PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: Qu Y-F, Wiens JJ. 2020 Higher temperatures lower rates of physiological and niche evolution. *Proc. R. Soc. B* **287**: 20200823.
http://dx.doi.org/10.1098/rspb.2020.0823

Received: 14 April 2020
Accepted: 19 June 2020

Subject Category:
Evolution

Subject Areas:
ecology, evolution, physiology

Keywords:
climate change, evolution, niche, phylogeny, physiology, vertebrates

Author for correspondence:
John J. Wiens
e-mail: wiensj@email.arizona.edu

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.5046640.

THE ROYAL SOCIETY
PUBLISHING

Higher temperatures lower rates of physiological and niche evolution

Yan-Fu Qu[1,2] and John J. Wiens[2]

[1]Jiangsu Key Laboratory for Biodiversity and Biotechnology, College of Life Sciences, Nanjing Normal University, Nanjing 210023, Jiangsu, People's Republic of China
[2]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

JJW, 0000-0003-4243-1127

Understanding rates and patterns of change in physiological and climatic-niche variables is of urgent importance as many species are increasingly threatened by rising global temperatures. Here, we broadly test several fundamental hypotheses about physiological and niche evolution for the first time (with appropriate phylogenetic methods), using published data from 2059 vertebrate species. Our main results show that: (i) physiological tolerances to heat evolve more slowly than those to cold, (ii) the hottest climatic-niche temperatures change more slowly than the coldest climatic-niche temperatures, and (iii) physiological tolerances to heat and cold evolve more slowly than the corresponding climatic-niche variables. Physiological tolerances are significantly and positively related to the corresponding climatic-niche variables, but species often occur in climates outside the range of these tolerances. However, mismatches between climate and physiology do not necessarily mean that the climatic-niche data are misleading. Instead, some standard physiological variables used in vertebrates (i.e. critical thermal maxima and minima) may reflect when species are active (daily, seasonally) and their local-scale microhabitats (sun versus shade), rather than their large-scale climatic distributions.

1. Introduction

As global temperatures rise, the survival of many species may hinge on their ability to rapidly shift their realized climatic niches to accommodate these new climatic conditions [1–5]. These niche shifts may occur through plastic changes (e.g. behavioural avoidance of high temperatures) or evolutionary change [6–8]. A crucial trait that may need to evolve rapidly to allow species to persist in warmer climates is their physiological tolerance to high temperatures [5]. Therefore, it is urgently important to understand evolutionary rates in physiological tolerances, rates of climatic-niche change, and the interrelationships between climatic niches and physiology.

Some papers have now addressed this intersection of physiological and climatic-niche evolution. However, most have not done so using appropriate phylogenetic methods. For example, in an influential and well-cited paper, Araújo *et al.* [9] suggested that physiological tolerances to heat evolve more slowly than tolerances to cold (e.g. due to different constraints on physiological processes at very high and low temperatures). They reviewed physiological data from ectotherms for critical thermal minima (CT_{min}) and maxima (CT_{max}), and similar variables for endotherms (upper and lower thermal neutral zones; UT_{max} and UT_{min}). They concluded that 'heat freezes niche evolution' (i.e. lowers the evolutionary rate), based on less variability among species in upper thermal tolerances (CT_{max}/UT_{max}) than in lower thermal tolerances (CT_{min}/UT_{min}). However, they did not infer rates of physiological or climatic-niche evolution. They also suggested that data on species' realized climatic niches may give misleading inferences about topics related to climatic niches (e.g. responses to climate change, niche evolution, invasive species), based on differences between climatic and physiological data. Grigg & Buckley [10] found greater phylogenetic signal in CT_{max} than CT_{min} in lizards. However, signal is not an estimate of rates for continuous variables [11]. Similarly, Hoffmann *et al.* [12] inferred greater constraints on upper than lower thermal limits in insects and squamate reptiles, again based on phylogenetic signal. Muñoz *et al.* [13] used phylogenetic methods [14] to directly compare evolutionary rates in upper and lower physiological tolerances among seven *Anolis* lizard species. They found lower rates for CT_{max} than CT_{min}.

We suggest that several important questions about the evolution of physiological tolerances and climatic niches should be broadly addressed using appropriate phylogenetic approaches. (1) Do physiological tolerances to heat (CT_{max}) evolve more slowly than physiological tolerances to cold (CT_{min}), as suggested in these previous studies? (2) Does heat freeze niche evolution? For example, do the hottest temperatures in species' realized climatic niches change more slowly than the coldest temperatures, possibly because of these asymmetric rates in physiological tolerances? (3) Does physiological evolution constrain climatic-niche evolution? Three subquestions may help resolve this. (a) Do physiological tolerances to extreme temperatures (CT_{max}, CT_{min}) evolve more slowly than the corresponding climatic-niche temperatures (hottest annual, coldest annual)? We expect lower rates in these physiological variables if their slow rates limit (constrain) rates of climatic-niche evolution. (b) Second, are there strong relationships among species between physiological tolerances to extreme heat and cold and corresponding niche temperatures? This was addressed by Araújo *et al.* [9], but without incorporating phylogeny. They concluded that physiological tolerances to cold were correlated with minimum niche temperatures, but tolerances to heat tended to be uncorrelated with maximum temperatures. (c) Do these physiological variables seem to limit where species can occur climatically? Specifically, do species occur only where maximum temperatures are less than their physiological tolerances to heat, and where minimum temperatures exceed their physiological tolerances to cold? (4) How are body temperatures related to physiological tolerances and climatic temperatures? For example, does variation in body temperatures across environments lower evolutionary rates in physiological tolerances by buffering individuals from extreme temperatures (e.g. [13,15])? Based on this idea, we might expect strong relationships between body temperatures and climatic variables and lower evolutionary rates in physiological tolerances than body temperatures. Alternatively, different species might maintain similar body temperatures across diverse environments, yielding weak relationships and similarly low rates in both body temperatures and physiological tolerances. To our knowledge, most of these questions have not been directly addressed before, or only at limited taxonomic scales. However, a recent study [16] found faster rates of niche evolution for coldest temperatures than hottest temperatures (in plants and vertebrates) but did not examine physiological variables.

Here, we address these questions using phylogenetic methods and physiological and climatic data from tetrapods. First, we compile physiological and climatic data from the literature for hundreds of amphibians, squamates, birds and mammals. We assemble time-calibrated phylogenies for each group (amphibians [17]; squamates [18]; birds [19]; mammals [20]). We then test our hypotheses using phylogeny-based methods designed to test for significant differences in evolutionary rates between variables [14] and infer relationships between variables [21]. Our results show lower evolutionary rates for physiological tolerances and climatic-niche variables associated with maximum temperatures, that climatic variables change more quickly than physiological variables, and climatic variables and physiological tolerances are significantly related.

2. Material and methods

(a) Physiological data

Physiological data for each species and corresponding references are given in electronic supplementary material, table S1. Body temperatures (T_b) reflect behavioural thermoregulation and available environmental temperatures (review in [22]). Data on T_b were for active animals in the field. Thermal tolerance limits in ectothermic vertebrates are typically estimated based on body temperatures associated with the loss of righting responses at upper and lower thermal limits [23,24]. These are referred to as critical thermal maxima (CT_{max}) and minima (CT_{min}). Endotherms can maintain a high and relatively constant active body temperature (T_a) through metabolic heat production (e.g. [25]). Birds and mammals with a broad thermoneutral zone can maintain their basal metabolism over a wide range of temperatures. Metabolic rates rise when environmental temperatures are above (UT_{max}) or below (UT_{min}) the thermoneutral zone [25]. Data were obtained on T_b (amphibians, squamates), T_a (birds, mammals), CT_{min} and CT_{max} (amphibians, squamates), and UT_{min} and UT_{max} (birds, mammals). We recognize that the physiological variables in ectotherms and endotherms are not strictly equivalent, and we do not compare them across groups. However, we treat them as conceptually similar (following [9]).

For amphibians, we obtained physiological data from literature sources [26–28]. We checked species names [29] and found 30 synonymous species. We deleted species with the same data under different names, and averaged values across conspecific taxa. We obtained data from 222 species, but removed 40 species absent from the tree, leaving physiological data from 182 species for one or more variables.

For squamates, we assembled published physiological data [3,10,27,28,30]. In one study [3], most T_b were from multiple populations, and we used these values when possible. We averaged T_b values across populations to obtain a single value for each species. Again, we checked species names (using [31]), found 80 synonyms, and renamed taxa and combined data from synonymous species. CT_{min} values from Brattstrom [30] were unusually low for 16 species. Specifically, values were less than 0°C (including species known to be active at high temperatures), whereas CT_{min} values from confamilial species were much higher. We therefore deleted CT_{min} data for these 16 species, as have other authors [27]. We retained a very low CT_{min} value (−3.7°C) from *Sceloporus jarrovii*, a species active in winter at high elevations [32]. We also removed 90 species absent from the tree, leaving 620 species. We also included the rhynchocephalian *Sphenodon punctatus*, but use 'squamates' for convenience.

We assembled bird data from various sources [25,33,34]. We preferentially used T_a data from Clarke & Rothery [34], who averaged values between sexes. We removed potentially erroneous UT_{max} values from 102 species [35]. We checked all species names [36] and deleted or combined 42 synonyms. We removed 42 species absent from the tree, leaving data for 618.

We summarized mammal data from various sources [25,28,34,37]. We renamed or combined 96 synonymous species [38], and removed 4 species absent from the tree. We removed UT_{max} data from 189 species (following [35]), leaving data for 628 species.

(b) Climatic data

Climatic data for each species are given in electronic supplementary material, table S2. We used three climatic variables: annual mean temperature (Bio1), maximum annual temperature (Bio5) and minimum annual temperature (Bio6). Most climatic data were from past studies of squamates [39], birds [40] and mammals [41]. These studies used the WorldClim dataset [42], using mean values across grid cells from range maps for each species and variable. For amphibians, we obtained range maps from IUCN [43] then used QGIS [44] to extract mean values from grid cells (from [42]) at 30″ spatial resolution.

There were also 313 squamate species, 130 birds and 36 mammals that lacked data in these datasets. We obtained distribution maps for birds [36], and obtained climatic data as described above (except for two, deleted Antarctic species, *Aptenodytes forsteri* and *A. patagonicus*). We obtained georeferenced locality data for squamate and mammal species from GBIF.org. We confirmed that sampled localities spanned each species' range and were not outside it (using [31,43]). We calculated mean climatic values across localities using QGIS and the WorldClim dataset. However, seven squamates had less than five georeferenced localities and were deleted.

(c) Phylogenies

The tree with maximum taxon sampling for each group is given in electronic supplementary material, datafiles S1–S4. We used Mesquite 3.04 [45] to prune trees to include only species with relevant data for each analysis. For birds, we used the consensus tree (containing all species) from the posterior distribution of 10 000 trees (from [19]; backbone tree from [46]).

We chose phylogenies that were time-calibrated (necessary for estimating rates) and had extensive species sampling. For some groups, phylogenies with less taxon sampling but better gene sampling suggest some alternative higher-level relationships (e.g. [47,48]). However, rate estimates should depend more on relationships and divergence times among closely related species, not higher-level relationships.

We also performed analyses using an alternative phylogeny for each group. These alternative trees (electronic supplementary material, Datafiles S5–S8) and results are described in electronic supplementary material, appendix S1. We also provide further justification there for the choice of trees used in the main analyses.

(d) Data analyses

For each group, we separately compared evolutionary rates in physiological tolerances to heat (CT_{max}/UT_{max}) and cold (CT_{min}/UT_{min}), body temperatures (T_b/T_a), and climatic-niche variables associated with extreme heat (Bio5) and cold (Bio6). We compared maximum-likelihood estimates of evolutionary rates (σ^2) from the Brownian motion model [14]. For each pair of variables for each group, we performed a likelihood-ratio test (LRT) comparing the likelihood for the different, observed rates for each variable and a model with constrained rates (equal between variables). Tests were performed using R code [14] in R 3.3.0 [49]. Rate comparisons were only made when comparing identical sets of species (i.e. with data for both variables).

We used phylogenetic generalized least-squares regression (PGLS; [21]) to test relationships between physiological and climatic variables. PGLS was performed in R using *caper* v.1.0.1 [50]. We used phylogenetic paired *t*-tests to evaluate whether climatic-niche variables (Bio5/Bio6) were significantly outside the range of physiological variables (CT_{max}/CT_{min}, UT_{max}/UT_{min}), using the R package *phytools* v.0.6–60 [51]. We applied a sequential Bonferroni correction [52,53] to tables of results with *p*-values.

Following most authors, we use 'niche evolution' to describe rate estimates for climatic-niche variables. However, we recognize that changes in the realized climatic niche among species can also reflect non-evolutionary processes, such as plasticity, extrinsic biotic factors and non-climatic abiotic factors.

(e) Methodological caveats

Here, we address several potential concerns about the data and methods used in our study. In general, there are many sources of error, but we were still able to find significant results in most groups. Furthermore, many limitations here are shared with earlier studies.

First, our taxon sampling is limited within each group, since relatively few species have physiological data. Nevertheless, our sampling is generally improved over previous studies. The least data were available for comparing CT_{min}/UT_{min} to CT_{max}/UT_{max}. Araújo *et al*. [9] had data for 26 amphibians, whereas we have 30. We also have more squamates (135/147) and birds (70/75). We have fewer mammals (133/321), but many mammalian data in previous studies [9] were problematic [35]. Our data for each group contains a mixture of closely related and distantly related species.

Second, incomplete sampling might bias rate estimates. However, our rate comparisons are only between sets of species with identical taxon sampling, and so this cannot bias these comparisons. More broadly, incomplete sampling does not appear to bias rate estimates [16,54]. Furthermore, limited sampling did not generally prevent us from finding significant patterns.

Third, incomplete sampling might influence PGLS analyses. However, simulations show that limited sampling (6% of species) does not bias phylogeny-based correlations [55] and has no impact on type-1 error rates (false positives). Limited sampling does reduce power [55], but we often obtained significant PGLS results.

Fourth, we only included climatic data for species with physiological data. Nevertheless, we included more than 600 species for these comparisons for most groups (but 182 for amphibians), and obtained some significant results for all groups. Our climatic datasets were broadly similar to our physiological datasets.

Fifth, there are potential geographical mismatches between physiological and climatic data. Physiological data were generally from few localities per species, whereas climatic data were from across the species's range. Furthermore, even for a single species, data from different physiological variables were sometimes from different localities. Thus, some mismatch between variables might be caused by mismatched variation across localities. This should be a source of random error, rather than bias. Nevertheless, we performed a set of analyses using only climatic data from populations from which physiological data were obtained (electronic supplementary material, table S5; details in electronic supplementary material, appendix S2). The results were similar to the main analyses, and did not show dramatically stronger physiology–climate relationships.

Sixth, we used a single model and rate estimate for each variable in each tree. Different models and rates might apply to different parts of each tree within each group (e.g. [39]). However, the approach we used [14] should be the most practical for comparing overall rates across large-scale trees for each group.

Seventh, our physiological data came from many sources. There may be some differences in how physiological variables were measured among studies. Previous authors combined data from the same sources used here (e.g. [9,27]). However, we removed problematic UT_{max} data for many birds and mammals used in earlier studies (following [35]). We also removed some problematic squamate data (see above). We still have concerns about the CT_{max}/CT_{min} data for amphibians, in terms of quality and taxon sampling. The amphibian results should, therefore, be taken with some caution.

Table 1. Comparison of evolutionary rates among physiological and climatic-niche variables. Physiological variables include body temperatures (T_b/T_a for ectotherms/endotherms), lower thermal tolerances (CT_{min}/UT_{min}) and upper thermal tolerances (CT_{max}/UT_{max}). Climatic variables include maximum annual temperatures (Bio5) and minimum annual temperatures (Bio6). Sample size (*n*) is the number of species included, and varies because only species with data for both variables were compared. Rates are not identical for the same variable in the same group when different numbers of species are included. Significant *p*-values ($p < 0.05$) are boldfaced. A sequential Bonferroni correction does not impact which results are considered significant in this table.

group	comparison	*n*	σ^2	$LRT_{d.f.} = 1$	*p*
amphibians	CT_{min} versus CT_{max}	30	0.38 versus 0.29	0.58	0.4476
	Bio5 versus Bio6	182	1.69 versus 1.51	0.61	0.4354
	CT_{min} versus Bio6	43	0.32 versus 1.94	27.37	**<0.0001**
	CT_{max} versus Bio5	96	0.24 versus 2.90	122.97	**<0.0001**
	T_b versus CT_{max}	10	0.61 versus 0.07	9.69	**0.0019**
squamates	CT_{min} versus CT_{max}	147	0.29 versus 0.15	16.42	**<0.0001**
	Bio5 versus Bio6	613	0.66 versus 1.26	62.72	**<0.0001**
	CT_{min} versus Bio6	177	0.40 versus 1.71	85.43	**<0.0001**
	CT_{max} versus Bio5	258	0.17 versus 0.72	123.39	**<0.0001**
	T_b versus CT_{min}	124	0.29 versus 0.40	2.92	0.0874
	T_b versus CT_{max}	173	0.28 versus 0.16	13.23	**0.0003**
birds	UT_{min} versus UT_{max}	75	2.65 versus 0.74	28.80	**<0.0001**
	Bio5 versus Bio6	636	3.96 versus 25.09	479.01	**<0.0001**
	UT_{min} versus Bio6	207	5.10 versus 8.48	13.27	**0.0003**
	UT_{max} versus Bio5	78	0.72 versus 3.91	50.04	**<0.0001**
	T_a versus UT_{min}	47	0.05 versus 2.61	120.64	**<0.0001**
	T_a versus UT_{max}	27	0.02 versus 0.25	35.88	**<0.0001**
mammals	UT_{min} versus UT_{max}	133	0.92 versus 0.49	12.89	**0.0003**
	Bio5 versus Bio6	628	3.82 versus 26.42	513.07	**<0.0001**
	UT_{min} versus Bio6	364	2.20 versus 6.18	93.13	**<0.0001**
	UT_{max} versus Bio5	134	0.49 versus 0.75	6.11	**0.0135**
	T_a versus UT_{min}	307	0.08 versus 2.18	620.38	**<0.0001**
	T_a versus UT_{max}	114	0.05 versus 0.43	106.69	**<0.0001**

Finally, we did not correct for potentially suboptimal acclimation temperatures on CT_{max} and CT_{min} measurements. However, analyses that did found very limited impact on CT_{max} and no impact on overall results for both variables [27].

3. Results

Physiological and climatic data are summarized in electronic supplementary material, table S3. The analyses (table 1) show that physiological tolerances to high temperatures evolve more slowly than tolerances to low temperatures. Rates (σ^2) for CT_{min}/UT_{min} are faster than for CT_{max}/UT_{max} in all groups (figure 1*a*). However, the difference in amphibians was not significant, and the sample size was limited ($n = 30$).

Our results (figure 1*b*; table 1) also show that the hottest temperatures in species' realized climatic niches change significantly more slowly than the coldest temperatures, except in amphibians. In amphibians, hottest temperatures change faster, but the difference is not significant.

Our results show mixed support for the idea that physiological evolution constrains climatic-niche evolution. Physiological tolerances to extreme temperatures do evolve more slowly than extreme climatic-niche temperatures (table 1): CT_{max}/UT_{max} evolve significantly more slowly than maximum temperatures in all groups (figure 1*c*), and CT_{min}/UT_{min} evolve significantly more slowly than minimum temperatures (figure 1*d*).

Furthermore, there are significant, positive relationships between physiological tolerances and extreme niche temperatures (table 2; figure 2). This includes both high temperatures (CT_{max}/UT_{max} versus maximum temperature: amphibians: $r^2 = 0.09$; squamates: $r^2 = 0.02$; birds: $r^2 = 0.21$; mammals: $r^2 = 0.11$) and low temperatures (CT_{min}/UT_{min} versus minimum temperature: amphibians: $r^2 = 0.53$; squamates: $r^2 = 0.09$; birds: $r^2 = 0.12$; mammals: $r^2 = 0.07$). We did not find a strong negative relationship between CT_{max} and maximum temperatures in squamates (as in [9]). Nevertheless, despite being positive and significant, many relationships had low r^2. Intriguingly, there are strong relationships between UT_{max} and UT_{min} in both birds and mammals, but not between CT_{max} and CT_{min} in squamates or amphibians (table 2).

On the other hand, species climatic distributions were not necessarily constrained by these physiological variables. In all four groups, species sometimes have higher values of maximum annual temperatures than CT_{max}/UT_{max} (amphibians = 6/96 species; squamates = 2/258; birds = 7/78;

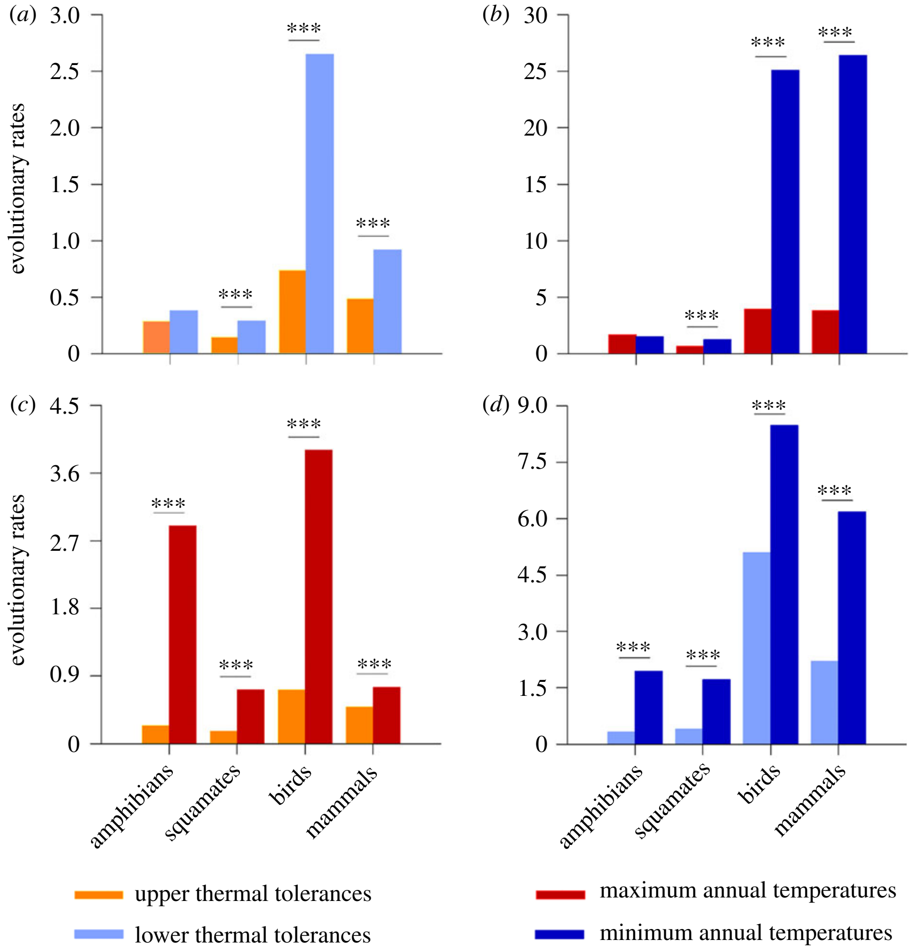

Figure 1. Comparisons of estimated evolutionary rates (σ^2) among physiological and climatic variables. (*a*) upper thermal tolerances (CT_{max}/UT_{max}) versus lower thermal tolerances (CT_{min}/UT_{min}), (*b*) maximum temperatures (Bio5) versus minimum temperatures (Bio6), (*c*) upper thermal tolerances versus maximum temperatures and (*d*) lower thermal tolerances versus minimum temperatures. Triple asterisks indicate significantly different rates (table 1). Rates can differ when different numbers of species are included. (Online version in colour.)

mammals = 35/134). Nevertheless, species have (overall) significantly higher values of CT_{max}/UT_{max} than maximum temperatures in all groups but amphibians, based on phylogenetic *t*-tests (electronic supplementary material, table S4). Species often have lower values for minimum temperatures than their CT_{min}/UT_{min} (amphibians = 16/43; squamates = 127/177; birds = 192/207; mammals = 354/364). Minimum temperatures were significantly lower than CT_{min}/UT_{min} in birds, but not in amphibians, squamates or mammals (electronic supplementary material, table S4).

Body temperatures (T_b/T_a) evolved more slowly than CT_{min}/UT_{min} in all groups (except in amphibians, with too few species: table 1). By contrast, T_b evolved significantly more quickly than CT_{max} in amphibians and squamates, whereas T_a evolved significantly more slowly than UT_{max} in birds and mammals. We found (table 2) that T_b was not significantly related to CT_{max} or CT_{min}, or with only weak relationships ($r^2 < 0.05$), except for T_b and CT_{max} in squamates ($r^2 = 0.15$; see also [10]). In amphibians, T_b was positively related to climatic variables (table 2). But for other groups, relationships were also generally weak and/or non-significant between T_b/T_a and climatic variables (table 2). In summary, these patterns support the idea that body temperatures change slowly (slower than physiological tolerances or intermediate between them), and are generally only weakly related to climate (except in amphibians). For brevity, we do not address these patterns further in the Discussion.

Overall, similar results were obtained using alternative trees (electronic supplementary material, appendix S1). These analyses confirmed that physiological tolerances to high temperatures evolve significantly more slowly than those to low temperatures in all four groups (even in amphibians, unlike the main analyses), and the hottest climatic-niche temperatures change more slowly than coldest temperatures. Physiological tolerances to extreme temperatures evolve more slowly than extreme climatic-niche temperatures (but not significantly for maximum temperatures in mammals). There were significant, positive relationships between physiological tolerances and extreme niche temperatures in all four groups. Other results were also broadly similar.

We also tested relationships between extreme physiological and climatic variables when data were obtained from the same localities, focusing on ectotherms (electronic supplementary material, appendix S2). These analyses confirmed that (i) extreme climatic-niche variables evolve faster than their corresponding physiological tolerances, (ii) CT_{min} and coldest temperatures are significantly related, (iii) species rarely occur where hottest temperatures are hotter than their CT_{max}, but often occur where coldest temperatures are lower than their CT_{min}. A notable difference is that CT_{max} and maximum temperatures were not significantly related in this dataset, in squamates or amphibians. Thus, weak relationships between physiological and climatic variables in the main analyses are not necessarily caused by a mismatch between localities for

Table 2. Relationships between pairs of climatic and physiological variables, based on phylogenetic regression (PGLS). Variables as in table 1. We did not include a relationship between T_b and $\mathrm{CT}_{\mathrm{min}}$ for amphibians because only two species had data for both variables. Significant associations ($p < 0.05$) are boldfaced, but p-values not significant after sequential Bonferroni correction are asterisked.

models	*n*	slope	r^2	*p*
amphibians				
$\mathrm{CT}_{\mathrm{max}} \sim \mathrm{Bio5}$	96	0.25	0.09	**0.0025**
$\mathrm{CT}_{\mathrm{min}} \sim \mathrm{Bio6}$	43	0.25	0.53	**<0.0001**
$\mathrm{CT}_{\mathrm{max}} \sim \mathrm{CT}_{\mathrm{min}}$	30	0.04	<0.01	0.7143
$T_b \sim \mathrm{CT}_{\mathrm{max}}$	10	−0.03	<0.01	0.9679
$T_b \sim \mathrm{Bio1}$	83	0.54	0.25	**<0.0001**
$T_b \sim \mathrm{Bio5}$	83	0.43	0.16	**0.0002**
$T_b \sim \mathrm{Bio6}$	83	0.30	0.14	**0.0005**
squamates				
$\mathrm{CT}_{\mathrm{max}} \sim \mathrm{Bio5}$	258	0.07	0.02	**0.0181***
$\mathrm{CT}_{\mathrm{min}} \sim \mathrm{Bio6}$	177	0.15	0.09	**<0.0001**
$\mathrm{CT}_{\mathrm{max}} \sim \mathrm{CT}_{\mathrm{min}}$	147	0.04	<0.01	0.4126
$T_b \sim \mathrm{CT}_{\mathrm{max}}$	173	0.52	0.15	**<0.0001**
$T_b \sim \mathrm{CT}_{\mathrm{min}}$	124	0.11	0.02	0.1641
$T_b \sim \mathrm{Bio1}$	518	0.12	0.03	**0.0001**
$T_b \sim \mathrm{Bio5}$	518	0.23	0.09	**<0.0001**
$T_b \sim \mathrm{Bio6}$	518	0.02	<0.01	0.3028
birds				
$\mathrm{UT}_{\mathrm{max}} \sim \mathrm{Bio5}$	78	0.33	0.21	**<0.0001**
$\mathrm{UT}_{\mathrm{min}} \sim \mathrm{Bio6}$	207	0.23	0.12	**<0.0001**
$\mathrm{UT}_{\mathrm{max}} \sim \mathrm{UT}_{\mathrm{min}}$	75	0.39	0.43	**<0.0001**
$T_a \sim \mathrm{Bio1}$	474	<0.01	<0.01	0.4781
$T_a \sim \mathrm{Bio5}$	474	0.01	<0.01	0.3111
$T_a \sim \mathrm{Bio6}$	474	<0.01	<0.01	0.7508
$T_a \sim \mathrm{UT}_{\mathrm{max}}$	27	0.02	0.01	0.6808
$T_a \sim \mathrm{UT}_{\mathrm{min}}$	47	<0.01	<0.01	0.9043
mammals				
$\mathrm{UT}_{\mathrm{max}} \sim \mathrm{Bio5}$	134	0.27	0.11	**<0.0001**
$\mathrm{UT}_{\mathrm{min}} \sim \mathrm{Bio6}$	364	0.15	0.07	**<0.0001**
$\mathrm{UT}_{\mathrm{max}} \sim \mathrm{UT}_{\mathrm{min}}$	133	0.44	0.52	**<0.0001**
$T_a \sim \mathrm{Bio1}$	571	−0.03	0.02	**0.0004**
$T_a \sim \mathrm{Bio5}$	571	−0.03	<0.01	**0.0244***
$T_a \sim \mathrm{Bio6}$	571	−0.02	0.03	**0.0001**
$T_a \sim \mathrm{UT}_{\mathrm{max}}$	114	0.04	0.01	0.1985
$T_a \sim \mathrm{UT}_{\mathrm{min}}$	307	<0.01	<0.01	0.8851

climatic and physiological data, since relationships can be weak when these data are matched.

4. Discussion

The relationships between physiological tolerances, climatic niches and evolution are of urgent importance as global warming potentially threatens much of global biodiversity. Here, we broadly test several hypotheses about rates of physiological and climatic-niche evolution. We find that rates of physiological evolution for upper thermal tolerances are slower than for lower thermal tolerances (figure 1*a*). We show that rates of change in maximum temperatures in the realized climatic niche are significantly slower than rates for minimum temperatures, and that rates of physiological evolution are slower than rates of climatic-niche evolution for these variables (figure 1*b–d*). We also show that physiological tolerances to high and low temperatures are significantly, positively related to both maximum and minimum temperatures (respectively) in the realized climatic niche (figure 2). By contrast, Araújo *et al.* [9] stated that tolerances to higher temperatures tend not to covary with maximum temperatures. However, we found that these relationships are often weak, and climatic-niche values are often outside the bounds of these physiological variables. Below, we address the potential causes of these patterns. We also address the idea that mismatches between physiological and climatic-niche values mean that climatic-niche data are misleading.

(a) Why are rates lower for higher temperatures?

Our results show that physiological tolerances to higher temperatures change more slowly than tolerances to lower temperatures, and that rates of niche change are slower for hottest temperatures than coldest temperatures. What might explain these patterns?

One potential explanation is that there are asymmetric constraints on rates of physiological evolution, and that physiological tolerances then limit the corresponding rates of climatic-niche evolution. Thus, there may be less change in maximum niche temperatures among species because the limited evolution of physiological tolerances to high temperatures constrains such shifts, whereas rapid evolution of physiological tolerances to cold allows species to adapt to environments with very different minimum temperatures. This is a particularly important hypothesis, because it implies that the limited rate of evolution of physiological tolerances to high temperatures will make species especially vulnerable to anthropogenic warming [9]. However, this hypothesis also raises the question of what explains the asymmetry in rates of physiological evolution. Araújo *et al.* [9] suggested that shared tolerances to high temperatures reflect negative impacts of high temperatures on membranes and proteins [56], whereas variation in lower thermal tolerances reflects different thermodynamic effects on reaction rates, especially those associated with ion homeostasis. They suggested that the former impacts may be more conserved.

Surprisingly, the hypothesis that these physiological variables explain variation in climatic niches has only mixed support in our results. We found lower evolutionary rates in physiological variables than in their corresponding climatic variables. We also found that relationships between climatic and physiological variables were positive and significant, but often weak (most $r^2 < 0.20$; table 2). More importantly, species often occur where minimum temperatures are lower than their lower physiological tolerances ($\mathrm{CT}_{\mathrm{min}}/\mathrm{UT}_{\mathrm{min}}$). This pattern implies that this physiological variable does not determine where species occur. By contrast, species often occur where maximum annual temperatures are below their upper physiological tolerances ($\mathrm{CT}_{\mathrm{max}}/\mathrm{UT}_{\mathrm{max}}$).

Why are these physiological variables uncoupled from these estimates of large-scale climate? For $\mathrm{CT}_{\mathrm{min}}$, many

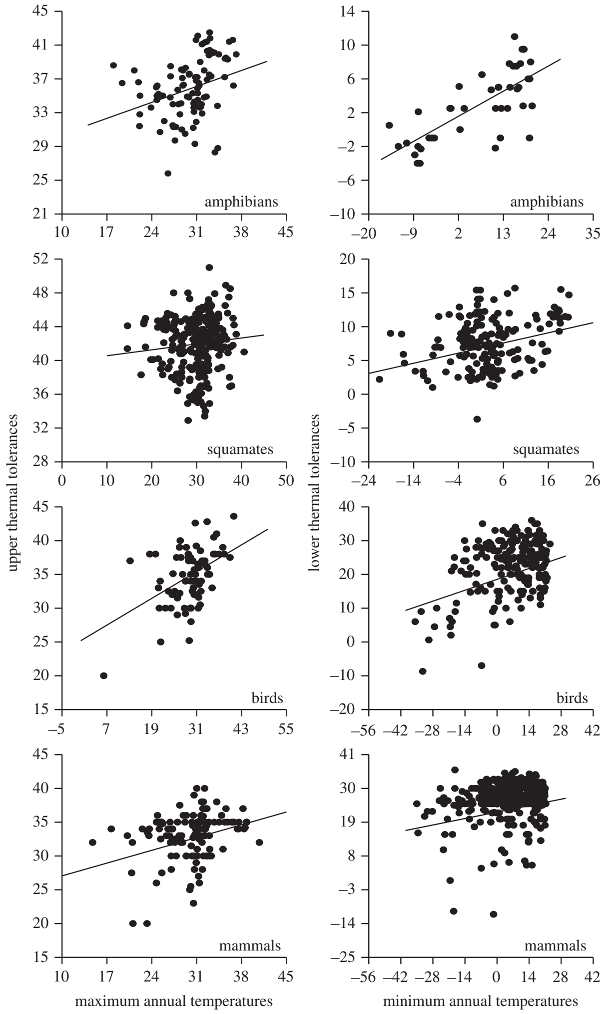

Figure 2. Relationships between physiological and climatic variables, including upper thermal tolerances (CT_{max}/UT_{max}) versus maximum annual temperatures (Bio5), and lower thermal tolerances (CT_{min}/UT_{min}) versus minimum annual temperatures (Bio6). For clarity, results are from the least-squares regression for raw data (PGLS results in table 2).

species of ectotherms may simply be inactive during cold weather. Thus, if the coldest temperatures are too low for locomotion, it may have few consequences. Similarly, species can occur in hotter climates than suggested by their CT_{max} by being active at cooler temperatures (e.g. at night or during rainy weather in amphibians). More generally, behavioural thermoregulation (e.g. occurring in cooler microclimates during hot weather) may allow species to occur in climatic conditions that differ from the range of values suggested by these physiological variables (e.g. [7,57]). Seasonal migration might also help explain these patterns in birds, especially for UT_{min} in birds (e.g. bird species that winter in the tropics can avoid cold winter temperatures).

Our results also imply an alternative (but non-exclusive) hypothesis to explain the low rates of physiological and niche evolution for maximum temperatures. Based on electronic supplementary material, table S3, the range of values among species for minimum niche temperatures is almost twice as large as for maximum temperatures, for all four groups (ranges for maximum temperatures = 25–32; ranges for minimum temperatures = 46–61). Thus, minimum temperatures may decrease strongly from the equator to the poles, but maximum temperatures can overlap broadly between temperate and tropical regions (e.g. [58,59]). Therefore, an alternative explanation for slower rates of physiological and niche evolution for high temperatures is that maximum temperatures are less variable across the globe than minimum temperatures. Indeed, previous studies have shown how (at least in lizards) CT_{min} changes strongly across latitudes whereas CT_{max} does not [57,60].

We acknowledge the potential 'chicken and egg' problem in discriminating between these two hypotheses, however. In other words, is there limited change in maximum temperatures among species because of limited evolution in physiological tolerances (constraining where a species can occur), or is there limited change in physiological tolerances to high temperatures because of limited variation in maximum temperatures across the globe? It is possible that both factors contribute to the lower rates for upper temperatures for the physiological and climatic variables, and that the importance of each factor varies among species. Intriguingly, estimates of σ^2 in squamates and mammals [61] suggest that species' maximum latitudes (i.e. in cooler climates) change more rapidly among species than their minimum latitudes (i.e. in warmer climates), showing how rates of change in distributions parallel the relevant rates in physiological variables.

A third, non-exclusive hypothesis is that many ectotherms use behavioural thermoregulation to avoid high temperatures, which helps constrain the evolution of CT_{max} across different environments (e.g. [13,15]). Thus, species may behaviourally avoid the highest temperatures rather than adapting to them physiologically. Conversely, behavioural thermoregulation may be less likely at lower temperatures, when individuals are inactive and unable to move (e.g. sleeping or seasonally inactive). Although this hypothesis is appealing, one might also argue that species in different environments could (in theory) avoid physiological evolution for different lower thermal tolerances by only being active at similar temperatures, the same as for upper temperatures. Overall, our results show a strong difference between rates of evolution for upper and lower temperature variables for both physiological tolerances and climatic niches, but the causes of these differences will require further study to elucidate.

(b) Do mismatches between climatic niches and physiological tolerances mean that climatic-niche data are 'misleading'?

Our results show relatively weak relationships between physiological variables and maximum and minimum climatic-niche temperatures (table 2; figure 2). Araújo *et al.* [9] suggested that conservatism in physiological tolerances to high temperatures would lead to mismatches between realized and fundamental niches. They also suggested that in studies of niche evolution 'if the currency of interest is rates of change in physiological aspects of the niche' then mismatches between physiology and climate would lead to 'erroneous conclusions' about niche conservatism and evolution based on climatic-niche data, including overestimating rates of niche evolution.

We think that many researchers analyse climatic-niche data not to estimate rates of physiological evolution, but rather to understand the causes and consequences of species distributions over space and time. Thus, researchers analyse climatic-niche data to address topics such as species responses to climate change (e.g. [5,62,63]), speciation (e.g. [64,65]), large-scale diversification patterns among clades (e.g. [40,41]), biogeography and species richness (e.g. [66,67]) and the distributions of introduced species (e.g. [68,69]). Physiological data might also be very relevant to explaining these distribution patterns, but understanding physiological evolution is not the primary goal.

Rather than necessarily indicating that climatic-niche data are wrong, mismatches between physiology and climatic distributions might instead indicate that some physiological variables do not necessarily determine species' climatic and geographical distributions. For example, our results show that many species occur where winters are colder than their CT_{min}, but it would be nonsensical to suggest that these climatic data were, therefore, misleading because of this mismatch with the physiological data.

We follow the idea here that the realized climatic niche is the set of climatic conditions where a species occurs (potentially determined by physiological tolerances, species interactions and other factors), whereas the fundamental climatic niche is the set of conditions where the species can occur given constraints of physiology alone [70]. Araújo *et al.* [9] implicitly treated species values of CT_{max} and CT_{min} as the species' fundamental climatic niche. However, CT_{max} and CT_{min} simply reflect the temperatures at which species can be active (or active without metabolic cost, for UT_{max}/UT_{min}). Importantly, these physiological variables may sometimes be more relevant to *when* species are active (daily and seasonally) and exactly where (e.g. microhabitat, sun versus shade [57,71]) rather than to large-scale climatic distributions and climate change.

In summary, mismatches between physiological and climatic-niche data do not necessarily mean that the physiological data are correct and climatic-niche data are misleading. Our results imply that these physiological variables may not reflect the large-scale climatic conditions where species can occur. This seems problematic for studies of species responses to climate change. Indeed, some studies suggest that recent climate-related species declines and extinctions may often be associated with changes in species interactions, not physiological tolerances (e.g. [72,73]). Thus, predicting species responses to climate change based on physiology alone might be problematic. Furthermore, many analyses of climate change that use physiological data incorporate additional factors, such as microclimate, behavioural thermoregulation, impacts of temperatures on activity schedules and acclimation (e.g. [3,27,60,74]). There are also alternative physiological measurements that may be even more relevant to species activity patterns and climatic distributions than CT_{max}/UT_{max} and CT_{min}/UT_{min}, such as voluntary thermal maxima (e.g. [75]). In theory, lethal thermal limits might predict species climatic distributions better than CT_{max}/UT_{max} and CT_{min}/UT_{min}, but this seems unlikely for upper limits (since most ectotherms occur at temperatures below CT_{max}, based on our results).

(c) Implications of evolutionary rates for climate change

Our results show that physiological tolerances to heat evolve relatively slowly, whereas maximum niche temperatures change more quickly. How do these rates compare to rates of climate change? Our rate estimates here do not have a straightforward interpretation in terms of units. However, analyses using alternative methods (with rates in °C per year) show that past rates of realized-niche change are much slower than rates of projected climate change, often by approximately 100 000-fold or more (tetrapods [76]; plants and animals [16,54]). Our results here show that physiological tolerances evolve more slowly than these realized climatic-niche variables. Thus, both physiological and niche rates seem too slow to keep pace with rapid, projected climate change. However, in contrast to these results, analyses of introduced vertebrate populations show that very rapid climatic-niche shifts are possible, much faster than projected rates of climate change [77]. These include shifts into regions with much hotter maximum temperatures than the native distributions. It seems unlikely that these maximum-temperature shifts generally occurred through rapid physiological evolution, since most occurred as species were introduced ('instantaneous' niche shifts). Further, analyses of recent responses to climate change suggest that rapid niche shifts in maximum annual temperatures may be crucial to the survival of plant and animal populations and species [5], but the mechanisms underlying these shifts remain unclear. Overall, we caution that neither realized climatic-niche data nor physiological data alone may fully predict how species respond to climate change. Slow rates of evolution for physiological tolerances to heat and maximum climatic temperatures may both be important, but are only two among many relevant factors.

(d) Summary

Here, we show that physiological tolerances to heat evolve more slowly than those to cold, that hottest temperatures in the climatic-niche evolve more slowly than coldest temperatures, and that physiological tolerances evolve more slowly than their corresponding climatic-niche variables. We also show significant positive relationships between physiological and climatic-niche variables, but these relationships are generally weak, and species can occur in climates outside those implied by these physiological variables. Therefore, we caution against equating species-level data for these physiological variables with the fundamental climatic niche, and using mismatches between climatic and physiological data to argue that climatic-niche data are misleading.

Data accessibility. All data are available as electronic supplementary material and from the Dryad Digital Repository: https://dx.doi.org/10.5061/dryad.m63xsj3zv [78].

Authors' contributions. Y.-F.Q. and J.J.W. designed the study and wrote the paper. Y.-F.Q. performed the analyses.

Competing interests. We have no competing interests to declare.

Funding. Y.-F.Q. was funded by the National Natural Science Foundation of China (grant nos 31670422 and 31770443), the Natural Science Foundation of Jiangsu Province (grant no. BK20161556) and the Priority Academic Program Development (PAPD) of Jiangsu Higher Education Institutions. J.J.W. was supported by the U.S. National Science Foundation grant no. DEB 1655690.

Acknowledgements. We thank the authors of previous studies for making their data available, and anonymous reviewers for valuable comments on the manuscript.

References

1. Holt RD. 1990 The microevolutionary consequences of climate change. *Trends Ecol. Evol.* **5**, 311–315. (doi:10.1016/0169-5347(90)90088-U)
2. Visser ME. 2008 Keeping up with a warming world: assessing the rate of adaptation to climate change. *Proc. R. Soc. B* **275**, 649–659. (doi:10.1098/rspb.2007.0997)
3. Sinervo B *et al*. 2010 Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**, 894–899. (doi:10.1126/science.1184695)
4. Hoffmann AA, Sgro CM. 2011 Climate change and evolutionary adaptation. *Nature* **470**, 479–485. (doi:10.1038/nature09670)
5. Román-Palacios C, Wiens JJ. 2020 Recent responses to climate change reveal the drivers of species extinction and survival. *Proc. Natl Acad. Sci. USA* **117**, 4211–4217. (doi:10.1073/pnas.1913007117)
6. Gienapp P, Teplitsky C, Alho JS, Mills JA, Merilä J. 2008 Climate change and evolution: disentangling environmental and genetic responses. *Mol. Ecol.* **17**, 167–178. (doi:10.1111/j.1365-294X.2007.03413.x)
7. Kearney M, Shine R, Porter WP. 2009 The potential for behavioral thermoregulation to buffer 'coldblooded' animals against climate warming. *Proc. Natl Acad. Sci. USA* **106**, 3835–3840. (doi:10.1073/pnas.0808913106)
8. Somero GN. 2010 The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *J. Exp. Biol.* **213**, 912–920. (doi:10.1242/jeb.037473)
9. Araújo MB, Ferri-Yanez F, Bozinovic F, Marquet PA, Valladares F, Chown SL. 2013 Heat freezes niche evolution. *Ecol. Lett.* **16**, 1206–1219. (doi:10.1111/ele.12155)
10. Grigg JW, Buckley LB. 2013 Conservatism of lizard thermal tolerances and body temperatures across evolutionary history and geography. *Biol. Lett.* **9**, 20121056. (doi:10.1098/rsbl.2012.1056)
11. Revell LJ, Harmon LJ, Collar DC. 2008 Phylogenetic signal, evolutionary process, and rate. *Syst. Biol.* **57**, 591–601. (doi:10.1080/10635150802302427)
12. Hoffmann AA, Chown SL, Clusella-Trullas S. 2013 Upper thermal limits in terrestrial ectotherms: how constrained are they? *Funct. Ecol.* **27**, 934–949. (doi:10.1111/j.1365-2435.2012.02036.x)
13. Muñoz MM *et al*. 2014 Evolutionary stasis and lability in thermal physiology in a group of tropical lizards. *Proc. R. Soc. B* **281**, 20132433. (doi:10.1098/rspb.2013.2433)
14. Adams DC. 2013 Comparing evolutionary rates for different phenotypic traits on a phylogeny using likelihood. *Syst. Biol.* **62**, 181–192. (doi:10.1093/sysbio/sys083)
15. Huey RB, Hertz PE, Sinervo B. 2003 Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am. Nat.* **161**, 357–366. (doi:10.1086/346135)
16. Liu H, Ye Q, Wiens JJ. 2020 Climatic niche evolution follows similar rules in plants and animals. *Nat. Ecol. Evol.* **4**, 753–763. (doi:10.1038/s41559-020-1158-x)
17. Pyron RA, Wiens JJ. 2013 Large-scale phylogenetic analyses reveal the causes of high tropical amphibian diversity. *Proc. R. Soc. B* **280**, 20131622. (doi:10.1098/rspb.2013.1622)
18. Zheng Y, Wiens JJ. 2016 Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4,162 species. *Mol. Phylogenet. Evol.* **94**, 537–547. (doi:10.1016/j.ympev.2015.10.009)
19. Jetz W, Thomas GH, Joy J, Hartmann K, Mooers AO. 2012 The global diversity of birds in space and time. *Nature* **491**, 444–448. (doi:10.1038/nature11631)
20. Rolland J, Condamine FL, Jiguet F, Morlon H. 2014 Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biol.* **12**, e1001775. (doi:10.1371/journal.pbio.1001775)
21. Martins EP, Hansen TF. 1997 Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *Am. Nat.* **149**, 646–667. (doi:10.1086/286013)
22. Camacho A, Rusch TW. 2017 Methods and pitfalls of measuring thermal preference and tolerance in lizards. *J. Therm. Biol.* **68**, 63–72. (doi:10.1016/j.jtherbio.2017.03.010)
23. Lutterschmidt WI, Hutchison VH. 1997 The critical thermal maximum: history and critique. *Can. J. Zool.* **75**, 1561–1574. (doi:10.1139/z97-783)
24. Qu YF, Li H, Gao JF, Xu XF, Ji X. 2011 Thermal preference, thermal tolerance and the thermal dependence of digestive performance in two *Phrynocephalus* lizards (Agamidae), with a review of species studied. *Curr. Zool.* **57**, 684–700. (doi:10.1093/czoolo/57.6.684)
25. Khaliq I, Hof C, Prinzinger R, Böhning-Gaese K, Pfenninger M. 2014 Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proc. R. Soc. B* **281**, 20141097. (doi:10.1098/rspb.2014.1097)
26. Feder ME, Lynch JF, Shaffer HB, Wake DB. 1982 Field body temperatures of tropical and temperate zone salamanders. *Smithson. Herpetol. Inf. Serv.* **52**, 1–23. (doi:10.5479/si.23317515.52.1)
27. Sunday JM *et al*. 2014 Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc. Natl Acad. Sci. USA* **111**, 5610–5615. (doi:10.1073/pnas.1316145111)
28. Bennett JM *et al*. 2018 GlobTherm, a global database on thermal tolerances for aquatic and terrestrial organisms. *Sci. Dat.* **5**, 180022. (doi:10.1038/sdata.2018.22)
29. University of California. 2019 AmphibiaWeb. See https://amphibiaweb.org. Accessed on 19 March 2019.
30. Brattstrom BH. 1965 Body temperatures of reptiles. *Am. Mid. Nat.* **73**, 376–422. (doi:10.2307/2423461)
31. Uetz P, Freed P, Hošek J. (eds) 2018 The reptile database, version 2018.10. See http://www.reptile-database.org. Accessed on 21 March 2019.
32. Ruby DE. 1977 Winter activity in Yarrow's spiny lizard, *Sceloporus jarrovi*. *Herpetologica* **33**, 322–332.
33. McNab BK. 1966 An analysis of the body temperatures of birds. *Condor* **68**, 47–55. (doi:10.2307/1365174)
34. Clarke A, Rothery P. 2008 Scaling of body temperature in mammals and birds. *Funct. Ecol.* **22**, 58–67.
35. Wolf BO, Coe BH, Gerson AR, McKechnie AE. 2017 Comment on an analysis of endotherm thermal tolerances: systematic errors in data compilation undermine its credibility. *Proc. R. Soc. B* **284**, 20162523. (doi:10.1098/rspb.2016.2523)
36. BirdLife International. 2017 Bird species distribution maps of the world. Version 2017.2. See http://datazone.birdlife.org/species/requestdis. (Accessed on 1 September 2018)
37. Clarke A, Rothery P, Isaac NJB. 2010 Scaling of metabolic rate with body mass and temperature in mammals. *J. Anim. Ecol.* **79**, 610–619. (doi:10.1111/j.1365-2656.2010.01672.x)
38. Burgin CJ, Colella JP, Kahn PL, Upham NS. 2018 How many species of mammals are there? *J. Mammal.* **99**, 1–11. (doi:10.1093/jmammal/gyx147)
39. Pie MR, Campos LLF, Meyer ALS, Duran V. 2017 The evolution of climatic niches in squamate reptiles. *Proc. R. Soc. B* **284**, 20170268. (doi:10.1098/rspb.2017.0268)
40. Cooney CR, Seddon N, Tobias JA. 2016 Widespread correlations between climatic niche evolution and species diversification in birds. *J. Anim. Ecol.* **85**, 869–878. (doi:10.1111/1365-2656.12530)
41. Castro-Insua A, Gómez-Rodríguez C, Wiens JJ, Baselga A. 2018 Climatic niche divergence drives patterns of diversification and richness among mammal families. *Sci. Rep.* **8**, 8781. (doi:10.1038/s41598-018-27068-y)
42. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005 Very high resolution interpolated climate surfaces for global land areas. *Int. J. Clim.* **25**, 1965–1978. (doi:10.1002/joc.1276)
43. IUCN. 2019 The IUCN red list of threatened species. Version 2019-1. See http://www.iucnredlist.org. Accessed on 21 March 2019.
44. Team QD. 2018 QGIS geographic information system. Open Source Geospatial Foundation Project. See http://qgis.osgeo.org.
45. Maddison WP, Maddison DR. 2011 Mesquite: A modular system for evolutionary analysis. Version 2.75. See http://mesquiteproject.org.
46. Hackett SJ *et al*. 2008 A phylogenomic study of birds reveals their evolutionary history.

Science **320**, 1763–1768. (doi:10.1126/science.1157704)

47. Jarvis ED *et al*. 2014 Whole genome analyses resolve early branches in the tree of life of modern birds. *Science* **346**, 1320–1331. (doi:10.1126/science.1253451)
48. Streicher JW *et al.* 2018 Evaluating methods for phylogenomic analyses, and a new phylogeny for a major frog clade (Hyloidea) based on 2,214 loci. *Mol. Phylogenet. Evol.* **119**, 128–143. (doi:10.1016/j.ympev.2017.10.013)
49. R Development Core Team. 2013 *R: a language and environment for statistical computing*. Vienna, Austria: R foundation for statistical computing. See http://www.R-project.org.
50. Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N. 2012 Comparative analyses of phylogenetics and evolution in R. R package version 0.5. See http://CRANR-projectorg/package=caper.
51. Revell LJ. 2012 Phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**, 217–223. (doi:10.1111/j.2041-210X.2011.00169.x)
52. Holm S. 1979 A simple sequentially rejective multiple test procedure. *Scand. J. Stat.* **6**, 65–70.
53. Rice WR. 1989 Analyzing tables of statistical tests. *Evolution* **43**, 223–225. (doi:10.1111/j.1558-5646.1989.tb04220.x)
54. Jezkova T, Wiens JJ. 2016 Rates of change in climatic niches in plant and animal populations are much slower than projected climate change. *Proc. R. Soc. B*. **283**, 20162104. (doi:10.1098/rspb.2016.2104)
55. Ackerly DD. 2000 Taxon sampling, correlated evolution, and independent contrasts. *Evolution* **54**, 1480–1492. (doi:10.1111/j.0014-3820.2000.tb00694.x)
56. Angilletta MJ. 2009 *Thermal adaptation: a theoretical and empirical synthesis*. Oxford, UK: Oxford University Press.
57. Huey RB, Deutsch CA, Tewksbury JJ, Vitt LJ, Hertz PE, Alvarez HJ. 2009 Why tropical forest lizards are vulnerable to climate warming. *Proc. R. Soc. B* **276**, 1939–1948. (doi:10.1098/rspb.2008.1957)
58. Addo-Bediako A, Chown SL, Gaston KJ. 2000 Thermal tolerance, climatic variability and latitude. *Proc. R. Soc. Lond. B* **267**, 739–745. (doi:10.1098/rspb.2000.1065)
59. Sunday JM, Bates AE, Dulvy NK. 2011 Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. B* **278**, 1823–1830. (doi:10.1098/rspb.2010.1295)
60. Huey RB, Kearney MR, Krockenberger A, Holtum JAM, Jess M, Williams SE. 2012 Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Phil. Trans. R. Soc. B* **367**, 1665–1679. (doi:10.1098/rstb.2012.0005)
61. Pie MR, Meyer ALS. 2017 The evolution of range sizes in mammals and squamates: heritability and differential evolutionary rates for low- and high-latitude limits. *Evol. Biol.* **44**, 347–355. (doi:10.1007/s11692-017-9412-0)
62. Thomas CD *et al*. 2004 Extinction risk from climate change. *Nature* **427**, 145–148. (doi:10.1038/nature02121)
63. Urban MC. 2015 Accelerating extinction risk from climate change. *Science* **348**, 571–573. (doi:10.1126/science.aaa4984)
64. Cadena CD *et al.* 2012 Latitude, elevational climatic zonation, and speciation in New World vertebrates. *Proc. R. Soc. B* **279**, 194–201. (doi:10.1098/rspb.2011.0720)
65. Jezkova T, Wiens JJ. 2018 Testing the role of climate in speciation: new methods and applications to squamate reptiles (lizards and snakes). *Mol. Ecol.* **27**, 2754–2769. (doi:10.1111/mec.14717)
66. Kozak KH, Wiens JJ. 2010 Niche conservatism drives elevational diversity patterns in Appalachian salamanders. *Am. Nat.* **176**, 40–54. (doi:10.1086/653031)
67. Lv X, Xia L, Ge D, Wu Y, Yang Q. 2016 Climatic niche conservatism and ecological opportunity in the explosive radiation of arvicoline rodents (Arvicolinae, Cricetidae). *Evolution* **70**, 1094–1104. (doi:10.1111/evo.12919)
68. Peterson AT. 2003 Predicting the geography of species' invasions via ecological niche modeling. *Q. Rev. Biol.* **78**, 419– 433. (doi:10.1086/378926)
69. Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C, Guisan A. 2012 Climatic niche shifts are rare among terrestrial plant invaders. *Science* **335**, 1344–1348. (doi:10.1126/science.1215933)
70. Soberón J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecol. Lett.* **10**, 1115–1123. (doi:10.1111/j.1461-0248.2007.01107.x)
71. Muñoz MM, Langham GM, Brandley MC, Rosauer D, Williams SE, Moritz C. 2016 Basking behavior predicts the evolution of heat tolerance in Australian rainforest lizards. *Evolution* **70**, 2537–2549. (doi:10.1111/evo.13064)
72. Cahill AE *et al.* 2013 How does climate change cause extinction? *Proc. R. Soc. B*. **280**, 2012890. (doi:10.1098/rspb.2012.1890)
73. Ockendon N *et al*. 2014 Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. *Global Change Biol.* **20**, 2221–2229. (doi:10.1111/gcb.12559)
74. Morley SA, Peck LS, Sunday JM, Heiser S, Bates AE. 2019 Physiological acclimation and persistence of ectothermic species under extreme heat events. *Global Ecol. Biogeogr.* **28**, 1018–1037. (doi:10.1111/geb.12911)
75. Camacho A, Rusch T, Ray G, Telmeco RS, Rodrigues MT, Angilletta MJ. 2018 Measuring behavioral thermal tolerance to address hot topics in ecology, evolution, and conservation. *J. Therm. Biol.* **73**, 71–79. (doi:10.1016/j.jtherbio.2018.01.009)
76. Quintero I, Wiens JJ. 2013 Rates of projected climate change dramatically exceed past rates of climatic-niche evolution among vertebrate species. *Ecol. Lett.* **16**, 1095–1103. (doi:10.1111/ele.12144)
77. Wiens JJ, Litvinenko Y, Harris L, Jezkova T. 2019 Rapid niche shifts in introduced species can be a million times faster than changes among native species and ten times faster than climate change. *J. Biogeogr.* **46**, 2115–2125. (doi:10.1111/jbi.13649)
78. Qu Y-F, Wiens JJ. 2020 Data from: higher temperatures lower rates of physiological and niche evolution. Dryad Digital Repository. (https://dx.doi.org/10.5061/dryad.m63xsj3zv)