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# The latitudinal diversity gradient and interspecific competition: no global relationship between lizard dietary niche breadth and species richness

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## ABSTRACT

**Aim** Dietary niche breadth has long been hypothesized to decrease towards lower latitudes as the numbers of competitors increase. Geographical variation in niche breadth is also hypothesized to be linked to high ambient energy levels, water availability, productivity and climate stability – reflecting an increased number of available prey taxa. Range size and body size are also hypothesized to be strongly and positively associated with niche breadth. We sought to determine which of these factors is associated with geographical variation in niche breadth across broad spatial scales and thus potentially drive the latitudinal diversity gradient.

**Location** Global.

**Methods** We collated volumetric dietary data for 308 lizard species. For each species, we gathered data on number of sympatric lizard species (a proxy for the number of competitors), annual temperature and precipitation, net primary productivity, seasonality, range size and body size. We examined the relationship between dietary niche breadth and focal parameters using both ordinary and phylogenetic generalized least squares regressions.

**Results** Niche breadth was positively related to annual precipitation, temperature seasonality and range size, and negatively related to body size. Lizard species richness increased towards lower latitudes. Dietary niche breadth, however, was unrelated to parameters reflecting diversity gradients, such as primary productivity, annual temperature, precipitation seasonality and, crucially, the number of potential competitors.

**Main conclusions** Contrary to prevailing ecological theory, competition is unrelated to dietary niche breadth. We found no support for interspecific competition driving the latitudinal diversity gradient. Rather, we found variation in niche breadth to be associated with water availability, climate stability, range size and body size. Our study casts doubt on the common assumption that tropical species are specialists, promoting greater alpha diversity, and on the assumption that the number of sympatric species is reflected in the intensity of interspecific competition.

## Keywords

Body size, climate, dietary niche breadth, interspecific competition, latitudinal diversity gradients, lizards, species range size, species richness.

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## INTRODUCTION

A species' niche breadth is defined as the suite of environments or resources that the species can inhabit or use (MacArthur, 1968). Niche breadth can influence, and be influenced by, competitive interaction. Determining the processes that drive global patterns of niche breadth therefore contributes to elucidating species distributions and interspecific interactions. Consequently, niche breadth is often invoked to explain the latitudinal diversity gradient (Pianka, 1966; Rohde, 1992; Forister *et al.*, 2015). Most studied taxa show a clear pattern of higher diversity in the tropics. Despite this pattern having been recognized for over 200 years (von Humboldt, 1808), the processes that drive and maintain the latitudinal diversity gradient remain unclear (Lomolino *et al.*, 2010). We investigated which processes are important drivers of global lizard dietary niche breadth patterns, focusing on the relationship between niche breadth and species richness.

A major tenet used to explain the greater species richness found in the tropics is that of interspecific competition. The view that competition is a dominant process explaining species richness is prevalent in the literature (Dobzhansky, 1950; Hutchinson & MacArthur, 1959; Rabosky & Hurlbert, 2015), so much so that it is referred to as the 'competitionist's paradigm' (Strong, 1980). This paradigm states that, in species-rich regions such as the tropics, competition (the strength of which is implicitly thought to increase with increasing species richness) drives niches to be narrower, i.e. to 'ecological specialization' (Dobzhansky, 1950; MacArthur, 1969). This specialization is a consequence of competitive pressure, due to an increase in species richness enabling the coexistence of more species along similar resource spectra (Hutchinson & MacArthur, 1959; Forister *et al.*, 2015). Thus, the interspecific competition hypothesis states (somewhat circularly; Rohde, 1992) that increased species richness at lower latitudes is driven by strong interspecific competition, resulting in the narrowing niche breadths that enable greater species packing along the resource axes. While the 'competitionist's paradigm' is often assumed in the literature (Dobzhansky, 1950; Hutchinson & MacArthur, 1959; Strong, 1980; Rabosky & Hurlbert, 2015), some studies have found no relationship between species richness and competition (Terborgh *et al.*, 1990; Pitman *et al.*, 1999; Wittmann *et al.*, 2013; Meiri *et al.*, 2014; Terborgh, 2015).

Current climate is strongly associated with broad-scale diversity gradients (Hawkins *et al.*, 2003), leading to a different prediction in relation to the geography of dietary niche breadths. The ambient energy, water availability and productivity hypotheses (Pianka, 1966; Rohde, 1992) all posit that in regions where a greater diversity of foods is available, feeding niches will be broader. They differ in regard to the specific factors associated with this diversity: temperature, water or primary productivity. According to the ambient energy hypothesis, diversity increases with temperature because high metabolic rates at higher temperatures may promote faster

speciation rates (Rohde, 1992), leading to a greater diversity of prey (Currie *et al.*, 2004). The water availability hypothesis posits that diversity increases with rainfall, because animals need access to water. It is expected to be most important in hot climates. The productivity hypothesis posits that diversity depends primarily on the conversion of energy into plant production (e.g. Hutchinson, 1959). Thus, the productivity hypothesis posits that animal population sizes increase in productive environments (Wright *et al.*, 1993) because greater levels of primary productivity facilitate a larger biomass of consumer populations (Clarke & Gaston, 2006) enabling an increase in prey species richness (Hurlbert, 2004).

Climatic stability has also been documented in the literature as a strong predictor of the latitudinal diversity gradient. Stable climates are thought to promote narrow physiological tolerances and specialization, leading to higher diversity and more stable population sizes (Pianka, 1966). Several studies suggest that the extent of seasonal fluctuations may control diversity patterns in prey: seasonal fluctuations may lead to an unpredictable diversity of prey types, thereby reducing the ability of predators to specialize on certain prey types and thus leading to dietary generalization (Hurlbert & Haskell, 2003; Clarke & Gaston, 2006). Species in stable climates, in contrast, have a more constant diversity of prey types, enabling specialization.

Species range size, or the range of resources that a species is able to use, can influence the latitudinal diversity gradient. Rapoport's rule predicts a positive relationship between species range size and latitude (Stevens, 1989), potentially due to the increased seasonal variability at higher latitudes selecting for broader climatic tolerances (Fernandez & Vrba, 2005). Brown (1984) suggested that species able to occupy larger range sizes should be able to use a wider range of resources. Slatyer *et al.* (2013) showed that generalist species do indeed have larger ranges than specialist species.

Body size may strongly influence dietary niche breadth. Large predators can catch and subdue both small and large prey, whereas small predators are restricted to feeding on small prey (Schoener, 1977; Vitt *et al.*, 2001). Costa *et al.* (2008), however, found that smaller lizards have wider dietary niche breadths than larger ones. This trend suggests that lizards conform to the optimal foraging theory. Optimal foraging theory states that larger lizards have narrower niches as a consequence of targeting fewer prey categories, which are more energetically favourable (MacArthur & Pianka, 1966).

We compiled a large macroecological dataset comprising detailed quantitative volumetric dietary data for 308 lizard species world-wide. We used this database to test seven competing hypotheses posited to explain dietary niche breadth, focusing on those that are thought to either cause, or be influenced by, diversity gradients:

1. The interspecific competition hypothesis: niche breadth will decrease as species richness increases from temperate to tropical regions.

2. The ambient energy hypothesis: niche breadth will increase as temperature increases from temperate to tropical regions.
3. The water availability hypothesis: niche breadth will increase with precipitation.
4. The productivity hypothesis: niche breadth will increase with net primary productivity.
5. The climate stability hypothesis: niche breadth will increase with seasonality.
6. The range size hypothesis: niche breadth will increase with range size.
7. The body size hypothesis: niche breadth will decrease as body size increases, conforming to optimal foraging theory.

## METHODS

### Species data

We collated detailed dietary data for 308 lizard species (following the taxonomy of the reptile database; Uetz, 2015) from mainland regions around the globe (Fig. 1) from an extensive literature review and from field collections. The niche breadths of island species may differ from those of their mainland relatives (e.g. Meiri *et al.*, 2005) and we therefore only used data from mainland populations. Data on maximum body mass for all species were calculated using snout-vent length and the conversion equations in Feldman

*et al.* (2016). Dietary data were based exclusively on stomach contents. We used a general 'plant' category and a 'vertebrate' category along with all order-level categories for each arthropod recorded in a lizard species' diet. Vertebrate and plant foods were not further divided because they are usually treated as single categories in the source papers. The dataset contains 27 prey categories. This is similar to Vitt & Pianka (2005), except that our data does not include harvesters, mites and psocoptera as separate categories. Harvesters were included with ants, mites with arachnids, and psocoptera were placed in 'miscellaneous' along with unidentified insects due to their extremely small volumetric percentages. We included the following categories not used by Vitt & Pianka (2005): Neuroptera, Ephemeroptera and insect eggs (see Appendices S1 and S2 in the Supporting Information).

We quantified volumetric dietary niche breadth using the volumetric proportion of different prey categories consumed by the lizard species for pooled stomachs. To calculate volumetric dietary niche breadth we used the inverse of Simpson's (1949) diversity measure (Pianka, 1973)

$$\text{niche breadth} = \frac{1}{\sum_{i=1}^n p_i^2}$$

where  $p$  is the proportional use of each prey category  $i$ . Niche breadth values range from 1 (exclusive use of a single

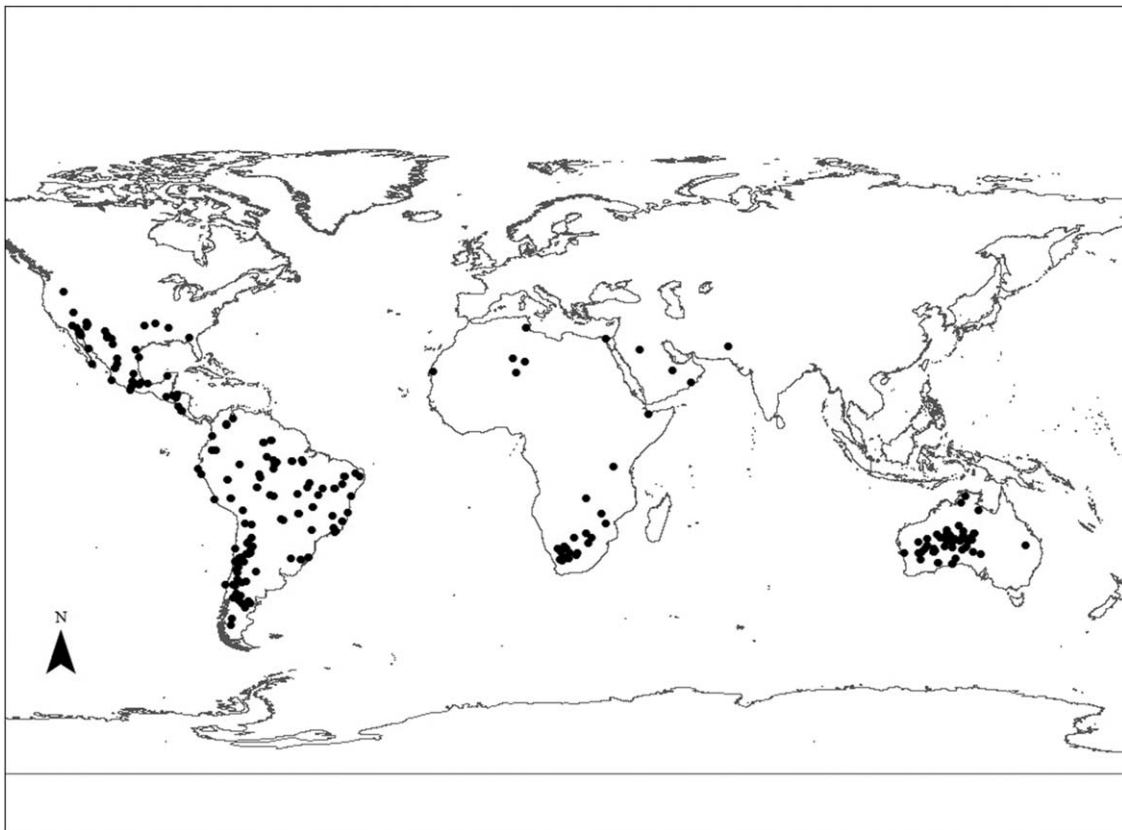


Figure 1 Distribution of lizard species for our dietary niche breadth data.

prey category) to  $n$  (use of all prey categories). We  $\log_{10}$  transformed niche breadth for the analyses. We had data for multiple populations for 50 of the 308 species. For these species we used the data only from the population for which niche breadth was highest, because the hypotheses we tested all postulate that niche breadth is constrained by biotic or abiotic factors, and the use of maximum dietary breadth is thus the most conservative. Nonetheless, we examined the effect that this choice had on the results of our analysis by conducting two sensitivity analyses: in one, we chose the population with the lowest niche breadths; in the other, we averaged niche breadth across locations (mean niche breadth, for which we also averaged geographical coordinates; see below). Results were similar for all three indices, and we thus only report the results of the analyses of maximum niche breadths.

The niche breadth values could be confounded by the number of individuals because we examined the pooled stomach contents of all individuals of a species. It is possible that larger niche breadths may simply represent that more individuals were sampled for a particular species. The Simpson's index we use, an algebraic transformation of Hurlbert's probability of an interspecific encounter, is a diversity index that has good statistical properties and is independent of sample size (Gotelli & Graves, 1996). Nevertheless, we tested for this effect by regressing sample size on volumetric niche breadth. The association between the two variables was not significant (sample size ranged from 5 to 1975:  $R^2 = 0.003$ ,  $P = 0.38$ ).

### Environmental data

We collected the latitude and longitude for the locality of each species' dietary data, following the data in the original publications and Google Earth. We then ascribed to each point locality climatic data obtained from WorldClim (Hijmans *et al.*, 2005) at 30-sec resolution. We selected the following four climate variables: mean annual temperature, mean annual precipitation, temperature seasonality and precipitation seasonality. Net primary productivity (NPP) was extracted from SEDAC at 0.25 decimal degrees (Imhoff *et al.*, 2004). To avoid spurious associations, these variables were selected because they are known to influence the distribution of species (Buckley *et al.*, 2012). In our dataset temperature, precipitation and primary productivity are weakly collinear. Therefore, they could be teased apart even though they are thought to be related to dietary niche breadth via a similar pathway. To estimate the potential effect of species richness on dietary niche breadth under the 'competitionist's paradigm', we calculated, for each species, the number of cohabiting lizards at the point where the study was undertaken as an index of competition intensity. We used lizard species distributions mapped by the Global Assessment of Reptile Distributions Working Group (GARD, <http://www.gardinitiative.org/>) in ArcGIS 10.0 to create a gridded total lizard species richness map for the studied localities. We overlaid our

species point locality data on the  $1^\circ \times 1^\circ$  grid, and extracted, for each locality in which dietary niche breadth was calculated, the total number of lizard species occurring in the same cell, as an index for the number of competitors. We used the GARD range maps for the 308 species for which we had obtained dietary data to calculate range size (in  $\text{km}^2$ ) in an equal-area Behrmann projection.

### Statistical analyses

To test for the latitudinal diversity gradient in our dataset, we performed a simple regression with  $\log_{10}$  mean species richness and latitude. We used ordinary least squares regressions (OLS) and phylogenetic generalized least squares regressions (PGLS) to examine the relationship between lizard dietary niche breadth and the predictor variables. All variables were  $\log_{10}$  transformed to comply with the assumptions of parametric tests. The data are not heteroscedastic (Studentized Breusch–Pagan test: Breusch–Pagan model (BP) = 9.91, d.f. = 7,  $P$ -value = 0.19).

Mean annual precipitation and NPP were strongly correlated (variance inflation factors (VIF) > 3; other predictor variables were not strongly intercorrelated). We thus compared two independent regression models for dietary niche breadth: one with all predictors except NPP (i.e. species richness, annual temperature and annual precipitation, temperature and precipitation seasonality, range size and body size) and another with the same predictors, except for annual precipitation, but with NPP. The dataset is the same in both cases. Models including mean annual precipitation had lower Akaike information criterion (AIC) values than models including NPP (Appendix S3). Therefore, we present models including mean annual precipitation rather than NPP.

Closely related species may have similar niche breadths. To correct for potential effects of phylogenetic relatedness on the dietary niche breadth of lizard species, we pruned the squamate phylogenetic tree of Pyron & Burbrink (2014) to include only the 218 species in our dataset that are represented in the tree. We used the resulting tree to correct for the effects of phylogenetic relatedness using PGLS. We used the maximum likelihood value of the scaling parameter  $\lambda$  (Pagel, 1999) to adjust the strength of phylogenetic non-independence, implemented in the R package 'caper' (Orme *et al.*, 2014). All statistical tests were performed using R 3.1.3 (R Development Core Team, 2015).

### RESULTS

Lizard species richness increases towards lower latitudes ( $R^2 = 0.77$ ,  $P < 0.001$ ; Table 1, Fig. 2). *Plica umbra*, a tropical forest species, has a narrow niche breadth: it mostly eats ants, as do many tropidurid species. *Scincella lateralis*, a temperate North American skink, *Aspidoscelis tigris*, a teiid from the south-western USA and northern Mexico, and *Homonota darwini*, a gecko from the temperate savannas of Patagonia, all had broad dietary niches, reflecting their generalist approach to eating whatever is available. It seems that dietary

**Table 1** The latitudinal gradient in our dataset.

Absolute latitude (mean)	Species in sample	Mean no. of competitors per species	SE	Mean niche breadth	SE
1.7	43	62.8	2.5	5.015	0.456
7.4	22	47.3	4.1	5.099	0.406
11.9	38	67.1	3.6	4.055	0.348
17.9	32	43.4	2.9	4.321	0.409
23.3	49	64.7	4.8	3.431	0.348
27.7	58	59.7	4.1	4.000	0.299
31.9	42	37.8	3.4	3.842	0.354
37.1	10	33.7	6.0	2.013	0.453
41.9	12	27.3	1.9	1.904	0.508
47.7	2	26.5	7.5	1.000	0.000

Absolute latitude is divided into 10 classes (mean of 5° latitude) with species in the sample representing the number of species with dietary data per latitude class. SE is standard error.

specialization is predominantly restricted to a small number of families, mostly of herbivorous species (e.g. the tropical *Iguana iguana* and *Ctenosaura defensor* and temperate *Phymaturus* species) and ant specialists, whereas dietary generalists are ubiquitous.

In the full OLS model dietary niche breadth is positively related to mean annual temperature, mean annual precipitation, temperature seasonality and range size, and negatively associated with body size ( $R^2 = 0.41$ ; Table 2, Fig. 3; see Appendix S4). Lizard species richness and precipitation seasonality are not significantly associated with lizard dietary niche breadth (Table 2). Lizard dietary niche breadth has a strong phylogenetic component ( $\lambda = 0.75$ ). The full PGLS model ( $R^2 = 0.15$ ; Table 2) is similar to the OLS model except for mean annual temperature, which is not significantly associated with lizard dietary niche breadth. Again, there is no association with precipitation seasonality or with lizard species richness ( $P = 0.88$ ).

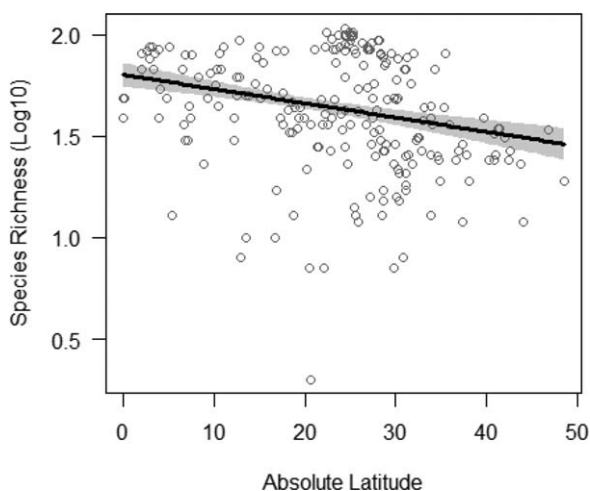
Results of models in which dietary niche breadth was analysed without species that consumed 80% or more plants or vertebrates – and were designated as herbivore and vertebrate

specialists – were broadly similar (Appendix S5). The full OLS model is similar to that obtained with the whole dataset except for mean annual temperature, temperature seasonality and body size, which were not significant. There is no association between lizard dietary niche breadth and lizard species richness ( $P = 0.15$ ). In this dataset niche breadth has a weaker phylogenetic component ( $\lambda = 0.41$ ). In the full PGLS model for this dataset lizard dietary niche breadth is positively related to mean annual precipitation and range size, as in the OLS model ( $R^2 = 0.10$ ). Again there is no association with either precipitation seasonality or lizard species richness ( $P = 0.68$ ; Appendix S5). Regardless of the dataset or analytical methods, all results share a stark commonality: that no relationship exists between lizard dietary niche breadth and lizard species richness.

## DISCUSSION

Our global lizard dietary niche dataset enabled us to concurrently test seven competing hypotheses that attempt to explain dietary niche breadth, including some that associate niche breadth with diversity gradients, and which are often portrayed as potential mechanisms maintaining high biodiversity in the tropics. We have shown that lizard dietary specialization is not due to an increase in species richness leading to a narrowing of niche breadth, as predicted by the interspecific competition hypothesis. Instead, we found that dietary specialization is predicted by the ambient energy, water availability, climate stability (for temperature only), range size and body size – supporting five of the associated hypotheses using the OLS (hypotheses 2, 3 and 5–7, but not 4 or 1) and supporting four of the associated hypotheses using PGLS (3 and 5–7, but not 2, 4 or 1).

Prey availability may influence dietary breadth (Petraitis, 1979). Data on lizard prey availability were unavailable in most of the sources. However, the taxonomic resolution of broad prey categories (mostly taxonomic orders), are most likely available across all the sampled locations (Vitt &

**Figure 2** Latitudinal diversity gradient.

**Table 2** A comparison of the relationship between dietary niche breadth and the predictor variables ( $\log_{10}$  transformed) for the global full models.

	OLS $R^2 = 0.41$ ( $P < 0.001$ ), d.f. = 7, 300		PGLS $R^2 = 0.15$ ( $P < 0.001$ ), d.f. = 7, 210	
	Slope $\pm$ SE	$P$	Slope $\pm$ SE	$P$
Species richness	0.077 $\pm$ 0.056	0.172	-0.011 $\pm$ 0.070	0.881
Annual temperature	0.430 $\pm$ 0.166	0.010	0.282 $\pm$ 0.177	0.114
Annual precipitation*	0.257 $\pm$ 0.047	<0.001	0.217 $\pm$ 0.059	<0.001
Temperature seasonality*	0.179 $\pm$ 0.059	0.003	0.207 $\pm$ 0.076	0.007
Precipitation seasonality	0.045 $\pm$ 0.071	0.529	0.055 $\pm$ 0.085	0.520
Range size*	0.067 $\pm$ 0.013	<0.001	0.045 $\pm$ 0.015	0.004
Body size*	-0.124 $\pm$ 0.019	<0.001	-0.090 $\pm$ 0.029	0.002

OLS, ordinary least squares regression; PGLS, phylogenetic generalized least squares regression; d.f., degrees of freedom; SE, standard error.

\*Significant PGLS associations are marked with an asterisk. (Appendix S5 provides a comparison of the relationship between dietary niche breadth and predictor variables ( $\log_{10}$  transformed) for the full OLS and PGLS models, excluding dietary specialists.)

Pianka, 2005), providing a conservative and comparable estimate of lizard dietary breadth for the focal species.

Given the strong phylogenetic signal in lizard dietary niche breadth, we focus our discussion on the results of the phylogenetic model. In both non-phylogenetic and phylogenetic regression models we consistently found no relationship between dietary niche breadth and species richness. It is possible species richness does not necessarily represent more competition, but rather species identity. Some species may be better competitors or related species may compete more with each other in a community (Meiri *et al.*, 2007, 2014).

If the presence of more species indicates stronger interspecific competition, as is usually assumed in the ecological literature (Dobzhansky, 1950; Hutchinson & MacArthur, 1959; Rabosky & Hurlbert, 2015), then the hypothesis that competition drives niche breadth is not supported by our data. The widely accepted (e.g. Rising, 1988; Laube *et al.*, 2013) 'competitionist's paradigm' states that an increased number of species in the tropics is driven by interspecific competition caused by limiting ecological resources such as food, which in turn results in greater specialization that allows 'species packing'. Increased lizard species richness in the tropics, however, is not associated with narrower feeding niches. Our findings correspond well with studies showing that interspecific competition is not associated with niche breadth along other niche axes. While some studies on herbivorous insects demonstrate specialization in tropical forests (Forister *et al.*, 2015), other studies have shown that Amazonian birds (Terborgh *et al.*, 1990) and Peruvian (Pitman *et al.*, 1999) and Brazilian trees (Wittmann *et al.*, 2013) are rarely restricted by habitat. Thus, tropical birds and trees, at least in Amazonia, are usually habitat generalists, not specialists. These findings support the hypothesis that interspecific competition is neither a mechanism for increased species richness in the tropics nor the result of this increased richness (Terborgh, 2015).

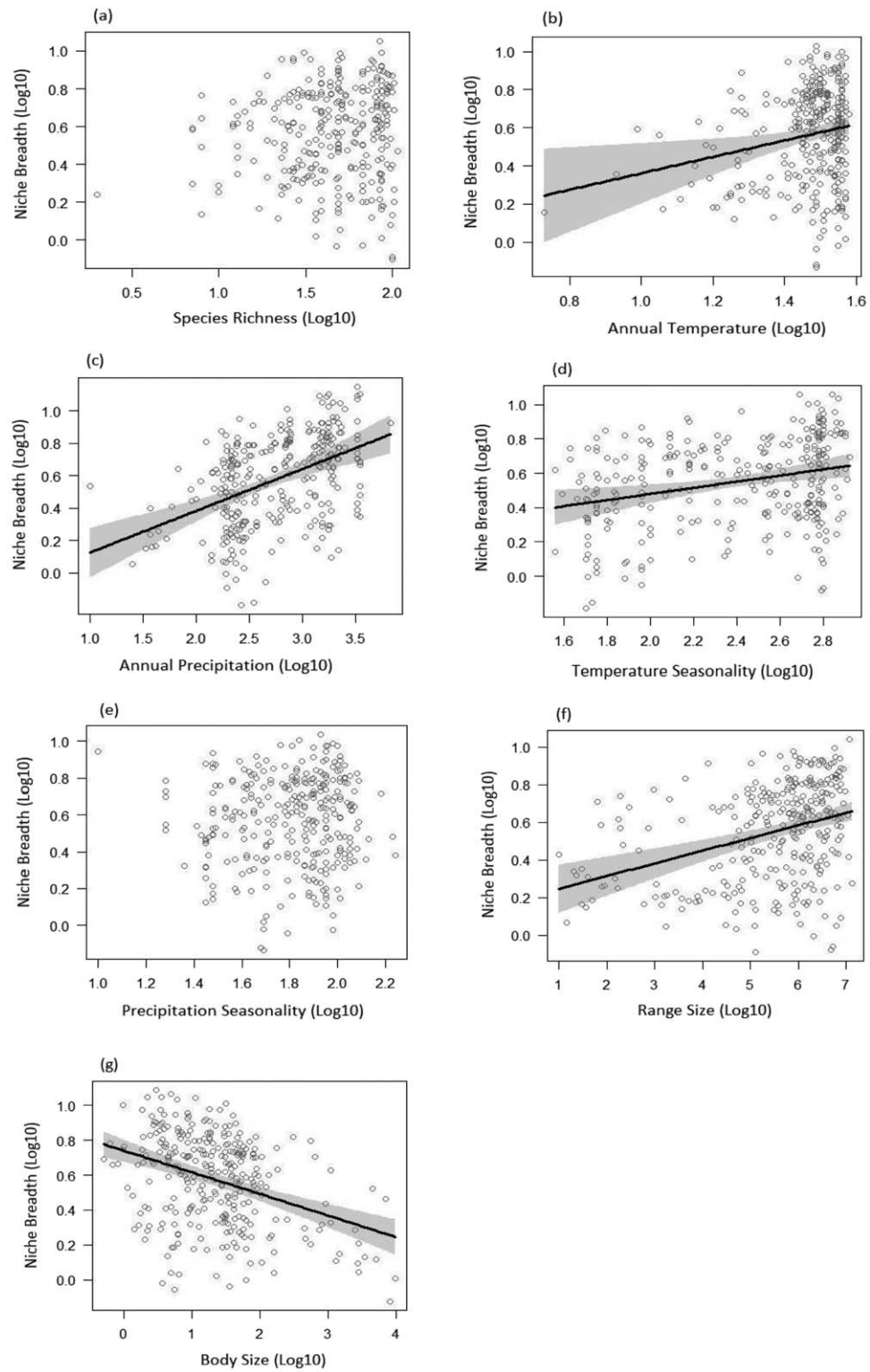
We found that lizard dietary niches are narrower in regions with lower rainfall. Annual precipitation strongly

influences diversity, especially at lower latitudes (Hawkins *et al.*, 2003). Rainfall is a major predictor of local diversity for a wide range of taxa (Canello *et al.*, 2014), with widespread patterns of increasing diversity along an increasing rainfall gradient (Sommer *et al.*, 2010). Arthropods are particularly sensitive to precipitation (Whittaker *et al.*, 2001), which in turn strongly affects the number of prey types available to a predator. Several insect prey groups are very sensitive to extreme rainfall events or to humidity in general, with many taxa preferring moist habitats (Progar & Schowalter, 2002). Changes in precipitation are potentially major drivers of insect community composition, which is reflected in dietary niche breadth. This supports present climate, specifically annual precipitation, as a mechanism driving dietary niche breadth.

Low seasonality in temperature (but not in precipitation) also emerges as an important climatic factor promoting narrower dietary niches of lizards. Stable climates are thought to promote narrow physiological tolerances and specialization, leading to higher diversity and more stable population sizes (Pianka 1966). Our findings correspond well with those of other studies showing that climatic stability drives dietary specialization in birds (Williams & Middleton, 2008) and spiders (Birkhofer & Wolters, 2012).

Smaller range sizes promote lizard dietary specialization. This supports studies demonstrating that generalist species have larger geographical ranges than specialist species (Brown 1984; Slatyer *et al.* 2013). Analogous to an explanation of Rapoport's rule, that larger species ranges result from broader physiological tolerances (Janzen 1967), we show that being a dietary generalist may promote range expansions. Causality, however, may also be reversed: a large geographical range may pre-adapt species to widen their dietary niche.

Our results contradict other studies reported for birds (Brandle *et al.*, 2002) and insects (Novotny & Basset, 1999) that support a positive body size–niche breadth relationship. Across lizard species, however, Costa *et al.* (2008) also found



**Figure 3** Full model ordinary least squares regression with the predictors displayed with their regression line and 95% confidence intervals when the predictors were significant in the model: (a) species richness, (b) annual temperature, (c) annual precipitation, (d) temperature seasonality, (e) precipitation seasonality, (f) range size and (g) body size.

that larger species have narrower feeding niches. Our study provides further support for the suggestion that lizards conform to the optimal foraging theory (MacArthur & Pianka, 1966). Larger lizards can select for larger, more profitable prey, thus eliminating the need to eat smaller prey, and thereby decreasing their dietary niche to become classified as

dietary specialists. We caution, however, that these findings may in part reflect a bias in the reporting of lizard dietary categories. Larger lizards tend to consume more plant and vertebrate food than smaller ones (Meiri, 2008). Vertebrates and plants, however, are usually reported under these headings in studies of lizard diets, rather than at the ordinal or

even class levels. Thus, it could be that although the large lizards we examined consume a variety of plant and vertebrate foods, they would still be classified as specialists in analyses such as ours. While future studies are needed to explore this relationship it is unlikely to affect our conclusions, as omitting vertebrate and plant specialists did not change our main results.

The latitudinal diversity gradient of increasing biodiversity from the poles to the equator is one of the most prominent in biogeography, yet our understanding of which processes are important in maintaining it remains unclear. Overall, our findings are consistent with the notion that climate is an important predictor of dietary specialization, with both less rainfall and more stable temperatures associated with narrower dietary niches, but are inconsistent with the view that the latitudinal diversity gradient is promoted by dietary specialization in the tropics. Trophic interactions between lizard species and their arthropod prey are sensitive to climate. It is likely that climatic conditions not only affect these interactions but also alter the functional role of other vertebrate predators in terrestrial ecosystems. The sensitivity of dietary niche breadth to climate has important implications for essential ecosystem functions that maintain increased species richness in the tropics, such as food web stability and energy flow (Tylianakis *et al.*, 2010). The synergistic effects of a narrow dietary niche and small range size augments the vulnerability of species to habitat loss and climate change (Slatyer *et al.* 2013). Based on our findings, the ‘competitionist’s paradigm’ seems to be the exception rather than the rule in explaining the latitudinal diversity gradient.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

**Appendix S1** Detailed methods for collection of dietary data.

**Appendix S2** Full dataset utilized in the analyses, including references for dietary data.

**Appendix S3** Comparing models without net primary productivity with models without annual precipitation.

**Appendix S4** Coefficients of correlation for ordinary least squares model.

**Appendix S5** A comparison of the relationship between dietary niche breadth and predictor variables for the best global full scale ordinary least squares and phylogenetic least squares models, without species that consumed 80% or more plants or vertebrates – and were designated as specialists.

## BIOSKETCHES

**Alison Gainsbury** is interested in the macroecology of lizards.

**Shai Meiri** studies the evolution and ecology of animal traits.

Editor: Jonathan Lenoir

## Appendix S1 – Detailed methods for collection of diet data.

Stomach contents were analyzed stomach mostly identifying each prey items to Order. Most prey are arthropods, this is representative of lizard diets and is supported by Shai *et al.* (2013) full dataset with 3048 global lizard species 80% of the species ate only arthropods. The vertebrate category consists of shed skin and vertebrate eggs. Prey items had recorded body length and width of intact prey items, and estimated individual prey volume (*Volume*) as an ellipsoid:

$$Volume = \frac{4}{3}\pi \left(\frac{l}{2}\right) \left(\frac{w}{2}\right)^2$$

where  $w$  = prey width and  $l$  = prey length. We used the proportion of prey volume of each prey category to calculate the inverse of Simpson index for volumetric dietary niche breadth (see Methods). The 27 prey categories were: (1) Annelida, (2) Ants, (3) Arachnida, (4) Chilopoda, (5) Cockroaches, (6) Coleoptera, (7) Collembola, (8) Dermaptera, (9) Diplopoda, (10) Diptera, (11) Ephemeroptera, (12) Hemiptera/Homoptera, (13) Hymenoptera (non-ants) , (14) Insect larvae and pupae, (15) Insect egg, (16) Isoptera, (17) Isopoda, (18) Lepidoptera, (19) Miscellaneous, (20) Mollusca, (21) Neuroptera, (22) Odonata, (23) Orthoptera, (24) Phasmids-Mantids, (25) Plant, (26) Scorpionida, (27) Vertebrate.







Tropiduridae	<i>Tropidurus torquatus</i>	29	-22.95	-43.01	1.90	134.0	4.68	1.52	2.33	3.09	1.65	11.89	1.59	6.94
Tropiduridae	<i>Uracentron flaviceps</i>	1670	0.00	-76.17	1.86	130.0	1.43	1.55	1.75	3.52	1.48	11.97	1.59	6.11
Varanidae	<i>Varanus breviceaudus</i>	26	-28.20	123.58	1.49	126.0	5.01	1.48	2.78	2.33	1.62	10.88	1.97	6.36
Varanidae	<i>Varanus caudolineatus</i>	13	-25.52	119.43	1.57	133.0	4.42	1.50	2.82	2.38	1.84	10.88	1.91	6.07
Varanidae	<i>Varanus eremius</i>	60	-25.14	127.08	2.16	202.0	1.76	1.52	2.80	2.31	1.69	10.82	1.99	6.47
Varanidae	<i>Varanus gouldii</i>	79	-28.20	123.58	3.84	670.0	2.90	1.48	2.78	2.33	1.62	11.03	1.97	6.80
Varanidae	<i>Varanus mertensi</i>	31	-16.79	136.13	3.54	542.0	1.70	1.56	2.59	2.85	2.08	11.26	1.92	6.08
Varanidae	<i>Varanus mitchelli</i>	23	-14.61	131.24	2.91	346.0	2.63	1.57	2.48	3.04	2.08	11.31	1.89	5.65
Varanidae	<i>Varanus panoptes</i>	64	-21.08	130.58	3.98	740.0	1.17	1.54	2.74	2.57	1.95	11.11	1.93	6.40
Varanidae	<i>Varanus tristis</i>	75	-28.20	123.58	2.74	305.0	1.59	1.48	2.78	2.33	1.62	11	1.97	6.78
Xantusiidae	<i>Lepidophyma flavimaculatum</i>	9	14.54	-87.15	1.86	153.0	2.12	1.50	2.22	3.12	1.90	11.71	1.76	5.42
Xantusiidae	<i>Lepidophyma smithii</i>	17	16.82	-99.83	1.45	112.0	1.20	1.57	1.89	3.08	2.09	11.65	1.23	4.69
Xantusiidae	<i>Xantusia vigilis</i>	24	33.90	-114.82	0.83	70.0	4.37	1.51	2.90	2.04	1.78	10.89	1.41	5.41
Xenosauridae	<i>Xenosaurus grandis</i>	25	18.88	-96.93	1.75	133.0	6.44	1.50	2.34	3.32	1.94	11.77	1.64	4.95
Xenosauridae	<i>Xenosaurus newmanorum</i>	37	21.38	-98.98	1.74	132.0	4.53	1.52	2.54	3.34	1.92	11.91	1.45	2.86
Xenosauridae	<i>Xenosaurus platyceps</i>	27	25.87	-97.50	1.60	121.0	4.34	1.52	2.69	2.85	1.83	11.74	1.73	3.56
Xenosauridae	<i>Xenosaurus rectocollaris</i>	65	18.30	-97.47	1.47	111.0	3.32	1.46	2.31	2.70	2.03	11.55	1.52	2.24

Species	Diet References
<i>Acanthocercus atricollis</i>	Reaney, L. T., & Whiting, M. J. (2002) Life on a limb: ecology of the tree agama ( <i>Acanthocercus a. atricollis</i> ) in southern Africa. <i>Journal of Zoology</i> , <b>257</b> , 439-448.
<i>Agama hispida</i>	Pianka, E. R. (1986) Ecology and natural history of desert lizards: analyses of the ecological niche and community structure. Princeton, NJ: Princeton University Press.
<i>Chlamydosaurus kingii</i>	Griffiths, A. D., & Christian, K. A. (1996) The effects of fire on the frillneck lizard ( <i>Chlamydosaurus kingii</i> ) in northern Australia. <i>Australian Journal of Ecology</i> , <b>21</b> , 386-398.
<i>Ctenophorus clayi</i>	Pianka (2013) Notes on the ecology and natural history of two uncommon terrestrial agamid lizards <i>Ctenophorus clayi</i> and <i>C. fordi</i> in the Great Victoria desert of Western Australia. <i>Western Australian Naturalist</i> , <b>29</b> , 85-93.
<i>Ctenophorus fordi</i>	Pianka (2013) Notes on the ecology and natural history of two uncommon terrestrial agamid lizards <i>Ctenophorus clayi</i> and <i>C. fordi</i> in the Great Victoria desert of Western Australia. <i>Western Australian Naturalist</i> , <b>29</b> , 85-93.
<i>Ctenophorus isolepis</i>	Pianka, E. R. (1986) Ecology and natural history of desert lizards: analyses of the ecological niche and community structure. Princeton, NJ: Princeton University Press.
<i>Ctenophorus maculatus</i>	Pianka, E. R. (2014) Notes on a collection of lizards from the Eucla sand dunes in Western Australia. <i>Western Australian Naturalist</i> , <b>30</b> , 155-161.
<i>Ctenophorus nuchalis</i>	Pianka, E. R. (1986) Ecology and natural history of desert lizards: analyses of the ecological niche and community structure. Princeton, NJ: Princeton University Press.
<i>Ctenophorus pictus</i>	Pianka, E. R. (2014) Notes on a collection of lizards from the Eucla sand dunes in Western Australia. <i>Western Australian Naturalist</i> , <b>30</b> , 155-161.
<i>Ctenophorus reticulatus</i>	Pianka, E. R. (1986) Ecology and natural history of desert lizards: analyses of the ecological niche and community structure. Princeton, NJ: Princeton University Press.
<i>Ctenophorus scutulatus</i>	Pianka, E. R. (1986) Ecology and natural history of desert lizards: analyses of the ecological niche and community structure. Princeton, NJ: Princeton University Press.
<i>Diporiphora amphibolurooides</i>	Pianka, E. R. (1986) Ecology and natural history of desert lizards: analyses of the ecological niche and community structure. Princeton, NJ: Princeton University Press.
<i>Diporiphora winneckeii</i>	Pianka, E. R. (1986) Ecology and natural history of desert lizards: analyses of the ecological niche and community structure. Princeton, NJ: Princeton University Press.
<i>Gowidon longirostris</i>	Pianka, E. R. (1986) Ecology and natural history of desert lizards: analyses of the ecological niche and community structure. Princeton, NJ: Princeton University Press.
<i>Laudakia melanura</i>	Meiri, S. Bauer, A.M, Chirio, L., Colli, G.R, Das, I., Doan, T.M., Feldman, A., Herrera, F.C., Novosolov, M., Pafilis, P., Pincheira-Donoso, D., Powney, G., Torres-Carvajal, O., Uetz, P. & Van Damme, R. (2013) Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. <i>Global Ecology and Biogeography</i> , <b>22</b> , 834-845.
<i>Moloch horridus</i>	Pianka, E. R. (1986) Ecology and natural history of desert lizards: analyses of the ecological niche and community structure. Princeton, NJ: Princeton University Press.
<i>Pogona minor</i>	Pianka, E. R. (1986) Ecology and natural history of desert lizards: analyses of the ecological niche and community structure. Princeton, NJ: Princeton University Press.
<i>Uromastyx acanthinura</i>	Meiri, S. Bauer, A.M, Chirio, L., Colli, G.R, Das, I., Doan, T.M., Feldman, A., Herrera, F.C., Novosolov, M., Pafilis, P., Pincheira-Donoso, D., Powney, G., Torres-Carvajal, O., Uetz, P. & Van Damme, R. (2013) Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. <i>Global Ecology and Biogeography</i> , <b>22</b> , 834-845.
<i>Uromastyx aegyptia</i>	Meiri, S. Bauer, A.M, Chirio, L., Colli, G.R, Das, I., Doan, T.M., Feldman, A., Herrera, F.C., Novosolov, M., Pafilis, P., Pincheira-Donoso, D., Powney, G., Torres-Carvajal, O., Uetz, P. & Van Damme, R. (2013) Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. <i>Global Ecology and Biogeography</i> , <b>22</b> , 834-845.
<i>Uromastyx alfredschmidti</i>	Meiri, S. Bauer, A.M, Chirio, L., Colli, G.R, Das, I., Doan, T.M., Feldman, A., Herrera, F.C., Novosolov, M., Pafilis, P., Pincheira-Donoso, D., Powney, G., Torres-Carvajal, O., Uetz, P. & Van Damme, R. (2013) Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. <i>Global Ecology and Biogeography</i> , <b>22</b> , 834-845.
<i>Uromastyx dispar</i>	Meiri, S. Bauer, A.M, Chirio, L., Colli, G.R, Das, I., Doan, T.M., Feldman, A., Herrera, F.C., Novosolov, M., Pafilis, P., Pincheira-Donoso, D., Powney, G., Torres-Carvajal, O., Uetz, P. & Van Damme, R. (2013) Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. <i>Global Ecology and Biogeography</i> , <b>22</b> , 834-845.
<i>Uromastyx macfadyeni</i>	Meiri, S. Bauer, A.M, Chirio, L., Colli, G.R, Das, I., Doan, T.M., Feldman, A., Herrera, F.C., Novosolov, M., Pafilis, P., Pincheira-Donoso, D., Powney, G., Torres-Carvajal, O., Uetz, P. & Van Damme, R. (2013) Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. <i>Global Ecology and Biogeography</i> , <b>22</b> , 834-845.
<i>Uromastyx occidentalis</i>	Meiri, S. Bauer, A.M, Chirio, L., Colli, G.R, Das, I., Doan, T.M., Feldman, A., Herrera, F.C., Novosolov, M., Pafilis, P., Pincheira-Donoso, D., Powney, G., Torres-Carvajal, O., Uetz, P. & Van Damme, R. (2013) Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. <i>Global Ecology and Biogeography</i> , <b>22</b> , 834-845.
<i>Uromastyx thomasi</i>	Meiri, S. Bauer, A.M, Chirio, L., Colli, G.R, Das, I., Doan, T.M., Feldman, A., Herrera, F.C., Novosolov, M., Pafilis, P., Pincheira-Donoso, D., Powney, G., Torres-Carvajal, O., Uetz, P. & Van Damme, R. (2013) Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. <i>Global Ecology and Biogeography</i> , <b>22</b> , 834-845.
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<i>Ophisaurus ventralis</i>	Hamilton, W. J., & Pollack, J. A. (1961) The food of some lizards from Fort Benning, Georgia. <i>Herpetologica</i> , <b>17</b> , 99-106.



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Family	According to the reptile database (Uetz, 2015). <a href="http://www.reptile-database.org/">http://www.reptile-database.org/</a>
Species	According to the reptile database (Uetz, 2015). <a href="http://www.reptile-database.org/">http://www.reptile-database.org/</a>
Sample Size (#of lizards)	Number of lizards sampled for the dietary niche breath calculation, following the data in the original publications
Latitude	Locality of species sampled for dietary data, following the data in the original publications and Google Earth
Longitude	Locality of species sampled for dietary data, following the data in the original publications and Google Earth
Log Mass (g)	Maximum body mass data for all species calculated using snout vent length and the conversion equations in Feldman <i>et al.</i> (2016)
Max SVL (mm)	Maximum snout vent length data for all species, following the data in Meiri (2008)
Niche Breadth	Volumetric diet niche breadth calculated by the inverse of Simpson's (1949) diversity measure, following the data in the original publications
Log Annual Temperature (degrees centigrade)	Locality of species (lat, lon) determined the climatic data obtained from the WorldClim database (Hijmans <i>et al.</i> , 2005) at 30 sec resolution
Log Seasonality in Temperature	Locality of species (lat, lon) determined the climatic data obtained from the WorldClim database (Hijmans <i>et al.</i> , 2005) at 30 sec resolution
Log Annual Precipitation (mm)	Locality of species (lat, lon) determined the climatic data obtained from the WorldClim database (Hijmans <i>et al.</i> , 2005) at 30 sec resolution
Log Seasonality in Precipitation	Locality of species (lat, lon) determined the climatic data obtained from the WorldClim database (Hijmans <i>et al.</i> , 2005) at 30 sec resolution
Log NPP	Locality of species (lat, lon) determined net primary productivity (NPP) extracted from SEDAC at 0.25 decimal degrees (Imhoff <i>et al.</i> , 2004)
Log Species Richness at locality	Lizard species distributions mapped by the global assessment of reptile distributions working group (GARD) in ArcGIS 10.0 created a gridded total lizard species richness map for the study localities
Log Species Range size (km <sup>2</sup> )	The GARD range maps for the 308 species for which we obtained dietary data were used to calculate range size (in Km <sup>2</sup> ) in an equal-area Behrmann projection
Diet References	Original publications containing the diet data

Appendix S3 - Comparing models without NPP to models without annual precipitation.

Mean annual precipitation and NPP were strongly correlated ( $vif > 3$ ; other predictor variables were not strongly intercorrelated). We thus started with two independent regression models (with dietary niche breadth as the response variable): one with all predictors except NPP ( $LNB \sim Lbodysize + Lsprich + Lrangesize + LSeasonTemp + LSeasonPrec + LAnnTemp + LAnnPrec$ ), and another with all predictors except annual precipitation ( $LNB \sim Lbodysize + Lsprich + Lrangesize + LSeasonTemp + LSeasonPrec + LAnnTemp + Lnpp$ ). The dataset is the same in both cases. We used the Akaike information criterion (AIC) to identify the best model among all possible combinations.

The FULL MODEL was: `modeltestall <- lm(LNB ~ Lbodysize + Lsprich + Lrangesize + LSeasonTemp + LSeasonPrec + LAnnTemp + LAnnPrec + Lnpp, data=dat)`

Checking for variance inflation factors using “library(car)” in R we received:

`vif(modeltestall)`

Lbodysize	Lsprich	Lrangesize	LSeasonTemp	LSeasonPrec	LAnnTemp	LAnnPrec	Lnpp
1.065863	1.310333	1.582019	3.789762	1.119022	1.970434	6.053198	7.930582

This shows that Annual precipitation and NPP are strongly co-linear with the other predictors

Thus we compared the two following models:

One with annual precipitation but no NPP:

`modeltestnonpp <- lm(LNB ~ Lbodysize + Lsprich + Lrangesize + LSeasonTemp + LSeasonPrec + LAnnTemp + LAnnPrec, data=dat)`  
`summary(modeltestnonpp)`

Residuals:

Min 1Q Median 3Q Max  
 -0.7052 -0.1865 0.0421 0.1962 0.4585

Coefficients:

Estimate Std. Error t value Pr(>|t|)  
 (Intercept) -1.67676 0.38329 -4.375 1.68e-05 \*\*\*  
 LMASS -0.12404 0.01882 -6.591 1.97e-10 \*\*\*  
 Lsprich 0.07738 0.05649 1.370 0.17179  
 Lrangesize 0.06723 0.01299 5.176 4.16e-07 \*\*\*  
 LSeasonTemp 0.17899 0.05892 3.038 0.00259 \*\*  
 LSeasonPrec 0.04501 0.07147 0.630 0.52932  
 LAnnTemp 0.43017 0.16579 2.595 0.00993 \*\*  
 LAnnPrec 0.25700 0.04723 5.442 1.10e-07 \*\*\*

---

Signif. codes: 0 ‘\*\*\*\*’ 0.001 ‘\*\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.243 on 300 degrees of freedom  
Multiple R-squared: 0.4083, Adjusted R-squared: 0.3945  
F-statistic: 29.57 on 7 and 300 DF, p-value: < 2.2e-16

And one with NPP but no annual precipitation (the data, response variables and other predictors are identical in the two models)

```
modeltestnoAnnPrec<-lm(LNB~ Lbodysize + Lsprich + Lrangesize + LSeasonTemp + LSeasonPrec
+ LAnnTemp + Lnpp , data=dat)
summary(modeltestnoAnnPrec)
```

Residuals:

```
   Min      1Q  Median      3Q      Max
-0.68999 -0.18974  0.03086  0.17977  0.49185
```

Coefficients:

```
      Estimate Std. Error t value Pr(>|t|)
(Intercept) -4.05223   0.78559  -5.158 4.54e-07 ***
LMASS       -0.12255   0.01890  -6.482 3.71e-10 ***
Lsprich      0.11962   0.05627   2.126 0.03434 *
Lrangesize  0.06864   0.01303   5.270 2.61e-07 ***
LSeasonTemp 0.20969   0.06567   3.193 0.00156 **
LSeasonPrec -0.01753   0.07105  -0.247 0.80532
LAnnTemp    0.28811   0.16615   1.734 0.08393 .
Lnpp        0.28688   0.05563   5.157 4.57e-07 ***
```

---

Signif. codes: 0 ‘\*\*\*\*’ 0.001 ‘\*\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.2441 on 300 degrees of freedom  
Multiple R-squared: 0.4028, Adjusted R-squared: 0.3888  
F-statistic: 28.9 on 7 and 300 DF, p-value: < 2.2e-16

using “library (MuMIn)” we calculated the AICc scores of the two models obtaining

	LAnnPrec	df	logLik	AICc	delta
modeltestnonpp	0.2570005	9	2.753055	13.09792	0
modeltestnoAnnPrec	NA	9	1.333594	15.93684	2.83892

Thus the model with precipitation but no NPP is superior and we used it in all the following analyses.  
vif (modeltestnonpp)

Lbodysize	Lsprich	Lrangesize	LSeasonTemp	LSeasonPrec	LAnnTemp	LAnnPrec
1.065629	1.280403	1.580271	3.027247	1.083201	1.894653	2.774455

Appendix S4- Coefficients of bivariate correlation between all pairs of predictor variables – and between each and log niche breadth (LNB).

	LNB	LBodysize	LAnnTemp	LSeasonTemp	LAnnPrec	LSeasonPrec	Lsprich	LRangesize
LNB	1							
LBodysize	-0.333433089	1						
LAnnTemp	0.384109736	-0.011703033	1					
LSeasonTemp	-0.221215896	0.152419517	-0.402634285	1				
LAnnPrec	0.372745081	-0.136140344	0.331890048	-0.781000396	1			
LSeasonPrec	-0.112866406	0.143578845	-0.006239089	-0.021457088	-0.096290157	1		
Lsprich	0.324265577	-0.123394487	0.410773744	-0.175300857	0.239237597	-0.089564032	1	
LRangesize	0.447890763	-0.020472274	0.533680523	-0.065706619	0.158837842	-0.163091064	0.342598466	1

LBodysize: Log maximum body mass (calculated from SVL)

LAnnTemp: Log mean annual temperature

LSeasonTemp: Log seasonality in temperature

LAnnPrec: Log mean annual precipitation

LSeasonPrec: Log seasonality in precipitation

Lsprich: Log species richness per locality

LRangesize: Log range size per species

See text on units, how each variable was quantified and where it derives from

Appendix S5 –A comparison of the relationship between dietary niche breadth and predictor variables (log 10 transformed) for the best global full scale OLS and PGLS models, without species that consumed 80% or more plants or vertebrates – and were designated as herbivore and vertebrate specialists. This dataset consists of 256 species (excluding the 52 specialist species). “df” is Degrees of Freedom and “se” is Standard Error. Significant PGLS associations are marked with an asterisk.

	OLS		PGLS	
	R <sup>2</sup> = 0.09 (p<0.001) df = 7, 248		R <sup>2</sup> = 0.08 (p=0.038) df = 7, 182	
	Slope ± se	p	Slope ± se	p
Species richness	0.056±0.063	0.369	-0.076±0.081	0.350
Annual temperature	-0.134±0.263	0.610	0.007±0.281	0.980
Annual precipitation *	0.170±0.057	0.003	0.159±0.071	0.028
Temperature seasonality	0.084±0.067	0.213	0.125±0.087	0.153
Precipitation seasonality	0.067±0.075	0.372	0.098±0.092	0.287
Range size *	0.041±0.016	0.011	0.050±0.020	0.012
Body size	-0.048±0.022	0.033	-0.048±0.030	0.113