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Hot, dry and different: Australian lizard richness is unlike that of mammals, amphibians and birds

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ABSTRACT

Aims (1) To map the species richness of Australian lizards and describe patterns of range size and species turnover that underlie them. (2) To assess the congruence in the species richness of lizards and other vertebrate groups. (3) To search for commonalities in the drivers of species richness in Australian vertebrates.

Location Australia.

Methods We digitized lizard distribution data to generate gridded maps of species richness and β-diversity. Using similar maps for amphibians, mammals and birds, we explored the relationship between species richness and temperature, actual evapotranspiration, elevation and local elevation range. We used spatial eigenvector filtering and geographically weighted regression to explore geographical patterns and take spatial autocorrelation into account. We explored congruence between the species richness of vertebrate groups whilst controlling for environmental effects.

Results Lizard richness peaks in the central deserts (where β-diversity is low) and tropical north-east (where β-diversity is high). The intervening lowlands have low species richness and β-diversity. Generally, lizard richness is uncorrelated with that of other vertebrates but this low congruence is strongly spatially structured. Environmental models for all groups also show strong spatial heterogeneity. Lizard richness is predicted by different environmental factors from other vertebrates, being highest in dry and hot regions. Accounting for environmental drivers, lizard richness is weakly positively related to richness of other vertebrates, both at global and local scales.

Main conclusions Lizard species richness differs from that of other vertebrates. This difference is probably caused by differential responses to environmental gradients and different centres of diversification; there is little evidence for inter-taxon competition limiting lizard richness. Local variation in habitat diversity or evolutionary radiations may explain weak associations between taxa, after controlling for environmental variables. We strongly recommend that studies of variation in species richness examine and account for non-stationarity.

Keywords
Australia, beta-diversity, biogeography, cross-taxon congruence, environmental correlates, lizards, macroecology, non-stationarity, species richness.

INTRODUCTION

Large-scale diversity gradients are often studied for individual higher taxa, and the environmental correlates of species richness in different taxa are often similar. These findings result from studies over a range of scales, both in total spatial extent and in the size of sampling units (e.g. Currie, 1991; Qian & Ricklefs, 2008; Field *et al.*, 2009). If the relationship between environmental factors and species richness is common to several higher taxa, congruence in the distribution of species richness across

those taxa can be expected. Cross-taxon congruence in richness, however, may be far from a universal phenomenon, as considerable variation exists (Prendergast *et al.*, 1993; Grenyer *et al.*, 2006; Mandelik *et al.*, 2007; Qian & Ricklefs, 2008). There is increasing evidence that non-stationarity in the environment–richness relationship is fairly common (Cassemiro *et al.*, 2007). We note that any assumption of congruence in richness requires not only that general correlations between environmental drivers and richness be common across higher taxa, but also that the geographical pattern of variation in these correlations must also be shared.

At large spatial scales, species richness is predicted by climatic conditions (Field *et al.*, 2009). The 'available energy hypothesis' suggests that species richness is limited by the amount of environmental energy (Wright, 1983), with temperature often used as a measure of environmental energy (Currie, 1991). Ectotherms such as reptiles are further constrained by temperature because temperatures influence their fecundity and survival rates (Adolph & Porter, 1993). A related theory, the 'environmental stress hypothesis', states that fewer species can tolerate harsh environments with low primary productivity (Fraser & Currie, 1996). Evapotranspiration (here actual evapotranspiration, AET) is a common measure of environmental stress in terrestrial environments, with lower AET equating to increased stress (Fraser & Currie, 1996; Costa *et al.*, 2007). Currie (1991) showed that reptile, amphibian, mammal and bird richness patterns in North America are all positively correlated with potential evapotranspiration. However, Schall & Pianka (1978) showed that non-scincid lizard richness is highest in deserts, and attributed this to the ability of poikilotherms to become inactive in times of stress. They suggested that thermoregulation of ectotherms is cheap in deserts, leading to high reptile species richness. Similarly, Pough (1980) argued that the physiological adaptations of lizards facilitate a low-energy lifestyle, allowing them to exploit various adaptive zones unavailable to homeotherms. Hawkins *et al.* (2005) suggested that the increase in aridity of western and central Australia since the Miocene may explain the current positive relationship between bird richness and AET. Some phylogenetic evidence from skinks, leaf-tailed geckos and pebble-mimic dragons supports the hypothesis that Miocene desertification drove diversification in Australian lizards (Rabosky *et al.*, 2007; Couper *et al.*, 2008; Shoo *et al.*, 2008). Although they are also ectothermic, amphibians are highly vulnerable to desiccation and are therefore expected to show a positive relationship with moisture variables (Semlitsch, 2003). Vermeij (1991) suggests that competition between major clades can lead to incongruent richness patterns between taxa. This suggestion is supported by Schall & Pianka (1978) and Milewski (1981; see also Morton & James, 1988), who propose competition between taxa as a possible determinant of species richness patterns in Australian lizards.

In this study we aim to map the species richness of Australian lizards and describe the patterns of range size and species turnover that underlie them. We aim to assess the congruence in species richness patterns of lizards and other vertebrate groups. We also investigate commonalities in the drivers of species richness in Australian vertebrates. We hypothesize that lizard richness will be positively correlated with temperature and negatively correlated with AET, as many species are highly adapted to harsh desert environments (Rabosky *et al.*, 2007). We hypothesize that the richness of birds and mammals, as homeotherms with high metabolic rates, will be positively correlated with AET along with amphibians which are highly vulnerable to desiccation. Thus we predict that the distribution of lizard richness in Australia will be incongruent with that of birds, mammals and amphibians, but congruent between different lizard clades.

METHODS

Species geographical range data

Using ArcGIS 9.1, we digitized vector range maps of all lizard species inhabiting mainland Australia (following the taxonomy of Uetz, 2006) compiling a database of 625 species range maps, approximately 95% of which are endemic to Australia (Uetz, 2006). Maps were taken primarily from Cogger (2000), supplemented from other sources (see Appendix S1 in Supporting Information). *Diplodactylus furcarcous*, *Gehyra kimberleyi*, *Lygosoma muelleri*, *Oreodeira gracilipes* and *Varanus timorensis* were excluded as they are believed to be junior synonyms of other taxa (Moody, 1988; Shea, 1991; Cogger, 2000). Point locality data were converted to polygons using a 1-km radius buffer. The polygon ranges were used to create a gridded species richness map on an equal-area Behrmann projection at a resolution of 96.49 km (approximately 1°). We excluded 155 coastal grid cells with less than 96% land cover (8909 km²) and all islands, including Tasmania, from the analysis in order to remove a confounding correlation between species richness and land area or insularity.

We therefore finally used the occurrences of 617 species within 751 grid cells to calculate species richness, β-diversity (using the modified Whittaker's index of Koleff *et al.*, 2003) and the distribution of median range size within grid cells for Australian lizards.

We also produced richness maps for Scincidae, Agamidae, Varanidae and Gekkonidae, treating the Gekkonidae + Pygopodidae clade (Han *et al.*, 2004) as a single family. Vector range map data for Australian mammals (Sechrest, 2003; Grenyer *et al.*, 2006), birds (Orme *et al.*, 2005) and amphibians (IUCN, 2004) were used to provide comparable richness surfaces on the same grid.

Congruence in species richness distributions

All statistical analyses were carried out using SAM (v.3.0, Rangel *et al.*, 2006). Visualization was performed in R v.2.8.0 (R Development Core Team, 2008), using the packages sp. (Pebesma & Bivand, 2005), maptools (Lewin-Koh *et al.*, 2008) and RColor-Brewer (Neuwirth, 2007). Initially, we used Pearson's correlations to explore the congruence in species richness surfaces amongst the four lizard clades and between all lizards,

mammals, amphibians and birds. We used Clifford *et al.*'s (1989) method for estimating effective degrees of freedom to correct the significance of the observed correlations in the face of demonstrable spatial autocorrelation.

We then used geographically weighted regressions (GWRs; see e.g. Fotheringham *et al.*, 2002; Foody, 2004; Cassemiro *et al.*, 2007) of lizard richness on the richness of the three other classes in turn to describe geographical variation in this relationship amongst taxa at local scales. Here, and in the environmental models described below, GWR was performed using a neighbourhood size of 10% of the dataset and a Gaussian distance-weighting function. We regressed all GWR surfaces on one another (lizard–mammal surface, lizard–bird surface, lizard–amphibian surface) in turn to quantitatively assess the similarity between the relationships of each higher-level taxon with lizards.

Environmental data

We estimated the relationship between species richness and four environmental variables: temperature, AET, mean elevation and elevation range (a common measure of habitat heterogeneity). Mean annual temperature data were averaged for the period 1961–90 at 10′ resolution interpolated from station means (New *et al.*, 2002). The mean values of annual AET are from the period 1950–90 at a 0.5° resolution (University of Delaware Global Climate Resource Pages, 2003). Elevation range (maximum minus minimum elevation within each grid cell, metres) and average elevation (metres) are taken from 30″ resolution data from the USGS (2003). Each variable was reprojected and area-weighted means were taken to reduce these finer resolution datasets to a single cell value in the Berhmann grid. The resulting environmental maps are shown in Appendix S2.

Modelling the environmental drivers of species richness

We used three parallel approaches to examine the relationship between the environmental variable set and the richness of the four vertebrate classes. First, we used spatially naïve multiple regression. Since autocorrelation in analyses of spatial data can lead to an increase in type-1 errors (Cliff & Ord, 1981), we used Moran's *I* (Appendix S3) and found strong evidence for spatial autocorrelation. We employed spatial eigenvector mapping (SEVM) with corrected Akaike information criterion (AIC_c)-weight model averaging to account for spatial covariation at multiple scales (Diniz-Filho & Bini, 2005; Dormann *et al.*, 2007). A truncation distance of 108.7 km, calculated in SAM, was used to create the spatial filters. Eigenvector filters were identified for each taxon that showed both a significant ($P < 0.05$) relationship with species richness and had sufficient ($r^2 > 0.02$) explanatory power. The filters successfully removed the spatial autocorrelation from the residuals of all models (not shown). These filters, together with the four environmental variables, formed the full model, and coefficients were calculated by AIC-weighted model averaging across all possible models. Finally, we used GWRs to visualize and account for regional differences in environmental models for all four lizard families and for all four vertebrate groups.

Testing for biotic interactions

We conducted limited *post hoc* testing for the stability of the environmental models of lizard richness to the introduction of richness terms for each of the other three vertebrate classes. In a GWR framework, we posit this allows an indication of regions where the richness of lizards interacts with that of another taxon, despite also reacting to environmental drivers. Areas of negative interaction between lizard richness and that of any other taxon, whilst holding the effects of the environment constant, are one possible signal of competition between groups structuring the richness of both (Milewski, 1981; Morton & James, 1988; Pianka, 1989; Vermeij, 1991). We ran three separate models, introducing birds, amphibians and mammals in turn, but did not examine higher-order interactions between other taxa and lizard richness.

RESULTS

Lizard species richness in continental Australia (Fig. 1a) varies between 27 and 94 species per cell (mean: 64 ± 12 SD). The main hotspot of lizard richness runs from central Australia west to the Hamersley Range and Pilbara coast. Subsidiary hotspots are found to the north of the Great Dividing Range around the Atherton Tableland on the east coast of Queensland, and in the Kimberley Plateau in northern Western Australia. Beta-diversity (Fig. 1b) is relatively low in the central to western hotspot of lizard species richness, and very low in the lowlands between the central deserts and the Great Dividing Range. Species turnover is high along the Great Dividing Range, and along the southern and western coasts. Lizard range sizes (Fig. 1c) are largest in the Great Australian Basin and in central-northern lowland areas, while the east coast and south-west corner are occupied by small-ranged species.

The geographical distribution of species richness within lizard families, although generally positive, shows low overall congruence (with the exception of Agamidae × Gekkonidae: $r = 0.616$, Table 1) with peaks of diversity in different locations (Fig. 2). Hotspots of richness for agamids and geckos are found, respectively, in central Australia and the highlands of Western Australia. Skinks are particularly species rich in central Australia and along the length of the east coast, while varanids show a relatively smooth latitudinal cline in species richness decreasing from Arnhem Land southward. Geographically weighted regression (Table 1b) confirms that, even at a local level, positive relationships are generally found between the species richness of lizard families.

Cross-taxon congruence

Lizards show a strikingly different distribution pattern from mammals, birds and amphibians in Australia. Mammal,
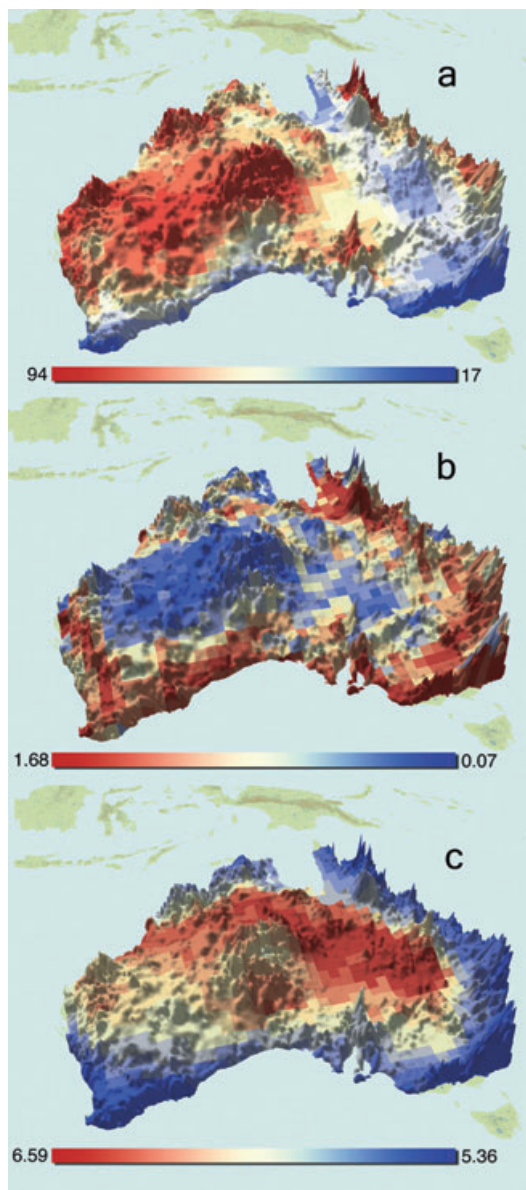
Figure 1 The geographic distribution of (a) lizard species richness (b) lizard β-diversity and (c) median range size in Australia on the equal area Behrmann projection grid draped over a topological surface at 10-arcmin resolution from http://www.ngdc.noaa.gov/mgg/global/global.html. Vertical extrusion is linear with elevation, colours are shaded in 20 equal-quantile bins (i.e. 5%-iles) from low (blue) to high (red). The base map is from the World Protected Areas Database GIS distribution.

Table 1 Congruence between lizard families corrected for spatial autocorrelation using (a) Clifford's method (Pearson's *r* above the diagonal, corrected *P*-values below the diagonal) and (b) median and inter-quartile slopes from geographically weighted regression.

(a)

Taxon	Agamidae	Gekkonidae	Scincidae	Varanidae
Agamidae	–	0.616	0.316	0.407
Gekkonidae	0.048	–	0.311	0.409
Scincidae	0.026	0.008	–	0.235
Varanidae	0.261	0.234	0.108	–

(b)

Taxon	Predictor	25%	Median	75%
Agamidae	Gekkonidae	0.127	0.359	0.566
Agamidae	Scincidae	0.093	0.167	0.221
Agamidae	Varanidae	−0.140	0.301	0.424
Gekkonidae	Scincidae	0.096	0.205	0.277
Gekkonidae	Varanidae	0.0002	0.339	1.054
Scincidae	Varanidae	0.299	0.579	0.762

See Appendix S5 for degrees of freedom and uncorrected *P*-values.

amphibian, mammal or bird species richness, all of which are significantly positively correlated with each other (Table 2a). However, the relationship between lizard richness and that of other vertebrates is clearly complex and dominated by local variation. GWR models of lizard species richness (Table 2b) show a range of responses: with mammals, the inter-quartile range of slopes is entirely positive, with birds this range is entirely negative, whilst with amphibians the inter-quartile range includes zero. Lizard richness is positively related to all other clades toward the Queensland coast, but in the rest of Australia these correlations are dominated by localized and taxon-specific positive and negative relationships (Fig. 3). All three GWR surfaces (lizard–mammal surface, lizard–bird surface, lizard–amphibian surface) were positively related with each other (all $P < 0.001$, d.f. = 749). The lizard–bird and lizard–amphibian GWR surfaces are highly and positively correlated ($r^2 = 0.744$), whereas the relationship between the lizard–mammal GWR surface and the other two-taxa GWR surfaces (lizard–bird GWR surface, lizard–amphibian GWR surface) is weaker ($r^2 = 0.248$ and $r^2 = 0.236$, respectively).

Environmental correlates of richness

The environmental models for all four vertebrate taxa are compared in Table 3, with both SEVM and GWR showing substantial improvements in explanatory power over simple ordinary least squares (OLS) models. The coefficients from these models are presented in Table 4. Elevation range was positively correlated with richness in all taxa. However, AET is consistently negatively related to lizard richness, but consistently positively related to richness in all other taxa. Lizard species richness

amphibian and bird species richness peaks on the east and northern coasts (Fig. 3), but the east coast shows generally low lizard richness. The Southwest Australia endemism hotspot identified by Myers *et al.* (2000) is also a richness hotspot of mammals, amphibians and, particularly, birds (Fig. 3) but relatively few lizard species occur there. In contrast, the Atherton Tableland in eastern Queensland is a richness hotspot for all four taxa.

Correcting for spatial autocorrelation, lizard species richness tends to be negatively, but not significantly, correlated with

Agamidae Richness

Scincidae Richness

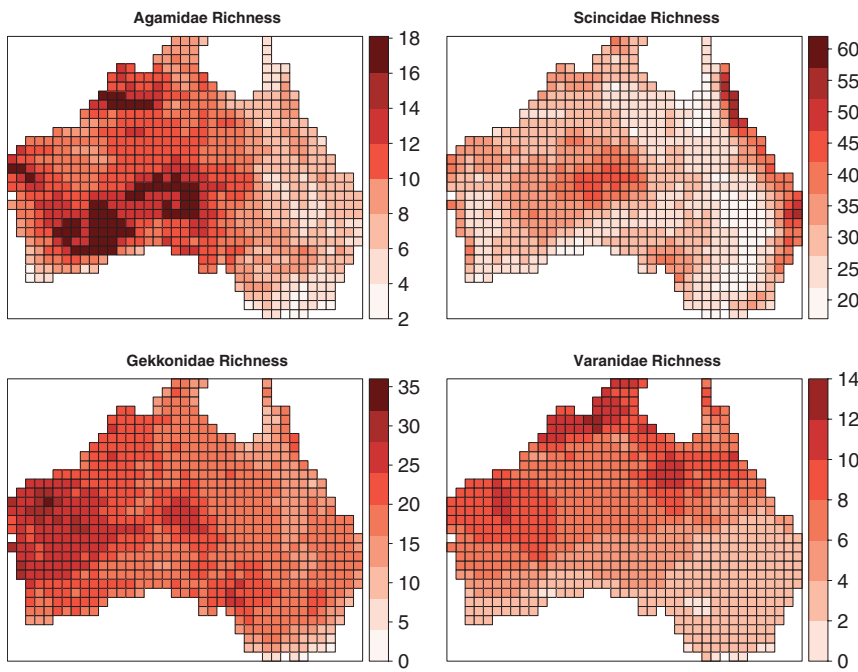**Gekkonidae Richness**

Varanidae Richness

Figure 2 Richness of Agamidae, Gekkonidae, Scincidae and Varanidae in Australia. Equal-area Behrmann projection. Correlations and geographically weighted regression (GWR) models of the congruence in these maps are shown in Table 1.
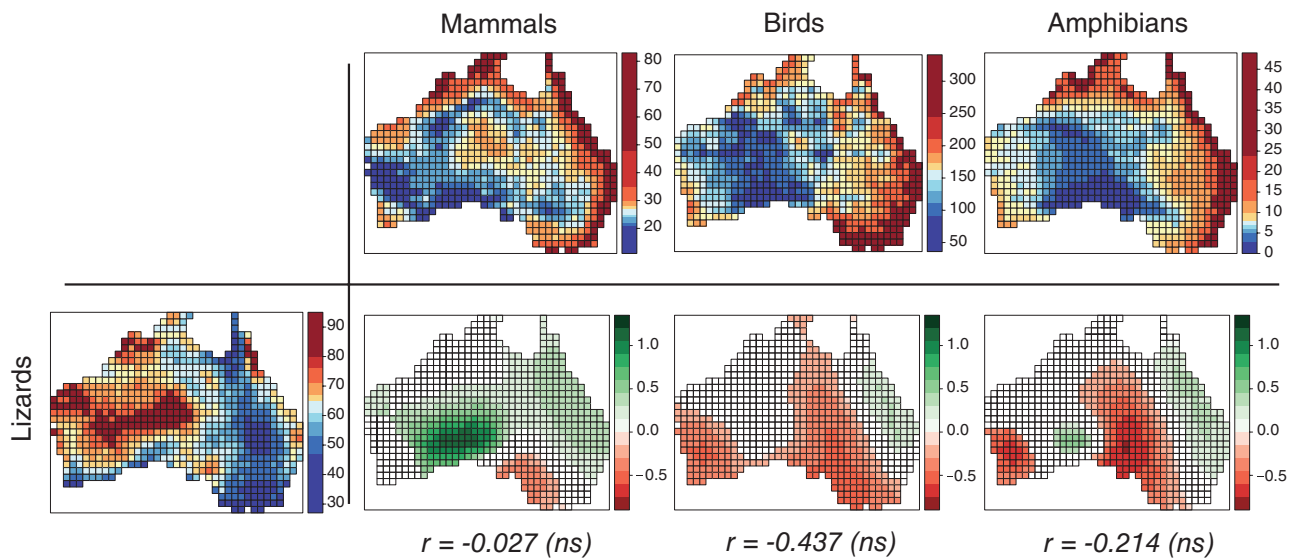
Mammals   Birds   Amphibians

Lizards

$r = -0.027$ (ns) $r = -0.437$ (ns) $r = -0.214$ (ns)

Figure 3 Richness of lizards (bottom left), mammals, birds and amphibians (top), and maps of the local geographically weighted standardized slopes of their relationships (bottom). White cells indicate non-significance of the local model at the focal cell ($\alpha = 0.05$). The Pearson correlation coefficient across the whole domain, with the accompanying Clifford-adjusted *P*-value, is given beneath each map for comparison. Correlations and geographically weighted regression (GWR) models of the congruence in these maps are shown in Table 2.

increases with temperature (although the Scincidae and Agamidae alone differ, Appendix S4) whilst bird species richness decreases with increasing temperature (Fig. 4). At a continental scale, amphibian species richness shows a negative relationship and mammalian species richness a positive relationship with temperature but both groups show substantial local variation. Species richness increases with mean elevation in lizards, decreases with it in birds and is not related to mean elevation in mammals and amphibians. Thus, it seems that while richness

increases with habitat diversity in all taxa, birds and amphibians are generally more diverse in cooler regions in Australia. The richness of birds, mammals and amphibians increases with increased water availability but lizard richness is highest in warm, dry regions.

The addition of the richness of any other vertebrate taxon did not qualitatively alter any of the environmental models of lizard richness, and the additional explanatory power of the resulting models is low (3–5%, Table 5). More strikingly, there is very little

Table 2 Cross-taxon congruence corrected for spatial autocorrelation using (a) Clifford's method (Pearson's *r* above the diagonal, corrected *P*-values below the diagonal with uncorrected *P*-values in brackets) and (b) median and inter-quartile slopes from geographically weighted regression. Clifford's corrected and uncorrected degrees of freedom are shown in (c).

(a)

Taxon	Lizards	Mammals	Birds	Amphibians
Lizards	–	−0.027	−0.437	−0.214
Mammals	0.915 (0.461)	–	0.653	0.856
Birds	0.176 (< 0.001)	0.004 (< 0.001)	–	0.754
Amphibians	0.455 (< 0.001)	< 0.001 (< 0.001)	0.003 (< 0.001)	–

(b)

Taxon	Predictor	25%	Median	75%
Lizards	Mammals	0.123	0.250	0.401
Lizards	Birds	−0.072	−0.031	−0.002
Lizards	Amphibians	−0.452	−0.088	0.131

(c)

Taxon	Lizards	Mammals	Birds	Amphibians	
Lizards	–	749	749	749	Uncorrected d.f.
Mammals	16.298	–	749	749	–
Birds	9.117	11.661	–	749	–
Amphibians	12.46	20.998	11.212	–	–
	Corrected d.f.				

Table 3 Model comparison between ordinary least squares (OLS) regression, spatial eigenvector filtering and geographically weighted regression.

	OLS	SEVM					GWR	
	r^2	No. of models	No. of filters	r^2	F		r^2	F
Lizards	0.513	4095	8	0.716	197.3		0.763	49.29
Birds	0.652	8191	9	0.766	351.5		0.796	33.98
Amphibians	0.757	65535	12	0.815	582.8		0.884	50.52
Mammals	0.733	65535	12	0.808	514.4		0.828	25.68

In each case, the adjusted r^2 is given and, for spatial eigenvector mapping (SEVM) and geographically weighted regression (GWR) models, an *F*-test of model improvement over OLS, all of which are significant ($P < 0.0001$). For SEVM models, the number of models averaged and the number of eigenvector filters is also shown. Four environmental parameters and an intercept are fitted in all models, hence the residual degrees of freedom are: OLS models, 746; GWR models (including 15.9 spatial degrees of freedom), 730.1; and for SEVM models the degrees of freedom are 746 minus the number of filters.

evidence for competitive structuring of vertebrate richness in Australia (Fig. 5). There are limited regions of locally negative relationships between lizards and both birds and amphibians. In no case are these local relationships significant, and they are set in a background of weakly positive or insignificant relationships between residual lizard richness and that of other taxa across most of Australia.

DISCUSSION

The richness pattern of Australian lizards is strikingly different from the generally congruent distributions of mammals, amphibians and birds. We reveal complex non-stationary rela-

tionships between lizard richness and that of mammals, birds and amphibians (Fig. 3), suggesting that different processes generate richness at different localities. Our findings differ from many of the published accounts of reptile richness drivers. For example, Schall & Pianka (1978) found that Australian total bird richness was not significantly correlated with lizard richness, whereas using the same non-spatially corrected statistical method we observe a significant negative relationship (Appendix S6b). There are a number of plausible reasons for this discrepancy. While we used the same main data source (Cogger's *Reptiles and amphibians of Australia*) the sixth edition we used has *c.* 60% more species, newly described since the first edition (1975) used by Schall and Pianka. Our analyses

Table 4 Model parameter estimates from ordinary least squares (OLS) regression, spatial eigenvector filtering and geographically weighted regression (GWR).

Predictor	OLS Coefficient	SEVM Coefficient	95% CI		GWR Coefficient	25%	75%
(a) Lizards							
Intercept	18.088*	33.099	28.67	37.52	38.12	30.66	48.08
Mean elevation	0.031*	0.009	0.004	0.01	0.02	0.01	0.03
Elevational range	0.010*	0.008	0.006	0.01	0.01	0.01	0.02
Mean AET	−0.026*	−0.016	−0.02	−0.01	−0.03	−0.04	−0.01
Mean temperature	2.028*	1.478	1.29	1.67	1.21	0.74	1.49
(b) Birds							
Intercept	254.993*	221.027	199.28	242.78	173.75	93.88	293.70
Mean elevation	−0.094*	−0.025	−0.04	−0.01	−0.09	−0.11	−0.05
Elevational range	0.047*	0.031	0.02	0.04	0.05	0.03	0.08
Mean AET	0.151*	0.126	0.11	0.14	0.15	0.10	0.20
Mean temperature	−6.354*	−5.102	−6.15	−4.05	−3.42	−7.36	−1.19
(c) Amphibians							
Intercept	4.327*	0.326	−2.27	2.93	−1.97	−7.8	4.68
Mean elevation	−0.002	0.003	0	0.01	−0.01	−0.01	0.002
Elevational range	0.006*	0.006	0.004	0.01	0.004	0.00	0.01
Mean AET	0.031*	0.028	0.026	0.03	0.03	0.02	0.03
Mean temperature	−0.322*	−0.162	−0.27	−0.06	−0.02	−0.25	0.36
(d) Mammals							
Intercept	10.864*	1.095	−2.31	4.5	8.74	2.22	25.14
Mean elevation	−0.003	0.003	0.00	0.01	−0.004	−0.01	0.00
Elevational range	0.016*	0.015	0.01	0.02	0.01	0.01	0.04
Mean AET	0.033*	0.038	0.036	0.04	0.03	0.02	0.04
Mean temperature	0.094	0.384	0.24	0.52	0.37	−0.42	0.57

AET, actual evapotranspiration.
Coefficients are given for each model. The significance of OLS estimates are shown using a *t*-test (*$P < 0.0001$); 95% confidence intervals (CI) from model averaging are shown for spatial eigenvector mapping (SEVM); and the inter-quartile range in local parameter estimates is shown for GWR. The numbers of filters used in the SEVM models are presented in Table 3.

are also at a finer resolution (10,000 vs. 57,600 km^2), and congruence has been shown to correlate strongly and positively with analytical spatial scale (Grenyer *et al.*, 2006). These factors, together with the non-stationarity we reveal in the correlates of richness and hence the possible dependence of richness patterns on different factors in different localities, may explain discrepancies between our works and other studies of lizard richness.

Lizard activity times and reproductive success are constrained by ambient temperature (Schall & Pianka, 1978; Adolph & Porter, 1993). We have shown that lizard richness is partly predicted by temperature in line with the 'available energy hypothesis' (Wright, 1983). Lizard richness generally decreases with increasing AET. Some high AET localities such as the northern Queensland coast are rich in lizard species. However, in the immediate neighbourhood of these localities, there are areas of high AET and low lizard richness such that both the general and local trends are negative (Fig. 4). The richness of other taxa increases with AET, providing evidence for the 'environmental stress' hypothesis. The peak in richness in dry conditions supports the hypothesis that lizard diversification is highest in hot,

arid environments (James & Shine, 2000; Hawkins *et al.*, 2003; Rabosky *et al.*, 2007). Richness of all taxa is positively related to elevation range, a common surrogate for habitat heterogeneity that may be associated with the number of habitats within a cell (Currie, 1991).

Phylogenetic affinities seem to affect species distribution. Pianka & Vitt (2003) illustrated how *Ctenotus* species are clustered around central Australia. Rabosky *et al.* (2007) likewise found that the increased aridification of Australia has catalysed the diversification of the species-rich *Ctenotus* and *Lerista*. We found that richness patterns between lizard families are not consistent across Australia, suggesting that phylogenetic relatedness partly explains lizard distribution. Further support for this is that lizard families are affected differently by the environmental variables (Table 1 and Appendix S6). Additional study using a dated phylogeny of Australian lizards could reveal the rates and the extent to which diversification generated distribution patterns.

James & Shine (2000) hypothesized that lizards which evolve in the large, climatically homogeneous, desert areas of Australia have large range sizes. Our measures of richness, β-diversity and
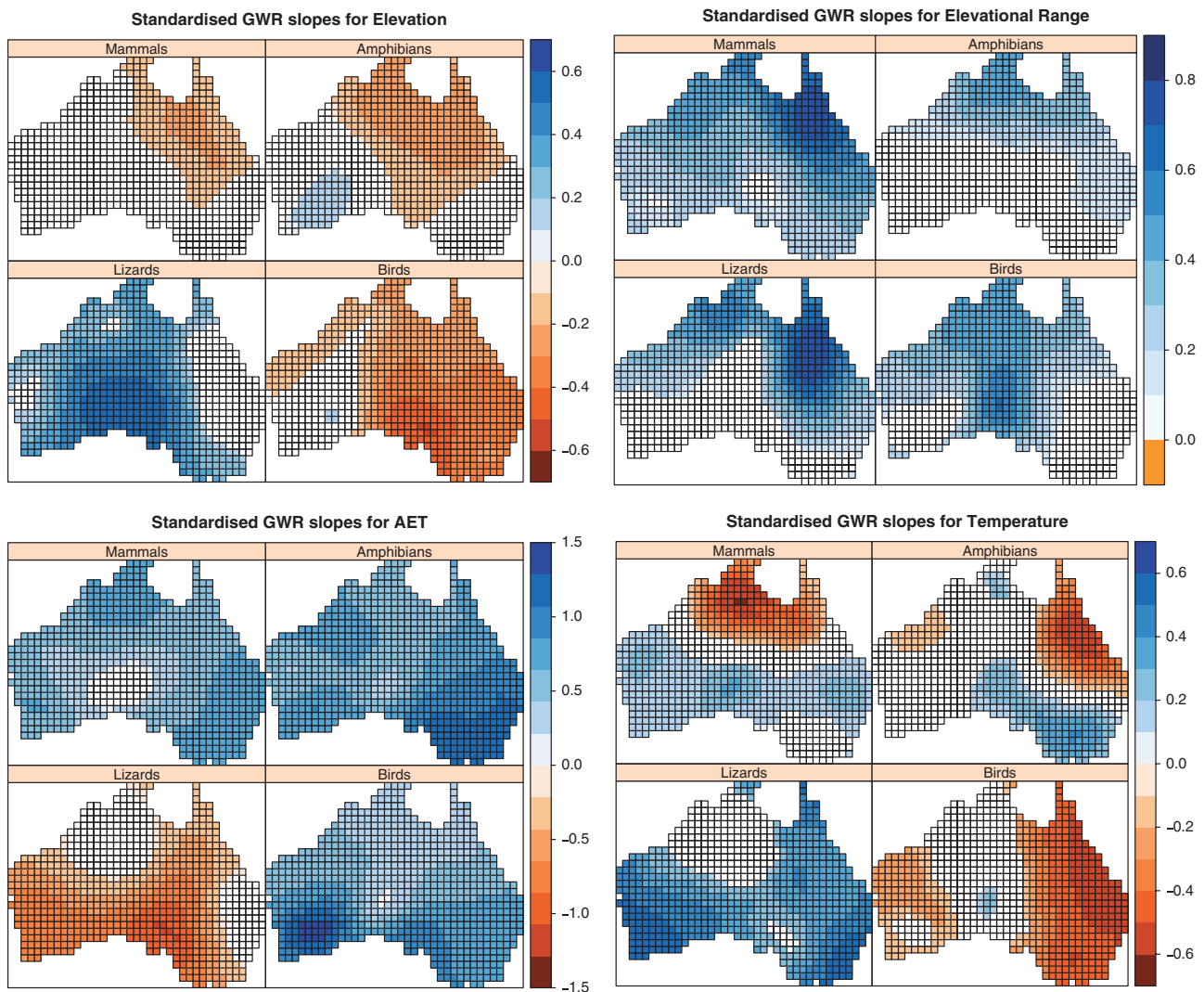
Figure 4 Maps of the component variation within the geographically weighted environmental regression models for all vertebrate classes. As above, white cells indicate non-significance of the local model at the focal cell (α = 0.05).

range size (Fig. 1), support this theory, with a diverse and relatively homogeneous lizard fauna dominating the deserts of western and central Australia. This diverse desert lizard fauna is further supplemented by a number of species of intermediate range size inhabiting the highlands of central Australia. The Great Australian Basin differs in having fewer, mostly large-ranged, species and, in contrast, the coast is generally dominated by a high turnover of small-ranged species. Interestingly, the low β-diversity and high α-diversity of Australian desert lizards contrast sharply with patterns seen in desert rodents in Australia and elsewhere (Kelt *et al.*, 1996).

It is important to consider the influence that environmental factors may have on shaping richness patterns. The incongruence between the richness of lizards and other vertebrate taxa can result from: different responses to environmental gradients; biotic interactions such as competition and predation (Schall & Pianka, 1978; Sweet & Pianka, 2007); or from different centres of diversification. We show that different taxa do respond differ-

ently to environmental variables. Milewski (1981) suggested that predation by and competition with mammals and birds influenced lizard species richness (see also Morton & James, 1988; Pianka, 1989). Controlling for the environmental variables, we find no evidence for a negative relationship between the species richness of lizards and other vertebrate taxa. While a negative correlation between the richness of taxa need not imply competition (Schall & Pianka, 1978; Gould & Calloway, 1980), we argue that a positive correlation provides some evidence against it. However, we do not rule out the effects of predation, which might actually be expected to result in a positive relationship between predator and prey richness. It has been argued that competition and predation pressures only operate at local scales (Whittaker *et al.*, 2001; but see Ricklefs, 2008); others suggest, however, that an evolutionary history of competition and predation may be important in shaping large-scale lizard distribution patterns (Milewski, 1981; Buckley & Jetz, 2007; Sweet & Pianka, 2007). Finally, we do not rule out the importance of
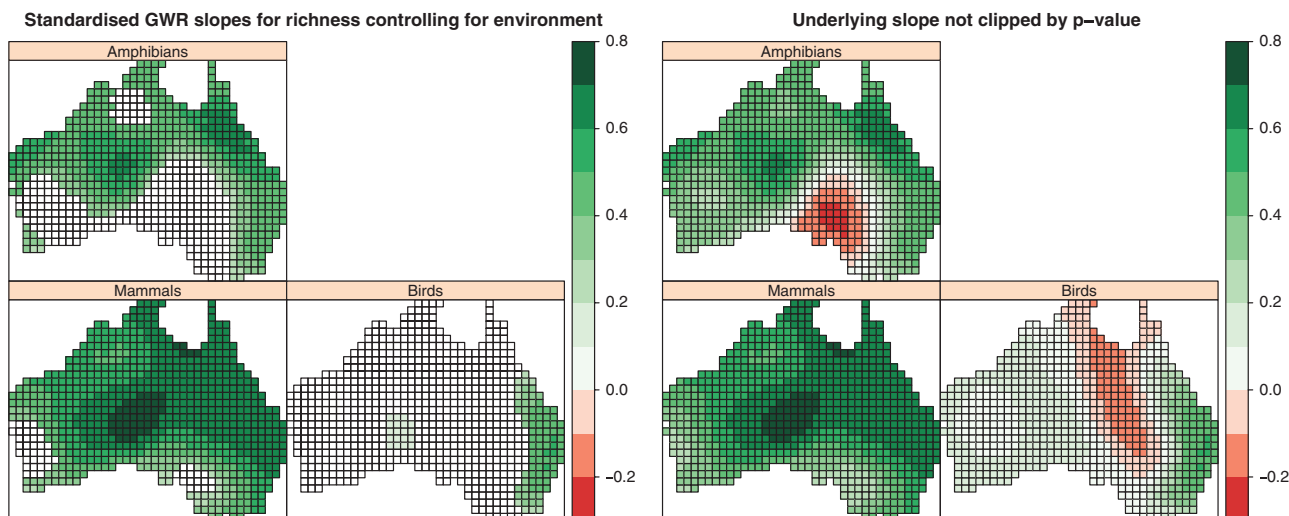
Standardised GWR slopes for richness controlling for environment   **Underlying slope not clipped by p-value**

Figure 5 The cross-taxon component of geographically weighted regressions of amphibian, bird and mammal richness on lizard richness, whilst controlling for environmental variables. Right, standardized slopes; Left, standardized slopes clipped by local significance (white cells indicate local α > 0.05).

Table 5 Environmental geographically weighted regression (GWR) models of lizard richness including species richness of other taxa.

Predictor	Coefficient	25%	75%
(a) Mammals (19.54 spatial d.f., r^2 = 0.82, F = 48.21)			
Intercept	32.94	21.41	40.81
Mean elevation	0.02	0.03	0.03
Elevational range	0.004	0.001	0.008
Mean AET	−0.04	−0.05	−0.03
Mean temperature	1.02	0.64	1.5
Mammalian richness	0.62	0.51	0.7
(b) Birds (19.37 spatial d.f., r^2 = 0.78, F = 45.42)			
Intercept	37.63	27.46	48.51
Mean elevation	0.02	0.02	0.03
Elevational range	0.01	0.01	0.02
Mean AET	−0.03	−0.04	−0.02
Mean temperature	1.22	0.71	1.7
Avian richness	0.02	0.002	0.03
(c) Amphibians (18.8 spatial d.f., r^2 = 0.80, F = 54.05)			
Intercept	38.63	30.43	47.42
Mean elevation	0.03	0.02	0.03
Elevational range	0.009	0.006	0.02
Mean AET	−0.04	−0.03	−0.03
Mean temperature	1.26	0.81	1.71
Amphibian richness	0.6	0.4	0.7

AET, actual evapotranspiration.
The median local coefficients are shown along with the inter-quartile range. Model adjusted r^2 values are shown, along with an *F*-test (all *P* < 0.0001) of model improvement over the ordinary least squares (OLS) models summarized in Table 3. Residual degrees of freedom are 745 minus the stated estimates of spatial degrees of freedom.

common areas of species radiations, such as those of bird and skink clades along the Australian east coast.

To conclude, richness patterns of mammals, birds and amphibians are highly congruent, while lizards follow a strikingly different pattern. This difference is caused by different responses to environmental gradients between the taxa but not by inter-taxon competition. We also strongly suggest that studies of variation in species richness examine and account for non-stationarity in environmental predictors of diversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Reference list of sources used to compile species distribution data.

Appendix S2 Gridded map of the mean elevation, elevation range, mean actual evapotranspiration (AET) and annual average temperature in Australia

Appendix S3 Moran's *I* correlogram showing spatial autocorrelation in lizard richness.

Appendix S4 Geographically weighted regression models of lizard family richness with the environmental variables.

Appendix S5 Results of lizard family congruence analysis.

Appendix S6 Results of vertebrate taxa congruence analysis.

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BIOSKETCH

Gary Powney is starting a PhD in evolutionary history as a determinant of species range dynamics. His main academic interests include species range dynamics, biodiversity and macroecology with particular emphasis on combining these subject areas to help inform conservation efforts of a wide range of taxa.

Editor: José Alexandre F. Diniz-Filho

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Appendix S2. Gridded map of the Mean Elevation (m), Elevation range (m), Mean AET (mm) and annual average temperature (^{o}C) in Australia.
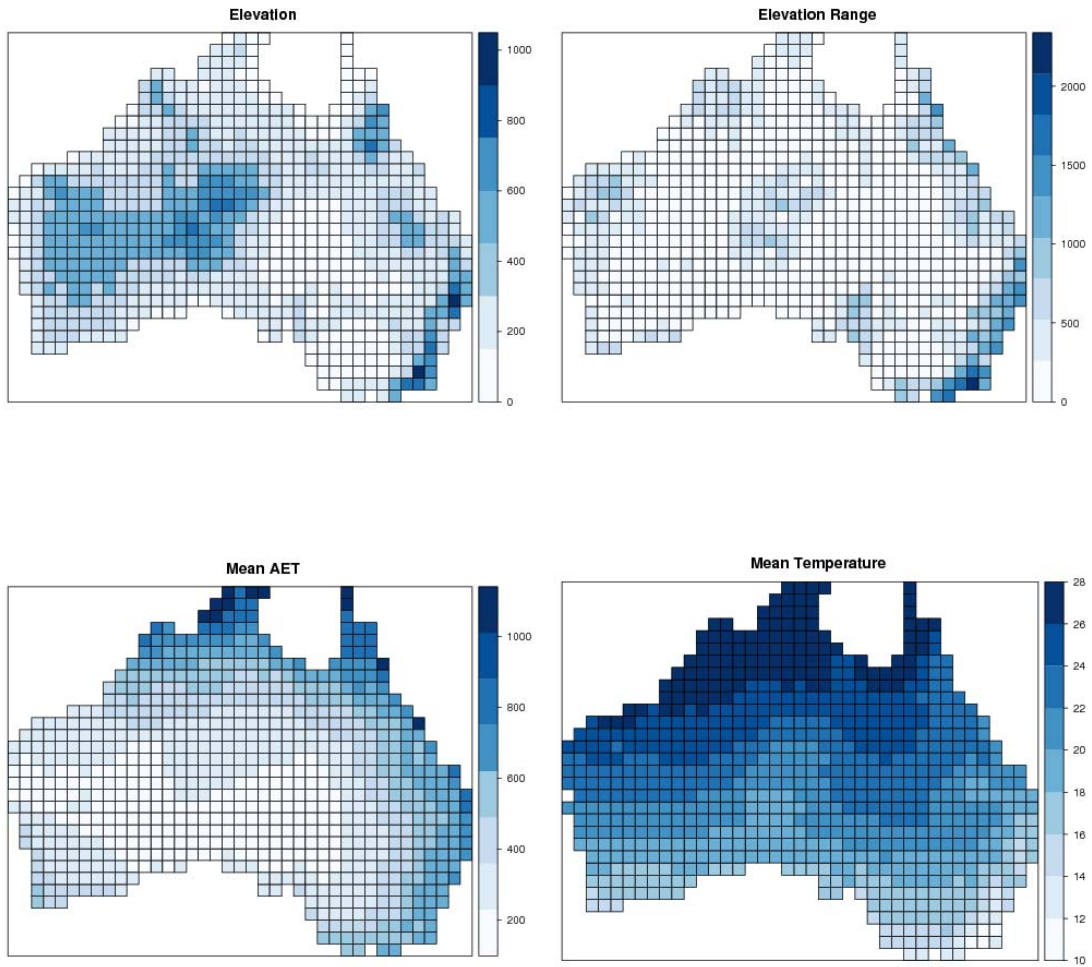
Appendix S3. Moran's I correlogram showing spatial autocorrelation in lizard richness. At short distances (0-1200km) there was positive spatial autocorrelation, while at long distances (1600-3500km) there was negative autocorrelation. Similar Moran's I correlograms were found when examining autocorrelation the richness patterns of lizard families.
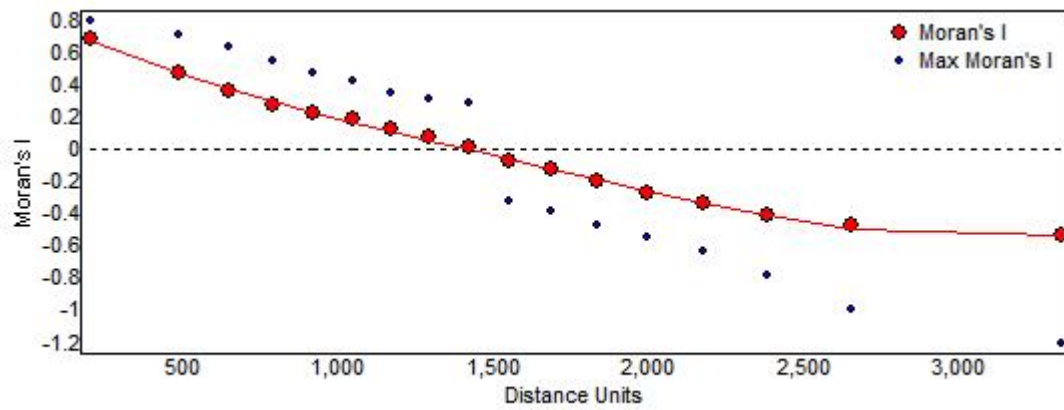
Appendix S4. Geographically-weighted regression models of lizard family richness with the environmental variables. GWR with Gaussian decay function adaptive bandwidth estimation by AICc amongst using 10-25% of cells as the neighbourhood.

Taxon	Predictor	Median B	Quartile lower	upper
Agamidae				
	Intercept	11.35608	4.6359	17.45
	Mean Elevation	0.00358	0.0016	0.006
	Elevational Range	0.00099	-0.0005	0.003
	Mean AET	-0.01466	-0.0092	-0.005
	Mean Temperature	0.08878	-0.1375	0.269
	Model df	20.858 (est) - 10% neighbours		
	of which spatial df	15.858 (est)		
	Error df	730.14		
	Adjusted R^2	0.8		
	F	71.38088	F vs. OLS	
Gekkonidae				
	Intercept	12.35518	8.2133	17.71
	Mean Elevation	0.00525	0.0041	0.007
	Elevational Range	0.00279	3E-05	0.004
	Mean AET	-0.00814	-0.0108	-0.006
	Mean Temperature	0.38697	0.1055	0.559
	Model df	20.858 (est) - 10% neighbours		
	of which spatial df	15.858 (est)		
	Error df	730.14		
	Adjusted R^2	0.765		
	F (p)	59.48319	F vs. OLS	
Scincidae				
	Intercept	21.99156	16.857	29.52
	Mean Elevation	0.00897	0.0022	0.015
	Elevational Range	0.00791	0.0056	0.012
	Mean AET	-0.0064	-0.0127	0.001
	Mean Temperature	0.23239	-0.2221	0.524
	Model df	20.858 (est) - 10% neighbours		
	of which spatial df	15.858 (est)		
	Error df	730.14		
	Adjusted R^2	0.602		
	F (p)	32.48514	F vs. OLS	
Varanidae				
	Intercept	-7.84675	-10.055	-4.746
	Mean Elevation	0.00412	0.0021	0.005
	Elevational Range	0.00111	0.0001	0.002
	Mean AET	-0.00158	-0.0028	-6E-05
	Mean Temperature	0.59542	0.3997	0.669
	Model df	20.858 (est) - 10% neighbours		
	of which spatial df	15.858 (est)		

Error df	730.14	
Adjusted R^2	0.858	
F	40.93694	F vs. OLS

Appendix S5. Results of lizard family congruence analysis, (a) is the Clifford's corrected and uncorrected degrees of freedom. While (b) is a comparison of corrected and uncorrected p-values using Clifford's method for accounting for spatial autocorrelation.

a)

Taxon	Agamidae	Gekkonidae	Scincidae	Varanidae	
Agamidae		749	749	749	*Uncorrected df*
Gekkonidae	8.651		749	749	
Scincidae	47.373	68.977		749	
Varanidae	7.433	8.215	46.042		
	Corrected df				

b)

Taxon	Agamidae	Gekkonidae	Scincidae	Varanidae	
Agamidae		<.001	<.001	<.001	*Uncorrected P*
Gekkonidae	0.048		<.001	<.001	
Scincidae	0.026	0.008		<.001	
Varanidae	0.261	0.234	0.108		
	Corrected p				