmest month and T_{min} : minimum temperature of coldest month (from Hijmans *et al.* 2005). CT_{max} : critical thermal maximum, CT_{min} : critical thermal minimum (Lethal Thermal minimum for amphibians), UCT: upper critical temperature for endotherms, LCT: lower critical temperature for endotherms. The residuals of regressing body mass and LCT in endotherms are plotted (Residuals LCT).

do so here, for reasons of disparate taxa and lack of phylogenies covering them, our findings are consistent with those of previous investigations, which have used a variety of approaches, and all of which have resulted in similar conclusions (e.g. Sunday *et al.* 2011, 2012; Hoffmann *et al.* 2013).

WHY WOULD EVOLUTION OF CLIMATIC NICHES BE ASYMMETRIC?

Our synthetic overview, and further analyses, unequivocally show that variation in thermal tolerances among terrestrial organisms is asymmetric (for syntheses of results see also Fig. S1). Specifically, a remarkable contrast of variability exists between interspecific tolerances to cold vs. heat among a large sample of terrestrial ectotherm, endotherm and plant species. The pattern also appears to hold true when intraspecific tolerances to cold vs. heat are measured among a small number of *Liolaemus* lizard species in South America. These results extend, to a wide variety of organisms, the finding for some terrestrial ectotherms that, generally, lower thermal limits are far more labile than upper limits (e.g. Addo-Bediako *et al.* 2000; Boher *et al.* 2010; Sunday *et al.* 2011; Grigg & Buckley 2013; Hoffmann *et al.* 2013). For a smaller set of ectotherm and endotherm species, we also show that critical limits to cold tend to correlate with metrics of ambient temperature, thus supporting the hypothesis that natural selection modulates physiological adaptation of species to lower temperatures. In contrast, critical limits to heat are, by and large, uncorrelated with metrics of environmental temperature partially supporting the hypothesis of conservatism of physiological tolerances to heat. These results also broaden previous evidence provided for terrestrial ectotherms that lower thermal limits are generally correlated with latitude (an indirect variable expected to correlate with metrics of ambient temperature), whereas upper thermal limits show much less geographical variation (e.g. Addo-Bediako *et al.* 2000; Sunday *et al.* 2011; Grigg & Buckley 2013). In consequence, they also implicitly suggest that the differences in range dynamics among marine and terrestrial species in response to changing climates, that have been identified previously on the basis of different asymmetries in tolerance (Sunday *et al.* 2012), may extend more broadly.

It might be argued, however, that phenotypic plasticity could reduce the extent of the differences in lability of upper and lower thermal tolerances. However, for a wide range of ectotherms evidence is accumulating that plasticity of upper limits is much reduced by comparison with plasticity of lower limits (see also Chown & Terblanche 2006; Hoffmann *et al.* 2013). How common this is for endotherms and plants is not yet clear, although it deserves explicit investigation for reasons that will become clear below (see also Piersma & Drent 2003).

Asymmetry in conservatism of lower and upper thermal limits is likely to be the consequence of different physiological processes operating near critical lower and upper thermal limits. With animals, variation in lower thermal limits is a consequence of differences in thermodynamic effects of temperature on reaction rates, and most likely those responsible for maintaining ion homeostasis (e.g. Hosler *et al.* 2000; MacMillan *et al.* 2012). In contrast, variation in tolerance to heat is mostly a consequence of limited variation in the ability of organisms to counter the destabilizing effects of high temperature on membranes and proteins (for review see Angilletta 2009). The latter processes involves, *inter alia*, ancient polypeptides that are

expected to be highly conserved across all forms of living organisms (e.g. Gupta & Golding 1993).

Likewise, cold acclimation of plants relies on adjusting metabolic processes (essentially photosynthesis and respiration) and on avoiding lethal freezing (e.g. Larcher 1995). Both aspects have been shown to be highly dynamic since plants not only adapt quickly to thermal environments but also acclimate and de-acclimate seasonally to low temperatures (e.g. Pagtera & Arorab 2013). Plants have also been shown to acclimate quickly to high temperatures (e.g. Sung *et al.* 2003). However, changes in lipid composition of the membranes and increased production of heat shock proteins, two basic processes involved in heat tolerance of plants, are typically not sufficient to enable them to cope with temperatures above 45 °C, except in exceptional circumstances, such as in the case of desiccated state of resurrection plants (e.g. Larcher 1995; Kappen & Valladares 2007). Thus, as is the case with animals, sound physiological reasons exist to explain why plants are more likely to exhibit higher variability and adaptive potential in their lower rather than their upper limits of thermal tolerance.

Higher order processes likely set thermal limits in marine organisms (Pörtner 2001), often resulting in close matches between range limits and thermal tolerances, with important consequences for range dynamics (Sunday *et al.* 2012). Although higher order processes have also been claimed to set thermal limits in terrestrial ectotherms (Pörtner 2001), several studies suggest that the latter is unlikely (e.g. Klok *et al.* 2004; McCue & Santos 2013). These profound differences between marine and terrestrial groups may partly account for the differences in the associations between ranges and tolerances found in marine and terrestrial organisms, with 'mismatches' being more common in terrestrial species (see the detailed treatment of tolerances, range filling and the impacts of climate change by Sunday *et al.* 2012).

Clearly, some organisms are able to develop substantial resistance to high temperatures, but this is rare (reviewed by Hoffmann *et al.* 2013). For example, lichens, bryophytes and vascular plants can increase their heat tolerance, with some species being able to recover from temperatures exceeding 80 °C and even 120 °C if these are experienced in desiccated state (e.g. Kappen & Valladares 2007). The same is true of some of several anhydrobiotic invertebrates (e.g. Watanabe *et al.* 2002). Perhaps, most notable are extremophilic microbes whose proteins can be synthesized at temperatures exceeding 100 °C (e.g. Kashefi & Lovley 2003). Several desert ant species are also known to tolerate temperatures exceeding 50 °C during short-term periods of activity (e.g. Wehner *et al.* 1992). However, the average upper thermal limit for insects in our data is 41.6 °C and temperatures above 47.8 °C are thought to be tolerated only temporarily by animals (Pörtner 2002).

In this context, an important question is whether complex terrestrial organisms can evolve hyperthermostability (the ability to maintain structural stability and function at high temperatures e.g. >50 °C) under specific circumstances. Forecasts are for ongoing increases in global temperatures that will, in many circumstances, exceed organismal upper thermal limits substantially constraining fitness (and ultimately survival) (e.g. Wahid *et al.* 2007; Kearney *et al.* 2009; Bozinovic *et al.* 2011). If organisms are unlikely to be able to alter upper thermal limits, by whatever mechanism, then extinction risk may be much higher than currently anticipated. However, behavioural regulation and microclimate availability may still provide important opportunities for improvement of performance and survival.

Ultimately, the question is whether conservatism of upper thermal tolerances among terrestrial organisms is due to hard physiological boundaries that prevent adaptation of organisms beyond given temperature limits, whether it is due to biogeographical legacies that set the context for evolution, or whether selection for tolerance of rare temperature events might be responsible for it. The biogeographical argument is as follows: Earth's climate has been predominantly warm throughout its history with pulses of cold climates coming and going (e.g. Ruddiman 2001). The planet was at its coldest known state between 850 and 550 million years ago (mya), and complex organisms evolved after this period (e.g. Romdal *et al.* 2013). Subsequently, two major glaciations occurred: the first between 325 and 240 mya; and the second at 35 mya, at the onset of the Oligocene. A shorter glaciation might have also taken place at about 430 mya (Ruddiman 2001). However, the critical issue for evolution is that the equatorial region has remained warm through glacial-interglacial cycles (between 30 and 40 °C between the Paleocene and the Pliocene, Fig. 6), while higher latitudes were exposed to marked climatic variation (from nearly 0 to -80 °C, Fig. 6). Thus, it is not surprising that the vast majority of clades evolved in the thermally stable and warm equatorial region (e.g. Jablonski *et al.* 2006; Romdal *et al.* 2013), while some clades were able to colonize higher latitudes via physiological adaptations to lower temperatures (e.g. Wiens & Donoghue 2004).

If the world remained warm during most of its history, with most species evolving in environments exposed to relatively high temperatures, better performance at higher temperatures (a thermodynamic effect – e.g. Asbury & Angilletta 2010) would be expected, and maximum performance temperatures would also be closer to thermal maxima than thermal minima, owing to irreversible enzyme inactivation at higher temperatures (i.e. thermal responses would be negatively skewed, as is the case – see Kingsolver 2009). Opportunities for speciation and evolution of thermal niches would thus occur through adaptive radiation in relatively colder and species poor areas (e.g. Gavrillets & Vose 2005). This reasoning could explain why most selective pressures favoured niche evolution in cold environments while little pressure existed for evolution of thermal niches in warm and stable environments (Donoghue & Moore 2003). However, it does not explain why so little evidence exists for thermal evolution above 50 °C.

Hard physiological boundaries, or selection for survival of rare, high extreme temperature at any latitude (absolute maximum temperatures vary much less across space than do absolute minima – see Addo-Bediako *et al.* 2000) are, at this stage, the two most plausible alternative explanations for conserved upper thermal limits. Distinguishing among these alternatives has not been the subject of detailed research. However, the former is, in our view, most plausible given that so few metazoan organisms, even in extreme environ-

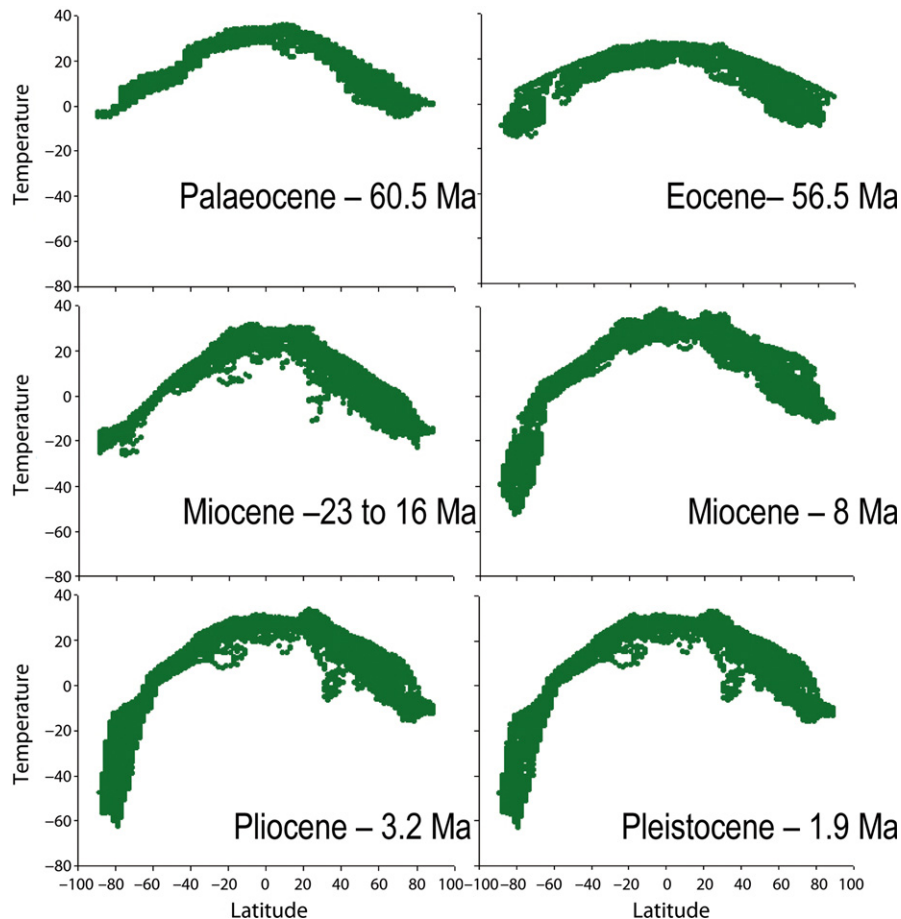


Figure 6 Changes in mean annual temperature values (°C) across latitude from the Paleocene to the Pliocene. Raw data to build the figure were based on GCM simulation hindcasts kindly provided by Persaram Batra (Miocene 23–26) and Paul Valdes and Alan Haywood (Palaeocene, Eocene, Miocene 8, Pliocene 3.2 and 1.9).

ments such as at marine hydrothermal vents (e.g. Ravaux *et al.* 2013), are able to exploit exceptionally hot, though energy rich, environments (i.e. much above 50 °C). Nonetheless, it is clear that explicit consideration of these alternatives is an important area for research.

Indeed, given that a few metazoans and plants seem to have evolved mechanisms to overcome temperature extremes (see above, and also Girguis & Lee 2006), understanding the biochemical and genetic basis of this ability, and how it might be promoted in other groups, is clearly important for the further development of conservation strategies for adapting to ongoing global temperature increases. Research on a variety of taxa is starting to address this question, especially from a genetic perspective, but consensus has yet to emerge (see Williams *et al.* 2012 for a brief overview). If upper thermal tolerance boundaries are indeed hard (or show limited ability to evolve), and the prospects for dispersal keeping pace with rates of change limited, then assisted migration (or managed relocation) may indeed become a preferred strategy, irrespective of its potential risks (e.g. Schwartz *et al.* 2012). In contrast, if upper boundaries are more malleable and can be altered through hybridization of populations or other approaches that might be considered a form of 'assisted evolution', then alternatives to wholesale relocations are plausible. Assisted evolution of domestic species has been a key component of human success, but has rarely been applied in this form in a conservation context (but see e.g. Jones & Monaco 2009).

NICHE CONSERVATISM LEADS TO NICHE SIMILARITY

High conservatism of upper thermal limits among terrestrial organisms suggests that many species are unlikely to evolve physiological tolerances to increased heat, especially when their climatic preferences are close to their upper thermal limits. In such cases, evolution of physiological tolerances will be impaired, and species persistence challenged unless species have other means to adapt to increased environmental temperatures – a topic now being thoroughly investigated (Deutsch *et al.* 2008; Huey *et al.* 2009; Clusella-Trullas *et al.* 2011; Kellermann *et al.* 2012b; Sunday *et al.* 2012; Grigg & Buckley 2013; Hoffmann *et al.* 2013). But another, more general and largely unnoticed consequence of niche conservatism is that fundamental niches, or at least the thermal components of the fundamental niches, are likely to be more similar among closely related species than is usually inferred with methodologies that relate geographical distributions of species with aspects of climate.

The idea that tolerances of species to environmental gradients varies continuously along those gradients was first proposed by Whittaker (1967). His ideas led to the development of the theory of gradient analysis and the continuum concept in community ecology, whereby species should gradually substitute each other along environmental gradients due to varying individual preferences and tolerances (see also Austin 1985). Even though these ideas were developed based on extensive empirical analyses of plant species distributions, we show here that the type of response curves of species in relation to the environment that were obtained for plants (e.g. Whittaker 1967) are unlikely to be fundamentally different from the response curves obtained for animals (see Fig. 7a). Indeed, the generality of such relationships has meant that the continuum concept underlies much of the thinking that motivates bioclimatic envelope modelling (alternatively termed ecological niche modelling,

habitat suitability modelling, or species distribution modelling; see for recent review of terminology Araújo & Peterson 2012), and that is used to infer species climatic niches based on associations between aspects of climate and species' geographical distributions (e.g. Austin 1985; Peterson *et al.* 2011). As shown in Fig. 7b, however, niche conservatism can cause the metabolic (thermal) response curves of different species to be more similar than expected if climatic niches were inferred from analysis of geographical distributions and species occupancies of thermal gradients. Although varying levels of conservatism might exist among traits affecting different dimensions of the fundamental niches (e.g. tolerance to water), our extensive analysis of lower and upper thermal limits among terrestrial organisms is consistent with the proposition that fundamental niches, or at least their thermal component, should be more similar among species than typically inferred with methods that relate the geographical distributions of species with their environment.

Even though interspecific and intraspecific differences between fundamental niches are expected due to niche evolution and/or phenotypic plasticity (see also e.g. Hoffmann *et al.* 2003; Klok & Chown 2003), we expected the thermal component of the fundamental niches to differ less within and among species than the thermal component of realized niches. Moreover, major interspecific and intraspecific differences between fundamental niches should be expected mainly at the tails of the species-temperature response curves, especially when these tails approach lower temperature limits (Fig. 7b). In contrast, limited overlap between realized niches of closely related species is likely to be more common and a consequence of historical climatic legacies (e.g. Ricklefs 2006), the effects of biotic interactions (e.g. Dobzhansky 1950), limited dispersal (e.g. Baselga *et al.* 2012) and, perhaps, variation in species tolerances to aspects of the environment that are not characterized by, but may also influence responses to thermal gradients.

CONSEQUENCES OF NICHE SIMILARITY FOR STUDIES IN ECOLOGY AND EVOLUTION

The extent to which functional traits, performance currencies, and the environment, vary across clades is a central question in ecology and evolution (e.g. Messier *et al.* 2010). Our prediction that fundamental niches are more similar across lineages than inferred from analysis of realized niches is of critical importance for a range of research questions. For example, uncritical analysis of realized climatic niches can lead to important mistakes when predicting the effects of climate change on species distributions, assessing the risk of species invasion, or making inferences about rates of niche evolution. Specifically, if realized niches are highly constrained by dispersal, biotic interactions, and/or resource utilization, as they are expected to be at low latitudes and altitudes (e.g. Dobzhansky 1950; Loehle 1998), then they are unlikely to provide accurate estimates of species tolerance limits to climate. When this is the case, projections from bioclimatic envelope models will have a tendency to overestimate the effects of climate change on species distributions, underestimate the risk of species invasions, and miscalculate rates of niche evolution. In contrast, if realized niches are mainly constrained by climate variables, as it expected to be the case at higher latitudes and altitudes, then greater similarity between realized niches and fundamental niches is expected with the consequence that bioclimatic envelope models are also more likely to provide

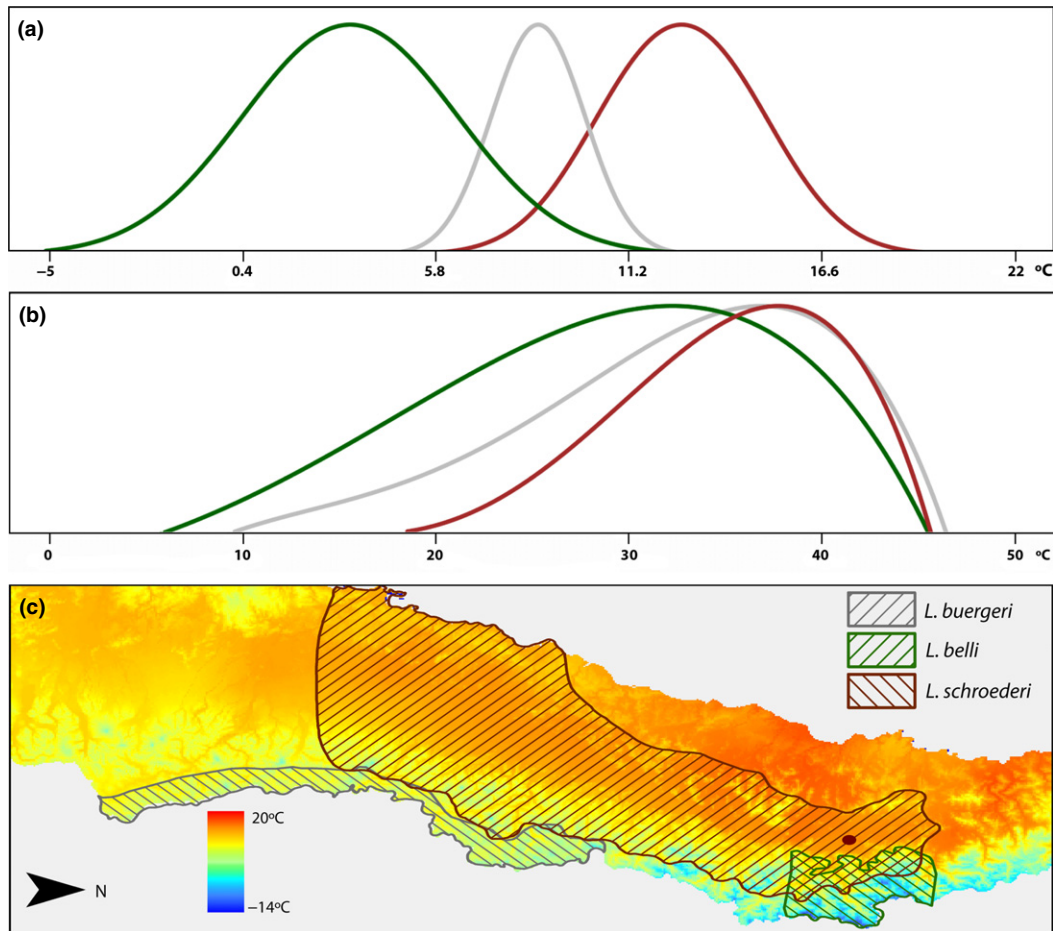


Figure 7 (a) Response curves estimated with bioclimatic envelope models (logistic regression) relating species distributions of three species of *Liolaemus* lizards in central Chile (see panel c) against mean annual air environmental temperatures (from Hijmans *et al.* 2005) (i.e. characterization of the realized niche for mean annual temperature); (b) empirical performance curves for the same species of *Liolaemus* (from F. Ferri-Yáñez, unpublished data) measured with sprint speed in laboratory conditions against body temperature (i.e. characterization of the fundamental niche for body temperature); and (c) geographical distributions of the three species of *Liolaemus* (from P.A. Marquet and C. Garín, unpublished data) overlaid on mean annual temperature.

accurate predictions. This outcome is most likely when thermal aspects of the environment–organism interaction are most significant, which is in any case often the outcome of many bioclimatic envelope models given the significance of the thermal environment for organisms (e.g. Walther *et al.* 2005; Kearney *et al.* 2010). Rates of environmental change may also play a role given differential organismal responses to them, particularly phenotypic plasticity (e.g. Terblanche *et al.* 2011), although plasticity is much less significant for upper thermal tolerance traits (see above).

Among work done recently, a comprehensive example of the significance of understanding fundamental thermal limits in the context of species distributions is provided by Sunday *et al.* (2012). They show how differences in the way upper and lower thermal limits vary among marine and terrestrial organisms have fundamental implications for understanding species distributions as climate continue to change. The *Liolaemus* lizards discussed above (see Fig. 7) provide a further example. Assume, for the sake of argument that a reasonable and similar correlation exists between increases in ambient temperature and increases in the body temperature of the species. If ambient temperatures increased uniformly across the gradient, populations of *Liolaemus schroederi* at the upper tail of the temperature gradient would be the first to go extinct unless behavioural adaptations enabled them

to persist under further warming (e.g. Huey *et al.* 2003). Assuming a similar interspecific relation between ambient and body temperatures, bioclimatic envelope models would be expected to correctly predict extinctions because the upper tail of the species–temperature response curve inferred with bioclimatic envelope models (Fig. 7a) as the lizard temperature reaches the upper thermal tolerance of the species as measured under laboratory conditions (Fig. 7b). In contrast, mismatches between the upper thermal tolerances and the upper tails of the species–temperature response curves, as is clear for the other two species, would cause failure of models to predict correctly extinctions under warming. For example, increased temperatures along the thermal gradient in Fig. 7b would cause bioclimatic envelope models to shift to the right and predict losses of climate suitability within existing ranges of *Liolaemus belli* and *Liolaemus buergeri*. However, if species are exposed to temperatures below their preferred body temperatures, increases in ambient temperature will increase their fitness. That is, models inferring niches from assessments of the relationship between geography and the environment would have a tendency to overestimate extinction risk in a climate warming scenario.

When realized niches for closely related species are segregated along the temperature gradient (Fig. 7a) and thermal fundamental niches are overlapping for them (Fig. 7b), one implication is that

several regions with suitable climate for the species are likely to be unoccupied. A low degree of equilibrium of species distributions with climate has already been reported for ectotherms (e.g. Munguía *et al.* 2012), endotherms (e.g. Monahan & Tingley 2012) and plants (e.g. García-Valdés *et al.* 2013), and one of the consequences for modelling of invasive species outside of their native ranges is that models will underestimate the extent of the areas that can be invaded. Another consequence is that tests of predictive success of models across invaded ranges will tend to generate high omission errors (invaded areas not predicted to be invaded by models) (e.g. Broennimann *et al.* 2007; Fitzpatrick *et al.* 2007) and these may invite potentially erroneous interpretations of shifts in fundamental niches. A pragmatic solution to improve inferences of physiological limits based on geographical distributions of species, is to model species distributions using both native and invaded ranges (Broennimann & Guisan 2008) or, whenever possible, to use historical distributional records (e.g. Nogués-Bravo *et al.* 2008).

Studies in evolution are also bound to be strongly affected by overestimation of niche differences across lineages. Specifically, if the currency of interest is rates of change in physiological aspects of the niche (e.g. Peterson *et al.* 1999; Hof *et al.* 2010; Kozak & Wiens 2010), then overestimation of niche differences among species will lead to inflation of evolutionary rates of the niche and this will lead to erroneous conclusions about niche conservatism and its importance in driving biodiversity patterns on earth.

CONCLUDING REMARKS

The activity of terrestrial animals and plants is limited by their thermal environment. Because environmental temperature varies in time and space, sometimes abruptly, organisms are continually challenged to maintain homeostasis. Here, we asked if physiological adaptation of species to current climate warming was likely, and what the consequences might be if this was not the case. For a large number of terrestrial ectotherms, endotherms and plants, we show that interspecific variation for lower thermal limits is greater than for upper limits. Similar patterns were found among individuals of the same species for a small number of South American lizard species, suggesting that selection could act at intraspecific level for lower thermal tolerances in cold environments, while reduced opportunities might exist for selection of upper tolerances under warm conditions. We also found for a sample of ectotherm and endotherm species that lower limits of tolerance tend to covary with ambient temperature, whereas upper thermal limits tend not to. In other words, natural selection seems to modulate physiological responses to lower temperatures more so than it does to upper temperatures. Two conclusions can be drawn from these results. First, rates of niche evolution vary for different traits. The implication is that controversy regarding rates of niche evolution vs. conservatism cannot be settled unless specific predictions are made and tested for different traits. Although similar statements have been made previously (e.g. Slobodkin & Rapoport 1974), the consequences of this reasoning for the niche conservatism debate have not always been fully appreciated (see for discussion Araújo & Peterson 2012). Second, and more importantly, hard boundaries seem to constrain evolution of upper thermal tolerances beyond given temperature limits. One consequence of strong conservatism of upper thermal limits among terrestrial organisms is that fundamental niches, particularly the upper tails of species-temperature response curves, should be more

similar among closely related species than typically inferred with bioclimatic envelope models or with multivariate approaches relating species distributions with environmental predictors (e.g. Hof *et al.* 2010; Kozak & Wiens 2010). Thus, realized niches of species living in cold environments will tend to underestimate upper thermal limits, potentially causing models to overestimate the effects of climate warming on biodiversity (see also Sunday *et al.* 2012). In contrast, realized niches for species in warm environments are closer to their physiological upper thermal limits. In such cases, further climate warming will cause models to predict correctly range contractions, unless species have other means to adapt to increased temperatures.

Improving understanding of the linkages between organisms and environments is critical for understanding rates of the evolution of niches, predicting the effects of climate change on biodiversity, and estimating the risk of invasive species (e.g. Wiens *et al.* 2010). To make progress in this field, greater interaction between otherwise disconnected disciplines is required. Specifically, there is need for greater coordination between empirical and theoretical research programmes that characterize the fundamental niches of species, and these efforts need to feed into the development of models of species geographical distributions that more explicitly account for the physiological mechanisms constraining species distributions (e.g. Buckley *et al.* 2010; Sunday *et al.* 2012; Kearney *et al.* 2013). Only with improved characterization of the physiological constraints on species distributions will researchers be able to quantify the additional contributions of non-climatic factors, such as dispersal and biotic interactions, in shaping ecological niches and geographical distributions.

ACKNOWLEDGEMENTS

This study is funded through the LINCglobal CSIC-PUC and the NICHE project (CGL2011-26852) of the Spanish Ministry of Economy and Competitiveness. M.B.A. also acknowledges the Integrated Program of IC&DT Call No 1/SAESCTN/ALENT-07-0224-FEDER-001755, and the Danish NSF for support. P.F.Y. is funded through a CSIC-JAE PhD studentship (2010 00735). F.B. acknowledges FONDECYT (1130015). P.A.M. acknowledges ICM (P05-002) and CONICYT (PFB-23). We thank Natália Melo for providing animal drawings for Figs 1–5, and the handling editor and six anonymous referees for constructive criticism of the manuscript (any potential error remains ours though).

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Editor, Dov Sax

Manuscript received 20 March 2013

First decision made 24 April 2013

Manuscript accepted 17 June 2013