

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

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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

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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

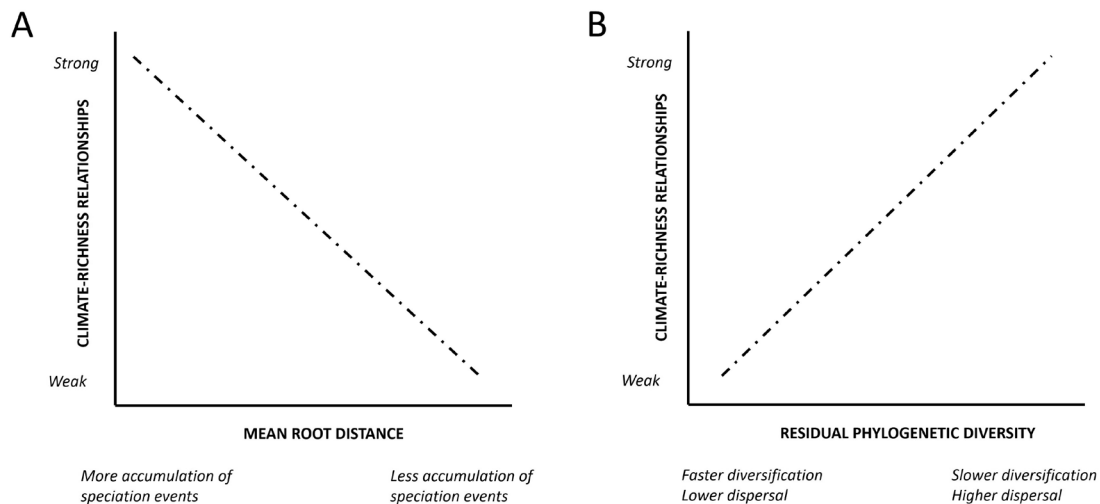
Hypothesis	Stationary expected relationships	Nonstationary predictions	References
Water–energy	Positive	Regions with a higher productivity (e.g. Chocó, Andes) have more species than regions with lower productivity (e.g. northern Mexico)	Hawkins <i>et al.</i> (2003); Evans <i>et al.</i> (2005)
Seasonality	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 higher *in situ* diversification and few dispersal events



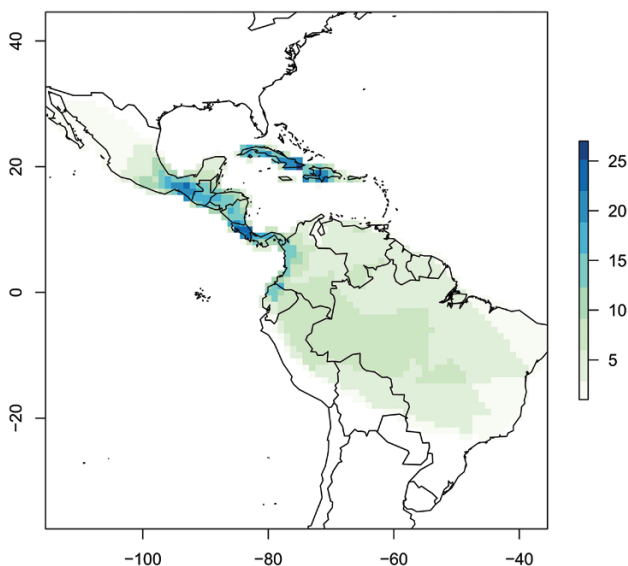
**Figure 1.** Nonmutually exclusive scenarios about the role of phylogenetic niche conservatism (PNC) and regional diversification mediating climate–richness relationships in *Anolis* lizards. If PNC drives climate–richness relationships, we expect that regions with more accumulation of lineages and 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.

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 Pacific islands (33 species) from our analyses for several



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

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 indicted 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).

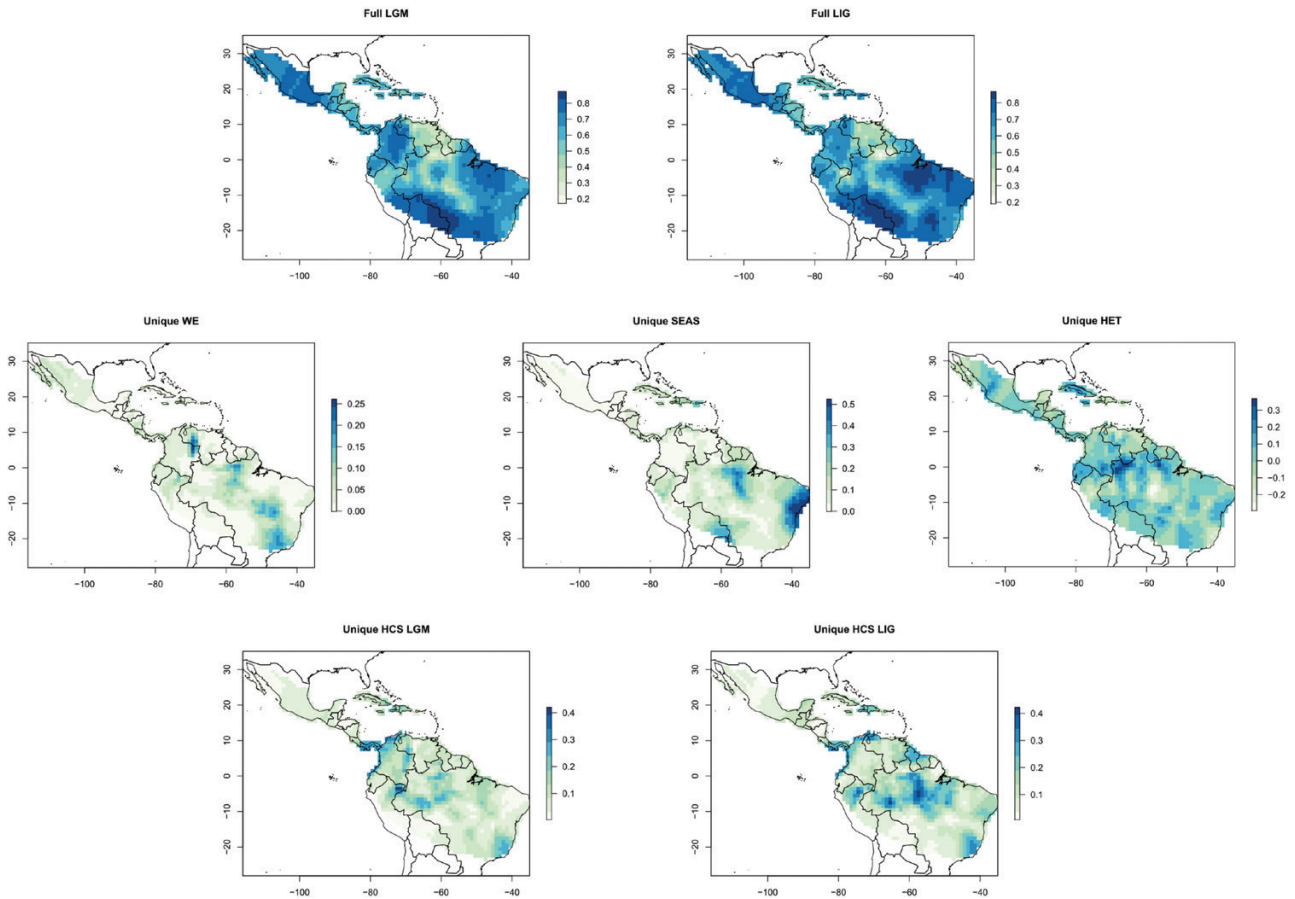
Strong differences between local regression parameters were found between the Greater Antilles and the mainland region (Table 4). We found lower local  $R^2$  values for the Greater Antilles relative to mainland areas (Supporting information, Fig. S7). Although local slopes also differed between regions, 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

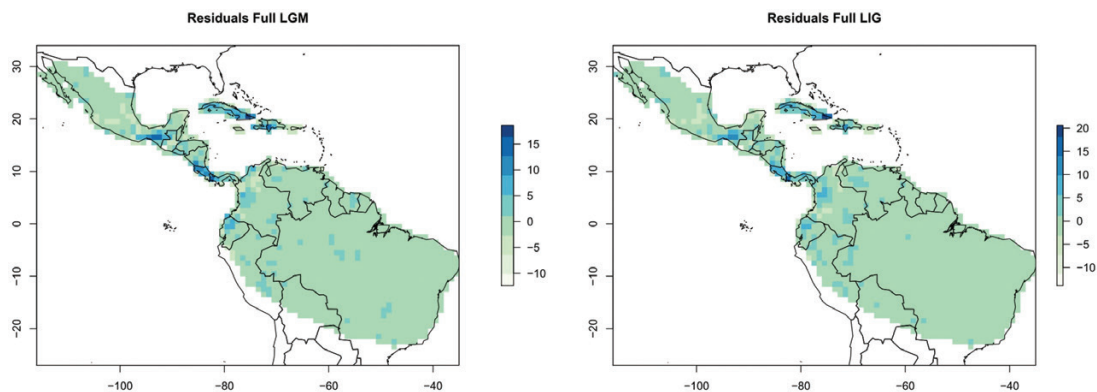
shared predictors were disentangled, we found that multiple environmental hypotheses act synergistically to explain the observed geographical gradient of species richness in *Anolis*. Although some researchers have suggested that different mechanisms drive species richness gradients independently (Currie, 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 species). In

**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.

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*.

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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.

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## SUPPORTING INFORMATION

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

**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.