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

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BIOSKETCH:

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.

ABSTRACT 50

Aim. Variation in body size across animal species underlies most ecological and 51
evolutionary processes shaping local- and large-scale patterns of biodiversity. For 52
well over a century, climatic factors have been regarded as primary sources of 53
natural selection on animal body size, ad hypotheses such as Bergmann's rule (the 54
increase of body size with decreasing temperature) have dominated discussions. 55
However, evidence for consistent climatic effects, especially among ectotherms, 56
remains equivocal. Here, we test a range of key hypotheses on climate-driven size 57
evolution in squamate reptiles across several spatial and phylogenetic scales. 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 62
net primary productivity as drivers of body mass across ~95% of extant squamate 63
species (9,733 spp.). We ran spatial autoregressive models of phylogenetically- 64
corrected median mass per equal-area grid cells. We ran models globally, across 65
separate continents, and for major squamate clades independently. We also 66
performed species-level analyses using phylogenetic generalized least square 67
models, and linear regressions of independent contrasts of sister species. 68

Results. Our analyses failed to identify consistent spatial patterns in body size as a 69
function of our climatic predictors. Nearly all continent- and family-level models 70
differed from one another, and species-level models had low explanatory power. 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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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

(*e.g.*,Siemann, Tilman & Haarstad, 1996; Gillooly, Brown, West, Savage & Charnov,   87

2001; Woodward *et al.*, 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; *cf*. Riemer, Gurlanick &   94

White, 2018) and interspecific (Blackburn & Hawkins, 2004; Olson *et al.*, 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 127

hypothesis' (Van Voorhies, 1996; Mousseau, 1997) both posit that seasonality drives 128

size clines. The former suggests that large size is selected for in seasonal 129

environments, as it allows for accumulation of food reserves to survive periods of 130

food scarcity. The latter suggests that short growing seasons in highly seasonal 131

climates lead to maturation at smaller size. The 'primary productivity hypothesis' 132

(Rosenzweig, 1968; Yom-Tov & Geffen, 2006) suggests that increased productivity 133

allows for the evolution of larger body sizes, which can be maintained by the 134

abundance of available food (Huston & Wolverton, 2011). These hypotheses are not 135

mutually exclusive, and the different putative climatic drivers of size evolution 136

covary across space. 137

We addressed a range of core hypotheses on the relationship between climate 138

and body size globally across squamates, the largest order of land vertebrates 139

(~10,350 species; Uetz, Freed & Hošek, 2018). Squamates are found on all continents 140

except Antarctica. Their distribution patterns differ considerably from other land 141

vertebrate groups, showing increased affinity for hot, arid regions (Roll *et al.*, 2017). 142

However, most studies on climatic size clines in squamates have been conducted on 143

species from temperate regions (*e.g.*, Ashton & Feldman, 2003; Olalla-Tárraga *et al.*, 144

2006; Pincheira-Donoso, Tregenza & Hodgson, 2007). Therefore, the more limited 145

scale of existing studies is unlikely to be representative of squamates, either 146

phylogenetically (*i.e.*, many families are not represented there), or geographically 147

(*i.e.*, the whole range of climatic conditions experienced by squamates is not 148

represented). Patterns detected might thus merely represent local or regional 149

trends. 150

Squamates in temperate regions often exhibit unique adaptations to cold 151

conditions (*e.g.*, Churchill & Storey, 1992; Voituron, Storey, Grenot & Storey, 2002; 152

Berman, Bulakhova, Alfimov & Mescheryakova, 2016). Such adaptations (*e.g.*, 153

prolonged hibernation) may mask or weaken climatic effects on body size 154

(Scholander, 1955). Furthermore, the small number of species in such regions might 155

lead to spatial patterns being driven by a few wide-ranging unusually small or 156

unusually large species (Slavenko & Meiri, 2015). 157

Crucially, while global-scale studies on size clines in endotherms have been 158

conducted (birds, Olson *et al.*, 2009; mammals, Riemer *et al.*, 2018), to date, only a 159

few studies have examined global size clines of an entire large clade of ectotherms 160

(apart from turtles; Angielczyk, Burroughs & Feldman, 2015; Rodrigues *et al.*, 2018), 161

making it impossible to infer a universal effect of climate on body size. 162

Our goals were to: a) examine the spatial patterns in body sizes of squamates; b) 163

test the leading current hypotheses linking body size and climate; and c) test 164

whether we find consistent support for these hypotheses across phylogenetic and 165

spatial scales. If climate consistently affects ectotherms' body sizes, we expect to 166

find qualitatively similar relationships between body size and the climatic variables 167

we examine, across squamate phylogeny and across space, and using different 168

methods (i.e., with either the species or the grid cell as the focus of analyses). 169

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METHODS 171

DATA COLLECTION 172

We used body mass (Feldman, Sabath, Pyron, Mayrose & Meiri, 2016) and 173

distribution data (Roll *et al.*, 2017) for ~95% (9,733 species) of the currently 174

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

measure of body size instead of other measures, such as SVL or total length, as these

cannot be easily compared between clades that differ greatly in their *bauplan* (see

e.g. figure S2c in Feldman *et al.*, 2016, where squamates of similar length differ by 2

orders of magnitude in mass). The mass data in Feldman *et al.* (2016) are size

maxima of squamate species, irrespective of sex, derived from SVL using clade-

specific length-mass allometric equations. Size maxima were used instead of means,

as they are more readily available in the literature, and also likely well represent the

potential sizes attainable by squamates, which have indeterminate growth. We $\log_{10}$-

transformed the mass data to normalize the otherwise strongly right-skewed body

size distribution (Feldman *et al.*, 2016). We used global temperature and

precipitation data for the 1979-2013 time period at 30 arc-second resolution

(CHELSA; Karger *et al.*, 2017). These were used to test three hypotheses: the 'heat

balance' hypothesis, using mean annual temperature (in degrees Celsius; BIO1); the

'water conservation' hypothesis, using mean annual precipitation (in mm/year;

BIO12); and the 'seasonality' hypothesis, using both temperature seasonality (annual

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

mm/year; BIO15). We also used global net primary productivity (NPP, in grams of

carbon / [year * m^2]) data for 1995 (SEDAC; Imhoff *et al.*, 2004) to test the 'primary

productivity' hypothesis. We tested these four hypotheses using two analytical

approaches (assemblage-level and species-level; see below). All statistical analyses

were performed in R v3.4.2 (R Core Team, 2017).

ASSEMBLAGE-LEVEL APPROACH

As squamate body size shows a strong phylogenetic signal (Blomberg, Garland Jr. 199

& Ives, 2003; Feldman *et al.*, 2016), we accounted for phylogenetic non- 200

independence using the Lynch method (Lynch, 1991). We used the variance- 201

covariance matrix derived from the latest species-level phylogeny of squamates 202

(Tonini, Beard, Ferreira, Jetz & Pyron, 2016) to fit a linear mixed effects model, with 203

body mass as the response and species identity mapped as a random effect, using 204

the *lmekin* function in the 'coxme' R package (Therneau, 2018). We omitted from the 205

analysis 41 species not included in the phylogeny. We treated the predicted values of 206

this model as the phylogenetic components of mass, attributed to shared 207

evolutionary history. The body size residuals from the phylogenetic components 208

were treated as the species components (the component of mass for each species 209

that cannot be explained by shared ancestry). We then overlaid the range maps for 210

all squamates (from Roll *et al*. 2017) onto an equal-area 96x96 km grid in a 211

Behrmann equal-area projection (roughly 0.86x0.86 degrees at the Equator) in 212

ArcGIS 10.0 (ESRI) and calculated the median of the species components for the 213

species assemblage in each grid cell. We also calculated the mean value of each of 214

our environmental predictors across the cell. We omitted island cells (all landmasses 215

smaller than Australia) from this analysis in order to remove the potential bias to our 216

results from effects of insularity on body size evolution (*e.g.*, Itescu *et al.*, 2018). 217

To account for spatial autocorrelation in the data, we fitted spatial autoregressive 218

(SAR) models (Dormann *et al.*, 2007). We defined the neighbourhood distance as the 219

distance (in km) at which global (or continental, in the continent analyses) Moran's I 220

dropped to 0, based on correlograms generated using the *correlog* function in the 221

'pgirmess' package (Giraudoux, 2017; Fig. S1.5-S1.8). We then ran multiple-predictor 222

SAR models using the *errorsarlm* 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   247

intervals from the resultant random distributions of median species component per   248

cell, to test whether observed median species components are lower, or higher, than   249

expected from their richness values.   250

                                                                                               251

SPECIES-LEVEL APPROACH   252

We used multiple-predictor phylogenetic generalized least square (PGLS)   253

regressions (Grafen, 1989), using the log_{10}-transformed mass of each species as the   254

response variable (after omitting all insular endemic species and species across   255

whose ranges we were lacking predictor variables), the mean of each environmental   256

variable across each species' range as predictors, and the latest phylogeny of   257

squamates (Tonini *et al.*, 2016) to estimate the expected covariance structure. After   258

omitting from the analysis 2,695 island-endemic species to remove a potential   259

insularity bias, and a further 701 species that were either not included in the   260

phylogeny or with missing data, we were left with 6,323 species. We ran the PGLS   261

models under a Brownian motion model of evolution and calculated the maximum   262

likelihood estimates of Pagel's λ, a measure of phylogenetic signal in the data   263

ranging from 0 (no signal) to 1 (strong phylogenetic signal under a Brownian motion   264

model of evolution), with the *pgls* function in the 'caper' package (Orme *et al.*,   265

2012).   266

This approach ignores spatial variation in the environmental predictor variables,   267

which can be substantial in extremely wide-ranging species. We therefore reran the   268

PGLS analyses after omitting those species with the 10% largest range sizes (leaving   269

5,691 species), which would be most heavily biased by averaging out environmental   270

predictors across their ranges, and compared the results of this analysis to those of the complete dataset.

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

RESULTS

ASSEMBLAGE-LEVEL APPROACH

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

correlated with the ratio of lizards to snakes in each cell – squamate assemblages are 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 $β$ = -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 (α = 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 α = 0.005; Table 2). The phylogenetic signal in the model 350

was very strong (λ = 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 (λ = 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

362

DISCUSSION 363

ASSEMBLAGE-LEVEL APPAROACH 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

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SPECIES-LEVEL APPROACH   450

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

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CONCLUSIONS 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 *et al.* (2017) are currently under embargo, and will be made publicly available   720

during 2018.   721

TABLES

Table 1. Results of the SAR analyses. A summary of the full model is given for each subset of the data. For each predictor, the standardised

regression slope is given. P-values for each predictor are indicated by *, **, ***, and n.s. (<0.05, <0.01, <0.005, and non-significant

respectively). Also given are Nagelkerke's Pseudo-R^2 values for each model, although we must stress these cannot be interpreted as

percentage of variance explained by the model.

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

	South America	0.42***	0.07*	-0.06*	0.21***	0.31***	0.42
Lizards	Global	0.33***	-0.02*	-0.2***	0.06***	0.00 (n.s.)	0.4
	Africa	0.18***	0.25***	-0.18***	0.15***	0.06 (n.s.)	0.35
	Asia	0.26***	-0.07***	-0.54***	-0.08***	-0.27***	0.48
	Australia	-0.38***	0.17***	0.33***	0.45***	0.29***	0.46
	Europe	0.72***	0.04 (n.s.)	0.13*	-0.03 (n.s.)	-0.25***	0.4
	North America	0.54***	-0.23***	-0.12 (n.s.)	-0.35***	0.08 (n.s.)	0.25
	South America	0.36***	0.23***	0.21***	-0.14***	-0.01 (n.s.)	0.29
Snakes	Global	0.0001***	-0.0001***	-0.0005***	-0.0001***	0.00002 (n.s.)	0.21
	Africa	-0.12***	-0.16***	0.25***	-0.36***	-0.09*	0.32
	Asia	0.63***	-0.34***	-0.38***	-0.28***	-0.006***	0.47
	Australia	-0.35***	-0.01 (n.s.)	-0.18***	0.4***	0.34***	0.67
	Europe	-0.28***	0.08*	-0.1 (n.s.)	0.1***	-0.01 (n.s.)	0.11

	North America	-0.1 (n.s.)	0.06 (n.s.)	0.38***	0.1***	0.09**	0.21
	South America	0.13***	-0.05 (n.s.)	0.26***	0.14***	0.18***	0.36

Table 2. Results of the PGLS analyses. A summary of the full model is given for the full dataset, and with the widest-ranging species omitted.

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

<0.005, and non-significant respectively).

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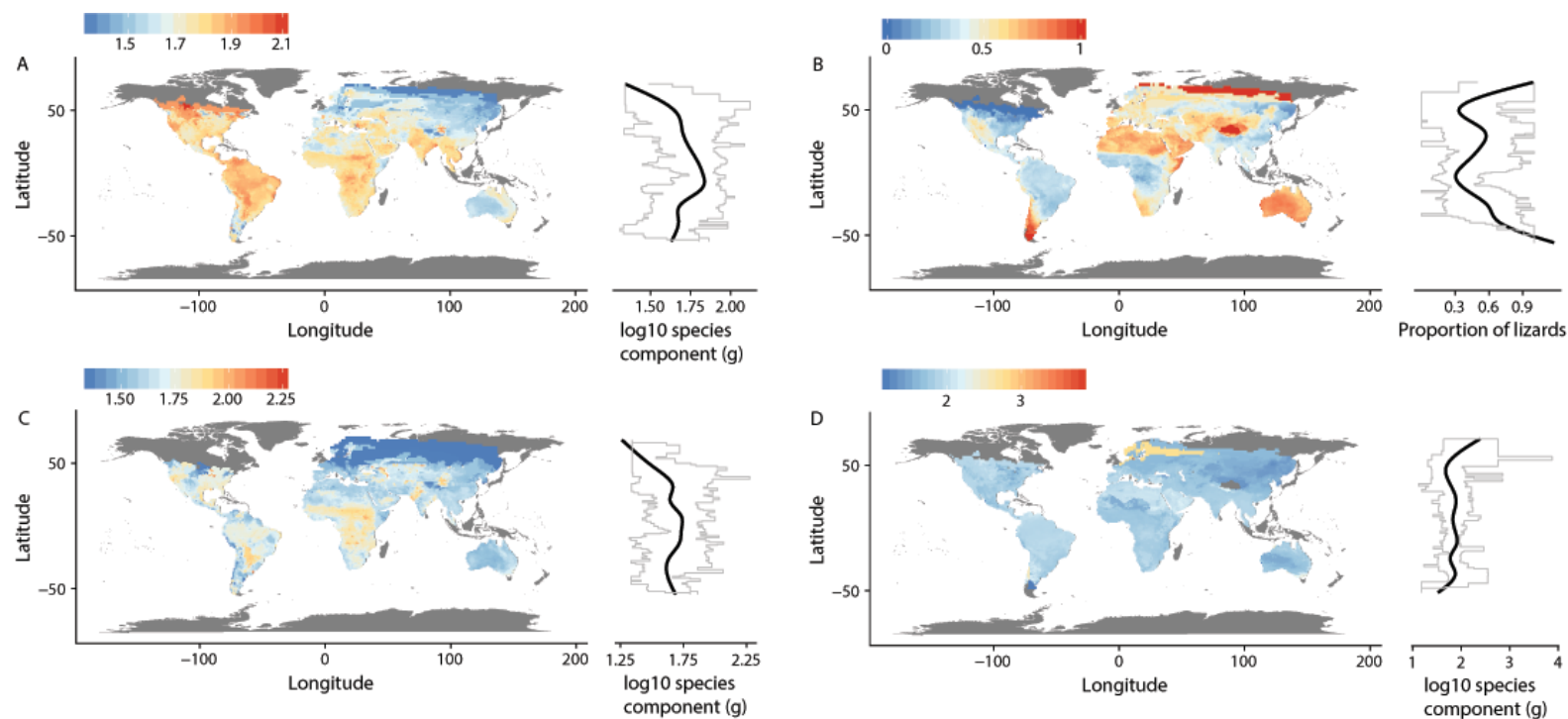
FIGURES

732

Figure 1. Maps showing the global distribution of a) median log10 species 733

component of mass (in grams) per cell of all squamates; b) proportion of lizard 734

species out of all squamates per cell; c) median log10 species component of mass (in 735

grams) per cell of lizards; and d) median log10 species component of mass (in grams) 736

per cell in snakes. Species components are the component of mass for each species 737

that cannot be explained by its evolutionary history (residuals from a phylogenetic 738

model of size evolution). Next to each map is a curve showing a generalized additive 739

model of each mapped variable (in black) and the minimum and maximum values of 740

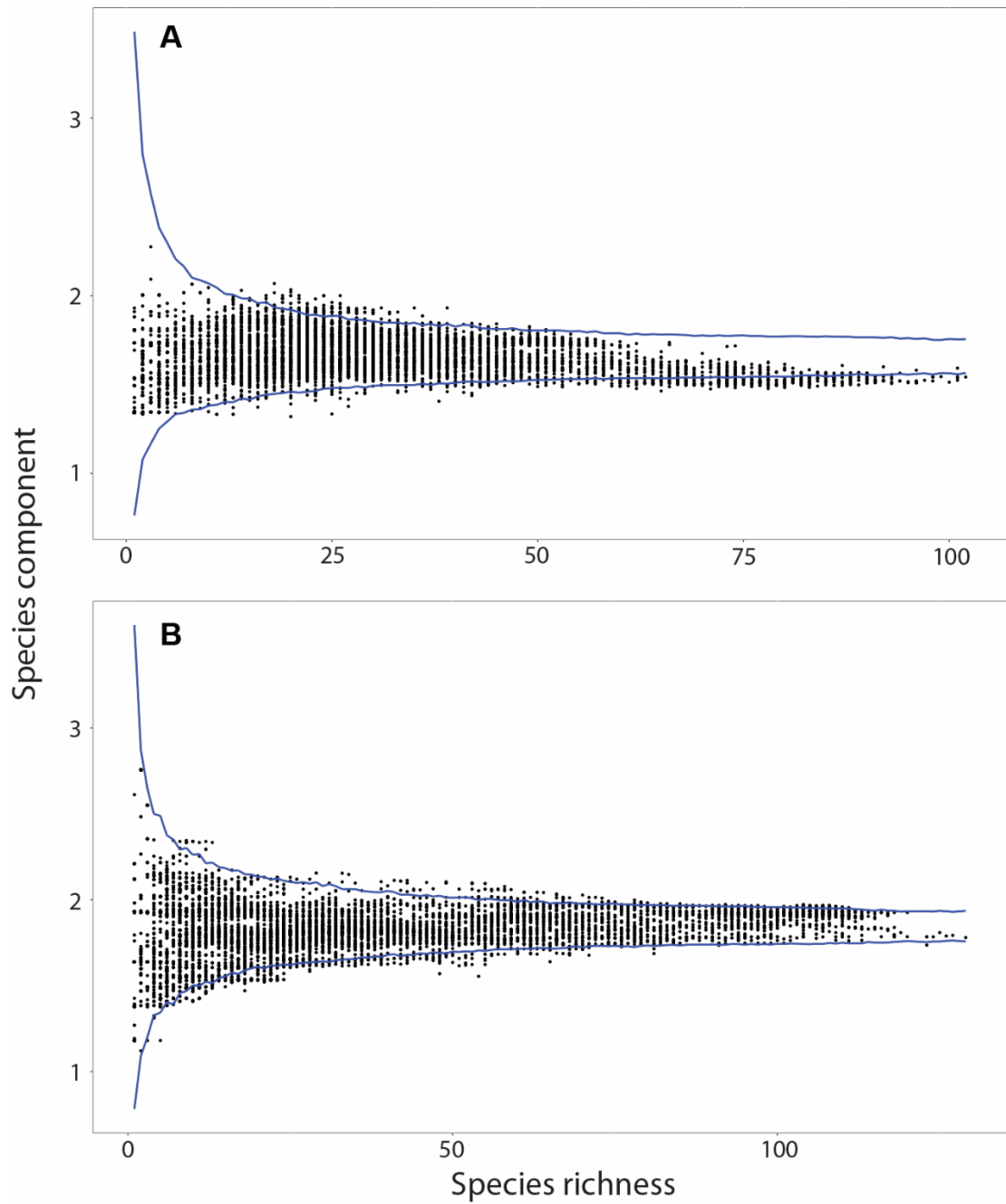each mapped variable per 96km latitudinal band (in grey). 741

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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
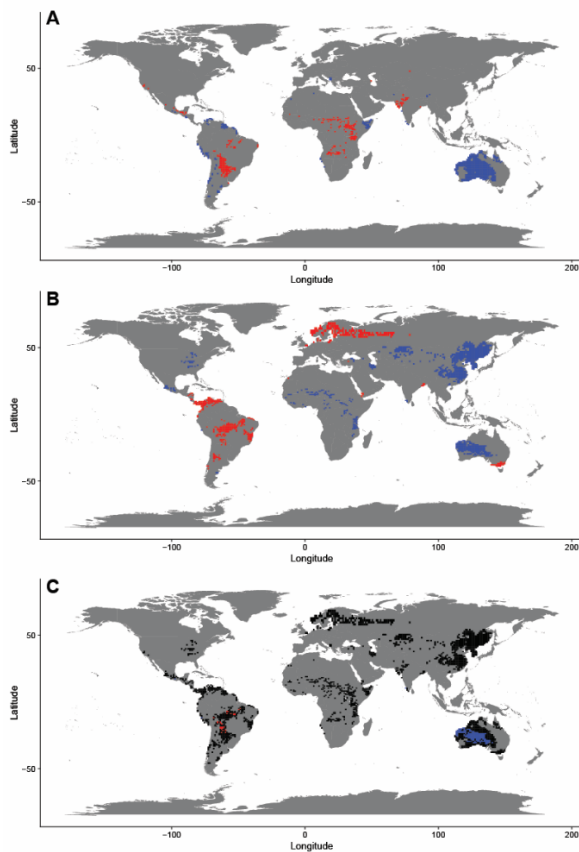
749

39

Figure 3. Maps showing cells of a) lizards and b) snakes with median species 751
components exceeding the 95% confidence intervals of 1000 randomized 752
distributions. Species components are the component of mass for each species that 753
cannot be explained by its evolutionary history (residuals from a phylogenetic model 754
of size evolution). Red cells have larger species components than expected by 755
chance, whereas blue cells have smaller species components than expected by 756
chance. c) Overlap between the two maps, black cells are where only lizards or 757
snakes (but not the other group) exceed expected values, light grey cells are where 758
both lizards or snakes exceed expected values (but not in the same direction), 759
whereas blue cells are where both are smaller than expected, and red cells are 760
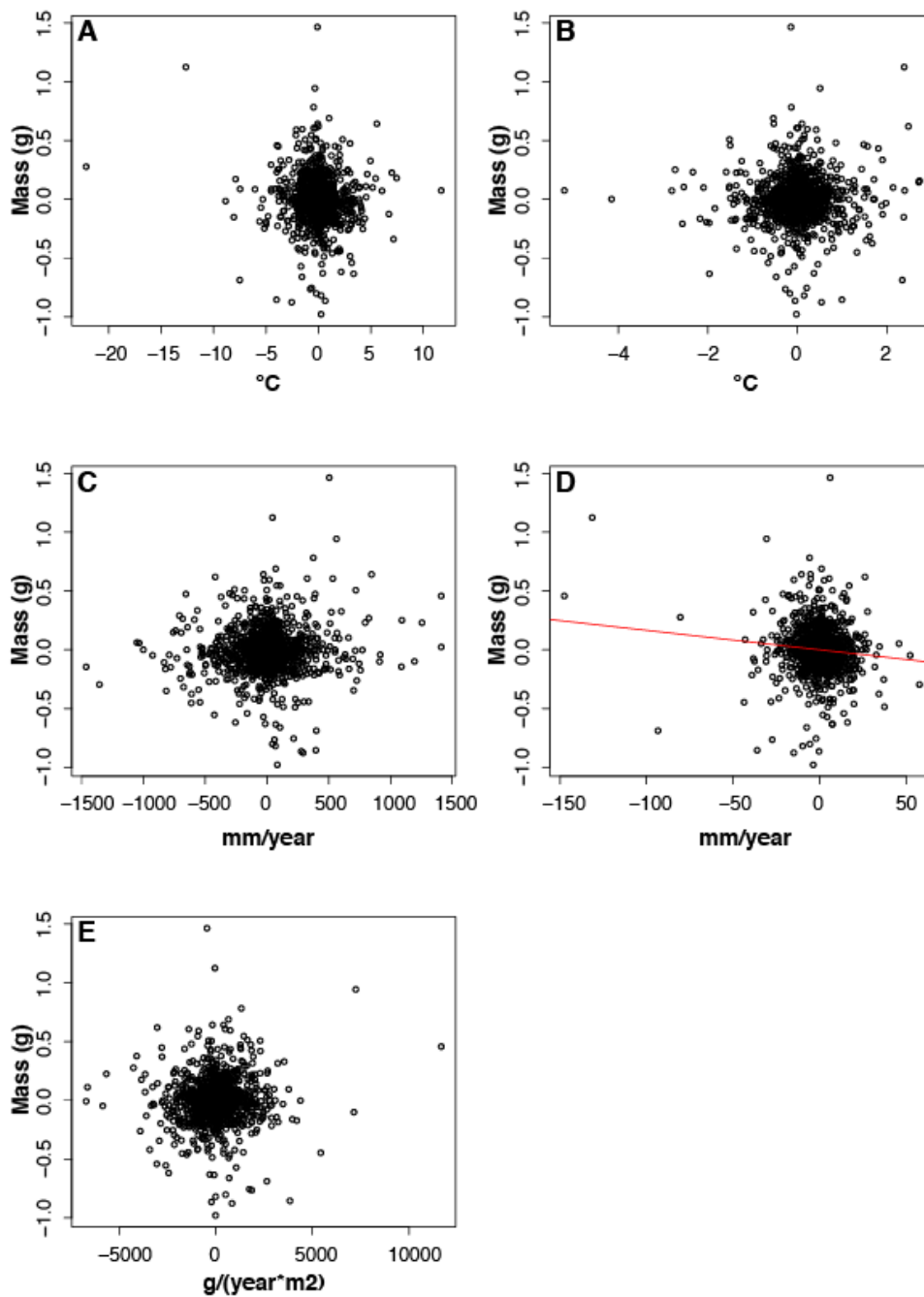where both are larger than expected. 761

762

Figure 4. Scatter plots of 1456 sister-species pairs. Shown are independent 763

contrasts of log10 mass (in grams) against a) mean annual temperature; b) 764

temperature seasonality; c) mean annual precipitation; d) precipitation seasonality; 765

and e) net primary productivity. Only the significant regression through the origin in 766

d) is represented by a red line. All other regressions are not significant. 767