LETTER

Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species

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Abstract

A key question in predicting responses to anthropogenic climate change is: how quickly can species adapt to different climatic conditions? Here, we take a phylogenetic approach to this question. We use 17 time-calibrated phylogenies representing the major tetrapod clades (amphibians, birds, crocodilians, mammals, squamates, turtles) and climatic data from distributions of > 500 extant species. We estimate rates of change based on differences in climatic variables between sister species and estimated times of their splitting. We compare these rates to predicted rates of climate change from 2000 to 2100. Our results are striking: matching projected changes for 2100 would require rates of niche evolution that are > 10 000 times faster than rates typically observed among species, for most variables and clades. Despite many caveats, our results suggest that adaptation to projected changes in the next 100 years would require rates that are largely unprecedented based on observed rates among vertebrate species.

Keywords

Adaptation, climate change, extinction, niche evolution, vertebrates.

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INTRODUCTION

Climate is changing rapidly, and this change may pose a major threat to global biodiversity (e.g. Thomas *et al.* 2004; Hof *et al.* 2011; Bellard *et al.* 2012). In the last 30 years, average global annual temperature has increased 0.6 °C, and by 2100 it is likely to increase an additional 4.0 °C or more (IPCC 2007). Rainfall will also be affected, and by 2100 some regions may experience a 30% decrease or increase in annual precipitation (IPCC 2007). Recent climate change has already driven many local populations to extinction, as shown by contractions at the warm-edge limits (low latitude or low elevation) of many species' geographical ranges (e.g. Chen *et al.* 2011; recent review in Cahill *et al.* 2013). Many authors predict that climate change will have a major negative impact on global biodiversity, especially when combined with other threats, such as habitat destruction (e.g. Hof *et al.* 2011). However, the extent to which species are threatened by climate change depends on the details of how they respond, including whether they can adapt to these changes evolutionarily.

Populations faced with climate change can respond in several different ways. These include dispersal to more suitable locations, persistence *in situ* through either phenotypic plasticity or evolutionary adaptation to changed conditions (either abiotic or biotic), or some combination of these processes (e.g. Holt 1990; Visser 2008). If dispersal, acclimation or adaptation do not occur, then the population may go extinct, especially if climate change pushes local conditions outside the fundamental climatic niche of the population or species (i.e. the set of temperature and precipitation conditions where the population or species can persist). Nevertheless, almost all models that have predicted future impacts of climate change have assumed that rates of evolutionary change in the climatic niche are negligible (e.g. Thomas *et al.* 2004; Deutsch *et al.* 2008; Schloss *et al.* 2012).

This raises a fundamental question: how quickly do species' climatic niches actually evolve? This question may be especially critical as human activities increasingly limit the ability of populations to track suitable climates over space, and given that unimpeded rates of movement may be slower than rates of climate change (e.g. Schloss *et al.* 2012).

There are many ways that the rate of climatic niche evolution can be addressed. Several studies have used or described a microevolutionary approach, utilising estimates of selection and heritability on relevant traits (e.g. Visser 2008; Sinervo *et al.* 2010; Hoffmann & Sgrò 2011). However, this approach may be difficult to apply to large numbers of species, especially if the relevant traits are unknown (e.g. physiology vs. traits related to species interactions). Another way that this question can be addressed is using comparisons among species. By documenting the climatic conditions where species occur, their realised climatic niches can be estimated (i.e. the set of climatic conditions where the species occurs, which must be included within the fundamental climatic niche). Time-calibrated phylogenies can then be used to estimate the time spans over which changes occur between climatic conditions occupied by closely related species. These rates can then be compared to projected rates of climate change in relevant climatic variables in the future. Some recent studies have focused on comparing rates of climatic niche evolution among clades using time-calibrated phylogenies (e.g. Smith & Beaulieu 2009; Kozak & Wiens 2010; Cooper *et al.* 2011; Fisher-Reid *et al.* 2012). Recent studies have also used phylogenetic analyses of climatic data to help predict species' responses to current changes (e.g. Lavergne *et al.* 2012) and to predict future shifts in geographical ranges (Lawing & Polly 2011). However, there has been little emphasis on absolute rates of climatic niche evolution among species and their relevance to rates of projected climate change.

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We acknowledge that this comparative approach has many limitations. For example, we do not know when on a branch a shift in climatic niche occurred, and rates of evolution within populations are not directly addressed. Furthermore, this approach does not address the evolution of physiological tolerances directly. Nevertheless, all approaches to predicting responses to future change have limitations, and insights from climatic niche evolution among species should not be ignored.

Here, we estimate absolute rates of climatic niche evolution for 540 species in 17 clades of terrestrial vertebrates, including groups of mammals, birds, lizards, snakes, turtles, crocodilians, salamanders and frogs. We use relatively comprehensive time-calibrated phylogenies to identify sister species. We then estimate climatic niche values for each species, including climatic variables whose future values have been projected (i.e. IPCC 2007). By combining climatic values for ancestral and extant species with age estimates of clades, we estimate rates of change among these species. We show that rates of climatic niche evolution among species are dramatically slower than rates of climate change expected in the next 100 years, typically by several orders of magnitude.

METHODS

Choice of clades and sister species

We focused on terrestrial vertebrates (tetrapods). Within Tetrapoda, we included clades within most major groups (Table 1), using two main criteria: (1) clades for which a time-calibrated molecular phylogeny was estimated using relaxed-clock methods, and (2) clades with relatively complete species sampling or containing subclades that were complete or nearly so (> 80%). We selected these well-sampled clades in an attempt to identify actual sister species, rather than species that merely appear closely related due to limited sampling. Comparing non-sister species may lead to underestimation of rates, e.g. if recently evolved species with highly divergent niches

are inadvertently excluded. However, we acknowledge that rates may still be underestimated for similar reasons if undescribed species interdigitate among these selected species pairs. For *Pteroglossus* (toucans), we used the lineages treated as separate by Patel *et al.* (2011). Some are currently ranked as subspecies, but many of these nevertheless appear to be morphologically and genetically distinct. Similarly, we also included a few distinct lineages that are not yet formally recognised as species in other clades (e.g. phrynosomatid lizards, plethodontid salamanders).

In most clades used here, trees are estimated with both nuclear and mitochondrial DNA sequences, and divergence times are estimated with multiple fossil calibration points (Table S1). In addition to incorporating diverse clades, the sampling of species also encompasses many geographical regions and biomes (including both arid and mesic and temperate and tropical conditions; see Table S1).

We generated a time-calibrated phylogeny for emydid turtles given that one was not available from previous studies. Furthermore, we estimated a new time-calibrated phylogeny for New World ranid frogs, given that a previous one (Wiens *et al.* 2009) lacked many species. Methodological details are described in Supplementary Appendix S1.

Climatic and locality data

We obtained climatic data for each species from georeferenced localities. Locality data were obtained from previous studies (Table 1) and from databases of museum specimen localities (e.g. GBIF, HerpNet). Locality data were carefully checked to confirm that localities spanned most of the species known geographical range whenever possible, and that no localities were outside the known range. Sample sizes of localities varied considerably among species (1 to >10 000), but seemed to generally reflect geographical range area, with more widely distributed species represented by more localities. We did not correct for differences in range size or numbers of localities among species, because differences in climatic

Table 1 Summary of vertebrate clades used to estimate rates of climatic niche evolution. When sampling of species within a clade was relatively incomplete, we used only species pairs within well-sampled genera and other subclades

Higher taxon	Clade	Species in tree	Species with estimated rates	Source for tree	Source for climatic data
Amphibians (frogs)	Hylini (Hylidae)	91 of ~181	26	Wiens *et al.* (2011a)	Wiens *et al.* (2011a)
Amphibians (frogs)	New World *Rana* (Ranidae)	48 of 48	30	Pyron & Wiens (2011) and this study	This study
Amphibians (salamanders)	Plethodontidae	250 of 431	90	Kozak & Wiens (2010)	Kozak & Wiens (2010)
Amphibians (salamanders)	Salamandridae	70 of 97	22	Wiens *et al.* (2011b)	This study
Squamate reptiles (lizards)	*Brookesia* (Chamaeleonidae)	28 of 30	20	Townsend *et al.* (2009)	Townsend *et al.* (2009)
Squamate reptiles (lizards)	Phrynosomatidae	117 of 138	46	Quintero & Wiens (2013)	Quintero & Wiens (2013)
Squamate reptiles (lizards)	*Plestiodon* (Scincidae)	37 of 43	24	Brandley *et al.* (2011)	This study
Squamate reptiles (snakes)	Lampropeltini (Colubridae)	31 of 31	20	Pyron & Burbrink (2009)	Pyron & Burbrink (2009)
Turtles	Emydidae	35 of ~43	10	Wiens *et al.* (2010) and this study	Stephens & Wiens (2009) and this study
Crocodilians	Crocodilians	23 of 23	18	Oaks (2011)	This study
Birds	*Aphelocoma* (Corvidae)	14 of 14	8	McCormack *et al.* (2011)	This study
Birds	Buteoninae (Accipitridae)	54 of 59	24	do Amaral *et al.* (2009)	This study
Birds	Furnariidae	285 of 293	148	Derryberry *et al.* (2011)	This study
Birds	Gruidae	15 of 15	8	Krajewski *et al.* (2010)	This study
Birds	*Pteroglossus* (Ramphastidae)	11 of 11	10	Patel *et al.* (2011)	This study
Mammals	Mustelidae	43 of 58	24	Koepfli *et al.* (2008)	This study
Mammals	Scandentia	20 of 20	12	Roberts *et al.* (2011)	This study

tolerances among species may be a major driver of differences in range size.

Climatic data were obtained from the WorldClim database (Hijmans *et al.* 2005) at a ~1 km^2 resolution. We obtained climatic data from each georeferenced locality using Hawth's Tools in Arc-Map 9.3 and the R package *raster* (Hijmans & van Etten 2012). The WorldClim database is based primarily on weather-station data (spatially interpolated to points between stations) and average values of climatic variables from 1950 to 2000. This database does not explicitly account for more recent climate changes. However, our distributional data are also based primarily on older records (i.e. locality data can potentially span from before the 1900s to the present day). In other words, our climatic and distributional data should both reflect patterns of climate and species distribution before very recent climatic changes (and possible range shifts caused by these changes).

We focused on six climatic variables, including annual mean temperature (Bio1), the highest and lowest temperatures recorded during the year (Bio5, Bio6), annual mean precipitation (Bio12) and the precipitation of the wettest and driest quarters of the year (Bio16, Bio17). These variables represent standard averages (Bio1, Bio12) and extreme values that may set species' range limits and reflect climatic tolerances. For some clades, climatic data were already available from previous studies (Table 1), but were from the same source (Hijmans *et al.* 2005) and same scale (~1 km^2). We estimated rates (see below) for each climatic variable for each species based on the mean value averaged across sampled localities. Means and standard errors of climatic variables for all species in all 17 clades (1153 species total) are provided in Appendix S3.

For migrant bird species (within Buteoninae, Furnariidae and Gruidae), we only included climatic data for months in which a species was actually present in a region, to avoid including conditions that individuals do not experience because of annual migration (see Appendix S4 for details).

Estimation of rates

To estimate a rate of climatic niche evolution for each species in each pair, we first reconstructed ancestral values for climatic variables across all species in the phylogenies using the Phylogenetic Generalized Least Squares approach (PGLS; Martins & Hansen 1997). We first found the best-fitting likelihood model of evolution for each climatic variable for each clade. We compared white noise (WN; no phylogenetic signal), Brownian Motion (BM) and Ornstein-Uhlenbeck (OU; single optimum) models using the *ape* (version 2.7-3; Paradis *et al.* 2004) and *geiger* (version 1.3-1; Harmon *et al.* 2008) packages in R version 2.13.2 (R Core Team 2012). The OU model had better fit than WN and BM for almost all variables in all clades, using the AIC (Table S2). To reconstruct ancestral values across the phylogeny we used PGLS in COMPARE 4.6b (Martins 2004) with the exponential model (OU) and alpha values estimated from the best fitting model. To assess robustness, we also conducted a set of analyses using reconstructions from the BM model with *ape*.

The rate of climatic niche evolution for each species for each variable was calculated as the absolute difference between the estimated ancestral value for the most recent ancestor of that species (i.e. the node uniting that species and its sister species) and the value for that species, divided by the age of that ancestor. For

example, a species that differed by 5 °C from its reconstructed ancestor that is 5 million years (Myr) old would have a rate of 1 °C/Myr. We acknowledge that there are several potential issues in estimating rates in this way, and we address these at length in the Discussion.

We obtained data on projected climate for 2080–99 for all localities, climatic variables and species (we use '2100' hereafter for brevity). Projected change depends on both emission scenarios and General Circulation Models (GCM). We used the Emission Scenario A2 (IPCC 2007), following Beaumont *et al.* (2008, p. 1143). We compiled data for 2080–99 from six GCMs: CCCMA-CGCM, CSIRO-MK3, HADCM3, CCSR-NIES, MPI-ECHAM5 and MRI-CGCM2.3.2 (http://www.ipcc-data.org). We used the original resolution of these models (1 degree^2) but bilinearly interpolated data to fit an equal area grid projection of 110 km^2. We performed spatial manipulations with the R packages *raster* (Hijmans & van Etten 2012) and *rgdal* (Bivand *et al.* 2013).

To estimate the future rate of climate change, we took the difference between present-day climate and projected climate for each locality, and divided this difference by 90 years (the midpoint of 2080–2100, minus 2000). We took the median and mean among all locality-specific rates for each species for each GCM model, but used the median for subsequent analyses given minimal difference from the mean. We then selected the minimum and maximum rates among all GCMs for each species, to incorporate uncertainty in the projections of future climate change. Finally, although we provide species-specific projections for climate change for each variable and species, these should not be used directly for conservation assessments, given the coarse spatial scale of the projected climate layers (110 km^2).

RESULTS

Across the 17 families of vertebrates, we obtained rate estimates for 540 species from 270 species pairs. Overall, rates of climatic niche evolution among species are dramatically slower than rates of projected climate change for 2000 to ~2100 (Figs 1 and 2; Tables 2 and 3; see Appendix S2 for all rate estimates). Rates estimated with the BM model are similar but generally lower than those estimated with the best-fitting OU model (see Figs S4, S5; Appendix S2). Below, we refer only to OU rates.

For annual mean temperature (Fig. 1), the mean species rate in most of the 17 clades is less than 1 °C/Myr, and only two clades show higher mean values (*Pteroglossus*: mean = 1.57, Salamandridae: mean = 1.73). The highest species rates within these clades are also typically less than 1 °C/Myr also, with some exceptions. In contrast, the IPCC estimated rates are ~4 °C for mean annual temperature in the next ~100 years, depending on location. We find that the rate of change observed among species is typically ~10 000–100 000 times slower than the expected rate of change from 2000 to 2100 (Table 2). This difference in rates can be smaller for some individual species under some climatic projections, but is always at least 500-fold (Appendix S5). Patterns are very similar for yearly minimum temperatures (Bio6) and maximum temperatures (Bio5), with mean rates typically less than 1 °C/Myr and maximum rates less than 7 (Appendix S5).

Patterns for precipitation are also similar (Fig. 2). For annual precipitation (measured in mm/year), mean rates within clades range from 11.3 mm/Myr (*Brookesia*) to 334.8 mm/Myr (*Pteroglossus*), with
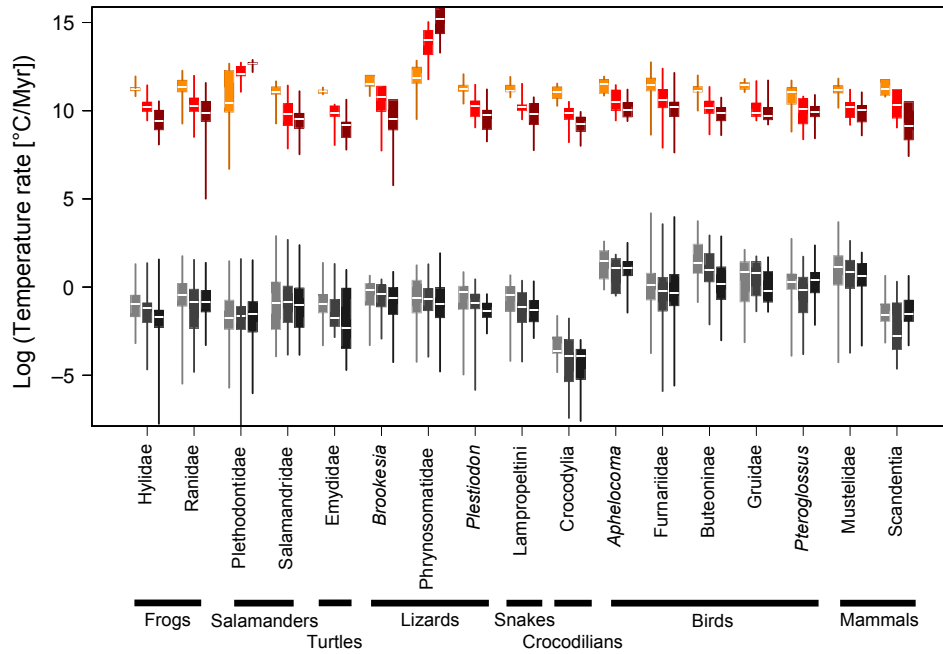
Figure 1 Rates of climatic niche evolution (for temperature) in vertebrates are much slower than projected rates of climate change. Rates are on a log10 scale. For each clade, the three boxplots are: left (grey) = minimum yearly temperature (Bio6); middle (black) = annual mean temperature (Bio1); right (black) = maximum yearly temperature (Bio5). The white horizontal line is the median rate among all species in the clade; the upper and lower limits of the box correspond to the first and third quartiles respectively. Whiskers indicate the range of species values. The orange, red and brown box plots and lines indicate projected rates of change for matching variables for 2000–2100 within the geographical ranges of these species (using the GCM giving the minimum difference in rates). Full results are in Appendix S5. Evolutionary rates are from the best-fitting OU model (see Fig. S4 for BM results). A few rate estimates (e.g. in phrynosomaitds) are outside the window of values shown here.
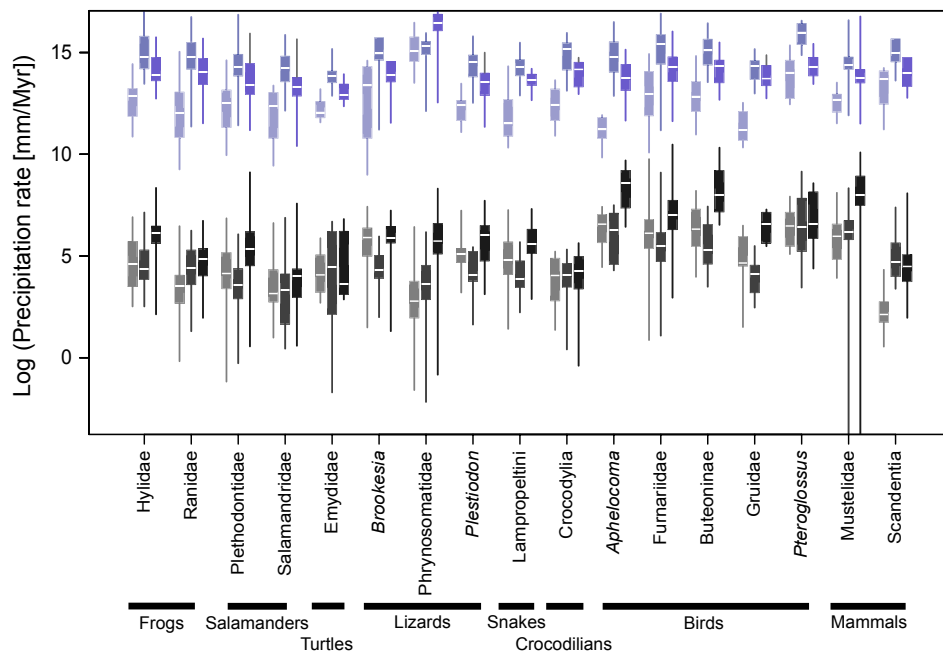

Figure 2 Rates of climatic niche evolution (for precipitation) in vertebrates are much slower than projected rates of climate change. Rates are on a log10 scale. For each clade, the three boxplots represent: left (grey) = driest quarter precipitation (x4; Bio17); middle (black) = total annual precipitation (Bio12); right (black) = wettest quarter precipitation (x4; Bio16). The white horizontal line is the median rate among all species in the clade; the upper and lower limits of the box correspond to the first and third quartiles respectively. Whiskers indicate the range of species values. The three purple box plots and lines indicate projected rates of change for matching variables for 2000–2100 within the geographical ranges of these species (using the GCM giving the minimum difference in rates). Full results are in Appendix S5. Evolutionary rates are from the best-fitting OU model (see Fig. S5 for BM results). A few rate estimates are outside the window of values shown here.

Table 2 Summary of differences between estimated rates of climatic niche evolution and projected climate change from 2000 to 2100 for annual mean temperature (Bio1), given the lowest and highest differences from current values among six GCMs. Values indicate how many times higher the projected rate of climate change is relative to estimated rates among species, including the mean and range of values among species within each clade. Rate estimates shown are based on the OU model. See Appendix S5 for full results, including all variables, all species, and results using the BM model

Clade		Lowest predicted change		Highest predicted change	
		Mean	Range	Mean	Range
Frogs	Hylidae	2.27×10^5	1.39×10^4–1.91×10^6	9.32×10^5	4.83×10^4–9.69×10^6
	Ranidae	4.65×10^5	3.63×10^3–6.52×10^6	9.77×10^5	2.11×10^4–1.45×10^7
Salamanders	Plethodontidae	2.30×10^{10}	5.49×10^4–2.07×10^{12}	3.23×10^{10}	7.27×10^4–2.91×10^{12}
	Salamandridae	1.68×10^5	9.94×10^2–1.76×10^6	5.17×10^5	4.45×10^3–3.15×10^6
Turtles	Emydidae	1.36×10^5	4.75×10^3–5.10×10^5	5.42×10^5	2.60×10^4–1.08×10^6
Lizards	*Brookesia*	1.33×10^5	1.68×10^3–6.49×10^5	2.44×10^5	2.31×10^4–1.14×10^6
	Phrynosomatidae	7.60×10^6	8.15×10^4–5.82×10^7	8.07×10^6	1.14×10^5–6.22×10^7
	Plestiodon	3.50×10^5	7.78×10^3–6.22×10^6	1.64×10^6	3.69×10^4–3.39×10^7
Snakes	Lampropeltini	2.26×10^5	1.40×10^4–1.06×10^6	7.35×10^5	6.67×10^4–4.93×10^6
Crocodilians	Crocodylia	5.35×10^6	1.03×10^5–3.78×10^7	1.42×10^7	3.45×10^5–9.33×10^7
Birds	*Aphelocoma*	3.71×10^4	3.19×10^3–1.33×10^5	9.88×10^4	1.40×10^4–2.56×10^5
	Furnariidae	2.00×10^5	5.72×10^2–1.01×10^7	4.04×10^4	1.86×10^3–2.22×10^7
	Buteoninae	4.34×10^4	8.23×10^2–6.98×10^5	8.71×10^4	4.44×10^3–1.09×10^6
	Gruidae	3.64×10^4	3.58×10^3–1.57×10^5	9.20×10^4	1.67×10^4–2.78×10^5
	Pteroglossus	9.22×10^4	4.19×10^3–3.35×10^5	3.11×10^5	1.53×10^4–1.42×10^6
Mammals	Mustelidae	7.25×10^4	1.13×10^3–1.04×10^6	2.45×10^5	6.68×10^3–3.97×10^6
	Scandentia	7.32×10^5	1.69×10^4–4.36×10^6	1.48×10^6	4.64×10^4–6.08×10^6

Table 3 Summary of differences between estimated rates of climatic niche evolution and projected rates of climate change from 2000 to 2100 for total annual precipitation (Bio12), given the lowest and highest differences from current values among six GCMs. Values indicate how many times higher the projected rate of climate change is relative to estimated rates among species, including the mean and range of values among species within each clade. Rate estimates shown are based on the OU model. See Appendix S5 for full results, including all variables, all species, and results using the BM model

Clade		Lowest predicted change		Highest predicted change	
		Mean	Range	Mean	Range
Frogs	Hylidae	1.04×10^5	1.24×10^3–7.18×10^5	2.78×10^5	3.77×10^3–1.41×10^6
	Ranidae	9.16×10^4	6.44×10^2–7.17×10^5	3.05×10^5	4.93×10^3–2.38×10^6
Salamanders	Plethodontidae	1.57×10^5	2.54×10^3–1.64×10^6	6.55×10^5	8.94×10^3–1.00×10^7
	Salamandridae	2.73×10^5	2.18×10^3–1.93×10^6	6.03×10^5	3.29×10^3–3.92×10^6
Turtles	Emydidae	5.91×10^5	7.91×10^2–5.49×10^6	2.49×10^6	3.38×10^3–2.32×10^7
Lizards	*Brookesia*	6.22×10^4	1.76×10^3–3.40×10^5	1.88×10^5	4.05×10^4–1.07×10^6
	Phrynosomatidae	1.85×10^6	3.88×10^2–6.88×10^7	3.19×10^6	3.43×10^3–1.09×10^8
	Plestiodon	6.16×10^4	1.22×10^3–4.05×10^5	2.54×10^5	1.36×10^4–2.63×10^6
Snakes	Lampropeltini	3.87×10^4	4.05×10^3–2.04×10^5	1.25×10^5	1.80×10^4–6.71×10^5
Crocodilians	Crocodylia	2.52×10^5	9.13×10^3–2.61×10^6	5.34×10^5	6.55×10^4–3.47×10^6
Birds	*Aphelocoma*	1.09×10^4	1.21×10^3–2.92×10^4	2.60×10^4	3.53×10^3–9.20×10^4
	Furnariidae	5.05×10^4	6.14–2.25×10^6	1.36×10^5	5.70×10^2–6.07×10^6
	Buteoninae	2.27×10^4	1.36×10^3–9.96×10^4	5.45×10^4	5.27×10^3–2.25×10^5
	Gruidae	6.15×10^4	1.82×10^3–2.71×10^5	2.35×10^5	2.00×10^4–8.05×10^5
	Pteroglossus	5.11×10^4	1.13×10^3–2.89×10^5	1.18×10^5	2.64×10^3–7.04×10^5
Mammals	Mustelidae	2.89×10^{12}	1.13×10^2–6.95×10^{13}	8.12×10^{13}	5.68×10^2–1.95×10^{15}
	Scandentia	4.17×10^4	9.58×10^2–1.81×10^5	1.75×10^5	4.12×10^3–4.11×10^5

an average of mean species rates among clades of 286. Maximum species rates within clades range from 39 to 9334 mm/Myr (*Brookesia* and *Pteroglosssus*). Again, rates are generally similar for changes in the precipitation of the wettest and driest quarters (Fig. 2). In contrast, projected changes in annual precipitation yields rates that are typically ~10 000–100 000 times faster than rates of niche evolution among species (Fig. 2; Table 3; Appendix S5). Changes for wettest and driest quarter precipitation are also similar, although the difference between past rates of change and projected changes are somewhat smaller for driest quarter precipitation, especially in some

species (but differences still typically ~1000–10 000 fold; Appendix S5).

DISCUSSION

Our results show that typical rates of climatic niche evolution among species across diverse vertebrate clades are dramatically slower than projected rates of anthropogenic climate change. Although there are many reasons why it may be problematic to directly compare estimates of past changes to future projections

(see below), our results show that the rate of projected climate change from 2000 to ~2100 is largely unprecedented in terms of the amount of climatic niche evolution that has occurred over the last several million years across hundreds of vertebrate species. These results are consistent with the observation that many populations are going locally extinct as climate changes, rather than simply adapting to altered climatic conditions. Specifically, numerous studies have documented range contractions at the lowest latitudes and elevations of species ranges (e.g. Chen *et al.* 2011; Cahill *et al.* 2013). Limited projections based on selection, heritability and temperature tolerances for lizards also concur that rates of evolution are too slow to keep pace with predicted rates of climate change (e.g. Sinervo *et al.* 2010), as do transplant experiments in plants (Etterson & Shaw 2001).

We acknowledge that there are many possible sources of error in these analyses, especially in extrapolating our results to predicting future impacts. However, most of these seem unlikely to overturn our basic conclusions. We group these based on whether they seem likely to be minor or major sources of error.

Minor sources of error

There are several sources of error that seem likely to be too small to overturn our major conclusions, given the magnitude of differences between past and projected rates. These include errors in estimating ages and relationships of species, niches of extant species and ancestral species, and failure to include some species or clades.

First, there may be errors in estimating the ages and relationships among species. Nevertheless, estimated ages seem unlikely to be incorrect by more than 10-fold (e.g. a species estimated as 2 Myrs old might actually be 200 000 years, but probably not 20 000 or 200 000 000). In contrast, observed rates of niche evolution among species and projected rates of climate change typically differ by ~10 000–100 000 fold. Similarly, errors in estimated phylogenies should change estimated rates very little. Most sister species sampled here are of similar age (Appendix S2). Given similar ages, changes in relationships among species should not dramatically change estimated rates. For example, if species A, B and C are of similar age, finding that A and B are sister taxa rather than B and C should have little impact on estimated rates. Mitochondrial introgression between species could lead to dramatic errors in both the phylogeny and divergence times, and many phylogenetic estimates are based at least partly on mitochondrial data (Table S1). However, if mitochondrial introgression led to dramatic errors, they would lead to overestimation of evolutionary rates in this case, rather than underestimation (i.e. distantly related species with divergent climatic niches might appear recently diverged, leading to higher estimated rates).

Similarly, these estimates might be changed by adding species belonging to these clades that are not included in our phylogenies (e.g. undescribed or unsampled species). However, these added species would have to be both dramatically younger and have strongly divergent climatic niches to significantly alter our main results. Both possibilities seem unlikely given the ages and limited climatic divergence among the species already included in these clades. A related issue is that some nominal species included here may later be divided into additional species by detailed phylogeographical studies. These subdivided species would likely be younger than the currently recognised species, and may sometimes have more divergent climatic niches.

But again, it seems unlikely that this will account for the large-scale difference between past rates and predicted rates. Furthermore, many species included here were already subdivided by detailed phylogeographical studies (e.g. some hylids, plethodontids and phrynosomatids), suggesting that such divisions will not overturn our results.

There may also be errors in our estimates of current climatic niches of these species and future climates. For example, many species have climatic data from few localities. In general, such species have smaller geographical ranges, and should occur in a limited climatic niche space, reducing potential errors (especially since rates are based on species means). The projections of future climate undoubtedly contain errors also, especially given their coarse spatial resolution. However, we know of no plausible scenario whereby these errors would explain the observed magnitude of differences in past vs. projected rates, especially given the general consistency of the estimated rates across clades, and that estimates of climatic niche variables for many species are based on hundreds and even thousands of georeferenced localities.

There may also be errors in reconstructing ancestral values for climatic variables, and such errors could influence estimated rates. However, the rates estimated here are for sister species pairs, and so should depend primarily on the similarity of the climatic niches of these sister species, and their estimated ages. For example, reconstruction methods might err in estimating ancestral trait values that are similar to an average of the values of the extant species, when the true ancestral values were more similar to those of one species or another (or more distant ancestors). But again, such errors should have only a minor impact on the estimated rates, given the similarity of these climatic variables for sister species (see below) and the time scales involved. Furthermore, even if climate and species distributions have changed dramatically in the recent past (e.g. due to Pleistocene glaciations), this does not mean that our ancestral trait estimates based on extant species climatic distributions are necessarily incorrect by orders of magnitude. Instead, many lines of evidence suggest that species shift their distributions over space to track their climatic niche as climate changes (e.g. Ackerly 2003). In fact, estimates of the past geographical distribution of climates are often based directly on this assumption (e.g. desert plants indicate desert climates, tropical plants indicate tropical climates). Or, put another way, just because some regions in northern North America were temporarily covered in ice does not mean that the species that occur there today were once adapted to living under glaciers.

We acknowledge that our study addresses only the realised niche and not the fundamental niche (Hutchinson 1957). Our data and analyses are based only on the climatic conditions where species occur, and not where they could occur based on their physiological tolerances to climate alone (fundamental niche). It may be that many species could occur under a broader range of conditions, but are prevented by non-climatic factors (such as non-climatic geographical barriers to dispersal and interactions with other species). Although our results do not directly address rates of change in physiological tolerances, it would be a mistake to assume that only physiological tolerances are relevant to explaining species responses to climate change. In fact, a recent review (Cahill *et al.* 2013) suggests that species interactions may be the major cause of local extinctions and population declines from climate change and climatic oscillations so far. Furthermore, phylogenetic analyses in salamanders suggest that species interactions (i.e. geographical overlap between clades) are critically important in determining rates of (rea-

lised) climatic niche evolution (Kozak & Wiens 2010). Analyses of species range limits for terrestrial ectotherms also suggest that the warm edges (low latitude and elevation) of many species are set by biotic interactions rather than physiological tolerances alone (Sunday *et al.* 2012). Thus, rate estimates based on the fundamental niche alone may be less relevant in predicting the ability of species to respond to future climate change. Instead, species interactions may be important in setting range limits, limiting rates of niche evolution and causing extinction when climate changes.

We also acknowledge that our sampling of vertebrate clades is not comprehensive. In theory, other well-sampled vertebrate clades with time-calibrated phylogenies could have been included, and more are becoming available all the time. In addition, the clades that we have included show a bias towards groups distributed in temperate North America and tropical Middle America, with more limited representation of South America, Europe, Asia, Madagascar, Africa and Australia (Table S1). Despite these limitations, we have included all major tetrapod clades (including both ectotherms and endotherms), and both temperate and tropical species on multiple continents, as well as clades that are diverse in mesic habitats (e.g. salamanders) and arid ones (e.g. phrynosomatid lizards). Given this, and the strong similarity in results across these diverse clades, it seems highly unlikely that including other clades will overturn the basic results for terrestrial vertebrates. Nevertheless, other clades (e.g. plants, arthropods, marine and freshwater groups) should be included in future studies.

Major sources of error

There are also some potentially major sources of error. Perhaps, the most important issue is that our rate estimates implicitly assume a constant amount of change over time. In fact, there could be dramatic changes in climatic niches over short time periods, followed (or preceded) by long periods of evolutionary stasis. This pattern could lead to dramatically underestimated rates. However, most species pairs included here have similar climatic niches, regardless of their age (Table S5). For example, for annual mean temperature, the median difference between sister species within a clade is < 2 °C for 7 clades, 2–4 °C for 7, and > 4 °C for only 3. So, the pattern is not of dramatic shifts leading to apparently slow rates over long time scales. Instead, climatic niches are generally similar between sister species, regardless of whether species are old or young. Therefore, it seems unlikely that species became very different over short time scales and then consistently diverged to become similar again, without leaving any trace in terms of dramatic differences among living species. Furthermore, recent studies of patterns of evolutionary change over time in body size (Uyeda *et al.* 2011) show that phenotypic traits may remain similar among populations and species over short time scales and only undergo major divergence at the scale of millions or tens of millions of years. Intriguingly, a recent review of climatic niche conservatism over different time scales also suggested that climatic niches tend to be highly conserved over time spans of up to tens or hundreds of thousands of years but diverge over longer time scales (Peterson 2011), suggesting similar patterns to those in body size. These lines of evidence suggest that our low rate estimates are not necessarily explained by rapid short-term changes and long term stasis. Similarly, rates may be underestimated if there is constant rapid evolution within a bounded set of trait values over long time scales (e.g. Hunt 2012). However, several addi-

tional analyses (Appendix S6) suggest that this hypothesis may not explain the low rates estimated here, including estimates of phylogenetic signal and OU-based estimates of phylogenetic half-life. Overall, deviations from rate constancy may be an important source of error in rate estimates in our study. Nevertheless, since projected changes for 2100 exceed typical climatic differences among many vertebrate sister species in many clades (see above, Table S4) rates of niche evolution seem unlikely to keep pace, regardless of this potential source of error in estimating rates for each species.

Also, rates of climatic niche evolution may be much higher among populations within species than the rates observed between species that we focus on here. For example, populations diverge over much more recent time scales than species. Furthermore, two sister species might show slow rates of niche evolution because they both contain many populations that occur in many climatically divergent localities, but have similar mean climatic values. However, species with small geographical ranges (i.e. few localities) also have low rates (Appendix S2), showing that our results are not simply an artefact of averaging climatic variation across the ranges of widespread species. In addition, analyses of three vertebrate clades suggest that within-locality seasonal variation explains much of the overall climatic niche variation within species (mean among species of ~75% for temperature and ~60% for precipitation), and that between-population variation is of less importance (Quintero & Wiens 2013). Regardless, estimating rates of climatic divergence among populations should be an important area for future research, and one that may be especially relevant for conservation. These analyses may also have many challenges, however, such as estimating when populations have split.

Another major issue is the possibility that species have not evolved at the maximum rate that they are capable of evolving at in the future. For example, rates of climatic niche evolution may be low due to the tendency of species to disperse when facing changing environmental conditions, rather than evolving to persist under those conditions (e.g. Ackerly 2003). Based on this argument, species and populations have not been forced to 'adapt or die' as they may soon have to, given the combination of rapid climate change and either slow dispersal or human modification of potential dispersal corridors. However, in many species, climate-induced range shifts may actually be driven by local extinction of populations at the edges of species ranges rather than by movement of individuals away from unfavourable conditions (but this is a poorly studied topic; see Cahill *et al.* 2013). Thus, apparent dispersal may actually reflect local extinction. Yet, gene flow may impede local adaptation across a species range, and so faster rates might be possible in isolated populations (Schiffers *et al.* 2012). A related issue is that conditions under which species have been forced to rapidly modify their climatic niches to persist are not represented in the time slice examined here (i.e. most species are 0.1–10 Myr old, so rapid niche evolution 25–30 Myr ago is not represented). However, even the fastest rates of climatic niche evolution in these clades are typically two or more orders of magnitude slower than projected rates (Tables 2 and 3). Furthermore, conditions where there may be rapid niche evolution should be represented (e.g. speciation, clades invading new regions). In summary, rates of climatic niche evolution estimated here might underestimate the maximum rates that are actually possible, but the issue is complex.

Finally, we emphasise that our results do not directly address whether these 540 species will survive impending climate change. This will depend on many factors, including impacts of human habitat modification on potential dispersal. Nevertheless, combining our (very coarse) climatic projections with current data for these species suggests that future conditions will be outside the current climatic niches of many species (Table S6), especially for temperature for many tropical species. These species may require extensive dispersal or niche evolution to survive projected changes.

CONCLUSIONS

We show that projected rates of climate change exceed typical rates of climatic niche evolution among vertebrate species by 10 000-fold or more, based on results from 17 clades and 540 species. These results do not necessarily mean that there will be widespread extinction of vertebrate species from climate change. For example, many species may be able to simply follow their climatic niche as it moves poleward in latitude or upward in elevation. However, these results do suggest that *in situ* adaptation of populations to changing climatic conditions would require rates of climatic niche evolution that are largely unprecedented among species in these clades. Clearly, the approach that we apply here should not be the only one used to address how quickly populations can respond to climate change. Experimental and modelling approaches will also be essential (e.g. Hoffmann & Sgrò 2011), as will comparative analyses of niches among populations below the species level. Our approach offers one way to address how quickly climatic niches evolve, and a similar approach could be applied to many other organisms. Finally, our results provide tentative support for the widespread practice of not including climatic niche evolution in modelling species responses to climate change.

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