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**Global patterns of body size evolution in squamate reptiles  
are not driven by climate**

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**Global patterns of body size evolution in squamate reptiles are not** 1  
**driven by climate** 2

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<b>BIOSKETCH:</b>	41
Alex Slavenko is a PhD student interested in biogeographical patterns of body size and life-history traits and the distribution of species, as well as the general biology of reptiles and amphibians. He is particularly interested in the patterns and evolution of such traits in insular environments.	42 43 44 45 46

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3	<b>Global patterns of body size evolution in squamate reptiles are not driven</b>	1
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6	<b>by climate</b>	2
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8		
9	Short running title: <b>Little effect of climate on squamate size</b>	3
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12		4
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15	<b>ABSTRACT</b>	5
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18		
19	<b>Aim.</b> Variation in body size across animal species underlies most ecological and	6
20		
21	evolutionary processes shaping local- and large-scale patterns of biodiversity. For well	7
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23	over a century, climatic factors have been regarded as primary sources of natural	8
24		
25	selection on animal body size, and hypotheses such as Bergmann's rule (the increase of	9
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27	body size with decreasing temperature) have dominated discussions. However, evidence	10
28		
29	for consistent climatic effects, especially among ectotherms, remains equivocal. Here,	11
30		
31	we test a range of key hypotheses on climate-driven size evolution in squamate reptiles	12
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33	across several spatial and phylogenetic scales.	13
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39	<b>Location.</b> Global.	14
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42	<b>Time period.</b> Extant.	15
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45	<b>Major taxa studied.</b> Squamates (lizards and snakes).	16
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49	<b>Methods.</b> We quantified the role of temperature, precipitation, seasonality and net	17
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51	primary productivity as drivers of body mass across ~95% of extant squamate species	18
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53	(9,733 spp.). We ran spatial autoregressive models of phylogenetically-corrected median	19
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55	mass per equal-area grid cells. We ran models globally, across separate continents, and	20
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3	for major squamate clades independently. We also performed species-level analyses	21
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5	using phylogenetic generalized least square models, and linear regressions of	22
6		
7	independent contrasts of sister species.	23
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11	<b>Results.</b> Our analyses failed to identify consistent spatial patterns in body size as a	24
12		
13	function of our climatic predictors. Nearly all continent- and family-level models differed	25
14		
15	from one another, and species-level models had low explanatory power.	26
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19	<b>Main conclusions.</b> The global distribution of body mass among living squamates	27
20		
21	varies independently from variation in multiple components of climate. Our study, the	28
22		
23	largest in spatial and taxonomic scale conducted to date, reveals that there is little	29
24		
25	support for a universal, consistent mechanism of climate-driven size evolution within	30
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27	squamates.	31
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35	<b>KEYWORDS:</b> Bergmann's rule, body mass, body size, ectotherms, phylogenetic	33
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37	comparative analyses, reptiles, size clines, spatial analyses	34
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## INTRODUCTION

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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; Gilgooly, 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

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3	& Rodríguez, 2009; Feldman & Meiri, 2014; Vinarski, 2014; Slavenko & Meiri, 2015;	57
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5	Rodrigues, Olalla-Tárraga, Iverso & Diniz-Filho, 2018) levels.	58
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8	The lack of consistency in the attempts to identify prevalent drivers of body size	59
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10	evolution in ectotherms may be partly due to the lack of applicability of the heat-related	60
11		
12	mechanism ( <i>i.e.</i> , Bergmann's original explanation) to ectotherms (Pincheira-Donoso <i>et</i>	61
13		
14	<i>al.</i> , 2008; Meiri, 2011; Slavenko & Meiri, 2015). Bergmann (1847) posited that reduced	62
15		
16	surface area-to-volume ratio in larger animals benefits heat conservation in colder	63
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18	climates, a mechanism sometimes known as the 'heat conservation hypothesis'.	64
19		
20	However, ectotherms produce negligible amounts of metabolic heat, and reduced	65
21		
22	surface area-to-volume ratios might result in less efficient thermoregulation in cold	66
23		
24	climates due to slower heating rates. Therefore, a trade-off exists between heat gain	67
25		
26	(more efficient in smaller ectotherms; Carothers, Fox, Marquet & Jaksic, 1997) and	68
27		
28	retention (more efficient in large ectotherms; Zamora-Camacho <i>et al.</i> , 2014). Thus, large	69
29		
30	body size in colder climates is predicted to compromise the need to achieve optimal	70
31		
32	body temperatures to initiate basic fitness-related activities in the first place (Pincheira-	71
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34	Donoso <i>et al.</i> , 2008).	72
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37	Alternative mechanisms for climate-driven body size-clines may be more applicable	73
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39	to ectotherms. The 'heat balance hypothesis' (Olalla-Tárraga <i>et al.</i> , 2006) predicts that	74
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41	thermoconformers exhibit a reverse pattern to the one predicted by Bergmann's rule,	75
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43	<i>i.e.</i> smaller bodies at lower temperatures because of the effect of body size on heating	76
44		
45	rates. The 'water availability hypothesis' (Ashton, 2002) suggests that large sizes, thus,	77
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47	small surface area-to-volume ratios, are beneficial in conserving water in dry habitats	78
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(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

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3 conditions experienced by squamates is not represented). Patterns detected might thus 101  
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5 merely represent local or regional trends. 102  
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8 Squamates in temperate regions often exhibit unique adaptations to cold conditions 103  
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10 (*e.g.*, Churchill & Storey, 1992; Voituron, Storey, Grenot & Storey, 2002; Berman, 104  
11  
12 Bulakhova, Alfimov & Mescheryakova, 2016). Such adaptations (*e.g.*, prolonged 105  
13  
14 hibernation) may mask or weaken climatic effects on body size (Scholander, 1955). 106  
15  
16 Furthermore, the small number of species in such regions might lead to spatial patterns 107  
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18 being driven by a few wide-ranging unusually small or unusually large species (Slavenko 108  
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20 & Meiri, 2015). 109  
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25 Crucially, while global-scale studies on size clines in endotherms have been 110  
26  
27 conducted (birds, Olson *et al.*, 2009; mammals, Riemer *et al.*, 2018), to date, only a few 111  
28  
29 studies have examined global size clines of an entire large clade of ectotherms (apart 112  
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31 from turtles; Angielczyk, Burroughs & Feldman, 2015; Rodrigues *et al.*, 2018), making it 113  
32  
33 impossible to infer a universal effect of climate on body size. 114  
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37 Our goals were to: a) examine the spatial patterns in body sizes of squamates; b) test 115  
38  
39 the leading current hypotheses linking body size and climate; and c) test whether we 116  
40  
41 find consistent support for these hypotheses across phylogenetic and spatial scales. If 117  
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43 climate consistently affects ectotherms' body sizes, we expect to find qualitatively 118  
44  
45 similar relationships between body size and the climatic variables we examine, across 119  
46  
47 squamate phylogeny and across space, and using different methods (*i.e.*, with either the 120  
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49 species or the grid cell as the focus of analyses). 121  
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## METHODS

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### DATA COLLECTION

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We used body mass (Feldman, Sabath, Pyron, Mayrose & Meiri, 2016) and

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distribution data (Roll *et al.*, 2017) for ~95% (9,733 species) of the currently described

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species of extant squamates (Uetz *et al.*, 2018). We used mass as our measure of body

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size instead of other measures, such as SVL or total length, as these cannot be easily

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compared between clades that differ greatly in their *bauplan* (see *e.g.* figure S2c in

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Feldman *et al.*, 2016, where squamates of similar length differ by 2 orders of magnitude

130

in mass). The mass data in Feldman *et al.* (2016) are size maxima of squamate species,

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irrespective of sex, derived from SVL using clade-specific length-mass allometric

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equations. Size maxima were used instead of means, as they are more readily available

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in the literature, and also likely well represent the potential sizes attainable by

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squamates, which have indeterminate growth. We  $\log_{10}$ -transformed the mass data to

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normalize the otherwise strongly right-skewed body size distribution (Feldman *et al.*,

136

2016). We used global temperature and precipitation data for the 1979-2013 time

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period at 30 arc-second resolution (CHELSA; Karger *et al.*, 2017). These were used to

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test three hypotheses: the 'heat balance' hypothesis, using mean annual temperature

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(in degrees Celsius; BIO1); the 'water conservation' hypothesis, using mean annual

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precipitation (in mm/year; BIO12); and the 'seasonality' hypothesis, using both

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temperature seasonality (annual range in degrees Celsius; BIO4) and precipitation

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seasonality (annual range in mm/year; BIO15). We also used global net primary

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productivity (NPP, in grams of carbon / [year \* m<sup>2</sup>]) data for 1995 (SEDAC; Imhoff *et al.*,

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3	2004) to test the ‘primary productivity’ hypothesis. We tested these four hypotheses	145
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5	using two analytical approaches (assemblage-level and species-level; see below). All	146
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7	statistical analyses were performed in R v3.4.2 (R Core Team, 2017).	147
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13	<b>ASSEMBLAGE-LEVEL APPROACH</b>	149
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15	As squamate body size shows a strong phylogenetic signal (Blomberg, Garland Jr. &	150
16		
17	Ives, 2003; Feldman <i>et al.</i> , 2016), we accounted for phylogenetic non-independence	151
18		
19	using the Lynch method (Lynch, 1991). We used the variance-covariance matrix derived	152
20		
21	from the latest species-level phylogeny of squamates (Tonini, Beard, Ferreira, Jetz &	153
22		
23	Pyron, 2016) to fit a linear mixed effects model, with body mass as the response and	154
24		
25	species identity mapped as a random effect, using the <i>lme4</i> function in the ‘coxme’ R	155
26		
27	package (Therneau, 2018). We omitted from the analysis 41 species not included in the	156
28		
29	phylogeny. We treated the predicted values of this model as the phylogenetic	157
30		
31	components of mass, attributed to shared evolutionary history. The body size residuals	158
32		
33	from the phylogenetic components were treated as the species components (the	159
34		
35	component of mass for each species that cannot be explained by shared ancestry). We	160
36		
37	then overlaid the range maps for all squamates (from Roll <i>et al.</i> 2017) onto an equal-	161
38		
39	area 96x96 km grid in a Behrmann equal-area projection (roughly 0.86x0.86 degrees at	162
40		
41	the Equator) in ArcGIS 10.0 (ESRI) and calculated the median of the species components	163
42		
43	for the species assemblage in each grid cell. We also calculated the mean value of each	164
44		
45	of our environmental predictors across the cell. We omitted island cells (all landmasses	165
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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).

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3 Species richness patterns can strongly affect size clines, with assemblage means and 187  
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5 medians, particularly in low-richness cells, often being sensitive to extremely large or 188  
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7 small-bodied species (Meiri & Thomas, 2007). We therefore used a permutation 189  
8  
9 approach to test if size clines could arise from spurious effects of richness patterns 190  
10  
11 (Olson *et al.*, 2009; Slavenko & Meiri, 2015). We randomly drew species from a pool of 191  
12  
13 all squamates, without replacement, to occupy cells while maintaining the original 192  
14  
15 richness distribution. The probability of drawing species from the pool was weighted by 193  
16  
17 each species' range size (from Roll *et al.*, 2017). We then calculated the median species 194  
18  
19 component for each random assemblage per cell. We repeated this procedure 1,000 195  
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21 times and calculated 95% confidence intervals from the resultant random distributions 196  
22  
23 of median species component per cell, to test whether observed median species 197  
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25 components are lower, or higher, than expected from their richness values. 198  
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### 35 SPECIES-LEVEL APPROACH 200

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37 We used multiple-predictor phylogenetic generalized least square (PGLS) regressions 201  
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39 (Grafen, 1989), using the  $\log_{10}$ -transformed mass of each species as the response 202  
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41 variable (after omitting all insular endemic species and species across whose ranges we 203  
42  
43 were lacking predictor variables), the mean of each environmental variable across each 204  
44  
45 species' range as predictors, and the latest phylogeny of squamates (Tonini *et al.*, 2016) 205  
46  
47 to estimate the expected covariance structure. After omitting from the analysis 2,695 206  
48  
49 island-endemic species to remove a potential insularity bias, and a further 701 species 207  
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51 that were either not included in the phylogeny or with missing data, we were left with 208  
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3 6,323 species. We ran the PGLS models under a Brownian motion model of evolution 209  
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5 and calculated the maximum likelihood estimates of Pagel's  $\lambda$ , a measure of 210  
6  
7 phylogenetic signal in the data ranging from 0 (no signal) to 1 (strong phylogenetic signal 211  
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9 under a Brownian motion model of evolution), with the *ppls* function in the 'caper' 212  
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11 package (Orme *et al.*, 2012). 213  
12  
13  
14  
15 This approach ignores spatial variation in the environmental predictor variables, 214  
16  
17 which can be substantial in extremely wide-ranging species. We therefore reran the 215  
18  
19 PGLS analyses after omitting those species with the 10% largest range sizes (leaving 216  
20  
21 5,691 species), which would be most heavily biased by averaging out environmental 217  
22  
23 predictors across their ranges, and compared the results of this analysis to those of the 218  
24  
25 complete dataset. 219  
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27  
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29  
30 In a complementary analysis, we compared independent size and climate contrasts of 220  
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32 all 1,456 sister-species pairs recovered from the phylogeny. While this greatly reduces 221  
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34 sample size, it also eliminates phylogenetic dependence, as any differences between 222  
35  
36 sister species in body size do not result from shared evolutionary history (Felsenstein, 223  
37  
38 1985), and compares species that tend to resemble each other most in traits that likely 224  
39  
40 affect body size (Bergmann, 1847). We ran linear regressions through the origin of 225  
41  
42 contrasts in mass between sister species against contrasts in each of the five 226  
43  
44 environmental predictors between sister species, and tested for significance with a 227  
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46 conservative alpha of 0.005 (Johnson, 2013; Benjamin *et al.*, 2018). 228  
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**RESULTS**

230

## ASSEMBLAGE-LEVEL APPROACH 231

Our analyses failed to identify a consistent latitudinal pattern in squamate body size 232

across different regions of the globe. Squamate assemblage body mass is largest in the 233

northern latitudes of North America, most of South America, inland Africa and the 234

Indian Subcontinent (Fig. 1a; Fig. S1.1). It is small in most of northern Eurasia, the Sahel 235

and the Horn of Africa, and in western and central Australia. Squamate species 236

components are positively correlated with mean annual temperature, mean annual 237

precipitation and NPP, and negatively correlated with precipitation seasonality (Table 1). 238

The spatial pattern in squamate species components is more strongly correlated with 239

the ratio of lizards to snakes in each cell – squamate assemblages are large-sized in cells 240

dominated by snakes, and small-sized in cells where most species are lizards (Fig. 1b; 241

SAR of adaptive component against lizard proportion, standardised  $\beta = -0.36$ ,  $p < 0.001$ , 242

Nagelkerke's pseudo- $R^2 = 0.39$ ). The pattern is clear even when accounting for 243

phylogenetic non-independence by comparing species components, but is even more 244

pronounced when examining the uncorrected mass data (Fig. S1.1). 245

Size-climate relationships are not geographically consistent – continent-level analyses 246

recovered models with different sets of predictors, with opposite correlation signs, and 247

with extremely different effect sizes, for each continent (Table 1). For instance, mean 248

annual temperature was positively correlated with squamate mass in Asia, Europe and 249

South America, but negatively correlated with mass in Australia and North America, and 250

uncorrelated with mass in Africa ( $\alpha = 0.005$ ). 251



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3	Further inconsistencies were found in the separate analyses of snakes and lizards	252
4		
5	(Table 1; Fig. 1c,d). Globally, lizard mass is positively correlated with mean annual	253
6		
7	temperature and seasonality in precipitation, and negatively correlated with seasonality	254
8		
9	in temperature. On the other hand, snake mass is positively correlated with mean	255
10		
11	annual temperature, and negatively correlated with mean annual precipitation and	256
12		
13	seasonality in temperature and precipitation globally. Body mass of neither snakes nor	257
14		
15	lizards is correlated with NPP. As with the global squamate models, snake and lizard	258
16		
17	continent-level models are substantially different to each other (Table 1).	259
18		
19	Family-level models also show large inconsistencies (Table S1.1). Each predictor was	260
20		
21	non-significant in 27-34% of the family models (across the 44 families with > 10 species),	261
22		
23	but often not in the same families ( <i>e.g.</i> , mean temperature and NPP were non-	262
24		
25	significant in 18 families each, but only in five of these were they both non-significant).	263
26		
27	When the predictors were significantly correlated with mass, the correlations often had	264
28		
29	opposite directions between families. For each of the predictors, positive correlations	265
30		
31	were found with mass in 27-41% of families, and negative correlations were found in 27-	266
32		
33	43% of the families (Fig. S1.4). Only four pairs of families had qualitatively identical	267
34		
35	models: Leiosauridae-Leptotyphlopidae, Hoplocercidae-Elapidae, Iguanidae-Colubridae,	268
36		
37	and Amphisbaenidae-Eublepharidae. These families are phylogenetically and	269
38		
39	ecologically very far from one another. All other family models were unique. These	270
40		
41	results hold even if we analyze only families with over 30 species. In this more restrictive	271
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43	dataset of 33 families, each predictor was non-significant in 27-36% of the models,	272
44		
45	positively correlated with mass in 24-45% of families, and negatively correlated with	273
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3 mass in 27-45% of families. There was no significant correlation between the species 274  
4 richness of a family and the number of significant predictors in its model (linear 275  
5 regression;  $p = 0.33$ ). 276  
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10 The permutation analyses showed that most of the observed median species 277  
11 components within cells could be expected by random processes of community 278  
12 assembly. In fact, only ~7% of lizard cells and ~11.5% of snake cells deviate from the 95% 279  
13 confidence intervals of the random distributions (Fig. 2; Fig. S1.2). These cells comprise 280  
14 somewhat distinct geographical units (Fig. 3; Fig. S1.3). Lizards are smaller than 281  
15 expected in many of the most species-rich cells (Fig. 2a; Fig. S1.2a), especially in 282  
16 Australia, and also in the Horn of Africa and along the coasts of South America. They are 283  
17 larger than expected in central South America, inland Africa and the northwest of the 284  
18 Indian subcontinent. Meanwhile, snakes are smaller than expected in western Australia, 285  
19 eastern Asia, some parts of the central Asian steppes, and inland Africa, and larger than 286  
20 expected in central and northern South America, much of northern Eurasia, and 287  
21 southeastern Australia. Only in very few cells in East Africa are both lizards and snakes 288  
22 larger, or smaller, than expected by chance (Fig. 3c). 289  
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#### 44 **SPECIES-LEVEL APPROACH** 291

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47 Our PGLS analyses revealed a positive relationship between squamate mass and 292  
48 temperature seasonality, and a negative relationship between mass and precipitation 293  
49 seasonality (at  $\alpha = 0.005$ ; Table 2). The phylogenetic signal in the model was very strong 294  
50 ( $\lambda = 0.93$ ), but the overall explanatory power was extremely low ( $R^2 = 0.01$ ). Omitting 295  
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3 the widest-ranging species from the dataset caused a marked change – the relationship 296  
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5 with seasonality in temperature became nonsignificant, but the positive correlation with 297  
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7 mean annual precipitation became significant. All other model parameters changed only 298  
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9 slightly ( $\lambda = 0.92$ ,  $R^2 = 0.02$ ). NPP and mean annual temperature were not significantly 299  
10  
11 correlated with mass in any of the models. 300  
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15 In the sister-species analysis we found a negative correlation between squamate 301  
16  
17 mass and precipitation seasonality, and no significant correlations with any of the other 302  
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19 predictor variables (Fig. 4). However, this model also had extremely low explanatory 303  
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21 power ( $R^2 = 0.01$ ). 304  
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## 24 25 26 27 28 29 **DISCUSSION** 306

### 30 31 32 **ASSEMBLAGE-LEVEL APPROACH** 307

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35 Our study provides the first truly global-scale analysis of the spatial patterns of body 308  
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37 size variation in squamates, the most speciose group among modern tetrapods, as a 309  
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39 function of multiple alternative climatic predictors. Our combined evidence from 310  
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41 multiple analytic approaches suggests that climate consistently fails to have an 311  
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43 identifiable effect on spatial patterns of squamate size. 312  
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48 Our core finding shows that spatial patterns in squamate body sizes are both weak 313  
49  
50 and inconsistent across phylogenetic and spatial scales. We thus conclude that climate 314  
51  
52 exerts weak direct selection pressure on squamate sizes, at least at the examined, 315  
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54 interspecific scales (but see also Pincheira-Donoso & Meiri, 2013, for intraspecific 316  
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3 comparisons). While squamates seem to display a global trend of decreasing in size 317  
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5 towards the poles (or a 'reverse Bergmann' pattern; Fig. 1a), this pattern is weak and 318  
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7 inconsistent across regions and lineages. Squamates are generally larger in the New 319  
8  
9 World, and the northernmost cells of North America contain assemblages with the 320  
10  
11 largest median sizes. This global pattern seems to be most strongly explained by the 321  
12  
13 ratio of lizard to snake species in each cell. The body size distribution of squamates is 322  
14  
15 strongly bimodal (Feldman *et al.*, 2016), as snakes are, on average, larger than lizards. 323  
16  
17 Snakes and lizards also differ in their spatial distribution patterns (Roll *et al.*, 2017). 324  
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19 Snakes show the common tetrapod pattern of richness peaking in the tropics, whereas 325  
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21 lizard richness peaks in warm, arid regions, particularly Australia. Thus, squamates are, 326  
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23 on average, large in snake-rich cells (*e.g.*, the Amazon Basin and Canada), and small in 327  
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25 lizard-rich cells (*e.g.*, Australia). The global latitudinal size patterns for lizards and snakes 328  
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27 are similarly unclear, with the strongest seeming to be a fall (in lizards) and rise (in 329  
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29 snakes) of body size in the northernmost latitudes (Fig 1c,d). This is likely due to the 330  
30  
31 effect of the very few, wide-ranging species, inhabiting extreme latitudes in the 331  
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33 Northern hemisphere (*e.g.*, *Zootoca vivipara* and *Vipera berus* are the only lizard and 332  
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35 snake species, respectively, in much of northern Eurasia, and the snake *Thamnophis* 333  
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37 *sirtalis* is the only squamate species in much of northern North America). The 334  
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39 inconsistency in patterns and in relationships with the climatic variables is especially 335  
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41 pronounced at the continent- and family-level analyses. No single climatic variable 336  
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43 displays a consistent relationship with squamate mass across scales. 337  
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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

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3 chance. This is markedly different from the result for birds, where many cell 359  
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5 assemblages cannot be explained by random processes (Olson *et al.*, 2009), yet are 360  
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7 similar to results for amphibians (Slavenko & Meiri, 2015). While this finding does not 361  
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9 necessarily imply that current size distributions were generated by random processes 362  
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11 alone (*i.e.*, our null model may be affected by the intrinsic imperfection of null models in 363  
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13 general; Gotelli, 2001), we cannot reject the null hypothesis. The relationship between 364  
14  
15 species richness and the median body size within cells is complex. Body sizes may be 365  
16  
17 either extremely large or extremely small in cells with low richness values purely by 366  
18  
19 chance, and squamate richness tends to be strongly correlated with climatic variables 367  
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21 (*e.g.*, Costa, Nogueira, Machado & Colli, 2007; Powney, Grenyer, Orme, Owens & Meiri, 368  
22  
23 2010; Morales-Castilla *et al.*, 2011; Lewin *et al.*, 2016). This poses a severe limitation for 369  
24  
25 inference using any grid-cell based analysis, as even large-scale, statistically significant 370  
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27 spatial patterns in body size may be merely spurious patterns, particularly due to 371  
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29 species' co-occurrence in multiple cells (Hawkins *et al.*, 2017). 372  
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38 Interestingly, the cells which deviate from random expectations are not randomly 373  
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40 distributed across the globe but seem to form distinct geographical units (Fig. 3). 374  
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42 Investigating the composition of squamate communities in these habitats might be a 375  
43  
44 promising avenue for uncovering the causes. For instance, lizards in Australian deserts 376  
45  
46 are much smaller than expected by chance (Fig. 3a). Lizard richness peaks in arid 377  
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48 Australia (Powney *et al.*, 2010; Roll *et al.*, 2017), and Australia's lizard fauna is 378  
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50 dominated by skinks (Cogger, 2014), which are generally small-bodied (Meiri, 2008). An 379  
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52 additional example is the higher than expected mass of snakes in a large portion of the 380  
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3 southern Amazon Basin (Fig. 3b). Patterns of body size distribution in South American 381  
4 snake assemblages are strongly affected by the contribution of the three most species- 382  
5 rich lineages: colubrids, xenodontines and dipsadids. Colubrid and xenodontine snakes 383  
6 (median mass 68.3 g) are much larger than dipsadids (median mass 35.4 g), and in the 384  
7 southern Amazon snake faunas are dominated by a combination of xenodontines and 385  
8 colubrids (see Fig. 25.6 in Cadle & Greene, 1993). Only in few places on the globe, 386  
9 however, are both lizards and snakes either smaller, or larger, than expected by chance 387  
10 (Fig. 3c), again demonstrating remarkable inconsistency in spatial body size patterns 388  
11 between the two groups. 389

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### 28 **SPECIES-LEVEL APPROACH**

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31 Our species-level analyses confirm the finding that body size among squamates varies 392  
32 independently from variation in climate. While we did find correlations between mass 393  
33 and our examined climatic variables, their explanatory power is extremely low, and 394  
34 most size variation is explained by shared ancestry. This is similar to previous findings in 395  
35 amphibians (Slavenko & Meiri, 2015). 396

36 Our study also serves as a demonstration of the importance of considering scale in 397  
37 ecological studies, both spatial (Wiens, 1989; Chave, 2013) and phylogenetic (Graham, 398  
38 Storch & Machac, 2018). Had we considered only the global scale analyses, we might 399  
39 have concluded that there is support for a reverse Bergmann's rule in squamate sizes. 400  
40 Only by examining our data across differing scales were we able to discern the 401

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3 inconsistency in patterns and realize that the global pattern is probably driven by 402  
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5 assemblage structure. In this case, our global scale analyses were a classic case of 403  
6  
7 comparing apples to oranges, considering the stark size differences between continents, 404  
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9 between lizards and snakes, and between different lineages within these groups. 405  
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13 We acknowledge that the interspecific approach ignores size variation at the 406  
14  
15 intraspecific level, arguably a more relevant scale for examinations of climate-driven size 407  
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17 evolution (Meiri, 2011). Some species indeed show intraspecific trends in size consistent 408  
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19 with climate-driven size evolution, particularly along elevational gradients (*e.g.*, 409  
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21 Zamora-Camacho *et al.*, 2014; *cf.* Pincheira-Donoso & Meiri, 2013). However, data on 410  
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23 range-wide intraspecific size variation are lacking for most squamate species. Testing 411  
24  
25 intraspecific relationships between climate and body size on a large sample of 412  
26  
27 squamates is beyond the scope of this work, though we acknowledge climate might be 413  
28  
29 an important factor shaping body size at this level. We doubt, however, that the effects 414  
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31 would be consistently predictable by any 'ecological rule' and suspect they might be 415  
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33 idiosyncratic and depend heavily on the natural history of each examined species. 416  
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## 42 43 44 **CONCLUSIONS** 418 45

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47 Collectively, our results suggest that climate is likely not an important driver of size 419  
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49 evolution in squamates as a group, despite exerting a strong influence on their spatial 420  
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51 distribution (Roll *et al.*, 2017), and therefore likely affecting spatial size distributions by 421  
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53 proxy. This is consistent with similar results for amphibians (Slavenko & Meiri, 2015), 422  
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3 and may be the case for terrestrial ectotherms in general. Recently, Riemer *et al.* (2018) 423  
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5 analysed an impressively large dataset of mammals and birds, and concluded that there 424  
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7 is little support for a general relationship between mass and temperature in 425  
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9 endotherms, despite previous evidence to the contrary (Ashton *et al.*, 2000; Meiri & 426  
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11 Dayan, 2003). While these results do not mean that temperature, and other climatic 427  
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13 variables, do not exert selection pressure on body size (and indeed they may apply to 428  
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15 some taxa), they do raise questions as to the generality of such evolutionary 429  
16  
17 mechanisms across all taxa. This is not to imply that climate is not an important driver of 430  
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19 size evolution, but rather that the causative mechanisms of size evolution may be 431  
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21 idiosyncratic and strongly lineage- and location-dependent. While this conclusion does 432  
22  
23 pose a difficulty for generalization, it also creates a promising avenue for future research 433  
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25 of size evolution on a case-by-case basis, and on multiple spatial and phylogenetic 434  
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27 scales. In any event, we advise caution in adopting such climate-size relationships as 435  
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29 general 'rules', at the very least until their generality has been properly tested on large, 436  
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31 extensive datasets. 437  
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**DATA ACCESSIBILITY**

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All data used for this study were previously published in other scientific publications and

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publicly available datasets and are properly cited. The distribution maps from Roll *et al.*

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(2017) are currently under embargo, and will be made publicly available during 2018.

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## TABLES

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**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.

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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

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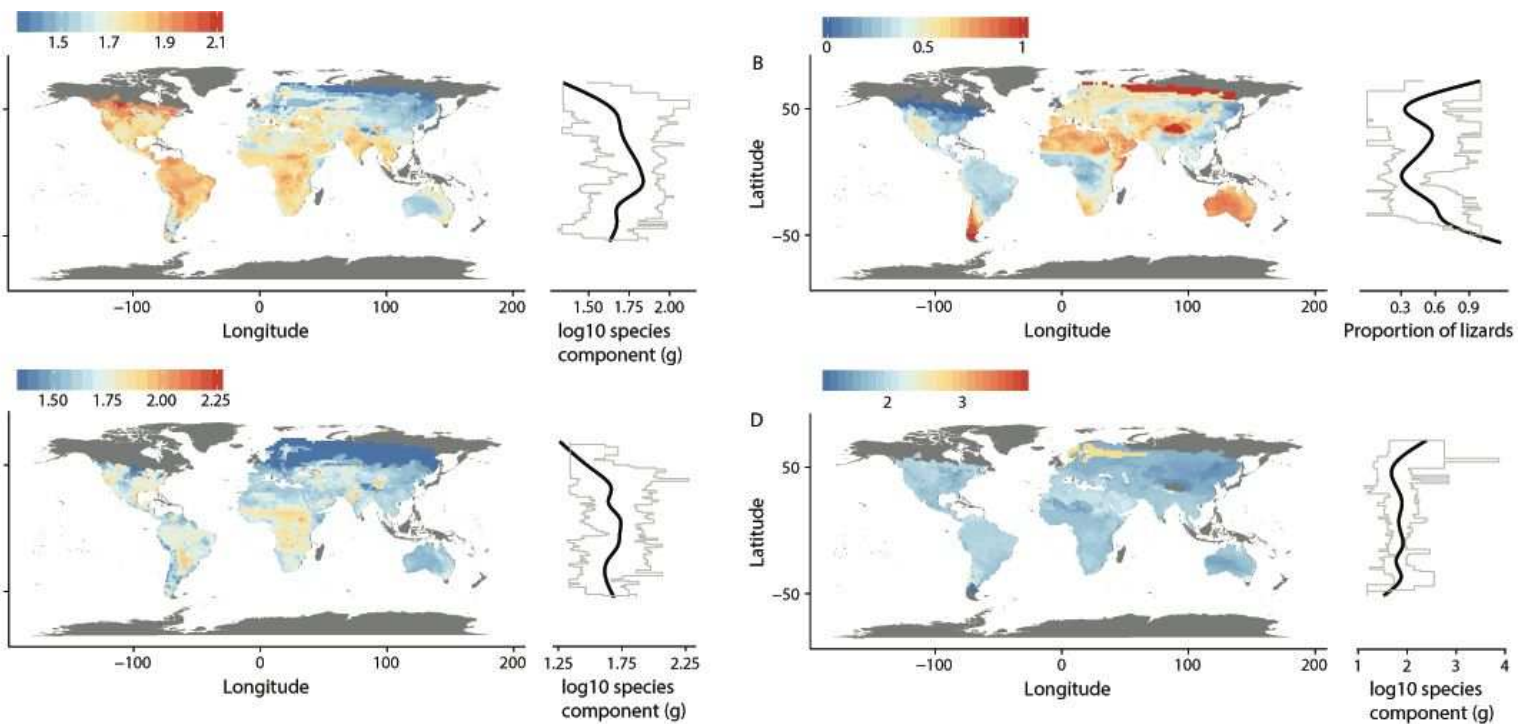
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**Table 2.** Results of the PGLS analyses. A summary of the full model is given for the full dataset, and with the widest-ranging species omitted. For each predictor, the standardised regression slope is given. P-values for each predictor are indicated 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	$\lambda$	$R^2$
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

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667

**Figure 1.** Maps showing the global distribution of a) median log<sub>10</sub> species component

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of mass (in grams) per cell of all squamates; b) proportion of lizard species out of all

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squamates per cell; c) median log<sub>10</sub> species component of mass (in grams) per cell of

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lizards; and d) median log<sub>10</sub> species component of mass (in grams) per cell in snakes.

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Species components are the component of mass for each species that cannot be

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explained by its evolutionary history (residuals from a phylogenetic model of size

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evolution). Next to each map is a curve showing a generalized additive model of each

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mapped variable (in black) and the minimum and maximum values of each mapped

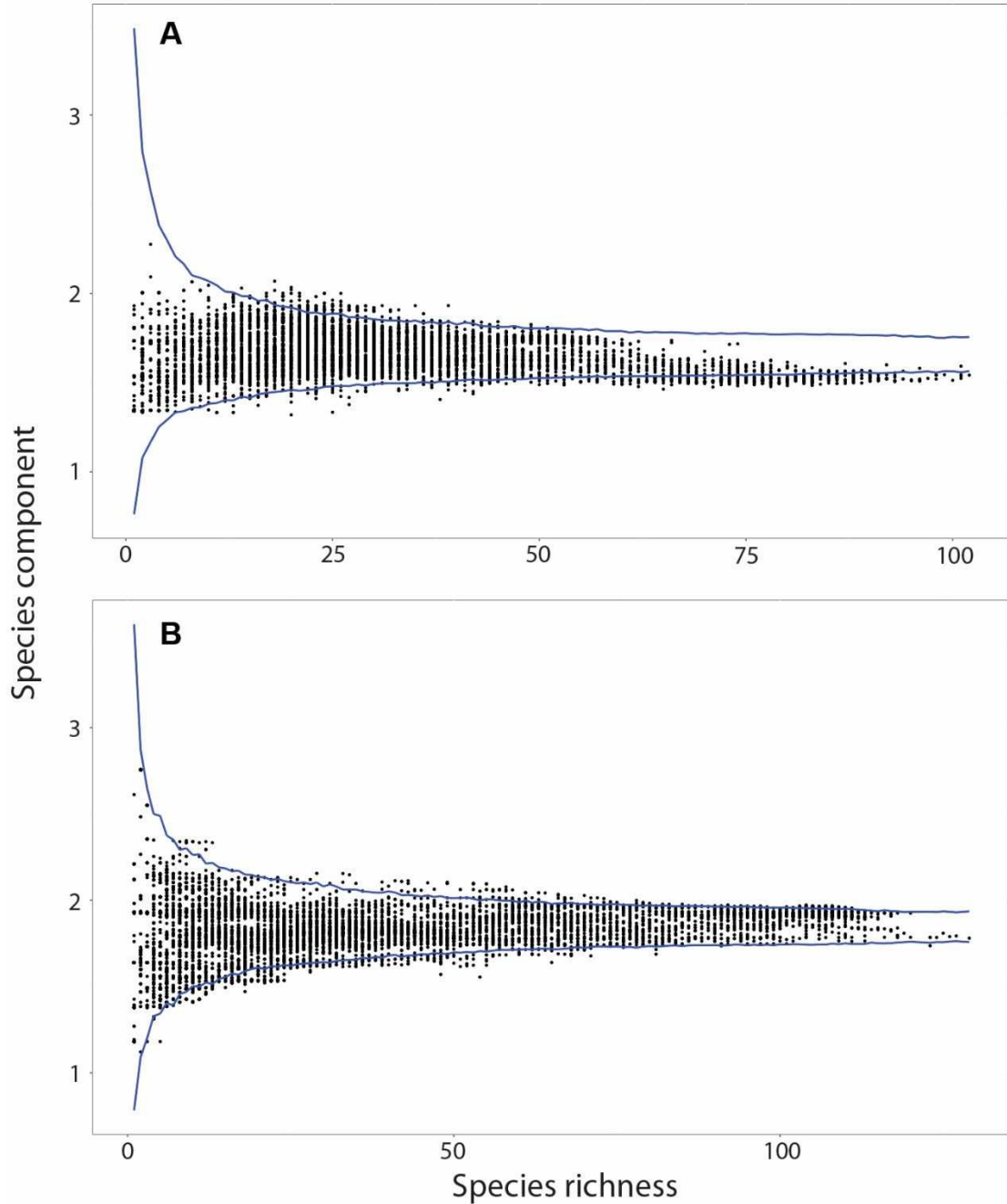
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variable per 96km latitudinal band (in grey).

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**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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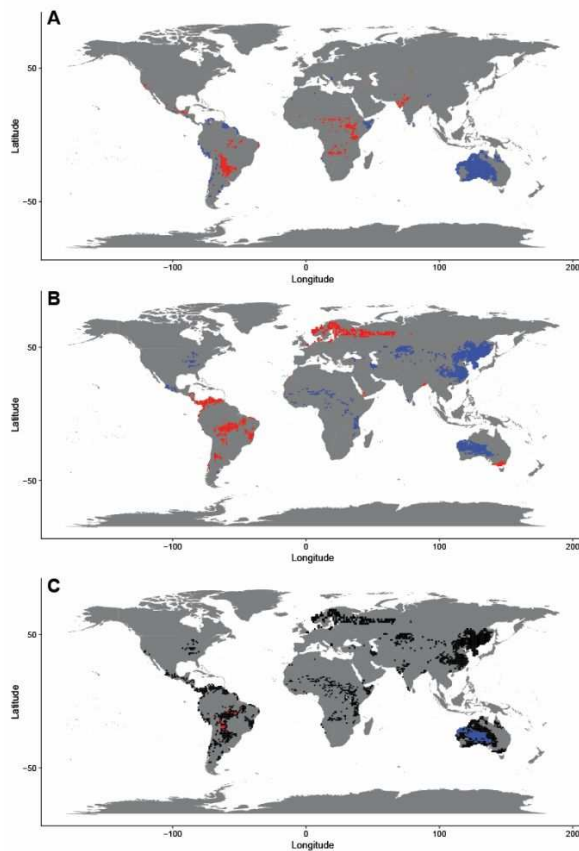
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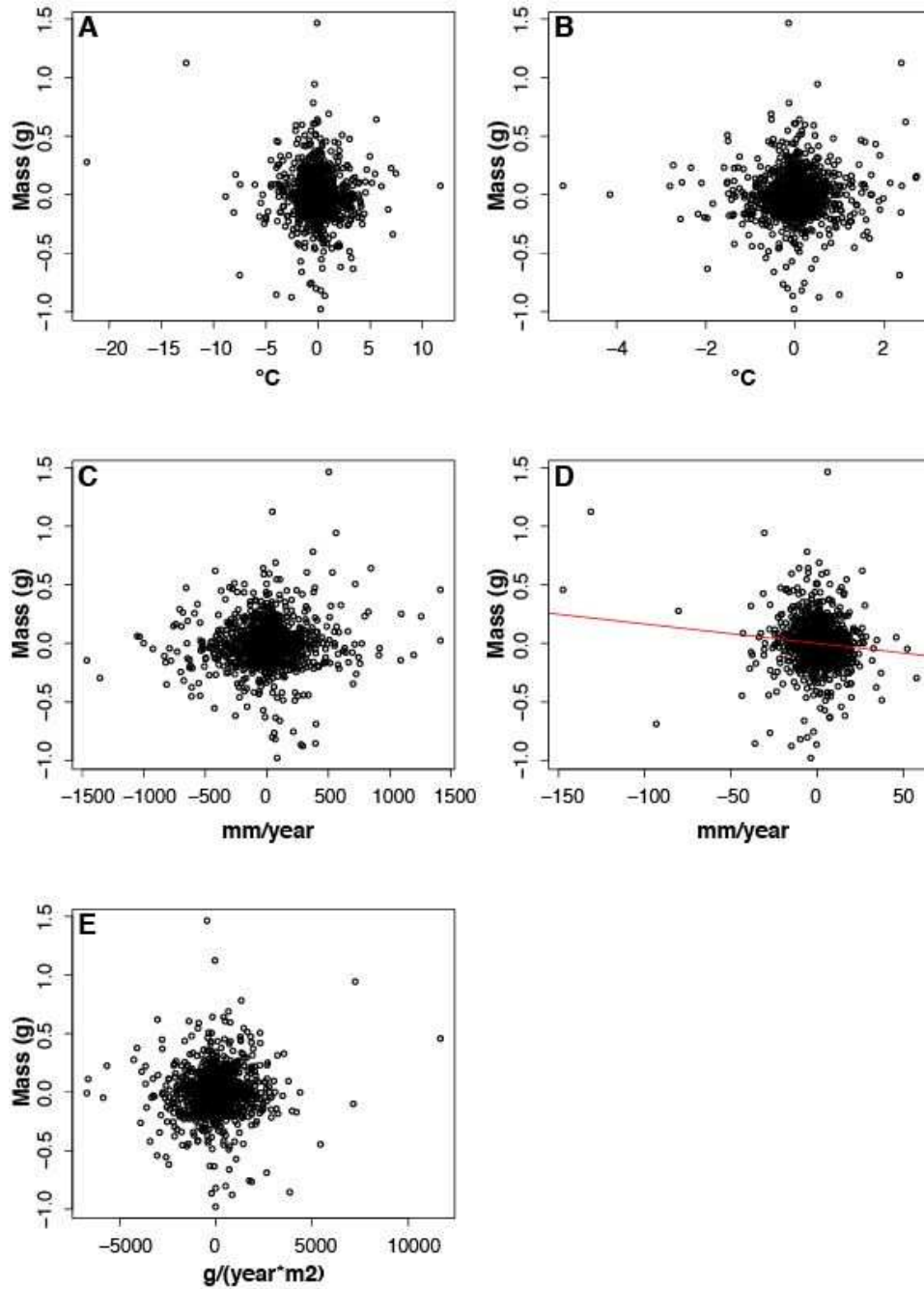
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**Figure 3.** Maps showing cells of a) lizards and b) snakes with median species components exceeding the 95% confidence intervals of 1000 randomized distributions. Species components are the component of mass for each species that cannot be explained 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

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3 expected values (but not in the same direction), whereas blue cells are where both are 694  
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5 smaller than expected, and red cells are where both are larger than expected. 695  
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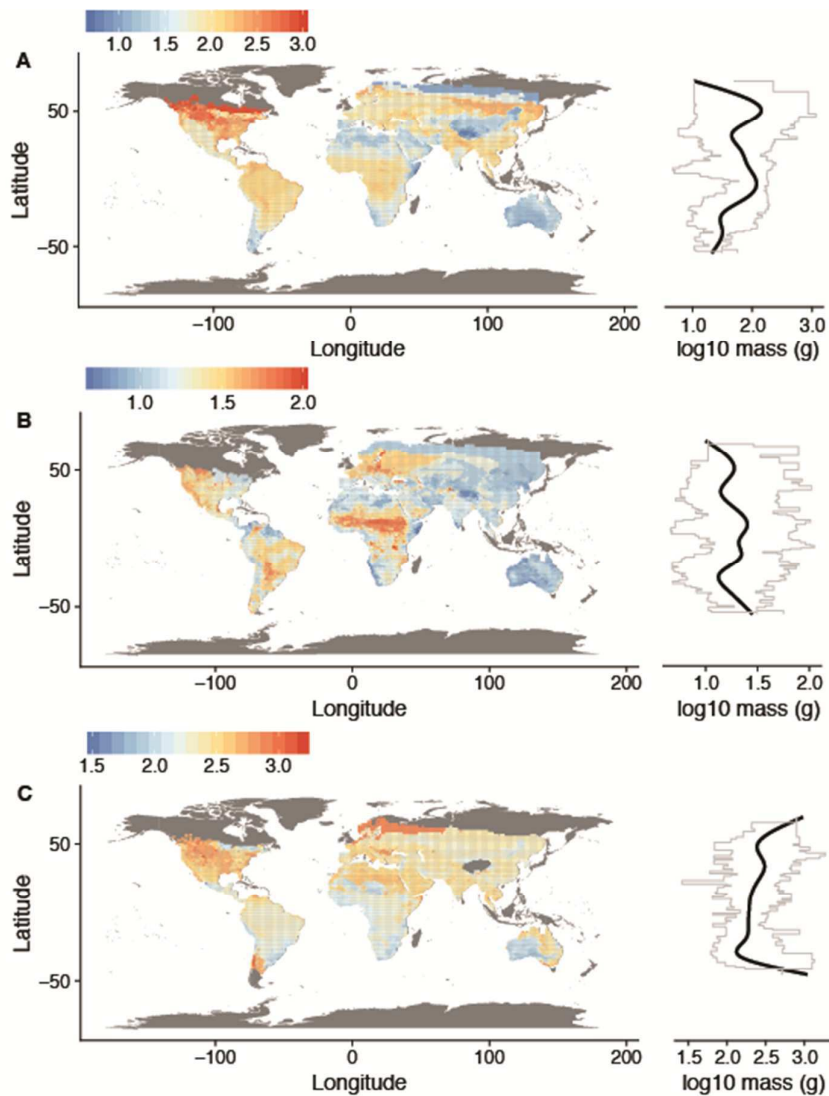
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3 **Figure 4.** Scatter plots of 1456 sister-species pairs. Shown are independent contrasts 697  
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5 of log<sub>10</sub> mass (in grams) against a) mean annual temperature; b) temperature 698  
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7 seasonality; c) mean annual precipitation; d) precipitation seasonality; and e) net 699  
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9 primary productivity. Only the significant regression through the origin in d) is 700  
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11 represented by a red line. All other regressions are not significant. 701  
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## 1 Appendix S1

2 Supplementary figures and table.



3

4 **Figure S1.1.** Maps showing global trends in log<sub>10</sub> median mass per cell (in grams;

5 uncorrected for phylogenetic non-independence) of a) squamates; b) lizards; and c)

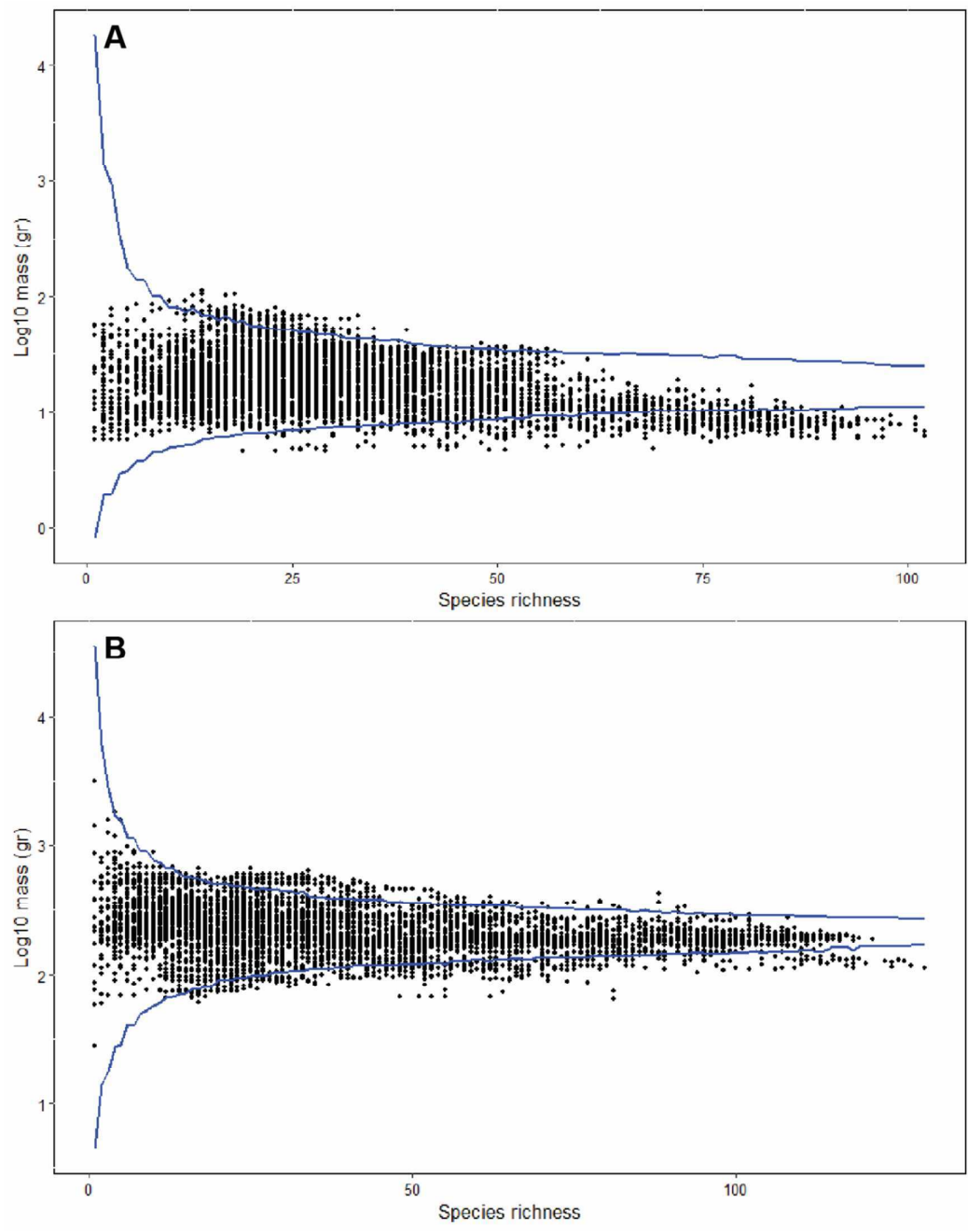
6 snakes. In all maps, colours range from blue for low values, to red for high values.

7 Next to each map is a curve showing a generalized additive model of each mapped

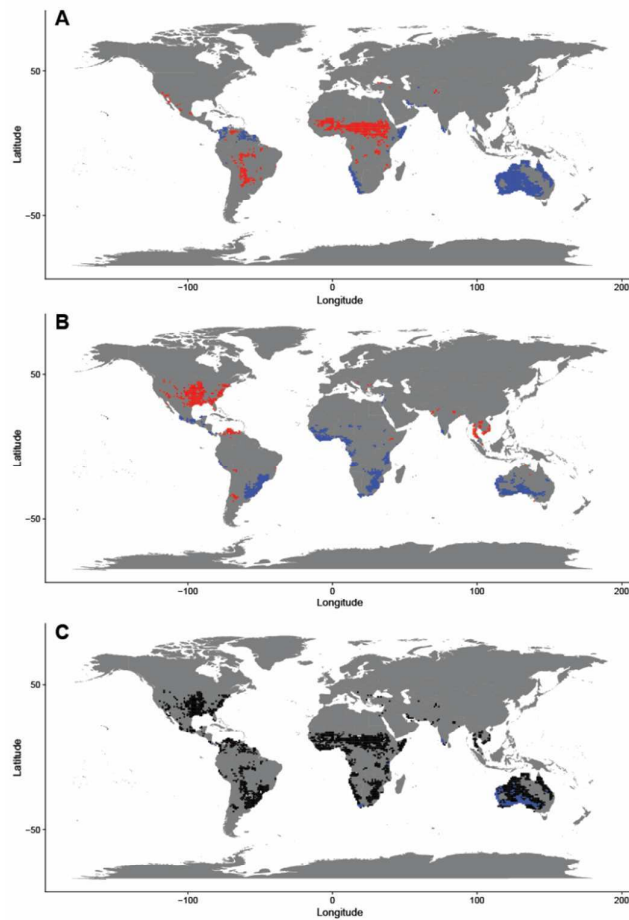
8 variable (in black) and the minimum and maximum values of each mapped variable

9 per 96km latitudinal band (in grey).

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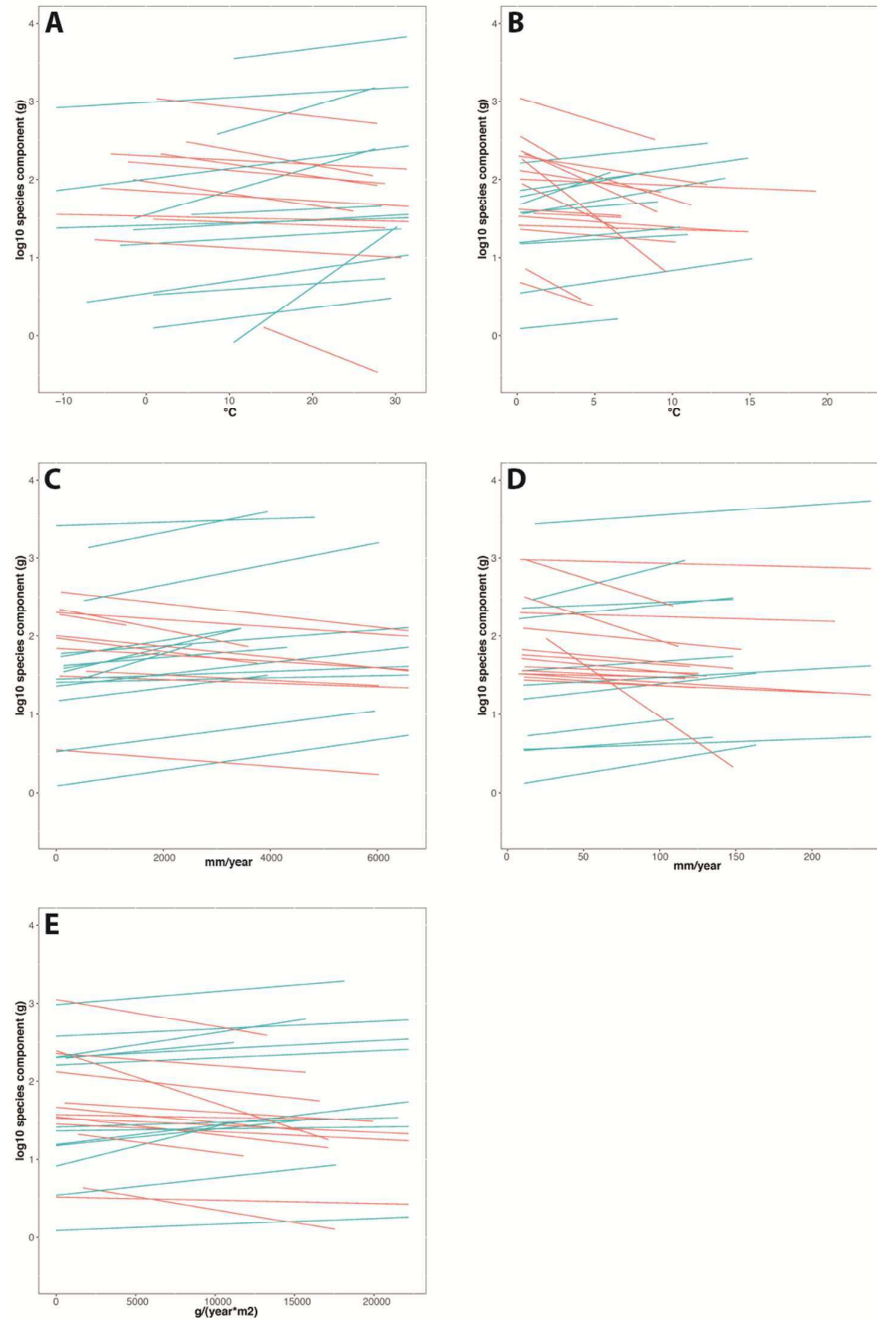
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11 **Figure S1.2.** Distribution of median mass (in grams; uncorrected for phylogenetic  
12 non-independence) of (a) lizards and (b) snakes per grid cell. Black circles represent  
13 observed values; blue lines represent 95% confidence intervals of 1000 randomized  
14 distributions.  
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17 **Figure S1.3.** Maps showing cells of a) lizards and b) snakes with median mass (in  
18 grams; uncorrected for phylogenetic non-independence) exceeding the 95%  
19 confidence intervals of 1000 randomized distributions. Red cells have larger masses  
20 than expected by chance, whereas blue cells have smaller masses than expected by  
21 chance. c) overlap between the two maps, black cells are where only lizards or  
22 snakes (but not the other group) exceed expected values, light grey cells are where  
23 both lizards or snakes exceed expected values (but not in the same direction),  
24 whereas blue cells are where both are smaller than expected, and red cells are  
25 where both are larger than expected.





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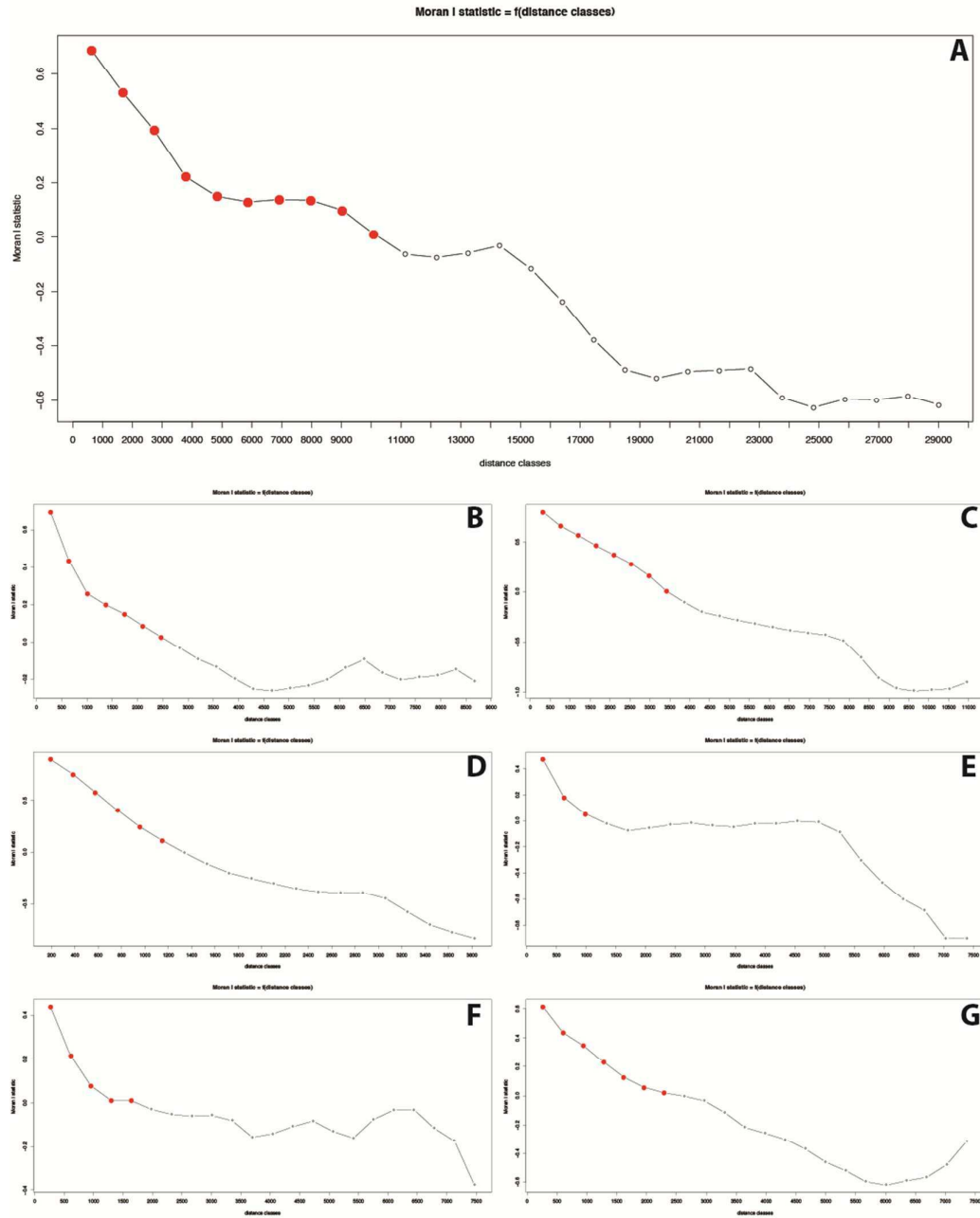
27 **Figure S1.4.** Regression plots of family-level SAR models of adaptive components

28 of mass against a) mean annual temperature; b) temperature seasonality; c) mean

29 annual precipitation; d) precipitation seasonality; and e) NPP. Each line represents

30 the model for a different family. Red lines are negative correlations, and blue lines

31 are positive correlations. Non-significant correlations are not shown.



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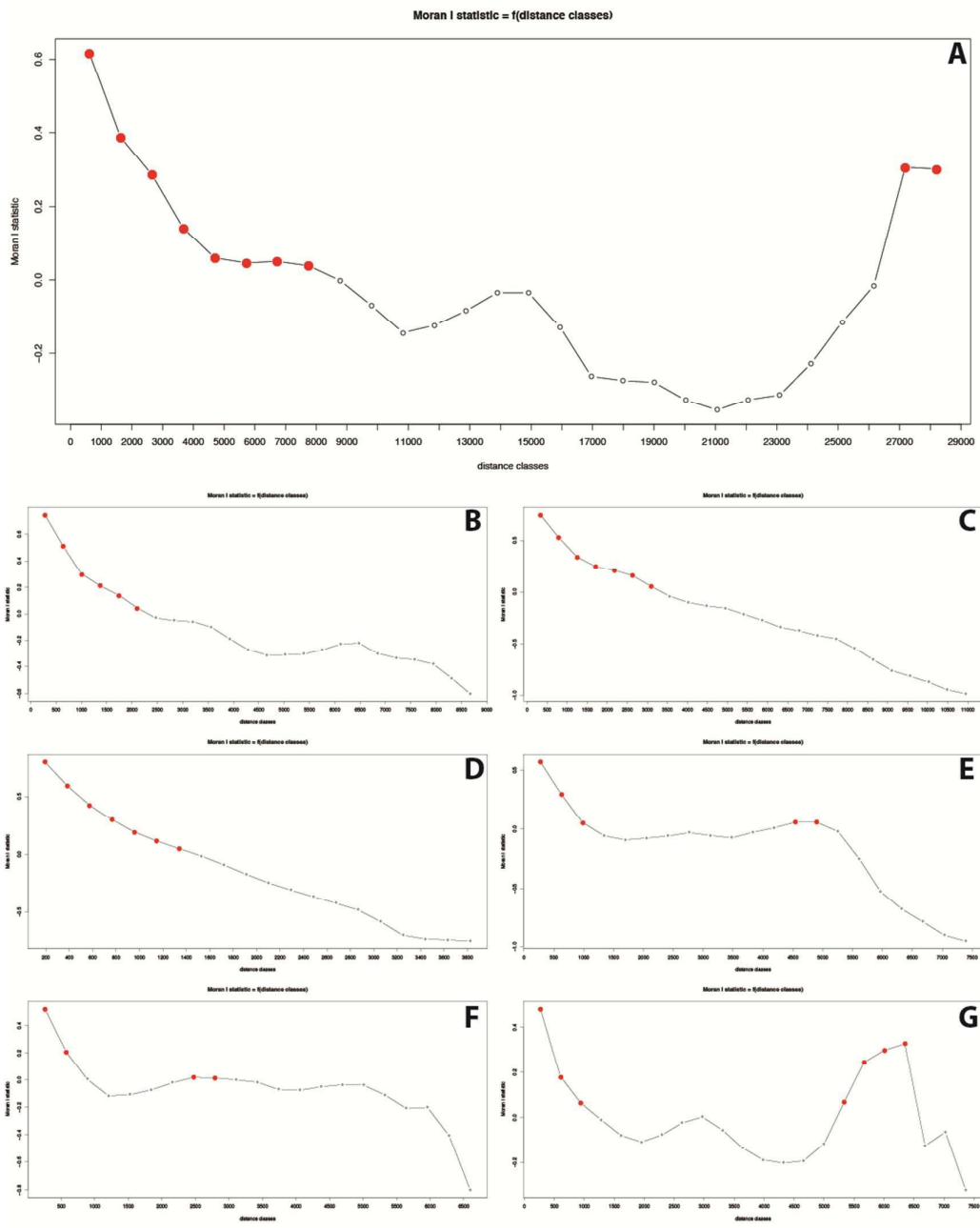
33 **Figure S1.5.** Correlograms of Moran's I of log<sub>10</sub> squamate adaptive components

34 a) globally; and in b) Africa; c) Asia; d) Australia; e) Europe; f) North America; g)

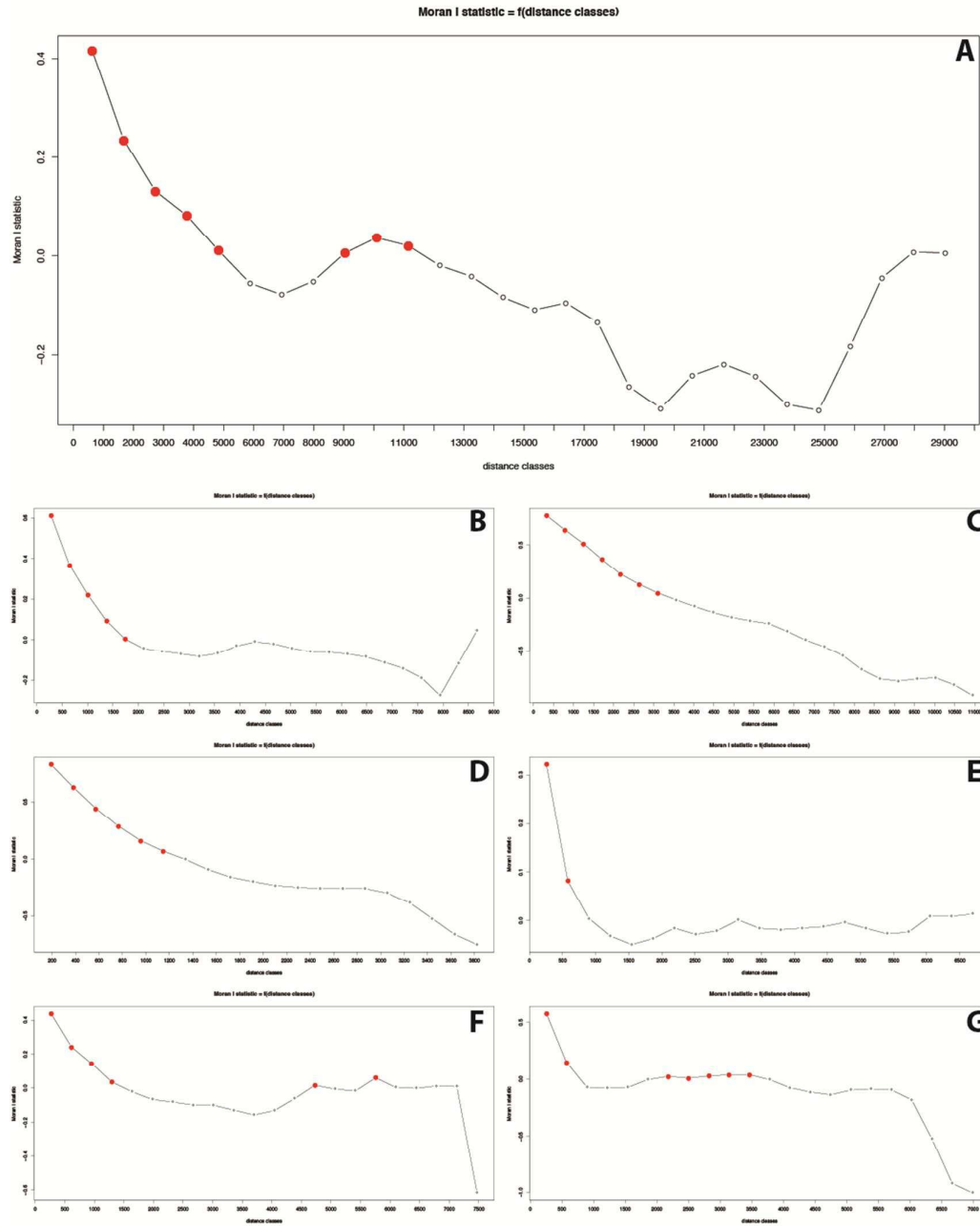
35 South America. Values exceeding 0 are marked by a red dot.

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



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**Figure S1.7.** Correlograms of Moran's I of log10 snake adaptive components a)

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globally; and in b) Africa; c) Asia; d) Australia; e) Europe; f) North America; g) South

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America. Values exceeding 0 are marked by a red dot.

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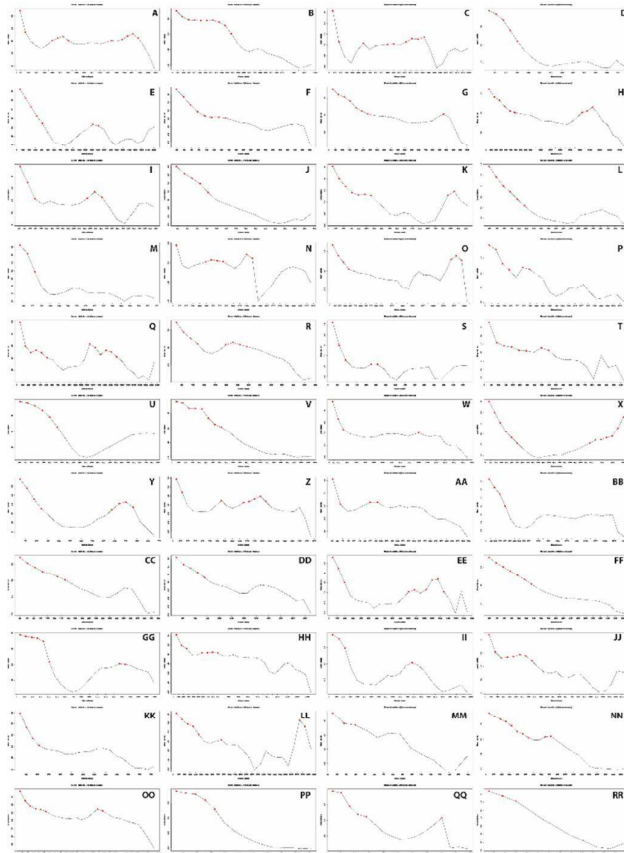
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48 **Figure S1.8.** Correlograms of Moran's I of log<sub>10</sub> adaptive components for the  
 49 following squamate families: a) Agamidae; b) Amphisbaenidae; c) Anguidae; d)  
 50 Anomalepididae; e) Boidae; f) Carphodactylidae; g) Chamaeleonidae; h) Colubridae;  
 51 i) Cordylidae; j) Crotaphytidae; k) Dactyloidae; l) Diplodactylidae; m) Diploglossidae;  
 52 n) Dipsadidae; o) Elapidae; p) Eublepharidae; q) Gekkonidae; r) Gerrhosauridae; s)  
 53 Gymnophthalmidae; t) Homalopsidae; u) Hoplocercidae; v) Iguanidae; w) Lacertidae;  
 54 x) Lamprophiidae; y) Leiosauridae; z) Leptotyphlopidae; aa) Liolaemidae; bb)  
 55 Natricidae; cc) Preatidae; dd) Phrynosomatidae; ee) Phyllodactylidae; ff)  
 56 Pygopodidae; gg) Pythonidae; hh) Scincidae; ii) Sphaerodactylidae; jj) Teiidae; kk)  
 57 Tropiduridae; ll) Typhlopidae; mm) Uropeltidae; nn) Varanidae; oo) Viperidae; pp)  
 58 Xantusiidae; qq) Xenodermatidae; rr) Xenosauridae. Values exceeding 0 are marked  
 59 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<sup>2</sup> values for each model

Family	Mean Annual Temperature	Mean Annual Precipitation	Temperature Seasonality	Precipitation Seasonality	NPP	Nagelkerke's Pseudo-R <sup>2</sup>	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



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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

For Peer Review

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