

# Climatic and evolutionary factors shaping geographical gradients of species richness in *Anolis* lizards

JULIAN A. VELASCO<sup>1\*</sup>, FABRICIO VILLALOBOS<sup>2,3</sup>, JOSE A. F. DINIZ-FILHO<sup>3</sup>,  
ADAM C. ALGAR<sup>4</sup>, OSCAR FLORES-VILLELA<sup>1</sup>, GUNTHER KÖHLER<sup>5</sup>, STEVEN POE<sup>6</sup>  
and ENRIQUE MARTINEZ-MEYER<sup>7</sup>

<sup>1</sup>Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Distrito Federal, Mexico 04510

<sup>2</sup>Red de Biología Evolutiva, Instituto de Ecología, A.C., Carretera Antigua a Coatepec 351, El Haya, 91070, Xalapa, Veracruz, Mexico

<sup>3</sup>Departamento de Ecologia, ICB, Universidade Federal de Goiás, Brasil

<sup>4</sup>School of Geography, University of Nottingham, Sir Clive Granger Building, Nottingham NG7 2RD, UK

<sup>5</sup>Senckenberg Forschungsinstitut und Naturmuseum, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

<sup>6</sup>Department of Biology, University of New Mexico, Albuquerque, NM, USA

<sup>7</sup>Instituto de Biología, Universidad Nacional Autónoma de México, DF and Centro del Cambio Global y la Sustentabilidad, AC, Villahermosa, Mexico

Received 5 October 2017; revised 4 December 2017; accepted for publication 5 December 2017

Understanding the climatic and historical factors shaping species richness is a major goal of ecology and biogeography. Consensus on how climate affects species richness is still lacking, but four potential and non-exclusive explanations have emerged: water–energy, where diversity is determined by precipitation and/or temperature; seasonality, where diversity is determined by seasonal variation in climate; heterogeneity, where diversity is determined by spatial variability in climate; and historical climatic stability, where diversity is determined by changes in climate through evolutionary time. Climate–richness relationships are also mediated by historical processes, such as phylogenetic niche conservatism and lineage diversification across regions. We evaluated the effect of climate on species richness gradients of *Anolis* lizards and tested the role of phylogenetic niche conservatism and regional diversification in the origin and maintenance of climate–richness relationships. Climate had a strong nonstationary relationship with species richness, with strong shared effects among several climate axes. Regional differences in climate–richness relationships suggest different assembly processes between regions. However, we did not find evidence for a role of evolutionary factors, such as phylogenetic niche conservatism or regional diversification, underlying these relationships. We suggest that evolutionary processes affecting climate–richness relationships in *Anolis* were probably obscured by high dispersal rates between regions.

**ADDITIONAL KEYWORDS:** climate – macroecology – macroevolution – phylogenetic niche conservatism – regional diversification.

## INTRODUCTION

Understanding the causes of variation in species richness across regions and clades is a fundamental goal of ecology (Wiens & Donoghue, 2004; Gotelli *et al.*, 2009).

The strong relationship between species richness and climate across continents, globally and through time suggests a causal effect of climate on species richness at multiple spatial scales (Currie *et al.*, 2004; Vázquez-Rivera & Currie, 2015), as well as a historical and evolutionary fingerprint on these patterns and relationships (Mittelbach *et al.*, 2007; Wiens *et al.*, 2010). The existence of both geographical and evolutionary

\*Corresponding author: E-mail: [jvelas@gmail.com](mailto:jvelas@gmail.com)

aspects implies that understanding how climate shapes richness gradients would be advanced by pursuing two components: first, studies must identify the climatic variables that predict species richness; and second, phylogenetic patterns linking climate and richness must be explored.

Numerous hypotheses have been proposed to explain climatic and phylogenetic components to species richness. For climatic predictors of species richness, the following four main hypotheses have been considered (Evans, Warren & Gaston, 2005; Field *et al.*, 2009; Tello & Stevens, 2010; Gouveia *et al.*, 2013): water–energy, where diversity is hypothesized to be determined by overall precipitation and/or temperature levels in a region; seasonality, where diversity is hypothesized to be determined by seasonal variation in climate; heterogeneity, where diversity is hypothesized to be determined by spatial variability in climate; and historical climatic stability, where diversity is hypothesized to be determined by changes in climate over millennia. For evolutionary effects (Mittelbach *et al.*, 2007), phylogenetic niche conservatism (PNC; Wiens & Donoghue, 2004; Wiens *et al.*, 2010) and geographical variation in diversification rates (Weir & Schluter, 2007; Rolland *et al.*, 2014) are currently the most prominent hypotheses to explain contemporary diversity gradients and their relationship with climate.

Several potential mechanisms might underlie these climate-based hypotheses. The water–energy hypothesis (Evans *et al.*, 2005) proposes that areas with higher productivity are hypothesized to support more individuals and therefore more species (Rohde, 1992; Srivastava & Lawton, 1998; Currie *et al.*, 2004; Allen & Gillooly, 2006; Table 1). The seasonality hypothesis proposes that within-year climate variation generates

larger demographic population fluctuations, thereby increasing species extinction for species with small population sizes (Janzen, 1967). Species occurring in seasonal areas usually have larger niches and range sizes that can reduce extinction risk, but at the same time the chance of speciation will also be reduced (Janzen, 1967; Stevens, 1989; Hurlbert & Haskell, 2003; Dalby *et al.*, 2014; Table 1). The heterogeneity hypothesis proposes that habitat complexity increases the *in situ* speciation rate probability through population fragmentation owing to the presence of more dispersal barriers that lead to reductions in gene flow (Kisel *et al.*, 2011; Table 1). Finally, the historical climatic stability hypothesis posits that regions with stable climates accumulate more species over time than regions with less stable climates (Jansson, 2003; Sandel *et al.*, 2011). Alternatively, strong climatic oscillations might influence net diversification rates by increasing extinction rates for species with low vagility or by reducing speciation rates for species with high vagility that can maintain gene flow while they track niches through space (Kisel *et al.*, 2011; Rakotoarinivo *et al.*, 2013; Table 1). Some of these climatically based hypotheses have been tested extensively (e.g. water–energy hypothesis; Field, O’Brien & Whittaker, 2005; Whittaker, 2007; Kreft & Jetz, 2007), whereas others (e.g. historical climatic stability hypothesis) have received less attention (but see Fine & Ree, 2006; Jetz & Fine, 2012), and their contribution to geographical species richness gradients remains largely unknown.

Conceptual and methodological advances have enabled the rigorous integration of a phylogenetic perspective in ecological studies (Jablonski, Roy & Valentine, 2006; Hernandez *et al.*, 2013), allowing tests of the role

**Table 1.** Global expected relationships between each hypothesis examined and species richness

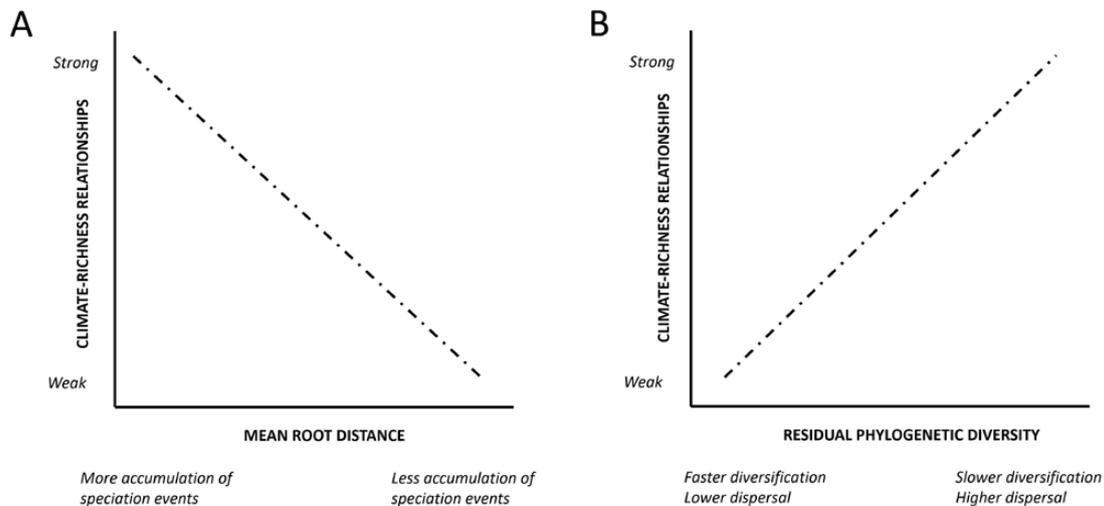
Hypothesis	Stationary expected relationships	Nonstationary predictions	References
Water–energy	Positive	Regions with a higher productivity (e.g. Chocó, Andes) have more species than regions with lower productivity (e.g. northern Mexico)	Hawkins <i>et al.</i> (2003); Evans <i>et al.</i> (2005)
Seasonality	Negative	Regions with lower seasonality in climate have more species (e.g. Chocó, Andes) than regions with higher seasonality (e.g. northern Mexico)	Klopfer (1959); Gouveia <i>et al.</i> (2013)
Heterogeneity	Positive	Regions with more complexity (e.g. mountains in Central America and the Andes) have more species than regions with lower complexity (e.g. Amazonian lowlands and northern Mexico)	Rahbek & Graves (2001); Tello & Stevens (2010)
Historical climatic stability	Negative	Regions with less climatic variability through time (e.g. Chocó, Amazonia) support more species than sites that are more variable (e.g. northern Mexico, Amazonia)	Araújo <i>et al.</i> (2008); Gouveia <i>et al.</i> (2013); Rakotoarinivo <i>et al.</i> (2013); Svenning <i>et al.</i> (2015)

of evolutionary processes in generating present-day geographical patterns of biodiversity (Morlon, 2014). Indeed, species richness gradients and the resulting climate–richness relationships are considered by some to result, at least in part, from evolutionary processes such as PNC (Wiens & Donoghue, 2004; Wiens & Graham, 2005) and variation in diversification rates across regions (Rolland *et al.*, 2014; Alves, Diniz-Filho & Villalobos, 2017; Schluter & Pennel, 2017). Evidence favouring the importance of PNC includes the confinement of older clades to their region of origin and the resulting accumulation of species in these regions (Jablonski *et al.*, 2006; Hawkins *et al.*, 2007; Romdal, Araújo & Rahbek, 2013). Under the PNC hypothesis, stronger climate–richness relationships are expected for older clades relative to younger clades (Hawkins *et al.*, 2012; Romdal *et al.*, 2013). In contrast to PNC, evidence favouring the importance of diversification rates in generating current geographical patterns comes from studies where spatial variation in speciation and extinction rates were found to generate nonrandom spatial gradients in species richness, independent of present-day conditions (Roy & Goldberg, 2007; Weir & Schluter, 2007; Rolland *et al.*, 2014).

Lizards of the genus *Anolis* provide an excellent system for examining the relative influence of climatic factors and historical processes on geographical patterns of diversity. *Anolis* lizards are likely to have originated in South America during the Palaeocene,

dispersed to Caribbean islands, and then back-colonized the mainland (Poe *et al.*, 2017). These lizards exhibit exceptional diversification in both the Caribbean (~180 species) and mainland regions (~220 species). Some studies suggest that assembly of anole faunas proceeds differently in insular and mainland regions (Algar & Losos, 2011; Stuart, Losos & Algar, 2012). Although previous studies have examined species richness patterns of *Anolis* across the mainland and islands, the roles of climate and evolutionary aspects in shaping overall geographical gradients of anoles remain unknown.

Here, we test the role of climatic and evolutionary factors in shaping geographical gradients of species richness in *Anolis* lizards at a broad spatial scale. First, we test whether climate is correlated with *Anolis* species richness while assuming that each climatic hypothesis contributes equally to the observed geographical gradients without nonstationary effects (Table 1). Second, we test whether the resulting climate–richness relationships are explained either by PNC or by regional diversification (Fig. 1). If PNC has played a role, we expect that regional assemblages in regions where lineages originated and accumulated more species will have a strong climatic signature. Conversely, if PNC has not played a role, we expect that these regional assemblages will exhibit a weak climatic signature (Fig. 1). Likewise, if regional diversification has shaped climate–richness relationships we expect that regional assemblages with



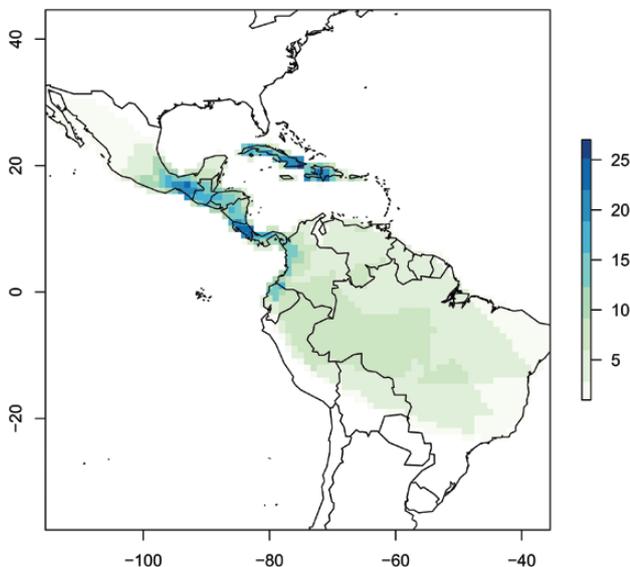
**Figure 1.** Nonmutually exclusive scenarios about the role of phylogenetic niche conservatism (PNC) and regional diversification mediating climate–richness relationships in *Anolis* lizards. If PNC drives climate–richness relationships, we expect that regions with more accumulation of lineages and speciation events will have a strong climate–richness relationship. In contrast, if PNC does not drive climate–richness relationships, we expect that regions with less accumulation of speciation events will have a weak climate–richness relationship. If regional diversification drives climate–richness relationships, we expect that regions with faster *in situ* diversification and low dispersal events will have a weak climate–richness relationship. In contrast, if regional diversification does not drive climate–richness relationships, we expect that regions with slow *in situ* diversification and high dispersal events will have a strong climate–richness relationship.

higher *in situ* diversification and few dispersal events will exhibit weak climate–richness relationships. Alternatively, if regional diversification has not played a role, we expect that regional assemblages with less *in situ* diversification and high dispersal will show a strong climate–richness relationship (Fig. 1).

## MATERIAL AND METHODS

### SPECIES DATA AND GEOGRAPHICAL GRADIENT OF SPECIES RICHNESS

We compiled occurrence records for 362 species of *Anolis* (from a total of 379 species; Poe *et al.*, 2017) from the Greater Antilles islands and Central and South America, i.e. throughout the range of *Anolis* (Velasco *et al.*, 2016). For each species with at least three records (296 species), we generated range maps representing the extent of occurrence using minimum convex polygons and removing nonland areas afterwards. The remaining 66 species with one or two records were added to the grid cell encompassing these records. We calculated the number of *Anolis* species by overlaying a grid of  $1^\circ \times 1^\circ$  (~12 544 km<sup>2</sup> cell size) covering the whole region where native anoles occur and counted the number of range maps overlapping each grid cell. We excluded coastal cells with < 25% of land surface to reduce potential area effects (Budic, Didenko & Dormann, 2016). Our grid system resulted in 1379 cells across the region (Fig. 2), from which a presence–absence matrix of 362 species by 1379 cells was generated for further analyses. We excluded Lesser Antillean species and species from other small Caribbean and



**Figure 2.** Geographical patterns of observed *Anolis* species richness.

Pacific islands (33 species) from our analyses for several reasons. First, these islands are occupied by only one or two species (Powell & Henderson, 2012), and island size is much smaller than the grid cell size used here; thus, there is no potential for high species richness. Second, there is evidence that anole assemblages on these islands result almost exclusively from dispersal from other sources (Poe *et al.*, 2017), and here we focus on areas where potential *in situ* speciation could have occurred (i.e. the Greater Antilles and mainland; Losos & Schluter, 2000). As we are interested in testing the role of climate on diversity gradients at regional scales, the exclusion of these small areas with low diversity will not be likely to affect our general results. In addition, we evaluated whether a mid-domain effect (Colwell & Less, 2000) can explain the observed pattern of species richness (Supporting information, Fig S1).

### ENVIRONMENTAL VARIABLES

To test the role of current (water–energy, seasonality and heterogeneity) and past (historical climatic variability) environmental characteristics on anole species richness, we used the following variables, grouped by climatic hypothesis: (1) water–energy (WE), annual mean temperature and annual precipitation; (2) seasonality (SEAS), temperature seasonality, temperature annual range and precipitation seasonality; (3) heterogeneity (HET), standard deviation of elevation, standard deviation of annual mean temperature and standard deviation of annual precipitation; and (4) historical climatic stability (HCS), climatic anomalies from temperature and precipitation, calculated as differences in current and past variables [e.g. we calculated anomaly in annual mean temperature (AMT) simply by subtracting current AMT from past AMT; Supporting information, Table S1]. We generated climatic anomalies for the Last Inter-Glacial period (LIG; ~130 000 years before present; Otto-Bliesner *et al.*, 2006) and the Last Glacial Maximum (LGM; ~21 000 years before present; Model for Interdisciplinary Research on Climate (MIROC) model; Hasumi & Emori, 2004] separately as measures of climate stability. Climatic variables were obtained from WorldClim (Hijmans *et al.*, 2005). We evaluated the collinearity of each predictor among hypotheses using Pearson’s correlation coefficient (Supporting information, Table S2). Given that collinearity among variables was low (Supporting information, Table S2), we feel confident in treating them independently.

### PHYLOGENETIC NICHE CONSERVATISM AND REGIONAL DIVERSIFICATION

We used a Bayesian phylogenetic estimation for all *Anolis* species (Poe *et al.*, 2017). We used the tree

with the minimal symmetric distance from the 50% majority rule consensus tree (MRC tree of Poe *et al.*, 2017). We calculated the mean root distance (MRD; Kerr & Currie, 1999; Hawkins *et al.*, 2006, 2007) and phylogenetic diversity (PD; Faith, 1992) of each grid cell in the domain using this tree. The MRD provides information about the relative levels of diversification among lineages and provides similar results to other recently developed metrics and approaches (e.g. Jetz *et al.*, 2012; Kennedy *et al.*, 2014; Pinto-Ledezma *et al.*, 2017). We classified species with lower root distance values and species with higher root distance values, operationalized as 30% (= close) and 70% (= far) percentiles of root distance values (Hawkins *et al.*, 2006; Pinto-Ledezma *et al.*, 2017).

Phylogenetic diversity is a metric that represents the summed branch lengths of a phylogenetic tree connecting species in an area (Faith, 1992; Vellend *et al.*, 2011). Given that PD is strongly correlated with species richness, we used residuals from a PD–species richness regression (with species richness as the independent variable) as a measure of regional diversification (residual PD; Davies & Buckley, 2011). The residual PD evaluates whether past evolutionary events (i.e. speciation, extinction and dispersal) have contributed to regional species assemblages (Davies & Buckley, 2011; Fritz & Rahbek, 2012), allowing us to differentiate regions with higher diversification rates and few dispersal events (i.e. low residual PD values) from regions with lower diversification rates and several dispersal events (i.e. high residual PD values; Davies & Buckley, 2012; Fritz & Rahbek, 2012). We mapped these metrics to visualize geographical patterns of regional diversification and faunal phylogenetic structure in *Anolis* (Supporting information, Fig. S1).

#### GLOBAL AND LOCAL CLIMATE–RICHNESS RELATIONSHIPS

We analysed a series of ordinary least squares (OLS) models and geographically weighted regression (GWR) models to evaluate the relationship between species richness and environmental variables (current and past climatic anomalies) for each time period (LGM and LIG). We used the GWR model to evaluate the nonstationary effect of environmental variables on species richness. We implemented a variance partitioning approach (Legendre & Legendre, 2012) with the aim of decomposing the effect of each predictor separately (i.e. independent effects) and in combination (i.e. shared effects) to predict geographical richness patterns (Fig. 2; see Supporting information, Table S1). We selected the model with the highest explanatory power using the Bayesian information criterion (BIC; Schwarz, 1978; Quinn & Keough, 2002). We evaluated whether parameters ( $R^2$ , slopes and residuals) from full

GWR models for LGM and LIG varied between regions using a spatial ANOVA. Statistical analyses were performed in Spatial Analysis in Macroecology (SAM) (Rangel, Diniz-Filho & Bini, 2010) and in the R environment.

#### EVOLUTIONARY DRIVERS OF CLIMATE–RICHNESS RELATIONSHIPS IN *ANOLIS* LIZARDS

We performed correlations between evolutionary metrics (MRD and residual PD) and local regression parameters ( $R^2$  and slopes) for GWR models to evaluate the effect of phylogenetic niche conservatism and regional diversification as drivers of climate–richness relationships for *Anolis* lizards. First, we tested whether phylogenetic niche conservatism (MRD) drives the climate–richness relationship (Fig. 1). Second, we tested whether regional diversification (residual PD) drives the climate–richness relationship (Fig. 1). We corrected the number of effective degrees of freedom in the presence of spatial autocorrelation in the correlation of GWR parameters with phylogenetic metrics using Dutilleul’s method (Dutilleul, 1993). We analysed these correlations for the Greater Antilles and the mainland separately. Furthermore, we analysed whether a null model eliminating the phylogenetic structure by randomizing species positions across the tree was able to explain the correlation between phylogenetic metrics and GWR parameters from full models. This null model describes a pattern where PNC and regional diversification do not have any impact on the resulting climate–richness relationships. We compared observed correlation values with expected correlation values without considering any phylogenetic effect and considered statistical significance if observed values fell outside the 95% confidence interval of the corresponding frequency distribution. All data used here were archived in Figshare at [https://figshare.com/articles/\\_/5669950](https://figshare.com/articles/_/5669950).

## RESULTS

#### GEOGRAPHICAL PATTERNS OF *ANOLIS* SPECIES RICHNESS

High species richness of *Anolis* occurs across the Greater Antilles (Cuba and Hispaniola), almost all of Central America (from the Isthmus of Tehuantepec in Mexico to Panama) and the Pacific slopes of the northern Andes (northwestern Colombia and Ecuador; Fig. 2). Lower *Anolis* richness was found in northern Mexico, the Caribbean coast of Colombia and Venezuela, and the Brazilian coast (Fig. 2). Geographical patterns of species with low root distance values showed higher richness in the Andes region, lower Central America and the Greater Antilles (Supporting information, Fig. S2).

In contrast, geographical patterns of species with high root distance values showed higher species richness in Middle America, Chocó, and the Andes region in South America (Supporting information, Fig. S2). Mapping residual PD values showed that the mid-portion of Middle America and the Andean region exhibited high values (Supporting information, Fig. S2). Conversely, low relative PD values were found mainly in the Greater Antilles, the Pacific coast of Mexico, Costa Rica, and Guajira province in Colombia (Supporting information, Fig. S2). We did not find evidence supporting a mid-domain effect generating the observed pattern of species richness (see Supporting information, Fig. S1).

#### CLIMATE–RICHNESS RELATIONSHIPS IN *ANOLIS* LIZARDS

The GWR models exhibited higher global  $R^2$  values than the OLS models (Table 2; Supporting information, Fig. S3). In addition, spatial nonstationarity effects of predictors on species richness were evident, with great geographical variation in regression coefficients across the Greater Antilles and the mainland (Supporting information, Fig. S4). The global expectations for regression coefficient values for each climate hypothesis were not fulfilled (Table 1; Supporting information, Fig. S4).

Full models for LGM and LIG periods exhibited the highest explanatory power (lower BIC scores and higher  $R^2$  values) relative to models for each hypothesis tested (i.e. WE, SEAS, HET and HCS;  $R^2$  values from full models increased, on average, from 0.642 to 0.785). The  $R^2$  values for models with each hypothesis (water–energy, seasonality, heterogeneity and historical climatic stability) were relatively similar for LGM and LIG (Table 3).

The  $R^2$  values for full models for LGM and LIG exhibited similar geographical patterns (Fig. 3). Higher  $R^2$  values were found in most parts of Mexico and eastern

Brazil, whereas low values were found in most parts of South America and the Greater Antilles (Fig. 3). The variance partitioning analysis revealed that the unique contributions of each hypothesis (i.e. independent effects of each hypothesis) were relatively minor and exhibited a strong nonstationary effect (Fig. 3; Table 3).

The signature of past climates, mainly from the LIG period, was strong on species richness patterns (Table 2; Fig. 3). For the LIG period, unique contributions of historical climatic stability were higher in Middle American highlands, the Chocó region and Western Amazonia (Fig. 3). Shared effects between two or more predictors exhibited higher contributions than unique models, particularly for effects that included past climatic anomalies (Table 3). Mapping of shared contributions indicated nonstationarity (Supporting information, Figs S5 and S6). Shared effects of water–energy and heterogeneity with historical climatic stability for the LIG period revealed higher contributions in some regions with high species richness (e.g. Central America; see Supporting information, Fig. S6).

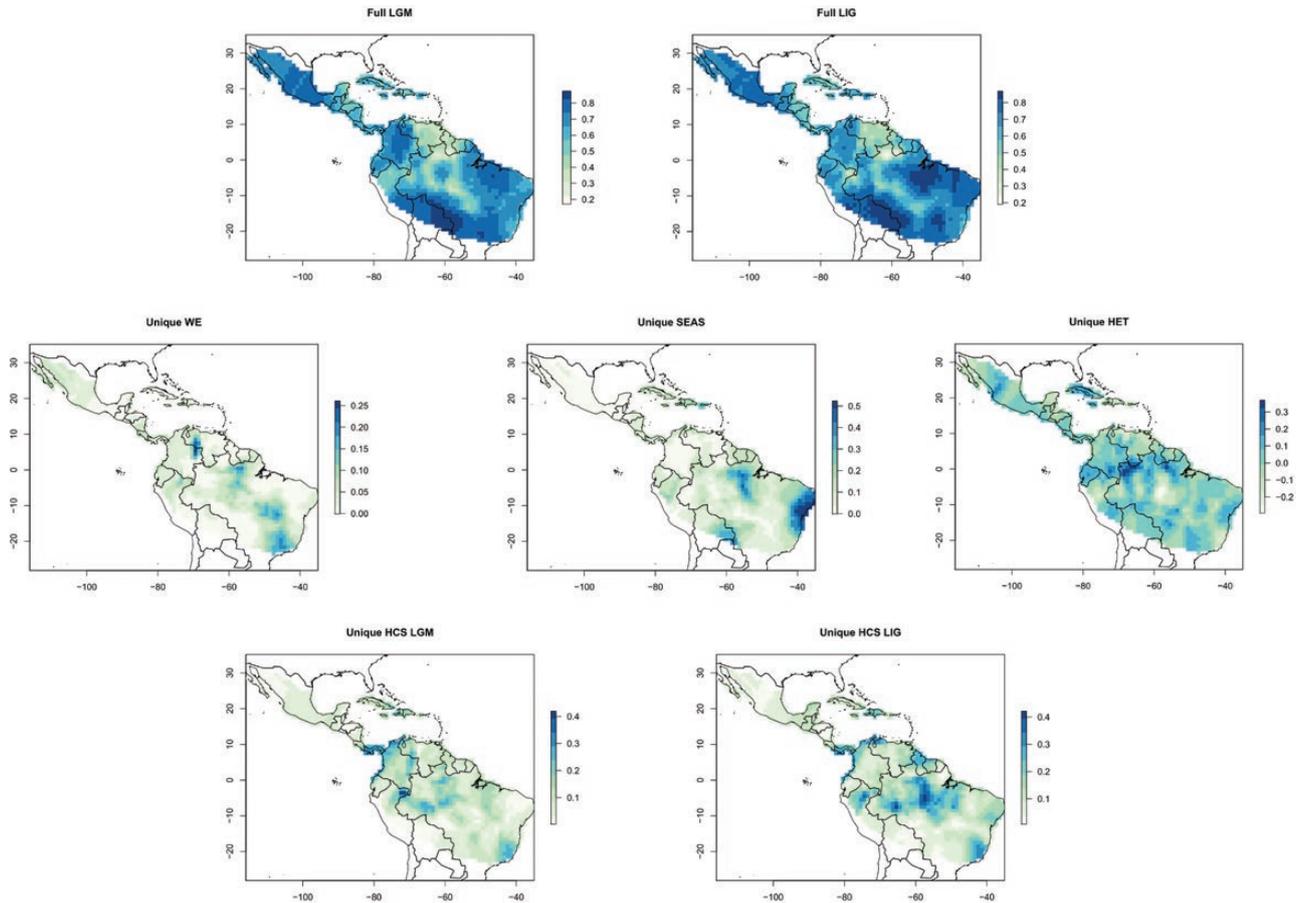
Strong differences between local regression parameters were found between the Greater Antilles and the mainland region (Table 4). We found lower local  $R^2$  values for the Greater Antilles relative to mainland areas (Supporting information, Fig. S7). Although local slopes also differed between regions, the nature of regional differences was dependent on the period examined (Table 4). For the LIG period, higher slopes were found for the Greater Antilles relative to mainland areas, but the opposite was found for the LGM period (Supporting information, Fig. S8).

Geographical patterns of the residuals from full and single models for both time periods were very similar (Fig. 4). High residuals were consistently found in the central portion of Middle America, corresponding to the Mexican and Guatemalan highlands and the Talamancan highlands in Costa Rica and Panama, and the Greater Antilles (Fig. 4).

**Table 2.** Bayesian model selection for full models and single hypothesis models (water–energy, seasonality, heterogeneity and historical climatic stability)

Model	GWR			OLS		
	$R^2$	BIC	$\Delta$ BIC	$R^2$	BIC	$\Delta$ BIC
Full LGM	0.780	2997.0	62.7	0.305	3866.2	410.4
Full LIG	0.789	2934.3	0.0	0.488	3455.8	0.0
WE	0.656	3021.1	86.8	0.140	4083.1	627.3
SEAS	0.609	3234.2	299.9	0.075	4186.0	730.3
HET	0.647	3115.4	181.1	0.213	3970.7	514.9
HCS LGM	0.648	3051.3	117.0	0.075	4198.9	743.1
HCS LIG	0.652	3151.0	216.7	0.243	3929.8	474.0

BIC, Bayesian information criterion;  $\Delta$ BIC, change in Bayesian information criterion; GWR, geographical weighted regression; HET, heterogeneity; HSC, historical climatic stability; LGM, Last Glacial Maximum (~21 000 years before present); LIG, Last Inter-Glacial period (~121 000 years before present); OLS, ordinary least squares;  $R^2$ , coefficient of determination; SEAS, seasonality; WE, water–energy.



**Figure 3.** Geographical patterns of full and unique contributions of each hypothesis explaining observed *Anolis* species richness gradients for the full models for the Last Glacial Maximum (LGM) and Last Inter-Glacial (LIG) periods. Unique HCS LGM, unique historical climatic stability for LGM; Unique HCS LIG, unique historical climatic stability for LIG; Unique HET, unique heterogeneity; Unique SEAS, unique seasonality; Unique WE, unique water–energy. See main text for details of variables analysed for each hypothesis.

#### EVOLUTIONARY DRIVERS OF CLIMATE–RICHNESS RELATIONSHIPS

We did not find a correlation between either MRD values or residual PD and GWR parameters ( $R^2$  and slopes, respectively; Table 5; Supporting information, Fig. S9). We also did not find a correlation when the Greater Antilles and the mainland were analysed separately (Supporting information, Fig. S10). Observed correlation values were well predicted by a null model simulating the absence of a role of phylogenetic niche conservatism and regional diversification on the resulting climate–richness relationships (Table 5; Supporting information, Fig. S11).

#### DISCUSSION

We present evidence for a strong control of past and current climate on geographical species richness gradients in *Anolis* lizards. When the effects of single and

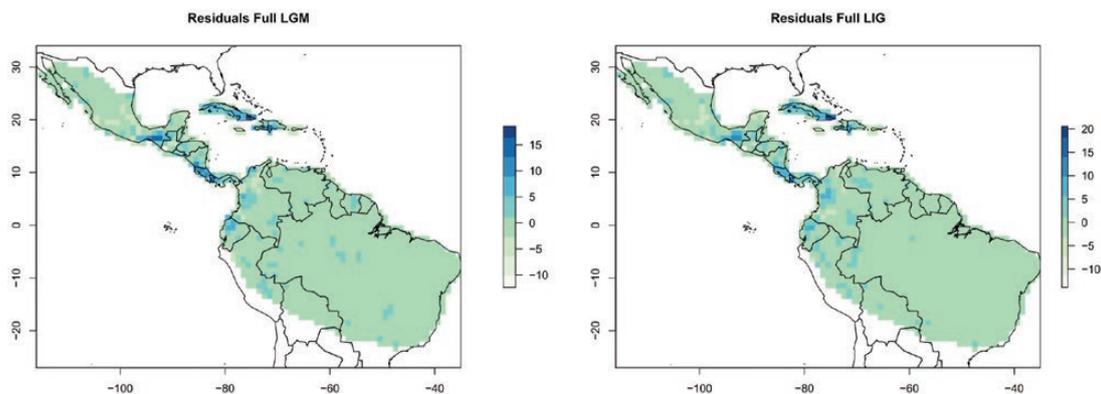
shared predictors were disentangled, we found that multiple environmental hypotheses act synergistically to explain the observed geographical gradient of species richness in *Anolis*. Although some researchers have suggested that different mechanisms drive species richness gradients independently (Currie, 1991; Field *et al.*, 2009), we found evidence for a complementary effect of these hypotheses on shaping anole species richness at regional scales (Tello & Stevens, 2010; Gouveia *et al.*, 2013). Moreover, pure effects of past climatic anomalies had a slightly larger impact than other predictors (Table 3). This result contrasts with other studies, in which palaeoclimate has played a strong role in species richness gradients (Rakotoarinivo *et al.*, 2013).

The signature of past climates from the LIG period on anole species richness was relatively higher than for the LGM (Table 3). This result suggests that cold temperatures from 21 000 years before present had

**Table 3.** Partial regression coefficients ( $R^2$ ) for pure and shared (denoted by s) contributions of the climatic hypothesis from geographical weighted regression models explaining observed *Anolis* species richness gradients for the Last Glacial Maximum and Last Inter-Glacial periods

Pure and shared effects	Last Glacial Maximum	Last Inter-Glacial
Pure WE	0.010	0.021
Pure SEAS	0.027	0.030
Pure HET	-0.054	0.023
Pure HCS	0.065	0.074
sWE + SEAS	0.004	-0.005
sSEAS + HET	0.054	-0.023
sWE + HET	0.092	0.048
sWE + HCS	0.013	0.002
sSEAS + HCS	0.004	0.001
sHET + HCS	0.075	-0.002
sWE + SEAS + HCS	0.010	0.019
sWE + SEAS + HET	-0.037	0.043
sSEAS + HET + HCS	-0.047	0.030
sWE + HET + HCS	-0.030	0.014
sWE + SEAS + HET + HCS	0.594	0.514

Negative partial  $R^2$  values are attributable to the opposite signal effects between predictors. HCS, historical climatic stability hypothesis; HET, heterogeneity hypothesis; SEAS, seasonality hypothesis; WE, water–energy hypothesis.



**Figure 4.** Geographical patterns of residuals of *Anolis* richness–climate relationships for the full models of the Last Glacial Maximum (LGM) and Last Inter-Glacial (LIG) periods.

a low impact on species ranges, at least on the mainland and Greater Antilles (but see Campbell-Staton, Edwards & Lobos, 2016; Campbell-Staton *et al.*, 2017). Furthermore, we found that climatic anomalies from the LIG period (~121 000 years before present) had a stronger effect in Middle America and the Greater Antilles than in South America. This result contrasts with some recent studies showing that adaptation to winter temperatures has played a role in the expansion of the northern limits in *Anolis carolinensis* (Campbell-Staton *et al.*, 2016, 2017). An evaluation of the individualistic responses of species ranges to the Quaternary climatic oscillations will be necessary to gain an understanding of the role of past climate on resulting species richness patterns.

Some macroecological studies have provided evidence that climate–richness relationships are stationary through space (Jetz, Rahbek & Lichstein, 2005). Our results show a strong nonstationary effect of multiple hypotheses on the species richness gradient in *Anolis* lizards. The nonstationary pattern was also evident in the unique and shared effects of each environmental hypothesis (Supporting information, Figs S5 and S6). This nonstationary pattern can be explained by differences in diversification histories of the main clades in the *Anolis* radiation (e.g. Dactyloa and Draconura clades; Poe *et al.*, 2017). For instance, the Dactyloa clade originated and diversified extensively in South America (67 species), with relative less diversification in Central America (seven

**Table 4.** Comparison of local parameters ( $R^2$  and slopes) from geographical weighted regression models between regions using a spatial ANOVA

Parameter	Model	Log likelihood	P-value
Local $R^2$ values	Full model LGM	2320.0	< 0.001
	Full model LIG	2404.3	< 0.001
	WE model	1994.2	< 0.001
	SEAS model	2097.2	0.157
	HET model	2151.6	< 0.001
	HCS LGM	2139.0	< 0.001
	HCS LIG	2118.4	0.745
Local slope value	Full model LGM	-3842.4	0.002
	Full model LIG	-3523.1	< 0.001
	WE model	-3248.3	< 0.001
	SEAS model	-2747.2	< 0.001
	HET model	-799.7	< 0.001
	HCS LGM	-2705.8	< 0.001
	HCS LIG	-2473.7	0.252

HCS, historical climatic stability hypothesis; HET, heterogeneity hypothesis; SEAS, seasonality hypothesis; WE, water–energy hypothesis.

**Table 5.** Pearson correlations between evolutionary metrics (mean root distance and residual phylogenetic diversity) and local parameters of richness–climate relationships for the Last Glacial Maximum and Last Inter-Glacial periods

	Observed $r$	P-value
MRD vs. local $R^2$ values, full model LGM	0.080	< 0.001
MRD vs. local $R^2$ values, full model LIG	0.119	< 0.001
MRD vs. local slopes, full model LGM	0.054	< 0.001
MRD vs. local slopes, full model LIG	-0.157	< 0.001
Residual PD vs. local residuals, full model LGM	-0.169	< 0.001
Residual PD vs. local residuals, full model LIG	-0.160	< 0.001

P-values are the probability that observed values of  $r$  from correlations between evolutionary metrics and geographical weighted regression parameters are higher than the null model average simulating the absence of phylogenetic structure and regional diversification effect on the resulting climate–richness relationships (1000 randomizations; see main text for details).

LGM, Last Glacial Maximum; LIG, Last Inter-Glacial; MRD, mean root distance; residual PD, residual phylogenetic diversity.

species). In contrast, the Draconura clade radiated extensively across the mainland (i.e. in Middle America and South America; [Poe et al., 2017](#)), occupying a large portion of the available climate space there ([Velasco et al., 2016](#)). These evolutionary differences are likely to have contributed to the contrasting species richness patterns in each clade. It is clear that a combination of historical biogeographical and lineage diversification

approaches will be necessary to clarify how the diversification dynamics have impacted the assemblage of anole species in both mainland regions.

Although speciation, extinction and dispersal have begun to be considered as processes that drive climate–richness relationships ([Ricklefs, 2006](#); [Kozak & Wiens, 2012](#); [Qian et al., 2015](#); [Schluter & Pennell, 2017](#)), we did not find evidence for a clear role of these processes in the climate–richness relationships of *Anolis* lizards. Neither phylogenetic niche conservatism nor regional diversification metrics were correlated with local regression parameters that capture climate–richness relationships. In addition, our results were not different from the null model describing a lack of phylogenetic structure and random diversification across the region. It is possible that the effect of evolutionary factors driving climate–richness relationships might leave a signature on taxa encompassing broad-scale climatic gradients (e.g. temperate vs. tropical regions; [Buckley et al., 2010](#); [Stevens, 2011](#); [Hawkins et al., 2012](#)) that is not evident within the range of *Anolis*.

The ability of the phylogenetic metrics used to capture recurrent dispersal movements across the region might also be a limitation of our work. [Poe et al. \(2017\)](#) inferred multiple dispersal events in *Anolis* lizards between continental regions, including several biotic exchanges between Middle America and South America. High dispersal rates between regions can obscure the evolutionary signature on the resulting climate–richness relationships because standard phylogenetic metrics do not capture the region of origin of a lineage, nor from where a lineage dispersed to a given region ([Roy & Goldberg, 2007](#)). A solution to this potential pitfall is to estimate speciation, extinction

and dispersal rates explicitly between regions (or grid cells; Rolland *et al.*, 2014; Pinto-Ledezma *et al.*, 2017) and how these processes are affected by climate. For instance, spatially explicit pattern-oriented simulations (Rahbek *et al.*, 2007; Rangel, Diniz-Filho & Colwell, 2007) might help to reveal the role of these processes in shaping climate–richness relationships in anoles.

Finally, our results support the idea that assembly processes driven by climate differ among insular and mainland regions in *Anolis* lizards. Previous research has provided evidence that oceanic islands promoted unique assembly processes in *Anolis* lizards (Stuart *et al.*, 2012). We find evidence of a weak climate signature on the insular anole assemblage, in contrast to the mainland assemblages. It is likely that other factors, including competitive interactions and dispersal limitations, played a role in shaping these species richness patterns, as documented in the Hispaniolan *Anolis* (Algar *et al.*, 2013). In fact, it is well established that Greater Antillean anole diversification has occurred as a response to adaptive specialization to microhabitat (Losos & Thorpe, 2004; Losos, 2009). It is still unknown whether a similar process played a substantial role in the evolution of mainland *Anolis*.

#### ACKNOWLEDGEMENTS

J.A.V. thanks the Posgrado de Ciencias Biológicas (PCB) programme of the Universidad Nacional Autónoma de México (UNAM), and the Consejo Nacional de Ciencia y Tecnología (Conacyt) for the graduate studies scholarship. J.A.V. is supported by a postdoctoral fellowship from Dirección General de Asuntos del Personal Académico (DGAPA) at Facultad de Ciencias of the UNAM. F.V. was supported by a Young Talents grant from the Science without Borders programme (Brazil) and Instituto de Ecología, A.C. Mexico. Work by J.A.F.D.-F. has been continuously supported by a Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) productivity fellowship and grants, and is now developed in the context of National Institutes for Science and Technology (INCT) in Ecology, Evolution and Biodiversity Conservation, supported by Ministério da Ciência, Tecnologia, Inovações e Comunicações/Conselho Nacional de Desenvolvimento Científico e Tecnológico (MCTIC/CNPq) (proc. 465610/2014–5) and Fundação de Amparo à Pesquisa do Estado de Goiás (FAPEG). We thank Michael Borregaard and two anonymous reviewers for their helpful comments. We thank L. Ochoa-Ochoa for her help with databases for Mexican anoles. J.A.V. and E.M.-M. conceived the study; J.A.V., F.V., J.A.F.D.-F. and A.C.A. designed methodology; J.A.V., A.C.A., O.F.-V., G.K. and S.P. collected the data; and

J.A.V. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

#### REFERENCES

- Algar AC, & Losos JB. 2011.** Evolutionary assembly of island faunas reverses the classic island–mainland richness difference in *Anolis* lizards. *Journal of Biogeography* **38**: 1125–1137.
- Algar AC, Mahler DL, Glor RE, Losos JB. 2013.** Niche incumbency, dispersal limitation and climate shape geographical distributions in a species-rich island adaptive radiation. *Global Ecology and Biogeography* **22**: 391–402.
- Allen AP, Gillooly JF. 2006.** Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. *Ecology Letters* **9**: 947–954.
- Alves DMCC, Diniz-Filho JAF, Villalobos F. 2017.** Geographical diversification and the effect of model and data inadequacies: the bat diversity gradient as a case study. *Biological Journal of the Linnean Society* **121**: 894–906.
- Araújo MB, Nogués-Bravo D, Diniz-Filho JAF, Haywood AM, Valdes PJ, Rahbek C. 2008.** Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography* **31**: 8–15.
- Buckley LB, Davies TJ, Ackerly DD, Kraft NJB, Harrison SP, Anacker BL, Cornell HB, Damschen EI, Grytnes JA, Hawkins BA, McCain CM, Stephens PR, Wiens JJ. 2010.** Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proceedings of the Royal Society B: Biological Sciences* **277**: 2131–2138.
- Budic L, Didenko G, Dormann CF. 2016.** Squares of different sizes: effect of geographical projection on model parameter estimates in species distribution modeling. *Ecology and Evolution* **6**: 202–211.
- Campbell-Staton SC, Cheviron ZA, Rochette, N, Catchen, J, Losos JB, Edwards SV. 2017.** Winter storms drive rapid phenotypic, regulatory, and genomic shifts in the green anole lizard. *Science (New York, N.Y.)* **357**: 495–498.
- Campbell-Staton SC, Edwards SV, Losos JB. 2016.** Climate-mediated adaptation after mainland colonization of an ancestrally subtropical island lizard, *Anolis carolinensis*. *Journal of Evolutionary Biology* **29**: 2168–2180.
- Colwell RK, Lees DC. 2000.** The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution* **15**: 70–76.
- Currie DJ. 1991.** Energy and large-scale patterns of animal- and plant-species richness. *The American Naturalist* **137**: 27–49.
- Currie DJ, Mittelbach GG, Cornell HV, Field, R, Guegan JF, Hawkins BA, Kaufman DM, Kerr JT, Oberdorff, T, O'Brien, E, Turner JRG. 2004.** Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters* **7**: 1121–1134.
- Dalby, L, McGill BJ, Fox AD, Svenning JC. 2014.** Seasonality drives global-scale diversity patterns in waterfowl (Anseriformes) via temporal niche exploitation. *Global Ecology and Biogeography* **23**, 550–562.

- Davies TJ, Buckley LB. 2011.** Phylogenetic diversity as a window into the evolutionary and biogeographic histories of present-day richness gradients for mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**: 2414–2425.
- Davies TJ, Buckley LB. 2012.** Exploring the phylogenetic history of mammal species richness. *Global Ecology and Biogeography* **21**: 1096–1105.
- Dutilleul, P. 1993.** Modifying the *t* test for assessing the correlation between two spatial processes. *Biometrics* **49**: 305–314.
- Evans KL, Warren PH, Gaston KJ. 2005.** Species–energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews of the Cambridge Philosophical Society* **80**: 1–25.
- Faith DP. 1992.** Conservation evaluation and phylogenetic diversity. *Biological Conservation* **61**: 1–10.
- Field R, Hawkins BA, Cornell HV, Currie DJ, Diniz-Filho JAF, Guégan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff, T, O'Brien EM, Turner JRG. 2009.** Spatial species–richness gradients across scales: a meta-analysis. *Journal of Biogeography* **36**: 132–147.
- Field R, O'Brien E, Whittaker, R. 2005.** Global models for predicting woody plant richness from climate: development and evaluation. *Ecology* **86**: 2263–2277.
- Fine PV, Ree RH. 2006.** Evidence for a time-integrated species–area effect on the latitudinal gradient in tree diversity. *The American Naturalist* **168**: 796–804.
- Fritz SA, Rahbek, C. 2012.** Global patterns of amphibian phylogenetic diversity. *Journal of Biogeography* **39**: 1373–1382.
- Gotelli NJ, Anderson MJ, Arita HT, Chao A, Colwell RK, Connolly SR, Currie DJ, Dunn RR, Graves GR, Green JL, Grytnes JA, Jiang YH, Jetz W, Lyons SK, McCain CM, Magurran AE, Rahbek C, Rangel TFLVB, Soberón J, Webb CO, Willig MR. 2009.** Patterns and causes of species richness: a general simulation model for macroecology. *Ecology Letters* **12**: 873–886.
- Gouveia SF, Hortal, J, Cassemiro FAS, Rangel TFLVB, Diniz-Filho JAF. 2013.** Nonstationary effects of productivity, seasonality, and historical climate changes on global amphibian diversity. *Ecography* **36**: 104–113.
- Hasumi, H, Emori, S. 2004.** *K-1 coupled GCM (MIROC) description*. Tokyo: Center for Climate System Research.
- Hawkins BA, Field R, Cornell HV, Currie DJ, Guégan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG. 2003.** Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **84**: 3105–3117.
- Hawkins BA, Diniz-Filho JAF, Jaramillo CA, Soeller SA. 2006.** Post-eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. *Journal of Biogeography* **33**: 770–780.
- Hawkins BA, Diniz-Filho JAF, Jaramillo CA, Soeller SA. 2007.** Climate, niche conservatism, and the global bird diversity gradient. *The American Naturalist* **170**(Suppl 2): S16–S27.
- Hawkins BA, McCain CM, Davies TJ, Buckley LB, Anacker BL, Cornell HV, Damschen EI, Grytnes, J-A, Harrison S, Holt RD, Kraft NJB, Stephens PR. 2012.** Different evolutionary histories underlie congruent species richness gradients of birds and mammals. *Journal of Biogeography* **39**: 825–841.
- Hernandez, C, Rodríguez-Serrano, E Avaria-Llautureo, J, Inostroza-Michael, O, Morales-Pallero, B, Boric-Bargetto, D, Canales-Aguirre CB, Marquet PA, Meade A. 2013.** Using phylogenetic information and the comparative method to evaluate hypotheses in macroecology. *Methods in Ecology and Evolution* **4**: 401–415.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005.** Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**: 1965–1978.
- Hurlbert AH, Haskell JP. 2003.** The effect of energy and seasonality on avian species richness and community composition. *The American Naturalist* **161**: 83–97.
- Jablonski D, Roy K, Valentine JW. 2006.** Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science (New York, N.Y.)* **314**: 102–106.
- Jansson, R. 2003.** Global patterns in endemism explained by past climatic change. *Proceedings of the Royal Society B: Biological Sciences* **270**: 583–590.
- Janzen, D. 1967.** Why mountain passes are higher in the tropics. *The American Naturalist* **101**: 233–249.
- Jetz W, Fine PV. 2012.** Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. *PLoS Biology* **10**: e1001292.
- Jetz W, Rahbek C. 2002.** Geographic range size and determinants of avian species richness. *Science (New York, N.Y.)* **297**: 1548–1551.
- Jetz W, Rahbek C, Lichstein JW. 2005.** Local and global approaches to spatial data analysis in ecology. *Global Ecology and Biogeography* **14**: 97–98.
- Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012.** The global diversity of birds in space and time. *Nature* **491**: 444–448.
- Kennedy JD, Wang, Z, Weir JT, Rahbek, C, Fjeldsa J, Price TD. 2014.** Into and out of the tropics: the generation of the latitudinal gradient among New World passerine birds. *Journal of Biogeography* **41**: 1746–1757.
- Kerr JT, Currie DJ. 1999.** The relative importance of evolutionary and environmental controls on broad-scale patterns of species richness in North America. *Ecoscience* **6**: 329–337.
- Kisel Y, McInnes L, Toomey NH, Orme CD. 2011.** How diversification rates and diversity limits combine to create large-scale species–area relationships. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**: 2514–2525.
- Klopfer PH. 1959.** Environmental determinants of faunal diversity. *The American Naturalist* **93**: 337–342.
- Kozak KH, Wiens JJ. 2012.** Phylogeny, ecology, and the origins of climate–richness relationships. *Ecology* **93**: sp8.
- Kreft H, Jetz W. 2007.** Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences of the United States of America* **104**: 5925–5930.
- Legendre, P, Legendre, L. 2012.** *Numerical ecology, 3rd edn.* Radarweg, the Netherlands: Elsevier.

- Losos JB. 2009.** *Lizards in an evolutionary tree: ecology and adaptive radiation of anoles*. Berkeley, CA: University of California Press.
- Losos JB, Schluter D. 2000.** Analysis of an evolutionary species–area relationship. *Nature* **408**: 847–850.
- Losos JB, Thorpe RS. 2004.** *Evolutionary diversification of caribbean anolis lizards*. In: Dieckmann U, Doebeli M, Metz JAJ, Tautz D, eds. *Adaptive speciation*. Cambridge: Cambridge University Press, 322–344.
- Mittelbach GG, Schemske DW, Cornell HV, Allen AP, Brown JM, Bush MB, Harrison SP, Hurlbert AH, Knowlton N, Lessios HA, McCain CM, McCune AR, McDade LA, McPeck MA, Near TJ, Price TD, Ricklefs RE, Roy K, Sax DF, Schluter D, Sobel JM, Turelli M. 2007.** Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* **10**: 315–331.
- Morlon H. 2014.** Phylogenetic approaches for studying diversification. *Ecology Letters* **17**: 508–525.
- Otto-Bliesner BL, Marshall SJ, Overpeck JT, Miller GH, Hu A. 2006.** Simulating Arctic climate warmth and icefield retreat in the last interglaciation. *Science (New York, N.Y.)* **311**: 1751–1753.
- Pinto-Ledezma JN, Simon LM, Diniz-Filho JAF, Villalobos, F. 2017.** The geographical diversification of Furnariidae: the role of forest versus open habitats in driving species richness gradients. *Journal of Biogeography* **44**: 1683–1693.
- Poe S, Nieto-Montes de Oca A, Torres-Carvajal O, De Queiroz K, Velasco JA, Truett B, Gray LN, Ryan MJ, Köhler G, Ayala-Varela F, Latella I. 2017.** A phylogenetic, biogeographic, and taxonomic study of all extant species of *Anolis* (Squamata: Iguanidae). *Systematic Biology* **66**: 663–697.
- Powell, R, Henderson RW. 2012.** Island lists of West Indian amphibians and reptiles. *Bulletin of the Florida Museum of Natural History* **51**: 85–166.
- Qian, H, Wiens JJ, Zhang, J, Zhang, Y. 2015.** Evolutionary and ecological causes of species richness patterns in North American angiosperm trees. *Ecography* **38**: 241–250.
- Quinn, G, Keough, M. 2002.** *Experimental design and data analysis for biologists*. Cambridge, UK: Cambridge University Press.
- Rahbek C, Graves GR. 2001.** Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences* **98**: 4534–4539.
- Rahbek, C, Gotelli NJ, Colwell RK, Entsminger GL, Rangel TFLVB, Graves GR. 2007.** Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proceedings of the Royal Society B: Biological Sciences* **274**: 165–174.
- Rakotoarinivo M, Blach-Overgaard A, Baker WJ, Dransfield J, Moat J, Svenning J. 2013.** Palaeoprecipitation is a major determinant of palm species richness patterns across Madagascar: a tropical biodiversity hotspot. *Proceedings of the Royal Society B: Biological Sciences* **280**: 20123048.
- Rangel TFLVB, Diniz-Filho JAF, Bini LM. 2010.** SAM: a comprehensive application for spatial analysis in macroecology. *Ecography* **33**: 46–50.
- Rangel TF, Diniz-Filho JA, Colwell RK. 2007.** Species richness and evolutionary niche dynamics: a spatial pattern-oriented simulation experiment. *The American Naturalist* **170**: 602–616.
- Ricklefs RE. 2006.** Evolutionary diversification and the origin of the diversity–environment relationship. *Ecology* **87**: sp7.
- Rohde, K. 1992.** Latitudinal gradients in species diversity. *Oikos* **65**: 514–527.
- Rolland J, Condamine FL, Jiguet F, Morlon H. 2014.** Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biology* **12**: e1001775.
- Romdal TS, Araújo MB, Rahbek, C. 2013.** Life on a tropical planet: niche conservatism and the global diversity gradient. *Global Ecology and Biogeography* **22**: 344–350.
- Roy K, Goldberg EE. 2007.** Origination, extinction, and dispersal: integrative models for understanding present-day diversity gradients. *The American Naturalist* **170** (Suppl 2): S71–S85.
- Sandel B, Arge L, Dalsgaard B, Davies RG, Gaston KJ, Sutherland WJ, Svenning JC. 2011.** The influence of late quaternary climate-change velocity on species endemism. *Science (New York, N.Y.)* **334**: 660–664.
- Schwarz GE. 1978.** Estimating the dimension of a model. *Annals of Statistics* **6**: 461–464.
- Schluter D, Pennell MW. 2017.** Speciation gradients and the distribution of biodiversity. *Nature* **546**: 48–55.
- Srivastava DS, Lawton JH. 1998.** Why more productive sites have more species: an experimental test of theory using tree-hole communities. *The American Naturalist* **152**: 510–529.
- Stevens GC. 1989.** The latitudinal gradient in geographical range: how so many species coexist in the tropics. *The American Naturalist* **133**: 240–256.
- Stevens RD. 2011.** Relative effects of time for speciation and tropical niche conservatism on the latitudinal diversity gradient of phyllostomid bats. *Proceedings of the Royal Society B: Biological Sciences* **278**: 2528–2536.
- Stuart YE, Losos JB, Algar AC. 2012.** The island–mainland species turnover relationship. *Proceedings of the Royal Society B: Biological Sciences* **279**: 4071–4077.
- Svenning JC, Eiserhardt WL, Normand S, Ordonez A, Sandel B. 2015.** The influence of paleoclimate on present-day patterns in biodiversity and ecosystems. *Annual Review of Ecology, Evolution, and Systematics* **46**: 551–572.
- Tello JS, Stevens RD. 2010.** Multiple environmental determinants of regional species richness and effects of geographic range size. *Ecography* **33**: 796–808.
- Vázquez-Rivera, H, Currie DJ. 2015.** Contemporaneous climate directly controls broad-scale patterns of woody plant diversity: a test by a natural experiment over 14,000 years. *Global Ecology and Biogeography* **24**: 97–106.
- Velasco JA, Martínez-Meyer, E, Flores-Villela, O, García, A, Algar AC, Köhler G, Daza JM. 2016.** Climatic niche attributes and diversification in *Anolis* lizards. *Journal of Biogeography* **43**: 134–144.
- Vellend, M, Cornwell WK, Magnuson-Ford, K, Mooers AØ. 2011.** Measuring phylogenetic biodiversity. In: Magurran AE, McGill BJ, eds. *Biological diversity: frontiers in measurement and assessment*. Oxford: Oxford University Press, 1–14.

- Weir JT, Schluter D. 2007.** The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science (New York, N.Y.)* **315**: 1574–1576.
- Whittaker, R. 2007.** Geographical gradients of species richness: a test of the water-energy conjecture of [Hawkins \*et al.\* \(2003\)](#) using European data for five taxa. *Global Ecology and Biogeography* **16**, 76–89.
- Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Jonathan Davies T, Grytnes JA, Harrison SP, Hawkins BA, Holt RD, McCain CM, Stephens PR. 2010.** Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* **13**: 1310–1324.
- Wiens JJ, Donoghue MJ. 2004.** Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution* **19**: 639–644.
- Wiens JJ, Graham CH. 2005.** Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics* **36**, 519–539.

## SUPPORTING INFORMATION

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

**Table S1.** Environmental variables included in each model.

**Table S2.** Average Pearson's correlation values between variables from each hypothesis examined.

**Figure S1.** Geographical patterns of observed *Anolis* species richness (top right) and predicted under a mid-domain null model (top left). Geographical patterns of *Anolis* species richness using only occurrence records (bottom left) and mid-domain effect randomizing occurrence record position across the domain (bottom right).

**Figure S2.** Geographical patterns of *Anolis* species richness, phylogenetic metrics (MRD, mean root distance; PD, phylogenetic diversity; and residual PD, residual phylogenetic diversity) and species richness for species belonging to lineages close to the root and far from the root of the anole phylogeny.

**Figure S3.** Correlograms of observed and estimated species richness and residuals from species richness–climate relationships for three regression models (top, GWR; middle, SAR; bottom, OLS). We compared the spatial autocorrelation in model residuals for three regression models (GWR, geographically weighted regression; OLS, ordinary least squares; and SAR, simultaneous autoregressive model) using Moran's *I* values for full models for the Last Glacial Maximum period (correlograms were similar for the Last Inter-Glacial period). Correlograms show that GWR methods control the presence of spatial autocorrelation in model residuals very well compared with SAR and OLS models. This suggests that parameter estimation in GWR models (predicted species richness,  $R^2$  and slopes) is not biased by spatial autocorrelation.

**Figure S4.** Boxplots illustrating the variation in regression coefficients for each variable from full models for the Last Glacial Maximum (LGM; top) and Last Inter-Glacial period (LIG; bottom). These plots show that explanatory variables were nonstationary across the entire domain and did not fulfil the global expectations (see Table 1 in the main text).

**Figure S5.** Shared contributions of climatic hypotheses for Last Glacial Maximum (LGM) period explaining observed *Anolis* species richness gradients: (1) water–energy; (2) seasonality; (3) heterogeneity; (4) historical climatic stability for LGM. See main text for details in variables for each hypothesis.

**Figure S6.** Shared contributions of climatic hypotheses for Last Inter-Glacial (LIG) period explaining observed *Anolis* species richness gradients: (1) water–energy; (2) seasonality; (3) heterogeneity; (4) historical climatic stability for LIG. See main text for details in variables for each hypothesis.

**Figure S7.** Boxplots of local  $R^2$  values from full models for the Last Glacial Maximum and Last Inter-Glacial periods for mainland (Middle America, South America) and islands (Greater Antilles).

**Figure S8.** Boxplots of local slope values from full models for the Last Glacial Maximum and Last Inter-Glacial periods for mainland (Middle America, South America) and islands (Greater Antilles).

**Figure S9.** Correlation between phylogenetic metrics [mean root distance (MRD) and residual phylogenetic diversity after control by species richness (residual PD)] and geographically weighted regression parameters ( $R^2$  and slopes) for Last Glacial Maximum (LGM) and Last Inter-Glacial (LIG) periods.

**Figure S9.** Correlation between phylogenetic metrics [mean root distance (MRD) and residual phylogenetic diversity after control by species richness (relative PD)] and geographically weighted regression parameters ( $R^2$  and slopes) for Last Glacial Maximum (LGM) and Last Inter-Glacial (LIG) periods for mainland and Greater Antilles.

**Figure S10.** Frequency distributions of determination coefficients ( $R^2$ ) for correlations between random residual phylogenetic diversity (PD; top), mean root distance (MRD; bottom) and observed residuals from geographically weighted regression (GWR) full models of the Last Glacial Maximum (LGM) and Last Inter-Glacial (LIG) periods.