ORIGINAL ARTICLE

Climatic niche conservatism and the evolutionary dynamics in species range boundaries: global congruence across mammals and amphibians

Miguel Á. Olalla-Tárraga[1,2]*[†], Lynsey McInnes[1,3]*[†], Luis M. Bini[4],
José A. F. Diniz-Filho[4], Susanne A. Fritz[5,6], Bradford A. Hawkins[7],
Joaquín Hortal[4,8,9], C. David L. Orme[1,3], Carsten Rahbek[5],
Miguel Á. Rodríguez[2] and Andy Purvis[1,8]

[1]Division of Biology, Imperial College London, Silwood Park Campus, Ascot, SL5 7PY, UK, [2]Department of Ecology, University of Alcalá, Alcalá de Henares, 28871, Spain, [3]Grantham Institute for Climate Change, Imperial College, London SW7 2AZ, UK, [4]Departamento de Ecologia, ICB, Universidade Federal de Goiás, CP 131, 74.001-970, Goiânia, GO, Brazil, [5]Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 København, Denmark, [6]Biodiversity and Climate Research Centre (BiK-F), D-60325 Frankfurt (Main), Germany, [7]Department of Ecology & Evolutionary Biology, University of California, Irvine, CA 92697, USA, [8]Centre for Population Biology, Imperial College London, Silwood Park Campus, Ascot, SL5 7PY, UK, [9]Departamento de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), C/José Gutiérrez Abascal 2, Madrid 28006, Spain

*Correspondence: Miguel Á. Olalla-Tárraga and Lynsey McInnes, Division of Biology, Imperial College London, Silwood Park Campus, Ascot, SL5 7PY, UK.
E-mail: miguel.olalla@uah.es;
lynsey.mcinnes01@imperial.ac.uk
[†]The first two authors contributed equally to this work, so order of authorship was decided by the 'coin-flip' method.

ABSTRACT

Aim Comparative evidence for phylogenetic niche conservatism – the tendency for lineages to retain their ancestral niches over long time scales – has so far been mixed, depending on spatial and taxonomic scale. We quantify and compare conservatism in the climatic factors defining range boundaries in extant continental mammals and amphibians in order to identify those factors that are most evolutionarily conserved, and thus hypothesized to have played a major role in determining the geographic distributions of many species. We also test whether amphibians show stronger signals of climatic niche conservatism, as expected from their greater physiological sensitivity and lower dispersal abilities.

Location Global; continental land masses excluding Antarctica.

Methods We used nearly complete global distributional databases to estimate the climatic niche conservatism in extant continental mammals and amphibians. We characterized the climatic niche of each species by using a suite of variables and separately investigate conservatism in each variable using both taxonomic and phylogenetic approaches. Finally, we explored the spatial, taxonomic and phylogenetic patterns in recent climatic niche evolution.

Results Amphibians and mammals showed congruent patterns of conservatism in cold tolerance, with assemblages of escapee species (i.e. those escaping most from the climatic constraints of their ancestors) aggregated in the North Temperate Zone.

Main conclusions The relative strength of climatic niche conservatism varies across the variables tested, but is strongest for cold tolerance in both mammals and amphibians. Despite the apparent conservatism in this variable, there is also a strong signal of recent evolutionary shifts in cold tolerance in assemblages inhabiting the North Temperate Zone. Our results thus indicate that distribution patterns of both taxa are influenced by both niche conservatism and niche evolution.

Keywords

Cold tolerance, diversification rates, geographic distribution, macroecology, macroevolution, phylogenetic niche conservatism, range edges, range size.

INTRODUCTION

Deciphering why species live where they do has long been a central issue in ecology and evolution (Darwin, 1859). The geographic range of a species reflects both its environmental tolerances and its geographical opportunities, now and in the past. Accordingly, ranges shift in response to environmental change (Parmesan & Yohe, 2003) and following specific

adaptations to cope with conditions beyond the range edge (Holt, 2003). Although some large-scale spatial patterns in geographic ranges have been found (such as a trend of increasing range size with distance from the equator; see Stevens, 1989), biogeographical and historical complexities make it unsurprising that closely related species often have very different range sizes (e.g. Freckleton *et al.*, 2002). If, however, large-scale range limits are largely governed by slowly evolving environmental tolerances (Wiens & Donoghue, 2004), then these limits will tend to be more similar among related species than are range sizes (Roy *et al.*, 2009).

Climatic niche conservatism has been defined as the tendency for species to retain aspects of their climatic niche over evolutionary time scales (Wiens & Graham, 2005). There has been debate recently over what constitutes niche conservatism: whether it is enough for phylogeny or taxonomy to explain significant variation in species traits or whether trait values specifically need to be more similar in closely related species than expected under a Brownian motion model of trait evolution (Harvey & Pagel, 1991; Losos, 2008; Wiens, 2008). We use the former, more permissive, definition. Under this view, niche conservatism is common and research attention switches from demonstrating it to measuring and comparing its strength in different traits, groups or regions. Different ecological characteristics often show widely different degrees of conservatism across the same set of species (Freckleton *et al.*, 2002). Here, we specifically test the strength of conservatism across a suite of potential range-limiting factors across two major vertebrate taxa, namely mammals and amphibians, to investigate which environmental aspects are most conserved within clades and are, therefore, implicated in having played the most important roles in limiting and structuring distributions at a broad scale (Soberón, 2007).

Detection of climatic niche conservatism (Harvey & Pagel, 1991; Wiens & Graham, 2005) depends on both taxonomic resolution and spatial scale (Losos, 2008; Wiens, 2008; Cooper *et al.*, 2010). Many genera and families are geographically restricted and so experience a limited range of environmental variation, making climatic niche conservatism harder to detect (Wiens & Graham, 2005). As an emergent species-level property, the range boundaries of species distributions are determined by biotic interactions, abiotic constraints or a combination of both. Hutchinson's (1978) niche concept provides a clear link between the observed geographical distribution of a species and the multiple biotic and abiotic dimensions limiting where a species can persist. While the fundamental niche represents all regions where a species could maintain a positive growth rate in the absence of biotic or dispersal limitation, observed species ranges correspond to realized niches, a subset of the fundamental niche (Soberón, 2007). Despite the difficulties involved in disentangling the relative contribution of biotic and abiotic factors in shaping observed range edges, there is strong support for climate as a major driver at continental and global scales (i.e. the Grinnellian niche, Soberón & Nakamura, 2009). Detection of conservatism in specific climatic requirements therefore suggests that those variables influence the broad-scale distribution of species and can be termed range-limiting factors (see also Cooper *et al.*, 2011, who made similar assumptions).

Despite the awareness that climatic niche conservatism may only become apparent at these broad spatial scales and higher phylogenetic levels, few phylogenetically inclusive global studies have been conducted to date. Hof *et al.* (2010) and Buckley *et al.* (2010) provide two exceptions. However, rather than investigate potentially important factors individually, Hof *et al.* (2010) instead used ordination techniques to derive single niche values for amphibians and Buckley *et al.* (2010) only investigated two climatic variables for continental mammals. Here, we use nearly complete global distributional databases to estimate conservatism in the climatic tolerances of two vertebrate taxa: continental mammals and amphibians. For each taxon, we compare the relative conservatism across a suite of potentially important variables to address the idea that different aspects of the niche may evolve independently (Freckleton *et al.*, 2002; Losos, 2008; Cooper *et al.*, 2010). We characterize the climatic niche of each species by using the suite of variables and separately investigate conservatism in each. Our goal is to identify those climatic factors that are most conserved within clades (and thus hypothesized to influence the distributions of many species in the clade) and those factors for which the tolerances of related species are more idiosyncratic. We also test whether the greater physiological sensitivity and lower dispersal abilities of amphibians compared to mammals have produced a stronger signal of conservatism in climatic range limits. Furthermore, we explore whether conservatism is stronger in the extreme values (minima or maxima) of environmental factors experienced by species in any part of their range than in whole-range averages. Finally, we map inferred recent changes in climatic tolerances to investigate spatial patterning in lineages that have escaped conservatism.

MATERIALS AND METHODS

Geographic distribution data for mammals and amphibians

Polygon shapefiles of the geographic ranges of each mammal and amphibian species were taken from the Global Mammal Assessment [GMA: http://www.iucnredlist.org/mammals; accessed 15 November 2008 (Schipper *et al.*, 2008)] and Global Amphibian Assessment [GAA: http://www.iucnredlist.org/amphibians; accessed 1 May 2008 (Stuart *et al.*, 2004)]. Because islands may be subject to different evolutionary processes, we excluded island endemics and any parts of species ranges that fell on islands. We also excluded wholly marine mammalian families within Cetartiodactyla, Carnivora and Sirenia, as well as the polar bear (*Ursus maritimus*) and the sea otter (*Enhydra lutris*). We matched the GMA species with the taxonomy of Wilson & Reeder (2005) as in Fritz & Purvis (2010), and the GAA with the taxonomy of Frost *et al.* (2006). The final data set contained 3878 mammal and 4165 amphibian species.

Environmental variables

Environmental variables came from the WorldClim database (Hijmans *et al.*, 2005; http://www.worldclim.org/current.htm) at 5 arc-min (= 0.083°) resolution and EDIT Geoplatform (http://edit.csic.es) at a resolution of 0.1°. Environmental factors thought to limit ranges of terrestrial vertebrates include ambient energy, primary productivity, water availability and their seasonal variation (Hawkins *et al.*, 2003). We chose four of the 19 BioClim variables available from WorldClim as well as normalized difference vegetation index (NDVI) remote-sensing data to address our hypotheses, on the basis of their importance for the ecology and distribution of vertebrates (see e.g. Aragón *et al.*, 2010). We used mean temperature of the warmest quarter (Bio10) and mean temperature of the coldest quarter (Bio11) to represent heat- and cold-tolerance and, together, tolerance to seasonal temperature variation. Similar alternative measurements such as maximum temperature of the warmest period or minimum temperature of the coldest period are probably too extreme and mostly capture outlier conditions unlikely to influence the long-term viability of all populations of each species. We used annual precipitation (Bio12) to capture cumulative water availability through a year, and precipitation seasonality (Bio15) to capture its seasonality, measured as the coefficient of variation of the weekly mean values. Finally, we used mean annual NDVI, calculated from monthly values for the period 1982–2000 (see EDIT Geoplatform, http://edit.csic.es, for details on data processing), to reflect primary productivity. We also calculated a measure of seasonality (coefficient of within-year variation) in NDVI, but it provided no additional information and was omitted from the final analyses. By using these fine-grain climatic datasets, we aim to characterize species climatic niches in a way that not only incorporates broad-scale macroclimatic effects, but also mesoscale climatic variation associated with elevational gradients. Note, however, that we do not attempt to characterize microclimatic factors that may be relevant for the habitat suitability of species at more local scales, e.g. micro-climatic variation in water availability for amphibians (Hillmann *et al.*, 2009).

We used the environmental variation within the geographic range of each species as a proxy of its realized niche (e.g. Hof *et al.*, 2010; Cooper *et al.*, 2011), under the assumption that distributions of species, at the coarse scale of our data, are primarily set by their environmental tolerances (Soberón & Nakamura, 2009; but see Pearson & Dawson, 2003). For each environmental variable, we characterized the tolerance of each species by calculating the mean, maximum and minimum values within its continental range (hereafter termed climatic niche measurements). At the coarse resolution of our analysis, our polygon-based range data (i.e. extent of occurrence) is congruent with survey-based data (see Hawkins *et al.*, 2008 and references therein) and, hence, is consistent with those that may be obtained from species distribution modelling approaches. We recognize that biotic interactions and different kinds of historical effects can also limit distributions, so our

measurements correspond to the realized rather than the fundamental niche (Soberón & Nakamura, 2009). However, quantitative genetic models (Case & Taper, 2000) suggest that even competitive limits may be strongest along steep environment gradients. Therefore, we assume that if we detect conservatism in any climatic extreme, it is in spite of any idiosyncratic effects.

We analyse these environmental variables separately, rather than processing them through a principal components analysis (as in e.g. Hof *et al.*, 2010), to preserve their interpretability and evaluate their individual importance. As expected, mean temperature of the warmest and coldest quarters are strongly correlated. This is, however, not a problem because we test each variable individually and are primarily interested in identifying which climatic variables are the most strongly conserved among species, with the aim of identifying that climatic factor along which related species diverge least. Finally, we also tested the absolute latitude of the centroid of each 0.1° grid cell, because latitude could be a proxy for as-yet-unidentified environmental factors (Hawkins & Diniz-Filho, 2004; see Appendix S1 in Supporting Information).

Data processing and statistical analyses

We first used a nested ANOVA to examine how variance in the climatic tolerances of species is partitioned among taxonomic levels (Hof *et al.*, 2010). Species were assigned to genera and families and these taxonomic levels were treated as random effects in a linear mixed-effects model fitted using restricted maximum likelihood with the R package 'nlme' (Pinheiro & Bates, 2000). Variance components were scaled to sum one. We tested the significance of each taxonomic level in two ways. First, we used likelihood ratio tests and Akaike's information criterion (AIC) values to compare the full model to models omitting a level. Second, we tested whether the 95% confidence intervals of each level's variance estimate included zero. We interpret greater than 50% variance explained above the species level as indicative of niche conservatism. To check whether the selection of this threshold may affect our perceptions on the existence of niche conservatism we additionally used more liberal (40%) and conservative (60%) thresholds for comparison. Very wide-ranging or narrowly distributed species can sometimes drive macroecological patterns (Jetz & Rahbek, 2002). Accordingly, we split species according to range size quartile and repeated the linear mixed-effects model within quartiles to test whether the taxonomic structure of niche conservatism varies with range size (see Appendix S1).

To complement the nested ANOVA analysis, we followed the approach of Roy *et al.* (2009) and quantified the tendency for tolerances to be more similar within than among genera, in units of the variable in question (rather than proportion of variance explained at higher taxonomic levels). For each climate niche measurement, the differences between pairs of species are calculated first for species within each genus and second for species across all genera. The test statistic is then

calculated as the median difference between these two distributions, and expresses the absolute magnitude of within-group similarity in the correct units. Differences were calculated separately for the three climate niche measurements (maximum, minimum and mean). We repeated this analysis at the family level (within- and between-family comparisons). Significance was assessed by randomly assigning taxonomic affinities across genera and families (depending on the level of analysis) while keeping the original number of species in each clade (1000 permutations).

Results of the analyses above could differ between mammals and amphibians simply if taxonomic levels are not comparable between the two groups. To assess the influence of family age on our results, we used Mann–Whitney *U*-tests to compare crown group ages of mammalian families taken from the mammal supertree (Fritz *et al.*, 2009), with amphibian family ages from each of two sources (Frost *et al.*, 2006; Roelants *et al.*, 2007). We also calculated ratios of genus-to-family ages (i.e. the average age of genera relative to their family age). Low values of this ratio indicate that genera are young relative to families. In two families of comparable age and conservatism, more variance would be attributed to genus level in the family with the lower ratio because the component genera have had less time for trait divergence. In the absence of a dated phylogeny, these results help indicate the extent to which our taxonomic results are truly comparable among the two taxa.

The validity of analyses of taxonomic structure, such as nested ANOVAs, depends on the extent to which taxonomic clustering directly reflects evolutionary relationships. We therefore also calculated Pagel's λ (Pagel, 1999), a measure of phylogenetic signal strength in comparative data, for our mammalian climatic niche measurements using the best available phylogeny (Fritz *et al.*, 2009) under the assumption that finding significant phylogenetic signal bolsters our inferences based on taxonomy (see also Roy *et al.*, 2009). We did not repeat this analysis for amphibians because Pagel's λ is a branch length transformation, and dating is not complete in the best-available amphibian phylogeny (see below).

Even if environmental tolerances are usually strongly conserved through evolutionary history, there will have been exceptions. Identifying lineages along which tolerances have shifted, and assemblages where many species show a change from ancestral environmental limits, may highlight the importance of adaptive innovations in structuring present-day assemblages. Ideally, we would assess divergent lineages by estimating ancestral states for the most conserved variable (i.e. mean temperature of the coldest quarter, see results below) and calculating the magnitude of deviations of species values from these to quantify independent evolution. However, currently available phylogenies may not be sufficiently resolved to permit these analyses; while the mammal supertree we use (Fritz *et al.*, 2009) is nearly complete, some parts of the tree are highly polytomous, and there is no well-resolved species-level amphibian phylogeny. Instead, we use the residuals from the

nested ANOVA as a coarse proxy of intra-generic evolution with negative values indicating an increased ability to tolerate cold.

For comparison, we also conducted phylogenetically explicit analyses using the mammal supertree (Fritz *et al.*, 2009) and a newly constructed genus-level amphibian supertree with all the species within each genus included as polytomies (Fritz & Rahbek, unpublished manuscript and see Appendix S2) and with all branch lengths set equal. We estimated ancestral states using a one-parameter maximum likelihood model (Brownian motion, Maddison, 1991) and estimated change in the cold tolerance of each species as the change in mean temperature of the coldest quarter along the terminal branch of the phylogeny leading to it. In well-resolved sections of the mammal tree, these changes estimate species-level change. In the amphibian tree, and within internally unresolved mammalian genera, they reflect deviations from the genus mean, as in the earlier analysis, but accounting for evolutionary relationships among genera. Given the reservations outlined above, these results must be interpreted with caution, but are still useful as an examination of the consistency of taxonomy- and phylogeny-based approaches.

For both methods, we combined these results with data on the occurrences of each species in the cells of a 96.5×96.5 km Behrmann projection global grid to calculate and map the mean inferred amount of recent evolution in cold tolerance within each grid cell, for amphibians and mammals separately. We also calculated cell-average differences between amphibians and mammals to map cross-taxon congruence.

We classified cells according to whether or not mean temperature in the coldest quarter dropped below 5 °C and defined species as escapees if any part of their range fell within these cold cells or as non-escapees if they were restricted to warmer climates. This threshold was defined on the basis of the relationship between temperature and plant growth (as measured by NDVI), following the procedure described in Olalla-Tárraga *et al.* (2006). We wished to test whether release from conservatism has impacted clade diversification by comparing the diversities of sister clades where one clade was exclusively composed of escapees and the other of non-escapees. However, because of polytomies in both the mammal and amphibian trees, only three valid phylogenetically independent contrasts were possible in each group precluding formal analysis.

Ideally, we would also have liked to estimate the effect of our binary character (escapee versus non-escapee) on diversification using a maximum likelihood-based model such as BiSSE (binary-state speciation and extinction, Maddison *et al.*, 2007). However, when we carried out this analysis on the dated mammal supertree (see Table S1a in Appendix S3), maximum likelihood extinction rates were estimated as zero for both character states, calling into question the validity of these results and suggesting that the lack of resolution or heterogeneity in rates across the phylogeny prevents robust conclusions being made at this time.

RESULTS

Nested ANOVAs show substantial variation in conservatism across climatic variables (Fig. 1, Table S1b in Appendix S3). Mean temperature in the coldest quarter was strongly conserved in both vertebrate classes: the proportion of variance explained above the species level across the three summary statistics (maximum, minimum and mean) ranged from 63.8% to 73.4% in amphibians and 50.3% to 65.8% in mammals (i.e. the sum of family and genus values in Table S1b). In amphibians, the highest proportion of variance for this variable was attributed to the family level, ranging from 40.0% to 48.5% across the three summary statistics. In mammals, however, although a similar amount of variance was explained above the species level, more of it was attributable to genera rather than families (Fig. 1). As for the consistency across climatic niche measurements, mean values generally showed as strong as or stronger taxonomic structure than did the minimum or maximum values.

Comparing within- and between-genus differences in climatic preferences to null expectations (Roy *et al.*, 2009) also indicated marked conservatism of mean temperature in the coldest quarter (Table 1). Results remained qualitatively the same after excluding monotypic genera (data not shown). Pagel's λ also indicates significant phylogenetic conservatism for the same set of variables in mammals (Table 1).

The observed signal in our nested ANOVAs was not an artefact of amphibian families being younger than those of mammals: they are older, whichever amphibian phylogeny is used [amphibians – Roelants *et al.* (2007): median = 66.1 Ma, Frost *et al.* (2006): 66.0 Ma, $n = 54$; mammals: median = 24.7 Ma, $n = 101$, Mann–Whitney U-test: $U = 325$ and $U = 316$, respectively, $P < 0.0001$].

The average ratio for genus-to-family ages was higher for amphibians (0.46) than mammals (0.33; Mann–Whitney U-test: $U = 6546$, $P < 0.0001$) which, even though ages were available for only 17% of amphibian genera, suggests that mammalian genera are relatively, as well as absolutely, younger than amphibian genera. This non-comparability of taxa between the two groups weakens comparisons of the depth of conservatism, but indicates that when conservatism is found to be stronger in amphibians, this conclusion is robust to taxonomic artefacts.

For both taxa, latitude (in absolute degrees) gave similar results to mean temperature in the coldest quarter (Fig. 1 and Table 1). We investigated whether the latitudinal signal was anything more than a proxy for climatic signal, but found no independent contribution of latitude (Appendix S1).

Global maps of the mean residuals from our nested ANOVA models highlighted regions where many of the species have recently shifted their tolerance to cold climates (Fig. 2). Results were qualitatively similar using ancestral trait reconstructions on phylogenies (Appendix S3), supporting the validity of our taxonomy-based analyses. As indicated by the strongly negative mean deviations (dark blue), mammal and amphibian assemblages inhabiting the northern Nearctic and Palaearctic regions can cope with much lower minimum temperatures in the coldest quarter than expected compared to their relatives (Fig. 2a,b, see also Appendix S3). On the contrary, few assemblages contained species whose cold tolerance is strongly under-predicted by phylogeny (red and orange cells in Fig. 2a,b). For both vertebrate classes, these under-predictions are clustered in northern Australia, Malaysia and the Ethiopian Highlands as well as in the Nubian Desert and southern parts of the Arabian Peninsula and Atlas Mountains for amphibians (see also Fig. S2 in Appendix S3). Our cross-taxon congruence map (Fig. 2c) picked out the latter regions, together with the
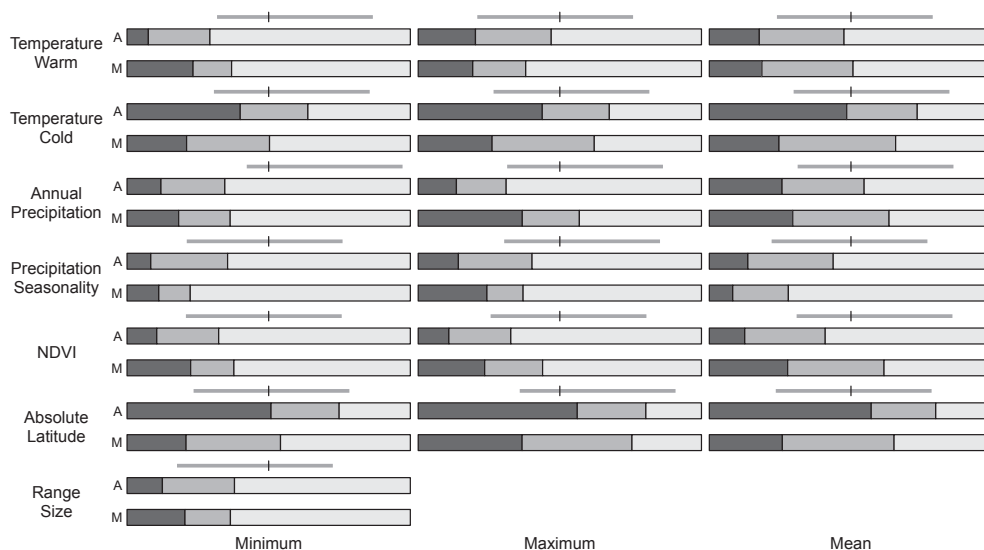
Figure 1 Taxonomic structure of the variance in climatic tolerances for amphibians (A) and mammals (M). The main bars show the proportion of variance attributed to families (dark grey), genera (mid grey) and species (light grey) by nested ANOVA. For each variable, the smaller bars show the relative sizes of the total variance associated with amphibians (left of the tick) and mammals (right of the tick). Abbreviations: Temperature warm/cold, mean temperature of the warmest/coldest quarter; NDVI, normalized difference vegetation index.

Table 1 Test statistics indicating whether species of amphibians and mammals are more similar in their climatic requirements within than between genera or families.

Taxon	Temp warm (°C)	Temp cold (°C)	Annual precipitation (mm)	Precipitation seasonality	NDVI	Absolute latitude (°)
Genus level comparisons						
Amphibians						
Max.	**0.3***	**1.6**	**−48.0***	**6.0**	0.0	**4.1**
Min.	**0.3***	**1.8**	**48.0**	**6.0**	**2.0**	**4.4**
Mean	0.1	**1.7**	**31.8***	**5.5**	0.0	**4.4**
Mammals						
Max.	**0.6**	**2.0**	**659.0**	**6.0**	**3.0**	**5.9**
Min.	**1.7**	**3.2**	**86.0**	**2.0***	**3.0**	**5.6**
Mean	**1.1**	**3.1**	**258.1**	**2.9**	**5.6**	**6.2**
Family level comparisons						
Amphibians						
Max.	**0.5**	**1.3**	**25.0***	**4.0**	**1.0**	**3.0**
Min.	**0.4**	**1.3**	**33.0**	**3.0**	**1.0***	**3.0**
Mean.	**0.4**	**1.3**	**48.5**	**3.5**	**1.0**	**3.0**
Mammals						
Max.	**0.2***	0.2	**293.0**	**4.0**	1.0	**0.5***
Min.	**0.9**	**0.8**	**33.0**	**−1.0***	**2.0**	**0.9**
Mean.	−0.4	**0.5**	**83.5**	0.3	**1.0**	**0.9**
Pagel's λ						
Mammals						
Max.	0.68	0.86	0.77	0.63	0.74	0.88
Min.	0.64	0.80	0.79	0.54	0.62	0.84
Mean.	0.84	0.88	0.71	0.88	0.90	0.86

Bold values are significant at $P < 0.001$, except values followed by * (significant at $P < 0.05$). Negative values indicate that closely related species are less similar than more distantly related species. Pagel's λ is 0 if there is no phylogenetic signal and 1 if the signal corresponds to expectation from Brownian motion; all values here are significantly different from 0 and 1 according to likelihood ratio tests.
Temp warm/cold, mean temperature of the warmest/coldest quarter; NDVI, normalized difference vegetation index.

Iberian and Italian peninsulas, as places where the mammals have evolved relatively greater cold tolerance than amphibians. Conversely, amphibian faunas of Canada, northern India and Patagonia have recently evolved greater cold tolerance than mammalian faunas there.

DISCUSSION

Our findings suggest that cold tolerance is a major limiting factor for the geographic distributions of both amphibians and mammals, apparently with broadly similar levels of conservatism in the two groups. Strong phylogenetic conservatism in cold tolerance has previously been reported for hylid frogs (Smith *et al.*, 2005; Wiens *et al.*, 2006). Our results show that the phenomenon is much more general, but that there are exceptions within each taxon – 'escapee' lineages that have shifted their cold tolerance. These expansions are associated with colonization of the North Temperate Zone, leading to the spatial aggregation of assemblages dominated by escapee species. Our results agree with a recent meta-analysis of experimental evidence (Sunday *et al.*, 2011) that showed that thermal tolerance breadth in terrestrial ectotherms – including amphibians – indeed changes latitudinally, mostly as a result of

increasing cold tolerance in northern temperate regions. Our results also reflect those of Cooper *et al.* (2011), who found greater conservatism of the thermal niche in tropical than temperate mammals.

Signals of conservatism in mammals and amphibians

While amphibians showed slightly stronger climatic niche conservatism than mammals for the most conserved variable, for other variables showing strong conservatism (e.g. annual precipitation), this conservatism was stronger in mammals than amphibians. These results also remained consistent under a more restrictive threshold for conservatism (60% variance accounted for above the species level). The variation in precipitation requirements across all amphibians is much more restricted than in mammals and the absence of strong phylogenetic signal in these variables may be due to this low variation and so be a simple reflection of the strict minimum water requirements of amphibians. Above this minimum, precipitation is no longer a limiting factor. Conversely, mammals are capable of persisting under a wider range of precipitation regimes, with conservatism for particular regimes apparent above the species level.
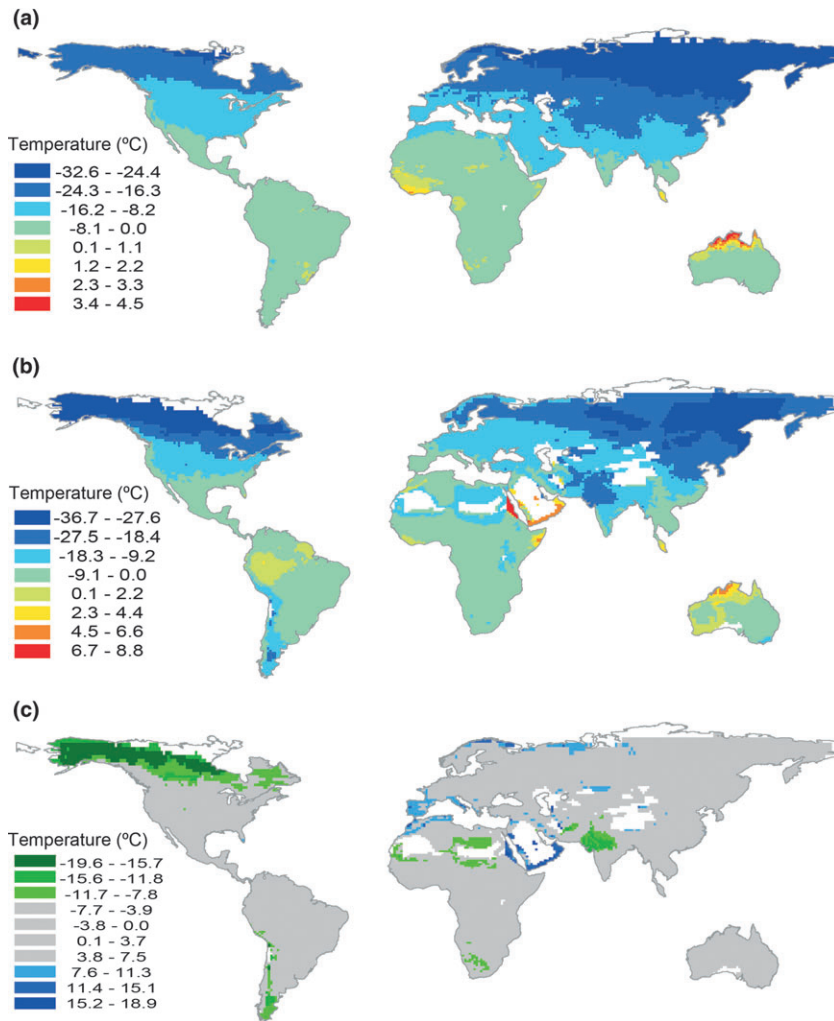
Figure 2 Spatial patterning of recent evolution in cold tolerance for mammals and amphibians. Mean assemblage (grid cell) values for recent evolution in cold tolerance calculated as the average residuals from a nested ANOVA (see main text) for the species occurring in each cell. (a) Mammals, (b) amphibians (equal-intervals above and below zero are used in the colour scale), and (c) their difference (amphibians minus mammals). Only extreme differences are coloured; white cells are unoccupied by amphibians; grey cells are those where the difference is small. The temperature range is for mean temperature of the coldest quarter.

Our results must be interpreted bearing in mind that amphibian and mammalian taxonomists may or may not be acting equivalently. Mammalian families are younger than amphibian families and, on average, mammalian genera are also younger relative to the age of their family than is the case for amphibians. This indicates that, for a given proportion of variance explained at the genus or family level, the variable in question is more conserved in amphibians than in mammals, as amphibians had more time for divergence. This does not mean that the mammalian signal is not real; simply that it is less 'impressive' than the amphibian one. The absence of a dated phylogeny for amphibians prevents more formal analyses of the rate of evolution of the climatic tolerances of this group (Ackerly, 2009). However, our observation that amphibians, with, on average, older families and older genera than mammals, have more limited variation and similarly strong levels of conservatism in cold tolerance, strongly suggests they must have evolved more slowly along this niche axis. Indeed,

the younger average age of mammalian genera and families may partly be a reflection of this faster rate of evolution (Simpson, 1953). Indeed, it is possible that differences in the branching patterns within clades may be contributing to the observed differences between the two groups (O'Meara *et al.*, 2006).

That most of the variation in amphibians was strongly structured at the family level for cold tolerance, but not for the remaining variables, may be due to the ectothermicity of this group. That is, even though many amphibian species (especially anurans) can regulate their body temperatures within narrow ranges through behavioural and physiological adjustments (see e.g. Hillmann *et al.*, 2009), as ectothermic organisms they rely on external sources for heat gain and are unable to produce metabolic heat to the levels of mammals. In colder environments, amphibian heating rates are lower and thermoregulation is severely limited, which, in turn, affects their operative temperatures and activity times. Under prolonged

cold conditions, amphibians survive by decreasing metabolic rates and resorting to overwintering strategies (i.e. spending most of the year inactive in burrows or under logs). These responses appear to have been established early in the evolutionary history of the clade and are consistent with a recent interpretation of the amphibian fossil record. Sahney *et al.* (2010) have suggested that climate aridification through the later Palaeozoic, which eventually led to the collapse of Carboniferous Coal Forests, favoured the ecological diversification of amniotes (reptiles) but had devastating effects on amphibian faunas. Mainly as a result of their limited capacity to adapt to the drier conditions that dominated Permian environments, many amphibian families failed to occupy new ecological niches (in terms of climate preference, body size or diet) and went extinct. A more nuanced understanding of the temporal dynamics of niche evolution and clade diversification in amphibians must await a well-resolved and dated amphibian phylogeny (e.g. Kozak & Wiens, 2006, 2010 for plethodontid salamanders).

Recent evolution of cold tolerance

Our map comparing the changes in cold tolerance of amphibians and mammals suggests that the amphibian species inhabiting the northern-most latitudes show more pronounced shifts in cold tolerance than mammals do. Amphibian species able to survive in northern parts of the Nearctic, Western Palaearctic and Siberia (seven anurans and the Siberian salamander) have evolved to tolerate freezing: they are able to convert 50% or more of their total body water into extracellular ice (Hillmann *et al.*, 2009). Conversely, mammals in the Iberian and Italian peninsulas have shifted their cold tolerance more than amphibians have. These mammalian faunas consist of species whose ranges stretch northwards into much colder areas, whereas the amphibian faunas are largely endemic to the peninsulas themselves so their cold tolerances reflect only Mediterranean minimum temperatures. This result may echo the different rates of emergence of the two groups from southern refugia following the retreat of the Pleistocene glaciers: while many mammal species have been able to expand out of these refugia, most amphibians have shown more limited recolonization abilities or greater specialization to Mediterranean habitats. Araújo *et al.* (2008) argue that the scarcity of amphibian species further north may result from either dispersal limitation or stronger physiological constraints stemming from their being ectotherms. It remains unresolved which hypothesis is more important; however, the fact that even wide-ranging European amphibians are limited by climate (Araújo *et al.*, 2008) and the successful dispersal of other 'poor' dispersers out of glacial refugia (e.g. some European trees, Svenning & Skov, 2007) suggest that physiological limitations may be more important in constraining amphibian rather than mammalian diversity, at least in Europe. Further research is needed to determine whether this limitation is due to the basic ecophysiological organization of the clade (as we suggest above) or to difficulties in evolving

new adaptations to cold environments for particular subclades only.

We wanted to test whether the hypothesis that species currently occupying northern latitudes are members of a relatively small number of 'escapee' clades nested within tropical clades (Jablonski *et al.*, 2006; Wiens *et al.*, 2006; Buckley *et al.*, 2010) and whether escape from conservatism has led to rapid diversification following entry into new niche space (Simpson, 1953). Due to the lack of resolution in both the mammal and amphibian phylogenies, we could identify few valid sister-clade contrasts, thus precluding formal analyses. If diversity only needs time and space to accumulate, diversification since the appearance of large geographical areas of new temperate and boreal environments in the Miocene should have produced many new species. However, other factors are probably necessary to build up diversity, in particular habitat heterogeneity, climatic stability and consistent energy availability (Stephens & Wiens, 2003; Mittelbach *et al.*, 2007; Kisel *et al.*, in press). Escapee clades may thus be depauperate due to higher rates of extinction during glacial cycles or due to selection for generalism favouring large-range species better able to cope with fluctuating climates (over geological time) and strong annual seasonality (Davies *et al.*, in press).

Niche conservatism in means versus extremes

We had hypothesized that the extreme values of environmental variables that species experience would relate most closely to the phylogenetically conserved physiological traits underlying species tolerances (Soberón & Nakamura, 2009), and therefore would show stronger conservatism than average values of environmental variables across species ranges. However, mean values of climatic variables had similar amounts of taxonomic structure as minima or maxima. These findings concur with those of Wiens *et al.* (2006) and Martin & Husband (2009) for mean and extreme values in hylid frogs and North American angiosperms, respectively. Given the broad-scale spatial autocorrelation in climatic variables, it is unlikely that slight discrepancies between actual and modelled distributions would cause grossly incorrect estimates of climatic requirements. Nevertheless, one possible explanation for the strong signals found for mean values is that they correlate better with actual tolerances than extreme values do simply because centres of distributions are easier to characterize than are extremes. Part of our signal strength could also stem from the spatial autocorrelation in climatic variation: related species may have similar climatic tolerances due to their geographic proximity (despite having very different range sizes if, for instance, one is a peripheral isolate of the other). Indeed, Cooper *et al.* (2011) found that the spatial component of various aspects of the mammalian climatic niche was significant for that reason. However, the congruence in conservatism for mean and extreme values suggests that our results are not driven purely by spatial proximity in range edges (e.g. abutting sister species) but rather reflect conserved climatic tolerances across the range.

Concluding remarks

All our environmental variables showed conservatism that was stronger than or similar to that for geographic range size itself, suggesting that much of the interspecific variation in range size might reflect that simple 'rules' such as threshold tolerances and dispersal limitation are being played out on a complex surface. Most vertebrate speciation is allopatric, contingent on the location and timing of formation of range-splitting barriers (Coyne & Orr, 2004). We here show that among related species and for certain climatic factors – cold tolerance in particular – climatic requirements remain similar following speciation events, while range sizes may be very different. With better-resolved phylogenies it will become possible to explore how niche conservatism and evolution have affected diversification within these two groups.

REFERENCES

Ackerly, D.D. (2009) Conservatism and diversification of plant functional traits: evolutionary rates versus phylogenetic signal. *Proceedings of the National Academy of Sciences USA*, **106**, 19699–19706.

Aragón, P., Lobo, J.M., Olalla-Tárraga, M.Á. & Rodríguez, M.Á. (2010) The contribution of contemporary climate to ectothermic and endothermic vertebrate distributions in a glacial refuge. *Global Ecology and Biogeography*, **19**, 40–49.

Araújo, M.B., Nogués-Bravo, D., Diniz-Filho, J.A.F., Haywood, A.M., Valdes, P.J. & Rahbek, C. (2008) Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography*, **31**, 8–15.

Buckley, L.B., Davies, T.J., Ackerly, D.D., Kraft, N.J.B., Harrison, S.P., Anacker, B.L., Cornell, H.V., Damschen, E.I., Grytnes, J.-A., Hawkins, B.A., McCain, C.M., Stephens, P.R. & Wiens, J.J. (2010) Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 2131–2138.

Case, T.J. & Taper, M.L. (2000) Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *The American Naturalist*, **155**, 583–605.

Cooper, N., Jetz, W. & Freckleton, R.P. (2010) Phylogenetic comparative approaches for studying niche conservatism. *Journal of Evolutionary Biology*, **23**, 2529–2539.

Cooper, N., Freckleton, R.P. & Jetz, W. (2011) Phylogenetic conservatism of environmental niches in mammals. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 2384–2391.

Coyne, J.A. & Orr, H.A. (2004) *Speciation*. Sinauer Associates, Inc., Sunderland, MA.

Darwin, C. (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life.* John Murray, London.

Davies, T.J., Buckley, L.B., Grenyer, R. & Gittleman, J.L. (in press) The influence of past and present climate on the biogeography of modern mammal diversity. *Philosophical Transactions of the Royal Society B: Biological Sciences*.

Freckleton, R.P., Harvey, P.H. & Pagel, M. (2002) Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist*, **160**, 712–726.

Fritz, S.A. & Purvis, A. (2010) Phylogenetic diversity does not capture body size variation at risk in the world's mammals. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 2435–2441.

Fritz, S.A., Bininda-Emonds, O.R.P. & Purvis, A. (2009) Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecology Letters*, **12**, 538–549.

Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., de Sá, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M. & Wheeler, W.C. (2006) The amphibian tree of life. *Bulletin of the American Museum of Natural History*, **297**, 8–370.

Harvey, P.H. & Pagel, M.D. (1991) *The comparative method in evolutionary biology*. Oxford University Press, Oxford.

Hawkins, B.A. & Diniz-Filho, J.A.F. (2004) 'Latitude' and geographic patterns in species richness. *Ecography*, **27**, 268–272.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufmann, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.

Hawkins, B.A., Rueda, M. & Rodriguez, M.Á. (2008) What do range maps and surveys tell us about diversity patterns? *Folia Geobotanica*, **43**, 345–355.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hillmann, S.S., Withers, P.C., Drewes, R.C. & Hillyard, S.D. (2009) *Ecological and environmental physiology of amphibians*. Oxford University Press, Oxford.

Hof, C., Rahbek, C. & Araújo, M.B. (2010) Phylogenetic signals in the climatic niches of the world's amphibians. *Ecography*, **33**, 242–250.

Holt, R.D. (2003) On the evolutionary ecology of species' ranges. *Evolutionary Ecology Research*, **5**, 159–178.

Hutchinson, G.E. (1978) *An introduction to population biology*. Yale University Press, New Haven, CT.

Jablonski, D., Roy, K. & Valentine, J.W. (2006) Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, **314**, 102–106.

Jetz, W. & Rahbek, C. (2002) Geographic range size and determinants of avian species richness. *Science*, **297**, 1548–1551.

Kisel, Y., McInnes, L., Toomey, N.H. & Orme, C.D.L. (in press) How diversification rates and diversity limits combine to create large-scale species–area relationships. *Philosophical Transactions of the Royal Society B: Biological Sciences*.

Kozak, K.H. & Wiens, J.J. (2006) Does niche conservatism promote speciation? A case study in North American salamanders. *Evolution*, **60**, 2604–2621.

Kozak, K.H. & Wiens, J.J. (2010) Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters*, **13**, 1378–1389.

Losos, J.B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, **11**, 995–1003.

Maddison, W.P. (1991) Squared-change parsimony reconstructions of ancestral states for continuous-valued characters on a phylogenetic tree. *Systematic Zoology*, **40**, 304–314.

Maddison, W.P., Midford, P.E. & Otto, S.P. (2007) Estimating a binary character's effect on speciation and extinction. *Systematic Biology*, **56**, 701–710.

Martin, S.L. & Husband, B.C. (2009) Influence of phylogeny and ploidy on species ranges of North American angiosperms. *Journal of Ecology*, **97**, 913–922.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V. *et al.* (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**, 315–331.

Olalla-Tárraga, M.Á., Rodríguez, M.Á. & Hawkins, B.A. (2006) Broad-scale patterns of body size in squamate reptiles of Europe and North America. *Journal of Biogeography*, **33**, 781–793.

O'Meara, B.C., Ané, C., Sanderson, M.J. & Wainwright, P.C. (2006) Testing for different rates of continuous trait evolution using likelihood. *Evolution*, **60**, 922–933.

Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature*, **401**, 877–884.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.

Pinheiro, J.C. & Bates, D.M. (2000) *Mixed-effects models in S and S-Plus*. Springer, New York.

Roelants, K., Gower, D.J., Wilkinson, M., Loader, S.P., Biju, S.D., Guillaume, K., Moriau, L. & Bossuyt, F. (2007) Global patterns of diversification in the history of modern amphibians. *Proceedings of the National Academy of Sciences USA*, **104**, 887–892.

Roy, K., Hunt, G., Jablonski, D., Krug, A.Z. & Valentine, J.W. (2009) A macroevolutionary perspective on species range limits. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1485–1493.

Sahney, S., Benton, M.J. & Falcon-Lang, H.J. (2010) Rainforest collapse triggered Carboniferous tetrapod diversification in Euramerica. *Geology*, **38**, 1079–1082.

Schipper, J., Chanson, J.S., Chiozza, F., Cox, N.A., Hoffmann, M., Katariya, V., Lamoreux, J., Rodrigues, A.S.L., Stuart, S.N., Temple, H.J. & Baillie, J. (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science*, **322**, 225–230.

Simpson, G.G. (1953) *The major features of evolution*. Columbia University Press, New York.

Smith, S.A., Stephens, P.R. & Wiens, J.J. (2005) Replicate patterns of species richness, historical biogeography, and phylogeny in Holarctic treefrogs. *Evolution*, **59**, 2433–2450.

Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, **10**, 1115–1123.

Soberón, J. & Nakamura, M. (2009) Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences USA*, **106**, 19644–19650.

Stephens, P.R. & Wiens, J.J. (2003) Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. *The American Naturalist*, **161**, 112–128.

Stevens, G.C. (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *The American Naturalist*, **133**, 240–256.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L. & Waller, R.W. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science*, **306**, 1783–1786.

Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2011) Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 1823–1830.

Svenning, J.-C. & Skov, F. (2007) Ice age legacies in the geographical distribution of tree species richness in Europe. *Global Ecology and Biogeography*, **16**, 234–245.

Wiens, J.J. (2008) Commentary on Losos (2008) Niche conservatism déjà vu. *Ecology Letters*, **11**, 1004–1005.

Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution*, **19**, 639–644.

Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 519–539.

Wiens, J.J., Graham, C.H., Moen, D.S., Smith, S.A. & Reeder, T.W. (2006) Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. *The American Naturalist*, **168**, 579–596.

Wilson, D.E. & Reeder, D.M. (eds) (2005) *Mammal species of the world: a taxonomic and geographic reference*. John Hopkins University Press, Baltimore, MD.

SUPPORTING INFORMATION

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

Appendix S1 Latitude and range size analysis.
Appendix S2 Amphibian phylogeny construction.
Appendix S3 Results of additional analyses.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCHES

Miguel Á. Olalla-Tárraga is an assistant professor broadly interested in biogeography and global change, with a particular emphasis on the macroecology, macroevolution and conservation of terrestrial vertebrates.

Lynsey McInnes is a PhD student interested in the macroecology and macroevolution of diversity limits. Her work employs phylogenetic and biogeographical approaches across different temporal and spatial scales.

Author contributions: M.Á.O.-T., L.M. and A.P. conceived the study and designed the analyses with contributions from L.M.B., J.A.F.D.-F., B.A.H., J.H., C.D.L.O., C.R. and M.Á.R; M.Á.O.-T. and L.M. performed the analyses; M.Á.O.-T., S.A.F., C.D.L.O., C.R. and M.Á.R. contributed data. M.Á.O.-T., L.M. and A.P. wrote the paper and all authors commented on the manuscript.

Editor: Peter B. Pearman