Running head: What factors controls the *Anolis* diversity?

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

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Abstract

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 (PNC) and regional diversification (RD) in the origin and maintenance of climate-richness relationships. Climate had a strong non-stationary 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 PNC or RD underlying these relationships. We suggest that evolutionary processes affecting climate-richness relationships in *Anolis* likely were obscured by high dispersal rates between regions.

Keywords: climate, regional diversification, phylogenetic niche conservatism, macroecology, macroevolution.

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 geographic and evolutionary 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; 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, four main hypotheses have been considered (Evans et al. 2005; Field et al. 2009; Tello and 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 *geographic variation in diversification rates* (Weir & Schluter 2007; Rolland et al.

2014) currently are the most prominent hypotheses to explain contemporary diversity gradients and its relationship with climate.

Several potential mechanisms may underlay 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; Allen & Gillooly 2006; Srivastava & Lawton 1998; Currie et al. 2004; 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 also will be reduced (Janzen 1967; Stevens 1989; Hurlbert & Haskell 2003; Dalby et al. 2014) (Table 1). The heterogeneity hypothesis proposes that habitat complexity increases *in situ* speciation rate probability through population fragmentation due to the presence of more dispersal barriers leading 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 track niches through space (Kisel et al. 2011; Rakotoarinivo et al. 2013) (Table 1). Some of these climatic-based hypotheses have been tested extensively (e.g., water-energy hypothesis; Field et al. 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 remain largely unknown.

Conceptual and methodological advances have enabled the rigorous integration of a phylogenetic perspective in ecological studies (Jablonski et al. 2006; Hernandez et al. 2013), allowing tests of the role of evolutionary processes in generating present-day geographic 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 phylogenetic niche conservatism (PNC; Wiens & Donoghue 2004; Wiens & Graham 2005) and variation in diversification rates across regions (Rolland et al. 2014; Alves et al. 2017; Schluter & Pennel 2017). Evidence favoring 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 et al. 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). Alternatively to PNC, evidence favoring the importance of diversification rates in generating current geographic 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* are an excellent system for examining the relative influence of climatic factors and historical processes on geographic patterns of diversity. *Anolis* lizards likely originated in South America during the Paleocene, 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 (~220 species) regions. Some studies suggest that assembly of anole faunas proceeds differently in insular and mainland regions (Algar & Losos 2011; Stuart et al. 2012). Although previous studies have examined species richness patterns of *Anolis* across 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 correlates 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 regional diversification (Figure 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 (Figure 1). Similarly, if regional diversification has shaped climate-richness relationships we expect that regional assemblages with 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 (Figure 1).

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 extent of occurrence using minimum convex polygons and removing non-land 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° x 1° (~12,544 km^2 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 less than 25% of land surface to reduce potential area effects (Budic et al. 2015). Our grid system resulted in 1379 cells across the region (Figure 1), 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 reasons. First, these islands are occupied by only one or two species (Powell and 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 are 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 likely will not affect our general results. In addition, we evaluated whether a mid-domain effect (Colwell & Less 2000) can explain the observed pattern of species richness (Supplementary 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; Table S1). We generated climatic anomalies for the Last Inter-Glacial (LIG; approx. 130,000 years before present; Otto-Bliesner et al. 2006) and the Last Glacial Maximum (LGM; approx. 21,000 years before present; MIROC model; Hasumi and 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 (Table S2). As collinearity among variables was low (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 in 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. 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 distances 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). As 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 and 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 among 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; Fritz & Rahbek 2012; Davies & Buckley 2012). We mapped these metrics to visualize geographical patterns of regional diversification and faunal phylogenetic structure in *Anolis* (Fig. S1).

Global and local climate-richness relationships

We analyzed 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 non-stationary effect of environmental variables on species richness. We implemented a variance partitioning approach (Legendre and 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 Table S1). We selected the model with the highest explanatory power using the Bayesian Information Criteria (BIC) (Schwarz 1978, Quinn and 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 SAM (Rangel et al. 2010) and in 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 test if 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 analyzed these correlations for the Greater Antilles and the mainland separately. Furthermore, we analyzed whether a null model eliminating the phylogenetic structure by randomizing species positions across the tree is able to explain the correlation between phylogenetic metrics and GWR parameters from full models. This null model describes a pattern where PNC and RD 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 Dryad at XXX.

Results

Geographic patterns of* Anolis *species richness

High species richness of *Anolis* occurs across the Greater Antilles (Cuba and Hispaniola), almost all of Central America (from 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 distances values showed higher richness in the Andes region, lower Central America, and the Greater Antilles (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 (Fig. S2). Mapping residual PD values showed that the mid portion of Middle America and the Andean region exhibited high values (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 (Fig. S2). We did not find evidence supporting a mid-domain effect generating the observed pattern of species richness (see Fig S1).

Climate-richness relationships in* Anolis *lizards

GWR models exhibit higher global R^2 values than OLS models (Table 2; Fig. S3). In addition, spatial non-stationarity effects of predictors on species richness were evident with great geographical variation in regression coefficients across the Greater Antilles and the mainland (Fig. S4). The global expectations for regression coefficient values for each climate hypothesis were not fulfilled (Table 1; 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, in average, from 0.642 to 0.785). R^2 values for models with each hypothesis (water-energy, seasonality, heterogeneity and historical climatic stability) were relatively similar for LGM and LIG (Table 4).

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 and 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 non-stationary effect (Fig. 3; Table 3).

The signature of past climates, mainly from the Last Inter-Glacial (LIG), was strong on species richness patterns (Table 2; Fig. 3). For the LIG period, unique contributions of historical climatic stability were higher in Middle America highlands, 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 non-stationarity (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 Fig. S6).

Strong differences between local regression parameters were found between the Greater Antilles and the mainland region (Table 3). We found lower local R^2 values for the Greater Antilles relative to mainland areas (Fig. S7). Although local slopes also differed between regions, the nature of regional differences was dependent on the period examined (Table 3). 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 (Fig. S8).

Geographic 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).

Evolutionary drivers of climate-richness relationships

We did not find a correlation between either MRD values or residual PD and GWR parameters (R^2, slopes, respectively) (Table 5; Figs S9). We also did not find a correlation when the Greater Antilles and the mainland were analyzed separately (Figs S10). Observed correlation values were well-predicted by a null model simulating the absence of phylogenetic structure and regional diversification effect on the geographical richness-climate pattern (Table 5; Figs 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 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 where paleoclimate has played a strong role in species richness gradients (Rakotoarinivo et al. 2013).

The signature of past climates from the Last-Inter Glacial period on anole species richness was relatively higher than for the Last Glacial Maximum (Table 3). This result suggests that cold temperatures from 21,000 BP had a low impact on species' ranges, at least on the mainland and Greater Antilles (but see Campbell-Staton et al. 2016; 2017). Furthermore, we found that climatic anomalies from the Last-Inter Glacial period (~121,000 BP) 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 understanding of the role of past climate on resulting species richness patterns.

Some macroecological studies provided evidence that climate-richness relationships are stationary through space (Jetz et al. 2005). Our results show a strong non-stationary effect of multiple hypotheses on species richness gradient in *Anolis* lizards. The non-stationary pattern was also evident in the unique and shared effects of each environmental hypothesis (Fig. S5-S6). This non-stationary 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 (7 species). By 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 likely 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 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; Qian et al. 2015; Kozak & Wiens 2012; Schluter and Pennell 2017), we did not find evidence for a clear role for these processes in the climate-richness relationships of *Anolis* lizards. Neither phylogenetic niche conservatism nor regional diversification metrics 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; Hawkins et al. 2012; Buckley et al 2010; Stevens 2011) which are not evident within the range of *Anolis*.

The ability of the phylogenetic metrics used to capture recurrent dispersal movements across the region may 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 origination region 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 explicitly speciation, extinction, and dispersal rates 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 et al. 2007) might help to reveal the role of these process 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 with the mainland assemblages. Probably 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 similar process played a substantial role in the evolution of mainland *Anolis*.

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Author's contributions

JAV and EMM conceived the study; JAV, FV, JAFDF and ACA designed methodology; JAV, ACA, OFV, GK, and SP collected the data, JAV analyzed the data and lead the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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

Hypothesis	**Stationary expected relationships**	**Non-stationary 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 et al. 2003; Evans et al. 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 et al. 2012
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) supports more species than sites that are more variable (e.g., northern Mexico, Amazonia)	Araujo et al. 2008; Gouveia et al. 2012; Rakotoarinivo et al. 2013; Svenning et al. 2015

Table 2. Bayesian model selection for full models and single hypothesis models (water energy, –WE; seasonality, –SEAS-, heterogeneity, –HET-, and historical climatic stability, –HSC). LGM: Last Glacial Maximum, ~21.000 years before present; LIG: Last Inter-Glacial, ~121.000 years before present). R^2: Coefficient of determination; GWR: Geographical weighted regression; OLS: Ordinary least squares. BIC: Bayesian Information Criterion; ΔBIC: Delta Bayesian Information Criterion.

		GWR			**OLS**	
Models	**R^2**	**BIC**	**ΔBIC**	**R^2**	**BIC**	**ΔBIC**
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

Table 3. Partial regression coefficients (R^2) for pure and shared (denoted by s) contributions of the climatic hypothesis from geographical weighted regression (GWR) models explaining observed *Anolis* species richness gradients for the Last Glacial Maximum and the Last Inter-Glacial periods. Negative partial R^2 values are due to the opposite signal effects between predictors. WE: Water-energy hypothesis; SEAS: Seasonality hypothesis; HET: Heterogeneity hypothesis; HCS: Historial climatic stability hypothesis.

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

Table 4. Comparison of local parameters (R^2 and slopes) from geographical weighted regression (GWR) models between regions using a spatial ANOVA. WE: Water-energy hypothesis; SEAS: Seasonality hypothesis; HET: Heterogeneity hypothesis; HSC: Historial climatic stability hypothesis.

Parameters	Models	Log-lik	*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 values	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

Table 5. Pearson correlations between evolutionary metrics (mean root distance, MRD and residual phylogenetic diversity, residual PD) and local parameters of richness-climate relationships for the Last Glacial Maximum (LGM) and the Last Inter-Glacial (LIG). *P*-values are the probability that observed *r* from correlations between evolutionary metrics and GWR 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).

	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
MR vs local slopes -full model LGM-	0.054	< 0.001
MR 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

Figure legends

Figure 1. Non-mutually exclusive scenarios about the role of phylogenetic niche conservatism (PNC) and regional diversification mediating climate-richness relationships in *Anolis* lizards. If PNC drive climate-richness relationships, we expect that regions with more accumulation of lineages and speciation events have a strong climate-richness relationship. By contrast, if PNC does not drive climate-richness relationships, we expect that regions with less accumulation of speciation events 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 have a weak climate-richness relationship. By 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.

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

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 the Last Inter-Glacial (LIG). Unique WE: unique Water-Energy; Unique SEAS: Unique Seasonality; Unique HET: Unique Heterogeneity; Unique HCS LGM: Unique Historical climatic stability for LGM; Unique HCS LIG: Unique Historical climatic stability for LIG. See main text for details in variables analyzed for each hypothesis.

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

Figure 1

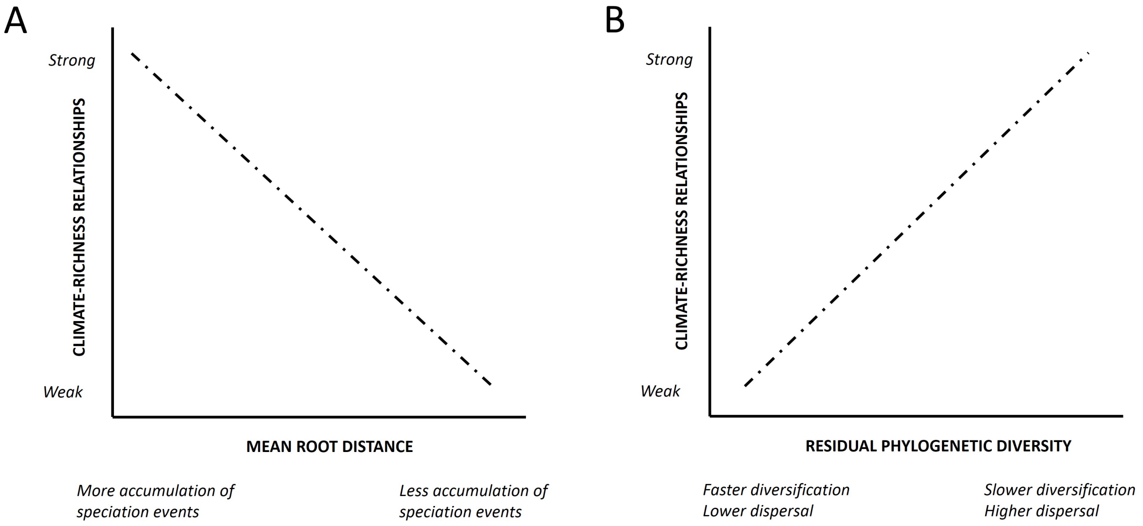

A
Strong
Weak
CLIMATE-RICHNESS RELATIONSHIPS
MEAN ROOT DISTANCE
More accumulation of speciation events
Less accumulation of speciation events
B
Strong
Weak
CLIMATE-RICHNESS RELATIONSHIPS
RESIDUAL PHYLOGENETIC DIVERSITY
Faster diversification
Lower dispersal
Slower diversification
Higher dispersal

Figure 2

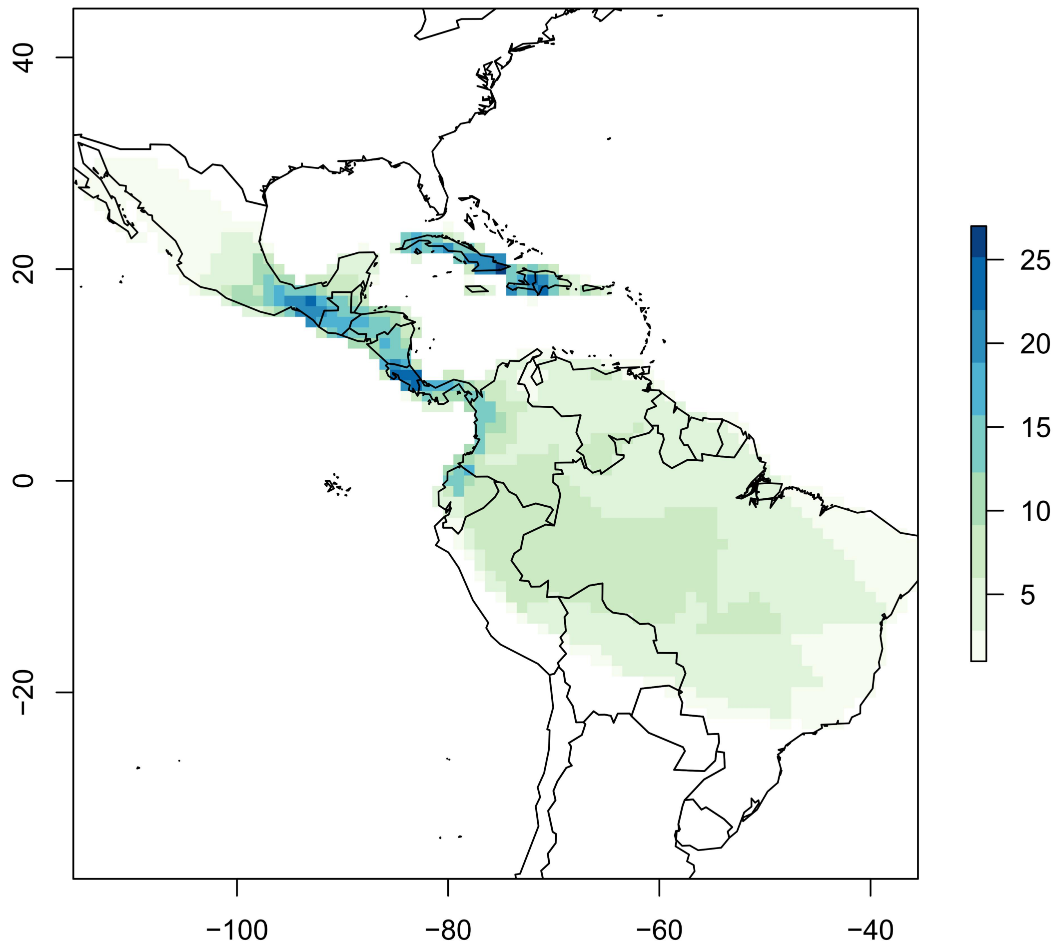
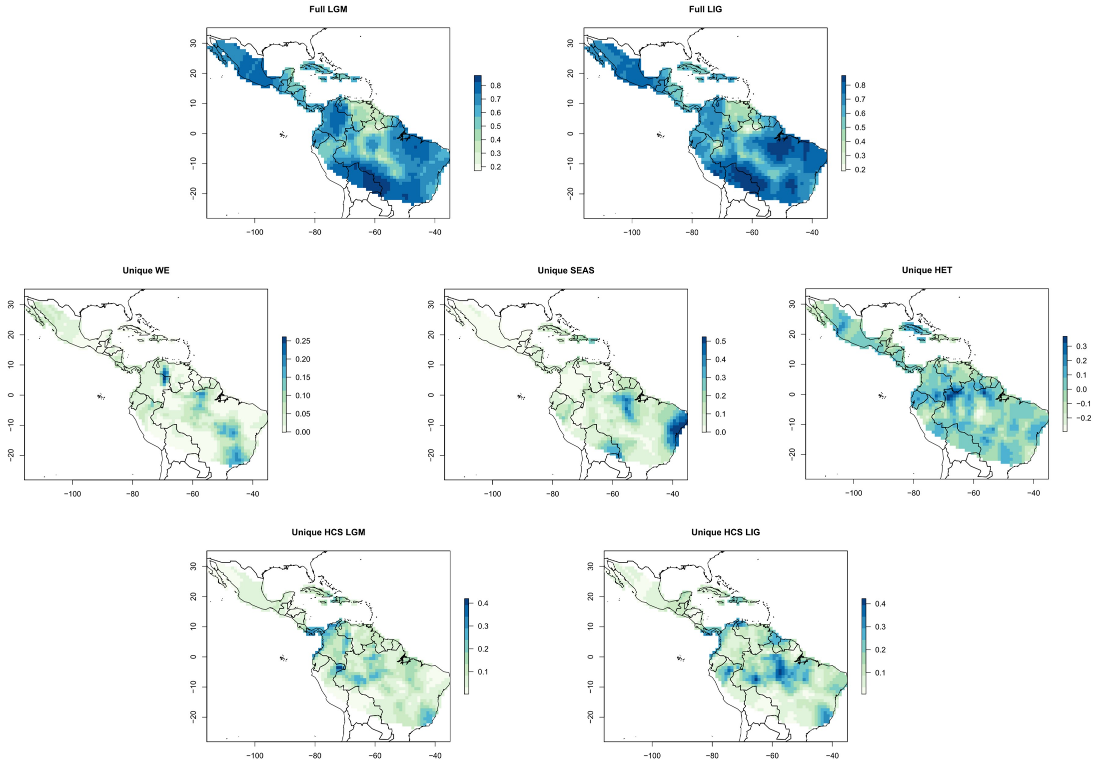


Figure 3


Full LGM
Full LIG
Unique WE
Unique SEAS
Unique HET
Unique HCS LGM
Unique HCS LIG
30
20
10
0
−10
−20
−100
−80
−60
−40
0.8
0.7
0.6
0.5
0.4
0.3
0.2
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0.20
0.15
0.10
0.05
0.00
0.5
0.4
0.3
0.2
0.1
0.0
0.3
0.2
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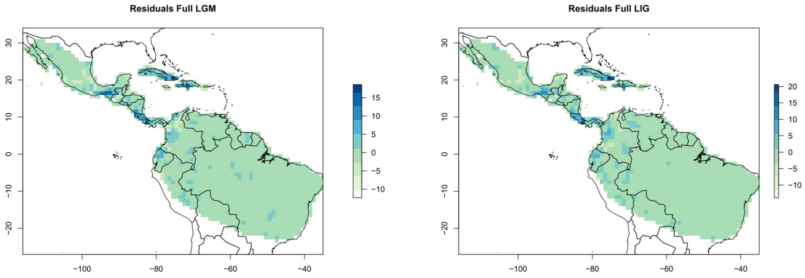
0.0
−0.1
−0.2
0.4
0.3
0.2
0.1

Figure 4


Residuals Full LGM
30
20
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−60
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−10
Residuals Full LIG
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−60
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−5
−10

SUPLEMENTARY MATERIAL APPENDIX

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

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Table S1. Environmental variables included in each model

	Variables included in each model
Full LGM -Last Glacial Maximum-	Annual mean temperature (AMT) Annual precipitations (AP) Temperature seasonality (TS) Temperature annual range (TAR) Precipitation seasonality (PS) standard deviation of Elevation (stdevElev) standard deviation of Annual mean temperature (stdevAMT) climatic anomalies for AMT from Last Inter-Glacial climatic anomalies for AP from the Last Glacial Maximum climatic anomalies for TS from the Last Glacial Maximum climatic anomalies for TAR from the Last Glacial Maximum climatic anomalies for PS from the Last Glacial Maximum
Full LIG -Last Inter-Glacial-	Annual mean temperature (AMT) Annual precipitations (AP) Temperature seasonality (TS) Temperature annual range (TAR) Precipitation seasonality (PS) standard deviation of Elevation (stdevElev) standard deviation of Annual mean temperature (stdevAMT) standard deviation of Annual precipitation (stdevAP) climatic anomalies for AMT from Last Inter-Glacial climatic anomalies for AP from the Last Inter-Glacial climatic anomalies for TS from the Last Inter-Glacial climatic anomalies for TAR from the Last Inter-Glacial climatic anomalies for PS from the Last Inter-Glacial
Single Water-Energy	Annual mean temperature (AMT) Annual precipitations (AP)

Single Seasonality	Temperature seasonality (TS)
	Temperature annual range (TAR)
	Precipitation seasonality (PS)
Single Heterogeneity	standard deviation of Elevation (stdevElev)
	standard deviation of Annual mean temperature (stdevAMT)
	standard deviation of Annual precipitation (stdevAP)
Single Historical climatic stability - LGM-	climatic anomalies for AMT from Last Inter-Glacial
	climatic anomalies for TS from the Last Glacial Maximum
	climatic anomalies for TAR from the Last Glacial Maximum
	climatic anomalies for PS from the Last Glacial Maximum
Single Historical climatic stability - LIG-	climatic anomalies for AMT from Last Inter-Glacial
	climatic anomalies for AP from the Last Inter-Glacial
	climatic anomalies for TS from the Last Inter-Glacial
	climatic anomalies for TAR from the Last Inter-Glacial
	climatic anomalies for PS from the Last Inter-Glacial

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

	Water-Energy	Seasonality	Heterogeneity	HCS LGM	HCS LIG
Water-Energy	1.000				
Seasonality	-0.483	1.000			
Heterogeneity	-0.025	-0.053	1.000		
HCS LGM	-0.133	0.088	-0.063	1.000	
HCS LIG	0.142	-0.131	-0.027	-0.072	1.000

We implemented a null modeling approach to establish whether a random arrangement of geographical ranges of species within the studied area can produce richness gradients similarly to those observed (i.e., a Mid-Domain effect; Colwell & Hurtt 1994; Colwell & Less 2000) (Fig. S1 top). We also implemented this null model using only occurrence records (Fig. S1 bottom). Randomizations of range positions across the domain were generated using R functions provided by Tello & Stevens (2012). Although this null model is useful to test whether the observed gradient of species richness can be driven by simply a randomization of ranges across the domain, it is still an open question of whether the data used here to generate the convex hulls polygons affect our resulting observed species richness.

Figure S1a. 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).

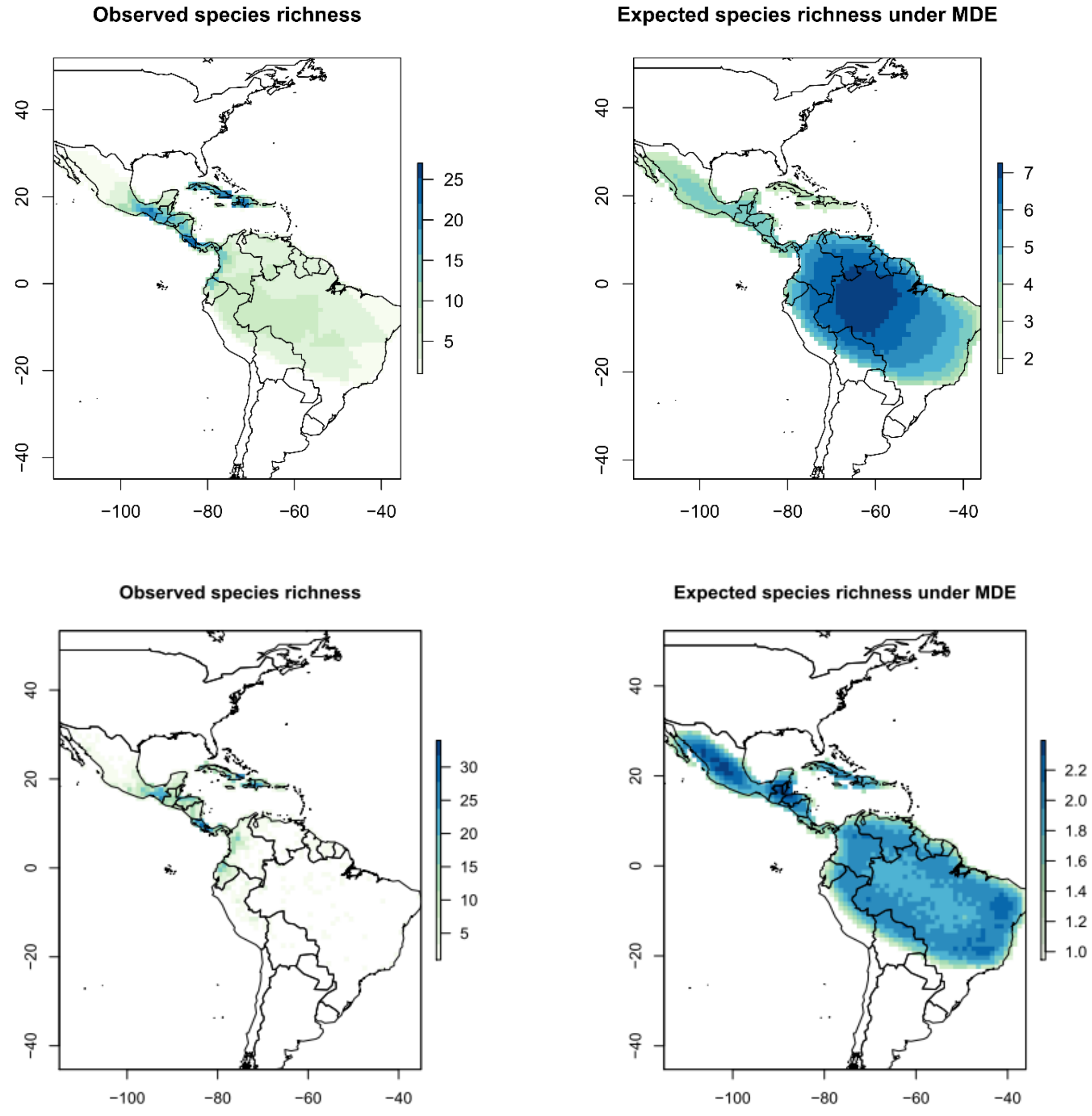

Figure S2. Geographical patterns of *Anolis* species richness, phylogenetic metrics (MRD: mean root distance; PD: phylogenetic diversity; and residual PD: residual phylogenetic diversity), and species richness for species belonging to lineages close to the root and far from the root of the anole phylogeny.

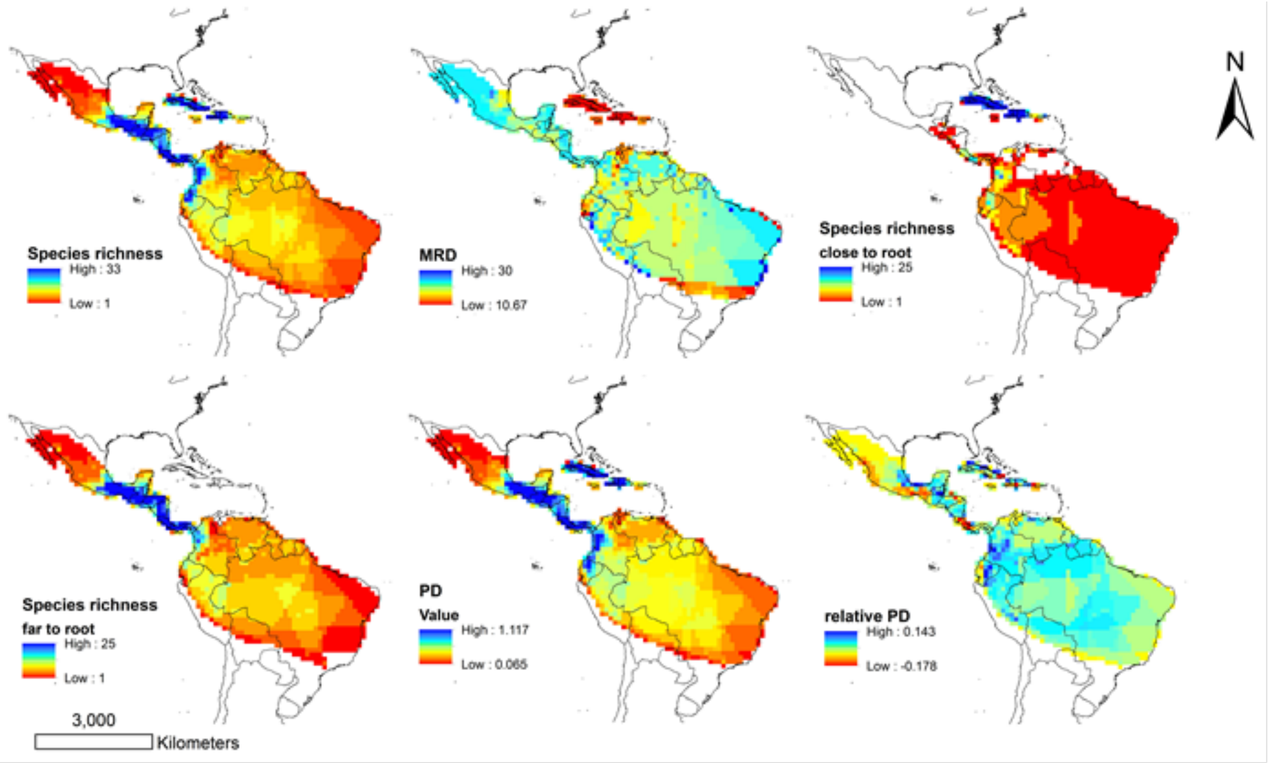

Figure S3. Correlograms of observed and estimated species richness and residuals from species richness-climate relationships for three regression models (top: GWR; middle: SAR; bottom: OLS). We compared the performance of three statistical models (OLS: ordinary least squares; SAR: simultaneous autoregressive model; and GWR: geographically weighted regression) used to estimate richness-climate relationships in *Anolis* lizards. We compared the spatial autocorrelation in model residuals for three regression models (OLS: ordinary least squares; SAR: simultaneous autoregressive model; and GWR: geographically weighted regression) using Moran's I values for full models for the Last Glacial Maximum period (correlograms were similar for the Last-Inter Glacial). Correlograms shown that GWR methods control very well the presence of spatial autocorrelation in model residuals than SAR and OLS models. This suggest that parameter estimation in GWR models (predicted species richness, R2, and slopes) are not biased by spatial autocorrelation.

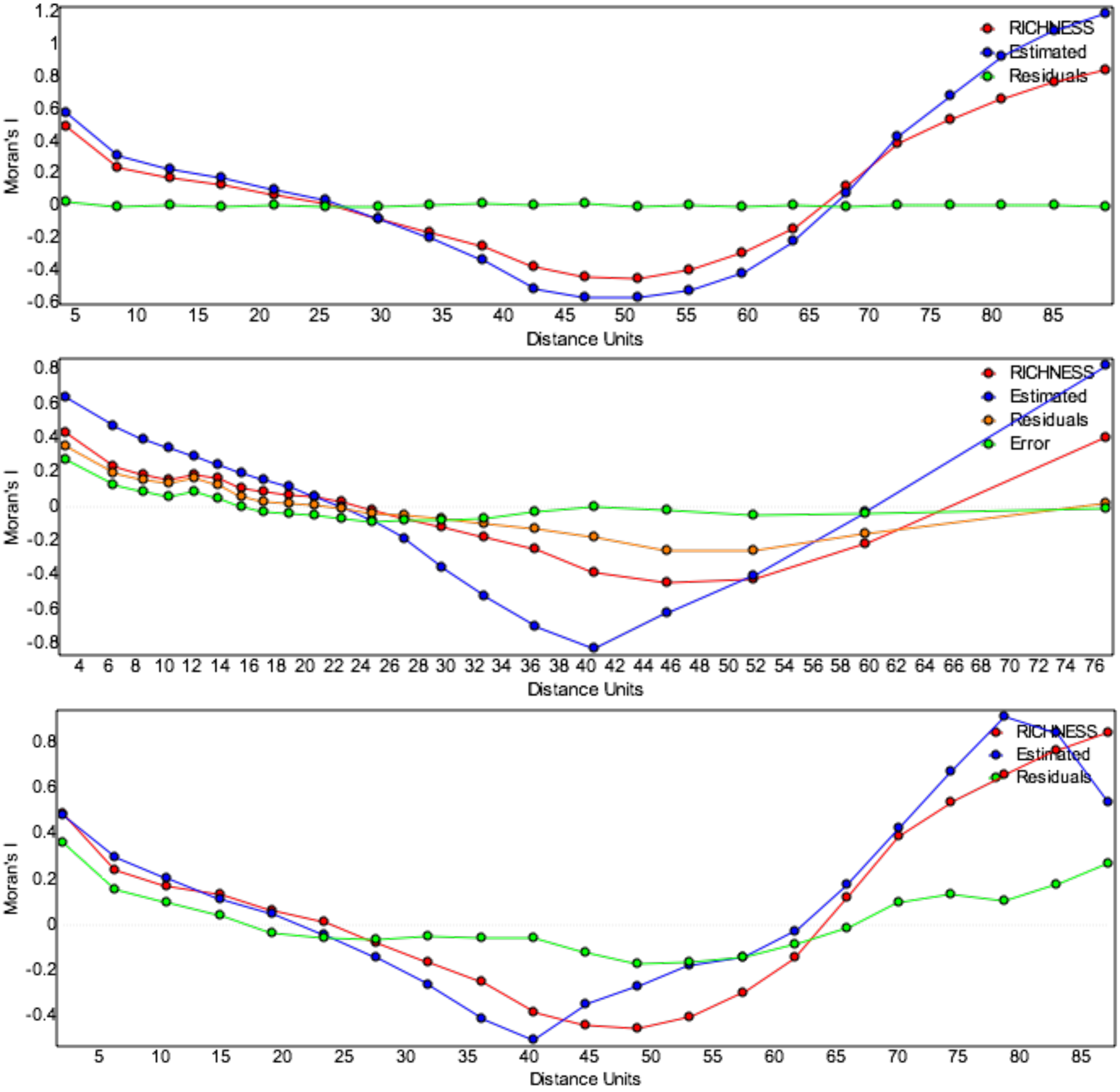

Figure S4. Boxplots illustrating the variation in regression coefficients for each variable from full models for LGM (top) and LIG (bottom). This plots show that explanatory variables were non-stationary across the entire domain and did not fulfill the global expectations (see Table 1 in the main text).

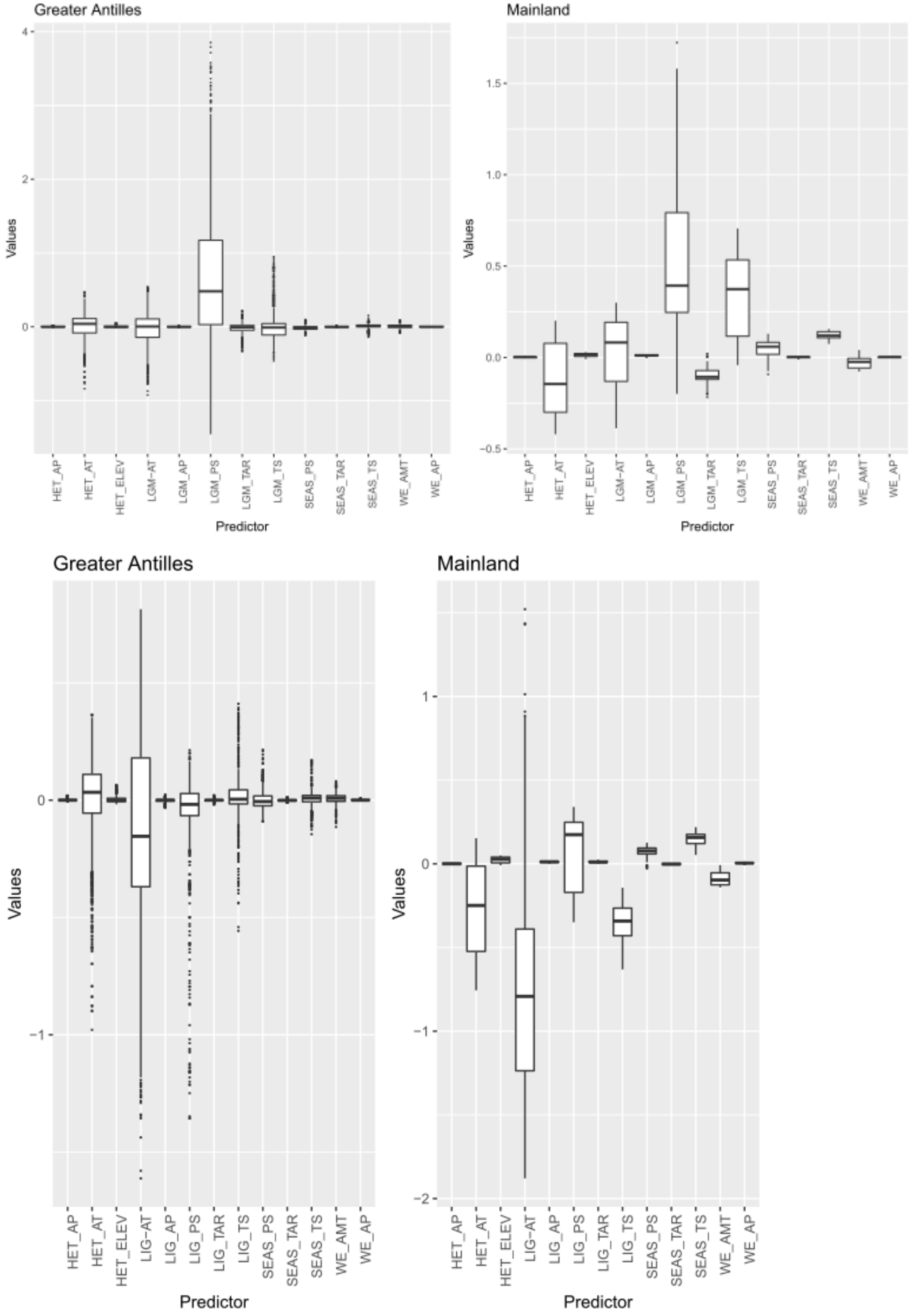

Figure S5. Shared contributions of climatic hypotheses for Last Glacial Maximum (LGM) explaining observed *Anolis* species richness gradients. 1: Water-Energy; 2: Seasonality; 3: Heterogeneity; 4: Historical Climatic Stability for LGM. See main text for details in variables for each hypothesis.

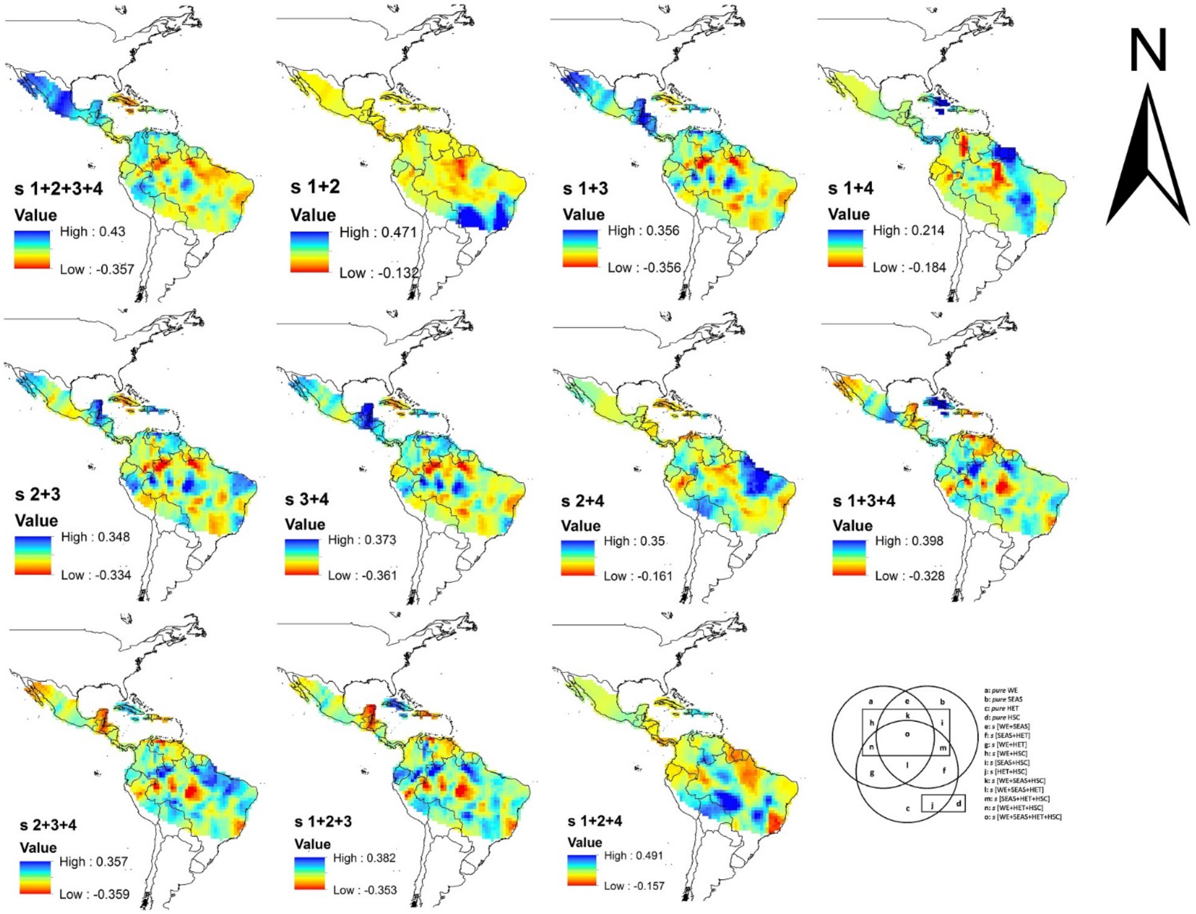

Figure S6. Shared contributions of climatic hypotheses for Last Inter-Glacial (LIG) explaining observed *Anolis* species richness gradients. 1: Water-Energy; 2: Seasonality; 3: Heterogeneity; 4: Historical Climatic Stability for LIG. See main text for details in variables for each hypothesis.

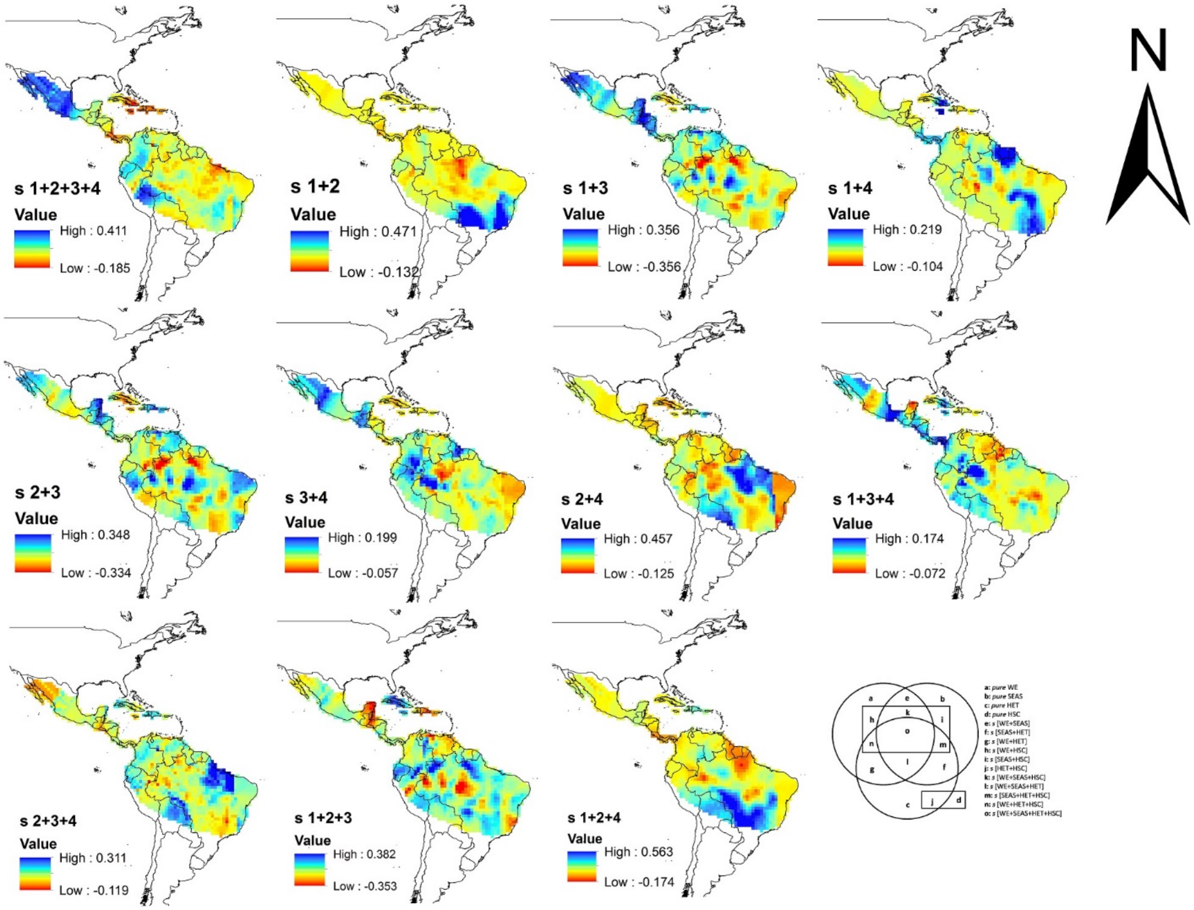
N
s 1+2+3+4
Value
High : 0.411
Low : -0.185
s 1+2
Value
High : 0.471
Low : -0.132
s 1+3
Value
High : 0.356
Low : -0.356
s 1+4
Value
High : 0.219
Low : -0.104
s 2+3
Value
High : 0.348
Low : -0.334
s 3+4
Value
High : 0.199
Low : -0.057
s 2+4
Value
High : 0.457
Low : -0.125
s 1+3+4
Value
High : 0.174
Low : -0.072
s 2+3+4
Value
High : 0.311
Low : -0.119
s 1+2+3
Value
High : 0.382
Low : -0.353
s 1+2+4
Value
High : 0.563
Low : -0.174
a
e
b
k
h
i
o
n
m
l
g
f
c
j
d
a: *pure* WE
b: *pure* SEAS
c: *pure* HET
d: *pure* HSC
e: *s* [WE+SEAS]
f: *s* [SEAS+HET]
g: *s* [WE+HET]
h: *s* [WE+HSC]
i: *s* [SEAS+HSC]
j: *s* [HET+HSC]
k: *s* [WE+SEAS+HSC]
l: *s* [WE+SEAS+HET]
m: *s* [SEAS+HET+HSC]
n: *s* [WE+HET+HSC]
o: *s* [WE+SEAS+HET+HSC]

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).

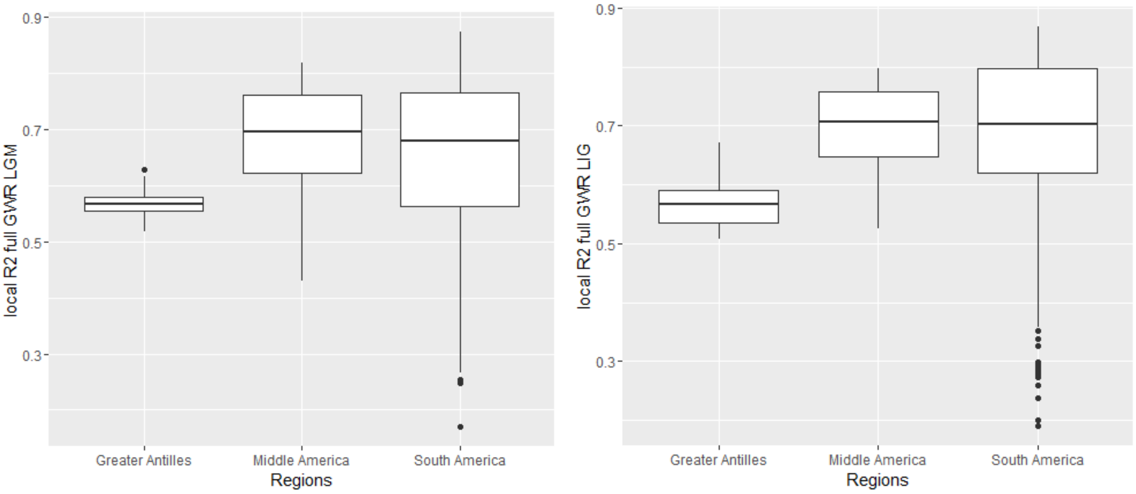

Figure S8. Boxplots of local slope values from full models for the Last Glacial Maximum and Last Inter-Glacial periods for mainland (Middle America, South America) and islands (Greater Antilles).

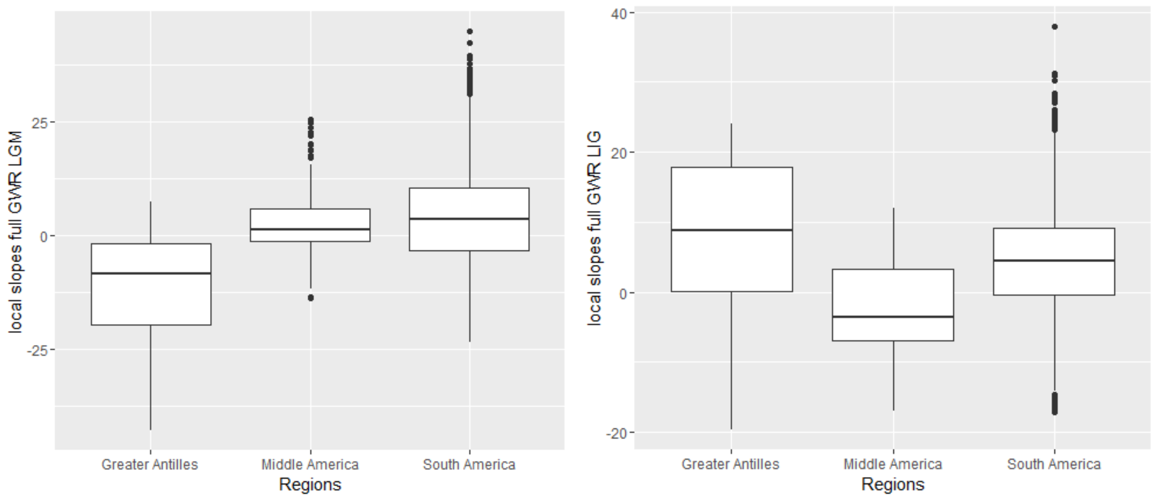

Figure S9. Correlation between phylogenetic metrics (mean root distance -MRD- and residual phylogenetic diversity after control by species richness -residual PD-) and geographically weighted regression parameters (R^2 and slopes) for Last Glacial Maximum (LGM) and Last Inter-Glacial (LIG).

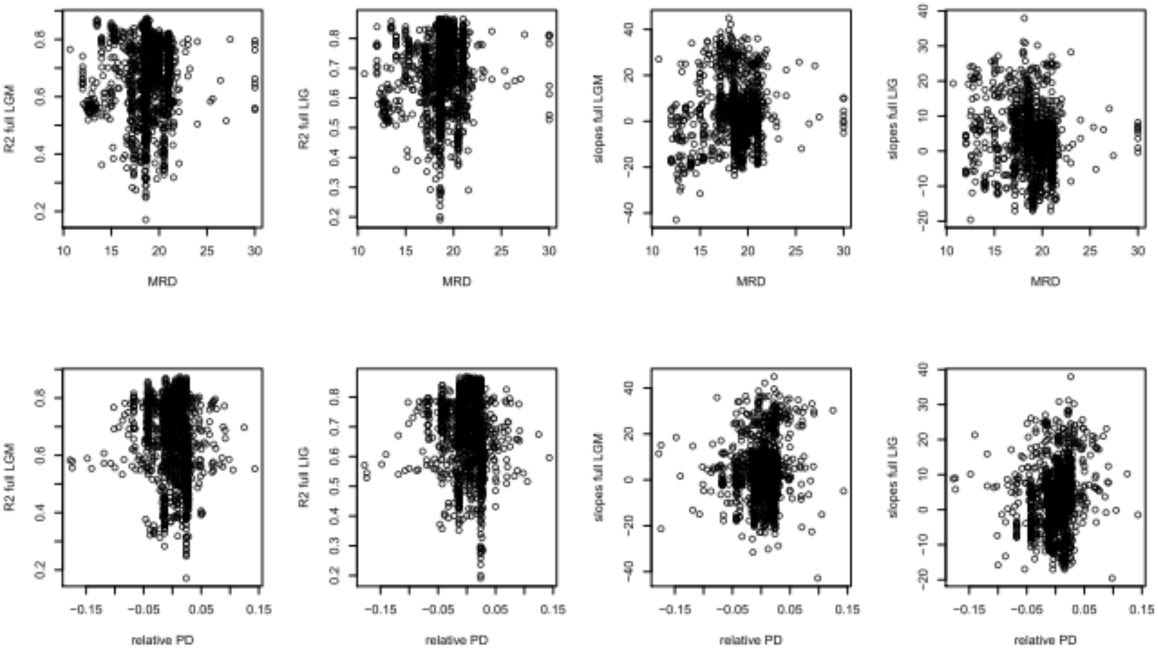

Figure S9. Correlation between phylogenetic metrics (mean root distance -MRD- and residual phylogenetic diversity after control by species richness -relative PD-) and geographically weighted regression parameters (R^2 and slopes) for Last Glacial Maximum (LGM) and Last Inter-Glacial (LIG) for mainland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

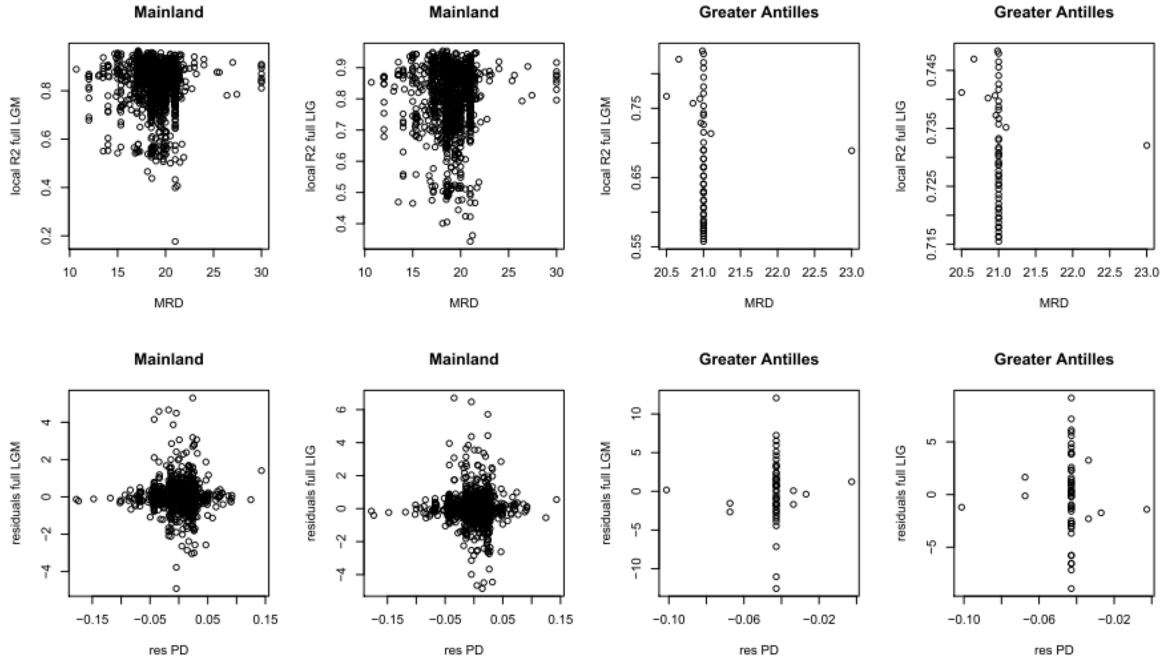

Figure S10. Frequency distributions of determination coefficients (R^2) for correlations between random residual PD (top), MRD (bottom) and observed residuals from GWR full models Last Glacial Maximum (LGM) and Last Inter-Glacial (LIG).