

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

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Alex Slavenko is a PhD student interested in biogeographical patterns of body size	42
and life-history traits and the distribution of species, as well as the general biology of	43
reptiles and amphibians. He is particularly interested in the patterns and evolution of	44
such traits in insular environments.	45
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ABSTRACT	50
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, and 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.	51 52 53 54 55 56 57 58
Location. Global.	59
Time period. Extant.	60
Major taxa studied. Squamates (lizards and snakes).	61
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.	62 63 64 65 66 67 68
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.	69 70 71

Main conclusions. The global distribution of body mass among living squamates 72
varies independently from variation in multiple components of climate. Our study, 73
the largest in spatial and taxonomic scale conducted to date, reveals that there is 74
little support for a universal, consistent mechanism of climate-driven size evolution 75
within squamates. 76

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KEYWORDS: Bergmann's rule, body mass, body size, ectotherms, phylogenetic 78
comparative analyses, reptiles, size clines, spatial analyses 79

INTRODUCTION	80
Climate is traditionally considered a primary source of natural selection	81
underlying the evolution of spatial, ecological and phylogenetic variation in animal	82
body sizes. Given that most ecological and evolutionary processes operating among	83
and within species are strongly influenced by body size (Peters, 1983), the	84
identification of predictable relationships between size and geography has offered a	85
key to elucidate the emergence of local- and large-scale patterns of biodiversity	86
(<i>e.g.</i> , Siemann, Tilman & Haarstad, 1996; Gillooly, Brown, West, Savage & Charnov,	87
2001; Woodward <i>et al.</i> , 2005; Slavenko, Tallowin, Itescu, Raia & Meiri, 2016).	88
Remarkably, this principle predates the theory of evolution by natural selection	89
itself. Bergmann's (1847) seminal work suggested that body size among closely	90
related mammal and bird species tends to increase towards colder geographic	91
regions (James, 1970). Such spatial body size gradients have been found to be	92
prevalent in endotherms, both at the intraspecific (Rensch, 1938; James, 1970;	93
Ashton, Tracy & de Queiroz, 2000; Meiri & Dayan, 2003; <i>cf.</i> Riemer, Gurlanick &	94
White, 2018) and interspecific (Blackburn & Hawkins, 2004; Olson <i>et al.</i> , 2009;	95
Torres-Romero, Morales-Castilla & Olalla-Tárraga, 2016) scales. In contrast, decades	96
of research conducted on a wide range of ectothermic organisms have uncovered	97
mixed support for climate-driven size clines either at the intraspecific (Ashton &	98
Feldman, 2003; Adams & Church, 2008; Pincheira-Donoso, 2010; Pincheira-Donoso &	99
Meiri, 2013; Zamora-Camacho, Reguera & Morena-Rueda, 2014) or interspecific	100
(Olalla-Tárraga, Rodríguez & Hawkins, 2006; Olalla-Tárraga & Rodríguez, 2007;	101
Pincheira-Donoso, Hodgson & Tregenza, 2008; Terribile, Olalla-Tárraga, Diniz-Filho &	102

Rodríguez, 2009; Feldman & Meiri, 2014; Vinarski, 2014; Slavenko & Meiri, 2015; 103
Rodrigues, Olalla-Tárraga, Iverso & Diniz-Filho, 2018) levels. 104

The lack of consistency in the attempts to identify prevalent drivers of body size 105
evolution in ectotherms may be partly due to the lack of applicability of the heat- 106
related mechanism (*i.e.*, Bergmann's original explanation) to ectotherms (Pincheira- 107
Donoso *et al.*, 2008; Meiri, 2011; Slavenko & Meiri, 2015). Bergmann (1847) posited 108
that reduced surface area-to-volume ratio in larger animals benefits heat 109
conservation in colder climates, a mechanism sometimes known as the 'heat 110
conservation hypothesis'. However, ectotherms produce negligible amounts of 111
metabolic heat, and reduced surface area-to-volume ratios might result in less 112
efficient thermoregulation in cold climates due to slower heating rates. Therefore, a 113
trade-off exists between heat gain (more efficient in smaller ectotherms; Carothers, 114
Fox, Marquet & Jaksic, 1997) and retention (more efficient in large ectotherms; 115
Zamora-Camacho *et al.*, 2014). Thus, large body size in colder climates is predicted to 116
compromise the need to achieve optimal body temperatures to initiate basic fitness- 117
related activities in the first place (Pincheira-Donoso *et al.*, 2008). 118

Alternative mechanisms for climate-driven body size-clines may be more 119
applicable to ectotherms. The 'heat balance hypothesis' (Olalla-Tárraga *et al.*, 2006) 120
predicts that thermoconformers exhibit a reverse pattern to the one predicted by 121
Bergmann's rule, *i.e.* smaller bodies at lower temperatures because of the effect of 122
body size on heating rates. The 'water availability hypothesis' (Ashton, 2002) 123
suggests that large sizes, thus, small surface area-to-volume ratios, are beneficial in 124
conserving water in dry habitats (especially for animals with permeable skins such as 125
amphibians). Therefore, large size is predicted to be selected for in arid climates. The 126

'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 * m²]) 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 *lme4* 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 *errorsarm* function in the ‘spdep’ package (Bivand *et al.*, 223
2011), with median species component per grid cell as the response variable and the 224
five environmental predictors. All Variance Inflation Factor (VIF) values were below 225
4. 226

To test whether the influence of environmental predictors is consistent across 227
scales, we performed several complementary analyses. First, we divided the dataset 228
into continents (Africa, Asia, Australia, Europe, North America, and South America). 229
We preferred delimitation to continents over biogeographical realms as preliminary 230
evidence suggests that squamates do not adhere well to the classical realm 231
boundaries (Maria Novosolov, pers. comm.). We then reran the SAR models, using 232
the same procedure to determine neighbourhood distance, for each continent. Next, 233
we analyzed lizards (including amphisbaenians) and snakes separately using the 234
same method. We then further divided squamates into families and analyzed all 44 235
families with at least 10 species (that are not island-endemic) separately using the 236
same method (see Table S1.1 in Supporting Information). 237

Species richness patterns can strongly affect size clines, with assemblage means 238
and medians, particularly in low-richness cells, often being sensitive to extremely 239
large or small-bodied species (Meiri & Thomas, 2007). We therefore used a 240
permutation approach to test if size clines could arise from spurious effects of 241
richness patterns (Olson *et al.*, 2009; Slavenko & Meiri, 2015). We randomly drew 242
species from a pool of all squamates, without replacement, to occupy cells while 243
maintaining the original richness distribution. The probability of drawing species 244
from the pool was weighted by each species' range size (from Roll *et al.*, 2017). We 245
then calculated the median species component for each random assemblage per 246

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 271
the complete dataset. 272

In a complementary analysis, we compared independent size and climate 273
contrasts of all 1,456 sister-species pairs recovered from the phylogeny. While this 274
greatly reduces sample size, it also eliminates phylogenetic dependence, as any 275
differences between sister species in body size do not result from shared 276
evolutionary history (Felsenstein, 1985), and compares species that tend to resemble 277
each other most in traits that likely affect body size (Bergmann, 1847). We ran linear 278
regressions through the origin of contrasts in mass between sister species against 279
contrasts in each of the five environmental predictors between sister species, and 280
tested for significance with a conservative alpha of 0.005 (Johnson, 2013; Benjamin 281
et al., 2018). 282

RESULTS 284

ASSEMBLAGE-LEVEL APPROACH 285

Our analyses failed to identify a consistent latitudinal pattern in squamate body 286
size across different regions of the globe. Squamate assemblage body mass is largest 287
in the northern latitudes of North America, most of South America, inland Africa and 288
the Indian Subcontinent (Fig. 1a; Fig. S1.1). It is small in most of northern Eurasia, the 289
Sahel and the Horn of Africa, and in western and central Australia. Squamate species 290
components are positively correlated with mean annual temperature, mean annual 291
precipitation and NPP, and negatively correlated with precipitation seasonality 292
(Table 1). The spatial pattern in squamate species components is more strongly 293

correlated with the ratio of lizards to snakes in each cell – squamate assemblages are 294
large-sized in cells dominated by snakes, and small-sized in cells where most species 295
are lizards (Fig. 1b; SAR of adaptive component against lizard proportion, 296
standardised $\beta = -0.36$, $p < 0.001$, Nagelkerke's pseudo- $R^2 = 0.39$). The pattern is 297
clear even when accounting for phylogenetic non-independence by comparing 298
species components, but is even more pronounced when examining the uncorrected 299
mass data (Fig. S1.1). 300

Size-climate relationships are not geographically consistent – continent-level 301
analyses recovered models with different sets of predictors, with opposite 302
correlation signs, and with extremely different effect sizes, for each continent (Table 303
1). For instance, mean annual temperature was positively correlated with squamate 304
mass in Asia, Europe and South America, but negatively correlated with mass in 305
Australia and North America, and uncorrelated with mass in Africa ($\alpha = 0.005$). 306

Further inconsistencies were found in the separate analyses of snakes and lizards 307
(Table 1; Fig. 1c,d). Globally, lizard mass is positively correlated with mean annual 308
temperature and seasonality in precipitation, and negatively correlated with 309
seasonality in temperature. On the other hand, snake mass is positively correlated 310
with mean annual temperature, and negatively correlated with mean annual 311
precipitation and seasonality in temperature and precipitation globally. Body mass of 312
neither snakes nor lizards is correlated with NPP. As with the global squamate 313
models, snake and lizard continent-level models are substantially different to each 314
other (Table 1). 315

Family-level models also show large inconsistencies (Table S1.1). Each predictor 316
was non-significant in 27-34% of the family models (across the 44 families with > 10 317

species), but often not in the same families (*e.g.*, mean temperature and NPP were 318
non-significant in 18 families each, but only in five of these were they both non- 319
significant). When the predictors were significantly correlated with mass, the 320
correlations often had opposite directions between families. For each of the 321
predictors, positive correlations were found with mass in 27-41% of families, and 322
negative correlations were found in 27-43% of the families (Fig. S1.4). Only four pairs 323
of families had qualitatively identical models: Leiosauridae-Leptotyphlopidae, 324
Hoplocercidae-Elapidae, Iguanidae-Colubridae, and Amphisbaenidae-Eublepharidae. 325
These families are phylogenetically and ecologically very far from one another. All 326
other family models were unique. These results hold even if we analyze only families 327
with over 30 species. In this more restrictive dataset of 33 families, each predictor 328
was non-significant in 27-36% of the models, positively correlated with mass in 24- 329
45% of families, and negatively correlated with mass in 27-45% of families. There 330
was no significant correlation between the species richness of a family and the 331
number of significant predictors in its model (linear regression; $p = 0.33$). 332

The permutation analyses showed that most of the observed median species 333
components within cells could be expected by random processes of community 334
assembly. In fact, only ~7% of lizard cells and ~11.5% of snake cells deviate from the 335
95% confidence intervals of the random distributions (Fig. 2; Fig. S1.2). These cells 336
comprise somewhat distinct geographical units (Fig. 3; Fig. S1.3). Lizards are smaller 337
than expected in many of the most species-rich cells (Fig. 2a; Fig. S1.2a), especially in 338
Australia, and also in the Horn of Africa and along the coasts of South America. They 339
are larger than expected in central South America, inland Africa and the northwest of 340
the Indian subcontinent. Meanwhile, snakes are smaller than expected in western 341

Australia, eastern Asia, some parts of the central Asian steppes, and inland Africa, 342
and larger than expected in central and northern South America, much of northern 343
Eurasia, and southeastern Australia. Only in very few cells in East Africa are both 344
lizards and snakes larger, or smaller, than expected by chance (Fig. 3c). 345

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SPECIES-LEVEL APPROACH 347

Our PGLS analyses revealed a positive relationship between squamate mass and 348
temperature seasonality, and a negative relationship between mass and 349
precipitation seasonality (at $\alpha = 0.005$; Table 2). The phylogenetic signal in the model 350
was very strong ($\lambda = 0.93$), but the overall explanatory power was extremely low (R^2 351
 $= 0.01$). Omitting the widest-ranging species from the dataset caused a marked 352
change – the relationship with seasonality in temperature became nonsignificant, 353
but the positive correlation with mean annual precipitation became significant. All 354
other model parameters changed only slightly ($\lambda = 0.92$, $R^2 = 0.02$). NPP and mean 355
annual temperature were not significantly correlated with mass in any of the 356
models. 357

In the sister-species analysis we found a negative correlation between squamate 358
mass and precipitation seasonality, and no significant correlations with any of the 359
other predictor variables (Fig. 4). However, this model also had extremely low 360
explanatory power ($R^2 = 0.01$). 361

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DISCUSSION 363

ASSEMBLAGE-LEVEL APPROACH 364

Our study provides the first truly global-scale analysis of the spatial patterns of 365
body size variation in squamates, the most speciose group among modern tetrapods, 366
as a function of multiple alternative climatic predictors. Our combined evidence from 367
multiple analytic approaches suggests that climate consistently fails to have an 368
identifiable effect on spatial patterns of squamate size. 369

Our core finding shows that spatial patterns in squamate body sizes are both 370
weak and inconsistent across phylogenetic and spatial scales. We thus conclude that 371
climate exerts weak direct selection pressure on squamate sizes, at least at the 372
examined, interspecific scales (but see also Pincheira-Donoso & Meiri, 2013, for 373
intraspecific comparisons). While squamates seem to display a global trend of 374
decreasing in size towards the poles (or a 'reverse Bergmann' pattern; Fig. 1a), this 375
pattern is weak and inconsistent across regions and lineages. Squamates are 376
generally larger in the New World, and the northernmost cells of North America 377
contain assemblages with the largest median sizes. This global pattern seems to be 378
most strongly explained by the ratio of lizard to snake species in each cell. The body 379
size distribution of squamates is strongly bimodal (Feldman *et al.*, 2016), as snakes 380
are, on average, larger than lizards. Snakes and lizards also differ in their spatial 381
distribution patterns (Roll *et al.*, 2017). Snakes show the common tetrapod pattern 382
of richness peaking in the tropics, whereas lizard richness peaks in warm, arid 383
regions, particularly Australia. Thus, squamates are, on average, large in snake-rich 384
cells (*e.g.*, the Amazon Basin and Canada), and small in lizard-rich cells (*e.g.*, 385
Australia). The global latitudinal size patterns for lizards and snakes are similarly 386
unclear, with the strongest seeming to be a fall (in lizards) and rise (in snakes) of 387
body size in the northernmost latitudes (Fig 1c,d). This is likely due to the effect of 388

the very few, wide-ranging species, inhabiting extreme latitudes in the Northern 389
hemisphere (*e.g.*, *Zootoca vivipara* and *Vipera berus* are the only lizard and snake 390
species, respectively, in much of northern Eurasia, and the snake *Thamnophis sirtalis* 391
is the only squamate species in much of northern North America). The inconsistency 392
in patterns and in relationships with the climatic variables is especially pronounced 393
at the continent- and family-level analyses. No single climatic variable displays a 394
consistent relationship with squamate mass across scales. 395

Overall, the support for the various hypotheses on climate-driven size evolution is 396
weak. Correlations consistent with all different hypotheses were found for all of the 397
hypotheses, but for none of them were these patterns consistent across scales and 398
models. The only correlation recovered in all global models (squamates, lizards, and 399
snakes) was a positive correlation between mass and mean temperature, which 400
would be consistent with 'heat balance hypothesis' under the assumption that all 401
squamates are thermoconformers. This, however, is a problematic assumption – 402
most squamates engage in thermoregulatory behaviour and are quite adept at 403
maintaining body temperatures higher than their surroundings (Meiri *et al.*, 2013). In 404
the continent level analyses, the only hypotheses supported for a majority of models 405
were the 'heat balance hypothesis' which was supported in five of six continents for 406
lizards, and the 'starvation resistance hypothesis' which was supported in five of six 407
continents for snakes, and the 'water availability', 'seasonality' and the 'primary 408
productivity' hypotheses, which were all supported in 53% of snake families. Note, 409
however, that hypotheses supported in most continents for snakes were never 410
supported in most continents for lizards and vice-versa. No hypothesis was 411
supported for most families in lizards or the Squamata as a whole. 412

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 436
arid Australia (Powney *et al.*, 2010; Roll *et al.*, 2017), and Australia's lizard fauna is 437
dominated by skinks (Cogger, 2014), which are generally small-bodied (Meiri, 2008). 438
An additional example is the higher than expected mass of snakes in a large portion 439
of the southern Amazon Basin (Fig. 3b). Patterns of body size distribution in South 440
American snake assemblages are strongly affected by the contribution of the three 441
most species-rich lineages: colubrids, xenodontines and dipsadids. Colubrid and 442
xenodontine snakes (median mass 68.3 g) are much larger than dipsadids (median 443
mass 35.4 g), and in the southern Amazon snake faunas are dominated by a 444
combination of xenodontines and colubrids (see Fig. 25.6 in Cadle & Greene, 1993). 445
Only in few places on the globe, however, are both lizards and snakes either smaller, 446
or larger, than expected by chance (Fig. 3c), again demonstrating remarkable 447
inconsistency in spatial body size patterns between the two groups. 448

SPECIES-LEVEL APPROACH

Our species-level analyses confirm the finding that body size among squamates 451
varies independently from variation in climate. While we did find correlations 452
between mass and our examined climatic variables, their explanatory power is 453
extremely low, and most size variation is explained by shared ancestry. This is similar 454
to previous findings in amphibians (Slavenko & Meiri, 2015). 455

Our study also serves as a demonstration of the importance of considering scale 456
in ecological studies, both spatial (Wiens, 1989; Chave, 2013) and phylogenetic 457
(Graham, Storch & Machac, 2018). Had we considered only the global scale analyses, 458

we might have concluded that there is support for a reverse Bergmann's rule in 459
squamate sizes. Only by examining our data across differing scales were we able to 460
discern the inconsistency in patterns and realize that the global pattern is probably 461
driven by assemblage structure. In this case, our global scale analyses were a classic 462
case of comparing apples to oranges, considering the stark size differences between 463
continents, between lizards and snakes, and between different lineages within these 464
groups. 465

We acknowledge that the interspecific approach ignores size variation at the 466
intraspecific level, arguably a more relevant scale for examinations of climate-driven 467
size evolution (Meiri, 2011). Some species indeed show intraspecific trends in size 468
consistent with climate-driven size evolution, particularly along elevational gradients 469
(*e.g.*, Zamora-Camacho *et al.*, 2014; *cf.* Pincheira-Donoso & Meiri, 2013). However, 470
data on range-wide intraspecific size variation are lacking for most squamate species. 471
Testing intraspecific relationships between climate and body size on a large sample 472
of squamates is beyond the scope of this work, though we acknowledge climate 473
might be an important factor shaping body size at this level. We doubt, however, 474
that the effects would be consistently predictable by any 'ecological rule' and 475
suspect they might be idiosyncratic and depend heavily on the natural history of 476
each examined species. 477

CONCLUSIONS 478 479

Collectively, our results suggest that climate is likely not an important driver of 480
size evolution in squamates as a group, despite exerting a strong influence on their 481

spatial distribution (Roll *et al.*, 2017), and therefore likely affecting spatial size 482
distributions by proxy. This is consistent with similar results for amphibians (Slavenko 483
& Meiri, 2015), and may be the case for terrestrial ectotherms in general. Recently, 484
Riemer *et al.* (2018) analysed an impressively large dataset of mammals and birds, 485
and concluded that there is little support for a general relationship between mass 486
and temperature in endotherms, despite previous evidence to the contrary (Ashton 487
et al., 2000; Meiri & Dayan, 2003). While these results do not mean that 488
temperature, and other climatic variables, do not exert selection pressure on body 489
size (and indeed they may apply to some taxa), they do raise questions as to the 490
generality of such evolutionary mechanisms across all taxa. This is not to imply that 491
climate is not an important driver of size evolution, but rather that the causative 492
mechanisms of size evolution may be idiosyncratic and strongly lineage- and 493
location-dependent. While this conclusion does pose a difficulty for generalization, it 494
also creates a promising avenue for future research of size evolution on a case-by- 495
case basis, and on multiple spatial and phylogenetic scales. In any event, we advise 496
caution in adopting such climate-size relationships as general 'rules', at the very least 497
until their generality has been properly tested on large, extensive datasets. 498

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DATA ACCESSIBILITY	717
All data used for this study were previously published in other scientific publications	718
and publicly available datasets and are properly cited. The distribution maps from	719
Roll <i>et al.</i> (2017) are currently under embargo, and will be made publicly available	720
during 2018.	721

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

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.

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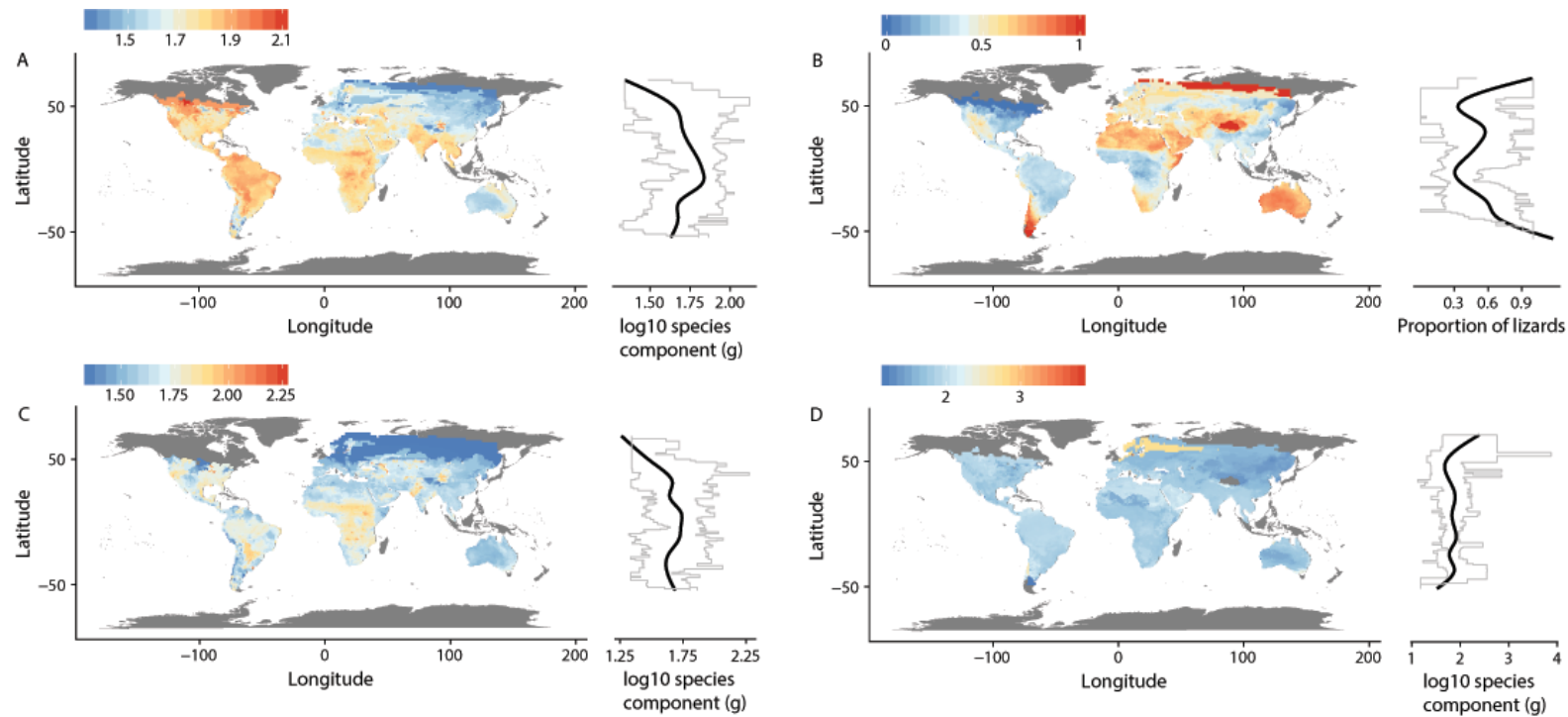
For each predictor, the standardised regression slope is given. P-values for each predictor are indicated by *, **, ***, and n.s. (<0.05, <0.01,

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<0.005, and non-significant respectively).

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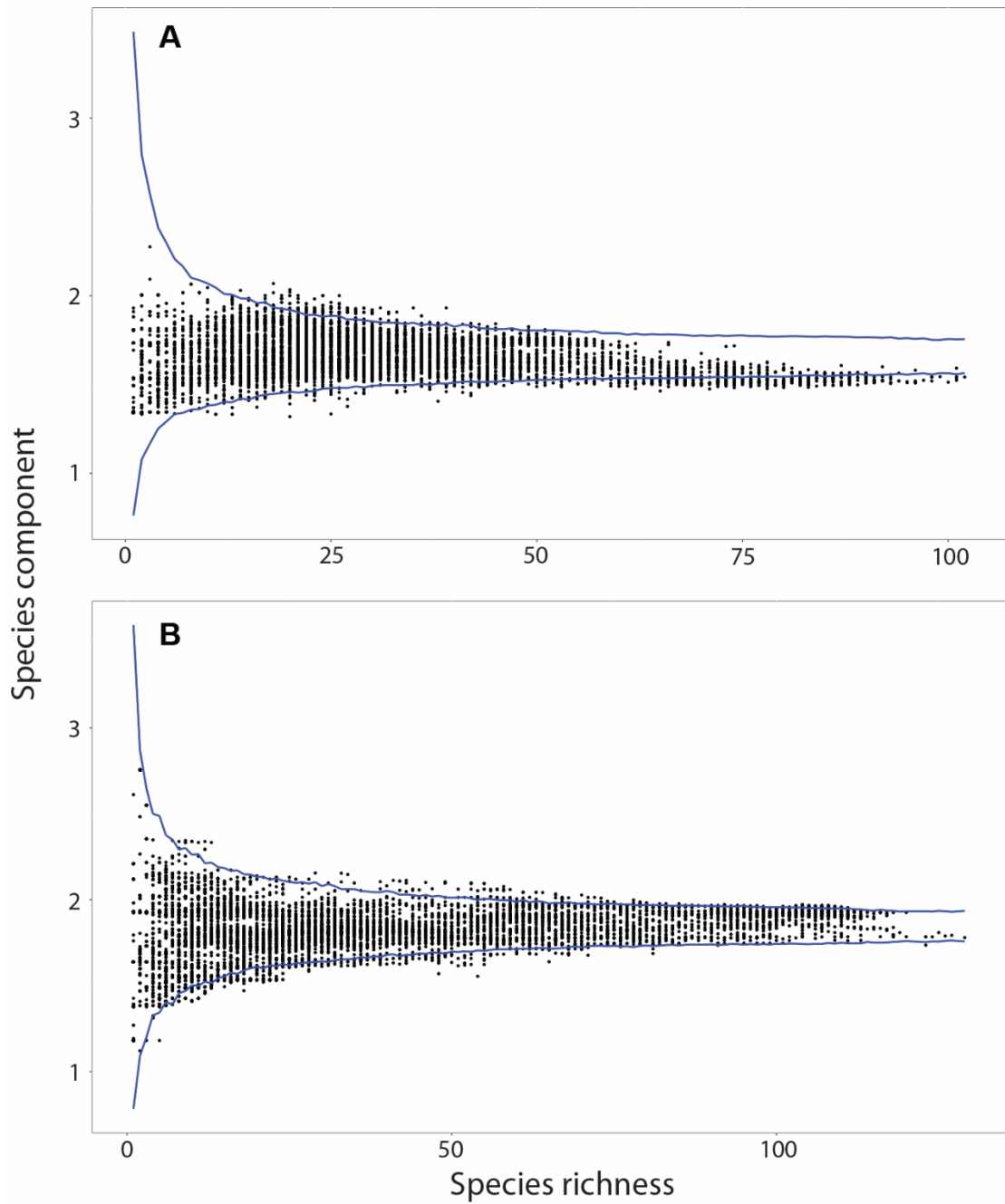
Model	Mean Annual Temperature	Mean Annual Precipitation	Temperature Seasonality	Precipitation Seasonality	Net Primary Productivity	λ	R^2
Full	0.02 (n.s.)	0.03*	0.07***	-0.04***	0.03**	0.93	0.01
Widest-ranging species omitted	0.004 (n.s.)	0.06***	0.02 (n.s.)	-0.05***	0.03**	0.92	0.02



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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).

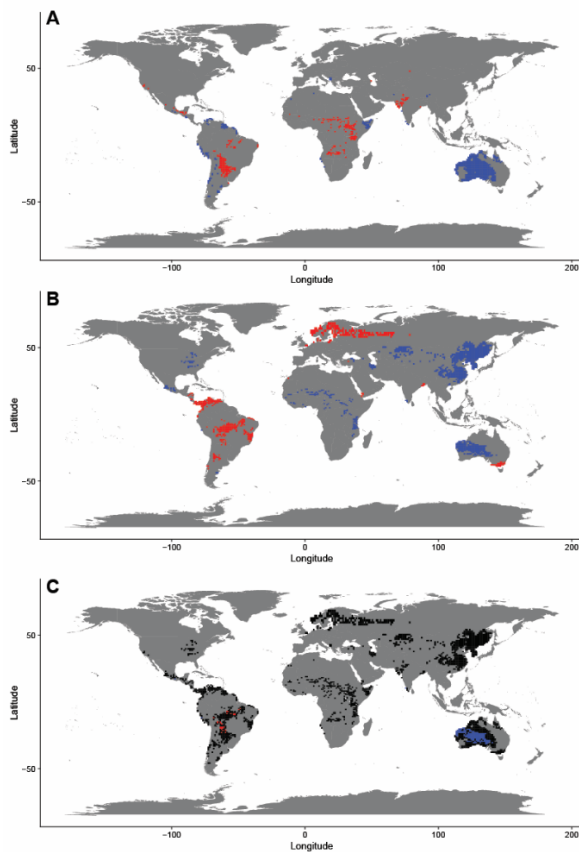
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Figure 2. Distribution of median species components of (a) lizards and (b) snakes 744
 per grid cell. Species components are the component of mass for each species that 745
 cannot be explained by its evolutionary history (residuals from a phylogenetic model 746
 of size evolution). Black circles represent observed values; blue lines represent 95% 747
 confidence intervals of 1000 randomized distributions. 748

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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.

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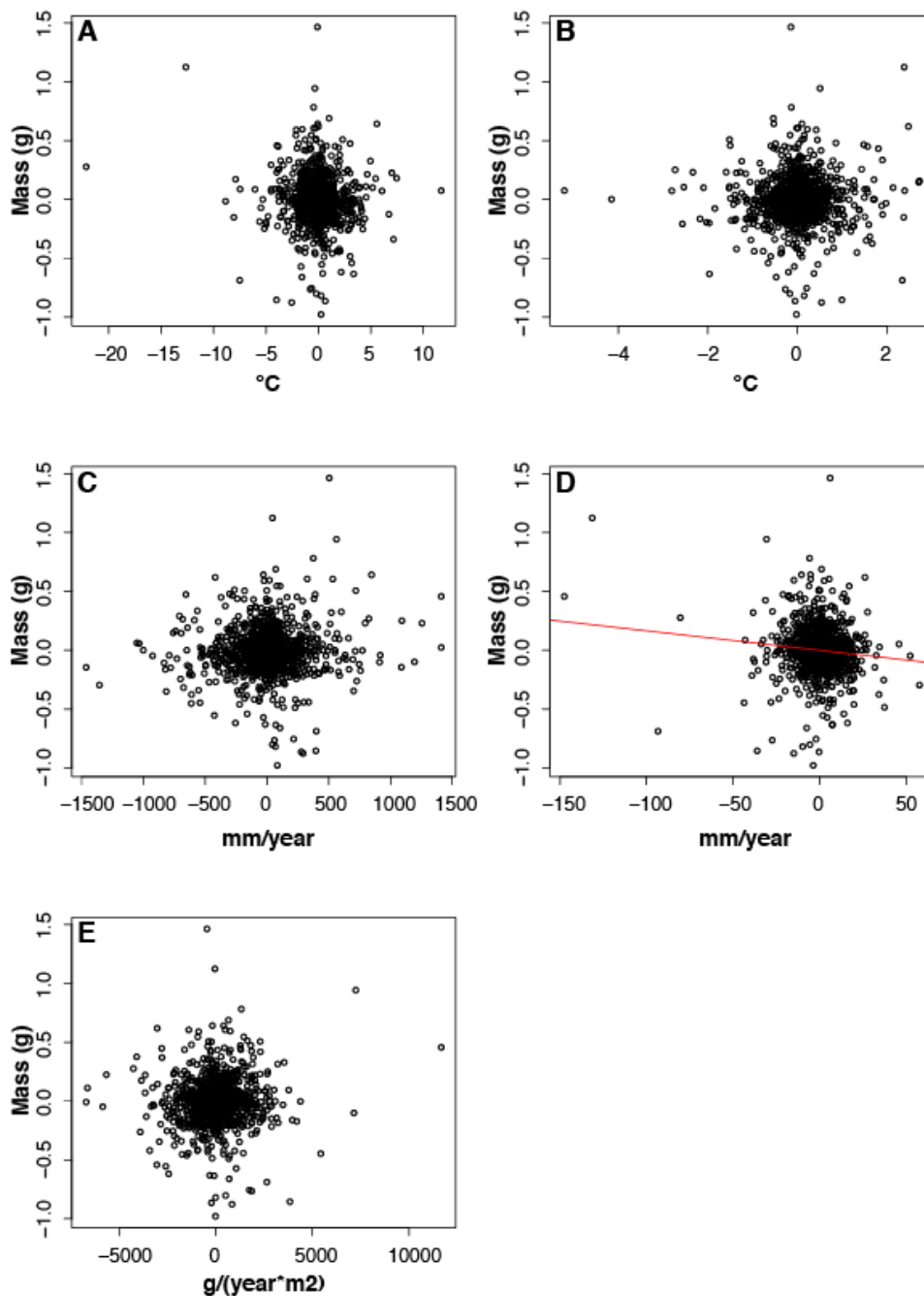
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 763 **Figure 4.** Scatter plots of 1456 sister-species pairs. Shown are independent
 764 contrasts of log₁₀ mass (in grams) against a) mean annual temperature; b)
 765 temperature seasonality; c) mean annual precipitation; d) precipitation seasonality;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