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Short running title: **Little effect of climate on squamate size**

ABSTRACT

Aim. Variation in body size across animal species underlies most ecological and evolutionary processes shaping local- and large-scale patterns of biodiversity. For well over a century, climatic factors have been regarded as primary sources of natural selection on animal body size, ad hypotheses such as Bergmann's rule (the increase of body size with decreasing temperature) have dominated discussions. However, evidence for consistent climatic effects, especially among ectotherms, remains equivocal. Here, we test a range of key hypotheses on climate-driven size evolution in squamate reptiles across several spatial and phylogenetic scales.

Location. Global.

Time period. Extant.

Major taxa studied. Squamates (lizards and snakes).

Methods. We quantified the role of temperature, precipitation, seasonality and net primary productivity as drivers of body mass across ~95% of extant squamate species (9,733 spp.). We ran spatial autoregressive models of phylogenetically-corrected median mass per equal-area grid cells. We ran models globally, across separate continents, and for major squamate clades independently. We also performed species-level analyses using phylogenetic generalized least square models, and linear regressions of independent contrasts of sister species.

Results. Our analyses failed to identify consistent spatial patterns in body size as a function of our climatic predictors. Nearly all continent- and family-level models differed from one another, and species-level models had low explanatory power.

Main conclusions. The global distribution of body mass among living squamates varies independently from variation in multiple components of climate. Our study, the largest in spatial and taxonomic scale conducted to date, reveals that there is little support for a universal, consistent mechanism of climate-driven size evolution within squamates.

KEYWORDS: Bergmann's rule, body mass, body size, ectotherms, phylogenetic comparative analyses, reptiles, size clines, spatial analyses

INTRODUCTION

Climate is traditionally considered a primary source of natural selection underlying the evolution of spatial, ecological and phylogenetic variation in animal body sizes. Given that most ecological and evolutionary processes operating among and within species are strongly influenced by body size (Peters, 1983), the identification of predictable relationships between size and geography has offered a key to elucidate the emergence of local- and large-scale patterns of biodiversity (*e.g.*,Siemann, Tilman & Haarstad, 1996; Gillooly, Brown, West, Savage & Charnov, 2001; Woodward *et al.*, 2005; Slavenko, Tallowin, Itescu, Raia & Meiri, 2016). Remarkably, this principle predates the theory of evolution by natural selection itself. Bergmann's (1847) seminal work suggested that body size among closely related mammal and bird species tends to increase towards colder geographic regions (James, 1970). Such spatial body size gradients have been found to be prevalent in endotherms, both at the intraspecific (Rensch, 1938; James, 1970; Ashton, Tracy & de Queiroz, 2000; Meiri & Dayan, 2003; *cf*. Riemer, Gurlanick & White, 2018) and interspecific (Blackburn & Hawkins, 2004; Olson *et al.*, 2009; Torres-Romero, Morales-Castilla & Olalla-Tárraga, 2016) scales. In contrast, decades of research conducted on a wide range of ectothermic organisms have uncovered mixed support for climate-driven size clines either at the intraspecific (Ashton & Feldman, 2003; Adams & Church, 2008; Pincheira-Donoso, 2010; Pincheira-Donoso & Meiri, 2013; Zamora-Camacho, Reguera & Morena-Rueda, 2014) or interspecific (Olalla-Tárraga, Rodríguez & Hawkins, 2006; Olalla-Tárraga & Rodríguez, 2007; Pincheira-Donoso, Hodgson & Tregenza, 2008; Terribile, Olalla-Tárraga, Diniz-Filho

& Rodríguez, 2009; Feldman & Meiri, 2014; Vinarski, 2014; Slavenko & Meiri, 2015; Rodrigues, Olalla-Tárraga, Iverso & Diniz-Filho, 2018) levels.

The lack of consistency in the attempts to identify prevalent drivers of body size evolution in ectotherms may be partly due to the lack of applicability of the heat-related mechanism (*i.e.*, Bergmann's original explanation) to ectotherms (Pincheira-Donoso *et al.*, 2008; Meiri, 2011; Slavenko & Meiri, 2015). Bergmann (1847) posited that reduced surface area-to-volume ratio in larger animals benefits heat conservation in colder climates, a mechanism sometimes known as the 'heat conservation hypothesis'. However, ectotherms produce negligible amounts of metabolic heat, and reduced surface area-to-volume ratios might result in less efficient thermoregulation in cold climates due to slower heating rates. Therefore, a trade-off exists between heat gain (more efficient in smaller ectotherms; Carothers, Fox, Marquet & Jaksic, 1997) and retention (more efficient in large ectotherms; Zamora-Camacho *et al.*, 2014). Thus, large body size in colder climates is predicted to compromise the need to achieve optimal body temperatures to initiate basic fitness-related activities in the first place (Pincheira-Donoso *et al.*, 2008).

Alternative mechanisms for climate-driven body size-clines may be more applicable to ectotherms. The 'heat balance hypothesis' (Olalla-Tárraga *et al.*, 2006) predicts that thermoconformers exhibit a reverse pattern to the one predicted by Bergmann's rule, *i.e.* smaller bodies at lower temperatures because of the effect of body size on heating rates. The 'water availability hypothesis' (Ashton, 2002) suggests that large sizes, thus, small surface area-to-volume ratios, are beneficial in conserving water in dry habitats (especially for animals with permeable skins such as amphibians). Therefore, large size is predicted to be selected for in arid climates. The ‘starvation resistance hypothesis’ (Lindsey, 1966; Boyce, 1979) and the ‘seasonality hypothesis’ (Van Voorhies, 1996; Mousseau, 1997) both posit that seasonality drives size clines. The former suggests that large size is selected for in seasonal environments, as it allows for accumulation of food reserves to survive periods of food scarcity. The latter suggests that short growing seasons in highly seasonal climates lead to maturation at smaller size. The ‘primary productivity hypothesis’ (Rosenzweig, 1968; Yom-Tov & Geffen, 2006) suggests that increased productivity allows for the evolution of larger body sizes, which can be maintained by the abundance of available food (Huston & Wolverton, 2011). These hypotheses are not mutually exclusive, and the different putative climatic drivers of size evolution covary across space.

We addressed a range of core hypotheses on the relationship between climate and body size globally across squamates, the largest order of land vertebrates (~10,350 species; Uetz, Freed & Hošek, 2018). Squamates are found on all continents except Antarctica. Their distribution patterns differ considerably from other land vertebrate groups, showing increased affinity for hot, arid regions (Roll *et al.*, 2017). However, most studies on climatic size clines in squamates have been conducted on species from temperate regions (*e.g.*, Ashton & Feldman, 2003; Olalla-Tárraga *et al.*, 2006; Pincheira-Donoso, Tregenza & Hodgson, 2007). Therefore, the more limited scale of existing studies is unlikely to be representative of squamates, either phylogenetically (*i.e.*, many families are not represented there), or geographically (*i.e.*, the whole range of climatic conditions experienced by squamates is not represented). Patterns detected might thus merely represent local or regional trends.

Squamates in temperate regions often exhibit unique adaptations to cold conditions (*e.g.*, Churchill & Storey, 1992; Voituron, Storey, Grenot & Storey, 2002; Berman, Bulakhova, Alfimov & Mescheryakova, 2016). Such adaptations (*e.g.*, prolonged hibernation) may mask or weaken climatic effects on body size (Scholander, 1955). Furthermore, the small number of species in such regions might lead to spatial patterns being driven by a few wide-ranging unusually small or unusually large species (Slavenko & Meiri, 2015).

Crucially, while global-scale studies on size clines in endotherms have been conducted (birds, Olson *et al.*, 2009; mammals, Riemer *et al.*, 2018), to date, only a few studies have examined global size clines of an entire large clade of ectotherms (apart from turtles; Angielczyk, Burroughs & Feldman, 2015; Rodrigues *et al.*, 2018), making it impossible to infer a universal effect of climate on body size.

Our goals were to: a) examine the spatial patterns in body sizes of squamates; b) test the leading current hypotheses linking body size and climate; and c) test whether we find consistent support for these hypotheses across phylogenetic and spatial scales. If climate consistently affects ectotherms' body sizes, we expect to find qualitatively similar relationships between body size and the climatic variables we examine, across squamate phylogeny and across space, and using different methods (i.e., with either the species or the grid cell as the focus of analyses).

METHODS

DATA COLLECTION

We used body mass (Feldman, Sabath, Pyron, Mayrose & Meiri, 2016) and distribution data (Roll *et al.*, 2017) for ~95% (9,733 species) of the currently described species of extant squamates (Uetz *et al.*, 2018). We used mass as our measure of body size instead of other measures, such as SVL or total length, as these cannot be easily compared between clades that differ greatly in their *bauplan* (see *e.g.* figure S2c in Feldman *et al.*, 2016, where squamates of similar length differ by 2 orders of magnitude in mass). The mass data in Feldman *et al.* (2016) are size maxima of squamate species, irrespective of sex, derived from SVL using clade-specific length-mass allometric equations. Size maxima were used instead of means, as they are more readily available in the literature, and also likely well represent the potential sizes attainable by squamates, which have indeterminate growth. We $\log_{10}$-transformed the mass data to normalize the otherwise strongly right-skewed body size distribution (Feldman *et al.*, 2016). We used global temperature and precipitation data for the 1979-2013 time period at 30 arc-second resolution (CHELSA; Karger *et al.*, 2017). These were used to test three hypotheses: the 'heat balance' hypothesis, using mean annual temperature (in degrees Celsius; BIO1); the 'water conservation' hypothesis, using mean annual precipitation (in mm/year; BIO12); and the 'seasonality' hypothesis, using both temperature seasonality (annual range in degrees Celsius; BIO4) and precipitation seasonality (annual range in mm/year; BIO15). We also used global net primary productivity (NPP, in grams of carbon / [year * m^2]) data for 1995 (SEDAC; Imhoff *et al.*,

2004) to test the ‘primary productivity’ hypothesis. We tested these four hypotheses using two analytical approaches (assemblage-level and species-level; see below). All statistical analyses were performed in R v3.4.2 (R Core Team, 2017).

ASSEMBLAGE-LEVEL APPROACH

As squamate body size shows a strong phylogenetic signal (Blomberg, Garland Jr. & Ives, 2003; Feldman *et al.*, 2016), we accounted for phylogenetic non-independence using the Lynch method (Lynch, 1991). We used the variance-covariance matrix derived from the latest species-level phylogeny of squamates (Tonini, Beard, Ferreira, Jetz & Pyron, 2016) to fit a linear mixed effects model, with body mass as the response and species identity mapped as a random effect, using the *lmekin* function in the ‘coxme’ R package (Therneau, 2018). We omitted from the analysis 41 species not included in the phylogeny. We treated the predicted values of this model as the phylogenetic components of mass, attributed to shared evolutionary history. The body size residuals from the phylogenetic components were treated as the species components (the component of mass for each species that cannot be explained by shared ancestry). We then overlaid the range maps for all squamates (from Roll *et al*. 2017) onto an equal-area 96x96 km grid in a Behrmann equal-area projection (roughly 0.86x0.86 degrees at the Equator) in ArcGIS 10.0 (ESRI) and calculated the median of the species components for the species assemblage in each grid cell. We also calculated the mean value of each of our environmental predictors across the cell. We omitted island cells (all landmasses smaller than Australia) from this analysis in order to remove the potential bias to our results from effects of insularity on body size evolution (*e.g.*, Itescu *et al.*, 2018).

To account for spatial autocorrelation in the data, we fitted spatial autoregressive (SAR) models (Dormann *et al.*, 2007). We defined the neighbourhood distance as the distance (in km) at which global (or continental, in the continent analyses) Moran's I dropped to 0, based on correlograms generated using the *correlog* function in the 'pgirmess' package (Giraudoux, 2017; Fig. S1.5-S1.8). We then ran multiple-predictor SAR models using the *errorsarlm* function in the 'spdep' package (Bivand *et al.*, 2011), with median species component per grid cell as the response variable and the five environmental predictors. All Variance Inflation Factor (VIF) values were below 4.

To test whether the influence of environmental predictors is consistent across scales, we performed several complementary analyses. First, we divided the dataset into continents (Africa, Asia, Australia, Europe, North America, and South America). We preferred delimitation to continents over biogeographical realms as preliminary evidence suggests that squamates do not adhere well to the classical realm boundaries (Maria Novosolov, pers. comm.). We then reran the SAR models, using the same procedure to determine neighbourhood distance, for each continent. Next, we analyzed lizards (including amphisbaenians) and snakes separately using the same method. We then further divided squamates into families and analyzed all 44 families with at least 10 species (that are not island-endemic) separately using the same method (see Table S1.1 in Supporting Information).

Species richness patterns can strongly affect size clines, with assemblage means and medians, particularly in low-richness cells, often being sensitive to extremely large or small-bodied species (Meiri & Thomas, 2007). We therefore used a permutation approach to test if size clines could arise from spurious effects of richness patterns (Olson *et al.*, 2009; Slavenko & Meiri, 2015). We randomly drew species from a pool of all squamates, without replacement, to occupy cells while maintaining the original richness distribution. The probability of drawing species from the pool was weighted by each species' range size (from Roll *et al.*, 2017). We then calculated the median species component for each random assemblage per cell. We repeated this procedure 1,000 times and calculated 95% confidence intervals from the resultant random distributions of median species component per cell, to test whether observed median species components are lower, or higher, than expected from their richness values.

SPECIES-LEVEL APPROACH

We used multiple-predictor phylogenetic generalized least square (PGLS) regressions (Grafen, 1989), using the log_{10}-transformed mass of each species as the response variable (after omitting all insular endemic species and species across whose ranges we were lacking predictor variables), the mean of each environmental variable across each species' range as predictors, and the latest phylogeny of squamates (Tonini *et al.*, 2016) to estimate the expected covariance structure. After omitting from the analysis 2,695 island-endemic species to remove a potential insularity bias, and a further 701 species that were either not included in the phylogeny or with missing data, we were left with

6,323 species. We ran the PGLS models under a Brownian motion model of evolution and calculated the maximum likelihood estimates of Pagel's λ, a measure of phylogenetic signal in the data ranging from 0 (no signal) to 1 (strong phylogenetic signal under a Brownian motion model of evolution), with the *pgls* function in the 'caper' package (Orme *et al.*, 2012).

This approach ignores spatial variation in the environmental predictor variables, which can be substantial in extremely wide-ranging species. We therefore reran the PGLS analyses after omitting those species with the 10% largest range sizes (leaving 5,691 species), which would be most heavily biased by averaging out environmental predictors across their ranges, and compared the results of this analysis to those of the complete dataset.

In a complementary analysis, we compared independent size and climate contrasts of all 1,456 sister-species pairs recovered from the phylogeny. While this greatly reduces sample size, it also eliminates phylogenetic dependence, as any differences between sister species in body size do not result from shared evolutionary history (Felsenstein, 1985), and compares species that tend to resemble each other most in traits that likely affect body size (Bergmann, 1847). We ran linear regressions through the origin of contrasts in mass between sister species against contrasts in each of the five environmental predictors between sister species, and tested for significance with a conservative alpha of 0.005 (Johnson, 2013; Benjamin *et al.*, 2018).

RESULTS

ASSEMBLAGE-LEVEL APPROACH

Our analyses failed to identify a consistent latitudinal pattern in squamate body size across different regions of the globe. Squamate assemblage body mass is largest in the northern latitudes of North America, most of South America, inland Africa and the Indian Subcontinent (Fig. 1a; Fig. S1.1). It is small in most of northern Eurasia, the Sahel and the Horn of Africa, and in western and central Australia. Squamate species components are positively correlated with mean annual temperature, mean annual precipitation and NPP, and negatively correlated with precipitation seasonality (Table 1). The spatial pattern in squamate species components is more strongly correlated with the ratio of lizards to snakes in each cell – squamate assemblages are large-sized in cells dominated by snakes, and small-sized in cells where most species are lizards (Fig. 1b; SAR of adaptive component against lizard proportion, standardised β = -0.36, $p < 0.001$, Nagelkerke's pseudo-R^2 = 0.39). The pattern is clear even when accounting for phylogenetic non-independence by comparing species components, but is even more pronounced when examining the uncorrected mass data (Fig. S1.1).

Size-climate relationships are not geographically consistent – continent-level analyses recovered models with different sets of predictors, with opposite correlation signs, and with extremely different effect sizes, for each continent (Table 1). For instance, mean annual temperature was positively correlated with squamate mass in Asia, Europe and South America, but negatively correlated with mass in Australia and North America, and uncorrelated with mass in Africa (α = 0.005).

Further inconsistencies were found in the separate analyses of snakes and lizards (Table 1; Fig. 1c,d). Globally, lizard mass is positively correlated with mean annual temperature and seasonality in precipitation, and negatively correlated with seasonality in temperature. On the other hand, snake mass is positively correlated with mean annual temperature, and negatively correlated with mean annual precipitation and seasonality in temperature and precipitation globally. Body mass of neither snakes nor lizards is correlated with NPP. As with the global squamate models, snake and lizard continent-level models are substantially different to each other (Table 1).

Family-level models also show large inconsistencies (Table S1.1). Each predictor was non-significant in 27-34% of the family models (across the 44 families with > 10 species), but often not in the same families (*e.g.*, mean temperature and NPP were non-significant in 18 families each, but only in five of these were they both non-significant). When the predictors were significantly correlated with mass, the correlations often had opposite directions between families. For each of the predictors, positive correlations were found with mass in 27-41% of families, and negative correlations were found in 27-43% of the families (Fig. S1.4). Only four pairs of families had qualitatively identical models: Leiosauridae-Leptotyphlopidae, Hoplocercidae-Elapidae, Iguanidae-Colubridae, and Amphisbaenidae-Eublepharidae. These families are phylogenetically and ecologically very far from one another. All other family models were unique. These results hold even if we analyze only families with over 30 species. In this more restrictive dataset of 33 families, each predictor was non-significant in 27-36% of the models, positively correlated with mass in 24-45% of families, and negatively correlated with mass in 27-45% of families. There was no significant correlation between the species richness of a family and the number of significant predictors in its model (linear regression; p = 0.33).

The permutation analyses showed that most of the observed median species components within cells could be expected by random processes of community assembly. In fact, only ~7% of lizard cells and ~11.5% of snake cells deviate from the 95% confidence intervals of the random distributions (Fig. 2; Fig. S1.2). These cells comprise somewhat distinct geographical units (Fig. 3; Fig. S1.3). Lizards are smaller than expected in many of the most species-rich cells (Fig. 2a; Fig. S1.2a), especially in Australia, and also in the Horn of Africa and along the coasts of South America. They are larger than expected in central South America, inland Africa and the northwest of the Indian subcontinent. Meanwhile, snakes are smaller than expected in western Australia, eastern Asia, some parts of the central Asian steppes, and inland Africa, and larger than expected in central and northern South America, much of northern Eurasia, and southeastern Australia. Only in very few cells in East Africa are both lizards and snakes larger, or smaller, than expected by chance (Fig. 3c).

SPECIES-LEVEL APPROACH

Our PGLS analyses revealed a positive relationship between squamate mass and temperature seasonality, and a negative relationship between mass and precipitation seasonality (at α = 0.005; Table 2). The phylogenetic signal in the model was very strong (λ = 0.93), but the overall explanatory power was extremely low (R^2 = 0.01). Omitting the widest-ranging species from the dataset caused a marked change – the relationship with seasonality in temperature became nonsignificant, but the positive correlation with mean annual precipitation became significant. All other model parameters changed only slightly (λ = 0.92, R^2 = 0.02). NPP and mean annual temperature were not significantly correlated with mass in any of the models.

In the sister-species analysis we found a negative correlation between squamate mass and precipitation seasonality, and no significant correlations with any of the other predictor variables (Fig. 4). However, this model also had extremely low explanatory power (R^2 = 0.01).

DISCUSSION

ASSEMBLAGE-LEVEL APPARAOACH

Our study provides the first truly global-scale analysis of the spatial patterns of body size variation in squamates, the most speciose group among modern tetrapods, as a function of multiple alternative climatic predictors. Our combined evidence from multiple analytic approaches suggests that climate consistently fails to have an identifiable effect on spatial patterns of squamate size.

Our core finding shows that spatial patterns in squamate body sizes are both weak and inconsistent across phylogenetic and spatial scales. We thus conclude that climate exerts weak direct selection pressure on squamate sizes, at least at the examined, interspecific scales (but see also Pincheira-Donoso & Meiri, 2013, for intraspecific comparisons). While squamates seem to display a global trend of decreasing in size towards the poles (or a 'reverse Bergmann' pattern; Fig. 1a), this pattern is weak and inconsistent across regions and lineages. Squamates are generally larger in the New World, and the northernmost cells of North America contain assemblages with the largest median sizes. This global pattern seems to be most strongly explained by the ratio of lizard to snake species in each cell. The body size distribution of squamates is strongly bimodal (Feldman *et al.*, 2016), as snakes are, on average, larger than lizards. Snakes and lizards also differ in their spatial distribution patterns (Roll *et al.*, 2017). Snakes show the common tetrapod pattern of richness peaking in the tropics, whereas lizard richness peaks in warm, arid regions, particularly Australia. Thus, squamates are, on average, large in snake-rich cells (*e.g.*, the Amazon Basin and Canada), and small in lizard-rich cells (*e.g.*, Australia). The global latitudinal size patterns for lizards and snakes are similarly unclear, with the strongest seeming to be a fall (in lizards) and rise (in snakes) of body size in the northernmost latitudes (Fig 1c,d). This is likely due to the effect of the very few, wide-ranging species, inhabiting extreme latitudes in the Northern hemisphere (*e.g.*, *Zootoca vivipara* and *Vipera berus* are the only lizard and snake species, respectively, in much of northern Eurasia, and the snake *Thamnophis sirtalis* is the only squamate species in much of northern North America). The inconsistency in patterns and in relationships with the climatic variables is especially pronounced at the continent- and family-level analyses. No single climatic variable displays a consistent relationship with squamate mass across scales.

Overall, the support for the various hypotheses on climate-driven size evolution is weak. Correlations consistent with all different hypotheses were found for all of the hypotheses, but for none of them were these patterns consistent across scales and models. The only correlation recovered in all global models (squamates, lizards, and snakes) was a positive correlation between mass and mean temperature, which would be consistent with 'heat balance hypothesis' under the assumption that all squamates are thermoconformers. This, however, is a problematic assumption –most squamates engage in thermoregulatory behaviour and are quite adept at maintaining body temperatures higher than their surroundings (Meiri *et al.*, 2013). In the continent level analyses, the only hypotheses supported for a majority of models were the 'heat balance hypothesis' which was supported in five of six continents for lizards, and the 'starvation resistance hypothesis' which was supported in five of six continents for snakes, and the 'water availability', 'seasonality' and the 'primary productivity' hypotheses, which were all supported in 53% of snake families. Note, however, that hypotheses supported in most continents for snakes were never supported in most continents for lizards and vice-versa. No hypothesis was supported for most families in lizards or the Squamata as a whole.

PERMUTATION ANALYSES

The results of our permutation tests show that almost all median species components per cell fall within the expected values, if species were assigned to cells by chance. This is markedly different from the result for birds, where many cell assemblages cannot be explained by random processes (Olson *et al.*, 2009), yet are similar to results for amphibians (Slavenko & Meiri, 2015). While this finding does not necessarily imply that current size distributions were generated by random processes alone (*i.e.*, our null model may be affected by the intrinsic imperfection of null models in general; Gotelli, 2001), we cannot reject the null hypothesis. The relationship between species richness and the median body size within cells is complex. Body sizes may be either extremely large or extremely small in cells with low richness values purely by chance, and squamate richness tends to be strongly correlated with climatic variables (*e.g.*, Costa, Nogueira, Machado & Colli, 2007; Powney, Grenyer, Orme, Owens & Meiri, 2010; Morales-Castilla *et al.*, 2011; Lewin *et al.*, 2016). This poses a severe limitation for inference using any grid-cell based analysis, as even large-scale, statistically significant spatial patterns in body size may be merely spurious patterns, particularly due to species' co-occurrence in multiple cells (Hawkins *et al.*, 2017).

Interestingly, the cells which deviate from random expectations are not randomly distributed across the globe but seem to form distinct geographical units (Fig. 3). Investigating the composition of squamate communities in these habitats might be a promising avenue for uncovering the causes. For instance, lizards in Australian deserts are much smaller than expected by chance (Fig. 3a). Lizard richness peaks in arid Australia (Powney *et al.*, 2010; Roll *et al.*, 2017), and Australia's lizard fauna is dominated by skinks (Cogger, 2014), which are generally small-bodied (Meiri, 2008). An additional example is the higher than expected mass of snakes in a large portion of the southern Amazon Basin (Fig. 3b). Patterns of body size distribution in South American snake assemblages are strongly affected by the contribution of the three most species-rich lineages: colubrids, xenodontines and dipsadids. Colubrid and xenodontine snakes (median mass 68.3 g) are much larger than dipsadids (median mass 35.4 g), and in the southern Amazon snake faunas are dominated by a combination of xenodontines and colubrids (see Fig. 25.6 in Cadle & Greene, 1993). Only in few places on the globe, however, are both lizards and snakes either smaller, or larger, than expected by chance (Fig. 3c), again demonstrating remarkable inconsistency in spatial body size patterns between the two groups.

SPECIES-LEVEL APPROACH

Our species-level analyses confirm the finding that body size among squamates varies independently from variation in climate. While we did find correlations between mass and our examined climatic variables, their explanatory power is extremely low, and most size variation is explained by shared ancestry. This is similar to previous findings in amphibians (Slavenko & Meiri, 2015).

Our study also serves as a demonstration of the importance of considering scale in ecological studies, both spatial (Wiens, 1989; Chave, 2013) and phylogenetic (Graham, Storch & Machac, 2018). Had we considered only the global scale analyses, we might have concluded that there is support for a reverse Bergmann’s rule in squamate sizes. Only by examining our data across differing scales were we able to discern the inconsistency in patterns and realize that the global pattern is probably driven by assemblage structure. In this case, our global scale analyses were a classic case of comparing apples to oranges, considering the stark size differences between continents, between lizards and snakes, and between different lineages within these groups.

We acknowledge that the interspecific approach ignores size variation at the intraspecific level, arguably a more relevant scale for examinations of climate-driven size evolution (Meiri, 2011). Some species indeed show intraspecific trends in size consistent with climate-driven size evolution, particularly along elevational gradients (*e.g.*, Zamora-Camacho *et al.*, 2014; *cf.* Pincheira-Donoso & Meiri, 2013). However, data on range-wide intraspecific size variation are lacking for most squamate species. Testing intraspecific relationships between climate and body size on a large sample of squamates is beyond the scope of this work, though we acknowledge climate might be an important factor shaping body size at this level. We doubt, however, that the effects would be consistently predictable by any 'ecological rule' and suspect they might be idiosyncratic and depend heavily on the natural history of each examined species.

CONCLUSIONS

Collectively, our results suggest that climate is likely not an important driver of size evolution in squamates as a group, despite exerting a strong influence on their spatial distribution (Roll *et al.*, 2017), and therefore likely affecting spatial size distributions by proxy. This is consistent with similar results for amphibians (Slavenko & Meiri, 2015), and may be the case for terrestrial ectotherms in general. Recently, Riemer *et al.* (2018) analysed an impressively large dataset of mammals and birds, and concluded that there is little support for a general relationship between mass and temperature in endotherms, despite previous evidence to the contrary (Ashton *et al.*, 2000; Meiri & Dayan, 2003). While these results do not mean that temperature, and other climatic variables, do not exert selection pressure on body size (and indeed they may apply to some taxa), they do raise questions as to the generality of such evolutionary mechanisms across all taxa. This is not to imply that climate is not an important driver of size evolution, but rather that the causative mechanisms of size evolution may be idiosyncratic and strongly lineage- and location-dependent. While this conclusion does pose a difficulty for generalization, it also creates a promising avenue for future research of size evolution on a case-by-case basis, and on multiple spatial and phylogenetic scales. In any event, we advise caution in adopting such climate-size relationships as general ‘rules’, at the very least until their generality has been properly tested on large, extensive datasets.

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DATA ACCESSIBILITY

All data used for this study were previously published in other scientific publications and publicly available datasets and are properly cited. The distribution maps from Roll *et al.* (2017) are currently under embargo, and will be made publicly available during 2018.

TABLES

Table 1. Results of the SAR analyses. A summary of the full model is given for each subset of the data. For each predictor, the standardised regression slope is given. P-values for each predictor are indicated by *, **, ***, and n.s. (<0.05, <0.01, <0.005, and non-significant respectively). Also given are Nagelkerke's Pseudo-R^2 values for each model, although we must stress these cannot be interpreted as percentage of variance explained by the model.

Model		Mean Annual Temperature	Mean Annual Precipitation	Temperature Seasonality	Precipitation Seasonality	Net Primary Productivity	Nagelkerke's Pseudo-R^2
Squamates	Global	0.29***	0.1***	-0.16***	0.01 (n.s.)	0.06***	0.48
	Africa	0.04 (n.s.)	0.22***	-0.13***	0.04 (n.s.)	0.14***	0.3
	Asia	0.44***	-0.13***	-0.64***	-0.22***	-0.14***	0.68
	Australia	-0.29***	0.34***	-0.1*	0.31***	-0.03 (n.s.)	0.64
	Europe	0.72***	0.14***	0.36***	0.03 (n.s.)	-0.08*	0.35
	North America	-0.18***	0.01 (n.s.)	0.36***	0.02 (n.s.)	0.14***	0.18
	South America	0.42***	0.07*	-0.06*	0.21***	0.31***	0.42

Lizards	Global	0.33***	-0.02*	-0.2***	0.06***	0.00 (n.s.)	0.4
	Africa	0.18***	0.25***	-0.18***	0.15***	0.06 (n.s.)	0.35
	Asia	0.26***	-0.07***	-0.54***	-0.08***	-0.27***	0.48
	Australia	-0.38***	0.17***	0.33***	0.45***	0.29***	0.46
	Europe	0.72***	0.04 (n.s.)	0.13*	-0.03 (n.s.)	-0.25***	0.4
	North America	0.54***	-0.23***	-0.12 (n.s.)	-0.35***	0.08 (n.s.)	0.25
	South America	0.36***	0.23***	0.21***	-0.14***	-0.01 (n.s.)	0.29
Snakes	Global	0.0001***	-0.0001***	-0.0005***	-0.0001***	0.00002 (n.s.)	0.21
	Africa	-0.12***	-0.16***	0.25***	-0.36***	-0.09*	0.32
	Asia	0.63***	-0.34***	-0.38***	-0.28***	-0.006***	0.47
	Australia	-0.35***	-0.01 (n.s.)	-0.18***	0.4***	0.34***	0.67
	Europe	-0.28***	0.08*	-0.1 (n.s.)	0.1***	-0.01 (n.s.)	0.11
	North America	-0.1 (n.s.)	0.06 (n.s.)	0.38***	0.1***	0.09**	0.21
	South America	0.13***	-0.05 (n.s.)	0.26***	0.14***	0.18***	0.36

Table 2. Results of the PGLS analyses. A summary of the full model is given for the full dataset, and with the widest-ranging species omitted. For each predictor, the standardised regression slope is given. P-values for each predictor are indicated by *, **, ***, and n.s. (<0.05, <0.01, <0.005, and non-significant respectively).

Model	Mean Annual Temperature	Mean Annual Precipitation	Temperature Seasonality	Precipitation Seasonality	Net Primary Productivity	λ	R^2
Full	0.02 (n.s.)	0.03*	0.07***	-0.04***	0.03**	0.93	0.01
Widest-ranging species omitted	0.004 (n.s.)	0.06***	0.02 (n.s.)	-0.05***	0.03**	0.92	0.02

FIGURES

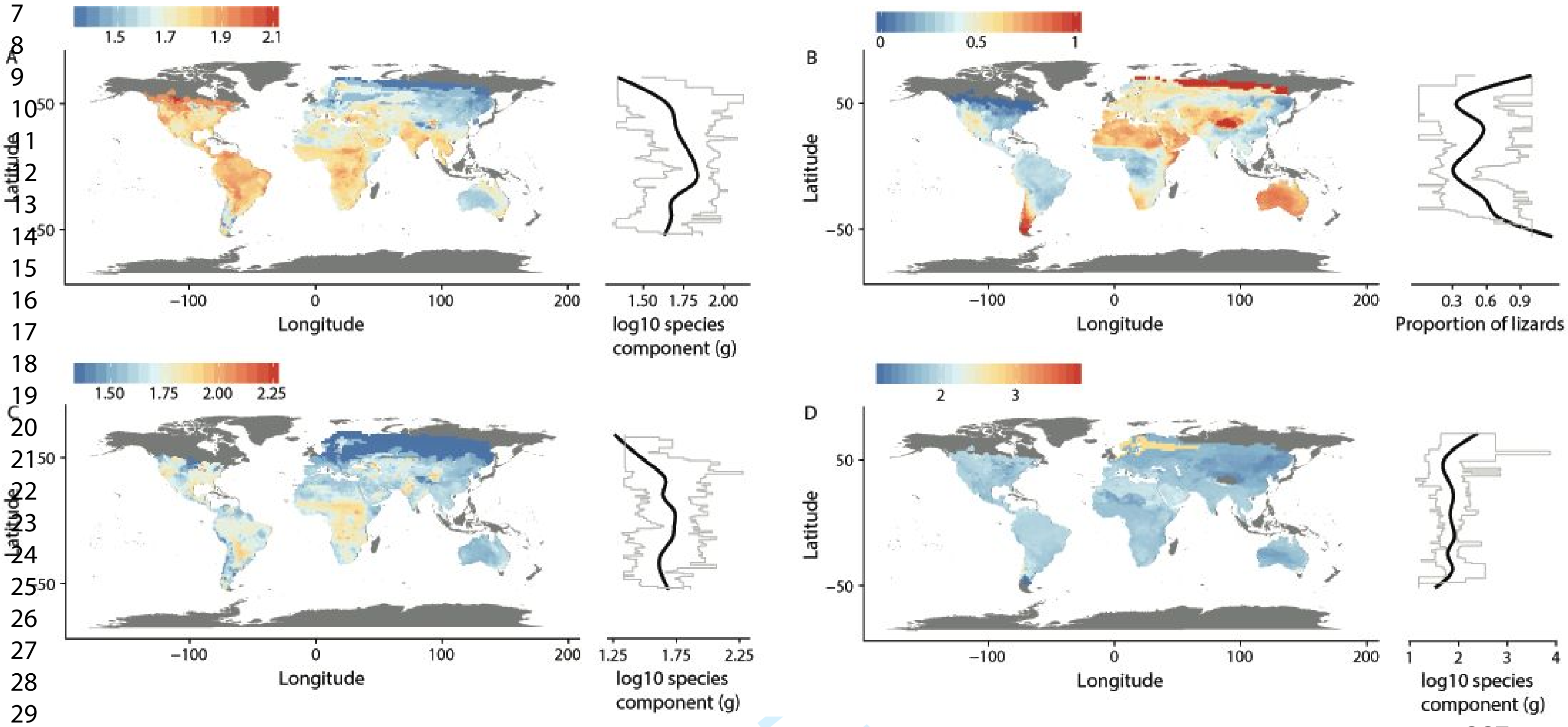

Figure 1. Maps showing the global distribution of a) median log10 species component of mass (in grams) per cell of all squamates; b) proportion of lizard species out of all squamates per cell; c) median log10 species component of mass (in grams) per cell of lizards; and d) median log10 species component of mass (in grams) per cell in snakes. Species components are the component of mass for each species that cannot be explained by its evolutionary history (residuals from a phylogenetic model of size evolution). Next to each map is a curve showing a generalized additive model of each mapped variable (in black) and the minimum and maximum values of each mapped variable per 96km latitudinal band (in grey).

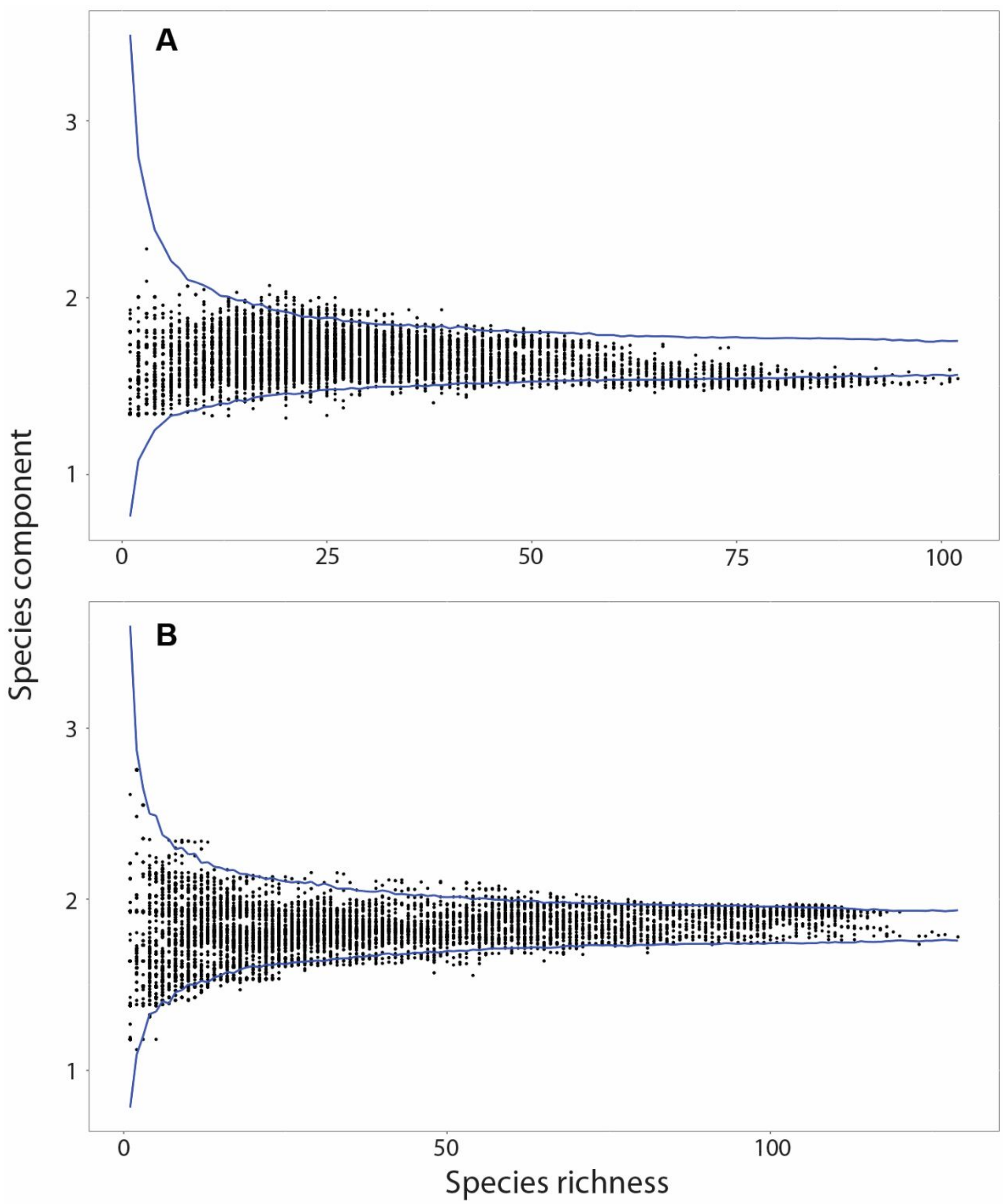

Figure 2. Distribution of median species components of (a) lizards and (b) snakes per grid cell. Species components are the component of mass for each species that cannot be explained by its evolutionary history (residuals from a phylogenetic model of size evolution). Black circles represent observed values; blue lines represent 95% confidence intervals of 1000 randomized distributions.

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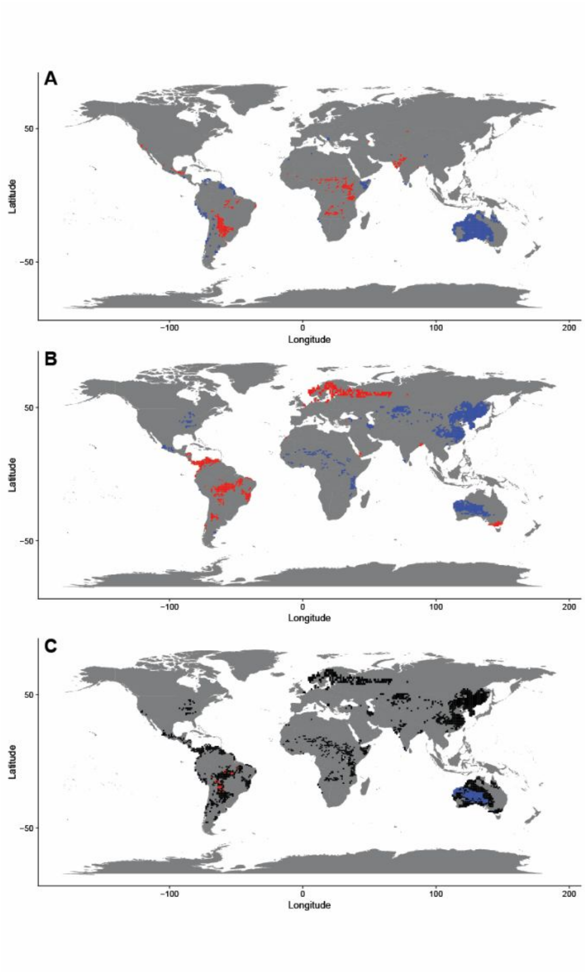

Figure 3. Maps showing cells of a) lizards and b) snakes with median species components exceeding the 95% confidence intervals of 1000 randomized distributions. Species components are the component of mass for each species that cannot be explained by its evolutionary history (residuals from a phylogenetic model of size evolution). Red cells have larger species components than expected by chance, whereas blue cells have smaller species components than expected by chance. c) Overlap between the two maps, black cells are where only lizards or snakes (but not the other group) exceed expected values, light grey cells are where both lizards or snakes exceed

expected values (but not in the same direction), whereas blue cells are where both are smaller than expected, and red cells are where both are larger than expected.

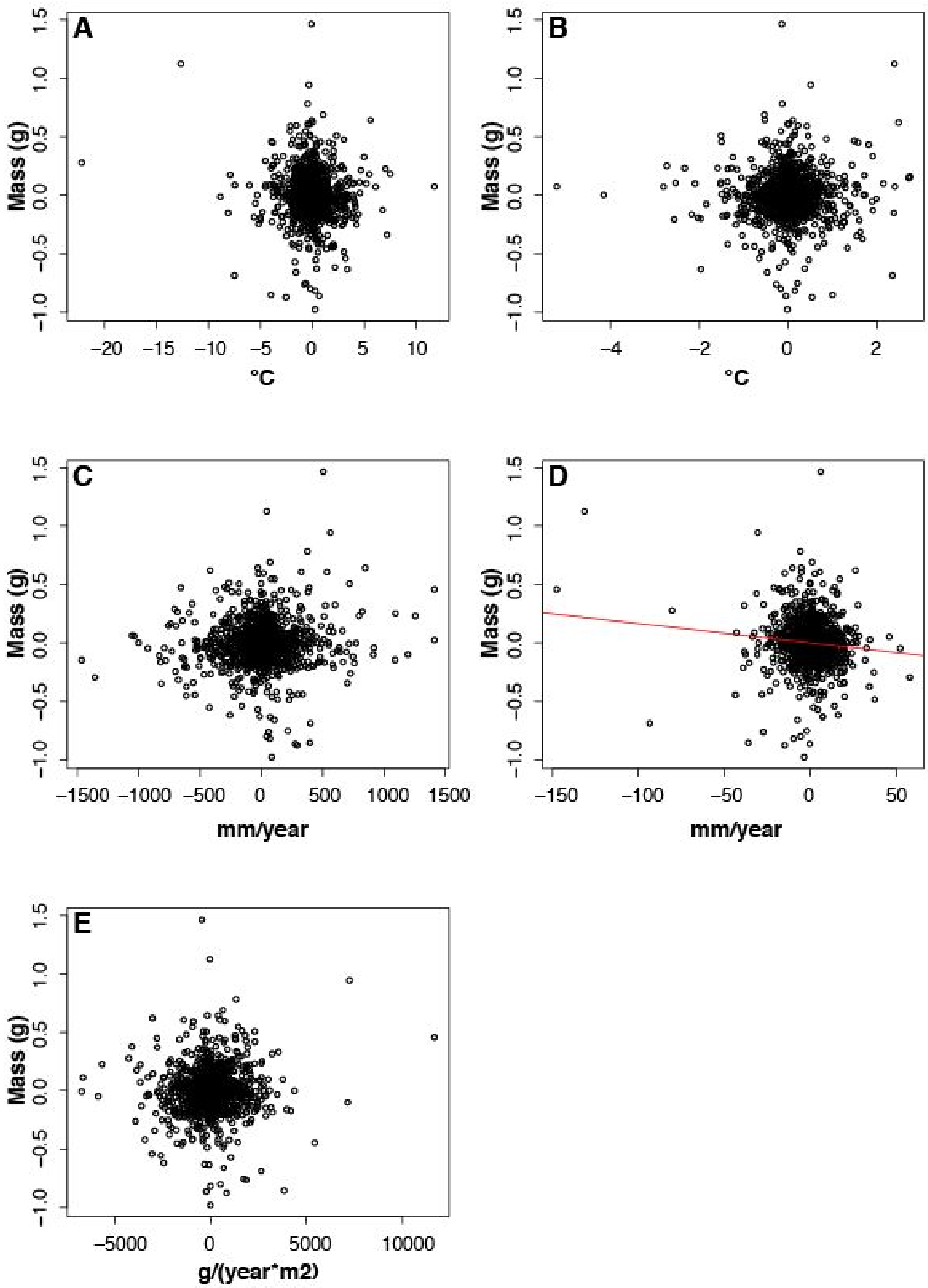

Figure 4. Scatter plots of 1456 sister-species pairs. Shown are independent contrasts of log10 mass (in grams) against a) mean annual temperature; b) temperature seasonality; c) mean annual precipitation; d) precipitation seasonality; and e) net primary productivity. Only the significant regression through the origin in d) is represented by a red line. All other regressions are not significant.

Appendix S1

Supplementary figures and table.

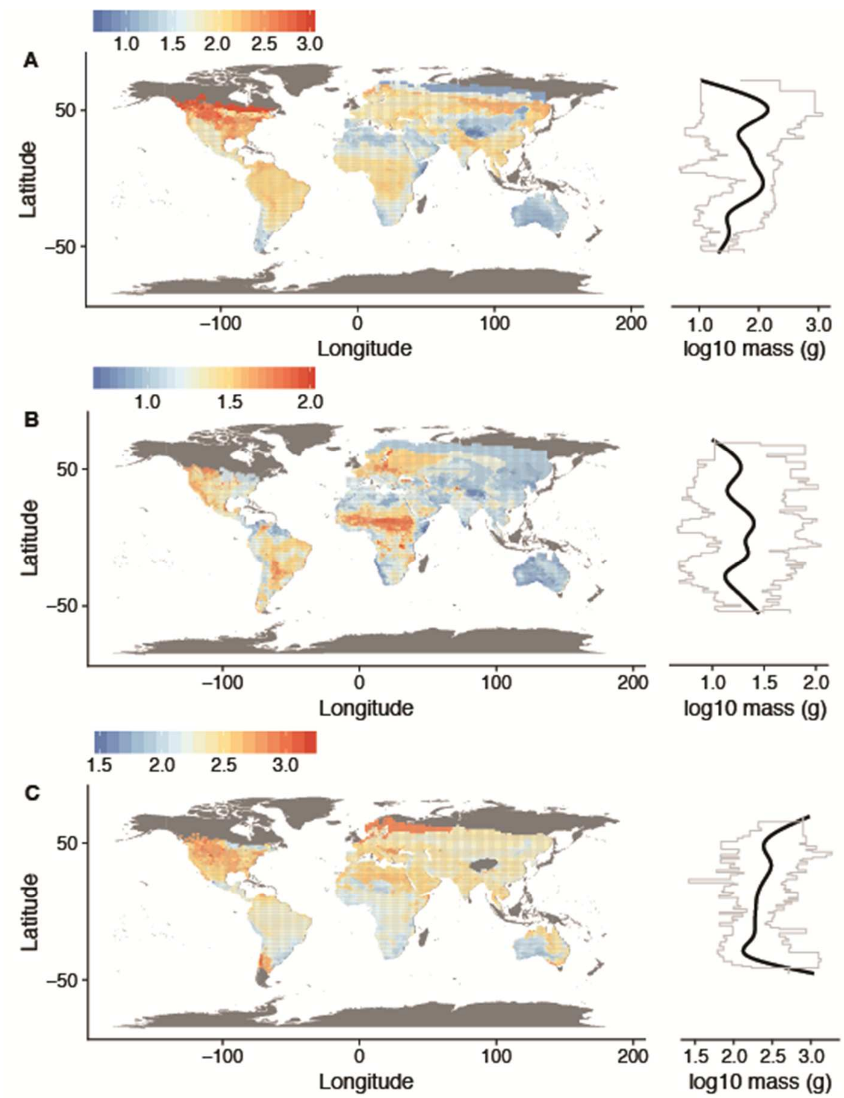

Figure S1.1. Maps showing global trends in log10 median mass per cell (in grams; uncorrected for phylogenetic non-independence) of a) squamates; b) lizards; and c) snakes. In all maps, colours range from blue for low values, to red for high values. Next to each map is a curve showing a generalized additive model of each mapped variable (in black) and the minimum and maximum values of each mapped variable per 96km latitudinal band (in grey).

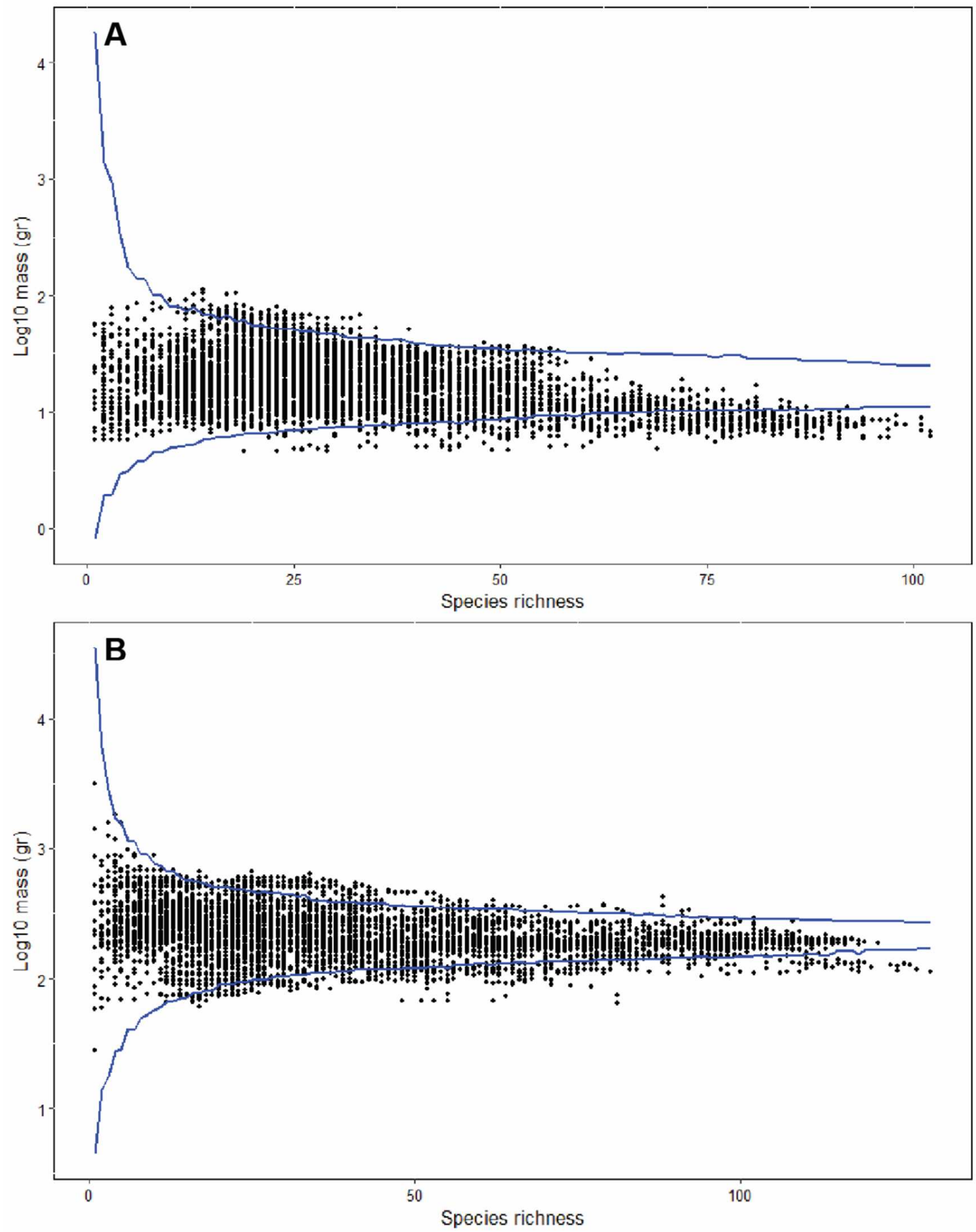

Figure S1.2. Distribution of median mass (in grams; uncorrected for phylogenetic non-independence) of (a) lizards and (b) snakes per grid cell. Black circles represent observed values; blue lines represent 95% confidence intervals of 1000 randomized distributions.

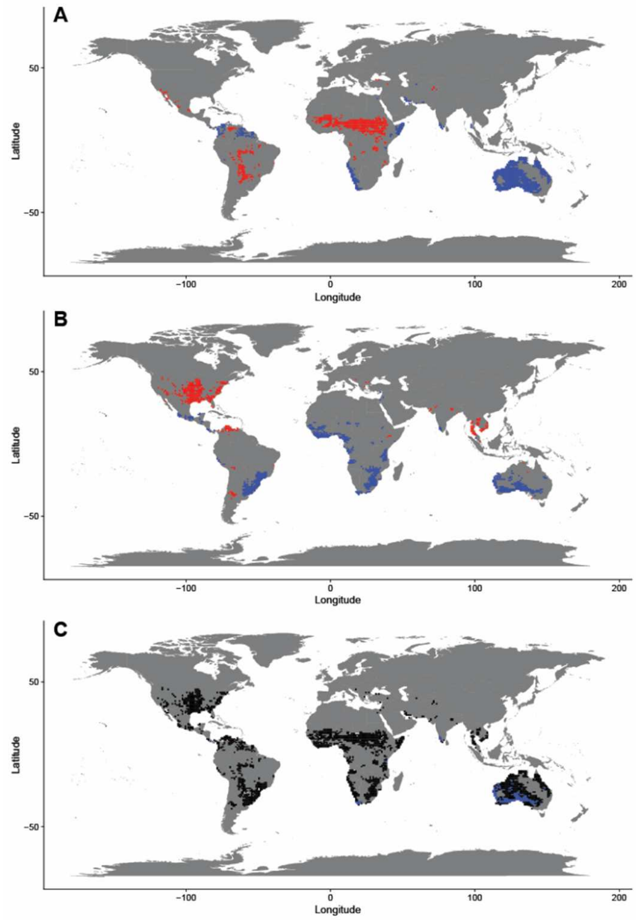

Figure S1.3. Maps showing cells of a) lizards and b) snakes with median mass (in grams; uncorrected for phylogenetic non-independence) exceeding the 95% confidence intervals of 1000 randomized distributions. Red cells have larger masses than expected by chance, whereas blue cells have smaller masses than expected by chance. c) overlap between the two maps, black cells are where only lizards or snakes (but not the other group) exceed expected values, light grey cells are where both lizards or snakes exceed expected values (but not in the same direction), whereas blue cells are where both are smaller than expected, and red cells are where both are larger than expected.

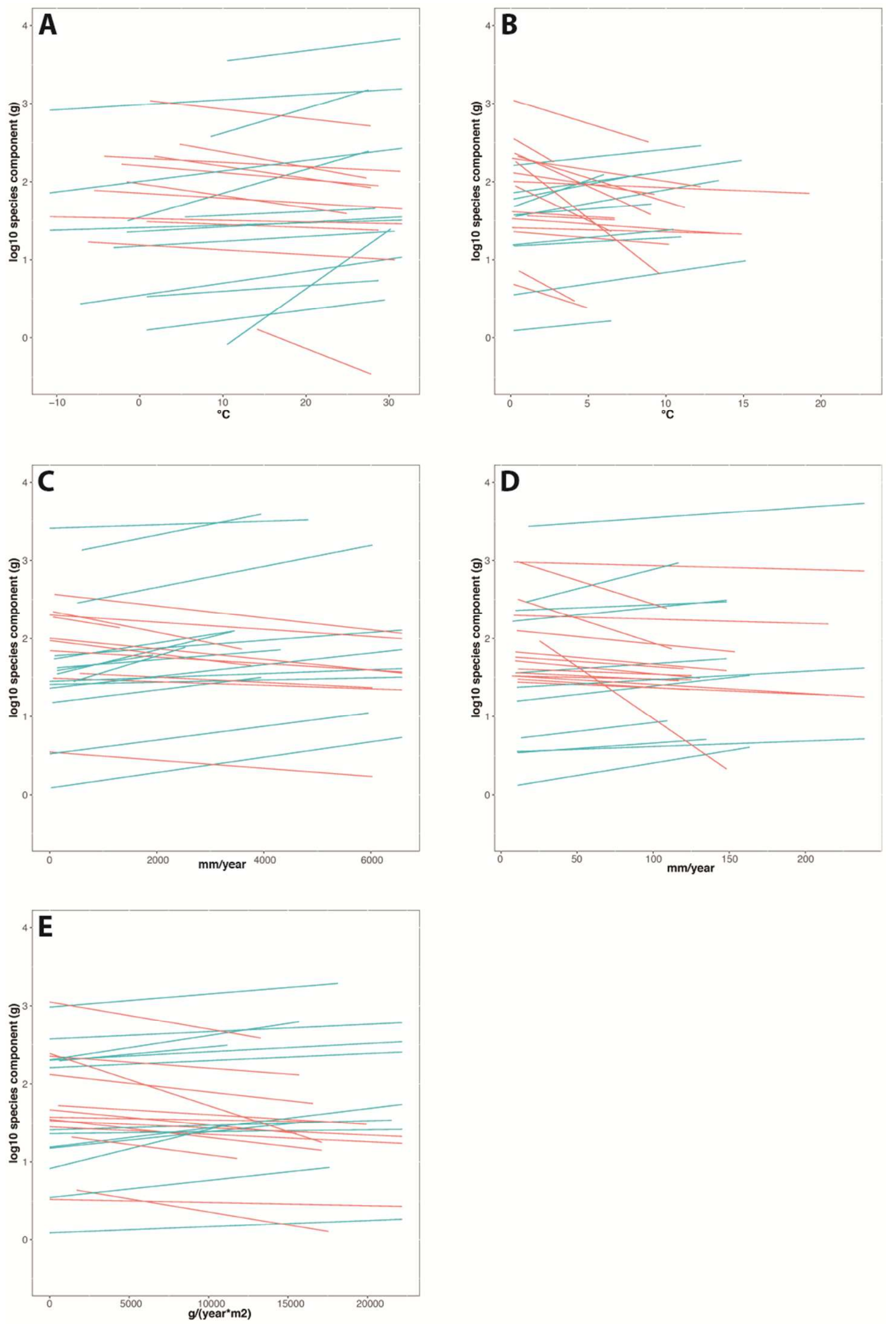

Figure S1.4. Regression plots of family-level SAR models of adaptive components of mass against a) mean annual temperature; b) temperature seasonality; c) mean annual precipitation; d) precipitation seasonality; and e) NPP. Each line represents the model for a different family. Red lines are negative correlations, and blue lines are positive correlations. Non-significant correlations are not shown.

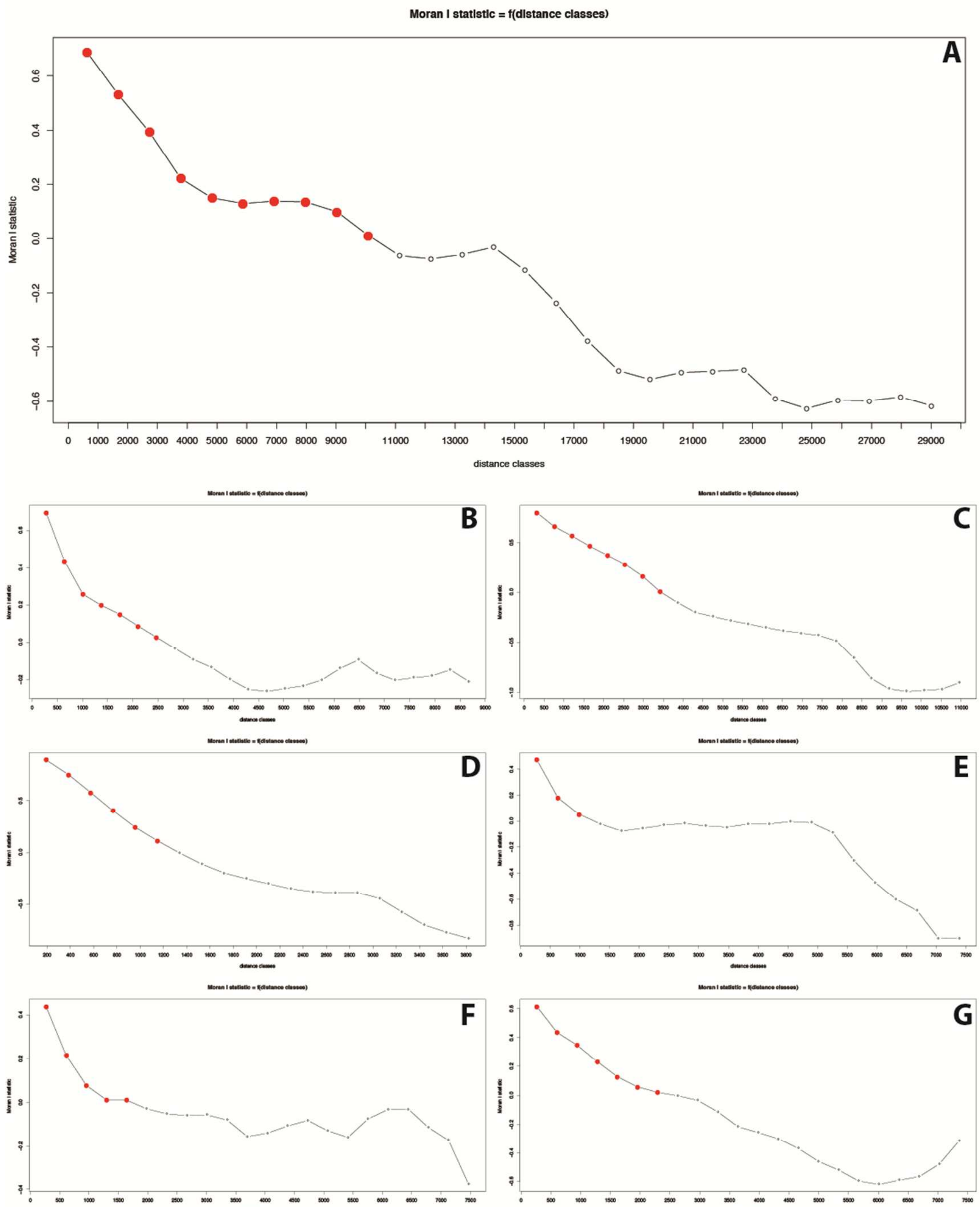

Figure S1.5. Correlograms of Moran's I of log10 squamate adaptive components a) globally; and in b) Africa; c) Asia; d) Australia; e) Europe; f) North America; g) South America. Values exceeding 0 are marked by a red dot.

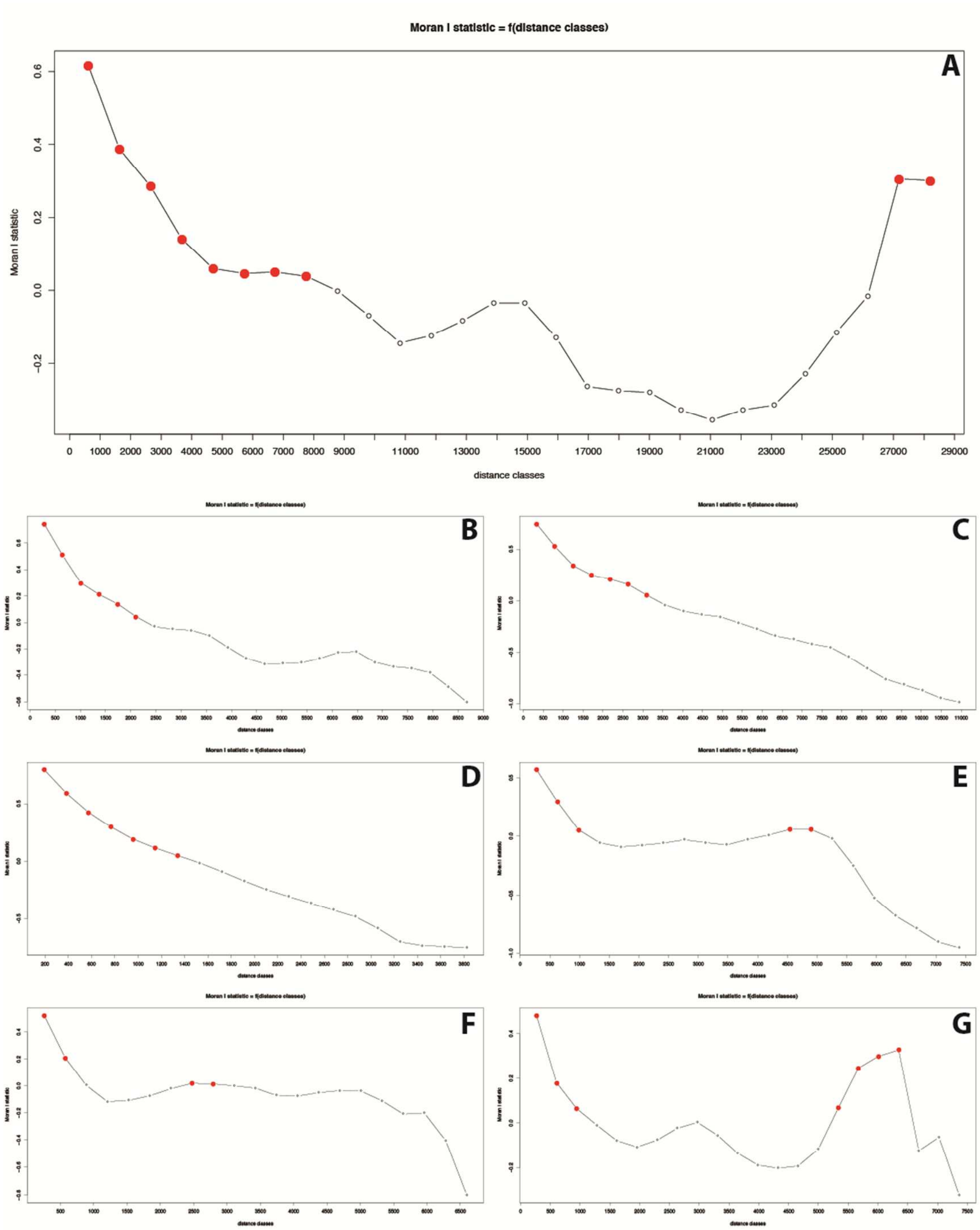

Figure S1.6. Correlograms of Moran's I of log10 lizard adaptive components a) globally; and in b) Africa; c) Asia; d) Australia; e) Europe; f) North America; g) South America. Values exceeding 0 are marked by a red dot.

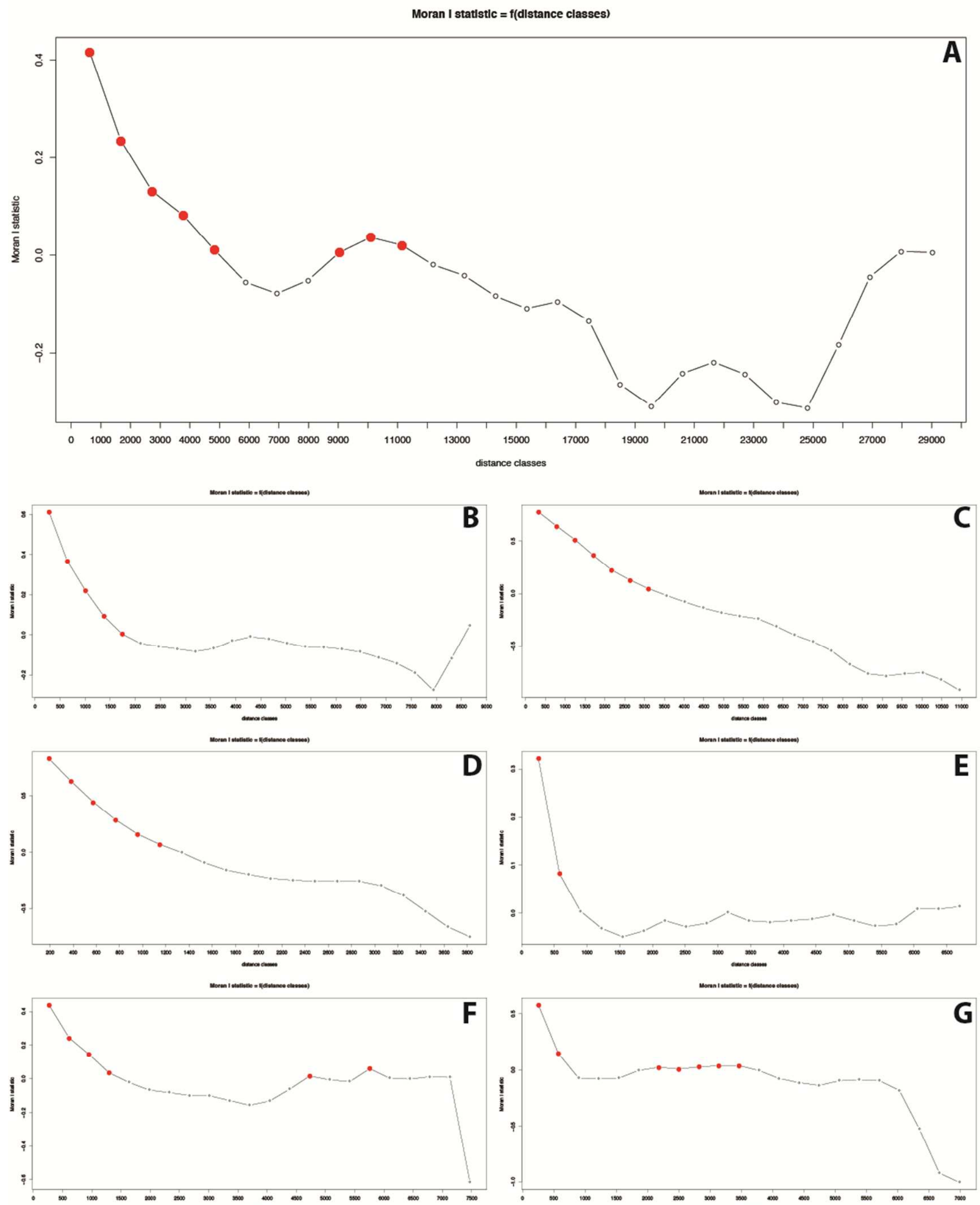

Figure S1.7. Correlograms of Moran's I of log10 snake adaptive components a) globally; and in b) Africa; c) Asia; d) Australia; e) Europe; f) North America; g) South America. Values exceeding 0 are marked by a red dot.

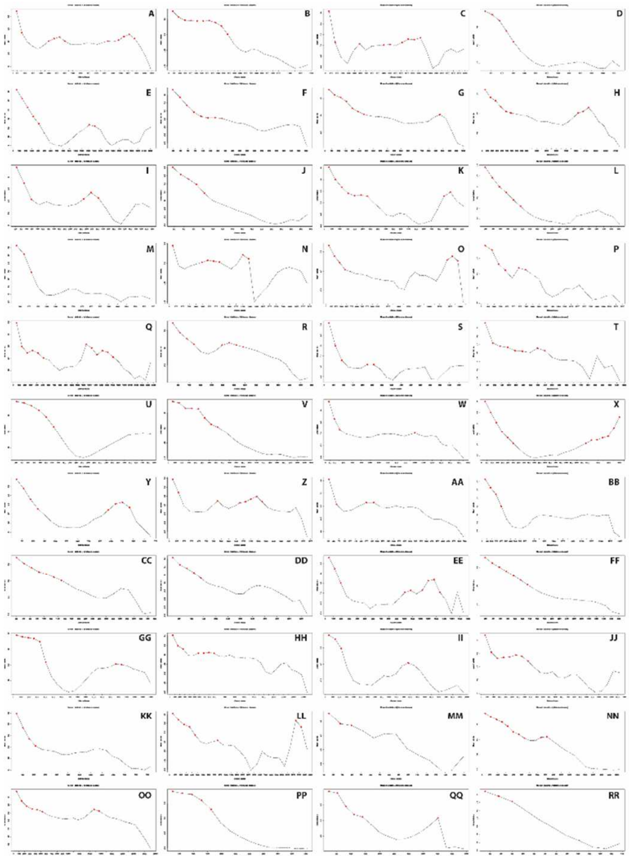

Figure S1.8. Correlograms of Moran's I of log10 adaptive components for the following squamate families: a) Agamidae; b) Amphisbaenidae; c) Anguidae; d) Anomalepididae; e) Boidae; f) Carphodactylidae; g) Chamaeleonidae; h) Colubridae; i) Cordylidae; j) Crotaphytidae; k) Dactyloidae; l) Diplodactylidae; m) Diploglossidae; n) Dipsadidae; o) Elapidae; p) Eublepharidae; q) Gekkonidae; r) Gerrhosauridae; s) Gymnophthalmidae; t) Homalopsidae; u) Hoplocercidae; v) Iguanidae; w) Lacertidae; x) Lamprophiidae; y) Leiosauridae; z) Leptotyphlopidae; aa) Liolaemidae; bb) Natricidae; cc) Pareatidae; dd) Phrynosomatidae; ee) Phyllodactylidae; ff) Pygopodidae; gg) Pythonidae; hh) Scincidae; ii) Sphaerodactylidae; jj) Teiidae; kk) Tropiduridae; ll) Typhlopidae; mm) Uropeltidae; nn) Varanidae; oo) Viperidae; pp) Xantusiidae; qq) Xenodermatidae; rr) Xenosauridae. Values exceeding 0 are marked by a red dot.

Table S1.1. Family-level SAR models of species components against environmental variables. A summary of the full model is given for each family. For each predictor, the standardised regression coefficient is given. P-values for each predictor are indicated by *, **, ***, and n.s. (<0.05, <0.01, <0.005, and non-significant respectively). Also given are Nagelkerke's Pseudo-R^2 values for each model

Family	Mean Annual Temperature	Mean Annual Precipitation	Temperature Seasonality	Precipitation Seasonality	NPP	Nagelkerke's Pseudo-R^2	Richness (non-insular species)
Agamidae	0.23***	-0.01 (n.s.)	-0.06*	-0.08***	0.2***	0.26	345
Amphisbaenidae	0.11***	0.17***	0.06***	0.18***	0.06***	0.45	157
Anguidae	0.51***	-0.07*	0.21***	0.07*	-0.14***	0.35	71
Anomalepididae	-0.22***	0.01 (n.s.)	-0.15***	0.11***	-0.21***	0.64	16
Boidae	0.16***	-0.17***	-0.34***	-0.29***	0.22***	0.6	37
Carphodactylidae	0.09 (n.s.)	0.58***	-0.25***	-0.15*	-0.16***	0.52	30
Chamaeleonidae	0.22***	0.1***	0.02 (n.s.)	0.25***	-0.03 (n.s.)	0.54	112
Colubridae	0.26***	-0.11***	-0.5***	-0.13***	-0.02 (n.s.)	0.49	653
Cordylidae	0.05 (n.s.)	0.14 (n.s.)	0.51***	-0.13*	-0.39***	0.37	66

Crotaphytidae	0.07 (n.s.)	-0.19***	0.04 (n.s.)	-0.04 (n.s.)	0.22***	0.47	12
Dactyloidae	0.03 (n.s.)	0.17***	0.35***	-0.13***	0.05*	0.37	231
Diplodactylidae	0.22***	0.66****	-0.07 (n.s.)	-0.2***	-0.05 (n.s.)	0.58	78
Diploglossidae	0.01 (n.s.)	0.07 (n.s.)	-0.2***	-0.01 (n.s.)	-0.19***	0.7	24
Dipsadidae	-0.27***	-0.03 (n.s.)	0.3***	0.22***	0.16***	0.39	679
Elapidae	-0.08***	-0.12***	-0.24***	-0.06***	0.14***	0.36	317
Eublepharidae	0.09***	0.15***	0.09***	0.2***	0.18***	0.84	25
Gekkonidae	0.15***	0.09***	-0.13***	0.01 (n.s.)	0.17***	0.29	669
Gerrhosauridae	0.38***	0.07 (n.s.)	0.17***	0.17***	0.16***	0.43	18
Gymnophthalmidae	-0.13***	-0.15***	-0.19*	-0.25***	-0.07*	0.22	245
Homalopsidae	-0.01 (n.s.)	-0.1*	-0.36***	-0.25***	-0.27***	0.21	33
Hoplocercidae	-0.3***	-0.35***	-0.3***	-0.79***	0.2***	0.65	19
Iguanidae	0.05***	-0.08***	-0.42***	-0.09***	0.01 (n.s.)	0.79	17
Lacertidae	0.19***	-0.01 (n.s.)	-0.08*	0.07***	-0.02 (n.s.)	0.23	285
Lamprophiidae	0.35***	-0.12***	0.34***	0.09***	0.26***	0.36	220

Leiosauridae	-0.09 (n.s.)	0.42***	0.06 (n.s.)	-0.26***	-0.24***	0.55	33
Leptotyphlopidae	-0.01 (n.s.)	0.11***	0.01 (n.s.)	-0.15***	-0.19***	0.38	102
Liolaemidae	-0.36***	-0.18**	-0.73***	0.00 (n.s.)	-0.14*	0.28	292
Natricidae	-0.24***	-0.09***	0.1***	-0.17***	0.1***	0.67	162
Pareatidae	-0.03 (n.s.)	-0.21***	0.31***	-0.15***	0.04 (n.s.)	0.47	14
Phrynosomatidae	-0.52***	-0.42***	-0.93***	0.13***	-0.26***	0.24	136
Phyllodactylidae	0.19***	0.43***	-0.25***	0.29***	0.07***	0.6	91
Pygopodidae	0.08 (n.s.)	0.2***	-0.22***	-0.35***	0.02 (n.s.)	0.44	44
Pythonidae	-0.09***	-0.06***	-0.01 (n.s.)	0.06***	0.08***	0.84	24
Scincidae	-0.06***	0.01 (n.s.)	-0.17***	-0.19***	-0.15***	0.23	911
Sphaerodactylidae	-0.21***	0.02 (n.s.)	0.57***	-0.02 (n.s.)	-0.05**	0.79	103
Teiidae	0.01 (n.s.)	-0.14***	0.02 (n.s.)	-0.16***	0.03 (n.s.)	0.23	117
Tropiduridae	0.18***	0.41***	0.16*	0.19***	-0.08**	0.32	120
Typhlopidae	-0.07***	0.02 (n.s.)	0.11***	-0.02 (n.s.)	0.22***	0.47	146
Uropeltidae	0.07 (n.s.)	-0.41*	-0.36***	0.21 (n.s.)	0.65***	0.37	38

Varanidae	0.07***	-0.16***	0.26***	-0.02 (n.s.)	0.19***	0.64	43
Viperidae	0.42***	-0.16***	-0.11***	0.02 (n.s.)	-0.01 (n.s.)	0.34	285
Xantusiidae	0.17***	0.11*	-0.6***	-0.39***	0.16***	0.84	32
Xenodermatidae	-0.19***	0.2***	-0.42***	-0.3***	-0.14***	0.82	14
Xenosauridae	-0.11 (n.s.)	0.62*	-0.31 (n.s.)	-0.07 (n.s.)	-0.28 (n.s.)	0.5	10