UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE GEOLOGÍA

ECOLOGÍA

DECONSTRUYENDO LOS PATRONES DE DIVERSIDAD DE LOS REPTILES ESCAMADOS (REPTILIA: SQUAMATA) EN AMÉRICA

TESIS POR ARTÍCULO CIENTÍFICO

DECONSTRUCTING THE DIMENSIONS OF THE ALPHA DIVERSITY IN THE SQUAMATE REPTILES (REPTILIA: SQUAMATA) ACROSS THE AMERICAS

QUE PARA OPTAR POR EL GRADO DE:

MAESTRO EN CIENCIAS BIOLÓGICAS

PRESENTA:

JUAN DANIEL VÁSQUEZ RESTREPO

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UNAM POSGRADO

POSGRADO CIENCIAS BIOLÓGICAS

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OFICIO CPCB/1022/2022

ASUNTO: Oficio de Jurado

M. en C Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión ordinaria (Virtual) del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día 29 de agosto del 2022 se aprobó el siguiente jurado para el examen de grado de **MAESTRO EN CIENCIAS BIOLÓGICAS** en el campo de conocimiento de Ecología **del** alumno **VÁSQUEZ RESTREPO JUAN DANIEL** con número de cuenta **521462631** por la modalidad de graduación de **tesis por artículo científico** titulado: **"Deconstructing the dimensions of the alpha diversity in the squamate reptiles (Reptilia: Squamata) across the Americas",** que es producto del proyecto realizado en la maestría que lleva por título: **"DECONSTRUYENDO LOS PATRONES DE DIVERSIDAD DE LOS REPTILES ESCAMADOS (REPTILIA: SQUAMATA) EN AMÉRICA",** ambos realizados bajo la dirección del **DR. JULIÁN ANDRÉS VELASCO VINASCO,** quedando integrado de la siguiente manera:

Presidente: **DR. ENRIQUE MARTÍNEZ MEYER**
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Vocal: **DR. CRISÓFORO FABRICIO VILLALOBOS CAMACHO**
Secretario: **DRA. LETICIA MARGARITA OCHOA OCHOA**

Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 07 de noviembre de 2022

COORDINADOR DEL PROGRAMA

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

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Dedicatoria

A México, a su gente, a sus dioses, su historia, su deliciosa comida, a sus símbolos, a lo que fueron, a lo que son y a lo que serán.

Índice

Resumen

La diversidad alfa es uno de los componentes más notables de las comunidades biológicas, la cual, pese a que tradicionalmente se ha explorado más desde la dimensión taxonómica, se extiende a otras como la filogenética o funcional. En este trabajo, nuestro objetivo fue documentar los patrones geográficos de diversidad alfa en estas tres dimensiones para los reptiles escamados (Reptilia: Squamata) en América, y a partir de esto, explorar los posibles mecanismos eco-evolutivos subyacentes. Recopilamos e integramos la información previamente disponible para casi 3000 especies de reptiles, pertenecientes a siete grupos monofiléticos dentro de la radiación Squamata. Posteriormente, utilizando un enfoque macroecológico deconstructivo, exploramos las relaciones de los patrones de las diversidades a nivel continental y a diferentes escalas filogenéticas mediante modelos geográficos autorregresivos y la espacialización de sus residuales. Encontramos un fuerte patrón latitudinal de acumulación de diversidad taxonómica hacia los trópicos, mientras que las diversidades filogenética y funcional se concentraron en regiones específicas con condiciones ambientales agrestes y/o heterogéneas. También encontramos diferencias al interior de los diferentes clados analizados, quienes mostraron tendencias y patrones geográficos contrastantes. Varias regiones en el continente exhiben patrones geográficos similares, lo que sugiere que procesos eco-evolutivos similares están moldeando los ensambles de reptiles a dicha escala. Sin embargo, la evidencia muestra también que, procesos no mutuamente excluyentes pueden operar de manera diferencial entre grupos.

Abstract

Alpha diversity is one of the most remarkable components of biological communities, which, although traditionally explored more from the taxonomic dimension, extends to other dimensions such as phylogenetic or functional. In this work, our objective was to document geographic patterns of alpha diversity in these three dimensions for squamate reptiles (Reptilia: Squamata) in the Americas, and from this, to explore possible underlying eco-evolutionary mechanisms. We compiled and integrated previously available information for nearly 3000 reptile species belonging to seven monophyletic groups within the Squamata radiation. Subsequently, using a deconstructive macroecological approach, we explored the relationships of patterns of diversities at the continental level and different phylogenetic scales through autoregressive geographic models and the spatialization of their residuals. We found a strong latitudinal gradient of taxonomic diversity with a large accumulation in tropical regions. Phylogenetic and functional diversity patterns were largely congruent given the high phylogenetic signal in the traits used, and higher values tended to be concentrated in harsh and/or heterogeneous environments. We found differences between major clades within Squamata that display contrasting geographical patterns. Several regions across the continent shared the same spatial mismatches between dimensions across clades, suggesting that similar eco-evolutionary processes are shaping these regional reptile assemblages. However, we also found evidence that non-mutually exclusive processes can operate differently across clades.

Introducción general

Desde el boom de la ecología de comunidades durante el siglo XX, el estudio de la biodiversidad se ha caracterizado por un enfoque taxonómico basado en los patrones de riqueza-abundancia (Maurer & McGill, 2011). Con el desarrollo de técnicas más sofisticadas para el análisis de datos y su integración con información filogenética, las brechas entre la ecología y la evolución se han ido reduciendo cada vez más, haciendo el estudio de la biodiversidad sumamente más complejo (McGill et al., 2019). Estos avances han permitido el reconocimiento de la biodiversidad como un concepto integrador que puede ser descompuesto en sus partes fundamentales (también llamadas dimensiones), entre las que se encuentran la taxonómica, la filogenética y la funcional (Colwell, 2009; Devictor et al., 2010; Jarzyna & Jetz, 2016; Ochoa-Ochoa, Mejía-Dominguez, Velasco, Dimitrov & Marske, 2020). Pese a que estas tres no son las únicas dimensiones que existen, si son las que han sido más estudiadas en las últimas décadas debido a que pueden ser fácilmente integradas, proporcionando conocimientos más profundos sobre los procesos ecológicos y evolutivos que les dan origen. Cada uno de estos componentes da cuenta de información complementaria no abarcada por los otros, y en conjunto, permiten describir de manera más completa la estructura y composición de las comunidades, así como los patrones de diversidad (Devictor et al., 2010).

El estudio de estas facetas de la biodiversidad a través de un enfoque macroecológico deconstructivo permite comprender mejor cómo se ha acumulado la biodiversidad a través del tiempo y el espacio (Marquet, Fernández, Navarrete y Valdovinos, 2004). Deconstruir implica tanto descomponer las dimensiones de la biodiversidad, descomponiendo los patrones biogeográficos por clado y/o región, como descomponer los patrones biogeográficos por procesos ecológicos o evolutivos que los producen. Normalmente, cuando se describen los patrones geográficos de diversidad, se asume que las especies o los clados son equivalentes, agrupando el papel de los fenómenos ecológicos y evolutivos en un solo resultado general (Marquet et al., 2004). En consecuencia, la perspectiva de deconstrucción macroecológica ayuda a interpretar los promotores y las escalas en las que una interacción de procesos eco-evolutivos está generando y manteniendo distintas facetas de la biodiversidad (Terribile, Diniz-Filho, Rodríguez & Rangel, 2009). Por ejemplo, adoptando una perspectiva deconstructiva podemos evaluar qué tipos de procesos eco-evolutivos operan diferencialmente a través de escalas espaciales y filogenéticas en diferentes taxones, como la oportunidad ecológica, el filtro ambiental, las interacciones bióticas o la dinámica de diversificación (Brown & Maurer 1989; Prinzing et al., 2008; Yoder et al., 2010; Gillman & Wright, 2013; Graham, Storch & Machac, 2018; Ochoa-Ochoa et al., 2020).

Para una introducción ampliada, véase el texto principal del manuscrito.

Discusión general y conclusiones

El enfoque deconstructivo implementado en este trabajó ayudó a analizar múltiples dimensiones de la biodiversidad a través de escalas filogenéticas, mostrando que, diferentes clados probablemente exhiben respuestas idiosincrásicas a las condiciones ambientales, y permitiendo así una visión más profunda sobre cómo se acumula la biodiversidad en una región y qué procesos eco-evolutivos están dando forma a estos patrones.

La deconstrucción macroecológica se refiere al análisis de los patrones de biodiversidad más allá del número de especies, patrones que pueden ser descompuestos a través de varios ejes. Por ejemplo, podemos examinar cómo varían las relaciones biodiversidad-ambiente en diferentes taxones en función de la geografía (por ejemplo, islas frente a continente), las escalas filogenéticas (por ejemplo, familias frente a órdenes), los rasgos de historia de vida (por ejemplo, vivíparos frente a ovíparos) o la fisiología (por ejemplo, endotermos frente a ectotermos). Este enfoque no es exclusivo para los reptiles escamados y puede utilizarse para comprobar si mecanismos ecológicos y evolutivos similares afectan a otros taxones de forma parecida. Aunque las trayectorias evolutivas idiosincrásicas pueden mostrar que algunos clados tienen una firma espacial particular en sus dimensiones de la biodiversidad, el valor de este enfoque es establecer si un gran clado exhibe respuestas similares a través de sus subgrupos a diferentes mecanismos que varían a través de la geografía.

La aplicación de un enfoque macroecológico deconstructivo en diferentes facetas de la biodiversidad mejora nuestra capacidad para establecer hipótesis eco-evolutivas espacialmente explícitas sobre los procesos que pueden estar dando forma a la biodiversidad. Son necesarios más estudios para comprobar el papel de otros factores ecológicos que promueven estos patrones geográficos de diversidad en Squamata. Nuestro enfoque se basa en la teoría macroecológica y macroevolutiva y, por lo tanto, puede utilizarse en otros taxones con el objetivo de comprobar cómo varían estos mecanismos eco-evolutivos a lo largo de la geografía.

Para una discusión ampliada, véase el texto principal del manuscrito.

Deconstructing the dimensions of alpha diversity in squamate reptiles (Reptilia: Squamata) across the Americas

Short running title: Squamata alpha diversity facets

Abstract

Aim: Our aim is to document the dimensions of current squamate reptile biodiversity in the Americas by integrating taxonomic, phylogenetic, and functional data, and assessing how this may vary across phylogenetic scales. We also explore the potential underlying mechanisms that may have originated the observed geographical diversity patterns.

Location: The Americas.

Time period: Present.

Major taxa: Squamata.

Methods: We used published data on the distribution, phylogeny, and body size of squamate reptiles to document the current dimensions of their alpha diversity in the Americas. We overlapped species ranges to estimate taxonomic diversity (TD) and calculated phylogenetic diversity using mean phylogenetic pairwise distance (MPD), speciation rate (DivRate), and Faith's index (PD). In addition, we estimated functional diversity as trait dispersion in the multivariate space using body size and leg development data. We implemented a deconstructive macroecological approach using spatial autoregressive models to understand how spatial mismatches between the three facets of diversity vary across phylogenetic scales, and the potential eco-evolutionary mechanisms driving these patterns across the geography.

Results: We found a strong latitudinal gradient of taxonomic diversity with a large accumulation in tropical regions. Phylogenetic and functional diversity patterns were largely congruent given the high phylogenetic signal in the traits used, and higher values tended to be concentrated in harsh and/or heterogeneous environments. We found differences between major clades within Squamata that display contrasting geographical patterns. Several regions across the continent shared the same spatial mismatches between dimensions across clades, suggesting that similar eco-evolutionary processes are shaping these regional reptile assemblages. However, we also found evidence that non-mutually exclusive processes can operate differently across clades.

Main conclusions: The implementation of a deconstructive macroecological approach across different facets of biodiversity enhances our capacity to establish spatially explicit eco-evolutionary hypotheses regarding the processes that may be shaping biodiversity. Further studies are necessary to test the role of additional ecological factors driving these geographic patterns of diversity across Squamata. Our approach is based on macroecological and macroevolutionary theory and therefore can be used in other taxa with the aim to test how these eco-evolutionary mechanisms are varying across geography.

Keywords
Deconstruction, functional diversity, macroecology, phylogenetic diversity, reptiles, taxonomic diversity

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Biosketch

Juan D. Vásquez-Restrepo is MSc. student at the National Autonomous University of Mexico. His areas of interest are the Systematics and Taxonomy of Neotropical reptiles, and the processes underlying their diversity. Currently, his research is focused on the macroecological study of the diversity patterns of the reptiles in the Americas at taxonomic, phylogenetic, and functional scales. In recent years he has also been working in scientific outreach for the conservation of these animals.

Author contributions: LMOO, JDVR and JAV conceived the ideas, and LMOO and OFV helped to refine and contextualize them. JDVR collected and analyzed the data. LMOO, JAV and OFV validated the results. JDVR wrote the first draft of the manuscript, and all authors contributed substantially to its revision and writing.

1. Introduction

Since the boom of community ecology during the 20th century, the study of biodiversity has been characterized by a taxonomic approach based on richness-abundance patterns (Maurer & McGill, 2011). With the development of more sophisticated techniques for data analysis and integration with phylogenetic data, the gaps between ecology and evolution have narrowed, making the study of biodiversity increasingly complex (McGill et al., 2019). These advances have allowed the recognition of biodiversity as an integrative concept that may be decomposed into its fundamental components (also called facets or dimensions), including taxonomic, phylogenetic, and functional diversity (Colwell, 2009; Devictor et al., 2010; Jarzyna & Jetz, 2016; Ochoa-Ochoa, Mejía-Dominguez, Velasco, Dimitrov & Marske, 2020). While these three are not the only existing facets, they have been heavily studied in the last decades since they can be relatively easily integrated, providing deeper insights about ecological and evolutionary processes. Each of these components accounts for complementary information not encompassed by the others, and they work together to more completely describe the structure and composition of communities and thus diversity patterns (Devictor et al., 2010).

The study of these biodiversity facets through a deconstructive macroecological approach allows a better understanding of how biodiversity has accumulated through time and space (Marquet, Fernández, Navarrete & Valdovinos, 2004). Deconstructing implies both decomposing dimensions of biodiversity, decomposing biogeographic patterns by clade and/or region, and decomposing biogeographic patterns by ecological or evolutionary processes that produce them. Usually when describing geographical biodiversity patterns, we assume that species or clades are equivalent, lumping the roles of ecological and evolutionary phenomena into one general result (Marquet et al., 2004). Accordingly, the macroecological deconstruction perspective helps to interpret drivers and scales where an interplay of eco-evolutionary processes is generating and maintaining distinct biodiversity facets (Terribile, Diniz-Filho, Rodríguez & Rangel, 2009). For instance, by adopting a deconstructive perspective we can evaluate which kinds of eco-evolutionary processes operate differentially across spatial and phylogenetic scales in different taxa, such as ecological opportunity, habitat filtering, biotic interactions, or diversification dynamics (Brown & Maurer 1989; Prinzing et al., 2008; Yoder et al., 2010; Gillman & Wright, 2013; Graham, Storch & Machac, 2018; Ochoa-Ochoa et al., 2020).

Analyzing the relationship between the different biodiversity dimensions in a geographical context may unveil the occurrence of particular ecological and evolutionary mechanisms in some geographical places or specific clades (Devictor et al., 2010; Safi et al., 2011). Mismatches between taxonomic (TD) and phylogenetic diversities (PD), in which certain regions exhibit more PD than expected by TD, suggest that dispersal predominates over *in situ* diversification (Davies & Buckley, 2011). Similarly, when more functional diversity (FD) is found in a region than expected by TD, ecological opportunity likely drives ecological diversification (Ricklefs, 2010; Stroud & Losos, 2016). These are not the only ecological and evolutionary processes that may help explain observed geographical mismatches between different facets, but they are among the most studied (see Table 1 for a more comprehensive review of potential mechanisms and hypotheses). Also, these eco-evolutionary mechanisms can operate at different spatial and phylogenetic scales and under distinct environmental conditions, and they are not necessarily mutually exclusive hypotheses (Ochoa-Ochoa et al., 2020).

Non-avian reptiles (hereafter reptiles) are an extraordinarily diverse group, comprising more than 11,000 species and occupying almost every biome at the global scale (Roll et al., 2017; Uetz et al., 2021). Among reptiles, the Squamata clade comprises about 97% of extant species, which have diversified since about 190 to 208 million years ago (Irisarri et al., 2017; Simões et al., 2018). The geographical patterns of some biodiversity facets in Squamata have been studied at broad phylogenetic and geographical scales (Wiens et al., 2012; Pyron, Burbrink & Wiens, 2013; Tonini et al., 2016; Roll et al., 2017; Vidan et al., 2019; Meseguer & Condamine, 2020). The recent availability of geographical, phylogenetic, and morphological information for many Squamata species (Feldman, Sabath, Pyron, Mayrose & Meiri, 2015; Meiri, 2018; Tonini et al., 2016; Roll et al., 2017) facilitates the study of how distinct facets of biodiversity emerge at different hierarchical levels of ecology and genealogy, and how different eco-evolutionary processes might drive these patterns. Reptiles exhibit a marked latitudinal diversity gradient, with more TD and PD accumulating along the tropical and subtropical belts (Roll et al., 2017; Gumbs et al., 2020). These diversities are highly asymmetric between subclades, with most families and genera containing few linages (Pincheira-Donoso, Bauer, Meiri & Uetz, 2013). Additionally, a hump-shaped relationship has recently been found for functional traits, where FD reach a peak towards the mid-values of TD (Vidan et al., 2019). However, the relationships among TD, FD, and PD are largely unknown, and spatial mismatches have not been explored in detail within an explicit geographical context for Squamata.

Here, we implement a deconstructive macroecological approach to evaluate how different ecological and evolutionary processes have shaped the geographical patterns of three biodiversity facets (TD, PD, and FD) in squamate reptiles across the American continent. We adopt a hypotheses-driven approach to evaluate how spatial mismatches differ across phylogenetic and spatial scales, and what eco-evolutionary processes may be driving these mismatch patterns.

First, we describe the geographical alpha diversities. Then, we evaluate how the geographical patterns of these three biodiversity facets among clades depart from the general one.

2. Methods

2.1 Geographic, phylogenetic and morphological data

We used previously published large-scale data for living Squamata in order to calculate diversity metrics and adjust our models. Distribution polygons were obtained from the IUCN Red List (https://www.iucnredlist.org), a time-calibrated phylogenetic tree from Tonini et al. (2016), and maximum body size data from Feldman et al. (2015). All data sources were subsampled to include only North, Central and South American taxa. In addition, due to data sources being published independently and in different years, their taxonomy was updated and standardized (see Operational Taxonomic Units section). We are aware that commission (false presences) and omission (false absences) errors make the use of polygonal range maps controversial, but for most reptiles, the large gaps for accurate presence records, as well as a lack of elevation data, ecological preferences, and/or species distribution models, make it impossible to refine them. Nevertheless, coarse species range maps have been regarded as useful for accounting for overall patterns at large spatial scales (Maréchaux, Rodrigues & Charpentier, 2016), particularly when most species have small ranges (Table S1).

2.2 Operational Taxonomic Units (OTUs)

The taxonomy for several groups varies among data sources, therefore, we updated and standardized it (Supplementary Files I) following the December 2020 update of The Reptile Database (TRDB, http://www.reptile-database.org). We treat species as Operational Taxonomic Units (OTUs). For groups with complex taxonomic histories, synonymized taxa and subspecies in the TRDB 2020 backbone taxonomy were not updated but rather provisionally named in quotation marks and assigned as distinct OTUs. Given that the focus of this study is not taxonomic, and recognizing that these groups may encompass high geographic, genetic, and/or morphological variation, we aim to avoid losing diversity information from such groups, despite some species limits being subject to discussion.

2.3 Tree uncertainty

Because the Tonini et al. (2016) supertree contains multiple polytomies derived from the combined method used to build it (phylogenetic inference + imputation), dichotomization was necessary for subsequent analysis. To do this, we randomly resolved the tree polytomies 100 times to non-zero length branches using the *fix.poly* command in the 'RRphylo' library (Castiglione et al., 2021). This function partitions the evolutionary time among the polytomous node descendants while keeping fixed the distance from the root to individual tips and their common ancestor. Stochastically resolving polytomies takes into account phylogenetic uncertainty (Figs. S1–S4) by exploring the parameter space while preserving the information in the dichotomous parts of the tree (Rangel et al., 2015). Then, phylogenetic metrics (see Dimensions of α diversity section) were calculated as the average result of the replicated set of analyses on the 100 randomly resolved trees.

2.4 Dimensions of α diversity

We included 3124 species of Squamata that are in common between the three data sets previously mentioned, representing nearly 90% of the data in each taxonomic group. The three dimensions of diversity (TD, PD, and FD) were evaluated for all included Squamata, and for each major monophyletic clade within it as recovered by Tonini et al. (2016): Amphisbaenia (101 spp.), Anguimorpha (108 spp.), Gekkota (234 spp.), Gymnophthalmoidea (360 spp.), Iguania (979 spp.), Scincoidea (92 spp.), and Serpentes (1249 spp.). Each group incorporates between 63–80% of the total OTUs for the Americas in the three data sets (Fig. S5). We excluded Dibamidae from the subgroups analyses because it is monotypic in America.

Geo-spatial analyses were conducted in a resolution of 55 km using the Behrmann equal-area projection (~ 0.5°). Taxonomic diversity (TD) was calculated as the number of species (S) in each cell after overlapping species distribution polygons. For phylogenetic diversity (PD), we used three different metrics based on tree branch lengths: mean pairwise phylogenetic distance (MPD), which represents the average phylogenetic distance or average time of divergence among species (Eme, Anderson, Myers, Roberts & Liggins, 2020); averaged speciation rate (DivRate), calculated as the inverse of the evolutionary distinctiveness (also referred as 'mean fair proportion'), which is a measure of how evolutionarily isolated a species is (Redding & Mooers, 2006; Isaac, Turvey, Collen, Waterman & Baillie, 2007; Title & Rabosky, 2018); and Faith's PD metric (Faith, 1992), expressed as the sum of the branch lengths of all species present in a cell. These metrics have been widely used in phylogenetic community ecology for describing community and assembly mechanisms (Swenson, 2019), and, except for Faith's PD, they show little mathematical correlation with species richness (Table S2; Oliveira et al., 2016). Available data for functional traits in reptiles are largely incomplete at our taxonomic scale of interest, being limited to maximum length, maximum estimated mass, and leg development (GARD, http://www.gardinitiative.org). We chose to use body mass and leg development as a proxy of functional diversity because: mass and leg development are related to species' physiology and ecology (Smith & Lyons, 2013; Rapacciuolo et al., 2017); and because body mass is a better proxy than the length in groups with length-mass allometry (Meiri, 2010; Feldman & Meiri, 2012). Functional diversity (FD) was estimated using a measure of trait dispersion in the multivariate space (FDis), calculated as the mean distance of individual species to the centroid of all species in the community (Laliberté & Legendere, 2010). We also used the MPD as an indirect surrogate of functional diversity, given that body mass (Pagel's $\lambda = 0.93 \pm 0.002$) and leg development exhibited a high phylogenetic signal (Pagel's $\lambda = 1$). When phylogenetic signal is present, clustering or overdispersion in a community may be informative on functions, under the assumption that closely related species are functionally similar (Swenson, 2019).

All analyses were conducted using Rstudio with R v.4.0.5. The presence-absence matrix and polygon overlapping were generated with the command *lets.presab* in the library 'letsR' v.4.1 (Villela & Villalobos, 2015). Phylogenetic diversity metrics were calculated using the package 'picante' v.1.8.2 (Kembel et al., 2010) and its functions *mpd*, *evol.distinct*, and *pd*. For functional diversity calculations, we used the function *fd_fdis* in the 'fundiversity' v.0.2.1 library (Grenié & Gruson, 2021).

2.5 Drivers of α diversity

To explore associations among the different diversity dimensions, we opted for a global regression analysis instead of a local one, given that global approaches are more suitable for general inferences (Jetz, Rahbek & Lichtein, 2005). To account for the high autocorrelation of the diversity facets (Fig. S6), we addressed their relationships using two types of spatial autoregressive models (Ver Hoef, Peterson, Hooten, Hanks & Fortin, 2018), the conditional autoregressive (CAR) and the simultaneous autoregressive (SAR). A key difference between CAR and SAR is that the former is "spatially memoryless" (Markov property), that is, it assumes that the value in a particular area is influenced by its neighbors and not by the neighbors of its neighbors (Ver Hoef, Hanks & Hooten 2018). For the SAR model, we adjusted both the spatial-lagged (SAR-SL), which accounts for spatial dependence auto-regressing the response variable on a spatially lagged version of itself (dependence comes from location), and the spatial error (SAR-SE), in which spatial dependence is accounted through an error term and the associated spatially lagged error term (dependence comes from unobserved variables). Thus, we adjusted five models for the PD ~ TD, FD ~ PD, and FD ~ TD relationships by each model type (Table 2), and spatialized the regressions' residuals of the best-fitted models in order to address the hypotheses regarding the underlying processes of the diversity facets (Table 1). Residuals from spatial autoregressive models can be decomposed (Haining, 2003) as the sum of the signal trend (non-spatial component) + signal stochasticity (spatially structured random variation) + noise (spatially unstructured random variation). In our case, most models' residuals (observed - fitted) tended to zero, making it impossible to detect a spatial pattern. For this reason, we subtracted the observed values from the trend signal only. Since residuals are random (non-significant Moran's I test), we included Faith's PD in this analysis, but omitted the DivRate because of its high phylogenetic uncertainty (Fig. S1–S2). Models were adjusted using the R package 'spatialreg v.1.1.5 (Bivand, Millo & Piras, 2021) and its functions *spautolm* (CAR), *lagsarlm* (SAR-SL), and *errorsarlm* (SAR-SE).

3. Results

3.1 Diversity patterns

The three facets of reptile alpha diversity in the Americas showed different geographic patterns across the continental landscapes. We do not discuss island diversities because they are underrepresented in our compiled dataset. A higher concentration of species richness was found to occur in the tropical region, including the Amazon Basin and its periphery, the biogeographic region of Chocó, the Andes, and Central America to southern Mexico (Fig. 1A). On the other hand, lower values of taxonomic diversity were recovered in temperate latitudes and the South American Arid Diagonal. Latitudinal profiles show two additional small diversity peaks, one located approximately in 30° N and the other in south-central Mexico. Higher speciation rates are concentrated in the high northern latitudes and southeastern South America, while low rates are observed in most of North and Central America, and in South America through the Pacific versant following the Andean line (Fig. 1B). Moreover, the MPD evidenced higher phylogenetic overdispersion in the arid region of North America, southern Mexico, the Chocó biogeographic region, the Andes, the Guiana Shield, the Caatinga biome, and the southernmost grasslands, scrubs, and steppes of South America (Fig. 1C). Most other regions exhibited intermediate values of phylogenetic distance, except for the most northern latitudes and some small spots in the Atlantic Forest. Likewise, functional diversity showed a similar pattern to the MPD, but did not include the biogeographic Chocó, the Guiana Shield, or the Caatinga (Fig. 1D). Functional diversity also exhibited a hump-shaped relationship with taxonomic diversity (Fig. 2A), with higher values at low to mid species-rich assemblies, suggesting functional equivalence or redundancy in the high specious ones. After accounting for the species effect, functional diversity showed a slightly negative but significant correlation ($R^2 = 0.07$, $p < 0.001$) with the speciation rate (Fig. 2B), which increased significantly ($R^2 = 0.47$, $p < 0.001$) with evolutionary time (Fig. 2C). Such a relationship between functional diversity and evolutionary time supports the assertion that closely related species are functionally similar. Of note, particular patterns emerged among the seven clades analyzed (Fig. 3) with contrasting regions of high diversity (Table 3), although patterns of speciation rate may be still obscured in some regions due to the phylogenetic uncertainness associated with some species-rich polytomous lineages (Figs. S1).

3.2 Spatial mismatches

For the PD ~ TD relationship, the MPD showed a predominance of negative residuals, indicating more phylogenetic clustering than expected by species richness (Fig. 4A). Despite this general pattern, however, some regions contain clumps of more negative values, specifically in eastern USA, central Mexico, the cis-Andean region in northwest South America, the Central Andes, and the Atlantic Forest. On the other hand, Faith's metric exhibited both positive and negative residuals, meaning the sum of evolutionary time was both more and less than the expected by the number of species, depending on the region (Fig. 4B). For instance, North and Central America (except central Mexico), the Chocó biogeographic region, the Northern Andes, the Guiana Shield, the Caatinga biome, and southeast South America showed positive values, while the Atlantic Forest, the main Amazon core, central Mexico, and the Central and Southern Andes showed negative ones. This suggests that in regions with both MPD and Faith's PD values being negative (e.g., the main Amazon core and the Atlantic Forest), low phylogenetic diversity may be driven by few dispersals coupled with many speciation events. On the contrary, in those regions with negative MPD and positive Faith's PD residuals (e.g., North and Central America, the Andes, Guiana Shield, Caatinga biome), dispersal is likely promoting higher phylogenetic diversity, but *in situ* speciation of these lineages is also taking place.

In the FD ~ PD relationship, FD was found to exhibit a trend of positive residuals with mean evolutionary time (Fig. 4C) and intermixed values for the accumulated evolutionary time (Fig. 4D). Most positive values are found in western North America and Central America, the Andes, and southern South America, while negative ones (only for Faith's PD) are located in the eastern USA, and the Amazon core and its periphery. This can be translated as more functional dispersion than expected by phylogenetic relatedness, which is likely driven by competitive interactions. As we mentioned before, MPD may be used as a surrogate for functional diversity, accounting for why the FD ~ TD pattern is virtually identical to that of PD ~ TD using the mean evolutionary time, although without negative residuals. Namely, the FD ~ TD relationship showed more functional dispersion than expected given the number of species, with a higher disparity in western North America, Central America, the Northern Andes, the main Amazon core and its periphery, and southern South America (Fig. 4E). On the contrary, lower values were observed in the cis-Andean portion of northwest South America, the Central Andes, and the Atlantic Forest. This residual structure is commonly associated with the availability of ecological space and/or ecological stability.

The clade-specific analyses showed different patterns among groups (Fig. 5; Table 4). The FD ~ PD and FD ~ TD patterns were more similar to each other than the PD ~ TD patterns. Moreover, depending on the phylogenetic metric used, patterns had slight differences in the magnitude of residuals and their presence in certain areas, although they generally were congruent and point in the same direction.

4. Discussion

4.1 Diversity patterns

The geographical patterns for taxonomic and phylogenetic diversity in squamate reptiles across the Americas are very similar to patterns seen in other taxa such as birds, mammals, and amphibians (Blackburn & Gaston, 1996; Davies, Buckley, Grenyer & Gittleman, 2011; Jenkins, Pimm & Joppa, 2013; Ochoa-Ochoa et al., 2020). They are also congruent with the global reptile patterns described by Roll et al. (2017) and Gumbs et al. (2020) in finding higher diversities in the tropics. However, the phylogenetic diversity pattern using Faith's PD differs substantially from our findings using the MPD, due to the former being a phylogenetic generalization of species richness (Chao & Jost, 2010). Concerning the functional diversity, we found a non-monotonic relationship with species richness, similar to a previous study focused solely on lizards (Vidan et al., 2019). Although Vidan et al. (2019) measured the functional diversity using a different approach, the resulting trend is the same as our findings, which supports the idea of functional redundancy in species-rich assemblages. The latitudinal diversity gradients, with two small peaks in the northern latitudes, is highly congruent with patterns observed in amphibians (Ochoa-Ochoa et al., 2020), suggesting that similar eco-evolutionary processes are likely involved in the origin and maintenance of biodiversity facets for both taxonomic groups. By implementing a deconstructive macroecological approach across phylogenetic scales, we found substantial differences between clades that exhibit disparate ecological and evolutionary trajectories. In addition, despite the fact that functional diversity estimation may be affected by the type and number of included traits, as well as the metric or index used, the geographical correspondence we found in several areas between this and the mean evolutionary time not only confirms that phylogenetic surrogates are very useful in the absence of functional traits, but also that the two traits we selected proved informative enough to recover functional patterns. We noticed that the overall geographical diversity patterns found across Squamata are strongly driven by highly speciose lineages, particularly snakes.

Consequently, the deconstructive approach implemented here helped analyze multiple dimensions of biodiversity across phylogenetic scales, showing that different clades likely exhibit idiosyncratic responses to environmental conditions, and thus allowing deeper insights about how biodiversity accumulates in a region and which eco-evolutionary processes are shaping these patterns (Marquet et al., 2004). Accordingly, the contrasting relationships between different dimensions among clades seem to indicate that functional and phylogenetic diversity are accumulated at different rates in a region.

Macroecological deconstruction refers to analyzing biodiversity patterns beyond the species number, and we can deconstruct patterns across several axes. For example, we can examine how biodiversity-environmental relationships in different taxa vary across geography (e.g., island vs. mainland), phylogenetic scales (e.g., families vs. orders), life-history traits (e.g., viviparous vs. oviparous) or physiology (e.g., endotherms vs. ectotherms) (Marquet et al., 2004). This approach is not exclusive to Squamate reptiles and can be used to test whether similar ecological and evolutionary mechanisms affect other taxa similarly. Although the idiosyncratic evolutionary trajectories can show that some clades have a particular spatial signature on their biodiversity facets, the worth of this approach is establishing whether a large clade exhibit similar responses across its clades to different mechanisms varying across geography.

4.2 Phylogenetic and taxonomic mismatch structure

Clade-specific mismatches across geography, in which an excess in positive residual values are observed, suggest that *in situ* diversification has been slow and that many reptile assemblages were likely shaped by multiple colonization events from nearby regions, and vice versa. The Mexican Transition Zone, for instance, recovered contrasting patterns across several clades. This region is well-known to harbor to a high biotic interchange between temperate and tropical biotas, thus historical dispersal events may be driving the high phylogenetic diversity found therein (DC hypothesis in Table 1). Unfortunately, the phylogenetic uncertainness associated with the speciation rate does not allow us for testing this explicitly. Phylogenetically distant lineages were also found in several arid or desert regions, such as northern Mexico and in some regions of South America such as the Caatinga, Cerrado, and the Chaco, which may be the result of a combination of dispersal and habitat filtering mechanisms (DC and HF hypotheses in Table 1) playing in concert to shape the membership of these regional assemblages. For example, recent studies have found evidence of multiple dispersal events towards these regions in several taxa (Antonelli et al., 2018). However, further work will be necessary to establish those functional traits which might have evolved by convergence.

In the case of gymnophthalmoids and iguanids that showed phylogenetic diversity values lower than expected by species richness in arid regions (e.g., northern Mexico), ecological opportunity and evolutionary rate (EO and ER hypotheses in Table 1) likely facilitate the generation of many different but closely related species. Some recent studies have found that arid regions in high latitudes facilitate diversification in several clades due to the occupation of widespread habitats across geography (e.g., phrynosomatid lizards; Wiens et al., 2013). It is also likely that many lineages exhibit idiosyncratic evolutionary trajectories across geography in these regions, where multiple factors including climate and geographical barriers facilitate species diversification at fine phylogenetic scales.

The contrasting patterns of positive and negative spatially intermixed residuals of phylogenetic diversity across different clades in different regions, but mainly in the tropic, suggest that these sites are key to understanding how diversity has assembled through time. We propose that these regions may work as macroevolutionary source-sink regions, where regional reptile assemblages are strongly shaped by *in situ* diversification occurring after dispersal. For example, reptile assemblages in the northwestern and southeastern portions of South America, including the Andes, the Chocó biogeographic region, and the Atlantic Forest, were likely shaped by the previously mentioned source-sink dynamics at a macroevolutionary scale, with each clade likely exhibiting particular trajectories of species and ecological diversification. These findings reinforce the idea that eco-evolutionary mechanisms have a scale-dependent effect across geography.

4.3 Functional mismatch structure

The high proportion of intermixed positive and negative residuals in the functional regression analyses of both phylogenetic and taxonomic diversity in some areas and in some clades, suggests that ecological space, competitive interactions, and/or habitat filtering mechanisms are operating predominantly (ES, CI, and HF hypotheses, respectively, in Table 1). These drivers may be acting differentially or synergistically. For instance, when higher functional diversity is expected given the phylogenetic structure, more ecological opportunities may allow functional disparity (EO in Table 1), but in phylogenetically clustered communities, past negative interactions led to trait divergence (EI in Table 1). Contrary, less functional diversity in phylogenetically distant assemblages may be indicative of habitat filtering. However, with our analysis it is not possible to discern which driver has a stronger effect or the partial contributions of each one however, the occurrence of these mismatches in harsh environments, or in regions with higher primary productivity or more complex habitat structure, may provide insights into the prevailing processes. Although monophyletic groups are the result of shared evolutionary history, not all their linages have been affected by the same eco-evolutionary mechanisms, deriving into multiple internal evolutionary histories. Furthermore, common regions where patterns exhibit similar trends suggests shared mechanisms among groups that effectively couple the biotas in such places, whereas the same mechanisms may not necessarily operate across similar regions.

In arid and dry zones, habitat filtering mechanisms and less environmental heterogeneity (HF and EH hypotheses in Table 1) tend to operate more strongly. Thus, low values of functional diversity are expected, as is the case of the North America deserts or the Arid Diagonal in South America. Nevertheless, we found the opposite for Squamata as a whole, and mixed evidence when decomposed into major clades. This may indicate limited ecological space (EO hypothesis in Table 1) driving intensive competitive interactions (CI hypothesis in Table 1), allowing species to diversify functionally despite the environmental pressure in the opposite direction. On the other hand, some clades like Gekkota, Gymnophthalmoidea, and Iguania showed low functional diversity in harsh environments that may be related with relaxed biotic interactions producing more trait homogenization and high niche packing by differential use of resources (Pianka, 1974), since when one niche dimension is broad, another is usually narrower (Costa-Pereira, Araújo, Souza & Ingram, 2019). Accordingly, we hypothesize that despite some mechanisms likely playing a strong role on a single facet of biodiversity, under certain environmental conditions other eco-evolutionary processes might be prevalent in other facets.

For Squamata, in regions with an extensive ecological space availability and heterogeneity (e.g., the Amazon core or the Andes), we found opposing patterns according to the metric used. That is, less functional diversity (EO and ES hypotheses in Table 1) than expected was found given the accumulated phylogenetic distance, and more for the mean phylogenetic distance. As we showed, functional diversity increases with evolutionary time, but this increase is likely asymptotic due to functions being limited by the number of species (there can not be more functions than species) and by environmental constraints. Therefore, as Faith’s PD accumulate more phylogenetic diversity in species-rich assemblages, it should exceed this asymptotic value, generating a "functional deficit" that obscures the pattern (Fig. 6). Furthermore, it is likely that ecological space in such tropical regions is already saturated, therefore limiting functional diversification. In addition, ecological stability (ES hypothesis in Table 1) in some regions may promote high functional diversity in different clades such as Amphisbaenia, Gekkota, Gymnophthalmoidea, Iguania, and Serpentes. These clades seem to share similarities in functional diversity in areas of past climatic stability (Costa et al., 2018), such as the Amazon core and north and northwestern South America. These contrasting patterns reinforce the idea that multiple eco-evolutionary processes may act in concert to drive ecological and species diversification in such regions.

Further studies including more ecological traits may help discern whether these clades really are ecologically similar and how they utilize the available functional and ecological space. The inclusion of more ecological traits in the estimation of functional diversity will also help identify in which regions clades saturate the ecological space.

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Data availability statement

The online version of this publication contains supplementary files that are available through the publisher’s website.

Supplementary Files I: Species list and taxonomic updates for each data source used.

Supplementary Files II: Supplementary figures and tables (indicated as Fig. S or Table S). All figures are also provided as independent files in best quality and full-size.

Supplementary Files III: Raster files generated in this study.

Deconstructing the dimensions of the alpha diversity in the squamate reptiles (Reptilia: Squamata) across the Americas

Juan D. Vásquez-Restrepo, Leticia M. Ochoa Ochoa, Oscar Flores-Villela, Julián A. Velasco

Tables

Table 1. Review of proposed ecological and evolutionary hypotheses and mechanisms driving biodiversity dimensions. When a driver promotes a facet diversification, it is indicated with a plus sign (+), while a minus sign (–) indicates that a driver constrains it. We only mention the most comprehensive studies for each hypothesis and acknowledge that these are not the only ones, therefore, we encourage readers to check additional sources cited within them.

Driver	Hypothesis	Intensity → Result	Reference
Ecological opportunity (EO)	Ecological space availability can promote or constrain species and trait diversification according to adaptive radiation theory.	> EO → + TD / + FD < EO → – FD	Ricklefs (2010) Yoder et al. (2010) Safi et al. (2011) Stroud & Losos (2016)
Habitat filtering (HF)	More extreme environmental conditions limit species numbers and trait diversification. Sites with harsh conditions tend to exhibit lineages more similar in traits. On the contrary, sites with less stressful conditions can promote trait diversification.	> HF → + TD[1] / ± PD[2] / – FD < HF → + PD / + FD	Safi et al. (2011) Götzenberger et al. (2012) Wiens, Kozak & Silva (2013) Ochoa-Ochoa et al. (2020)
Competitive interactions (CI)	Biotic interactions among co-occurring species with similar ecological requirements lead to competitive exclusion, therefore promoting more trait dissimilarity. On the contrary, relaxed interactions promote more trait homogenization.	> CI → + FD < CI → – FD	Safi et al. (2011) Götzenberger et al. (2012)
Evolutionary Interaction (EI)	A negative correlation is expected between phylogenetic and trait dispersion if negative interactions occur among more related species. This is a particular case of the CI involving past interactions that cause trait divergence.	> CI → – PD / + FD	Prinzing et al. (2008)

Evolutionary rate (ER)	The rate at which lineages evolve promotes or constrains diversification. When high, many different but closely related species are generated. On the contrary, species diversity is expected to be driven by the arrival of foreign distantly-related species.	> ER → + TD / – PD < ER → + TD / + PD	Davies & Buckley (2011)
Effective evolutionary time (EET)	Species will accumulate fastest in areas where temperatures are higher, which also promotes higher mutation rates, fast selection, and more niche diversification. This is a particular case of the ER, including temperature as an *ad hoc* hypothesis explaining the rates.	> EET → + TD / – PD / + FD < EET → – TD / + PD / – FD	Gillman & Wright (2013)
Evolutionary time (ET)	The time a lineage has been in a geographic area is positively related to the amount of diversity accumulated. With longer times and high speciation rates, phylogenetic diversity is low and depends on dispersal, while with low speciation rates, phylogenetic diversity is affected by old lineages.	> ET → + TD > ET & > ER → + TD / – PD > ET & < ER → + TD / + PD	Mittelbach et al. (2007)
Dispersal-Colonization (DC)	The movement of the species in space increases the number of non-related species among sites.	> DC → + TD / + PD < DC → – PD	Davies & Buckley (2011)
Environmental heterogeneity (EH)	The heterogeneity of environmental conditions can promote or constrain trait diversification. For instance, heterogeneous conditions promote more phenotypic diversification, while homogeneous conditions constrain phenotypic variation.	> EH → + FD < EH → – FD	Safi et al. (2011)

Ecological stability (ES)	Stability in ecological conditions can promote or constrain species and trait diversification. Together with environmental heterogeneity, it can differentially drive diversity dimensions.	> ES & > EH → + TD / + PD / + FD > ES & < EH → – TD / + PD < ES & > EH → + TD / + PD / + FD < ES & < EH → – TD / – PD	Mittelbach et al. (2007) Colville et al. (2020)
Random Sampling (RS)	Given most functional traits have phylogenetic signal with no negative interactions, large randomly assembled communities will be phylogenetically overdispersed and will contain more trait variance.	> RSH → + PD / + FD < RSH → – PD / – FD	Prinzing et al. (2008)

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[1] There is evidence that some groups (e.g., phrynosomatid and liolaemid lizards) may diversify in extreme environmental conditions (Wiens, Kozak & Silva, 2013; Esquerré, Brennan, Catullo, Torres-Pérez & Keogh, 2018).

[2] In harsh environments, PD may be high despite habitat filtering when a lineage has evolved *in situ* for a long time (Wiens et al., 2013), as well as when environmental conditions convergently filter eco-physiological species that are not closely related. On the contrary, PD is constrained.

Table 2. Global models used to fit the relationships among diversity facets. The best model for each relationship is highlighted in **bold**. Data by clade are available in Tables S3–S9.

Model	**Type**	**AICc**	**Residuals autocorrelation**	
			Moran's I	***p***
PD ~ TD (MPD)	CAR	89600	-0.09	1
	SAR-LM	88830	-0.03	1
	SAR-EM	**87050**	**-0.07**	**1**
PD ~ TD (Faith's PD)	CAR	126817	-0.05	1
	SAR-LM	133821	0.18	< 0.001
	SAR-EM	**120600**	**-0.06**	**1**
FD ~ PD (MPD)	**CAR**	**-21790**	**-0.13**	**1**
	SAR-LM	-18144	0.02	< 0. 001
	SAR-EM	-19643	-0.08	1
FD ~ PD (Faith's PD)	CAR	-16745	-0.10	1
	SAR-LM	-16502	-0.06	1
	SAR-EM	**-17384**	**-0.07**	**1**
FD ~ TD	**CAR**	**-17245**	**-0.10**	**1**
	SAR-LM	-16440	-0.06	1
	SAR-EM	-16868	-0.07	1

Table 3. Summary of the diversity patterns of squamate reptiles in continental America. We only describe areas with the highest values based on the last 25% of the data (quantile maps are available in Fig. S8).

Group	Species richness	Speciation rate	Evolutionary time	Functional diversity
Amphisbaenia	East South America, mainly in the Cerrado biome	Southeast South America and part of the Caribbean islands	Main Amazon core, Guiana Shield, and southeast South America in Paraguay and northern Argentina	Guiana Shield and the Cerrado biome
Anguimorpha	Scattered across central México	Patchy from Guatemala to northern Mexico, and western North America	Scattered across central-south Mexico, northern Mexico, and adjacent USA	Northern portion of the Baja California peninsula and adjacent USA, scattered across the Pacific versant of Mexico, and Uruguay
Gekkota	Hispaniola and Cuba	Patchy, in the Caribbean islands, Baja California peninsula, central Mexico, trans-Andean Colombia, Central Andes in Peru, and the southern portion of South America	Central America, northwestern Amazon, and patchy across east South America	Central America, and scattered across the western and southern Amazon, and the Cerrado biome
Gymnophthalmoidea	The Guiana Shield and the main Amazon core	Northern Mexico and adjacent USA, the Yucatán peninsula, along the Andes from Colombia to the Bolivian Amazonia, the Atlantic Forest, and the Lesser Antilles	Central America, northwestern Amazon, Guiana Shield, patchy across Ecuador and Peru, northeast and southeast South America	Northwestern South America, scattered across the Amazon core, and the Cerrado biome

Iguania	Costa Rica, the Chocó biogeographic region, and Cuba	Southern, eastern, and northeastern South America, also central Mexico	Eastern USA, central Mexico to middle Central America, northwestern South America, the main Amazon core, and patchy across eastern South America	Northern and northwestern South America, through Central America to central Mexico, and scattered in the Caribbean islands
Scincoidea	Eastern USA, scattered across Central America, and eastern South America	Central America, southwest Amazon in Colombia, Ecuador, and Peru, and northeast South America	Central America and northern portion of the Baja California peninsula and adjacent USA	Eastern USA, northern Mexico, scattered in middle Central America, and northern Amazon
Serpentes	Main Amazon core and the Atlantic Forest	Northwest North America, the Andes, and southeast South America	North and northwestern South America, Caatinga biome, Central Andes to central-north Argentina, northwestern North America, and patchy across northern Mexico and the Caribbean islands	Southern USA to north-central Mexico, scattered across Central America, northwestern and northern South America, the Central Andes, central Argentina, and the Caatinga and Cerrado biomes

Table 4. Summary of the spatial mismatches for squamate reptiles in continental America. We only describe areas with the highest positive/negative values based on the first and last 10% of the data (quantile maps are available in Fig. S9).

Group		PD ~ TD	FD ~ PD	FD ~ TD
Amphisbaenia	+	The main Amazon core, the Guiana Shield, and part of southeast South America	Northern South America in the Guiana Shield and scattered across the Cerrado biome	Northern South America in the Guiana Shield and scattered across the Cerrado biome

	–	East South America and part of the Caribbean islands	The northwest, northeast, and southeast portions of South America, and part of the Caribbean islands	The northeast and southeast portions of South America, and part of the Caribbean islands
Anguimorpha	+	Scattered across Mexico	The northern portion of the Baja California peninsula and southeast South America in Uruguay	The northern portion of the Baja California peninsula and southeast South America in Uruguay
	–	Southeast South America and western USA	Scattered across Mexico	Scattered across Mexico
Gekkota	+	Scattered across Mexico, Central America, and the Amazon and its periphery	Scattered across the Atlantic versant of southern Mexico to Central America, part of the western Amazon, and the Cerrado biome	Scattered across the Atlantic versant from southern Mexico to Central America, and part of the western Amazon
	–	Southern South America, northern Venezuela, the Caribbean islands, and part of the Andes from southern Colombia	Scattered across the Pacific versant of Mexico to Central America, Cuba, the Chocó and the Andes of Colombia, and northeast South America	Baja California peninsula, Cuba, the Chocó and the Andes of Colombia, and part of southern South America
Gymnophthalmoidea	+	North, northwestern, and southeastern portions of South America, and scattered across the Lesser Antilles, Central America, and the Ecuadorian and Peruvian Andean foothills	Northwestern South America, and scattered across the Cerrado biome and the Central Andes foothills	Northwestern South America, and scattered across the Cerrado biome and the Central Andes foothills
	–	From southern to northern Mexico and adjacent USA, Hispaniola, and the Andes from Ecuador to Bolivia	From southern to northern Mexico and adjacent USA, the Pacific versant of Colombia and Ecuador, and patchy across the Atlantic Forest	From southern to northern Mexico and adjacent USA, the Pacific versant of Colombia and Ecuador, and patchy across the Atlantic Forest
Iguania	+	Eastern USA, and scattered across Central America, northwestern South America, the southern Amazon, and the Caatinga and Cerrado biomes	Central America, the northwestern portion of South America, and part of eastern Amazon	Central America and the northwestern portion of South America

	–	Central Mexico, the South American Arid Diagonal, and some Caribbean islands	Western and eastern USA, the South American Arid Diagonal, part of the southeast and northeast South America	Western USA and the Florida peninsula, the South American Arid Diagonal, and part of southeastern South America
Scincoidea	+	Along the Atlantic versant of Central America, and scattered in south-central and southwest USA	Northern Mexico and adjacent USA, Florida peninsula, and the northern Amazon	Northern Mexico and adjacent USA, and the Florida peninsula
	–	Eastern and northeastern South America and scattered in North America	Mainly in the main Amazon core and the central-south portion of South America	Mainly in the main Amazon core and the central-south portion of South America
Serpentes	+	The northern portion of South America, the South American Arid Diagonal, northwestern North America, and scattered across the Caribbean islands	Scattered across North America, part of Central and northwestern South America, the Caatinga biome, and patchy across the Central Andes and the southern portion of South America	Scattered across North America, part of northwestern South America, and patchy across the Central Andes and the southern portion of South America
	–	Scattered across North and Central America, and the southern and southeast portions of South America	Patchy across the northern portion of North America, south-central Mexico, western and southern Amazon, the Atlantic Forest, and the Caribbean islands	Patchy across the northern portion of North America, south-central Mexico, scattered in the Amazon, the Atlantic Forest, and the Greater Antilles

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Figures

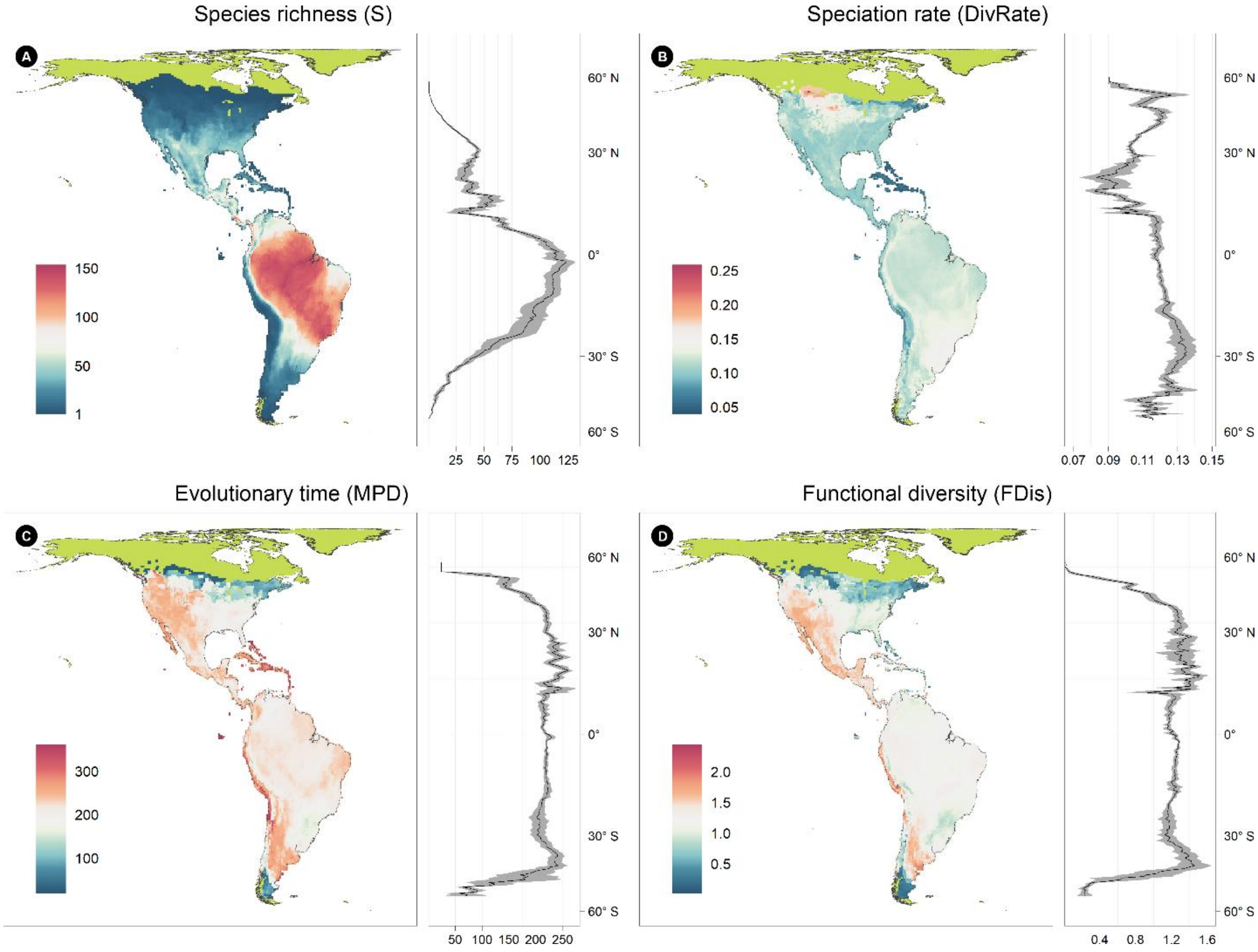

Figure 1. Geographical variation in taxonomic (**A**), phylogenetic (**B**–**C**), and functional diversity (**C**–**D**) for squamate reptiles in the Americas. Regions with no data are colored in light green. Maps are in Berhamnn equal-area projection. Faith's PD is not included due to its high correlation with species richness, but is available in Fig. S7. This figure is color-blind friendly and is also provided in best quality and full-size in Supplementary Files II. Raster files are available in Supplementary Files III.

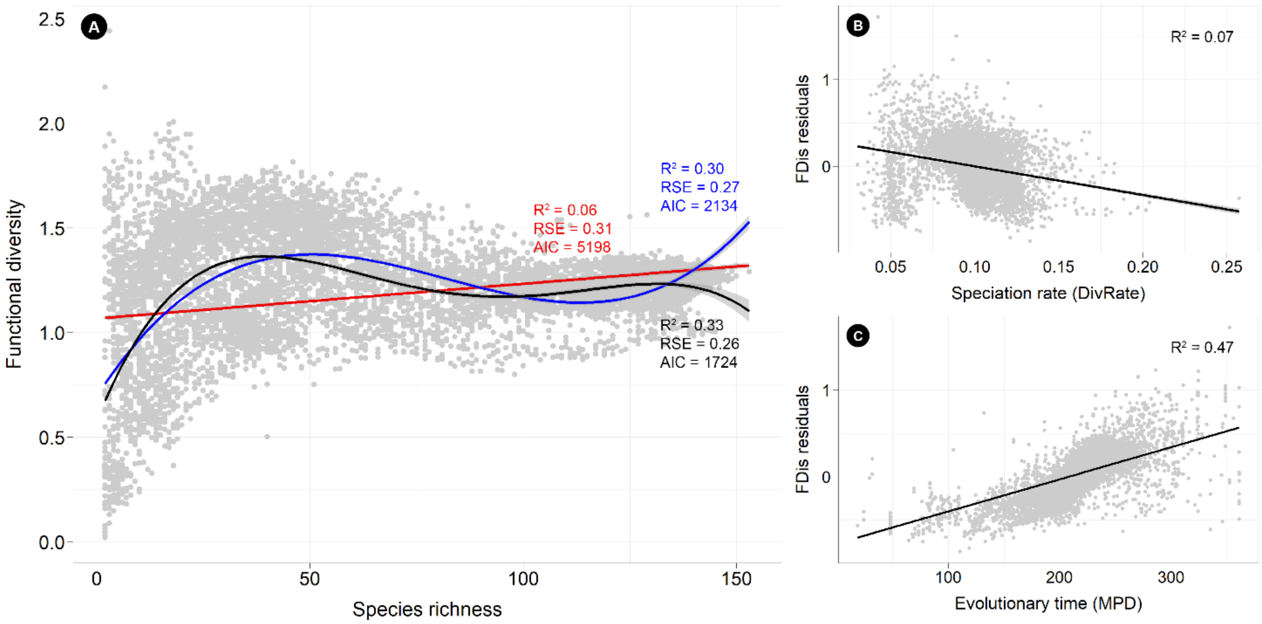

Figure 2. Relationship between functional diversity vs. species richness (**A**), functional diversity species-richness corrected vs. speciation rate (**B**), and functional diversity species-richness corrected vs. evolutionary time (**C**). Colored lines in **A** represent three different models (red: lineal, blue: 3rd degree polynomic, black: 4th degree polynomic).

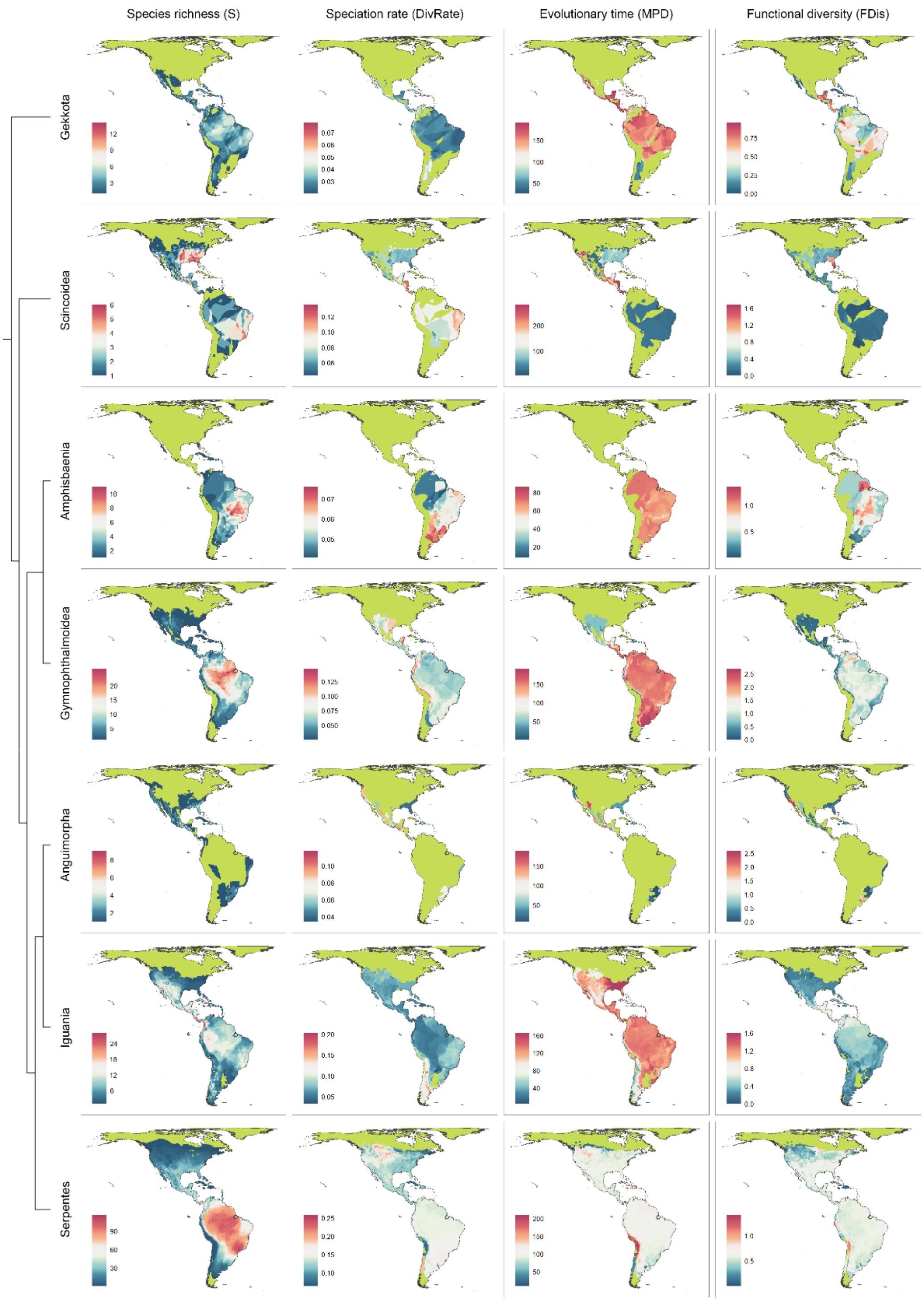

Figure 3. Diversity metrics for squamate reptiles in the Americas. Regions with no data are colored in light green. For DivRate, MPD, and FDis, pixels with a single species are not showed. Maps are in Berhamnn equal-area projection. Faith's PD is not included due to its high correlation with species richness, but is available in Fig. S7. This figure is color-blind friendly and is also provided in best quality and full-size in Supplementary Files II.

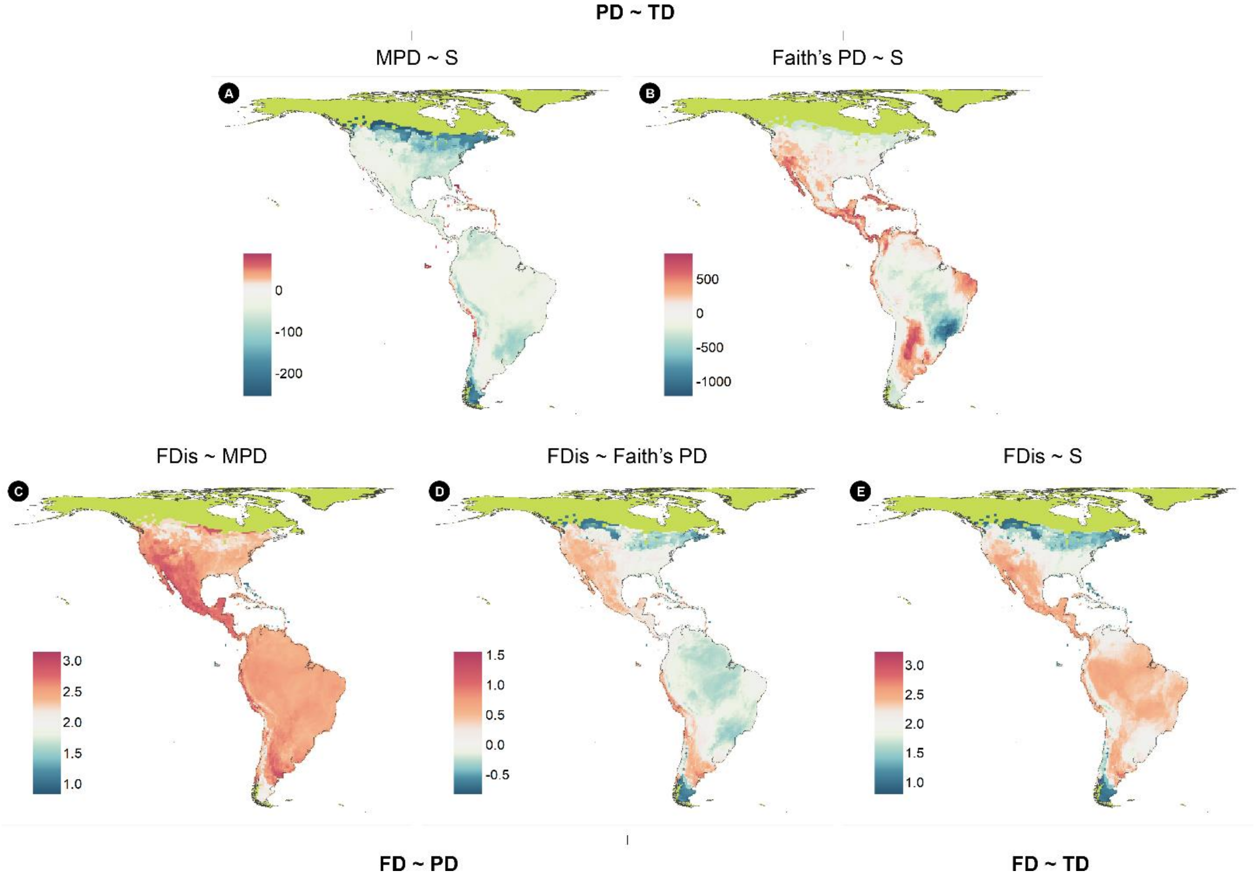

Figure 4. Regression residuals for the adjusted PD ~ TD (**A**–**B**), FD ~ PD (**C**–**D**), and FD ~ TD (**E**) models. Regions with no data are colored in light green. This figure is color-blind friendly and is also provided in best quality and full-size in Supplementary Files II.

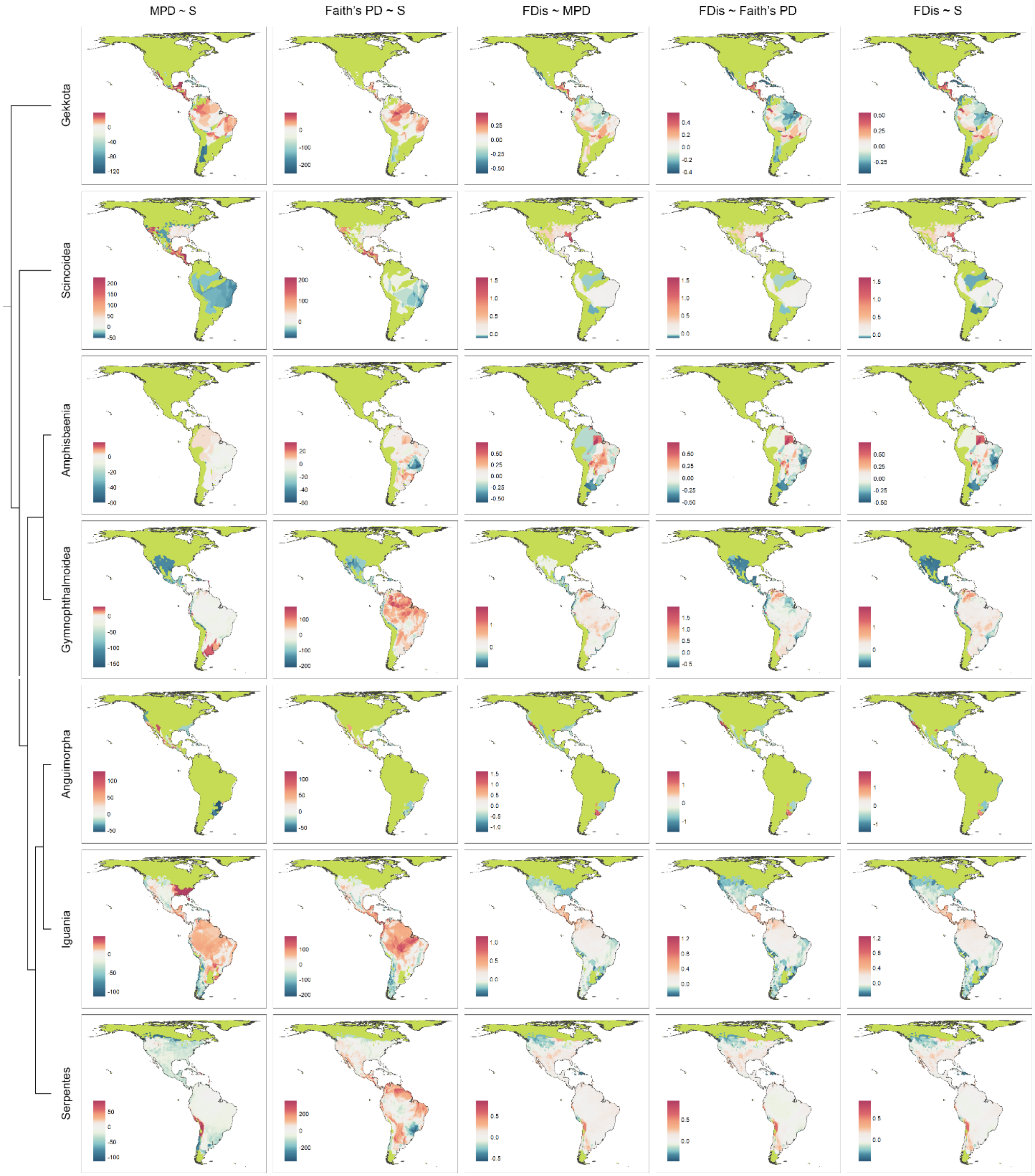

Figure 5. Geographic mismatches by clade. Regions with no data are colored in light green. Maps are in Berhamnn equal-area projection. This figure is color-blind friendly and is also provided in best quality and full-size in Supplementary Files II.

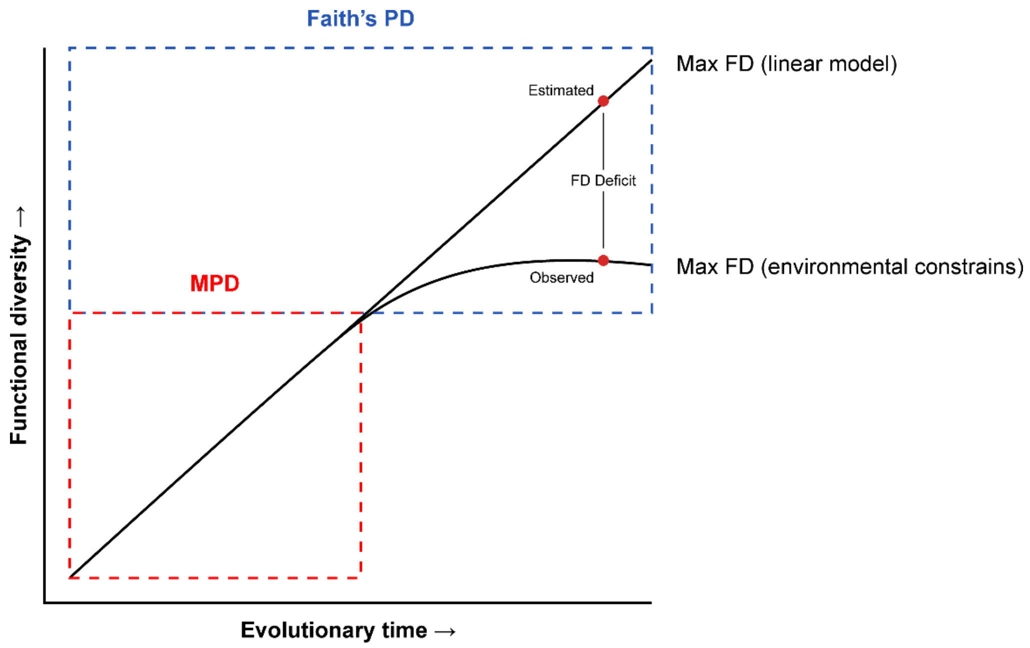

Figure 6. Schematic representation of the functional deficit caused by the use of different phylogenetic measures.

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Supplementary Files II: Figures

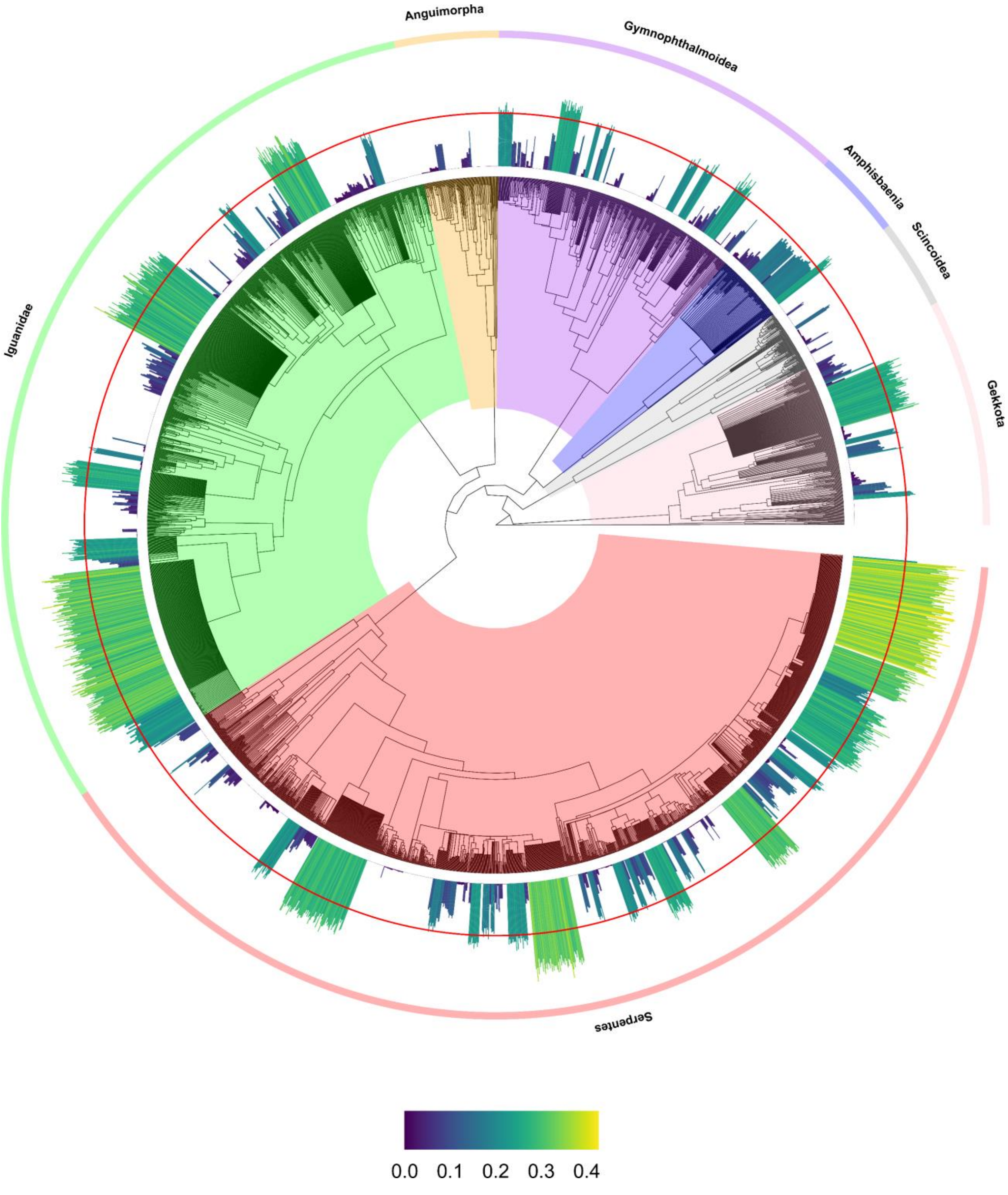

Figure S1. Coefficient of variation of the DivRate (per species) for the Tonini et al. (2016) tree. The red line indicates the 20% threshold. Higher variation is found within highly diverse polytomous genera like: *Anolis* (Iguanidae), *Atractus* (Serpentes), *Dipsas* (Serpentes), *Erythrolamprus* (Serpentes), *Liolaemus* (Iguanidae) *Micrurus* (Serpentes), *Tantilla* (Serpentes).

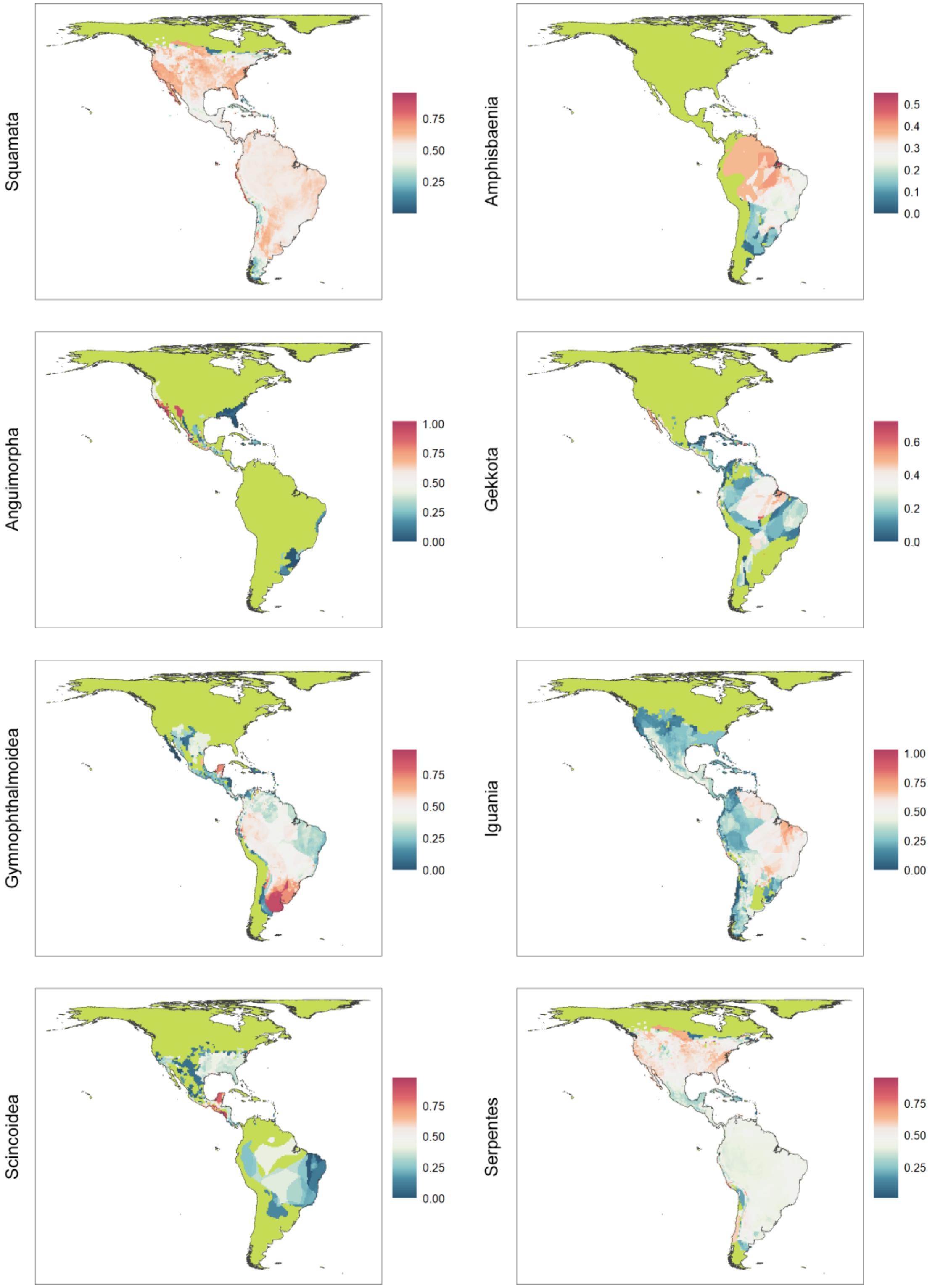

Figure S2. Coefficient of variation in speciation rate (DivRate) for the 100 random tree dichotomizations in the geographical space. Regions with no data are colored in light green.

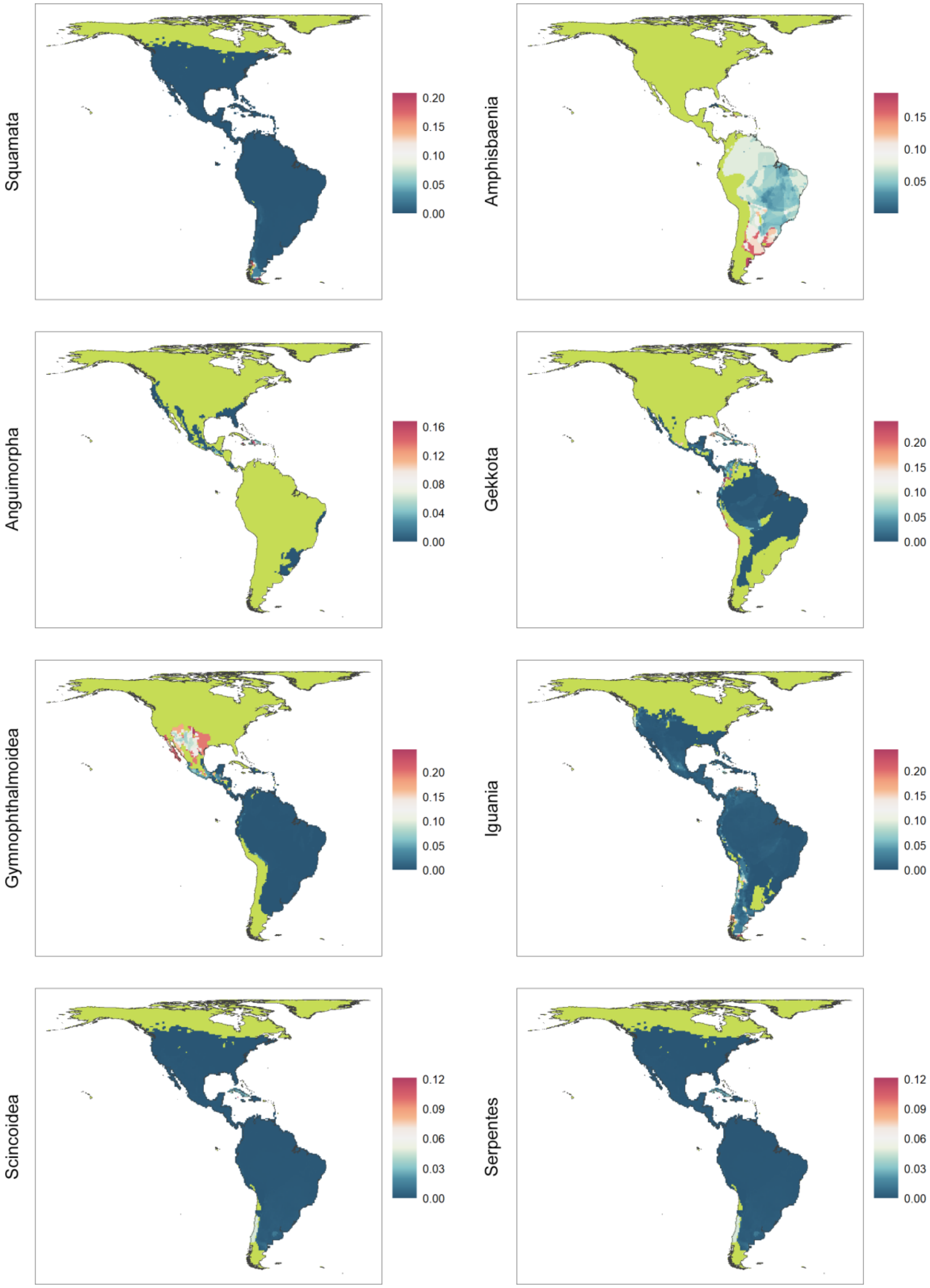

Figure S3. Coefficient of variation in evolutionary time (MPD) for the 100 random tree dichotomizations in the geographical space. Regions with no data are colored in light green.

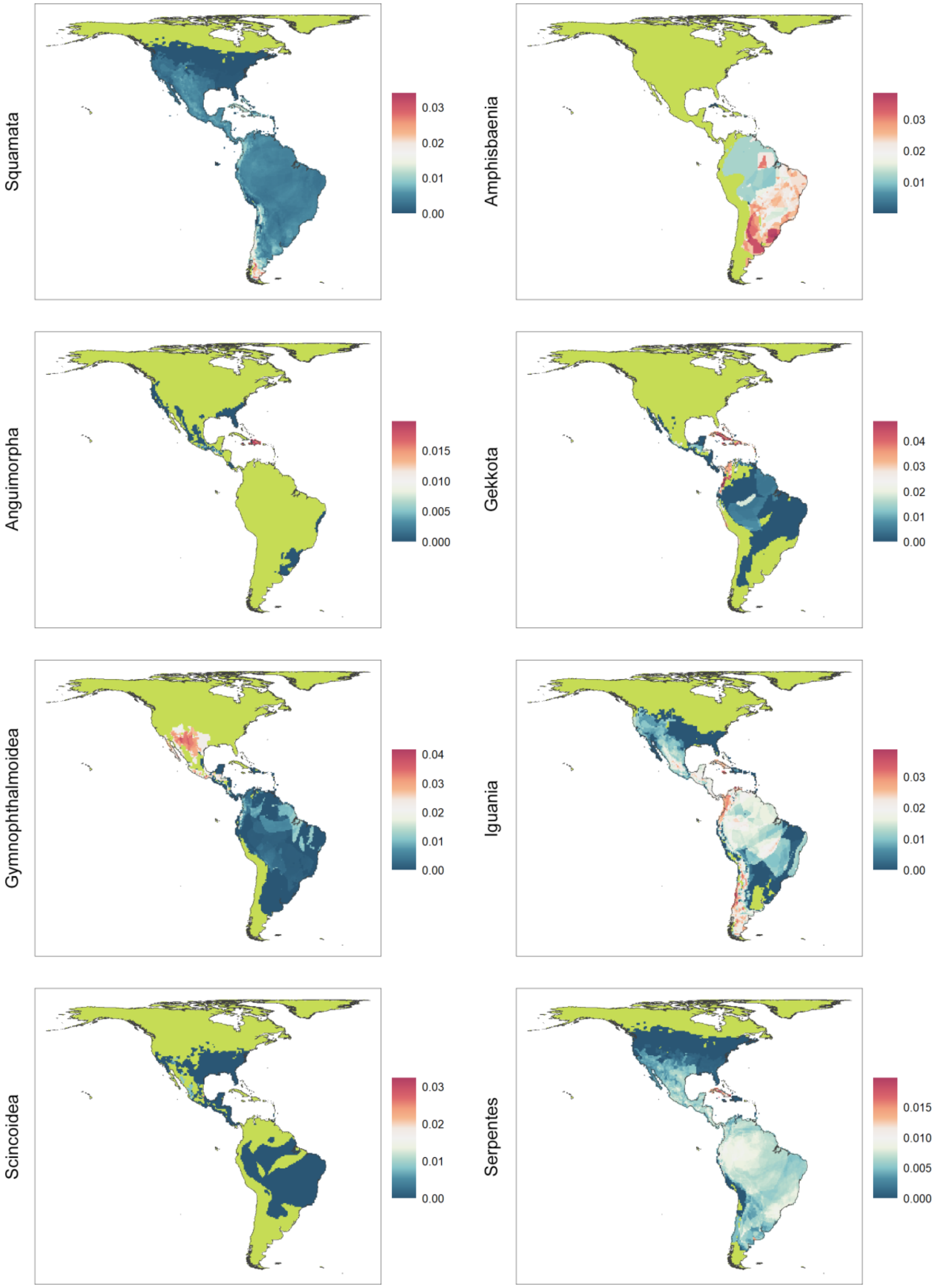

Figure S4. Coefficient of variation in Faith's metric (Faith's PD) for the 100 random tree dichotomizations in the geographical space. Regions with no data are colored in light green.

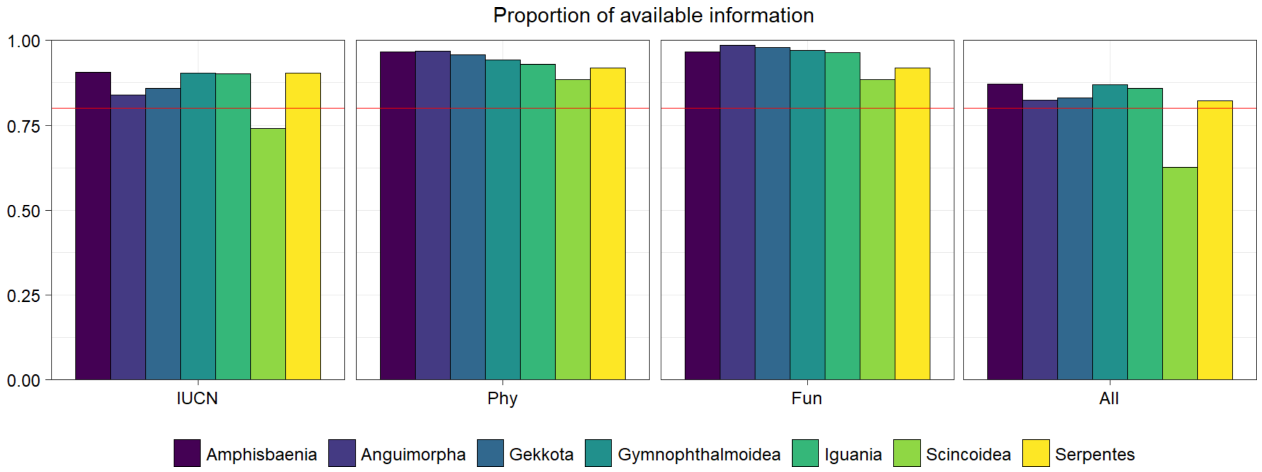

Figure S5. Available and missing information for squamate reptiles in the Americas. Bar plots show the proportional completeness by clade of the combined tree datasets (Amphisbaenia: **116 spp.**, Anguimorpha: **131 spp.**, Gekkota: **282 spp.**, Gymnophthalmoidea: **414 spp.**, Iguania: **1139 spp.**, Scincoidea: **147 spp.**, Serpentes: **1520 spp.**). The horizontal red line indicates 80%.

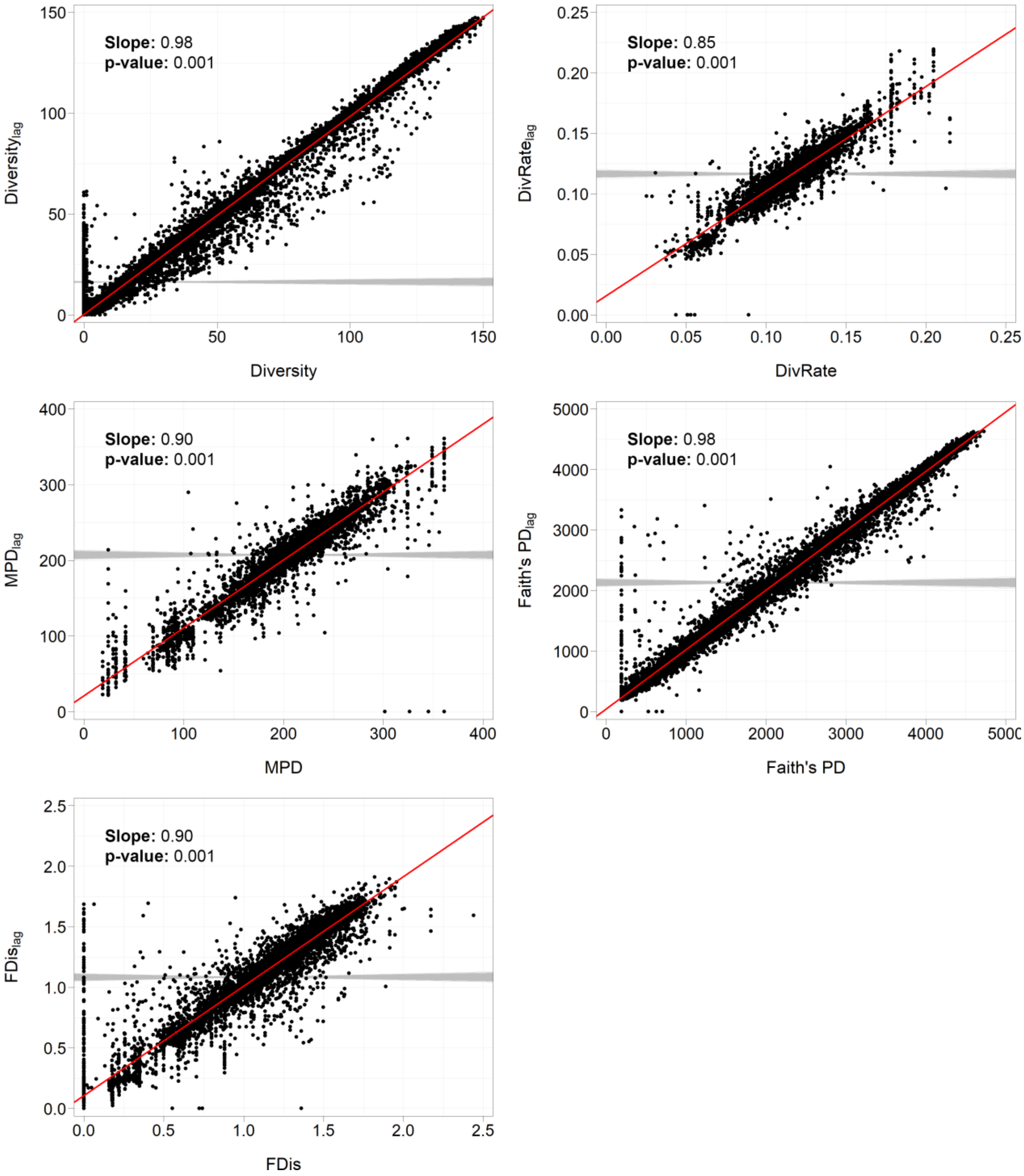

Figure S6. Spatial autocorrelation Moran's I test for the diversity metrics used. The slope of each relationship between the metric and its lagged values is equivalent to the Moran's I statistic, where higher values indicate higher autocorrelation. Grey shadows are the slopes for the 999 null models based on random permutations.

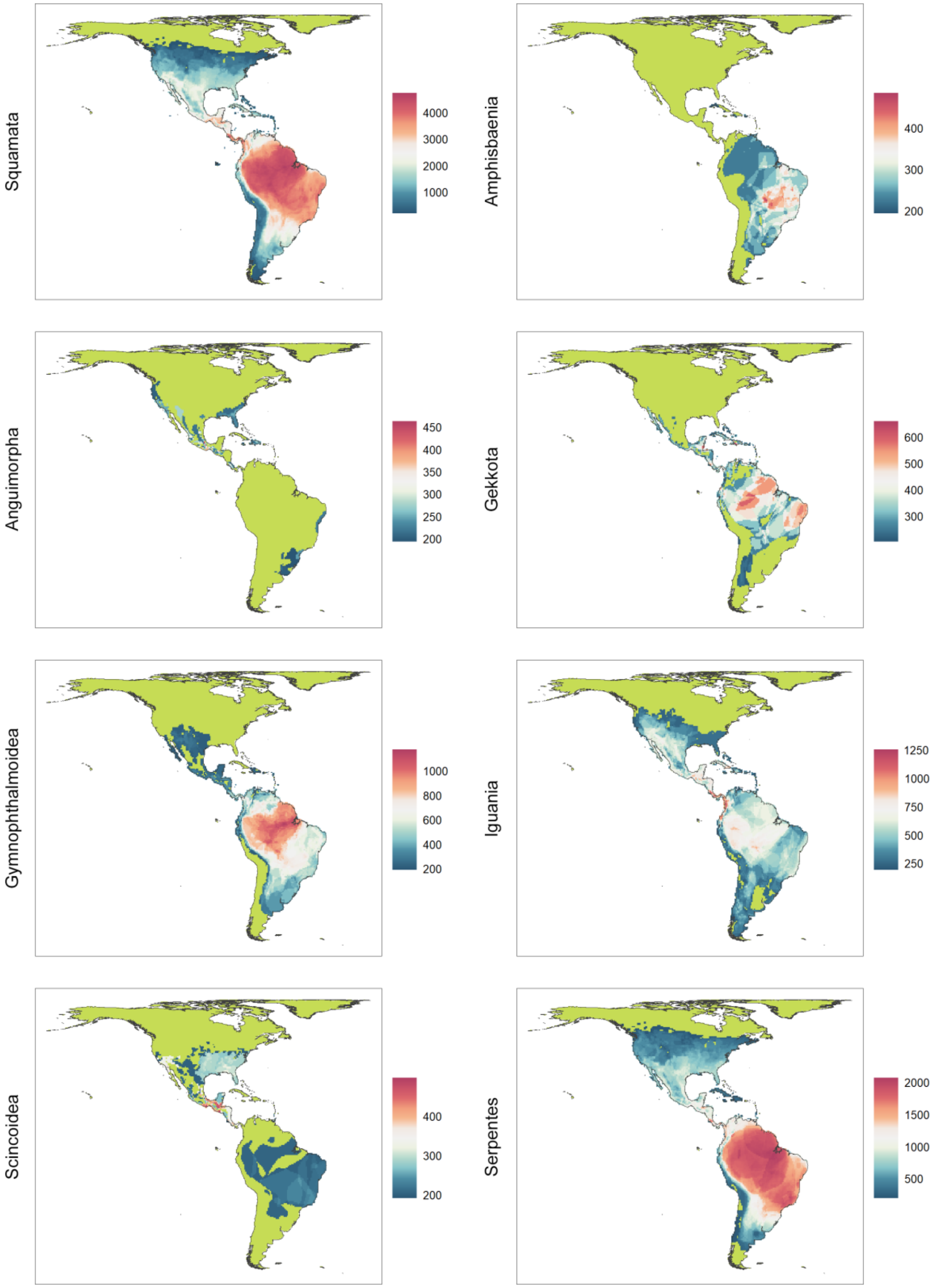

Figure S7. Faith's PD for Squamata and its subclades. Regions with no data are colored in light green. Pixels with a single species are not showed. Maps are in Berhamnn equal-area projection.

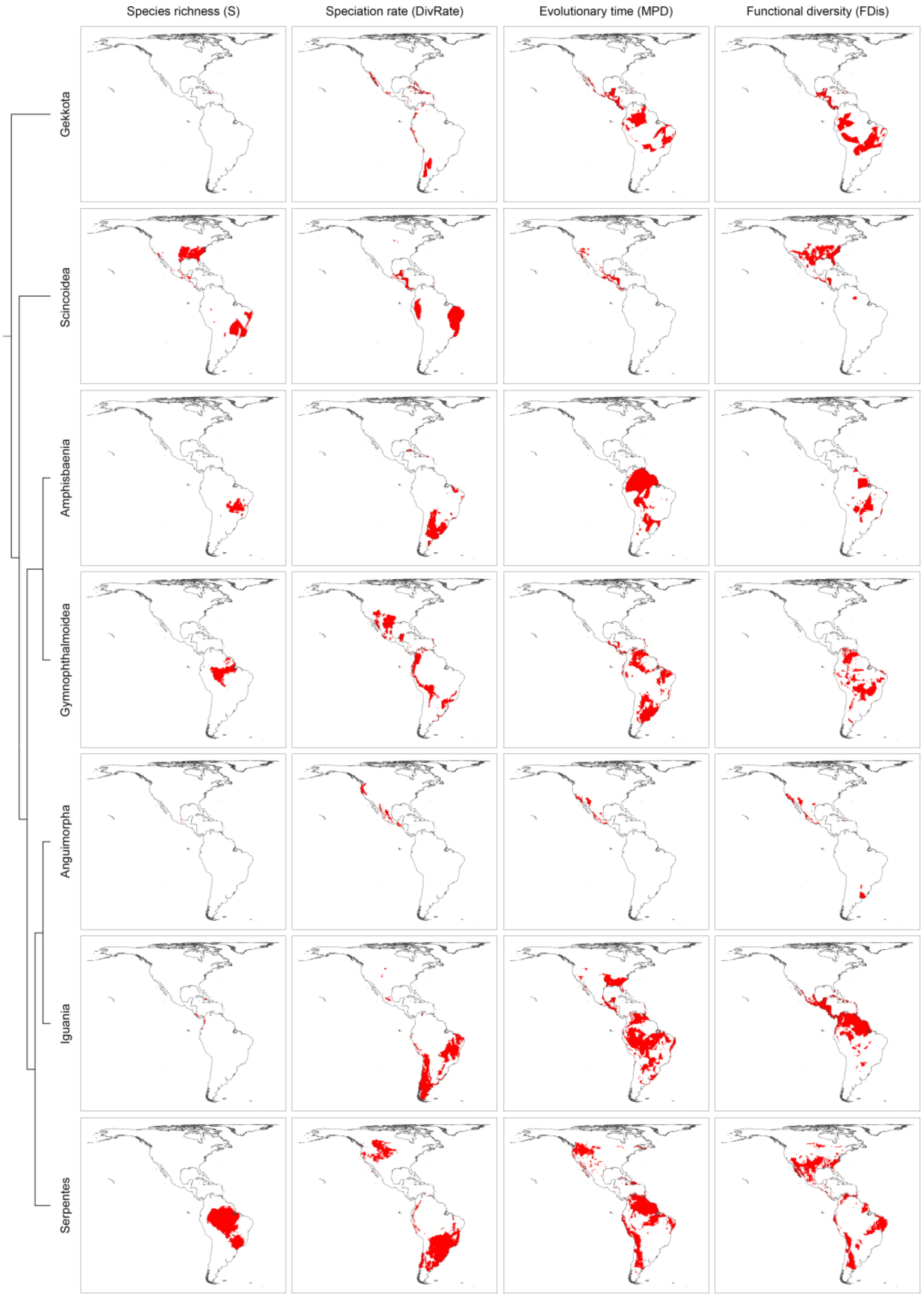

Figure S8. Highest values of diversity metrics for the squamate reptiles in the Americas based on the last 25% of the data. For DivRate, MPD, and FDis, pixels with a single species are not shown. Maps are in Berhamnn equal-area projection. This figure is also provided in the best quality and full-size in Supplementary Files II.

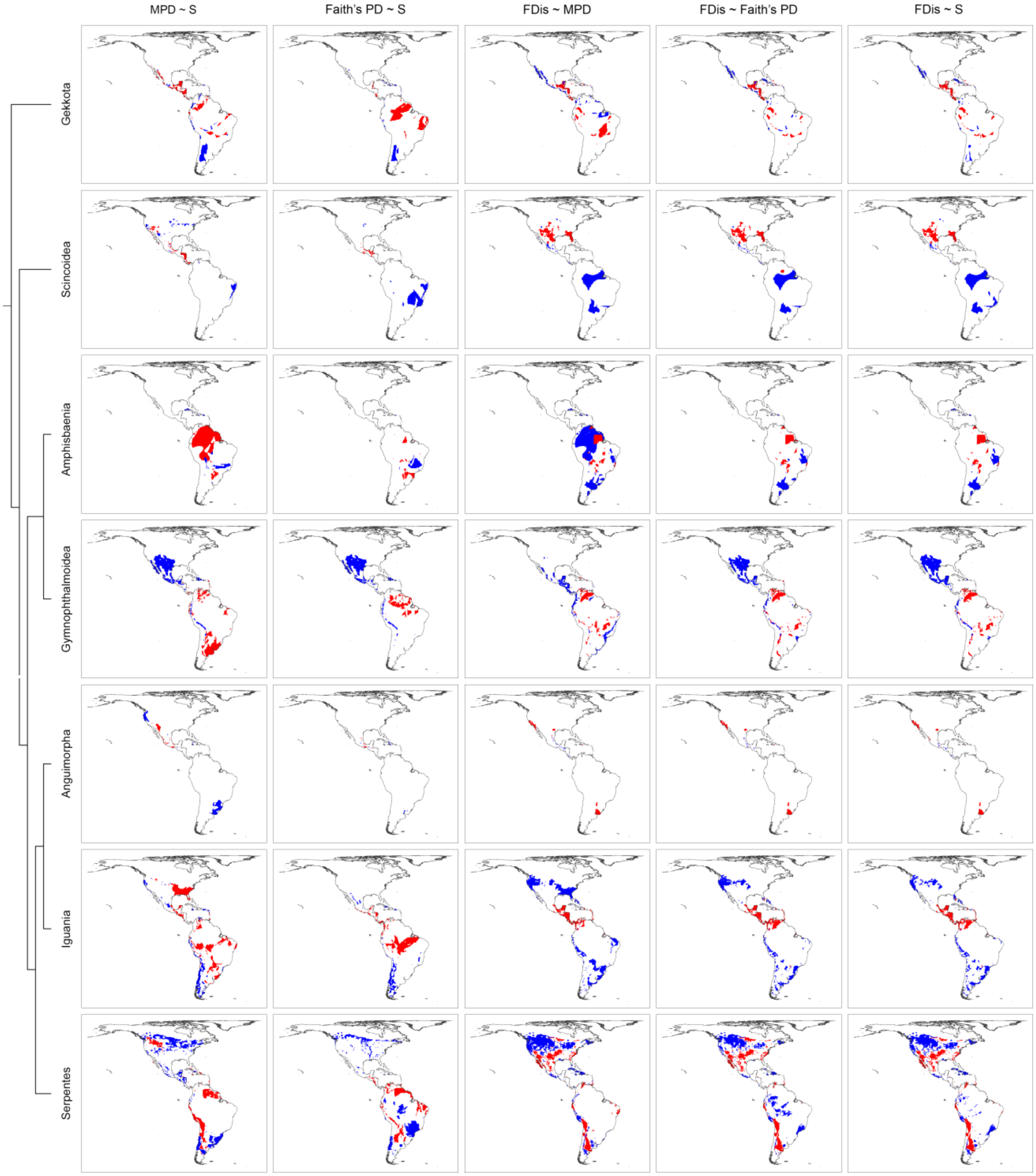

Fig. S9. Highest positive (red) and negative (blue) values of geographic mismatches by clade based on the first and last 10% of the data. Maps are in Berhamnn equal-area projection. This figure is also provided in best quality and full-size in Supplementary Files II.

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Supplementary Files II: Tables

Table S1. Proportion of species per IUCN polygon area.

	Area (in km^2)	Number of species	Proportion	
			Relative	Accumulated
Less than 100000 km^2	< 10	98	0.03	0.69
	10 – 100	313	0.10	
	100 – 1000	460	0.15	
	1000 – 10000	626	0.20	
	10000 – 100000	653	0.21	
More than 100000 km^2	100000 – 1000000	604	0.19	0.31
	1000000 – 10000000	342	0.11	
	> 10000000	28	0.01	

Table S2. Spearman’s and Kendall’s rank correlation among the metrics used. Values above the diagonal indicate the rho (ρ) for Spearman’s, while below-diagonal values indicate the tau (τ) for Kendall’s. All coefficients were significantly different from zero ($p < 0.001$).

	S	MPD	DivRate	Faith’s PD	FDis
S	–	0.07	0.24	0.98	0.22
MPD	0.04	–	-0.37	0.18	0.81
DivRate	0.16	-0.29	–	0.19	-0.27
Faith’s PD	0.90	0.12	0.10	–	0.29
FDis	0.15	0.66	-0.21	0.20	–

Table S3. Global models used to fit the relationships among diversity facets in Amphisbaenia. The best model for each relationship is highlighted in **bold**.

Model	Type	AICc	Residuals autocorrelation	
			Moran's I	*p*
PD ~ TD (MPD)	CAR	18888	-0.10	1
	SAR-LM	19289	0.01	0.168
	SAR-EM	**17768**	**-0.08**	**1**
PD ~ TD (Faith's PD)	CAR	28014	-0.01	0.914
	SAR-LM	32631	0.48	0
	SAR-EM	**25147**	**-0.03**	**1**
FD ~ PD (MPD)	CAR	-7995	-0.07	1
	SAR-LM	-8344	-0.03	1
	SAR-EM	**-8463**	**-0.03**	**1**
FD ~ PD (Faith's PD)	CAR	-8499	-0.06	1
	SAR-LM	-8488	0.00	0.677
	SAR-EM	**-9041**	**-0.02**	**0.999**
FD ~ TD	CAR	-8326	-0.06	1
	SAR-LM	-8435	-0.01	0.914
	SAR-EM	**-8885**	**-0.03**	**0.999**

Table S4. Global models used to fit the relationships among diversity facets in Anguimorpha. The best model for each relationship is highlighted in **bold**.

Model	**Type**	**AICc**	**Residuals autocorrelation**	
			Moran's I	***p***
PD ~ TD (MPD)	CAR	9292	-0.18	1
	SAR-LM	9289	-0.07	1
	SAR-EM	**9268**	**-0.08**	**1**
PD ~ TD (Faith's PD)	CAR	9002	-0.14	1
	SAR-LM	9195	0.24	0
	SAR-EM	**8595**	**-0.05**	**0.994**
FD ~ PD (MPD)	**CAR**	**-387**	**-0.07**	**1**
	SAR-LM	-222	-0.05	0.998
	SAR-EM	-307	-0.14	1
FD ~ PD (Faith's PD)	**CAR**	**-351**	**-0.20**	**1**
	SAR-LM	-222	-0.05	0.997
	SAR-EM	-284	-0.10	1
FD ~ TD	**CAR**	**-232**	**-0.15**	**1**
	SAR-LM	-175	-0.06	0.999
	SAR-EM	-218	-0.07	1

Table S5. Global models used to fit the relationships among diversity facets in Gekkota. The best model for each relationship is highlighted in **bold**.

Model	**Type**	**AICc**	**Residuals autocorrelation**	
			Moran's I	***p***
PD ~ TD (MPD)	CAR	35042	-0.14	1
	SAR-LM	35270	-0.03	1
	SAR-EM	**33757**	**-0.11**	**1**
PD ~ TD (Faith's PD)	CAR	39832	-0.13	1
	SAR-LM	41275	0.39	0
	SAR-EM	**36709**	**-0.07**	**1**
FD ~ PD (MPD)	CAR	-10710	-0.12	1
	SAR-LM	-9856	-0.01	0.755
	SAR-EM	**-10798**	**-0.06**	**1**
FD ~ PD (Faith's PD)	CAR	-9916	-0.12	1
	SAR-LM	-9635	-0.04	1
	SAR-EM	**-10154**	**-0.06**	**1**
FD ~ TD	CAR	-9763	-0.12	1
	SAR-LM	-9594	-0.04	1
	SAR-EM	**-9971**	**-0.06**	**1**

Table S6. Global models used to fit the relationships among diversity facets in Gymnophthalmoidea. The best model for each relationship is highlighted in **bold**.

Model	Type	AICc	Residuals autocorrelation	
			Moran's I	***p***
PD ~ TD (MPD)	CAR	49576	-0.10	1
	SAR-LM	50296	-0.03	1
	SAR-EM	**49157**	**-0.08**	**1**
PD ~ TD (Faith's PD)	CAR	58706	-0.13	1
	SAR-LM	62243	0.26	0
	SAR-EM	**56195**	**-0.03**	**1**
FD ~ PD (MPD)	CAR	-8715	-0.08	1
	SAR-LM	-7819	0.04	0
	SAR-EM	**-8964**	**-0.04**	**1**
FD ~ PD (Faith's PD)	CAR	-7239	-0.08	1
	SAR-LM	-7260	-0.02	1
	SAR-EM	**-7549**	**-0.04**	**1**
FD ~ TD	CAR	-7099	-0.07	1
	SAR-LM	-7176	-0.03	1
	SAR-EM	**-7265**	**-0.04**	**1**

Table S7. Global models used to fit the relationships among diversity facets in Iguania. The best model for each relationship is highlighted in **bold**.

Model	**Type**	**AICc**	**Residuals autocorrelation**	
			Moran's I	***p***
PD ~ TD (MPD)	CAR	62630	-0.11	1
	SAR-LM	62181	-0.05	1
	SAR-EM	**61726**	**-0.07**	**1**
PD ~ TD (Faith's PD)	CAR	78222	-0.05	1
	SAR-LM	82465	0.34	0
	SAR-EM	**73503**	**-0.05**	**1**
FD ~ PD (MPD)	CAR	-25199	-0.12	1
	SAR-LM	-24529	-0.06	1
	SAR-EM	**-25427**	**-0.08**	**1**
FD ~ PD (Faith's PD)	CAR	-24052	-0.12	1
	SAR-LM	-24445	-0.07	1
	SAR-EM	**-24605**	**-0.08**	**1**
FD ~ TD	CAR	-23972	-0.12	1
	SAR-LM	-24353	-0.08	1
	SAR-EM	**-24481**	**-0.08**	**1**

Table S8. Global models used to fit the relationships among diversity facets in Scincoidea. The best model for each relationship is highlighted in **bold**.

Model	**Type**	**AICc**	**Residuals autocorrelation**	
			Moran's I	***p***
PD ~ TD (MPD)	CAR	42429	-0.10	1
	SAR-LM	42310	-0.05	1
	SAR-EM	**42248**	**-0.05**	**1**
PD ~ TD (Faith's PD)	CAR	39910	-0.05	1
	SAR-LM	41477	0.06	0
	SAR-EM	**39005**	**-0.06**	**1**
FD ~ PD (MPD)	**CAR**	**-13394**	**-0.12**	**1**
	SAR-LM	-13227	-0.07	1
	SAR-EM	-13284	-0.09	1
FD ~ PD (Faith's PD)	**CAR**	**-13387**	**-0.13**	**1**
	SAR-LM	-13271	-0.07	1
	SAR-EM	-13349	-0.09	1
FD ~ TD	**CAR**	**-13272**	**-0.12**	**1**
	SAR-LM	-13229	-0.08	1
	SAR-EM	-13258	-0.08	1

Table S9. Global models used to fit the relationships among diversity facets in Serpentes. The best model for each relationship is highlighted in **bold**.

Model	Type	AICc	Residuals autocorrelation	
			Moran's I	***p***
PD ~ TD (MPD)	CAR	71996	-0.09	1
	SAR-LM	71393	-0.02	1
	SAR-EM	**69811**	**-0.07**	**1**
PD ~ TD (Faith's PD)	CAR	101901	-0.02	0.999
	SAR-LM	107638	0.25	0
	SAR-EM	**95901**	**-0.04**	**1**
FD ~ PD (MPD)	CAR	-30716	-0.10	1
	SAR-LM	-30658	-0.04	1
	SAR-EM	**-30757**	**-0.06**	**1**
FD ~ PD (Faith's PD)	CAR	-30330	-0.10	1
	SAR-LM	-30577	-0.05	1
	SAR-EM	**-30860**	**-0.06**	**1**
FD ~ TD	CAR	-30577	-0.10	1
	SAR-LM	-30563	-0.05	1
	SAR-EM	**-30727**	**-0.06**	**1**