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ORIGINAL ARTICLE

Mean body sizes of amphibian species are poorly predicted by climate 1

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ABSTRACT

Aim Climate is thought to exert a strong influence on animal body sizes. We examined the relationship between amphibian body size and several climatic variables to discern which climatic variables, if any, affect amphibian size evolution.

Location Europe and North America.

Methods We assembled a dataset of mean sizes of 356 (out of 360) amphibian species in Europe, the USA and Canada, and tested how they are related to temperature, precipitation, primary productivity and seasonality. First, we examined the body size distributions of all the species inhabiting equal-area grid cells (of 96.3 km × 96.3 km) using randomizations to account for the effects of species richness. Second, we examined the relationship between mean species body size and the environmental predictors across their ranges accounting for phylogenetic effects.

Results The observed amphibian body size distributions were mostly statistically indistinguishable from distributions generated by random assignment of species to cells. Median sizes in grid cells were negatively correlated with temperature in anurans and positively in urodeles. The phylogenetic analysis revealed opposite trends in relation to temperature. In both clades most climatic variables were not associated with size and the few significant relationships were very weak.

Main conclusions Spatial patterns in amphibian body size probably reflect diversity gradients, and relationships with climate could result from spurious effects of richness patterns. The large explanatory power of richness in the grid-cell analysis, and the small explanatory power of climate in the interspecific analysis, signify that climate per se has little effect on amphibian body sizes.

Keywords

Amphibians, Bergmann's rule, ectotherms, Europe, grid-cell analysis, North America, phylogenetic analysis, size clines.

INTRODUCTION

Climate has been shown to have a strong effect on large-scale body-size gradients of endotherms (e.g. intraspecific: James, 1970; Ashton *et al.*, 2000; Ashton, 2002a; interspecific: Blackburn & Hawkins, 2004; Olson *et al.*, 2009). However, despite years of intense study, its effect on continental-level gradients in ectotherms is still debated (e.g. intraspecific: Ashton & Feldman, 2003; Pincheira-Donoso & Meiri, 2013; interspecific: Olalla-Tárraga *et al.*, 2006; Pincheira-Donoso *et al.*, 2008; Terribile *et al.*, 2009; Feldman & Meiri, 2014). Several hypotheses have been proposed to explain the effect of climate on body size. The heat conservation hypothesis (Bergmann, 1847) posits that a reduced surface area-to-volume ratio in larger animals gives them an advantage in conserving heat in cold climates. However, the applicability of this hypothesis to ectotherms is debated because they do not generate substantial heat by metabolic activity. Alternative

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hypotheses regarding geographical patterns of body size may therefore be more relevant to ectotherms. The primary productivity hypothesis (Rosenzweig, 1968) posits that animals evolve larger sizes in more productive areas, where abundant resources help maintain a larger size (McNab, 2010). The water availability hypothesis (Ashton, 2002b) posits that a small surface area-to-volume ratio facilitates water conservation in dry environments and body size thus increases in arid areas. The starvation resistance hypothesis (Lindsey, 1966; Boyce, 1979) posits that large body size is selected for in seasonal areas because larger animals have greater food reserves, which they utilise more slowly, enabling them to survive long periods of food scarcity. In contrast, the seasonality hypothesis (Van Voorhies, 1996; Mousseau, 1997) proposes the opposite: in seasonal regions, where the growing season is short, there is less time for growth and so animals mature at a smaller size. A common feature of all these hypotheses is that they each posit a role for climate, whether direct or indirect, in shaping size clines.

Relationships between body size and environmental factors are often examined by dividing space into grid cells and assigning some measure of central tendency (e.g. mean and median) of body size to each. This mean or median is then regressed against different environmental factors. While this approach is straightforward, it does have several limitations. First, spatial data are spatially autocorrelated, and this autocorrelation needs to be accounted for using statistical methods such as simultaneous autoregression of spatial errors (SAR; Dormann *et al.*, 2007). Second, the method is sensitive to species richness, especially when using mean body size. Because species are not randomly assigned to cells, and because of greater spatial turnover of small species, the mean body size is usually small in species-rich cells (Brown & Nicoletto, 1991; Cardillo, 2002; Olson *et al.*, 2009), probably for reasons independent of climatic selection on size itself. Most species within clades are small, and species richness increases towards the tropics. Size ranges, however, are spatially relatively uniform (Brown & Nicoletto, 1991). Spatial trends in body size could therefore merely reflect diversity gradients, as more small-bodied species can be found in species-rich cells. Thus community assembly processes could create spatial body size patterns without climate-based selection on size. Richness therefore needs to be accounted for.

Mean body size of species within grid cells may also be a poor measure of central tendency of body size, as it is sensitive to the skewness of the body size frequency distribution, making the median or mode superior size indices (Meiri & Thomas, 2007). Furthermore, selection does not act on cross-species averages (Adams & Church, 2011). The assumption that the central tendency of body size in each grid cell is being optimized is therefore problematic. Last, and perhaps most importantly, grid-cell analyses do not account for phylogeny. Spatial trends in body size could reflect taxon turnover and not actual adaptations to different environmental pressures. A method for incorporating phylogeny into assemblage-level grid-cell analyses, phylogenetic eigenvector regression, exists (Diniz-Filho *et al.*, 1998). However, this method has severe statistical limitations and probably does not adequately account for the effects of phylogeny (Adams & Church, 2011; Freckleton *et al.*, 2011).

Using data on the amphibians in Europe and North America, we used two methods to determine whether climate is related to amphibian body size: a spatial grid cell-based approach and an interspecific phylogenetic approach. The second approach is conservative because it does not encapsulate the entire range of body sizes and environments a species inhabits. It also examines each species once only, whereas a grid-cell test uses a species in all the grid cells it inhabits (and therefore gives much more weight to larger ranged species). Interspecific tests allow phylogeny to be taken into account and compare closely related species, accounting for the possibility of a size cline merely reflecting taxon turnover (Meiri & Thomas, 2007). A grid-cell approach thus examines how size distributions of assemblages change over space, while a species-level phylogenetic approach examines how size evolves within and between clades. The two methods are complementary and allowed us to examine both the spatial and phylogenetic components of amphibian size variation.

MATERIALS AND METHODS

Species data

Europe and North America are inhabited by 360 extant amphibian species (excluding island endemics; Frost, 2012). These include 141 species of anurans (40 in Europe and 101 in North America) and 219 species of urodeles (29 in Europe and 190 in North America), including many species that have been recently described or split. These values are *c.* 30% higher than those used in previous analyses (122 anurans and 153 urodeles; Olalla-Tárraga & Rodríguez, 2007). Olalla-Tárraga & Rodríguez (2007) omitted five species of small, northern North American frogs, which have physiological adaptations to cold climates, arguing that these adaptations necessitate their removal from body-size analyses. We reason that having physiological or behavioural adaptations to climate does not preclude adaptations in the form of body size or shape to deal with the same selective pressures (Mayr, 1956). The removal of such species is likely to have a strong bias on the results of size–climate analyses because all are small, inhabit cold climates and have very large ranges, thus affecting size estimates in multiple grid cells. We therefore included these species in our analyses.

We obtained mean body sizes for all species from field guides (for North America: Behler & King, 1979; Degenhardt *et al.*, 1996; Conant & Collins, 1998; Stebbins, 2003; Lemm, 2006; Jensen *et al.*, 2008; Brennan & Holycross, 2006; Beane [3] *et al.*, 2010; Stebbins & McGinnis, 2012; for Europe: Arnold, 2002; Kwet, 2009; Masó & Pijoan, 2011) and primary literature (see Appendix S1 in Supporting Information), using as many sources as we were able to find for each species to reduce possible bias. Body mass may be a better index for body size than length, as it also takes shape into account (Feldman & Meiri, 2013). Indeed, the longest urodele in our dataset, *Amphiuma tridactylum* (mean total length 758.5 mm), weighs ~~only~~ about 50% less than the fifth longest, *Cryptobranchus alleganiensis* (mean total length 450 mm) (Martin & Hutchison, 1979). However, amphibian masses are rarely reported, forcing us to use body length as a measure of body size. The standard body size measurement for anurans is the snout–vent length (SVL). Total length (TL = SVL + tail length) is a more common measurement for urodeles. We therefore used SVL as the size index for anurans and TL as the size index for urodeles, and analysed both orders separately.

We used mean body sizes of each species, as opposed to maximum body sizes (which is the most common index in similar studies; e.g. Olalla-Tárraga & Rodríguez, 2007), because the mean is less dependent on sample size. It probably also represents species better, because maximum body sizes can reflect extreme outliers rather than the population as a whole. Where mean body size was unavailable we calculated the mid-point between the maximum and minimum adult body size data or, preferably, the average of mean male and mean female body sizes. When multiple means were available for a species (e.g. from different sources) we calculated the average of all published means. Length data were $\log_{10}$ transformed for all analyses.

We downloaded ArcGIS shapefiles (ESRI, Redlands, CA, USA) of individual amphibian species distribution maps from the IUCN Red List database (IUCN, 2012). Several species lack IUCN distribution maps, having been recently split from other species or not yet assessed. For these we digitized distribution maps from field guides (Conant & Collins, 1998; Beane *et al.*, 2010; Masó & Pijoan, 2011), the primary literature and online databases (Recuero *et al.*, 2006; Crespi *et al.*, 2010; Caudata.org, 2012; Garcia-Porta *et al.*, 2012; Jockusch *et al.*, 2012; Streicher *et al.*, 2012; Wielstra *et al.*, 2013; Green *et al.*, 2014) using ArcGIS 10.0 (ESRI).

We omitted four species for which we did not have mean body size estimates (*Aneides iecanus*, *Aneides niger*, *Batrachoseps nigriventris* and *Plethodon ainsworthi*). This left us with 141 species of anurans (40 in Europe and 101 in North America) and 215 species of urodeles (29 in Europe and 186 in North America).

To account for the effects of phylogenetic non-independence on resulting patterns, we used a phylogeny of extant amphibians from Pyron & Wiens (2011). We modified this tree using the latest phylogeny of Ambistomatidae (Williams *et al.*, 2013) and added species missing from the phylogeny of Pyron & Wiens (2011) from published accounts using PhyloWidget (Jordan & Piel, 2008). We scaled the branches using cladogram transform in FigTree 1.3.1 (Rambaut, 2010) to create an ultrametric tree, as branch lengths were missing from the source trees. The final composite phylogeny was used for the study; the full list of sources used in its compilation are given in Appendix S2.

Environmental data

We downloaded temperature and precipitation data from WorldClim (http://www.worldclim.org; Hijmans *et al.*, 2005), and net primary productivity (NPP) data from the Socioeconomic Data and Applications Center (SEDAC) website (http://sedac.ciesin.columbia.edu/es/hanpp.html; Imhoff *et al.*, 2004). We extracted data on mean, minimum and maximum annual temperatures, temperature seasonality (the standard deviation of temperature across months; all in degrees centigrade), mean annual precipitation, and minimum and maximum precipitation of the driest and wettest month (in mm/year). WorldClim data were for the period of 1950–2000 at a spatial resolution of 1/10 degree. Data on mean annual NPP (in grams of carbon × (1/[year × m^2]); log transformed) were at a quarter-degree scale.

Statistical analyses

Grid-cell analysis

For the grid-cell analysis we used median body sizes within grid cells, with a 96.3 km × 96.3 km (*c.* 1° × 1° at the equator) grid on a Behrmann equal area projection (ESRI). We accounted for spatial autocorrelation using SAR (Dormann *et al.*, 2007) with the spdep package in R (Bivand *et al.*, 2011). We ran the same analyses using the minimum and maximum values of body size per grid cell as the response variable, to examine how body size distributions are affected by climatic variables. If climate exerts strong selection pressure on size (e.g. if small size is selected against in cold regions), it is reasonable to assume that extreme sizes will be affected more strongly than median sizes. Extreme sizes, however, are more likely to be found in species-rich cells. Hence we used richness as a predictor in all analyses. As R^2 values are impossible to derive from SAR models, we calculated Nagelkerke pseudo R^2 values as an estimate of goodness-of-fit of models using the BaylorEdPsych package in R (Beaujean, 2012).

To test further for the effects of species richness and range size on amphibian size in grid-cell assemblages, we ran randomization tests. We generated 1000 random datasets of amphibian assemblages per grid cell (using observed richness values), where the probability of selecting a species for the assemblage was proportional to its range size (Olson *et al.*, 2009), to calculate the null distribution of median body sizes per grid cell. We then compared this null distribution with our observed values. Such a test does not capture the continuous nature of ranges (i.e. randomized ranges are allowed be to disjunct). However, randomizing continuous ranges would also result in changing the distribution of richness values and the ratio between species-poor and species-rich cells. Therefore, our tests appeared to be adequate for examining whether or not the observed richness distribution could generate, by random processes alone, the observed body size distributions.

Interspecific analysis

We used the mean, minimum and maximum values of the environmental factors across each species' distribution as size predictors, to account for environmental variability across each species' range. Because of the high collinearity between mean, minimum and maximum values, we ran the analyses separately for each set of factors (e.g. mean temperature, mean precipitation and mean NPP versus maxima of all measures). We omitted two hybrid species (*Pelophylax esculentus* and *Pelophylax grafi*; Frost, 2012) and the paraphyletic *Batrachoseps major* (Jockusch *et al.*, 2001) from the phylogenetic analyses. We also omitted *Batrachoseps robustus* and *Eurycea robusta*, for which no phylogenetic data were available. The dataset therefore comprised 139 anuran species (38 in Europe, 101 in North America) and 212 urodele species (29 in Europe, 183 in North America).~~A~~

~~B~~

We ran a phylogenetic generalized least square (PGLS) regression (Freckleton *et al.*, 2002) using the CAPER package in R (Orme *et al.*, 2012) to estimate the maximum likelihood value of the scaling parameter λ. All statistical analyses were performed in R 3.0.2 (R Core Team, Vienna, Austria) using the RSTUDIO 0.98.978 (RStudio Inc., Boston, MA, USA) interface.

Some urodele species are obligatory cave-dwellers (*Proteus anguinus* in Europe; Sindaco *et al.*, 2006; *Eurycea rathbuni*, *Eurycea robusta*, *Eurycea spelaea*, *Eurycea tridentifera*, *Eurycea wallacei*, *Gyrinophilus gulolineatus* and *Gyrinophilus palleucus* in North America; Green *et al.*, 2014). We re-ran all analyses (both SAR and PGLS) without the cave-dwelling species. The results of these analyses did not differ qualitatively from those obtained using the complete dataset (data not shown). We therefore present the results from the complete dataset. We also ran the analyses separately for North America and Europe (for each order). The results of these separate analyses are shown in Appendix S3.

RESULTS

Grid-cell analysis

Three factors were correlated with median body size in both orders: richness, mean temperature and temperature seasonality (Table 1). Median anuran body size decreased with increasing richness (Fig. 1a and Fig. 2a), temperature and seasonality. The size of the smallest anurans within grid cells decreased with richness, temperature, seasonality and NPP, and increased with precipitation. The size of the largest anurans showed opposite trends with most of these variables: it increased with richness, temperature and NPP, and decreased with seasonality and precipitation (Table 1). The removal of all the climatic variables from the model caused very limited reduction in pseudo R^2 (0.58 with and 0.55 without climatic variables). While caution should be used in the interpretation of pseudo R^2 values, these results suggested that climatic variables were not strong predictors of median SVL. Furthermore, while there seemed to be a latitudinal trend in median sizes of European anurans (but note the Balkans), median sizes in North American grid cells showed no clear latitudinal trend but rather complex longitudinal ones (Fig. 2a).

Urodele body size showed trends that were mostly opposite to those of the anurans (Fig. 1b and Fig. 2b). Median body size increased with increasing temperature and seasonality. Urodele median TL was also negatively correlated with mean NPP, although, as with anurans, there was no clear latitudinal trend in North America (Fig. 2b). Both minimum and maximum TL of urodeles increased with temperature. However, they showed divergent trends in respect to richness and NPP, and while the size of the smallest urodeles increased with seasonality and precipitation, the size of the largest was uncorrelated with either of these variables (Table 1). The removal of climatic variables from this model likewise resulted in a very minor decrease of pseudo R^2 (0.82 with and 0.8 without climatic variables), suggesting that,

Table 1 Summary table of the simultaneous autoregression of spatial errors (SAR) models of anuran and urodele body size (snout–vent length for anurans and total length for urodeles) for species from Europe and North America, against climatic variables and species richness. For each order, models were recorded with median, maximum and minimum size as the response parameter. The slope was recorded for each predictor (with *P*-values in parentheses). Non-significant predictors are denoted n.s. NPP, net primary productivity.

		Model		
Order	Predictor	Median	Maximum	Minimum
Anura	Richness	–0.006 (<0.001)	0.005 (<0.001)	–0.012 (<0.001)
	Mean temperature	–0.002 (<0.001)	0.002 (<0.001)	–0.008 (<0.001)
	Temperature Seasonality	–0.011 (<0.001)	–0.013 (<0.001)	–0.014 (<0.001)
	Mean precipitation	n.s. (0.93)	-2.26×10^{-5} (<0.001)	5.18×10^{-5} (0.04)
	Mean NPP	n.s. (0.16)	0.016 (0.002)	–0.052 (<0.001)
	Pseudo R^2	0.58	0.82	0.78
Urodela	Richness	–0.005 (<0.001)	0.009 (<0.001)	–0.01 (<0.001)
	Mean temperature	0.006 (<0.001)	0.01 (<0.001)	0.002 (0.03)
	Temperature Seasonality	0.024 (<0.001)	n.s. (0.07)	0.033 (<0.001)
	Mean precipitation	n.s. (0.51)	n.s. (0.63)	1.84×10^{-5} (0.04)
	Mean NPP	–0.045 (<0.001)	0.05 (<0.001)	–0.013 (<0.001)
	Pseudo R^2	0.82	0.83	0.83

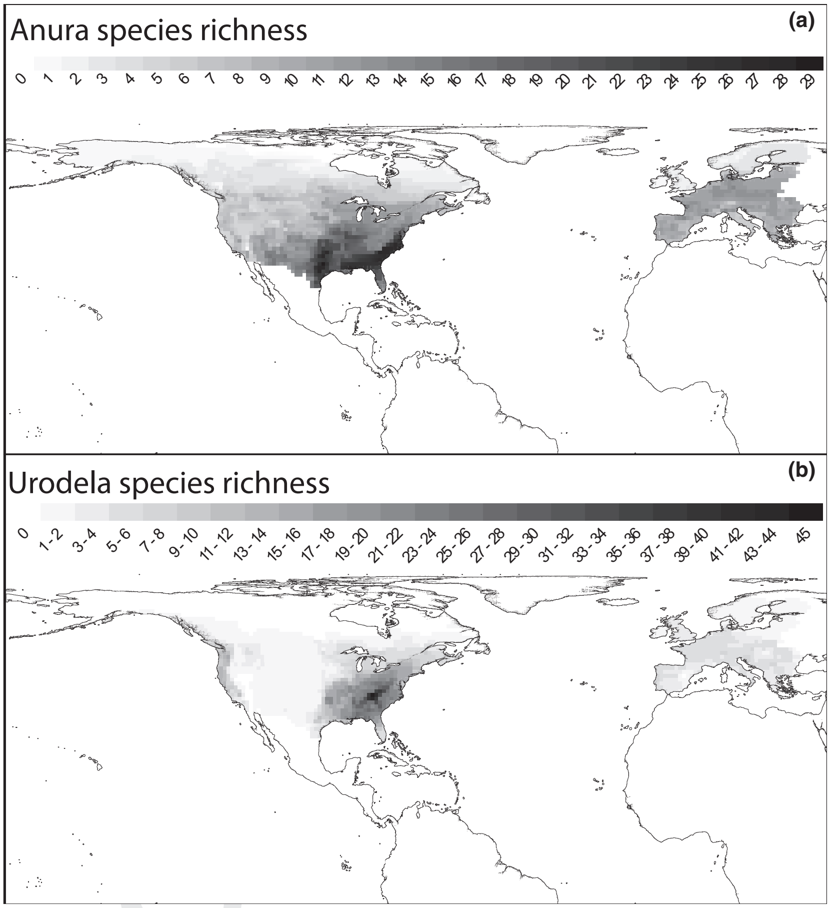

Figure 1 Behrmann equal area projection maps of species richness of (a) anurans and (b) urodeles from Europe and North America, on a 96.3 km × 96.3 km (*c.* 1° × 1° at the equator) scale.

similar to anurans, climatic variables were not strong predictors of median TL.

Randomization tests

Most anuran median SVL values fell within the 95% confidence intervals generated by random assignment of species to grid cells, apart from the richest cells (richness > 22) and a few species-poor cells, in which size was smaller than expected by chance (Fig. 3a). The distribution of urodele median TL across grid cells did not differ much from the null model, with nearly all observed values falling within the 95% confidence intervals, apart from a few species-poor cells (Fig. 3b). Therefore, observed body size distributions were not statistically distinguishable from those generated by random assignment of species to grid cells, except for the most speciose anuran cells and a few species-poor anuran and urodele cells.

Interspecific analysis

Maximum likelihood values of λ were 0.831 and 0.938 for the anuran and urodele models, respectively (both λ values significantly differed from zero at $P < 0.05$), signifying a strong phylogenetic signal. Anuran SVL increased with maximum temperature (slope = 0.009, $P = 0.005$, $F_{2,137} = 8.08$, $R^2 = 0.056$) but not with mean or minimum temperatures ($P = 0.44$ and 0.98, respectively), while urodele TL decreased with increasing mean (slope = –0.007, $P = 0.009$, $F_{2,210} = 6.86$, $R^2 = 0.032$) and minimum temperature (slope = –0.005, $P < 0.001$, $F_{2,210} = 13.82$, $R^2 = 0.062$). The effect of temperature was very weak even in the statistically significant analyses, with the models explaining less than 7% of the variation in anuran and urodele body size. No other environmental factors were correlated with body size in either amphibian order.

DISCUSSION

Most of the variation in urodele and anuran median body size within grid cells can be explained by random assignment of species to grid cells with unequal richness, i.e. climatic body size trends could merely reflect extant diversity gradients and result from spurious effects of richness. In extremely species-rich cells anuran body sizes are lower than expected according to the null model, suggesting some other mechanism is shaping the size distributions (Olson *et al.*, 2009). These cells are predominantly in south-east USA and are probably home to larger proportions of small-bodied hylid frogs (Vitt & Caldwell, 2014) than other cells, causing the median body sizes to be lower than expected. The small size of hylid frogs probably reflects their largely

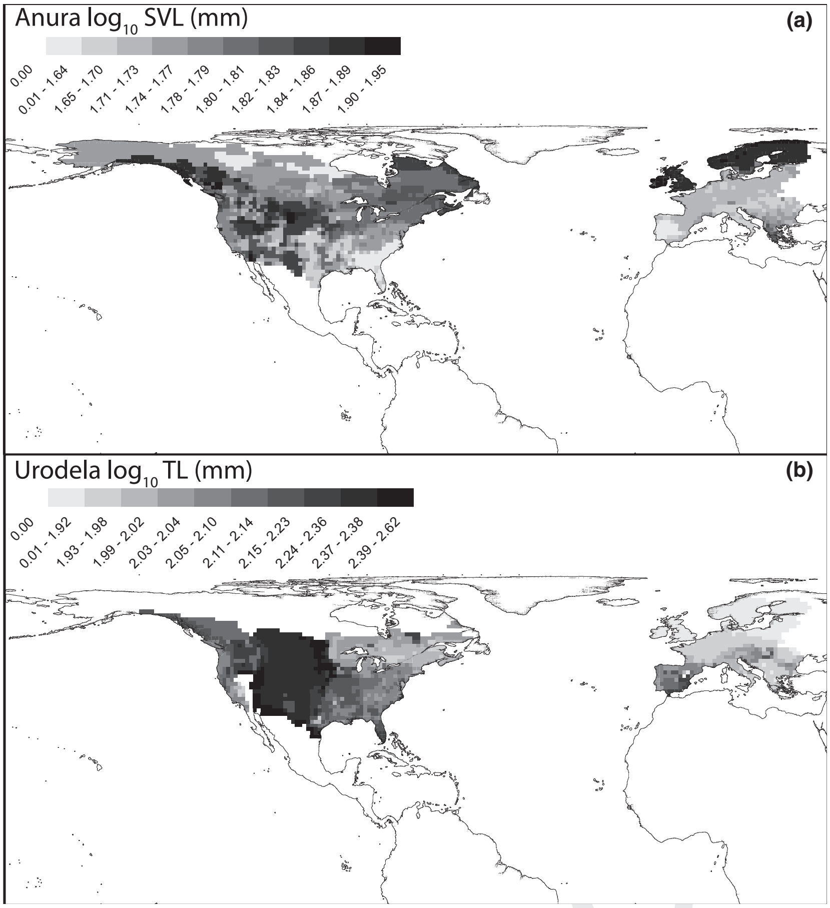

Figure 2 Behrmann equal area projection map of median (a) snout–vent length (SVL) of anuran and (b) total length (TL) of urodele species (mm; log-transformed) from Europe and North America, on a 96.3 km × 96.3 km (*c.* 1° × 1° at the equator) scale.

arboreal lifestyle rather than the result of climatic selection per se.

We found the two amphibian orders to have opposite trends in relation to temperature: anuran median body size decreases with mean annual temperature (Bergmann's rule) while urodele median body size increases with mean annual temperature (the converse) and seasonality in temperature. However, maximum body size of anurans increases with increasing temperature (corrected for species richness), meaning that warm areas are home to both extremely small and extremely large anurans, suggesting that the body size of anurans is not constrained by temperature. Grid cells with such properties simply have many anurans, and it is thus unsurprising to find both small and large species in them. The apparent decrease in median SVL of anurans with temperature probably reflects the right skewed distribution of anuran body sizes within grid cells rather than climate-mediated selection on size.

Olalla-Tárraga & Rodríguez (2007) suggested that a converse Bergmann's rule in urodeles could be explained because they are thermoconformers while anurans are thermoregulators, and therefore smaller urodeles are more effective at gaining heat from the environment. This argument is difficult to accept for several reasons. First, some anurans appear to be poor thermoregulators and others can be active at low

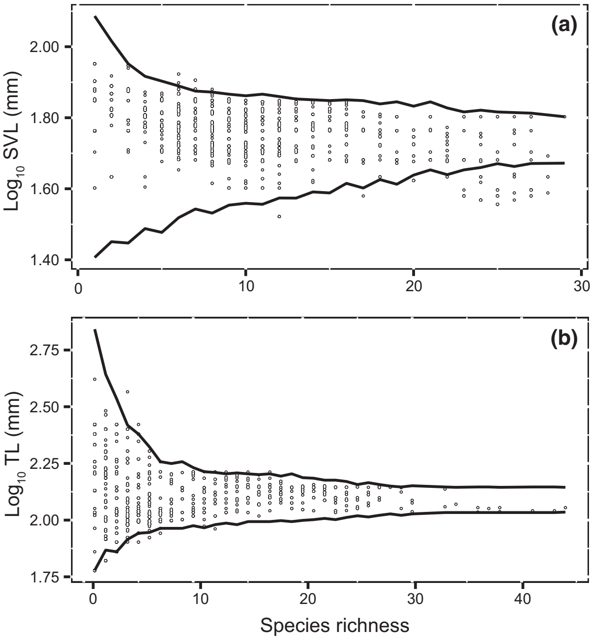

Figure 3 Distribution of median (a) anuran snout–vent length (SVL) and (b) urodele total length (TL) per grid cell of species from Europe and North America. White circles represent observed values; black lines represent 95% confidence intervals of 1000 randomized distributions.

body temperatures (Navas, 2002). Second, many urodeles effectively engage in thermoregulatory behaviour (e.g. Spotila, 1972; Heath, 1975; Wells, 2007; Ficetola *et al.*, 2010). Third, our results do not support a decrease in anuran body size with temperature per se. The weak association between size and climate in both clades may imply that these relationships represent the actions of yet unknown variables, rather than reflecting strong inherent differences in the selection regimes faced by anurans and urodeles.

The interspecific analyses revealed opposite trends to those discerned by the grid-cell analysis. We found that anuran body size increases with increasing mean annual temperature, while urodele body size decreases with the same variable. However, these trends are weak, explaining only a small fraction of the variance in size. This effect size may be too small to be biologically meaningful. Perhaps ambient temperatures simply do not exert a strong selective pressure on amphibian body sizes, although they serve as strong environmental buffers to amphibian distribution (Buckley & Jetz, 2007).

It is possible the interspecific analysis failed to determine actual trends because it does not fully capture the size variability within each species' range. Indeed, species inhabiting large ranges experience a wealth of different environmental pressures and are more likely to exhibit size clines (Meiri *et al.*, 2007). The faults of the grid-cell method, however, seem larger, as it appears to be highly sensitive to the methodological effects of species richness. Furthermore, it does not account for phylogeny, the effect of which seems to be very large in determining amphibian body size (as is evident in the high values of λ). Therefore, trends in body size distributions uncovered using grid-cell methods probably do not represent changes in the population level in response to selection, as natural selection does not act on cross-species averages (Adams & Church, 2011; Gaston & Chown, 2013). Rather, observed anuran body size trends could be driven by a few, wide-ranging species, for example the medium-sized *Lithobates sylvaticus* (the only anuran in much of northern Canada and Alaska), *Bufo bufo* and *Rana temporaria* (the only anurans in most of the British Isles and Scandinavia, and the largest anurans in Europe), and be more related to community assembly rather than size evolution.

While this study offers some insight into body-size clines in amphibians, there is yet more work to be done. We reinforce previous recommendations of a large-scale, macroecological approach, combining both spatial and phylogenetic methods, to tackle this question, as both methods reveal different aspects of size trends. North America and Europe, while large and home to one hotspot of urodele diversity (Buckley & Jetz, 2007), are relatively similar in climate. Our results suggest other driving mechanisms behind size trends in amphibians besides climate, and studies on a larger geographical scale, encompassing more taxa and greater environmental variability, could help unravel those mechanisms.

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SUPPORTING INFORMATION

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

Appendix S1 A full list of mean body sizes by species.
Appendix S2 Composite phylogeny of amphibians in North America and Europe.
Appendix S3 Results for North America and Europe analysed separately.

BIOSKETCHES

Alex Slavenko is a PhD student interested in biogeographical patterns of body size and life-history traits and the distribution of species, as well the general biology of reptiles and amphibians. He is particularly interested in the patterns and evolution of such traits in insular environments.

Shai Meiri is interested in the tempo and mode of the evolution of traits, and in the natural history of land vertebrates.

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