UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE BIOLOGÍA

BIOLOGÍA EVOLUTIVA

PATRONES Y PROCESOS EN LA DIVERSIFICACIÓN Y RIQUEZA DE ESPECIES

DEL GÉNERO *ANOLIS*

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

Julian Andres Velasco Vinasco

TUTOR PRINCIPAL DE TESIS: Dr. Enrique Martínez Meyer, Instituto de Biología, UNAM.
COMITÉ TUTOR: Dr. Oscar Flores Villela, Facultad de Ciencias, UNAM.
Dr. Andrés García Aguayo, Instituto de Biología, UNAM.

MÉXICO, D.F.   **NOVIEMBRE, 2015.**

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UNAM
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Dr. Isidro Ávila Martínez
Director General de Administración Escolar, UNAM
P r e s e n t e

Me permito informar a usted que en la reunión del Subcomité por Campo de Conocimiento de Ecología y Manejo Integral de Ecosistemas del Posgrado en Ciencias Biológicas, celebrada el día 14 de septiembre de 2015, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del alumno **VELASCO VINASCO JULIAN ANDRES** con número de cuenta **512451077** con la tesis titulada: **"Patrones y procesos en la diversificación y riqueza de especies del género *Anolis*"**, realizada bajo la dirección del **DR. ENRIQUE MARTÍNEZ MEYER:**

Presidente:	DRA. ELLA GLORIA VÁZQUEZ DOMÍNGUEZ
Vocal:	DR. OCTAVIO RAFAEL ROJAS SOTO
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Suplente:	DR. ALEJANDRO GONZÁLEZ VOYER
Suplente	DR. AURELIO RAMÍREZ BAUTISTA

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

A T E N T A M E N T E
"POR MI RAZA HABLARA EL ESPIRITU"
Cd. Universitaria, D.F. a 9 de noviembre de 2015.

DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA
COORDINADORA DEL PROGRAMA

POSGRADO EN CIENCIAS BIOLOGICAS
COORDINACIÓN

c.c.p. Expediente del (la) interesado (a).

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Decía Bernardo de Chartres que somos como enanos a los hombros de gigantes. Podemos ver más, y más lejos que ellos, no por la agudeza de nuestra vista ni por la altura de nuestro cuerpo, sino porque somos levantados por su gran altura.

Juan de Salisbury, *Metalogicon* 1159 (III, 4)

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RESUMEN

Uno de los objetivos de la biología evolutiva es tratar de explicar y entender los factores que controlan dinámicas de diversificación de especies en diferentes grupos taxonómicos. Es bien conocido que la diversidad de especies entre linajes es resultado del efecto de factores ecológicos y evolutivos operando a escalas espaciales y temporales. Los procesos últimos que determinan la riqueza de un linaje en una región geográfica son la especiación, extinción y dispersión. Sin embargo, hay evidencia que los procesos de generación de diversidad tienden a estar mediados por variaciones en atributos ecológicos de las especies. En este sentido, la geografía y los atributos ecológicos de las especies juegan un papel clave en la dinámica de diversificación y los patrones de diversidad. Las lagartijas Neotrópicales del género *Anolis* son un excelente modelo de estudio para explorar efectos conjuntos de la geografía y el clima en la diversificación de especies y los gradientes geográficos de diversidad. El género *Anolis* (Squamata: Dactyloidae) es un ejemplo de radiación adaptativa. Se ha establecido que la diversidad de especies en el Caribe es producto de la diversificación adaptativa. Sin embargo, y a diferencia del Caribe, no es claro en las faunas continentales de *Anolis* qué procesos ecológicos y evolutivos controlan estos patrones. Pocos estudios han explorado el papel que juega la geografía y el clima en la diversificación de especies y los patrones regionales de riqueza. En su conjunto esta tesis ofrece una perspectiva integral de la diversificación ecológica del género *Anolis* a escalas filogenéticas y geográficas grandes. Los resultados obtenidos sugieren que la dinámica de diversificación de nichos ecológicos a escalas geográficas es diferente de las dinámica de nichos ecológicos a escalas locales. Estos resultados sugieren que los procesos evolutivos subyacentes en la diversificación ecológica son diferentes entre *Anolis* continentales y los *Anolis* del Caribe.

ABSTRACT

Understanding the ecological and evolutionary drivers of diversification is one of the central goals of evolutionary biology. It is well known that species diversity results from a effect of ecological and evolutionary processes operating across spatial and temporal scales. In particular, the ultimate processes controlling regional species richness are speciation, extinction and dispersal. However, recent studies have found that these evolutionary and biogeographic processes are also controlled by species' traits. Accordingly, both the geographical context and ecological niche play a key role shaping species diversification dynamics and therefore control how species richness is assembled at regional scales. *Anolis* lizards are an excellent model system to study the role of geography and climate as controls of species diversification and geographical species richness patterns. Although Insular anole diversity might be explained by geographical and evolutionary factors, it is still unclear whether the same factors control species diversification and species diversity in mainland settings. In particular, the role of geography and climate on species diversification and species richness in mainland anole faunas it is unknown. My general aim in this dissertation is to understand the role of ecological and evolutionary factors driving species diversification and geographical patterns of species richness in *Anolis* lizards. In general, I show a comprehensive picture of how coarse-grain ecological niche traits have shaped evolutionary radiation in *Anolis* lizards and how they have had a deep impact in the diversity and endemism patterns across regions. Also, I provide support for a contention about a distinction between ecological diversification at coarse-grain and fine-grain scales during the evolutionary history of *Anolis* lizards. Finally, I provide evidence suggesting that mainland and insular anole fauna follow different evolutionary trajectories.

INTRODUCCIÓN

Entender los procesos ecológicos y evolutivos responsables de la variación geográfica en la diversidad de especies es quizás una de las cuestiones más interesantes dentro de la biogeografía y biología evolutiva (Brown & Lomolino 1998). Ejemplos de estos patrones se pueden observar en los gradientes de diversidad latitudinal (Mittelbach et al. 2007), altitudinal (McCain & Grytnes 2010), profundidad oceánica (Witman & Roy 2009) y las diferencias en diversidad entre islas y continentes (MacArthur & Wilson 1967). Varias hipótesis ecológicas y evolutivas se han propuesto para explicar estos gradientes de diversidad. Por ejemplo, el gradiente de diversidad latitudinal se explica por diferencias en tasas de diversificación (especiación menos extinción) entre regiones tropicales y templadas, donde los linajes tropicales tienden a especiar más y extinguirse menos que los templados (Rolland et al. 2014; Pyron & Wiens 2013; Jetz et al. 2012). Además, las especies tropicales tienden a exhibir una tendencia fuerte a mantener los nichos ecológicos de sus ancestros (i.e., conservadurismo filogenético de nicho; Wiens and Graham 2005, Wiens et al. 2010, Pyron et al. 2014). Sin embargo, aún no es clara la relación existente entre el nicho ecológico y las tasas de diversificación y, por consiguiente, los patrones geográficos de riqueza de especies resultantes. Bajo este contexto, el concepto de nicho ecológico es clave para entender la dinámica de diversificación de especies y los mecanismos de ensamble de especies a escalas regionales.

Aunque el concepto de nicho ecológico es clave para entender aspectos de la distribución de especies y su habilidad para colonizar ciertas regiones (Schoener 2009; Holt 2009; Soberón 2014; Schurr et al. 2012), siempre ha existido gran confusión en la literatura con respecto a su definición, alcance, utilidad y operatividad (McInerny & Etienne 2012a, b, c; Soberón 2014). Dentro de la plétora de definiciones de nicho ecológico que se han formulado, rescato tres que considero son las más importantes: el concepto Grinnealliano (Grinnell 1917), el concepto Eltoniano (Elton 1927) y el concepto Hutchinsoniano (Hutchison 1957; 1978). El

nicho Grinnelliano se refiere a los requerimientos ambientales de una especie en función de la geografía (Grinnnell 1917). Por su parte, el nicho Eltoniano hace referencia al papel o *rol* funcional que ocupa una especie dentro de una comunidad o ambiente biótico y a sus efectos locales (Elton 1927). Finalmente, el concepto de Hutchinson plantea que el nicho es la sumatoria de todos los factores ambientales que permiten la existencia indefinida de una especie, y se conceptualiza como un híper-volumen de n-dimensiones (Hutchinson 1957, 1978). La definición de nicho de Hutchinson provee una aproximación más cuantitativa e integral que incluye tanto al concepto de Grinnell como al de Elton (Chase & Leibold 2003). Las dimensiones de nicho en términos de Grinnell (nicho Grinnelliano) y de Elton (nicho Eltoniano) son radicalmente diferentes y están muy relacionadas con la escala espacial en la cual se examinan. Adicionalmente, Hutchinson planteó dos tipos de nicho: el nicho fundamental y el nicho efectivo (*realized niche*, en inglés). El nicho fundamental se refiere a las condiciones ambientales que permiten la existencia indefinida de una especie excluyendo el efecto de las interacciones bióticas. El nicho efectivo por su parte considera el efecto tanto de los factores ambientales como las interacciones bióticas en la presencia de una especie (Hutchinson 1957; 1978). El término existencia indefinida hace referencia a los procesos demográficos que determinan la presencia de una población sin inmigración (Maguire 1973; Hutchinson 1978; Holt 2009). En este sentido, la definición de Hutchinson se puede expresar de forma explícita en términos demográficos (i.e., tasas de nacimiento y muerte per capitas) y cómo varían a través de la geografía y el ambiente (Maguire 1973; Hutchinson 1978; Holt 2009; Schurr et al. 2012). Por lo tanto, aquí se puede apreciar de forma muy clara la relación directa entre el nicho ecológico y la dinámica de los rangos geográficos de las especies (Pulliam 2000; Holt 2009). A lo largo de esta tesis haré referencia al concepto de nicho de Hutchinson, entendido como el conjunto de variables ambientales a gran escala (e.g., clima) que permiten que una población persista en el tiempo sin inmigración (i.e., con tasas de crecimiento poblacional intrínseco positivas – población fuente-) y sin considerar el

efecto potencial de las interacciones bióticas (i.e., *el nicho fundamental Grinnelliano*; Holt 2009; Soberón & Nakamura 2009; Peterson et al. 2011).

La estimación del nicho ecológico requiere información detallada de la dinámica demográfica de una especie a lo largo de su rango geográfico o de un gradiente ambiental (Schurr et al. 2011). Sin embargo, esa información poblacional es escasa, por lo que se han propuesto varias aproximaciones conceptuales y metodológicas para la estimación de los nichos ecológicos. Las aproximaciones más conocidas son a través del uso de modelos estadísticos de tipo mecanísticos y de tipo correlativo. Los modelos mecanísticos explícitamente incorporan el enlace causal entre los atributos funcionales de un organismo y el ambiente donde vive (Kearney & Porter 2004, 2009). Estos modelos permiten *aproximarse* mucho mejor al nicho fundamental, pero son prohibitivos para muchas especies por la cantidad de información ecológica y fisiológica que demandan (Kearney & Porter 2009). Por su parte, los modelos correlativos buscan encontrar una asociación estadística (correlación) entre la presencia de una especie y el ambiente a escala geográfica (Peterson et al. 2011). La ventaja de los modelos correlativos radica en su facilidad de implementación y la flexibilidad en cuanto a los requerimientos de datos (Kearney et al. 2010). Numerosas técnicas para generar modelos correlativos de nicho ecológico se han desarrollado en los últimas dos décadas (Franklin 2009), y se desarrollan modelos cada vez más complejos y computacionalmente más intensivos (e.g., modelos de distribución de especies jerárquicos Bayesianos hSDM; Vielledent et al. 2014). Los modelos correlativos son los más usados en ecología, evolución y biogeografía (Peterson et al. 2011; Franklin 2009).

Los modelos de nicho ecológico se han empleado para examinar las dinámicas de nicho a través del tiempo y del espacio (Pearman et al. 2008; Peterson et al. 1999; Graham et al. 2004). Por un lado, existe evidencia teórica y empírica (Holt & Gaines 1992; Holt & Gomulkiewicz 1997; Holt 2014; Peterson et al. 1999; Martínez-Meyer et al. 2004, 2006; Peterson 2011) sugiriendo que los nichos

ecológicos evolucionan muy lentamente dentro y entre especies. Este fenómeno se conoce como conservadurismo de nicho ecológico y su extensión varía dependiendo de la escala temporal y espacial en la que se examina (Wiens & Graham 2005; Losos 2008; Wiens et al. 2010; Crisp and Cook 2012; Pyron et al. 2014). Algunos autores argumentan que el conservadurismo de nicho, referido a la tendencia a que las especies emparentadas retengan los atributos de nicho ecológico de sus ancestros, puede considerarse como un patrón y proceso al mismo tiempo (Wiens & Graham 2005; Wiens 2008). Por otra parte, otros autores argumentan que el conservadurismo de nicho es sólo un patrón y que debe referirse únicamente al fenómeno donde las especies muy emparentadas son ecológicamente más similares que lo que podría esperarse bajo un modelo de movimiento browniano (Losos 2008; Figura 1).
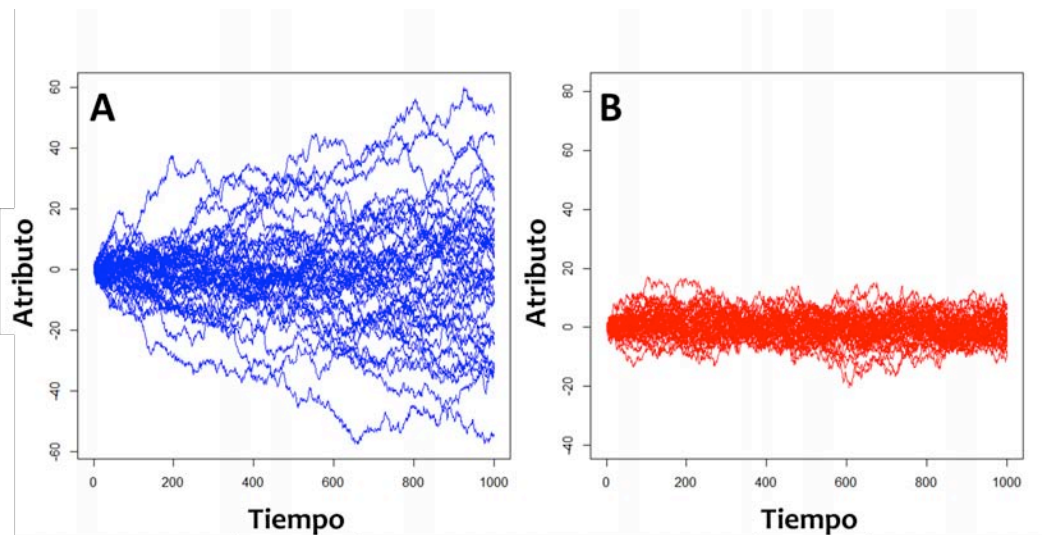
Figura 1. Representación gráfica de 1000 simulaciones del modelo de movimiento browniano (A) y del modelo Ornstein-Uhlenbeck (B). Un modelo de movimiento browniano puede ser apropiado para describir la evolución de un atributo continuo (e.g., tamaño corporal) como un camino aleatorio a través del espacio disponible de valores para ese atributo. Este modelo ha sido usado para evaluar hipótesis de evolución de atributos como un proceso de diversificación no constreñida (Felsenstein 1985, Freckleton et al. 2002, Blomberg et al. 2003). Por su parte, el modelo Ornstein-Uhlenbeck describe un proceso donde los atributos evolucionan hacia un óptimo selectivo y exhiben una fuerte constricción evolutiva. Este modelo puede describir atributos que evolucionan bajo selección estabilizadora, por ejemplo si exhiben conservadurismo de nicho (Hansen 1997; Butler & King 2004).

De igual forma, Losos (2008) resalta la importancia de distinguir entre señal filogenética (i.e., la tendencia de especies emparentadas a ser más similares que lo que podría esperarse por un proceso evolutivo aleatorio) y conservadurismo de nicho. La señal filogenética puede aparecer si los atributos de una especie evolucionan siguiendo un modelo de movimiento browniano, el cual puede ser generado por deriva génica o selección natural fluctuando aleatoriamente en el tiempo (Losos 2008; Revell et al. 2008). En este sentido, el que exista señal filogenética no es suficiente para demostrar conservadurismo de nicho, pero la ausencia de señal sí es un indicio de la no existencia de conservadurismo de nicho (Losos 2008).

Diferentes estudios recientes han explorado la dinámica evolutiva de nicho ecológico usando métodos comparativos filogenéticos modernos (e.g., Kostikova et al. 2014; Wiens et al. 2013; Pyron & Wiens 2013; Schnitzler et al. 2012; Boucher et al. 2011; Kozak & Wiens 2010). Sin embargo, hasta la fecha no existen estudios donde se haya evaluado el desempeño y la precisión de estos métodos para evaluar la dinámica de los nichos en el tiempo y el espacio, en particular los supuestos de los modelos evolutivos subyacentes (O'Meara 2012; Pennell & Harmon 2013; Garamszegi 2014; Harmon et al. 2010).

Aunque se reconoce que el nicho ecológico fundamental puede ser visualizado como una extensión fenotípica de una población, y por lo tanto este se encuentra sujeto a evolución por selección natural u otros procesos (Holt 1992; Holt & Gaines 1992), no es claro si estos modelos son buenos descriptores de la dinámica evolutiva del nicho ecológico. Algunos trabajos teóricos han encontrado que usar índices para medir señal filogenética (e.g., índice K de Blomberg, Blomberg et al. 2003; *lambda* de Pagel, Pagel 1999; I de Moran, Gittleman & Kot 1990; C promedio de Abouheif, Abouheif 1999) y derivar conclusiones acerca del conservadurismo filogenético de nicho resulta ser problemático cuando los supuestos de los modelos se han violado (Revell et al. 2008; Münkemüller et al. 2012; Münkemüller et al.

2015). Por ejemplo, Münkemüller et al. (2015), a partir de simulaciones de atributos de nicho bajo varios modelos evolutivos (e.g., movimiento browniano, Ornstein-Uhlenbeck, y deriva) concluyen que estos índices son muy sensibles a violaciones de los supuestos del modelo. En particular, Münkemüller et al. (2015) encontraron que los índices tienden a mostrar baja señal filogenética cuando los nichos evolucionan bajo un modelo Ornstein-Uhlenbeck con un solo óptimo evolutivo (un modelo que describe una dinámica de selección natural estabilizadora). Por el contrario, cuando los nichos evolucionan bajo el mismo modelo pero con varios óptimos evolutivos, los índices tienden a mostrar mayor señal filogenética que lo esperado bajo un modelo de movimiento browniano. Estos resultados sugieren que los índices de señal filogenética son útiles para medir conservadurismo de nicho sólo cuando los datos (i.e., atributos de nicho ecológico y la filogenia) se ajustan a un modelo de movimiento browniano (Münkemüller et al., 2015). Sin embargo, este no parece ser el caso para los estudios que han examinado la evolución del nicho ecológico Grinnelliano en varios grupos taxonómicos (veáse Velasco et al., *en revisión* – capítulo 3-; Algar & Mahler, 2015; Boucher et al. 2012). Además, el supuesto que los nichos ecológicos exhiben un sólo óptimo bajo un modelo Ornstein-Uhlenbeck a través de la historia evolutiva de un taxón, no parece ser muy realista (Velasco et al., *en revisión*, capítulo 3). Es claro que un entendimiento de cual es el modelo nulo apropiado para evaluar la dinámica evolutiva de nicho ecológico es clave para entender la asociación entre el nicho ecológico y la diversificación de especies.

Existen factores tanto intrínsecos (e.g., nicho ecológico) como extrínsecos (e.g., clima y eventos biogeográficos históricos), que actúan como controladores de dinámicas de diversificación y ensamble de especies (Ricklefs 2012; Rabosky 2013; Wiens 2011). Por un lado, algunos estudios han comenzado a explorar la relación entre la evolución de nicho ecológico y la diversificación de especies (Rabosky et al. 2013; Pyron & Wiens 2013; Pyron & Burbrink 2012; Gómez-Rodríguez et al. 2014; Bonetti & Wiens 2014; Kostikova et al. 2014). En particular, se ha evaluado si la amplitud de nicho climático y la especialización influyen en las tasas de

diversificación de especies (Gómez-Rodríguez et al. 2014; Bonetti & Wiens 2014). En este sentido, uno puede suponer que los grupos taxonómicos ricos en especies exhiban mayor diversidad de nichos climáticos (y probablemente menor solapamiento de nicho) que grupos pobres en riqueza de especies (Rabosky 2012a, Ricklefs 2012, Rabosky et al. 2013; Velasco et al. *En prensa*: capítulo 1). Esta predicción es consistente con escenarios de diversificación dependiente de la diversidad donde la dinámica de especiación está acoplada con la divergencia de nicho, y a medida que transcurre el tiempo, los linajes y regiones llegan a saturarse ecológicamente (Schluter 2000; Rabosky 2009; 2013). En contraste, si la diversificación no es dependiente de la diversidad, es decir sólo del tiempo y del área geográfica (Wiens 2011; Cornell 2013), se podría esperar que la tasa de evolución de nicho no esté acoplada con la tasa de diversificación. Es decir, que la evolución de nicho no este relacionada con eventos cladogenéticos. En este sentido se podría esperar que los nichos ecológicos sean similares y amplios para especies pertenecientes a clados ricos en especies (Cornell 2013).

Finalmente, el clima y su variación a nivel geográfico juega un papel clave en los patrones geográficos de riqueza y endemismo de especies (Wiens & Donoghue 2004, Gotelli et al. 2009; Wiens 2011; Cornell 2013). En este sentido, se han propuesto dos tipos de hipótesis generales, una ecológica y la otra evolutiva, para explicar cómo el clima determina la riqueza regional de especies (Mittelbach et al. 2007, Currie et al. 2004). La hipótesis ecológica plantea que los cambios ambientales a través del tiempo explican los cambios de riqueza y ensamble de especies a través de la geografía (Evans et al. 2005; Field et al. 2009; Tello & Stevens 2010; Gouveia et al. 2013). Dentro de esta hipótesis se incluyen al menos cuatro tipos de mecanismos: (i) agua-energía, (ii) estacionalidad, (iii) heterogeneidad ambiental y (iv) estabilidad climática histórica. En cuanto a la hipótesis evolutiva se incluyen el conservadurismo de nicho (Wiens and Donoghue 2004) y la diversificación regional (Buckley et al. 2010; Rolland et al. 2014) como responsables de los gradientes de diversidad de especies y las relaciones clima-diversidad

resultantes. Sin embargo, solo de forma reciente se han comenzado a integrar la hipótesis evolutiva junto con la ecológica para explicar cual de las dos tiene un impacto mayor como controlador del número y composición de especies en una región (Rangel et al. 2007; Algar et al. 2009).

En esta tesis se explora el papel de factores extrínsecos (clima y eventos biogeográficos) e intrínsecos (nicho climático) como controladores de dinámicas de diversificación y la riqueza de especies de lagartijas del género *Anolis* (Squamata: Dactyloidae) en la región Neotropical. La combinación de diferentes métodos y conceptos en esta tesis, como son los métodos para estimar los nichos ecológicos, los métodos comparativos filogenéticos basados en modelos evolutivos explícitos y los métodos biogeográficos modernos (métodos paramétricos), permite someter a prueba hipótesis evolutivas y ecológicas relacionadas con los factores que controlan la diversificación y la riqueza de especies a escala regional. Se presentan tres capítulos donde se evaluaron los factores reguladores de diversidad regional en lagartijas del género *Anolis*.

En el capítulo I, evalué la relación entre los atributos de nicho ecológico (amplitud y posición media de nicho Grinnelliano) y tasas de diversificación en *Anolis*. En este capítulo se evalúa sí las diferencias de nicho climático entre diferentes linajes de *Anolis* están relacionadas con su diversificación total (riqueza de especies) y las tasas de diversificación de especies (especiación y extinción). También, se evalúa si los clados ricos en especies (i.e., con mayor diversificación total) tienden a exhibir mayor diversidad de nichos climáticos, que los clados pobres en especies (i.e., con menor diversificación total).

En el capítulo II, exploré el papel de los factores climáticos y evolutivos sobre los gradientes geográficos de riqueza de especies de lagartijas *Anolis*. En este capítulo, investigué la contribución de factores únicos y compartidos de cuatro hipótesis climáticas (agua-energía, estacionalidad, heterogeneidad y estabilidad climática) usando regresiones geográficas ponderadas con un enfoque de partición

de varianza. De igual forma, sometí a prueba la hipotésis que el conservadurismo de nicho y la diversificación regional controlan las relaciones del clima y la riqueza en ensambles de *Anolis*.

Finalmente, en el capítulo III, evalué el papel de los eventos biogeográficos históricos y la dinámica evolutiva de nichos climáticos en el endemismo insular de lagartijas *Anolis* en el Caribe. A partir de una reconstrucción biogeográfica histórica evalué si la vicarianza o dispersión jugaron un papel en la distribución de los principales clados de *Anolis* insulares. Adicionalmente, evalué cómo el conservadurismo y convergencia de nicho climático condicionan el endemismo excepcional de *Anolis* en el Caribe, donde casi todas las especies son endémicas de una sola isla.

CAPÍTULO I

Atributos de nicho climático y diversificación en lagartijas

Anolis.

ORIGINAL ARTICLE

Climatic niche attributes and diversification in *Anolis* lizards

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ABSTRACT

Aim The aim of this study was to test the link between climatic niche dynamics and species diversification in *Anolis* on islands and on the mainland. We tested the hypotheses that lineages in warmer climates and with narrow climate niches diversified more than lineages in cold climates and with broad climate niches. We also tested the hypothesis that species-rich clades exhibit greater niche diversity than species-poor clades.

Location Neotropics.

Methods We collated occurrence records for 328 *Anolis* species to estimate niche breadth, niche position and occupied niche space (as a proxy for niche diversity). We compared niche breadth between insular and mainland *Anolis* species and among *Anolis* clades, controlling for the potential confounding effect of range size. Using two approaches (clade-based and QuaSSE) we explored the association between niche metrics and diversification rates in *Anolis* lizards.

Results We found that Caribbean *Anolis* had a narrower niche breadth and niche space occupation compared to mainland anoles after controlling for range size differences. There was a significant association between niche traits (mean niche position and niche breadth) and diversification in anoles. Anole lineages with narrow niche breadths and that occupy warmer areas exhibited higher speciation rates than those with broader niche breadths and that occupy cold areas. Similarly, clades with higher total diversification exhibit more niche diversity than clades with lower total diversification.

Main conclusions Climatic niche attributes play a role in anole diversification with some differences between mainland and insular anole lineages. Climatic niche differences between regions and clades likely are related to differences in niche evolutionary rates. This also suggests that climate plays a strong role in shaping species richness between and within mainland and islands.

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INTRODUCTION

Species richness in a clade or region results from the interplay of ecological and evolutionary factors operating at different spatial and temporal scales (Wiens, 2011; Cornell, 2013). Species richness in a region can ultimately be explained by differences in diversification rates (i.e. speciation minus extinction) and dispersal events (Wiens & Donoghue, 2004; Wiens, 2011). Although species diversification is known to be influenced by ecological factors within a particular region (Wiens, 2011; Cornell, 2013; Machac *et al.*, 2013), there is still little understanding of how variation in

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ecological factors affects species diversification, and thus species richness, across phylogenetic and geographical scales.

Ecology, diversification and species richness are linked through the niche concept (Hutchinson, 1957; Soberón & Nakamura, 2009; Ricklefs, 2012). For instance, some recent studies have shown that speciation rates are coupled with rates of niche evolution (Rabosky, 2012a; Rabosky & Adams, 2012; Rabosky *et al.*, 2013). Accordingly, clades displaying a high degree of species richness are expected to have greater niche diversity than clades with low species richness (Rabosky, 2012a; Ricklefs, 2012; Rabosky *et al.*, 2013). This prediction is an expected outcome during adaptive radiation where slowdowns in diversification occur as ecological space is filled and species' niches become narrow due to competition (Schluter, 2000; Rabosky, 2009). In this way, niche divergence can drive cladogenesis. Alternatively, diversification may not be ecologically constrained but rather, they may be time or area dependent (Wiens, 2011). In cases where cladogenesis is decoupled from niche evolution, we would expect lineages to have greater niche similarity and large niche breadths (Cornell, 2013). The above scenarios have been explored mostly using phenotypic traits related to habitat use (Schluter, 2000; Harmon *et al.*, 2003). Only recently some studies have explored the role of coarse-grain climatic niche attributes in clade diversification (Kozak & Wiens, 2010; Pyron & Burbrink, 2012; Schnitzler *et al.*, 2012; Machac *et al.*, 2013; Wiens *et al.*, 2013; Kostikova *et al.*, 2014).

The climatic niche is defined as the set of climatic variables at a coarse resolution with an influence on the intrinsic and instantaneous population growth rates of a species at a geographical scale (Soberón, 2007; Peterson *et al.*, 2011). It is useful to establish whether climatic niche requirements can explain differences in species richness and diversification among regions and clades. This definition considers climatic niche as a population-level trait and not as an individual-level trait, which is implicit in definitions incorporating critical physiological boundaries. Accordingly, several studies have explored the link between climatic niche attributes and

diversification (Kozak & Wiens, 2010; Schnitzler *et al.*, 2012). For instance, Kozak & Wiens (2010) suggested that high rates of climatic niche evolution might promote increases in diversification rates. However, a causal link between diversification rate and climatic niche evolution is difficult to establish (Schnitzler *et al.*, 2012). In order to clarify the link between niche dynamics, diversification and species richness, clear predictions about how climatic niche attributes (e.g. niche space and niche breadth) facilitate increases or slowdowns in diversification rates are needed.

In this paper, first, we hypothesize a link between climatic niche metrics (i.e. niche position and niche breadth) and diversification in *Anolis* lizards. For niche position, we predict that lineages occupying warmer and drier areas (where anole diversity is higher; Losos, 2009; Algar & Losos, 2011) tend to diversify more than lineages adapted to cold and very humid conditions (where their diversity is lower). For niche breadth, we predict that clades composed of climatic niche specialist species (i.e. with narrow niche breadths) will have higher diversification rates than lineages composed of climatic niche generalist species (i.e. wide niche breadths) (Futuyma & Moreno, 1988; Cantalapiedra *et al.*, 2011; Cadena *et al.*, 2012; Wiens *et al.*, 2013). This hypothesis predicts a negative relationship between diversification rates and niche breadth, a relationship that likely is mediated by climatic niche conservatism (Gómez-Rodríguez *et al.*, 2015). Second, we hypothesize that clades with high species richness (and likely high diversification rates) will have a high degree of niche diversity (i.e. more occupied niche space) than clades poor in species (Ricklefs, 2012). This is consistent with a scenario where cladogenesis is driven by niche evolution rates (Harmon *et al.*, 2003; Rabosky *et al.*, 2013).

We test these hypotheses for *Anolis* lizards, which occur mainly in the Caribbean islands and on the mainland from Mexico to southern Brazil. They are species-rich on both the islands (*c.* 160 species) and the mainland (*c.* 230 species; Table 1). The evolutionary history of Caribbean *Anolis* has been subjected to intense research in the last several decades

Table 1 Clades recognized in *Anolis* radiation, species richness, range size (log10 km^2), age, net diversification rates (Net divers. rates; extinction fraction 0.9/0.1), occupied niche space (Occ. niche space), niche breadth (log10) and distribution.

Clade	Species richness	Range size	Age (Ma)	Net divers. rates	Occ. niche space	Niche breadth	Distribution
Anolis	44	5.095	30.090	0.054/0.102	3.076	1.542	Bahamas, Cayman islands, Cuba, Hispaniola, south of Florida
Lesser Antilles *Dactyloa*	9	3.210	25.510	0.021/0.059	1.34	1.513	Southern Lesser Antilles
Mainland *Dactyloa*	83	7.053	30.980	0.072/0.122	16.496	2.640	Lower Central America and South America
Audantia	9	4.921	22.860	0.023/0.059	7.968	1.779	Hispaniola and satellite islands
Chamaelinorops	16	4.863	30.850	0.028/0.067	7.432	1.704	Hispaniola and satellite islands
Ctenonotus	36	4.945	30.870	0.047/0.093	5.2	1.779	Bahamas, Hispaniola, Puerto Rico, Virgin Islands, Northern Lesser Antilles
Deiroptyx	21	5.270	32.100	0.033/0.073	4.861	1.704	Cuba, Hispaniola, Puerto Rico
Xiphosurus	11	5.170	30.030	0.021/0.057	4.199	1.736	Cuba, Hispaniola, Puerto Rico and satellite islands
Cuban *Norops*	18	5.110	28.950	0.029/0.068	1.986	2.640	Cuba
Jamaican *Norops*	7	4.090	25.270	0.016/0.049	2.575	1.382	Jamaica
Mainland *Norops*	150	7.140	32.310	0.090/0.142	14.148	2.707	Middle and South America

(Losos, 2009). There is evidence that their diversification in the Greater Antilles is related to island size and colonizing time, with speciation rates declining over time as a function of area (Rabosky & Glor, 2010). This pattern suggests that regional species richness in the Greater Antilles is controlled by area and potentially by competitive interactions (Losos & Schluter, 2000; Rabosky & Glor, 2010). Specifically, we predict that *Anolis* lizards with narrow climatic niches and specialization towards particular climate regimes have diversified more than those that tolerate a wide range of climate conditions (Kozak & Wiens, 2010).

In this paper, we compare climatic niche attributes in *Anolis* between regions and clades, to assess whether niche position and specialization have driven diversification in these lizards. We evaluate the available climatic space in each region to explore patterns of niche occupation in *Anolis* clades inhabiting the islands and the mainland. Although there are substantial niche differences between insular and mainland anoles, niche traits were associated with cladogenesis in both anole faunas.

MATERIALS AND METHODS

Anolis records

We mapped 13,579 georeferenced locality records for 328 *Anolis* species from the Caribbean islands (145 species, 3134 locality records) and the mainland (183 species, 10,445 locality records), drawn from the Global Biodiversity Information Facility (GBIF, http://gbif.org), HerpNET (http://www.herpnet.org/), Algar & Losos (2011), Ochoa-Ochoa & Flores-Villela (2006) and other databases not publicly available (e.g. GK database). Some herpetological collections for which *Anolis* locality data are not available via the Internet (e.g. GBIF or HerpNet), namely ICN (Colección de Anfibios y Reptiles, Instituto de Ciencias Naturales, Bogotá Colombia), MHUA (Museo de Herpetología de la Universidad de Antioquia, Medellín, Colombia) and QCAZ (Colección de Anfibios y Reptiles, Pontificia Universidad Católica de Ecuador, Quito, Ecuador), were georeferenced using national gazetteers and the point-georeferencing method with a spatial precision of ~1 km (Chapman & Wieczorek, 2006). We carefully revised each record in our database and eliminated erroneous, doubtful and duplicate records (i.e. identical records from two or more sources).

Climatic niche metrics in *Anolis* lizards

We estimated the climatic niche represented by temperature and precipitation variables drawn from the WorldClim database (Hijmans *et al.*, 2005) using the occurrence records of 328 species. Our climatic niche estimates encompass the realized niche as is common in geographical information system approaches (Peterson *et al.*, 2011). To estimate the niche breadth for each *Anolis* species, we used maximum Mahalanobis distances (Rotenberry *et al.*, 2006) – a statistical technique for ecological niche modelling based on presence-only records (Peterson *et al.*, 2011). The Mahalanobis distance measures the space between two points in a n-dimensional coordinate system accounting for unequal variances and correlation between variables (Xian *et al.*, 2008). Distances are simply calculated as a standardized difference between the value of any point (i.e. a species' record) and the mean values from all points from the climate space (Rotenberry *et al.*, 2006). Also, we estimated niche breadth using Euclidean distances and ran a correlation of niche breadth between both distance methods, which was highly significant ($P < 0.0001$).

We characterized the available climatic space for each region in which each clade occurs. For each island in the Greater Antilles, we extracted values for bioclimatic variables for all pixels (1 km² pixel size). For the mainland, we generated a minimum convex polygon (MCP) for Middle American and South American anole records with a buffer of 1000 km in each area. Note that here Middle America refers to the countries of Central America and Mexico. This polygon potentially represents at least the dispersal or movement area for mainland anole species (Peterson & Soberón, 2012; Saupe *et al.*, 2012). We clipped all bioclimatic rasters using this polygon and extracted values for all 19 variables from a random set of pixels (> 100,000 pixels of 1 km² each for South America and > 25,000 pixels of 1 km² each for Middle America). We conducted a principal components analysis (PCA) with all 19 bioclimatic variables from species records and points from each region (see Appendix S1 in Supporting Information). For each anole species, we calculated the mean of the scores of the first PC as an estimate of niche position. Finally, we calculated range size for each species as the area within the MCP enclosing all records for individual species and for anole clades. The MCP was only used to calculate range sizes, which were used as covariates for comparisons of niche breadth between clades and regions.

Phylogenetic estimation

We generated a time-calibrated phylogeny using an *Anolis* dataset extracted from a recent Squamata phylogeny (Pyron *et al.*, 2013). Our anole tree comprises 207 anole species, representing 53% of the total number of recognized anole species (Uetz, 2014). Although sampling was very complete for the Caribbean anole species (87%, 19 species missing), it was very incomplete for the mainland species (76 species, 32% of all known species). We also included 32 outgroups based on the topological position of *Anolis* in the Iguania phylogeny (Townsend *et al.*, 2011). The assembled matrix included 233 taxa and 12,896 sites corresponding to nine genes included in Pyron *et al.* (2013). We used their alignment to maintain consistency among studies. We used only two calibration points due to the low availability of fossil samples. First, using a normal distribution prior, we calibrated the root with the crown-group pleurodont iguanian *Saichangurvel* (Conrad & Norell, 2007) from the Late

Campanian (70.6 ± 0.6 Ma; Townsend et al., 2011). Second, a lognormal prior with a minimum age of 23 Ma was used to calibrate the Anolis chlorocyanus group based on an unnamed fossil from the Dominican Republic putatively assigned to this clade (de Queiroz et al., 1998). We placed this anole fossil at the stem of the chlorocyanus group (A. aliniger, A. chlorocyanus, A. coelestinus, A. singularis) following Nicholson et al. (2012). We implemented a relaxed clock method with uncorrelated rates among branches using the software BEAST 1.8.0 (Drummond et al., 2012). We did not implement a highly parameterized partitioned analysis as the ingroup (Anolis) is represented almost entirely by one single gene (ND2). As suggested by JMODELTEST 2.0 (Guindon & Gascuel, 2003; Darriba et al., 2012), we used the GTRGI model of evolution for the entire dataset. We initiated two runs starting from a random tree and ran these for 40 million generations sampling every 1000 following a burn-in of 2 million generations. The number of generations required to reach stationarity was determined by examining marginal probabilities in TRACER 1.6 (Rambaut et al., 2014). For each run, the posterior sampling of trees yielded an effective sample size of > 200 for all parameter models. Both runs were combined as they gave similar results, and node and branch parameters were summarized on the maximum clade credibility tree (see Fig. S1 in Appendix S2). The resulting tree was very similar in topology to recent phylogenetic estimates of Anolis lizards using the same datasets (Mahler et al., 2010; Nicholson et al., 2012; Gamble et al., 2014; Prates et al., 2015). In particular, Prates et al. (2015) generated a calibrated tree for a subset of Anolis species (some species from Dactyloa clade, Anolis carolinensis and some species from Norops clade) using three fossils as calibration points and lying outside the Anolis ingroup (one in the root and two inside the outgroup). Their estimated dates for the most recent common ancestor of Anolis are very similar to our estimated dates (see Prates et al., 2015).

Climatic niche attributes and diversification in Anolis lizards

The clade-based approach

We implemented a clade-based approach to correlate occupied climatic niche space with species richness. Nicholson et al. (2012, their fig. 4) recognized eight clades in the Anolis phylogeny and raised them to the rank of genus (but see Poe, 2013). We used these same names as clades to compare niche attributes. Although the criteria to delimit these clades are arbitrary, the same problem occurs with the use of recognized taxa of a given rank (e.g. family or genus level); additionally, some of these clade names for anoles have been used by some herpetologists for almost three decades (Guyer & Savage, 1986; Savage, 2002). We separated the Norops clade into three – Cuban Norops, Jamaican Norops and mainland Norops – and also split the Dactyloa clade – Lesser Antillean Dactyloa and mainland Dactyloa (Table 1). We obtained species richness

data for each clade from Nicholson et al. (2012). For each clade, we calculated occupied niche space as the summed variances of the first four PC scores (see above). This measure of occupied niche space can be considered a proxy for niche diversity, analogous to the measures of morphological variance used in studies of morphological disparity (Foote, 1997; Wainwright, 2004; Ricklefs, 2012). We can use the species richness (ln species richness) of anole clades as a direct estimator of the total diversification in each clade (the Ω estimator in Rabosky, 2009) because anole clade diversity was not correlated with age ($R^2 = 0.30$, $P = 0.124$) (Rabosky, 2009, 2012b; Rabosky & Adams, 2012). In addition, we calculated net diversification rates for each anole clade using the method-of-moments estimator (Magallón & Sanderson, 2001), based on the crown-group age (obtained from our calibrated tree) and the total number of described species for each clade, and using two values for relative extinction rate (0.9 and 0.1). We tested for a relationship between occupied niche space, clade area (log10 geographical area) and species richness (ln species richness) and net diversification rates in Anolis clades using a path analysis. We repeated the same analysis using only insular clades. This approach allowed us to incorporate all of the anole species for which we had compiled climate data.

The QuaSSE approach

We implemented a quantitative-state speciation and extinction model (QuaSSE; FitzJohn, 2012) to correlate niche attributes (mean niche position and niche breadth) with diversification rates (FitzJohn, 2010). The QuaSSE approach uses a maximum likelihood method to evaluate whether a distribution of continuous character states is associated with higher or lower speciation rates (FitzJohn, 2010). This method has been used previously to find associations between climate and diversification rates in other taxonomic groups (Pyron & Wiens, 2013; Kostikova et al., 2014). We explored whether mean niche position and niche breath were associated with speciation rates in Anolis lizards. These niche metrics describe the ecological niche of a species across a set of environmental axes (Schoener, 1989; Thuiller et al., 2005). The QuaSSE approach identifies whether lineages exhibiting lower or higher niche positions/broader or narrower niche breadths are correlated with higher speciation rates in Anolis.

We generated four models in which speciation rates were fitted according to a particular function: (1) a constant function (trait variation has no influence on speciation rate); (2) a linear function (a linear increase in a trait is associated with a linear increase in speciation rate); (3) a sigmoid function (there is an association between speciation rates and a continuous trait exhibiting a sigmoidal function); and (4) a modal function (where intermediate values for a trait are associated with a higher speciation rate). In addition, we generated another set of models, but assuming a directional trend in the evolution of the particular trait (FitzJohn, 2012). We kept extinction rates constant among models because QuaSSE is known for its difficulty detecting

differences in extinction rates (FitzJohn, 2010). We conducted the same analysis but only for the Caribbean species by pruning all mainland species from the phylogeny. We did not conduct a specific analysis for mainland species only due to the limited taxon sampling for these species (see above). Models were compared using the Akaike information criterion (AIC; Burnham & Anderson, 2002) and we selected as the best models those with the lowest AIC scores (Burnham & Anderson, 2002). As QuaSSE calculations are quite complex and computationally extensive (FitzJohn, 2012), we only performed a QuaSSE analysis for each variable with the best topology selected from our BEAST analysis. Therefore, we were not able to evaluate the potential effects of phylogenetic uncertainty on correlations between speciation rates and niche traits. Finally, we performed a rarefaction analysis for the Caribbean anole tree to evaluate the impact of missing species on the QuaSSE analysis. We randomly pruned species in a sequence of percentages (10%, 15%, 20%, 25%, 30%, 35%, 40%, 45% and 50%) and generated a QuaSSE analysis for each dataset with these pruned trees. The aim was to evaluate whether QuaSSE is sensitive to missing species and therefore to explore the potential impact of taxon incompleteness on the association between traits and diversification (see Appendix S3).

RESULTS

Anole climatic niches

The first two axes of the PCA explained 46.6% and 22.4% of the total variance of climatic variables in *Anolis* lizards (69% in total). Both axes were mainly related to temperature variables (see Appendix S1). The first axis was mainly associated with the minimum temperature of the coldest month (bio 6) and the second axis was mainly associated with the maximum temperature of the warmest month (bio 5; see Appendix S1). We used the mean PC scores of the first axis for each species as a metric of average niche position.

Niche breadth between insular and mainland *Anolis* lizards and among *Anolis* clades

Caribbean *Anolis* species did not have lower niche breadth values than their mainland counterparts (Fig. 1a; $F_{1,330} = 3.32$, $P < 0.069$). However, after controlling for geographical range size effects, niche breadths do differ between regions (ANCOVA; $F_{1,308} = 4.24$, $P < 0.040$). Furthermore, we did not find any differences in niche breadth between clades (Fig. 1b; $F_{10,321} = 1.57$, $P < 0.114$), but we did detect differences after controlling for range size differences (ANCOVA; $F_{10,299} = 2.35$, $P = 0.011$).

Occupied niche space in *Anolis* clades and available climate space

Comparisons of occupied niche space with available climate conditions across regions revealed that the occupation of niche space differed strikingly between insular and mainland lineages (Figs 2 & 3). Insular anole clades seem to occupy almost all climate conditions available on each of the Greater Antilles islands, except Jamaica (Fig. 2). In contrast, mainland anoles occupy only a portion of all available climate conditions both in Middle America and South America. The *Norops* clade occupies a larger niche space than *Dactyloa* does in Middle
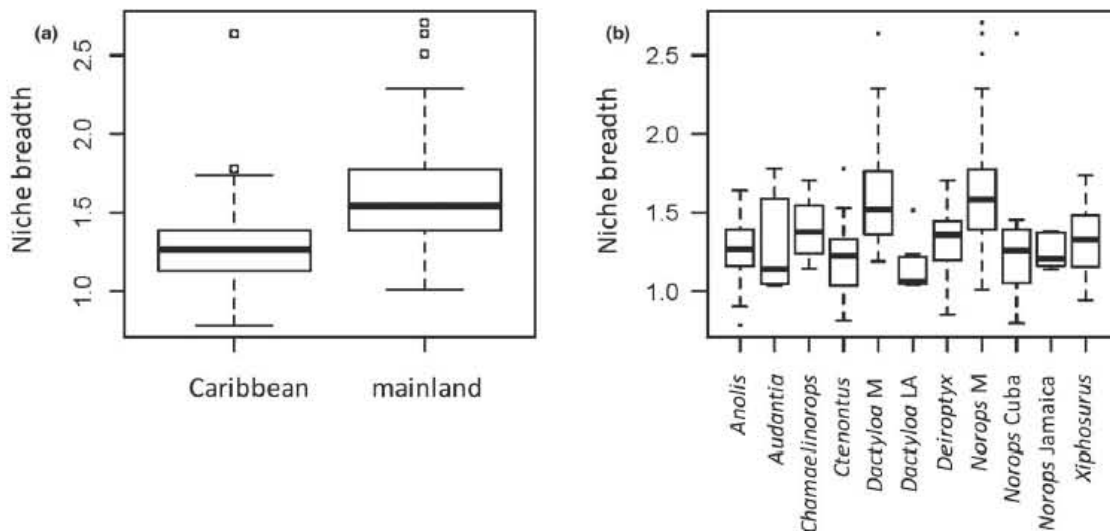

Figure 1 Box plots of niche breadth values for Caribbean and mainland *Anolis* species (a) and *Anolis* clades (b). Niche breadth was estimated using maximum Mahalanobis distances to the niche centroid for 19 bioclimatic variables in a multidimensional climatic niche space. *Dactyloa* LA *Dactyloa* Lesser Antilles *Dactyloa* M: mainland *Dactyloa Norops* M: mainland *Norops*.
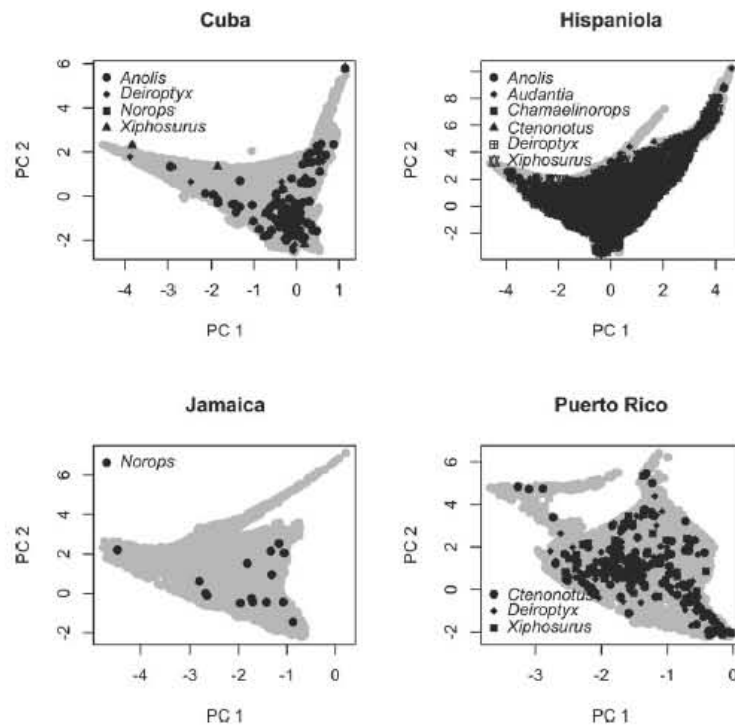
Figure 2 Occupied climate niche space for Caribbean anole clades in each one of the Greater Antilles islands. Light grey points represent the available climate conditions in each island extracted from each pixel (see text for details).

America, but in South America both clades occupy similar portions of the niche space (Fig. 3).

The clade-based approach

Path analysis revealed a significant correlation between species richness (total diversification) and occupied niche space for all anole clades ($R = 0.71$, $P = 0.015$; Fig. 4a). Furthermore, occupied niche space had an indirect influence on species richness through clade area (partial $r = 0.79$). Average niche breadth was not correlated with species richness ($R = 0.02$, $P = 0.950$; Fig. 4b), nor did it have any indirect influence on species richness through clade area (partial $r = 0.22$). For insular clades, niche attributes (occupied niche space and average niche breadth) were not correlated with species richness (Fig. 4c,d). Similar results were obtained using net diversification rates for *Anolis* clades (see Fig. S2 in Appendix S2). This suggests that our results were robust to differences in the diversification metrics used (i.e. total diversification and net diversification rates).

The QuaSSE approach

We found an association between niche attributes (niche position and niche breadth) and speciation rates for all *Anolis* lizards (Table 2). For niche position and niche breadth,

we found that the best model was one with a humped directional trend (Table 2, Fig. 5 upper; though according to AIC values for niche breadth this model had no more support than the linear model with a directional trend). This suggests that speciation rates are higher in lineages occupying warmer areas and for lineages with very narrow niches and some with large niches. For Caribbean anoles, we found that the best model for niche position was one with a directional linear trend (Table 2, Fig. 5 bottom left; again, comparing AIC values for this model had no more support than the hump model with a directional trend). The best model for niche breadth for Caribbean anoles was one with a humped directional trend (Table 2; Fig. 5 bottom right). This suggests that speciation rates are higher in Caribbean anole lineages occupying warmer regions and with very small niches than in lineages occupying cold climates and with large niches. Finally, the association between niche traits and speciation rates for Caribbean *Anolis* lizards found here was stable to the different percentage of random taxon pruning (see Appendix S3). Therefore, our QuaSSE analyses were robust to the taxonomic incompleteness in our dataset.

DISCUSSION

In this study, we found evidence of an association between niche traits and cladogenesis in *Anolis* lizards. First, we found

that anole species occurring in warmer and drier regions tend to diversify more than species in humid and cold regions. This result was consistent for mainland and Caribbean anole species. In particular, Caribbean anole clades tend to occupy all available climate space in comparison with mainland anoles. This suggests that Caribbean clades are not likely constrained by an inability to expand their climatic niche limits, but rather, by the limited Caribbean climate space (Algar & Mahler, 2015). In fact, Caribbean species might not be

prevented from inhabiting cold conditions by evolutionary constraints on cold tolerance, which can evolve quickly (Leal & Gunderson, 2012; Muñoz et al., 2014), but rather by climatic availability in the region (Algar & Mahler, 2015). The limited climatic space, coupled with the high species richness of these clades, suggests substantial niche overlap in insular species, though this may be mediated in part by narrower niche breadths. Furthermore, the high degree of similarity in niche traits for Caribbean anoles suggests that climate niche convergence might be a widespread phenomenon across the Greater Antilles, as found for phenotypic traits (Losos et al., 1998; Mahler et al., 2013). This pattern might be the result of a combination of reduced climatic space in the region and a strong effect of stabilizing selection on climatic niches (Sedio et al., 2013; Wüest et al., 2015).

Mainland clades occupy only a portion of the climatic space within their accessible area (Peterson et al., 2011), but these clades still exhibited greater niche breadth and broader niche space values than insular clades. Mainland clades may have been prevented from exploiting the complete available climate space either because of insufficient time for niche diversification (though this is unlikely for the Dactyloa clade given its age: 30 Ma; see Table 1), inability to adapt to extreme climate conditions, strong biotic interactions or dispersal constraints. As mainland anole species tend to be absent from regions with extreme temperatures (e.g. mountaintops exceeding 3000 m or desert areas), anoles may have physiological constraints that prevent them from inhabiting regions with these extreme climate conditions. However, whether mainland anoles are more limited in range by current climate, dispersal limitations or biotic interactions than Caribbean anoles are (Algar et al., 2013), remains unknown.

We found strong evidence of a negative relationship between niche breadth and diversification rates. This suggests that niche specialization, particularly towards warmer and drier climates, has driven anole diversification. This association between niche specialization and cladogenesis suggests a strong role of climate in anole diversification. Similar results have been found in lampropeltine snakes, for which lineages occurring in warm conditions had higher speciation rates

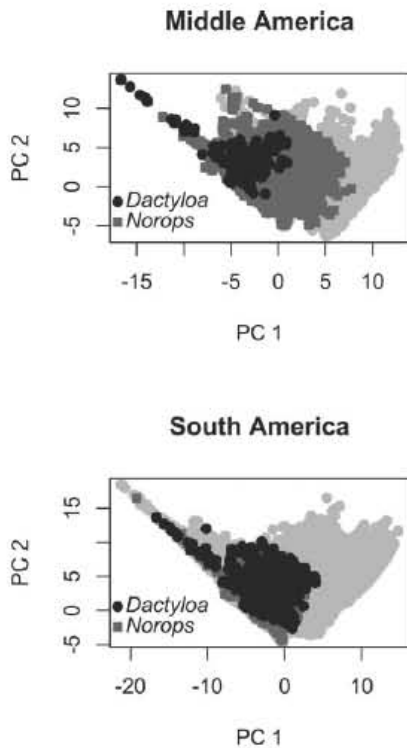## Middle America

South America

Figure 3 Occupied climate niche space for mainland anole clades in Middle America and South America. Light grey points represent the available climate conditions in each mainland region extracted from a random sample of pixels (see text for details).
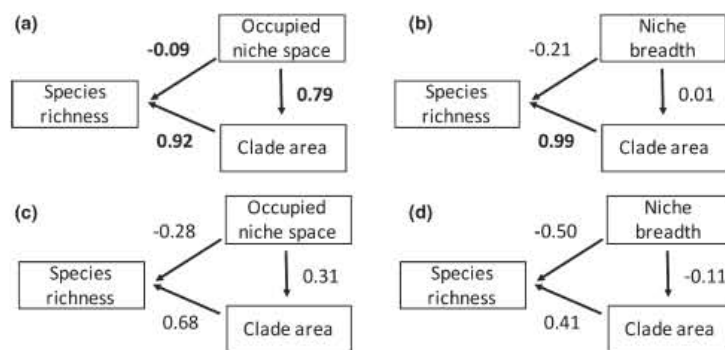

Figure 4 Direct and indirect effects of climatic niche traits (occupied niche space and niche breadth) on species richness for all anole clades (a, b), and only for insular clades (c, d). Statistically significant correlation coefficients are in bold (P < 0.05).

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Table 2 QuaSSE models of the relationship between climatic niche metrics (niche position and niche breadth) and speciation rates in all *Anolis* and only Caribbean *Anolis* lizards. Best-fitting models according to delta AIC (Akaike information criterion) values are in bold. Pars: number of parameters; lnL: ln likelihood; ΔAIC: Delta AIC; Weights: model weights.

			Niche position				Niche breadth			
	Model	Pars	lnL	AIC	ΔAIC	Weights	lnL	AIC	ΔAIC	Weigths
All *Anolis*	Minimal	3	−937.95	1881.9	48	0.00	−683.31	1372.6	45	0.00
	Linear	4	−937.89	1883.8	50	0.00	−683.22	1374.5	47	0.00
	Sigmoidal	6	−937.06	1886.1	52	0.00	−682.91	1377.8	51	0.00
	Hump	6	936.28	1884.5	51	0.00	−682.81	1377.6	50	0.00
	Linear (drift)	5	−917.36	1844.7	11	0.00	−659.16	1328.3	1	0.23
	Sigmoidal (drift)	7	−917.92	1849.8	16	0.00	−662.35	1338.7	12	0.00
	Hump (drift)	7	−909.91	1833.8	0	0.38	−656.58	1327.2	0	0.38
Caribbean *Anolis*	Minimal	3	−652.3	1310.5	24	0.00	−391.7	789.5	16	0.00
	Linear	4	−652.2	1312.5	26	0.00	−391.7	791.4	18	0.00
	Sigmoidal	6	−651	1314	27	0.00	−391.7	795.3	22	0.00
	Hump	6	−649.4	1310.8	24	0.00	−391.7	795.3	22	0.00
	Linear (drift)	5	−638.4	1286.8	0	0.38	−391.4	792.7	20	0.00
	Sigmoidal (drift)	7	−641.2	1296.3	9	0.00	−379.5	773.1	0	0.38
	Hump (drift)	7	−637.2	1288.3	1	0.23	−391.7	797.3	24	0.00
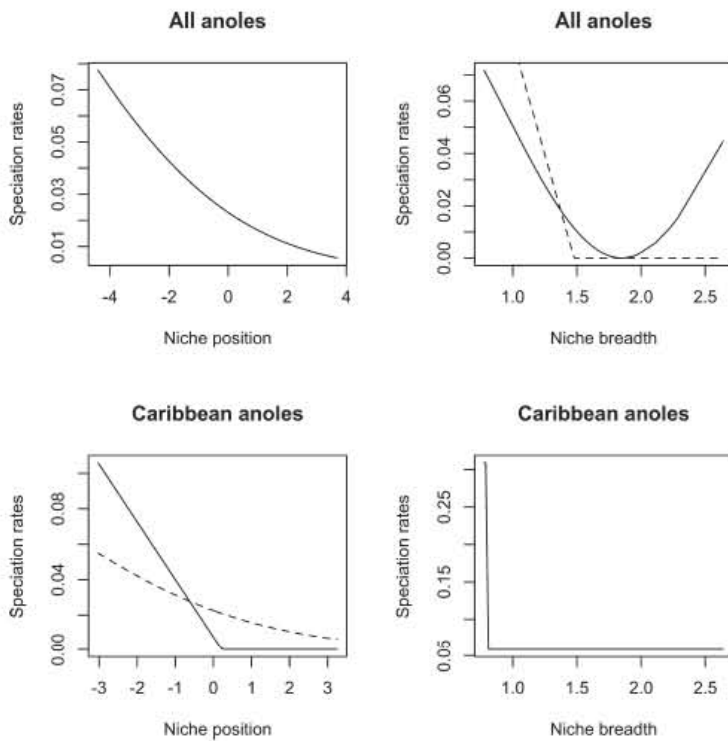
Figure 5 Relationships between niche traits (mean niche position and niche breadth) and speciation rates for all anoles lizards (upper) and Caribbean anoles only (bottom) using the quantitative-state speciation and extinction model approach. Dotted lines represent alternative models according to delta Akaike information criterion values (see Table 2).

(Pyron & Burbrink, 2012). Finally, we found that clades with higher species richness tend to exhibit more niche diversity (occupied niche space) than species-poor clades. These results support the hypothesis that cladogenesis is coupled with climate niche divergence in *Anolis* lizards (Rabosky, 2012a; Rabosky *et al.*, 2013). Recently, Gómez-Rodríguez

et al. (2015) suggested that a negative relationship between niche width and diversification rates would be expected under a scenario of niche conservatism (Wiens, 2004). In contrast, they suggested that a positive relationship would be expected under a scenario of climatic niche divergence (Moritz *et al.*, 2000). However, it is not clear how these

niche conservatism or niche divergence patterns can shape diversification dynamics at regional scales. In our opinion, the evolutionary mechanisms underlying the correlation between climatic niche traits and speciation dynamics are still unknown.

Our study is the first to examine how climatic niches vary among *Anolis* lizards at large phylogenetic and geographical scales, and how climatic niche traits are related to species diversification. We found that Caribbean and mainland anoles exhibit striking differences in niche traits (after controlling for range size effects) and these are correlated with speciation rates. Specifically, we found that lineages with narrow niches and that are specialized to warmer areas have diversified more than lineages with large niches and specialized to cold regions. Niche differences in insular and mainland anoles suggest that different evolutionary processes (niche divergence or niche conservatism) might be operating between regions, as in the case of ecomorphological traits (Pinto *et al.*, 2008). However, it is crucial that a more comprehensive phylogeny for mainland anoles be incorporated to corroborate these findings using comparative phylogenetic methods. Finally, our study found interesting macroecological and macroevolutionary patterns, but more research is necessary to identify the potential evolutionary mechanisms driving these patterns.

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SUPPORTING INFORMATION

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

Appendix S1 Results of the principal components analysis for 19 bioclimatic variables.

Appendix S2 Supplementary figures.

Appendix S3 Effects of missing species on the QuaSSE analysis.

BIOSKETCH

Julián A. Velasco is carrying out his PhD studies at the Instituto de Biología, Universidad Nacional Autónoma de México. His doctoral research focuses on understanding the ecological and evolutionary processes responsible for species richness gradients and diversification in *Anolis* lizards. He addresses several evolutionary and ecological topics using a combination of conceptual and methodological approaches including niche modelling, geospatial analysis, historical biogeography and macroecology.

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CAPÍTULO II

Factores climáticos y evolutivos formando gradientes geográficos de riqueza de especies en lagartijas *Anolis*.

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

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ABSTRACT

Understanding the role of ecological and evolutionary factors on geographical gradients of species richness is one of the most active research arenas in ecology and biogeography. Consensus on which climatic components determine richness is still lacking, but four factors have been proposed: water-energy, seasonality, heterogeneity, and historical climatic stability. In addition, the resulting richness-climate relationships may be mediated by historical processes, such as phylogenetic niche conservatism (-PNC- the evolutionary trend to retain ecological traits among related species) and differences in species diversification rates across regions (regional diversification). Here, we evaluated the contribution of unique and shared predictors of four climatic hypotheses on the geographical species richness gradients of Neotropical *Anolis* lizards using a partitioning approach. In addition, we evaluated the role of PNC and regional diversification in the origin and maintenance of the resulting richness-climate relationship. Our results show that climate has a non-stationary relationship with *Anolis* species richness with most of the effect shared among climate axes. Regional differences in species richness-climate relationships suggest differential assembly processes between mainland and insular settings. As we did not find evidence for a role of PNC and regional diversification shaping anole richness-climate relationships, we suggest that geographical species richness patterns in *Anolis* lizards are now decoupled from the evolutionary factors that generated them during the assembly process.

Keywords: *Anolis, assembly, climate, diversification, geographical ecology, lizards, macroecology, phylogenetic niche conservatism*

INTRODUCTION

Understanding the causes of species richness variation across regions and lineages is one of the fundamental questions in ecological and evolutionary studies (Wiens and Donoghue 2004, Gotelli et al. 2009). The relationship between species richness and climate across continents, globally, and through time suggests a causal effect of climate on species richness at broad spatial scales (Currie et al. 2004, Vázquez-Rivera and Currie 2015), via one or several potential processes (Mittelbach et al. 2007, Wiens et al. 2010). Therefore, understanding how climate shapes richness gradients requires two stages: First, to identify the climatic axes that promote or constrain richness, and second to identify the biological processes linking climate and richness. Numerous hypotheses have been proposed for each of these stages. For stage one, four main factors related to current and past climatic factors have been considered (Evans et al. 2005, Field et al. 2009, Tello and Stevens 2010, Gouveia et al. 2013), namely: (i) water-energy, (ii) seasonality, (iii) environmental heterogeneity, and (iv) historical climatic stability. For stage two, a number of evolutionary and ecological factors have been proposed (Mittelbach et al. 2007) with phylogenetic niche conservatism (PNC; Wiens and Donoghue 2004, Wiens et al. 2010) and geographic variation in diversification rates (Weir and Schluter 2007, Wiens 2011) currently being the most prominent ones (Rolland et al. 2014).

Multiple causal mechanisms have been hypothesized for each one of these environmental hypotheses. For instance, at least nine mechanisms are known for the water-energy hypothesis (Evans et al. 2005, Tello and Stevens 2010), including direct

effects on population sizes by allowing more individuals in higher productive areas, and therefore more species (Srivastava and Lawton 1998, Currie et al. 2004). Other mechanisms state that productivity increases speciation rates and reduces extinction rates (Rohde 1992, Allen and Gillooly 2006). However, much of these causal mechanisms has not been tested rigorously and therefore lacks strong empirical support.

For the seasonality hypothesis, the proposed mechanisms relies on within-year climatic variability generating large population fluctuations and increasing species extinction risk. Accordingly, species occurring in seasonal areas will have wider niches and larger range sizes, with less chances for speciation (Janzen 1967, Hurlbert and Haskell 2003, Williams and Middleton 2008, Tello and Stevens 2010, Dalby et al. 2014). Mechanisms for the environmental heterogeneity hypothesis indicate that habitat complexity increases the number of dispersal barriers and promotes population fragmentation with reductions in gene flow. In these cases, habitat complexity might directly elevate diversification rates by increasing the number of *in situ* speciation events (Kisel et al. 2011). Finally, causal mechanisms underlying the historical climatic stability hypothesis make it likely that areas with stable climates will accumulate species over time (Jansson 2003, Sandel et al. 2011, Rakotoarinivo et al. 2013). In contrast, strong climatic oscillations might influence directly net diversification rates by increasing extinction rates for species with low vagility, or by reducing speciation rates for species with high vagility, which can track its niches across geography and increases gene flow between populations (Kisel et al. 2011,

Rakotoarinivo et al. 2013). Although some of these climatic hypotheses have been tested extensively (e.g., water-energy hypothesis: see for instance Field et al. 2005, Whittaker 2007, Kreft and Jetz 2007), others (e.g., historical climatic stability hypothesis; but see Fine and Ree 2006, Jetz and Fine 2012) have received less attention and its contribution to geographical species richness gradients of many taxa remain unknown.

Recent conceptual and methodological advances have reinvigorated the integration of the historical perspective in ecological studies (Jablonski et al. 2006, Cavender-Bares et al. 2012, Hernandez et al. 2013), allowing tests of historical evolutionary processes generating present-day geographic patterns of biodiversity (Wiens and Donoghue 2004). Indeed, species richness gradients and the resulting richness-climate relationships are now thought to result, at least in part, from historical processes such as the phylogenetic niche conservatism (PNC; Wiens and Donoghue 2004, Wiens and Graham 2005, Algar et al. 2009, Hawkins and McCain 2012), and variation of diversification rates across regions (Rolland et al. 2014). Evidence favoring these historical processes includes the overall confinement of old clades to their region of origin (e.g., tropical regions) whereas derived clades can be present at regions more distant from their origin (e.g., temperate regions) (Jablonski et al. 2006, Hawkins et al. 2007, Romdal et al. 2013), and the stronger richness-climate relationship for old clades compared to the one observed for derived clades (Hawkins and McCain 2012).

Lizards of the Neotropical genus *Anolis* are an excellent system to examine the relative influence of climatic factors and historical processes on geographic patterns of diversity. *Anolis* lizards likely originated in South America during the Paleocene (~60 million of years ago), dispersing to the Caribbean islands and then back-colonizing the mainland (Nicholson et al. 2005, Losos 2009). Although these lizards exhibit exceptional diversification in both the Caribbean (~150 species) and mainland (~240 species) (Losos 2009), some recent studies suggests that the assembly of the anole faunas differ between insular and mainland regions (Algar and Losos 2011, Stuart et al. 2012). In particular, Stuart *et al.* (2012) suggested that higher turnover of anole species among islands and between islands and mainland is indicative of a unique assembly process in the Caribbean islands. Although these studies have examined species richness patterns of *Anolis* within both insular and mainland regions and between them, key questions related to the potential role of the climatic factors to shape geographical gradients via evolutionary processes of anoles remain open.

In this paper, we tested the role of climatic and evolutionary factors on geographical gradients of species richness in *Anolis* lizards at broad spatial scales. First, we evaluate the unique and shared contributions of the four climatic hypothesis (water-energy, seasonality, heterogeneity, and historical climatic stability) on species richness via a geographical weighted regression (GWR) with a partitioning approach (Tello and Stevens 2010, Gouveia et al. 2013). Second, we evaluated the role of PNC and regional diversification on the richness-climate relationships in *Anolis* lizards. If

PNC has played an important role, we predict that regional assemblages composed of "basal" species would exhibit a strong signature with climate. In contrast, assemblages composed of "derived" species would exhibit a weak climatic signature (Buckley et al. 2010, Hawkins and McCain 2012). In addition, if regional diversification has driven the assembly of anole faunas, we predict that regions showing faster *in situ* diversification and low dispersal events will have a weak climatic signature (i.e., higher residual from richness-climate models). Conversely, if regional diversification has not driven the assembly of faunas, we predict that regions with slow *in situ* diversification and high dispersal will have a strong climatic signature (i.e., lower residuals from richness-climate models) (Buckley et al. 2010).

MATERIALS AND METHODS

Species data and geographical gradient of species richness

We compiled occurrence records for 300 *Anolis* species from the Caribbean and mainland and generated range maps for each species representing their extents of occurrence (Velasco *et al*. in review). We generated minimum convex polygons for each species with at least three records and removed non-land areas afterwards (292 species). The eight remaining species with one or two records were added to the grid cell encompassing these records. We calculated the number of *Anolis* species by overlying a grid of 1° x 1° (~12544 km^2 pixel size) covering the whole region where native anoles occur and counted the number of range maps overlapping in each grid cell. We excluded those coastal cells with less than 25% of land surface. Our grid

system resulted in 1247 cells across the region, from which a presence-absence matrix of 300 species by 1247 cells was created for further analyses.

Spatial diversification and phylogenetic niche conservatism

We generated a combined phylogeny for 253 *Anolis* lizards based on morphological and DNA data (see Appendix 1). To incorporate missing species in the phylogeny with range maps (80 species), we used information from taxonomic or systematic accounts and original descriptions to add them to the phylogeny using the phytools R package (Revell 2012) (see Appendix 1). For the resulting tree, polytomies were randomly resolved and all branch lengths were set to unity. Species from the Lesser Antilles and other small Caribbean islands were pruned from our resulting tree (33 species). These small islands have a low diversity (one or two species per island; Losos 1990) and therefore their exclusion does not affect our general results.

We calculated mean-root distance (MRD) and phylogenetic diversity (PD) using our phylogenetic hypothesis. MRD is a metric that represents the level of evolutionary derivedness of a local fauna, and was calculated as the average number of nodes separating a species from the root of the phylogeny (Kerr and Currie 1999). Species were classified as "basal" or "derived" using 30% and 70% percentiles of root distance values, respectively (Hawkins et al. 2006) and we then calculated species richness for each group. According to the PNC hypothesis, basal faunas should exhibit a stronger relationship with climate than faunas composed of derived species (Wiens and Donoghue 2004, Buckley et al. 2010).

Phylogenetic diversity is a metric that represents the summed branch lengths

of a phylogenetic tree connecting species by its geographical proximity (Faith 1992,

Vellend et al. 2011), and here was calculated for each grid cell. As PD is strongly

correlated with species richness (R^2=0.82, $p < 0.0001$), we calculated residuals for a

PD-species richness regression as a measure of regional diversification (henceforth

we call this as relative PD). This metric evaluates whether past evolutionary events

(i.e., speciation, extinction, and dispersal) have contributed to regional species

assemblages (Davies and Buckley 2011, Fritz and Rahbek 2012), allowing us to

differentiate among regions with faster diversification rates and few dispersal events

(low relative PD values) from regions with slower diversification rates and several

dispersal events (high relative PD values; Fritz and Rahbek 2012, Davies and Buckley

2012). PD and MRD were calculated using the R package *picante* (Kembel et al.

2010). We mapped these metrics to explore geographical patterns of regional

diversification and evolutionary derivedness in *Anolis*.

Environmental variables

To test the role of current (water-energy, seasonality, and heterogeneity) and

past (historical climatic variability) climate hypotheses on anole species richness, we

used the following variables: (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 that were calculated as differences in

current and past variables (Table S2). 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). For the LGM, we excluded AMT because we did

not find differences among temporal periods. All climatic variables were obtained

from the WorldClim database (Hijmans et al. 2005), and calculations were made in

ArcGIS 9.3 (ESRI 2009).

Climate-richness relationships

We performed a series of ordinary least squares models (OLS) and

geographical weighted regression (GWR) models to correlate the number of species

of *Anolis* lizards in each grid cell with current and past climatic variables separating

analyses for each time period (LGM and LIG). First, we built models for the complete

set of hypotheses (WE, SEAS, HET, and HSC) for each time period (Last Glacial

Maximum and Last Inter-Glacial, respectively) (hereafter "full model LGM" and "full

model LIG"). Also, we built models for each hypothesis separately (hereafter "single

WE", "single SEAS", "single HET", "single HSC-LGM", and "single HSC-LIG") (Figure

1A; see Table A2). We selected the model with the highest explanatory power using

the Bayesian Information Criteria (BIC) also known as Schwarz's Bayesian Criterion

(Schwarz 1978, Quinn and Keough 2002). We calculated local GWR regression

parameters (R^2 and slope) for each cell from full and single models (Fotheringham et al. 2002) (Figure 1A).
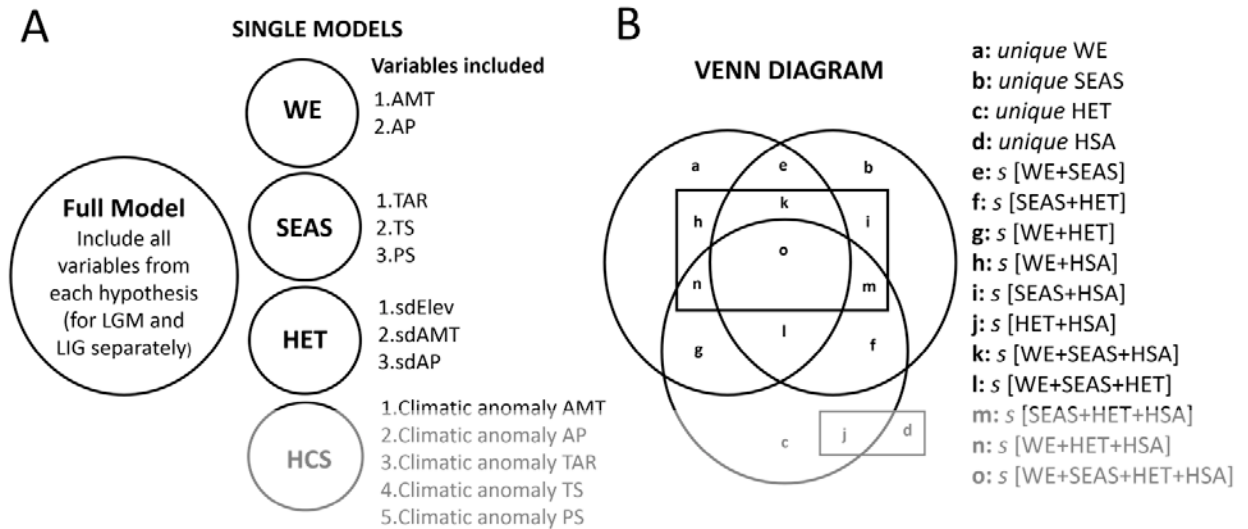

Figure 1. Diagram representing richness-climate models implemented. (a) Full models (larger circle) were built using all single hypotheses (small circles: Water-Energy, Seasonality, Heterogeneity, and Historical Climatic Stability) for each time period (Last Glacial Maximum,LGM and Last Inter-Glacial, LIG). Variables used for each hypothesis are listed at the right-hand side of each circle (AMT: annual mean temperature; AP: annual precipitation; TS: temperature seasonality; PS: precipitation seasonality; stdevElev: standard deviation of annual mean temperature; stdevAP: standard deviation of annual precipitation; see main text for details about how were calculated). (b) Venn diagram representing the variation partitioning analysis implemented. We partitioned variation in species richness among four hypotheses: Water-Energy (WE), Seasonality (SEAS), Heterogeneity (HET) and Historical Climatic Stability (HCS). Fractions *a, b, c, d* represent variation in species richness associated with the *unique* effects of each one of the four hypotheses. In other words, this represents variation in species richness explained only by a single hypothesis maintaining constant the effect of the remaining hypothesis. Fractions *e, f, g, h, i, j* represent variation associated with the *shared* effects by two hypotheses. Fractions *k, l, m, n* represent variation associated with the *shared* effects by three hypotheses, finally, *o* represents variation associated to the intersection of all four hypotheses.

We implemented a variance partitioning approach (Legendre and Legendre 2012) with the aim of decomposing the effect of each predictor separately (i.e., pure effects) and in combination (i.e. shared effects) in determining geographical richness patterns (Figure 1B). This approach allowed us to estimate pure effects of a predictor

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(or shared effects for two predictor) while controlling the effects from other predictors. We conducted this approach for both time periods (LGM and LIG) (Figure 1B). Finally, we compared parameters from full GWR models for LGM and LIG among Greater Antilles, Middle America and South America to explore for potential differences between regions. All statistical analyses were performed in the macroecological software SAM (Rangel et al. 2010).

Evolutionary drivers of richness-climate relationships in Anolis *lizards*

We performed correlations between evolutionary metrics (MRD and PD) and parameters for full GWR models (e.g., residuals, R^2, slopes) in order to evaluate the effect of PNC and regional diversification as drivers of richness-climate relationships for *Anolis* lizards. First, we tested the effect of PNC by performing a correlation between MRD (as a metric of PNC) and GWR parameters. According to the PNC hypothesis, we expected a negative correlation between these parameters. This negative correlation would suggest that regional assemblages composed of "basal" species (low MRD values) exhibit a strong signature of climate (revealed by higher values in GWR parameters -local R^2 and slopes-), whereas regional assemblages composed by "derived" species (high MRD values) exhibit a weak signature of climate (reflected in lower GWR parameters).

Second, we tested whether regional diversification drives variation in species richness that was not explained by climate factors. For this, we correlated the residuals from the full GWR models (for LGM and LIG time periods) and relative PD

values. We expected that regional assemblages dominated by slow diversification rates and colonization of multiple lineages (high relative PD values) exhibit a strong signature of climate (reflected in low residuals from full GWR models). In contrast, we expected that regional assemblages dominated by fast diversification rates of lineages (low relative PD values, suggesting elevated *in situ* speciation), exhibit a weak signature of climate (reflected by high residuals from full GWR models). We implemented the Dutilleul's method (Dutilleul 1993) to correct the number of effective degrees of freedom in the presence of spatial autocorrelation in GWR parameters.

Correlations between evolutionary metrics (MRD and relative PD) and GWR parameters were compared against a null model in which we eliminated the phylogenetic structure by randomizing species across the tree. This null model describes a scenario in which PNC and regional diversification do not have any impact on the observed climate-richness relationships. In other words, the null model envisions a situation where climate-richness relationships emerge only as a result of the spatial cohesiveness and overlap of species ranges. We shuffled the tips in the original tree 1000 times. Then, we calculated the evolutionary metrics (MRD and relative PD) for each random tree and correlated these metrics with the observed GWR parameters. We generated frequency distributions of the 1000 coefficients of determination (R^2) for each comparison (random MRD vs. GWR R^2 and slopes for LGM and LIG; random relative PD vs. GWR residuals for LGM and LIG). We

considered statistical significance of such coefficients if observed values fell outside the 95% confidence interval of the corresponding frequency distribution.

RESULTS

Geographic patterns of species richness and evolutionary metrics

High species richness of *Anolis* lizard species occurs across the Greater Antilles, the mid portion of the Guatemalan highlands, the Talamancan highlands (Costa Rica and Panama) and the northern Andes (Colombia and Ecuador) (Figure 2A). Lower diversity was found towards northern Mexico, the Caribbean coast in Colombia and Venezuela, and the Brazilian coast (Figure 2A). Species richness from "basal" lineages was higher in the Andes region, lower Central America, and the Greater Antilles (Figure 2B). In contrast, species richness from "derived" lineages was higher in Middle America, Chocó, and the Andes region in South America (Figure 2C). PD was highly correlated with species richness (R^2=0.82, $p < 0.0001$). Mapping relative PD values showed that the mid portion of Middle America and the Andean region exhibited high values (Figure 2D). Conversely, low relative PD values were found mainly in the Greater Antilles, the Pacific coast of Mexico, Costa Rica, and Guajira province in Colombia (Figure 2D).
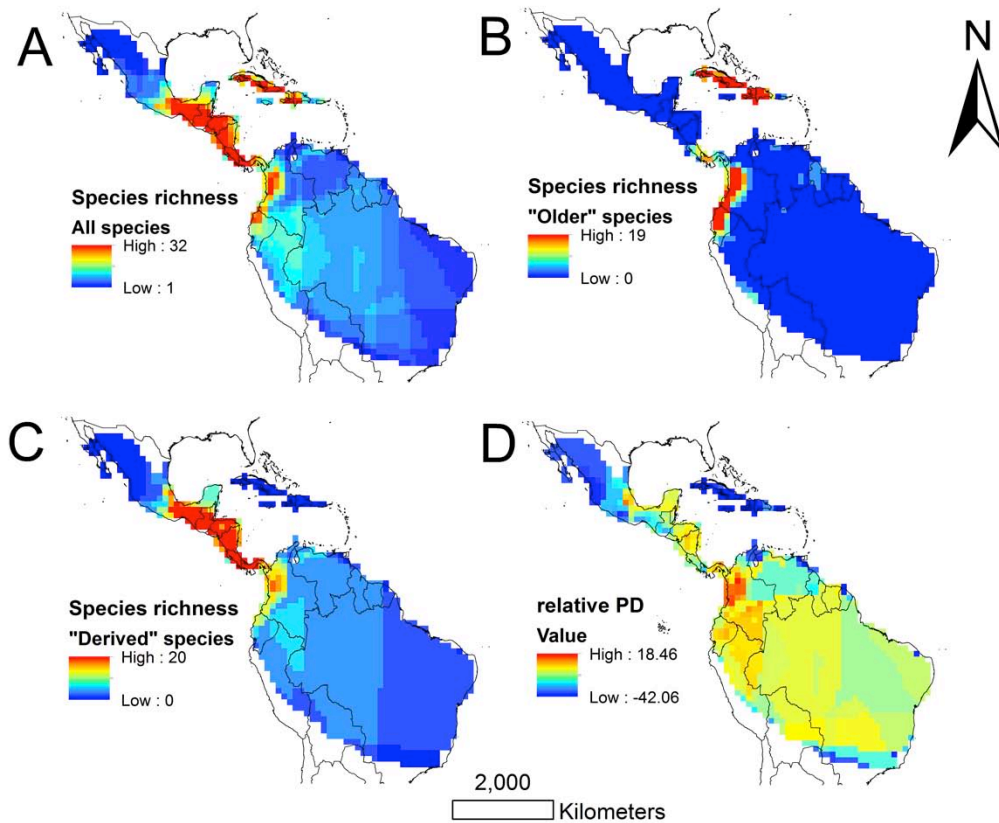
Figure 2. (a) Geographical patterns of *Anolis* species richness. Species richness for (b) "basal" and (c) "derived" *Anolis* species; (d) relative phylogenetic diversity (relative PD).

Climate-richness relationships

A comparison of statistical analyses revealed that GWR models always performed better than OLS models (Table 1; Appendix S2). These results suggest a strong non-stationary effect in richness-climate relationships for *Anolis* lizards. In all cases, full models for LGM and LIG periods exhibited highest explanatory power, indicated by lower BIC scores and higher R^2 values, than single models for each hypothesis tested (i.e., water-energy, seasonality, heterogeneity and historical climatic stability). R^2 values for single hypotheses (water-energy, seasonality,

heterogeneity and historical climatic stability) were relatively similar for LGM and

LIG (Table 1).

Table 1. Regression parameters for full models and single hypotheses (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). GWR: Geographical weighted regression; OLS: Ordinary least squares. BIC: Bayesian Information Criteria.

Models	GWR			OLS		
	R^2	BIC	Δ BIC	R^2	BIC	Δ BIC
Full model for Last Glacial Maximum	0.736	2589	65.6613	0.292	3749	212.998
Full model for Last Inter-Glacial	0.766	2523	0	0.352	3536	0
Water-Energy (WE)	0.654	2653	130.169	0.104	3973	436.167
Seasonality (SEAS)	0.619	2792	268.344	0.04	4066	529.161
Heterogeneity (HET)	0.642	2715	191.612	0.213	3817	280.602
Historical climatic stability (HSC) -LGM	0.689	2605	81.5196	0.068	4036	499.738
Historical climatic stability (HSC) –LIG-	0.689	2537	13.9455	0.118	3875	338.606

R^2 values for full models for LGM and LIG exhibited similar geographical

patterns (Figure 3 and 4). 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 (Figure 3 and 4). However, the variance partitioning analysis

revealed that the unique contribution of each predictor (i.e., *unique* models where

effects of other predictors are held constant; see Figure 1B) were relatively minor and

exhibited a strong non-stationary effect (Figure 3 and 4; Table 2). In particular, the

signature of past climates (mainly from Last Inter-Glacial, LIG) was strong on species

richness patterns (Table 1; Figure 3 and 4). In this time period, unique contributions

for historical climatic stability were higher (higher partial coefficients) in Middle

America highlands, Chocó region, and Western Amazonia (Figure 4).

Table 2. 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; HSC: Historial climatic stability hypothesis.

Pure and shared effects	Last Glacial Maximum	Last Inter-Glacial
pure WE	0.02	0.01
pure SEAS	0.02	0.01
pure HET	0.02	0.03
pure HSC	0.03	0.06
sWE+SEAS	0.00	0.01
sSEAS+HET	0.00	0.00
sWE+HET	0.03	0.04
sWE+HSC	0.00	0.01
sSEAS+HSC	0.01	0.02
sHET+HSC	0.01	0.00
sWE+SEAS+HSC	0.01	0.00
sWE+SEAS+HET	-0.04	-0.03
sSEAS +HET+HSC	-0.01	-0.01
sWE+HET+HSC	0.01	0.00
sWE+SEAS+HET+HSC	0.63	0.62

Figure 3. Geographical patterns of full and unique contributions of each hypothesis explaining observed *Anolis* species richness gradients for the Last Glacial Maximum (LGM). WE: Water-Energy; SEAS: Seasonality; HET: Heterogeneity; CA: Climatic Anomaly. See main text for details in variables analyzed for each hypothesis. Upper right: Venn diagram representing hypotheses evaluated in this study. Each lowercase letter represents unique (denoted by ***unique***) or shared (denoted by ***s***) contributions of climatic hypotheses to observed geographical patterns of *Anolis* species richness (see Figure 1B).
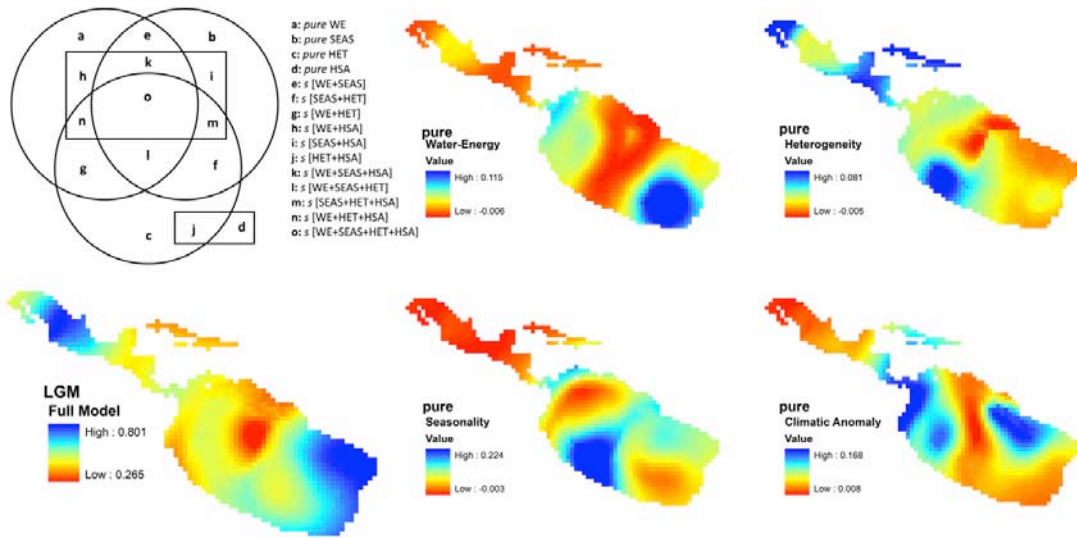

Figure 4. Geographical patterns of full and unique contributions of each hypothesis explaining observed *Anolis* species richness gradients for the Last Inter-Glacial (LIG). WE: Water-Energy; SEAS: Seasonality; HET: Heterogeneity; CA: Climatic Anomaly. See main text for details in variables analyzed for each hypothesis. Upper right: Venn diagram representing hypothesis evaluated in this study. Each lowercase letter represents unique (denoted by ***pure***) or shared (denoted by ***s***) contributions of climatic hypotheses to observed geographical patterns of *Anolis* species richness (see Figure 1B).
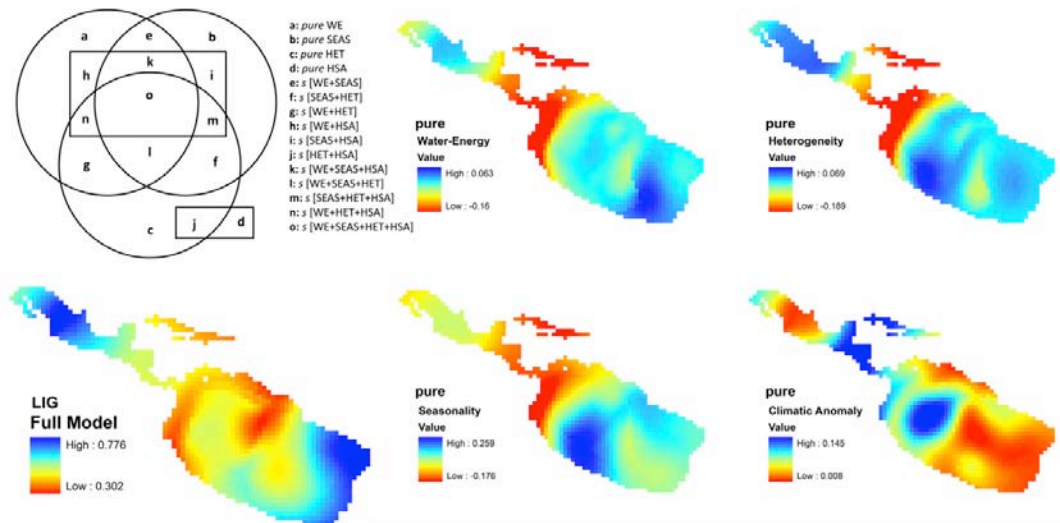
Shared effects between two or more predictors exhibited higher contributions than unique models, particularly for models that included past climatic anomalies (Table 2). Again, mapping of model contributions for shared contributions were strongly non-stationary (Figure S1 and S2 in Appendix S3). Shared effects of water-energy and heterogeneity with historical climatic stability for LIG revealed higher contributions in regions with high species richness Figure S1 and S2 in Appendix S3).

We found differences in regression parameters of full models between regions (Table 3). In particular, we found lower local R^2 values for the Greater Antilles than mainland areas, perhaps driven by a lower climatic variation in the Caribbean islands in comparison with mainland (Figure S3 in Appendix S3). Although local slopes also differed between regions, this was related to the period examined (Table 3). For the LIG period, higher slopes were found for the Greater Antilles in comparison with mainland areas, but the opposite was found for the LGM period (Figure S4 in Appendix S3).

Table 3. Comparison of local parameters (R^2 and slopes) of richness-climate relationships between regions (*p*-values). MA: Middle America; SA: South America; GA: Greater Antilles. WE: Water-energy hypothesis; SEAS: Seasonality hypothesis; HET: Heterogeneity hypothesis; HSC: Historial climatic stability hypothesis.

| Parameters	Models	MA vs SA	SA vs GA	MA vs GA
Local R^2 values	Full Model LGM	< 0.001	< 0.001	< 0.001
	Full Model LIG	< 0.001	< 0.001	< 0.001
	WE Model	< 0.001	< 0.001	< 0.001
	SEAS Model	< 0.001	< 0.001	< 0.001
	HET Model	< 0.001	>0.07	< 0.001
	HCS LGM	< 0.001	> 0.5	< 0.001
	HCS LIG	> 0.5	> 0.07	> 0.1
Local slope values	Full Model LGM	< 0.001	< 0.001	>0.5
	Full Model LIG	>0.1	< 0.01	< 0.05
	WE Model	< 0.001	< 0.001	< 0.001
	SEAS Model	< 0.001	< 0.001	< 0.001
	HET Model	< 0.001	< 0.001	< 0.001
	HCS LGM	< 0.001	< 0.001	> 0.5
	HCS LIG	< 0.001	< 0.001	< 0.001
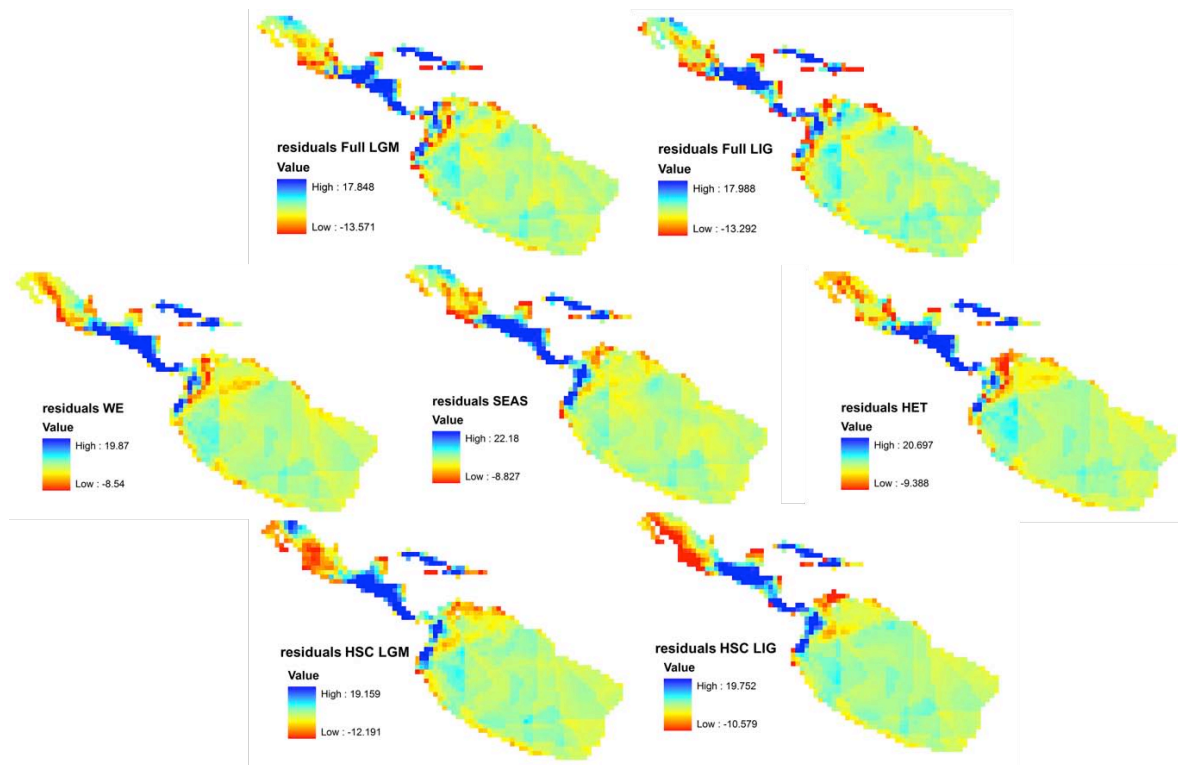
Figure 5. Geographical patterns of residuals of *Anolis* richness-climate relationships for the Last Glacial Maximum (LGM) and the Last Inter-Glacial (LIG). WE: Water-Energy; SEAS: Seasonality; HET: Heterogeneity; HCS: Climatic Anomaly. See main text for details in variables analyzed for each hypothesis.

Geographic patterns of residuals for full and single models for both time periods were very similar (Figure 5). 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 (Figure 5).

Evolutionary drivers of richness-climate relationships

We did not find evidence for a significant correlation between either MRD values or relative PD and GWR parameters (R^2, slopes, and residuals, respectively) (Table 4; Figure S5 and S6 in Appendix S3). These observed correlation values were predicted by a null model simulating the absence of PNC and regional diversification effect on the geographical richness-climate pattern (Figure S7 and S8 in Appendix S3).

Table 4. Correlations between evolutionary metrics (mean root distance, MRD and relative phylogenetic diversity, relative 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^2 from correlations between evolutionary metrics and GWR parameters are higher than the null model average (1000 randomizations; see main text for details).

	Observed R2	*p*-value
MRD vs local R^2 values -full model LGM-	0.00	0.000
MRD vs local R^2 values -full model LIG-	0.01	0.000
MR vs local slopes -full model LGM-	0.00	0.000
MR vs local slopes -full model LIG-	0.01	0.000
Relative PD vs. local residuals -full model LGM-	0.00	0.000
Relative PD vs. local residuals -full model LIG-	0.00	0.000

DISCUSSION

A debate about the importance of single factors as predictors of diversity gradients is currently taking place (e.g., water-energy vs. seasonality), and more importantly, how the climate-diversity relationship varies across geographical regions (Jetz and Rahbek 2002, Davies et al. 2007, Tello and Stevens 2010, Gouveia et al. 2013). In this study, we provide evidence for a strong relationship between species richness of anole lizards and environmental predictors in the Neotropical realm. The variance partitioning strategy used here allowed us to disentangle the unique effects of each climatic hypothesis tested. These unique contributions were similar but very small (Table 1). Shared effects of two or more hypotheses were more important than individual ones (Table 1). These results suggest that geographical patterns of anole species richness may be explained by single, or synergy of several environmental factors, but that correlational analyses through space cannot disentangle their effects.

Our results are consistent with findings in other taxonomic groups (e.g., bats, Tello and Stevens 2010) and suggest that factors driving anole species richness in the Neotropical realm are complex with multiple non-stationary effects (Foody 2004, Eiserhardt et al. 2011, Gouveia et al. 2013). In particular, it was clear that insular and mainland regions exhibited differences in the contribution of climatic factors to species richness patterns (Table 3; Figure S1 and S2 in Appendix 3). This suggests that the signature of climatic conditions on the assembly of anole faunas and regional diversification was very different between insular and mainland regions (Algar and Losos 2011, Stuart et al. 2012), which may arise because Caribbean islands exhibit a

restricted climatic space and thus less climatic variability in comparison with the mainland (Velasco et al. in review).

We did not find evidence for a role of phylogenetic niche conservatism or regional diversification on the resulting richness-climate relationships in *Anolis* lizards. Observed values for these correlations were not different from null models describing the absence of an effect of PNC and regional diversification on richness-climate relationships. It is likely that higher concentration of species richness and its correlation with climate may be explained by additional factors not examined in this study. For instance, high diversity and endemism of animals and plants in the central portion of Middle America (Campbell 1999, Pennington et al. 2004) is considered to be a result of tectonic activity in the Miocene, likely promoting diversification rates in this groups (Castoe et al. 2009, Daza et al. 2010). For the Greater Antilles, it is well recognized that anole diversity results from exceptional diversification (high speciation with low extinction rates) related to ecological specialization (Losos and Schluter 2000, Algar and Losos 2011). Accordingly, we suggest that high diversity in the central portion of Middle America (from the Norops clade) might be also a result of elevated *in situ* speciation rates associated with tectonic events during the Miocene. Studies on the biogeography of this region have shown a complex pattern of dispersal and vicariance events that difficult the understanding of diversification patterns in this region (Flores-Villela and Martínez-Salazar 2009). Therefore, further studies should integrate historical biogeographical and lineage diversification

approaches to clarify the diversification dynamics and regional assembly in this region.

Mapping the evolutionary metrics for *Anolis* lizards provided insights on diversification and colonization dynamics on anole faunas. On one hand, regions with low relative PD are hypothesized to exhibit fast diversification of few lineages, because rapid diversification tend to result in shorter branches in terminal taxa (Davies and Buckley 2011, Fritz and Rahbek 2012). On the other, regions with high relative PD are hypothesized to reflect either slow diversification or colonization of multiple lineages (Davies and Buckley 2011, Fritz and Rahbek 2012), as is the case of lower Central America and northern South America where there is a mixing of basal (*Dactyloa*) and derived (*Norops*) anole clades. We found that the Greater Antilles exhibited low relative PD suggesting fast diversification, consistent with previous studies showing that insular anoles assemblages have been shaped by diversification rates dependent on geographical area (Algar and Losos 2011). In contrast, the central portion of Middle America and the Andes region exhibited high relative PD values consistent with slow diversification rates. This suggests that mainland anole assemblages, particularly in those areas of exceptional species richness (Figure 1), have likely been generated by a combination of *in situ* speciation and several dispersal events of multiple lineages from surrounding regions (Davies and Buckley 2011, Fritz and Rahbek 2012).

Mapping of species richness in "basal" and "derived" lineages revealed that higher species richness of "basal" species in the Andes and Greater Antilles,

suggesting that faunal assembly in these regions likely occurred early in the anole radiation. Conversely, higher species richness of "derived" clades occurred in Middle America, suggesting later colonization (Nicholson et al. 2005). In the lower portion of Central America and northwestern Colombia, there is a mixing of "basal" (*Dactyloa* clade) and "derived" (*Norops* clade) species. It is possible that the emergence of the Panama land bridge played a significant role in the assembly process within this region (Leigh et al. 2014).

Several studies have found evidence for a strong signature of past climatic anomalies on geographical species richness patterns, particularly in temperate regions (Svenning and Skov 2007, Svenning et al. 2009, Hortal et al. 2011). However, very few studies have been conducted to explore these effects on tropical-restricted groups (but see Rakotoarinivo et al. 2013). Our study is, to our knowledge, among the first ones exploring the effects of past climatic anomalies beyond the LGM (>21,000 ybp) for a strict Neotropical lineage. The signature of past climates from LIG on geographical species richness patterns of anoles was relatively higher than for the LGM. This suggests that past cooling from the LGM (21,000 ybp) had low impacts on species richness of *Anolis* lizards. In addition, our results revealed that climatic anomalies from LIG were stronger in Middle America and the Greater Antilles than in South America. However, it is still necessary to test the effect of past climates on the geographical ranges dynamics of anoles. For instance, to evaluate how geographical ranges have contracted or expanded facing Pleistocene climatic oscillations and how these range shifts have an effect on species richness patterns.

In conclusion, our study shows that species richness at broad spatial scales for *Anolis* lizards results from a synergistic effect of past and current climatic factors with notable differences in richness-climate relationships among insular and mainland regions. We found little support for evolutionary factors (PNC and diversification) shaping richness-climate relationships across geography. We suggest that anole regional assemblages are not shaped solely by PNC and regional diversification but also by other ecological processes (e.g., dispersal and species interactions; Algar et al. 2013) mediated by climate. Although it there is evidence for a role of evolutionary factors driving richness-climate relationships, in particular PNC, such relationships may act primarily across broad-scale climatic gradients (e.g., temperate vs. tropical regions), rather than within tropical regions. Furthermore, climatic niche dynamics may not be well captured by phylogenetic patterns as described here and evidence from other approaches might be necessary. In general, our results support previous findings suggesting that assembly processes in *Anolis* lizards differ among insular and mainland regions, but are still dominated by climate factors.

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CAPÍTULO III

La vicarianza antigua y el conservadurismo de nicho climático

explican el endemismo insular de *Anolis* en las islas del Caribe

Ancient vicariance and climatic niche conservatism explain insular endemism in an iconic radiation of lizards.

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ABSTRACT

Aim: We test the role of historical biogeographic events and climatic niche dynamics (niche conservatism and niche convergence) on exceptional insular endemism of *Anolis* lizards in the Caribbean islands.

Location: Caribbean islands

Methods: We reconstruct historical biogeographic events using a time-calibrated Caribbean anole phylogeny. We used modern phylogenetic comparative methods to evaluate climatic niche dynamics (niche conservatism and niche convergence) across time and space (between and within islands). Furthermore, we used ecological niche modeling tools to predict suitable climate for species outside their native areas (i.e., across the entire Caribbean region).

Results: We find evidence that anoles colonized Caribbean islands during the late Eocene-early Oligocene coinciding with the emergence of the Aves Ridge and the GAARlandia landmass. Mostly anoles clades diversified after the GAARlandia break-up and few dispersal events are necessary to explain distribution patterns across islands. Single-island endemic species are climatically restricted to native islands exhibiting very similar climatic niches. We found evidence of recent strong climatic niche conservatism and past climatic niche divergence.

Main conclusions: Our results suggest that exceptional endemism in Caribbean anole lizards might be explained by ancient vicariance events and strong climatic niche conservatism.

Keywords: Niche dynamics, climatic niche disparity, niche convergence, climatic suitability, lizards, *Anolis*, GAARlandia, Aves Ridge

INTRODUCTION

Insular systems are a well-known example of unique diversity in biogeography, which is reflected in an elevated number of endemic species (MacArthur & Wilson, 1967; Losos & Ricklefs, 2010). High insular endemism results from a combination of factors, such as colonization, speciation, island size, isolation and environmental uniqueness (Kier *et al.* 2009; Losos and Ricklefs 2010). Recently, research has begun to integrate speciation as a main driver of island endemism (Kisel & Barraclough, 2010; Qian & Ricklefs, 2012). However, little is known about the role of ecological niche dynamics, understood as the balance of phylogenetic niche conservatism (PNC; i.e., the tendency of related species to retain ancestral ecological traits) and niche convergence on shaping patterns of island diversity and endemism (Hosner *et al.* 2014).

Ecological niche theory predicts that species' geographical ranges at coarse-grain scales are constrained by a set of abiotic, biotic factors and dispersal limitations (Peterson *et al.* 2011). For endemic insular species, range limits are chiefly constrained by strong dispersal barriers rather than ecological or climatic factors (Brown & Lomolino, 1998). However, few tests have been conducted to disentangle the importance of geographical and ecological barriers on range limits of insular endemic species. Accordingly, it is still unknown whether insular species exhibit suitable ecological niche conditions outside its native areas and what factors play a role as drivers of current distribution and endemism.

Niche conservatism and niche convergence patterns emerge from ecological niche dynamics across time and space (Donoghue & Edwards, 2014). Accordingly, these two patterns might contribute to explain the high endemism in many insular systems. For instance, if insular diversity is shaped only by dispersal events, species colonizing an island might exhibit similar climatic requirements (environmental filter). This resulting niche similarity might emerge either by PNC or niche convergence as a consequence of evolving towards similar climatic regimes. In contrast, if insular diversity is shaped by *in situ* speciation, species might exhibit higher niche similarity by PNC and eventually niche evolution would occur as a result of climatic opportunity (Algar & Mahler, 2015). Use of modern phylogenetic comparative methods might enable us to discern between both evolutionary scenarios: PNC or niche convergence (Mahler *et al.* 2013; Bravo *et al.* 2014). Although there is theoretical evidence that multiple evolutionary processes can drive niche similarity (Revell *et al.* 2008), the distinction between both patterns is a crucial step to understanding how species evolved their ecological niches at coarse-scales (Bravo *et al.* 2014).

Anolis lizards are a well-known example of adaptive radiation in both insular and mainland settings (Losos, 2009). In particular, insular anole diversity in the Caribbean region is explained by a combination of geographical, ecological and evolutionary factors (Losos, 2009). Caribbean anole species are notable single-island endemics, with some exceptions which were driven by human activities (Helmus *et al.* 2014). This exceptional endemism is reflected in high species turnover rates between islands explained by geographical and environmental factors (Stuart *et al.* 2012). However, past biogeographic events and climatic niche dynamics might contribute to explain how these exceptional patterns were shaped. Although it is well known that dispersal and vicariance events drove species diversification in insular systems (Bacon *et al.* 2012), these factors have been seldom tested as drivers of anole endemism in the Caribbean islands. We suggest here that unique anole faunas were

driven by a combination of historical events and strong niche conservatism reflected in a poor climatic suitability for each species outside its native areas.

Here, we reconstruct the historical biogeography of Caribbean *Anolis* lizards to infer the roles of dispersal and vicariance in shaping current anole insular diversity and endemism. Furthermore, we test whether climatic niche conservatism or niche convergence was pervasive across the anole radiation and discuss how either of these factors shaped endemism in the Caribbean islands. Specifically, we test whether anole species are climatically restricted to its native islands or they can find widespread climatic conditions across islands. In addition, we tested whether species' niches are more similar within than among islands.

MATERIALS AND METHODS

Phylogenetic estimation and divergence times

We generated a time-calibrated phylogeny using an *Anolis* dataset extracted from a recent Squamata phylogeny (Pyron *et al.* 2013). The assembled matrix comprises nine genomic regions (12S, 16S, BDNF, cytb, ND2, ND4, NT3, R35 and RAG1) and 207 anole species, representing 53% of the total anole diversity (Uetz, 2014). Caribbean anole species sampling is nearly complete (83%, only 26 species missing). We included five outgroups based on the topological position of *Anolis* in the Iguania phylogeny (Townsend *et al.* 2011). We used two fossil calibration points. First, using a normal distribution prior we calibrated the root with the crown-group pleurodont iguanian *Saichangurvel* (Conrad *et al.* 2007) from the Late Campanian (70.6 ± 0.6 Mya) (Townsend *et al.*, 2011). Second, a lognormal prior with a minimum age of 23 mya was used to calibrate a Dominican amber fossil from the *Anolis chlorocyanus* group (de Queiroz *et al.* 1998). We implemented an uncorrelated relaxed clock method with uncorrrelated rates among branches using the software BEAST 1.8.1 (Drummond *et al.* 2012). We used the GTRGI model of evolution for the unpartitioned dataset as suggested by jModeltest v. 2 (Darriba *et al.* 2012). We decided not to partition the dataset as the Anole dataset is mostly

comprised by the ND2 region and the remaining genes were used to have a good estimate of the tree root. We started two runs from a random tree for 40 million generations sampling every 1000. The log files were checked for stationarity and convergence using Tracer 1.6. After discarding 4 million generations as a burn-in period, a maximum clade credibility tree was annotated to summarize node and branch parameters. We pruned mainland anole species and our resultant tree was composed of 130 Caribbean species (Appendix S1 in Supporting Information). This topology was very similar to other recent Caribbean anole phylogenies generated using the same data (Mahler *et al.* 2010; Rabosky & Glor, 2010).

Parametric biogeographic analysis

We investigated the historical biogeography for Caribbean *Anolis* lizards using parametric approaches based on a maximum likelihood framework implemented in the newly developed BioGeoBEARS package in R (Matzke, 2013). We estimated ancestral ranges for each node and compared different models of range expansion (e.g., dispersal-extinction-cladogenesis -DEC-, dispersal-vicariance analysis –DIVA-, and BayArea) using the time-calibrated phylogeny. BioGeoBEARS incorporates a new parameter to estimate the "probability" of founder-event speciation (+J), an important process in island biogeography (Matzke, 2014). We assigned species to each Greater Antilles islands and treated Lesser Antilles as a single unit. Therefore we used five areas for the analysis: Lesser Antilles, Puerto Rico, Cuba, Hispaniola, and Jamaica.

We performed an unconstrained analysis where dispersal is constant across time and space (i.e., equal dispersal costs). Although this scenario ignores the geological history of Caribbean landmasses, we used it here as a null biogeographic model. In addition, we performed a time-stratified scenario based on the geological model from Iturralde-Vinent & MacPhee (1999). We penalized strongly against dispersal across water assigning a very low probability (d=0.01) when landmasses were separated and a probability of 1 when landmasses were united. We built cost dispersal matrices based on Iturralde-Vinent & MacPhee (1999) for four time periods

as follows: **(1) Late Eocene-early Oligocene (35-33 mya):**) during this narrow time frame all Greater Antilles, except Jamaica were connected as a single landmass (GAARlandia). Also, a land connection between GAARlandia and South America emerged, known as the Aves Ridge. We assigned dispersal probability of 1 for all transitions between islands, except for Jamaica. This cost matrix was set at the root of tree based on our divergence estimates (Fig. 1) **(2) Late Oligocene (27-25 mya):** During this period, Cuba was fragmented in three landmasses and Hispaniola was divided in two (Northern and Southern). Southern Hispaniola was connected to Puerto Rico, and the Lesser Antilles remained isolated. We assigned dispersal probability from 1 to transitions between connected landmasses and 0.01 between separated landmasses. **(3) Middle Miocene (16-14 mya):** Cuba remained fragmented and Hispaniola was connected again and with a slight land connection with Puerto Rico. The Lesser Antilles were separated. We assigned dispersal probability of 0.01 between all landmasses. **(4) Pliocene to present (5-0 mya):** All landmasses were separated and dispersal probability was set to 0.01 between islands. Finally, we compared the fit of several unconstrained and constrained biogeographic models using the Akaike information criteria (AIC).

Climatic niche convergence and niche dynamics through time

We extracted occurrence records for 130 Caribbean *Anolis* species from a database of 13,864 locality records for *Anolis* species compiled from several sources (Velasco *et al.*, in review). We extracted climatic information from 19 variables from WorldClim for each species locality record and performed two principal component analyses (PCA): one including only temperature related variables (bio1 to bio11) and another with only precipitation variables (bio12 to bio19). For each species, we calculated the mean of the scores for the first PC axis for only temperature (thermal niche position) and precipitation (hydric niche position).

We tested whether climatic niche variation in Caribbean anole lineages is consistent with a scenario of adaptive convergence. We used the recently published

method called SURFACE (Ingram & Mahler, 2013). This method uses a phylogeny and niche traits metrics to fit an Ornstein-Uhlenbeck (OU) model in which lineages evolved toward convergent climatic regimes (adaptive peaks) in a macroevolutionary landscape. An OU model describes an evolutionary process that includes two components: a deterministic tendency to evolve toward optimal states (i.e., adaptive regimes), and a stochastic component that is interpreted as evolutionary changes by natural selection and genetic drift (Butler & King, 2004). The method allows identifying the maximum number of convergent adaptive peaks without an *a priori* delimitation according to the phylogeny. SURFACE starts with a model with a single adaptive regime for all species and then increases the number of adaptive regimes using a stepwise model selection procedure based on Akaike Information Criterion (AICc). A new peak shift is added at each step and seeks for an improvement of the model fit (forward phase). In the backward phase, the final set of previously identified regimes is collapse to find further improvements of model fit. SURFACE finds the maximum number of adaptive regimes that best fit the data and identify which clades are convergent towards the same adaptive peaks. We then tested whether our convergent pattern for climatic niche differed from one expected by a null Brownian motion model (BM). We compared our observed convergence parameter (delta k) with 500 simulated delta k under a BM process.

We examined the tempo of climatic niche diversification across the phylogeny using disparity-through time (DTT) plots (Harmon *et al*. 2003). DTT plots estimate the average niche disparity among subclades relative to total disparity in the entire phylogeny and compared this observed value against a mean expectation from a null model generated under Brownian motion. Disparity is calculated as average pairwise Euclidean distance for each niche trait for the entire tree and then for subclades defined by nodes in that tree. For instance, the first splitting event in the phylogeny divided this in two subclade and disparity is calculated for each one. The next splitting event, divided the tree in three and again disparity is calculated for each subclade. Relative disparity is standardized dividing the subclade disparity by the

entire disparity and is averaged for all lineages occurring in a particular divergence time (i.e., a node). Values approaching 0 indicate that niche variation is partitioned as among-subclade differences, suggesting that subclades exhibit little niche variation in comparison with the entire clade. Conversely, values approaching 1 indicate that subclades contain substantial niche variation and can exhibit a high niche overlap occupying similar regions of climatic space (i.e., niche convergence). Finally, it computes a niche disparity index (MDI in Harmon *et al.* 2003) as the overall difference in relative disparity of a clade compared with to a null hypothesis simulated with a Brownian motion model (Harmon et al. 2003). Negative MDI values indicate lower subclade disparity than expected under a null model, suggesting that niche disparity was accumulated early in the history of a clade, as opposed to positive MDI values that indicate higher subclade disparity than expected under a null model, suggesting that niche disparity was concentrated toward the tips of the tree (Harmon *et al.* 2003). Here, we generated DTT plots for species' niche mean position and calculated the MDI index using our anole tree. We compared the MDI index against a mean expectation of 1000 simulated values under a BM model.

Internal climatic niche structure

We tested whether endemic Caribbean *Anolis* species find potential climatic conditions outside their native island (endemism area) using a niche modeling approach. We generated ecological niche models across the entire Caribbean region for species with more than 10 unique occurrence records. We used three algorithms (GAM: Generalized Additive Model; SRE: Surface Range Envelop; Maxent: Maximum Entropy) implemented in the Biomod2 library in R (Thuiller *et al.* 2009) and 19 bioclimatic variables from WorldClim database at 30 arc-seconds resolution (Hijmans *et al.* 2005). We compared performance of these algorithms using three standard validation metrics (TSS: true skill statistics; ROC: receiver operating characteristic; and Kappa statistic; Fig. S1 in Appendix S2). Finally, we showed results just for Maxent because it was the only algorithm that identified suitable

climatic conditions outside native islands for most species. We used default settings in Maxent, except clamping and extrapolation options that were turned off. Although we tested different regularization values, we did not find differences in AUC values (Fig. S2 in Appendix S2). Each model was calibrated using 50 replicates by splitting the dataset into training and testing using 25% of occurrence records for testing. We used 10th percentile threshold as cut-off to convert Maxent probabilities into binary estimates of presence and absence (Liu *et al*., 2005). Pixels predicted as present were classified as native or outer according information about current native distribution for each species.

We calculated distance to the niche centroid for each model as a proxy of maximum climatic suitability across Caribbean islands (Martinez-Meyer *et al*. 2013). We compared ecological distances between native islands versus outer islands for each clade controlling for potential effects of area (log10) and geographical distance to islands (square root). Finally, we compared whether niche similarity was higher between species inhabiting the same island against other islands using the Schoener index implemented in the ENMtools software (Warren *et al*. 2008).

RESULTS

Caribbean anole biogeography

Our estimated dates are congruent with a recent study where divergence times were estimated for main anoles clades (Prates *et al*. 2015). Our dating analysis suggests the *Anolis* lizards (Dactyloidae) originated during late Paleocene-Early Eocence (68-37 mya). At least two colonization events are necessary to explain current anole diversity in Caribbean islands. The first one occurred during late Eocene-early Oligocene transition (45-33 mya), and explains most of the Caribbean anole diversity. The second one explains the distribution of the dactyloid anoles (Dactyloa clade) in the southern Lesser Antilles and occurred during middle Oligocene- early Miocene (31-20 mya) (Fig. 1). The estimated dates for the first

colonization event is temporally congruent with the emergence of a land bridge (the Aves Ridge) that connected northeastern South America with proto-Antilles (Fig. 1).
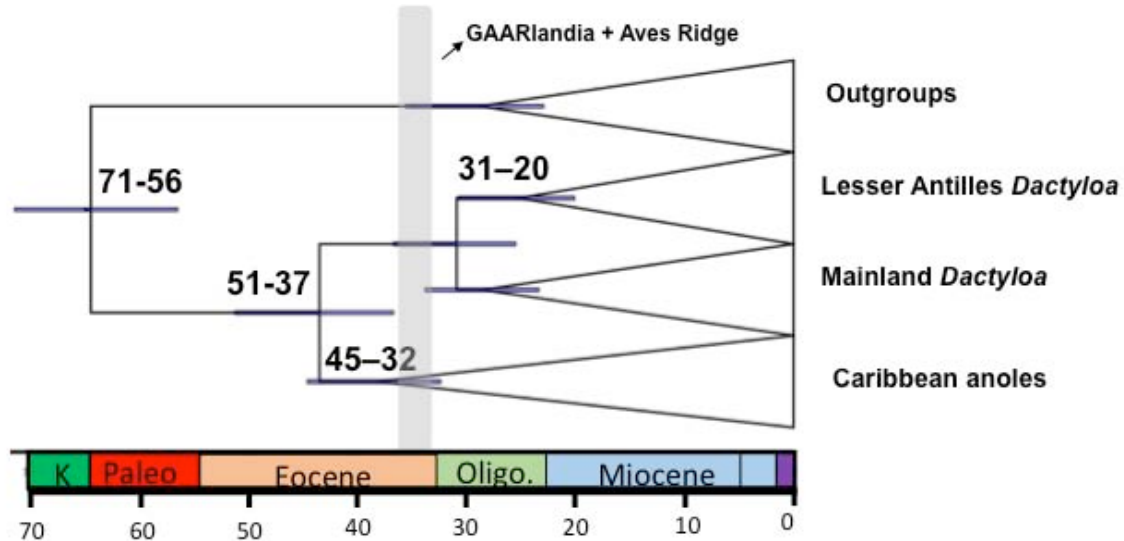

Figure 1. Divergence times between clades of *Anolis* lizards and pleurodont iguanian lizards (see main text for details). Horizontal blue bars in each node indicate 95% credibility intervals of node ages. Vertical gray bar indicates the timing of the emergence of the Aves Ridge during the Eocene-Oligocene transition (35-33 mya; Iturralde-Vinent and MacPhee 1999). This bridge is hypothesized as a land connection between southeastern South America and Antilles and probably was used by anoles to reach the Caribbean landmass known as GAARlandia. Main anole clades were collapsed for a better visualization (see Fig. 2).

Ancestral range estimation

Comparison of biogeographic models (DEC vs. DEC+J) reveals that models that included the jump dispersal parameter "j" increased significantly the likelihood of the best model (Table 1). Furthermore, the best models were those that included dispersal constraints given a palaeogeographical reconstruction and allowed a maximum number of four areas for ancestral areas (Table 1). This suggests that dispersal constraints played a strong role driving current distribution of Caribbean *Anolis* lizards. The selected best model estimated an ancestral range for all Caribbean anoles as a composite area by ACD (A: Lesser Antilles; C: Cuba; and D: Hispaniola; Fig. 2). We inferred several dispersal and vicariance events according this best model

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estimated. Six range expansions were counted when all islands were merged in GAARlandia (Fig. 2) and two oceanic dispersals events are necessary to explaint the current distribution of several species. The fist one was a dispersal from Cuba to Jamaica for the *Norops* clade (Fig. 2). The second one involved dispersal from Puerto Rico to Northern Lesser Antilles explaining the current distribution for *Anolis acutus* (Fig. 2). The early separation of Cuba and Hispaniola explains the distribution of *Anolis lucius* in Cuba (Fig. 2).

Table 1. Comparison of DEC and DEC+J models on historical biogeography of Caribbean *Anolis* lizards. Constrained (C) models incorporate dispersal constraints in the model formulation based on Caribbean paleogeographic models (Iturralde-Vinent and MacPhee model 1999; Iturralde-Vinent 2006; see main text for details). Unconstrained (Unc) models consider equal dispersal probability between islands (i.e., equal to 1). Max.Anc.Areas: Maximum number of areas allowed in ancestral range estimates.

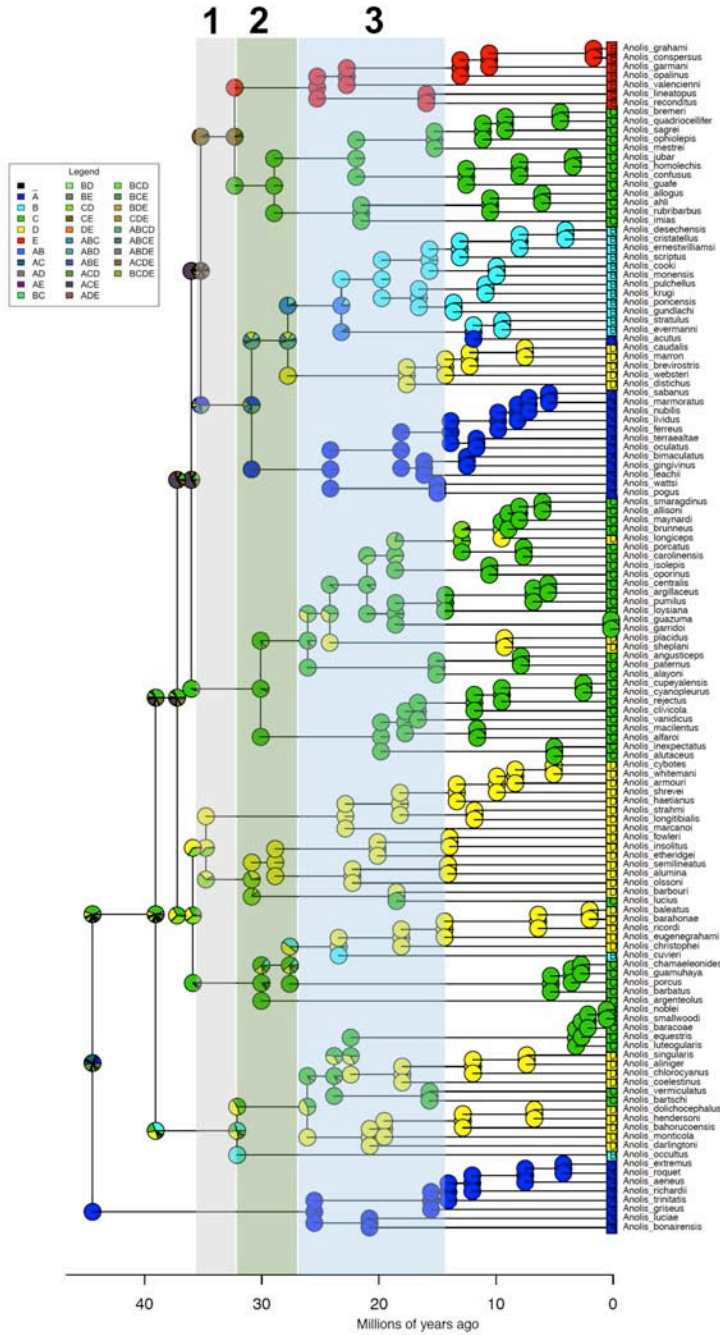| Type	Max.Anc.Areas	Model	LnL	p	d	e	j	AIC	ΔAICc	w
C	**4**	DEC	-71.5	2	0.01	0	0	146.9	19.2	0.0
		DEC+J	**-60.9**	**3**	**0**	**0**	**0.11**	**127.8**	**0.0**	**0.7**
	2	DEC	-77.0	2	0.01	0	0	158.0	30.2	0.0
		DEC+J	-61.6	3	0	0	0.12	129.1	1.4	0.3
Unc	**4**	DEC	-72.5	2	0	0	0.01	149.0	21.2	0.0
		DEC+J	-72.5	3	0	0	0.01	151.0	23.2	0.0
	2	DEC	-95.8	2	0	0	0	195.5	67.8	0.0
		DEC+J	-72.3	3	0	0	0.02	150.5	22.8	0.0

Figure 2. Ancestral range estimations for Caribbean *Anolis* lizards using the DECj model in BioGEOBEARS package (Matzke 2014). States at nodes represent estimates of ancestral ranges before the speciation event. Capital letters refers to geographic areas as follows: A) Lesser Antilles, B) Puerto Rico, C) Cuba, D) Hispaniola and E) Jamaica. Vertical light bars indicate the hypothesized emergence of Caribbean landmasses: 1) emergence of the Aves Ridge and GAARlandia (35-33 mya); 2) GAARlandia (33-27 mya); 3) land connection between Puerto Rico and Hispaniola (27-15 mya).

Climatic niche convergence

The evolution of climatic niche for most anole species was towards hot and dry environmental conditions. We discovered five convergent climate regimes (color large points) and four non-convergent regimes (black or grey large points) (Fig. 3; Table 2). These non-convergent regimes were reconstructed as ancestral climatic regimes for Caribbean anoles (Fig. 3a). Most climatic niche shifts seem to be involved with dispersal between or within-islands. Only one climate regime evolved toward cold temperatures (yellow color in Fig. 3a,b) composed by three lineages (6 species). Only one climate regime evolved to wet conditions (light blue in Fig. 3a,b) composed by four lineages (6 species). These results suggest that evolution of cold tolerance and rainy conditions in Caribbean *Anolis* has been rare and current species descend from ancestors adapted to hot and dry conditions (grey color in Figure 3a,b). The resulting pattern of climatic niche convergence differs from a null model generated under Brownian motion process (Fig. 3c; p-value < 0.01).

Table 2. Akaike criterion information and convergence parameters for each model from the backward phase of the SURFACE approach. AICc: Akaike Information Criterion corrected; Δ AICc: Delta Akaike Information Criterion corrected; k': Number of distinct climatic regimes after collapsing convergent regimes; Δk: Reduced number of regimes after accounting for climatic niche convergence; k' conv: Number of convergent regimes reached by multiple shifts. Selected best model in bold.

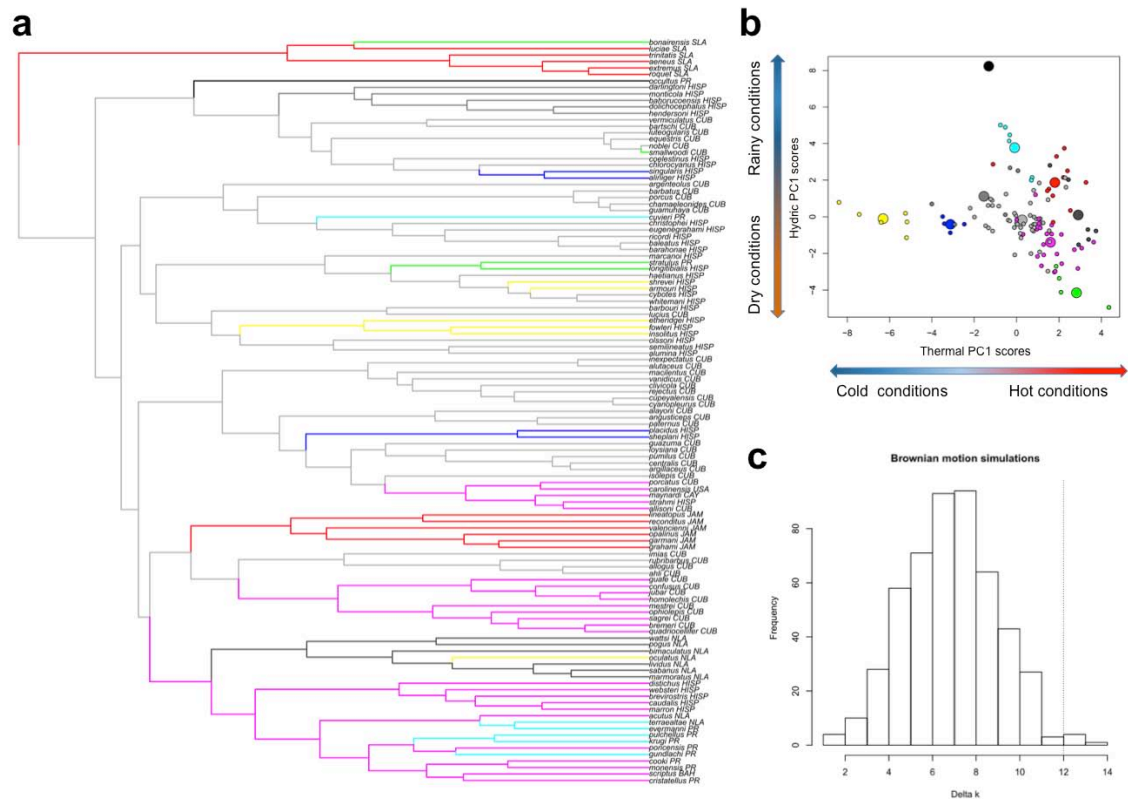| Regime	AICc	Δ AICc	k'	Δk	k' conv
1	836.1517	56.6966	22	0	0
2	813.0863	33.6312	19	3	3
3	793.7743	14.3192	15	7	7
4	779.5912	0.1361	11	11	6
5	**779.455**	**0**	**10**	**12**	**6**

Figure 3. Convergent evolution of climatic niche in the Caribbean *Anolis* lizards. a) Calibrated phylogeny for Caribbean *Anolis* lizards with climatic niche data and with adaptive regimes identified by SURFACE approach. Colored branches represent convergent adaptive peaks (or climatic regimes) and gray or black branches represent non-convergent regimes. b) Climatic spae occupied by the Caribbean *Anolis* species. Large colored circles represent the same convergent adaptive regimes identified in the phylogeny and small colored circles represent species that have evolved around these adaptive optima. Large gray or black circles represent the same non-convergent regimes identified in the phylogeny. Small gray or black circles correspond to species that have evolved toward these regimes. c) Histogram of 500 delta k values (true level of convergence) simulated under a Brownian motion model. The dashed line represent the observed true level of convergence in our dataset (Observed delta k = 12; mean simulated delta k = 7.34; *p*-value < 0.001). CUB: Cuba; HISP: Hispaniola; JAM: Jamaica; PR: Puerto Rico; NLA: Northern Lesser Antilles; SLA: Southern Lesser Antilles; CAY: Cayman island; BAH: The Bahamas; USA: United States of America.

Both climatic niche tracking and niche shifts were recurrent patterns across the entire Caribbean anole radiation, likely related with some few dispersal events. For instance, when *Norops* clade colonized Jamaica, this clade evolved toward rainy climatic regime (large red point in Fig. 3b), whereas some Cuban *Norops* species evolved toward drier climatic regime (large magenta point in Fig. 3b). The ancestral

niche reconstructed for this clade occupied a non-convergent regime with intermediate climatic conditions (large gray point in Fig. 3b). In contrast, most species from *Anolis* clade evolved toward a non-convergent intermediate climatic regime (large gray point in Figure 3b). Two species from this clade (*A. placidus* and *A. sheplani*) evolved toward a cooler regime (large blue point in Figure 3b) and a subclade that occurs in several islands (*A. porcatus* in Cuba; *A. carolinensis* in Florida; *A. maynardi* in Cayman islands; *A. strahmi* in Hispaniola; *A. allisoni* in Cuba) evolved toward a hotter and drier climatic regime (large magenta point in Fig. 3b). These two examples shown that multiple evolutionary processes might underlie these niche conservatism and niche evolution patterns in Caribbean *Anolis* lizards.

Climatic niche dynamics through time

Disparity-through time plots for niche metrics show that Caribbean anoles exhibit higher levels of average subclade niche disparity than expected under a null model (Fig. 4a,b). These higher values indicate a greater occupation of climatic space by subclades and extensive niche overlap in relation to the niche disparity of the entire lineage. According to DTT plots, relative disparity for climatic niche was close to 1 during early phases of anole diversification (Fig. 4a,b). As anole diversification occurred, relative disparity decreased toward 0 values (Fig. 4a,b). A positive departure from a null model (higher observed values than expected) suggests that climatic niche diversification increased through time (thermal NDI=0.105, p<0.001; water NDI=0.399; p<0.001). In other words, anoles diversified extensively through climatic niche dimensions as reflected by an acceleration of its evolutionary rates (i.e., positive NDI values).
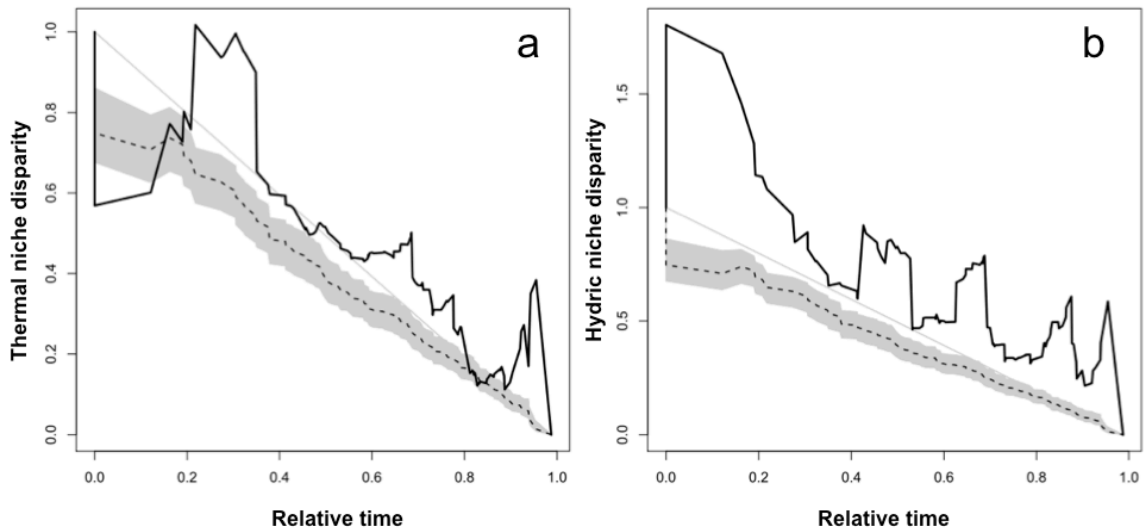
Figure 4) Disparity through time plots (DTT) for a) thermal and b) hydric niche mean position values for the Caribbean *Anolis* lizards. Relative time indicates the entire temporal span of the phylogeny from 0 (i.e., root) to 1 (i.e., tips).

Climatic niche structure and niche similarity

Boxplots of ecological distances between Caribbean islands showed that anole species tend to exhibit climatic niche conditions close to optimal niche conditions within their native islands (Fig. 5). In other words, for most anole species the optimal niche conditions tend to be found in native islands than outer islands. This pattern was maintained after controlling for distance and area (Table 3). Furthermore, niche similarity was higher for sympatric species occurring in Greater Antilles islands than for other species, except for those in Puerto Rico (Fig. S3 in Appendix S2).

Table 3. Comparisons of ecological distances of climatic niche conditions between native and outer islands for each anole clade controlling for geographical area (log10) and geographical distance (square root). Clade assignment was based on Nicholson *et al.* (2012; see Table S1 in Appendix S1).

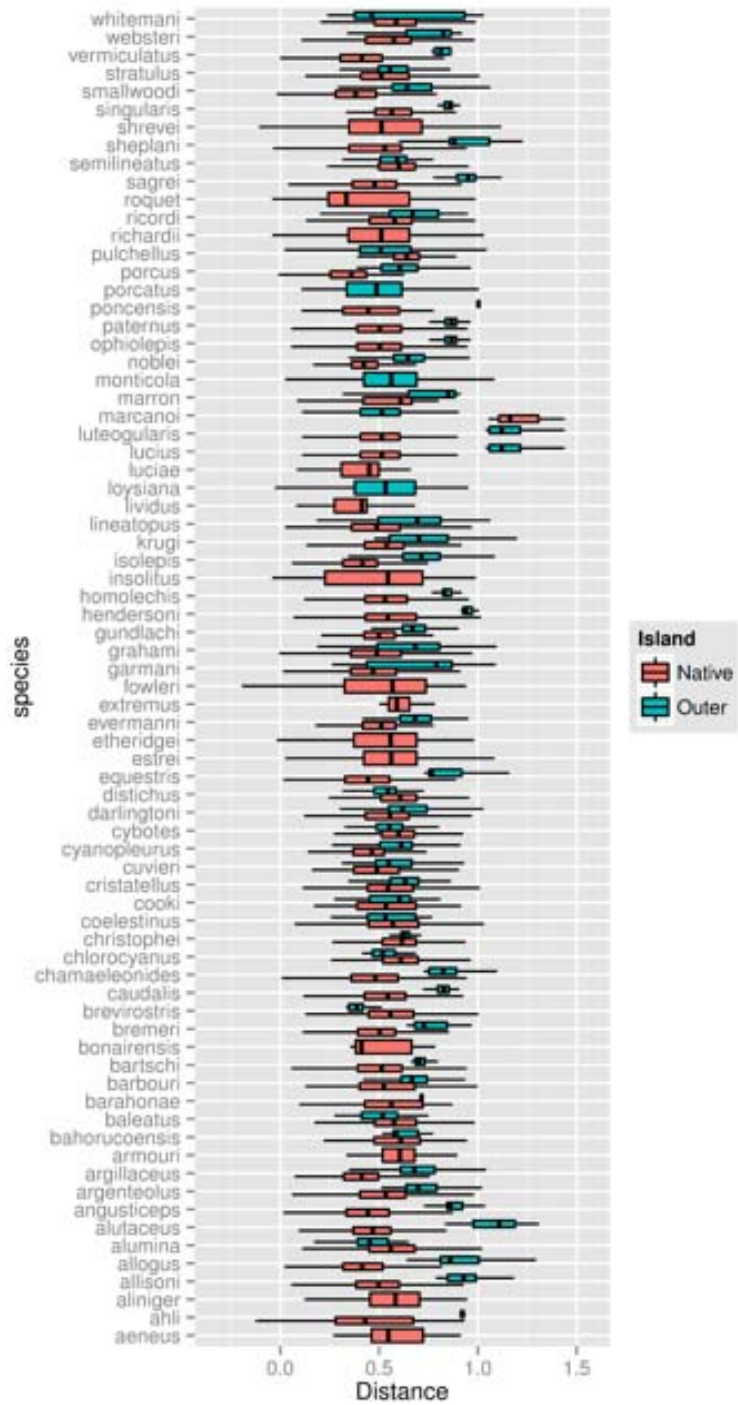| Clades	F	*p*-value	Area	*p*-value	Distance	*p*-value
Anolis	24093.20	0.00	939.30	0.00	25.60	0.00
Audantia	9.60	0.00	8.90	0.00	89.00	0.00
Chamaelinorops	328.90	0.00	8.10	0.00	163.00	0.00
Ctenonotus	535.80	0.00	515.50	0.00	782.60	0.00
Dactyloa	0.70	0.41	0.50	0.47	NA	NA
Deiroptyx	328.90	0.00	8.10	0.00	163.00	0.00
Norops	13094.40	0.00	1656.60	0.00	179.30	0.00
Xiphosurus	1089.40	0.00	835.00	0.00	32.50	0.00

Figure 5) Comparisons of ecological distances (Euclidean distances) from climatic niche structure for Caribbean anole species between native islands (N) vs. outer islands (Out).

DISCUSSION

Historical biogeography of Caribbean* Anolis *lizards

Our divergence estimates and distributions for Caribbean anole species fit a historical scenario well where anoles colonized Caribbean islands from South America, likely through the Aves Ridge, when all islands formed GAARlandia (Iturralde-Vinent & MacPhee, 1999; Iturralde-Vinent, 2006). The first estimated divergence event coincided temporally with the emergence of the Aves Ridge (33-35 mya). This idea conflicts with previous biogeography studies for Caribbean faunas. For instance, a previous work hypothesized that anoles colonized the Caribbean by over-water dispersal events from South America (Hedges *et al*. 1992: the over-water dispersal scenario). Alternatively, it has been suggested that anoles colonized a proto-Antillean arc from South America, when this arc formed a land connection between North and South America during the mid-Cretaceous (Rosen, 1975: the vicariance scenario). Our results provide support for a third alternative scenario based on a geological model for the Caribbean basin proposed by Iturralde-Vinent & MacPhee (1999).

Our phylogenetic results support an onset of Caribbean anole radiation during the middle Eocene and late Oligocene (45-33 mya; Fig. 1), conflicting with the dates estimated previously (~100 mya, see Nicholson *et al*. 2012). We consider the older dates estimated by Nicholson *et al*. (2012) were strongly influenced by the incorrect assignment of the Mexican amber anole fossil (*Anolis electrum*†; Lazell, 1965) to their anole tree. As Castañeda *et al*. (2014) showed the phylogenetic position of this fossil is extremely ambiguous to be assigned with confidence to any anole clade. Furthermore, divergence times estimated by Prates *et al*. (2015), using different calibration points, recovered similar dates to those obtained in this study.

We infer several ancient dispersal events coinciding in time with the emergence of GAArlandia. Therefore, it is likely that most dispersal events between islands occurred across land connection. Break-up of GAARlandia explains the

isolation of several anole clades on the Caribbean islands. These results suggest that dispersal was low despite past land connections and that anoles are not good dispersers as previously thought (Williams, 1969; Losos, 2009). The poor dispersal ability for many species is likely related with climatic niche constraints.

Climatic niche dynamics in Caribbean Anolis *lizards*

Climatic niche dynamics suggest that both evolutionary patterns (niche convergence and niche conservatism) were pervasive through the Caribbean *Anolis* history. The few available climatic conditions for species outside their endemic islands support the contention that strong niche conservatism has likely played a greater role than strong geographical barriers in driving anole insular endemism. This hypothesis also is supported by the higher niche similarity observed in each of the Greater Antilles islands.

We found that climatic niche divergence was accumulated early in the anole radiation. Our results support the contention that anoles have evolved to occupy available climates in each island after dispersal occurred. Niche divergence events likely occurred after the GAARlandia break-up and species were left isolated in each climate. Anole lizards likely colonized GAARlandia when the climate was hot and dry, before the Eocene-Oligocene glacial maximum (Zachos *et al*. 2008). After the GAARlandia break-up, which coincided with the Middle Miocene Climatic Optimum, anoles evolved toward colder and wetter climate conditions (Zachos *et al*. 2008). Furthermore, it is possible that rates of climatic niche evolution were higher during this period and then slowed down as species occupied all available climatic space. However, it its necessary to test whether evolutionary rates were variable across time and whether shifts in tempo and mode for niche traits are associated with climatic and geologic events.

The fact that many distantly related groups in Caribbean anoles likely originated in isolation within each island and then observed convergent climatic niche evolution might be the result of adaptation towards similar climatic regimes in

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each island (Boucher *et al*. 2011). It is probable that strong stabilizing selection would operate in climatic niches in single-island endemics (Holt & Gaines, 1992; Holt, 1996). The observed niche shifts towards cooler temperatures in the Caribbean region seem to represent independent evolutionary adaptation (i.e., niche convergence). These independent adaptions in some lineages toward cooler conditions have been faster, as in the case of *Cybotes* clade in Hispaniola (Muñoz *et al*. 2014).

Caribbean anole endemicity

Environmental differences between islands are considered as drivers of endemism and higher species turnover in the Caribbean anoles (Stuart *et al*. 2012). However, in recent times several species have colonized other islands mediated by human shipping. It seems that low anole diversity facilitates colonization from other sources (Helmus *et al*. 2014). However, we found that these small islands and banks show suitable climatic conditions for many endemic species, mainly from Cuba (Fig. S4 in Appendix S2). Therefore, these islands have the potential to be colonized by invasive anole species, not only because they are depauperated, but also because they apparently hold suitable climatic conditions to allow alien species' establishment. We suggest that low climate suitability in large islands might be an additional constraining factor to impede successful colonization of invasive anole species.

Conclusions

Our results suggest that climatic niche divergence occurred early in the Caribbean anole radiation and species have exhibited strong niche conservatism related to island geography. This early niche divergence likely occurred after the GAARlandia break-up. When anoles reach the Caribbean islands, these islands held hotter and drier conditions than today, thus species have evolved toward cooler and wetter conditions. Anoles eventually adapted to the available climates in each island in isolation reinforcing niche conservatism patterns. All these results support the

contention that climatic niche dynamics and ancient biogeographic events have driven insular endemism in *Anolis* lizards. A next step is testing whether these same factors operate in another Caribbean taxonomic groups or in mainland settings to have a more integral comprehension of the evolutionary and biogeographic processes in the region. Our study also shows that a combination of approaches (historical biogeography, phylogenetic comparative methods and ecological niche modeling) as implemented here provides multiple lines of evidences to test hypotheses about causes of insular endemism.

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Supporting Information

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

Appendix S1 Phylogenetic estimation for Caribbean anoles and main clades occurring in the Caribbean islands

Appendix S2 Performance and validation metrics for ecological niche models for Caribbean anole species.

Biosketch

Julián A. Velasco is carrying out his Ph.D studies at the Instituto de Biología, Universidad Nacional Autónoma de México. His current research focuses on understanding the ecological and evolutionary processes responsible for diversification, endemism and geographical species richness gradients in vertebrate taxa.

Enrique Martínez-Meyer is full-time researcher at the Instituto de Biología of the Universidad Nacional Autónoma de México. His main research lines are the biological responses of environmental change, ecological niche theory and its application to biogeography, and the ecology of mammals.

DISCUSIÓN GENERAL

Es posible descubrir los patrones e inferir los mecanismos ecológicos y evolutivos responsables de la diversificación y ensamble de especies de *Anolis* a través de un enfoque integrativo, donde se combinan aproximaciones conceptuales y metodológicas (Meseguer et al. 2014; Evans et al. 2014; Wiens et al. 2006). Esta tesis presenta un análisis de cómo el clima promueve la diversidad de especies de *Anolis* en un contexto explícito a nivel geográfico y filogenético. En términos generales se encontró que el clima y el nicho ecológico, a escala geográfica, han repercutido en la forma como la diversidad de especies de *Anolis* se ha acumulado a través del tiempo y del espacio. La combinación de estos contextos, geografía y filogenia, permite abordar cuestiones acerca de la dinámica evolutiva de grupos taxonómicos que han diversificado extensivamente, como es el caso de las lagartijas del género *Anolis*.

La relación encontrada entre la diversidad de nichos climáticos y la diversificación de especies sugiere que el clima es un factor importante durante los procesos cladogenéticos en el género *Anolis*, y en particular para los linajes continentales. Así mismo, las diferencias encontradas entre faunas continentales e insulares sugieren que las diferencias en la disponibilidad ambiental en ambas regiones es un factor importante que debe considerarse en conjunto con las diferencias geográficas (e.g., área). En este sentido, sugiero que la oferta ambiental determina en gran medida cómo la evolución de nichos climáticos en *Anolis* ha

ocurrido. Estos resultados refuerzan la hipótesis que la oportunidad ecológica

controla la dinámica de diversificación y radiación adaptativa en este grupo icónico.

Las diferencias entre regiones insulares y continentales sugieren que la

relación del clima con la riqueza y diversificación de especies presenta un patrón no

estacionario muy fuerte. En particular, algunas regiones continentales muestran que

la riqueza no esta explicada por factores climáticos actuales y del Quaternario, por

ejemplo, la porción media de Mesoamérica. De igual forma, encontrar que la firma

climática del periodo inter-glacial (hace ~121,000) fue mayor que la del máximo

glacial (hace ~21,000) sugiere que el enfriamiento del último glacial probablemente

tuvo un impacto menor en los patrones de riqueza y endemismo. Estos resultados

sugieren que el clima tiene un papel más directo, en contraste con el

conservadurismo de nicho y la diversificación, en la formación de los patrones

geográficos de riqueza de especies de *Anolis*. En otras palabras, la acumulación

regional de especies obedece más a que las especies comparten nichos similares,

que a procesos cladogenéticos *in situ*.

Finalmente, el papel de eventos biogeográficos históricos resulta ser

importante para analizar los patrones de diversidad resultantes. La evidencia sugiere

que las *Anolis* Caribeños comenzaron a diversificar justo despues de colonizar el

Caribe. Esta colonización ocurrió muy probablemente a través de la conexión

temporal conocida como la Cresta de Aves (*Aves Ridge*, en inglés) que emergió entre

el nororiente de Suramérica y las Antillas hace 35 millones de años. Los principales

eventos cladogenéticos en los *Anolis* Caribeños parecen estar asociados con eventos tempranos de vicarianza-dispersión de las proto-Antillas o GAARlandia. De igual forma, se encontró que estos eventos históricos parecen estar asociados con patrones de divergencia temprana en nichos climáticos. Aparentemente, cuando los linajes se quedaron aislados geográficamente en cada isla, y el clima fue haciéndose más frio desde el Eoceno hasta la actualidad, las especies se fueron adaptando y convergieron a ocupar los regímenes climáticos disponibles en cada isla.

Finalmente, con respecto al endemismo insular en *Anolis*, es decir donde la mayoria de especies son endémicas a una sola isla, se encontró que para casi todas las especies las condiciones ecológicas óptimas están dentro de sus islas nativas y muy pocas en otras islas. Esto sugiere que las especies están muy adaptadas a las condiciones climáticas en sus áreas nativas y por lo tanto la capacidad de colonizar y mantener poblaciones viables en otras islas es baja.

CONCLUSIONES GENERALES

La relación de atributos de nicho climático (i.e., posición, amplitud y volumen de espacio de nicho ocupado) están relacionados con diferentes métricas de diversificación total en *Anolis*. Sin embargo, la falta de una asociación entre clados del Caribe sugiere que esta asociación nicho-diversificación está direccionada principalmente por los dos clados continentales.

El clima actual y pasado contribuyó a la formación del gradiente geográfico de diversidad en *Anolis*. El no encontrar evidencia del conservadurismo de nicho, así como la diversificación regional de especies mediando la relaciones clima-riqueza de *Anolis*, sugiere un papel clave del clima en la acumulación de especies a nivel regional.

Los eventos de vicarianza que fragmentaron las Antillas cuando formaban una sola masa terrestre, los patrones de conservadurismo y convergencia de nicho climático y la disponibilidad climática baja por fuera de áreas nativas, explican el patrón excepcional de endemismo de *Anolis* en el Caribe, donde casi todas las especies son endémicas a una sola isla.

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ANEXOS

Capítulo I.

Appendix S1. **Results of the Principal Components Analysis for 19 bioclimatic variables.**

We conducted a Principal Component Analysis with 19 bioclimatic variables for species records and points from each region (see main text for details). The values shown below correspond to the loadings for each bioclimatic variable, eigenvalues and percent of variance for the first four PC axis.

Variables	PC1	PC2	PC3	PC4
BIO1 = Annual Mean Temperature	-0.264	-0.286	-0.001	-0.014
BIO2 = Mean Diurnal Range	0.256	-0.043	0.032	0.290
BIO3 = Isothermality	-0.207	0.196	-0.333	-0.158
BIO4 = Temperature Seasonality	0.221	-0.135	**0.424**	0.096
BIO5 = Max Temperature of Warmest Month	-0.130	**-0.419**	0.192	0.154
BIO6 = Min Temperature of Coldest Month	**-0.301**	-0.136	-0.126	-0.123
BIO7 = Temperature Annual Range	0.264	-0.124	0.276	0.247
BIO8 = Mean Temperature of Wettest Quarter	-0.197	-0.355	0.113	0.023
BIO9 = Mean Temperature of Driest Quarter	-0.277	-0.219	-0.055	-0.018
BIO10 = Mean Temperature of Warmest Quarter	-0.188	-0.378	0.199	0.028
BIO11 = Mean Temperature of Coldest Quarter	-0.290	-0.176	-0.156	-0.046
BIO12 = Annual Precipitation	-0.268	0.211	0.112	0.259
BIO13 = Precipitation of Wettest Month	-0.244	0.152	-0.059	**0.482**
BIO14 = Precipitation of Driest Month	-0.190	0.247	0.362	-0.178
BIO15 = Precipitation Seasonality	0.164	-0.114	-0.399	0.365
BIO16 = Precipitation of Wettest Quarter	-0.248	0.154	-0.052	**0.475**
BIO17 = Precipitation of Driest Quarter	-0.198	0.250	0.361	-0.163
BIO18 = Precipitation of Warmest Quarter	-0.128	0.226	0.228	0.243
BIO19 = Precipitation of Coldest Quarter	-0.222	0.152	0.092	0.055
Eigenvalues	**3.088**	**1.990**	**1.479**	**1.131**
Variance	**0.502**	**0.209**	**0.115**	**0.067**
Accumulated Variance	**0.502**	**0.711**	**0.826**	**0.893**

Appendix S2. Supplementary figures

Figure S1. Calibrated phylogeny for *Anolis* lizards generated using Bayesian Markov Chain Monte Carlo analysis implemented in BEAST (Drummond *et al.* 2012). Numbers in the nodes are Bayesian posterior probabilities.
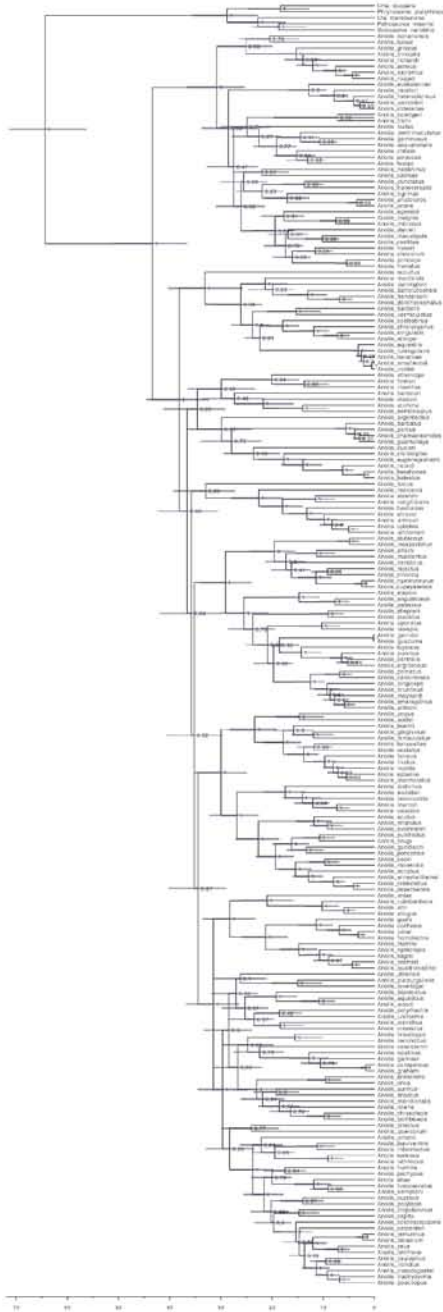
Figure S2. Direct and indirect effects of niche traits on net diversification rates in all anole clades (a,b) and only insular clades (c,d). Statistically signification correlation coefficients are in bold (p < 0.05). Net diversification rates were estimated using extinction fraction of 0.9 and 0.1. As path analysis were very similar with both extinction fractions, we only shown effects using 0.9 extinction fraction.
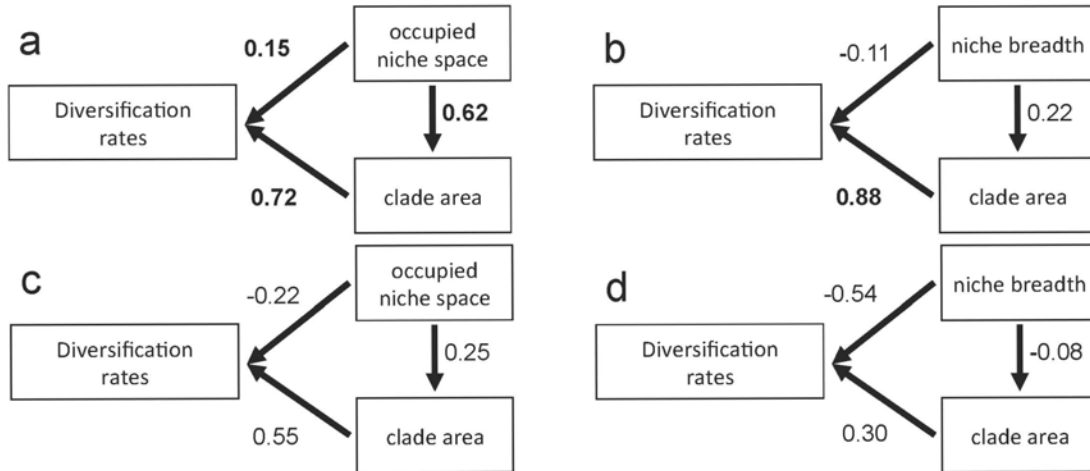
Appendix S3. Effects of missing species on the QuaSSE analysis.

Effects of missing species in the phylogeny on the association of niche traits and diversification using QuaSSE approach. We generate nine datasets, each one with a percentage of taxon incompleteness. Each dataset was generated randomly pruning a percentage of taxa from the Caribbean anole tree (i.e., 10%, 15%, 20%, 25%, 30%, 35%, 40%, 45% and 50%). With each dataset we performed QuaSSE analysis and evaluate the association between niche metrics (mean niche position and niche breadth) and diversification in Caribbean anole lizards. Best-fitting models according to ΔAIC values are in bold. In all cases all models selected found an association between niche traits and speciation rates.

	% total taxa	% pruned taxa	Model	Mean niche position		Niche breadth	
				AIC	ΔAIC	AIC	ΔAIC
dataset 1	76.7	10	minimal	1154.4	18.1	837.2	19.5
			linear	1156.3	20.0	839.1	21.5
			sigmoid	1158.3	22.0	843.1	25.5
			humpshaped	1156.6	20.3	825.4	7.8
			drift.linear	**1136.3**	**0.0**	**817.6**	**0.0**
			drift.sigmoid	1151.9	15.6	823.7	6.1
			drift.humpshaped	1137.8	1.5	825.9	8.3
dataset 2	72.0	15	minimal	1096.7	20.5	778.2	20.7
			linear	1098.7	22.5	780.2	22.7
			sigmoid	1101.1	24.9	784.2	26.7
			humpshaped	1098.5	22.3	762.6	5.1
			drift.linear	**1076.1**	**0.0**	**757.5**	**0.0**
			drift.sigmoid	1080.5	4.4	763.4	5.9
			drift.humpshaped	1100.4	24.3	764.0	6.5
dataset 3	68	20	minimal	1003.5	13.8	720.7	6.4
			linear	1005.5	15.8	722.6	8.3
			sigmoid	1007.0	17.3	726.7	12.4
			humpshaped	1003.7	13.9	726.7	12.4
			drift.linear	**989.7**	**0.0**	724.3	9.9
			drift.sigmoid	991.5	1.8	**714.3**	**0.0**
			drift.humpshaped	991.5	1.8	728.7	14.3
dataset 4	64	25	minimal	943.6	15.5	633.5	18.9
			linear	945.6	17.5	635.5	20.8
			sigmoid	947.8	19.7	638.2	23.6
			humpshaped	945.6	17.5	639.4	24.8
			drift.linear	**928.1**	**0.0**	**614.7**	**0.0**
			drift.sigmoid	934.2	6.1	620.2	5.5
			drift.humpshaped	930.0	1.9	624.5	9.8
dataset 5	60	30.0	minimal	1374.0	16.5	622.4	15.7
			linear	1375.5	18.0	624.3	17.6

	% total taxa	% pruned taxa	Model	Mean niche position		Niche breadth	
				AIC	ΔAIC	AIC	ΔAIC
			sigmoid	1379.4	21.9	628.2	21.5
			humpshaped	1367.6	10.0	628.2	21.5
			drift.linear	1377.5	20.0	**606.7**	**0.0**
			drift.sigmoid	1371.0	13.5	610.8	4.1
			drift.humpshaped	**1357.5**	**0.0**	606.7	0.0
dataset 6	54	35.0	minimal	801.3	4.5	563.0	4.6
			linear	803.3	6.5	564.9	6.6
			sigmoid	804.0	7.2	568.9	10.6
			humpshaped	797.0	0.2	568.9	10.6
			drift.linear	**796.8**	**0.0**	566.5	8.1
			drift.sigmoid	800.8	4.0	**558.3**	**0.0**
			drift.humpshaped	798.8	2.0	570.9	12.6
dataset 7	51.3	40.0	minimal	734.2	8.3	473.2	12.2
			linear	735.9	10.0	475.2	14.2
			sigmoid	738.5	12.6	478.3	17.3
			humpshaped	737.7	11.7	479.1	18.1
			drift.linear	**725.9**	**0.0**	**461.0**	**0.0**
			drift.sigmoid	732.8	6.9	469.3	8.3
			drift.humpshaped	729.4	3.5	464.6	3.6
dataset 8	46.7	45.0	minimal	656.2	18.1	469.8	11.7
			linear	658.1	20.1	471.8	13.7
			sigmoid	658.6	20.6	475.8	17.7
			humpshaped	657.7	19.7	475.8	17.7
			drift.linear	**638.0**	**0.0**	473.3	15.2
			drift.sigmoid	640.9	2.9	**458.1**	**0.0**
			drift.humpshaped	642.4	4.4	461.3	3.2
dataset 9	42.7	50.0	minimal	590.7	5.4	390.4	3.5
			linear	592.7	7.4	392.2	5.3
			sigmoid	595.9	10.6	395.3	8.3
			humpshaped	593.8	8.5	396.3	9.3
			drift.linear	**585.3**	**0.0**	**387.0**	**0.0**
			drift.sigmoid	589.1	3.8	387.1	0.2
			drift.humpshaped	595.8	10.5	397.7	10.8

Capítulo II.

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

Appendix 1. Phylogenetic estimation for *Anolis* lizards.

We estimated phylogenetic relationships for 253 *Anolis* species and an outgroup taxa (*Basiliscus basiliscus*) from a combined matrix with morphological and molecular data (mitochondrial and nuclear DNA). We obtained morphological data from Poe (2004), Velasco & Hurtado (2014), Poe & Yañez-Miranda (2007), Poe et al. (2009) and Velasco (2008). Molecular data were from Nicholson (2002), Nicholson et al. (2005) and Castañeda & de Queiroz (2011). The mitochondrial DNA sequences of molecular data correspond to a continuous fragment encompassing six complete genes (ND2, tRNATrp, tRNAAla, tRNAAsn, tRNACys, tRNATyr and the origin of light-strand replication before ending shortly after the start of COI; see Nicholson et al. 2005 for details). The nuclear DNA is from the internal transcribed spacer region (ITS; see Nicholson, 2002 for details). We performed alignments for the mitochondrial DNA using Muscle (Edgar 2004) with default parameters. The alignment for the nuclear DNA sequence was obtained from the Poe´s matrix (Poe 2004). Final alignments were checked by eye and manually adjusted. A matrix of 1929 characters (1506 parsimony-informative) for 255 species was obtained. We used maximum parsimony implemented in the TNT software (Goloboff et al. 2008). All characters were equally weighted and gaps were treated as missing data. We performed random sectorial searches producing three independent hits of tree best length. For each hit, we made searches with 50 replicates of Wagner trees using TBR (tree-bisection and reconnection algorithm) followed by 100 ratchet and five tree drift rounds, and finally submitting these resultant trees to five tree fusing cycles. We obtained 576 optimal trees of length 31889 steps (CI=0.82; RI=0.49) and generated a 50% majority-rule consensus tree. Polytomies in this consensus tree were randomly resolved. Nodal support was estimated using bootstrapping with 500 random addition searches holding 10 trees per replicate. Because reliable branch lengths were not obtained due to the nature of data (incompleteness for some species, e.g., only scored for some morphological characters or scores for only a DNA marker), we set all branch lengths to unity (Figure 1; see below). To incorporate missing species in the phylogeny with range maps (80 species), we used information from taxonomic or systematic accounts and original descriptions to add them to the phylogeny using the phytools R package (Revell 2012; see Table 1 for species included; see below). For the resulting tree, polytomies were randomly resolved and all branch lengths were set to unity.

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Velasco & Hurtado. (2014). A new green anole lizard of the "Dactyloa" clade (Squamata: Dactyloidae) from the Magdalena river valley of Colombia. *Zootaxa* 3785 (2): 201-216 .

Figure 1. A majority-rule consensus parsimony tree for 253 *Anolis* species lizards combining morphological and molecular data.

Table 1. Taxa added to the phylogeny based on taxonomic and systematic information. MRCA: most recent common ancestor.

| species	Placement in the tree	References
alvarezdeltoroi	MRCA *cobanensis-parvicirculatus*	Nieto-Montes de Oca, 1996
anisolepis	MRCA *crassulus-sminthus*	Smith et al., 1968
apletophallus	MRCA *limifrons-zeus*	Köhler & Sunyer, 2008
beckeri	MRCA *pentaprion-petersi*	Kohler, 2010
bellipeniculus	MRCA for phenacoasurs clade	Myers and Donnelly 1996
binotatus	similar to *granuliceps*	JAV personal observation
boettgeri	MRCA *fasciatus-ruizi*	Poe et al., 2008
bombiceps	MRCA *chyrsolepis-lineatus*	Dangiolella et al. 2011
campbelli	MRCA *alvarezdeltoroi-cobanensis-parvicirculatus*	Kohler & Smith, 2008
caquetae	MRCA *puntactus* group	Williams 1974
carlostoddi	MRCA for phenacoasurs clade	Myers & Donnelly, 1996
charlesmyersi	MRCA *beckeri-pentaprion*	Kohler, 2010
cristifer	MRCA *pentaprion* group	Kohler & Acevedo, 2004
cryptolimifrons	MRCA *limifrons* group	Köhler & Sunyer, 2008
cuscoensis	MRCA *boettgeri*	Poe et al., 2008
cusuco	closely related to *laeiventris*	McCranie et al., 2000
cymbops	MRCA *schiedii* group	Cope, 1864, Nieto Montes de Oca, 1994
danieli	danieli_Palmar	JAV personal observation
darlingtoni	MRCA *hendersoni*	Nicholson et al. 2012
datzorum	MRCA *laeviventris*	Kohler etal., 2007
dissimilis	sister to *calimae*	Prates etal 2014
duellmani	MRCA *schiedei* group (*cobanensis-parvicirculatus-alvarezdeltoroi*)	Fith & Henderson, 1973
fortunensis	MRCA *kemptoni* (*exsul, gruuo, kemptoni, pandoensis, pseudokemptoni*)	Ponce & Kohler., 2008
fugitivus	MRCA *cyanopleurus* group (*Anolis alutaceus* group from Nicholson et al. 2012)	Garrido, O. H. 1975.
fungosus	MRCA *pentaprion* group (*fungosus, ibague, ortonii, pentaprion, sulcifrons, utilensis,* and *vociferans*)	Uetz 2014; Myers 1971
gracilipes	external similarity with *notopholis*	JAV personal observation
gruuo	MRCA *kemptoni* (*exsul, gruuo, kemptoni, pandoensis, pseudokemptoni*)	Ponce & Kohler 2008
haguei	related to *crassulus* (also *anisolepis*)	Stuart 1942; Smith et al. 1968
hobartsmithi	MRCA *schiedei* group (*cobanensis-parvicirculatus-alvarezdeltoroi*)	Nieto-Montes de Oca 2001
huilae	sister with *boettgeri*	Poe et al 2008
johnmeyeri	*johnmeyeri* is closely related to *purpurgularis* and *pijolense*. MRCA *schiedei* group	Uetz 2014
juangundlachi	MRCA *cyanopleurus*	Garrido, O. H. 1975.
koopmani	MRCA *Chamaelinorops* clade (*alumina, barbouri, christophei, darlingtoni, fowleri, insolitus, olssoni, semilineatus*)	Rand 1961
loysiana	MRCA *loysiana* group (*argillaceus, centralis, pumilis*)	Nicholson et al. 2012

species	Placement in the tree	References
lynchi	MRCA *lyonotus* group (*lionotus, macrolepis, oxilophus, poecilopus, rivalis*)	Miyata et al. 1985
lyra	related to *vittigerus* (in Poe et al. 2009: sister to *bicaorum, lemurinus*)	Poe et al. 2009
macrolepis	MRCA *lionotus* group (*lionotus, oxilophus, poecilopus, rivalis, lynchi*)	Nicholson 2002
macrophallus	related to *cupreus*	Kohler & Kreutz 1999
magnaphallus	similar to *pachypus* and *tropidolepis*, in Poe & Ibañez (2007) is sister to *tropidolepis*	Poe & Ibañez 2007
matudai	MRCA *schiedei* group	Nieto-Montes de Oca 1994
megalopithecus	*eulaemus* subgroup (*gemmosus, ventrimaculatus*)	Personal observation
milleri	MRCA *schiedei* group	Smith 1950
monteverde	related to *altae*	Kohler 2009
morazani	MRCA *crassulus* group (*amplisquamosus, crassulus, heteropholidotus, muralla, sminthus, wermuthi*)	Townsend & Wilson, 2009
muralla	MRCA *crassulus* group (*amplisquamosus, crassulus, heteropholidotus, muralla, sminthus, wermuthi*)	Kohler et al. 1999
naufragus	MRCA *schiedei* group	Campbell et al. 1999
occultus	MRCA Deiroptyx clade (*darlingtoni-argenteolus* clade)	Nicholson et al. 2012
omiltemanus	MRCA *gadovi* group (*gadovi, dunni, utowanae, schmidti*)	Davies 1954
parilis	MRCA *kunayalae, mirus*	Poe etal 2007
petersii	related to *biporcatus*, in Poe & Ibañez (2007) is nested in a clade with *pentaprion-vociferans*	Poe & Ibañez 2007
phyllorhinus	MRCA *puntactus*, forming a clade with *transversalis*	Prates et al. 2012
pijolensis	MRCA *schiedei* group	McCranie et al. 1993
pseudokemptoni	MRCA *kemptoni* (*exsul, gruuo, kemptoni, pandoensis, pseudokemptoni*)	Ponce & Kohler 2008
pseudopachypus	similar to *pachypus* and *tropidolepis*	Kohler et al. 2007
pygmaeus	MRCA *laeviventris* subseries (*cusuco, intermedius, kreutzi, laeviventris, salvini, megapholidotus, nebuloides, simmonsi, cuprinus, isthmicus, subocularis, rodriguezi*)	Nicholson 2002
quaggulus	related to *humilis*	Poe & Ibañez 2007
rivalis	MRCA *lionotus* group (*lionotus, oxilophus, poecilopus, rivalis, lynchi*)	Williams, 1984
rodriguezi	MRCA *laeviventris* subseries (*cusuco, intermedius, kreutzi, laeviventris, salvini, megapholidotus, nebuloides, simmonsi, cuprinus, isthmicus, subocularis, pygmaeus*)	Nicholson 2002
rupinae	MRCA *hendersoni* species group	Nicholson et al. 2012

species	Placement in the tree	References
salvini	MRCA *pentaprion* group (*fungosus, ibague, ortonii, pentaprion, sulcifrons, utilensis, and vociferans*)	Kohler 2007
santamartae	related *solitarius*	Poe 2004, Nicholson et al. 2012
schiedii	MRCA *schiedii* group	Nieto-Montes de Oca 1994
schmidti	sinonim de *nebulosus*	Nieto-Montes de Oca et al. 2013
scypheus	related to *nitens*	Nicholson et al. 2012
serranoi	similar to *lemurinus*	Kohler 1999
simmonsi	sinonim de *nebuloides*	Nieto-Montes de Oca et al. 2013
soinii	sister to *transversalis* (sp A) in Poe et al. 2008	Poe et al. 2008
sulcifrons	similar to *pentaprion*	Myers 1971
terueli	*Anolis carolinensis* species group (*allisoni, smaragdinus*)	Nicholson et al. 2012
unilobatus	similar to *sericeus* and *wellbornae*	Kohler & Vesely 2010
vaupesianus	MRCA *punctatus* group	Williams 1982
vescus	*Anolis alutaceus* species group (*alfaroi-vanidicus*)	Nicholson et al. 2012
vittigerus	related to *lyra*. In Poe et al. 2009 nested with *bicaorum* and *lemurinus*	Poe et al. 2009
wampuensis	similar to *humilis, tropidonotus, uniformis*	McCranie & Kohler 2001
wellbornae	similar to *sericeus* and *unilobatus*	Kohler & Vesely 2010
wermuthi	related to *crassulus* group (*sminthus, heteropholidotus*)	Kohler & Obermeier 1998
yoroensis	similar to *cupreus* and *macrophallus*	McCranie et al. 2001

Appendix S2. Performance of statistical models

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 S1. Correlograms of observed and estimated species richness and residuals from species richnness-climate relationships for three regression models (top: GWR; middle: SAR; bottom: OLS)

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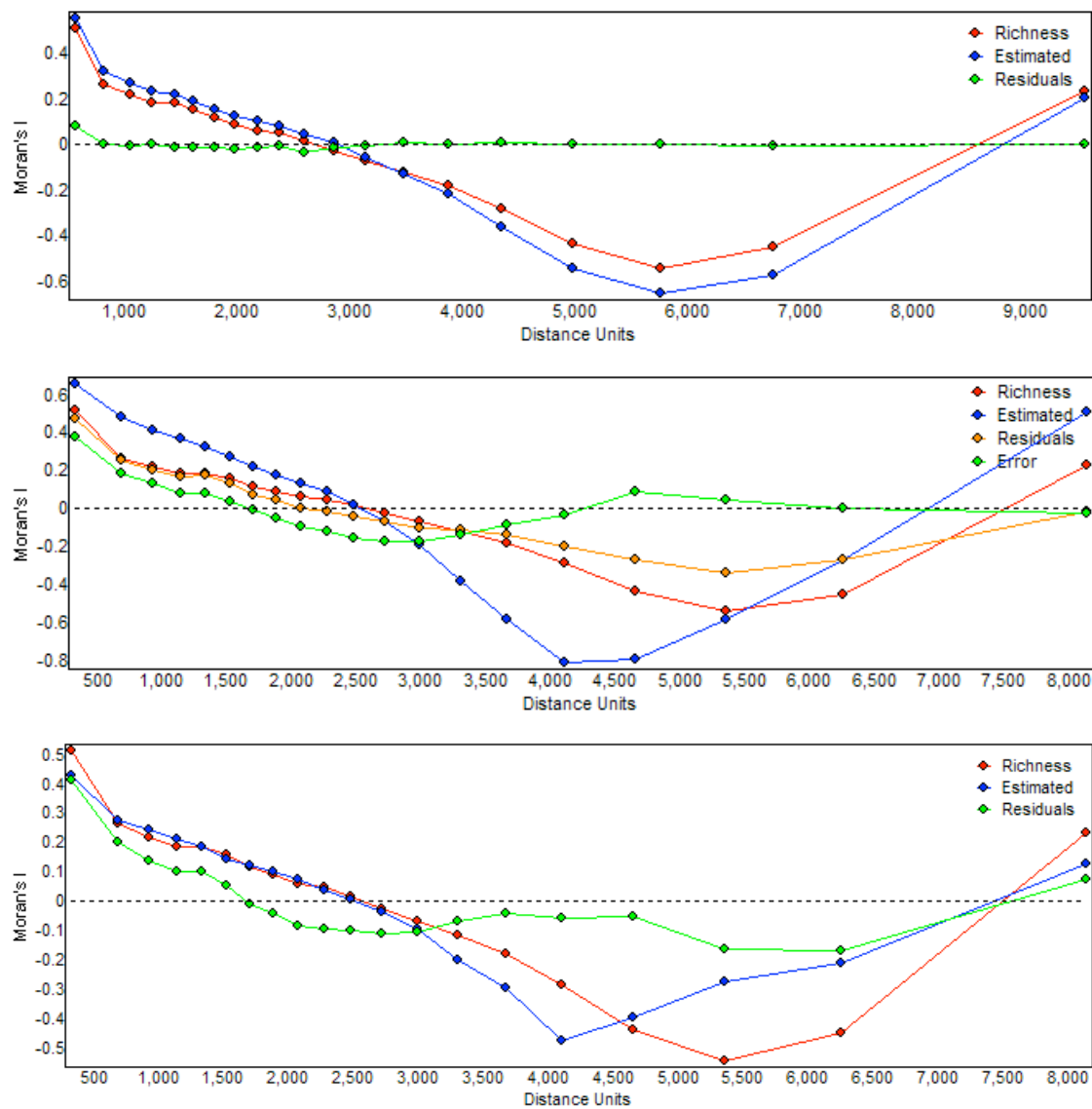
Appendix S3. Additional tables and figures

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) standard deviation of Annual precipitation (stdevAP) 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 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
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

Figure S1. Shared contributions of climatic hypotheses for Last Glacial Maximum (LGM) explaining observed *Anolis* species richness gradients. WE: Water-Energy; SEAS: Seasonality; HET: Heterogeneity; HCS: Historical Climatic Stability for LGM. See main text for details in variables for each hypothesis. Upper right: Venn diagram representing hypothesis evaluated in this study and where each lowercase letter represent unique (denoted by *unique*) or shared (denoted by s) contributions (see main text for details).
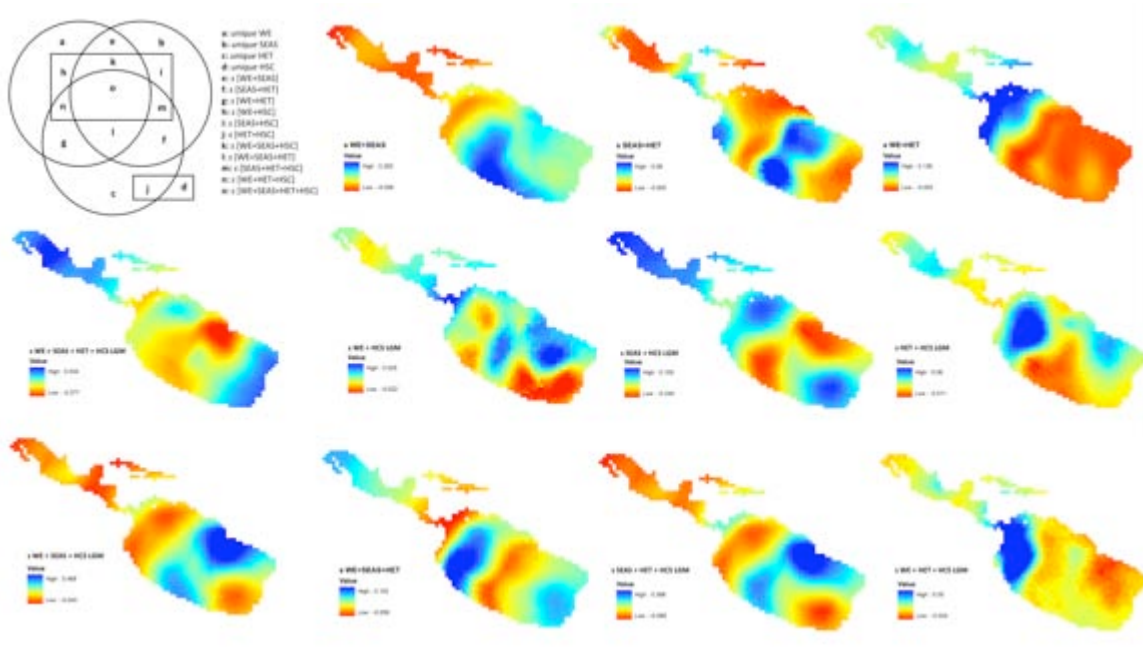
Figure S2. Shared contributions of climatic hypotheses for Last Inter-Glacial (LIG) explaining observed *Anolis* species richness gradients. WE: Water-Energy; SEAS: Seasonality; HET: Heterogeneity; HCS: Historical Climatic Stability for LIG. See main text for details in variables for each hypothesis. Upper right: Venn diagram representing hypothesis evaluated in this study and where each lowercase letter represent unique (denoted by *unique*) or shared (denoted by s) contributions (see main text for details).
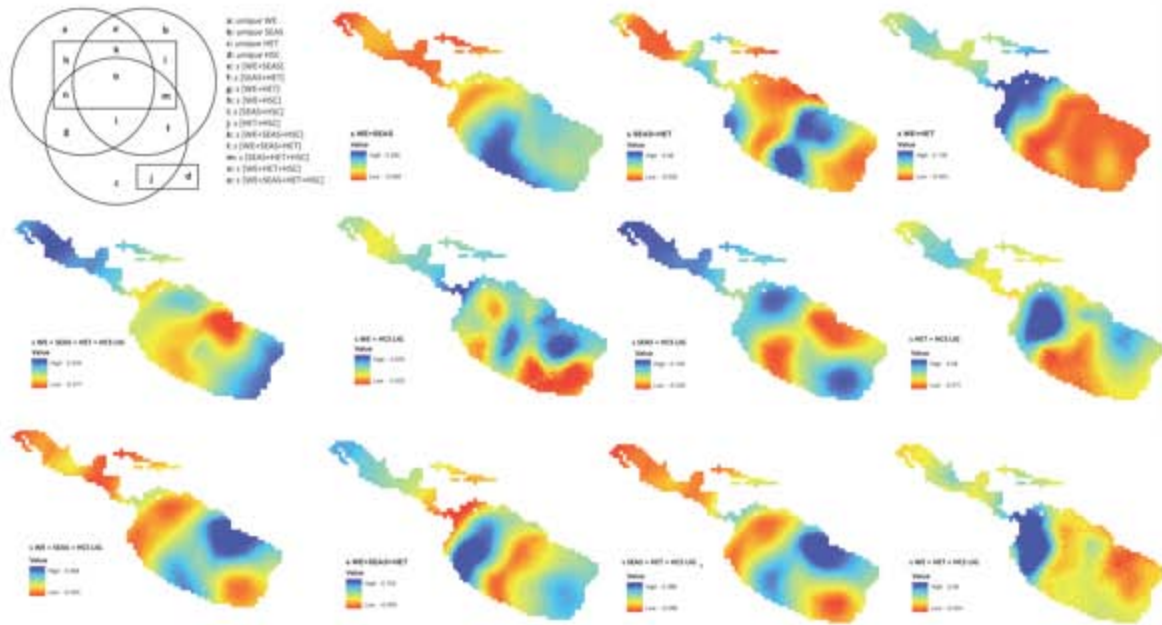
Figure S3. Boxplots of local R^2 values from full models for the Last Glacial Maximum and Last Inter-Glacial periods for mainland (Middle America, South America) and islands (Greater Antilles).
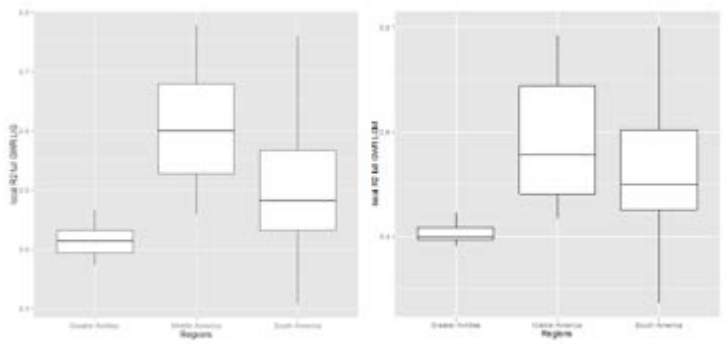
Figure S4. Boxplots of local slope values from full models for the Last Glacial Maximum and Last Inter-Glacial periods for mainland (Middle America, South America) and islands (Greater Antilles).
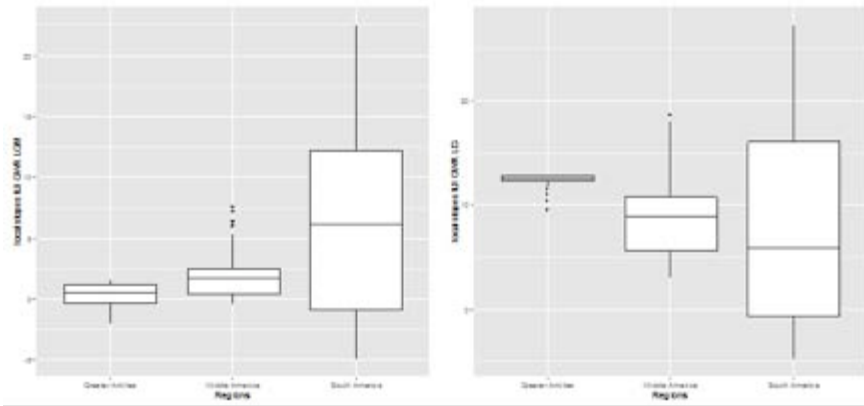
Figure S5. Correlation between faunal evolutionary derivedness (mean root distance -MRD-) and geographically weighted regression parameters (R^2 and slopes)
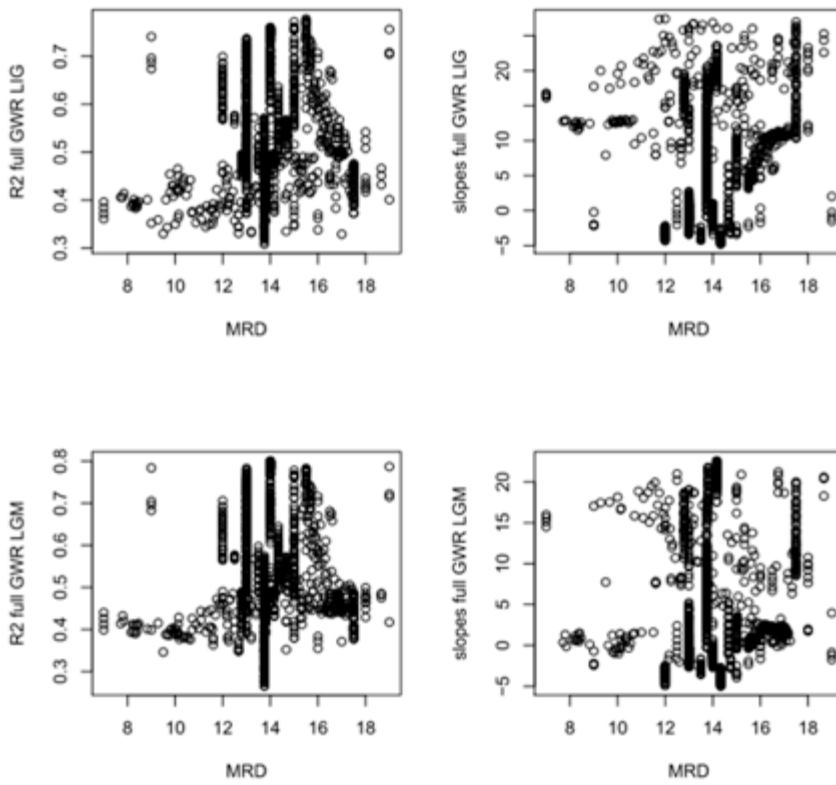
Figure S6. Correlation between regional diversification (relative PD) and residuals of geographically weighted regression models for Last Glacial Maximum (LGM) and Last Inter-Glacial (LIG).
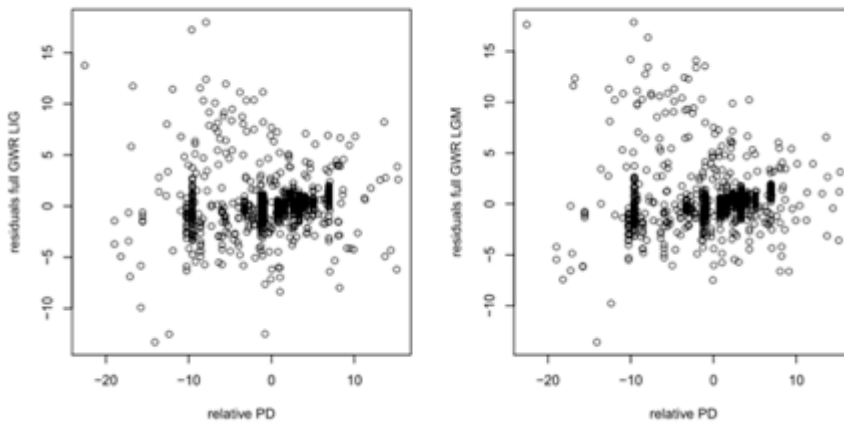
Figure S7. Frequency distributions of determination coefficients (R^2) for correlations between random MRD and observed GWR parameters (R^2, slopes) for full models for Last Glacial Maximum (LGM) and Last Inter-Glacial (LIG).
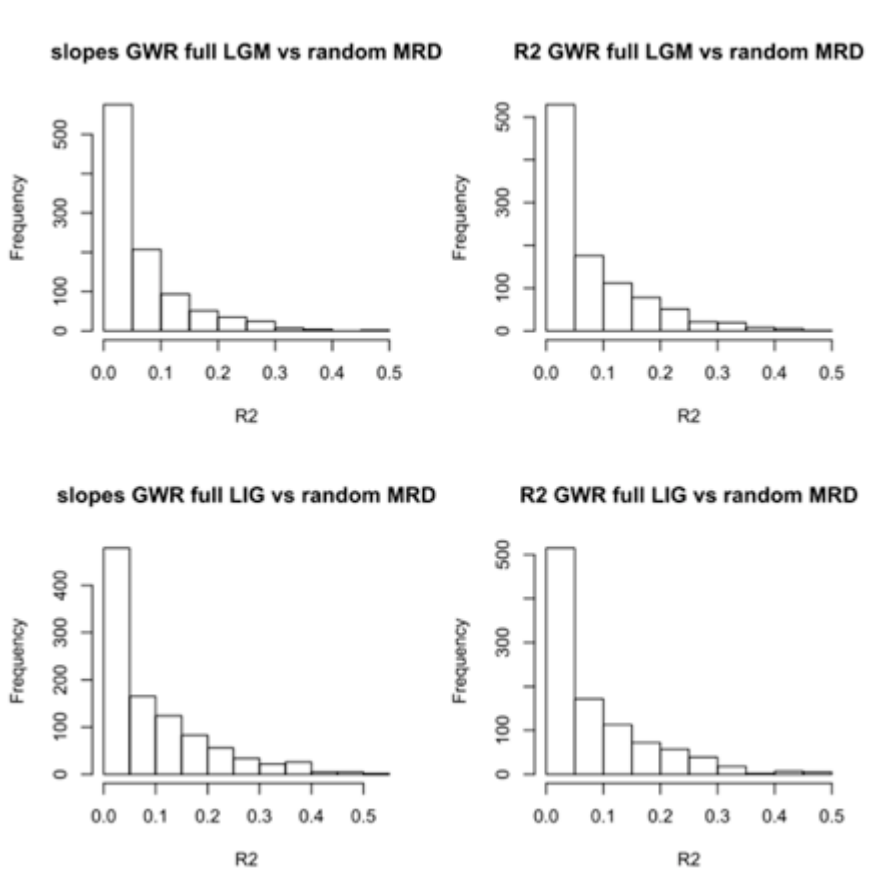
Figure S8. Frequency distributions of determination coefficients (R^2) for correlations between random relative PD and observed residuals from GWR full models Last Glacial Maximum (LGM) and Last Inter-Glacial (LIG).
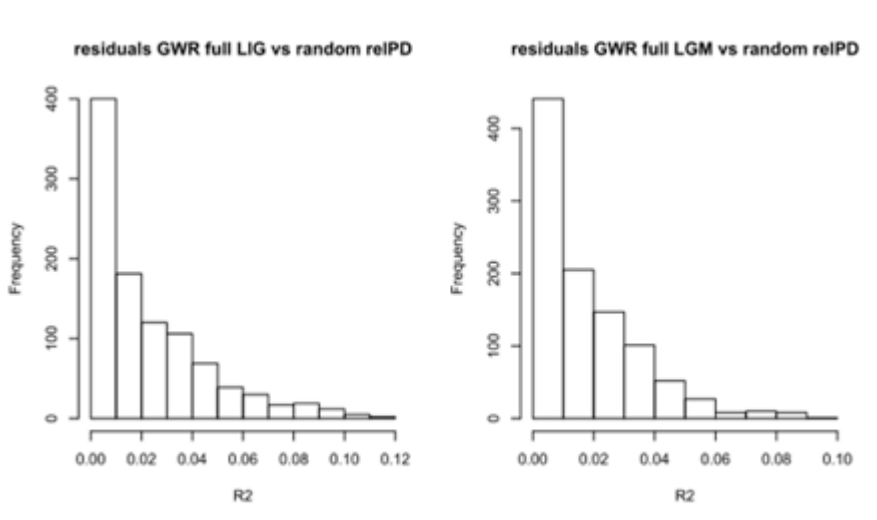
Capítulo III.

Ancient vicariance and climatic niche conservatism explains insular endemism in an iconic radiation of lizards.

Appendix S1. Phylogenetic estimation for Caribbean anoles and main clades occurring in the Caribbean islands.

Figure S1) Calibrated tree for Caribbean *Anolis* lizards generated using Bayesian Markov Chain Monte Carlo analysis implemented in BEAST (Drummond et al. 2012), with branches proportional to absolute ages (in millions of years). Blue bars in each node indicate 95% confidence intervals of node ages. Blue arrow indicates the MRCA for all Caribbean *Anolis* except for clade *Dactyloa* from Lesser Antilles. A large blue bar crossing the tree represents the timing of emergence of the GAARlandia and the Aves Ridge (Iturralde-Vinent and MacPhee 1999). Clade assignment was based in Nicholson et al. (2012).
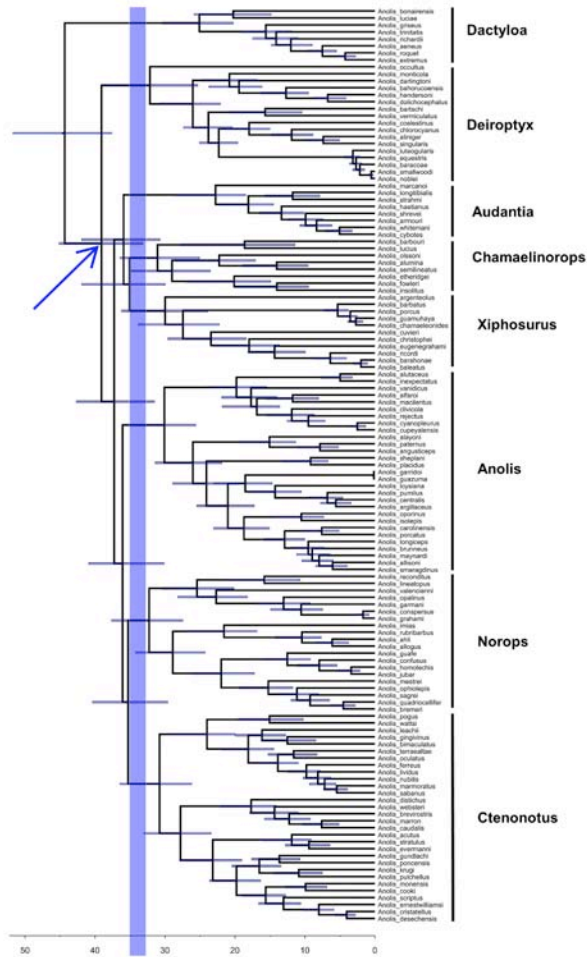

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Table S1. *Anolis* clades occurring in the Caribbean islands*. Only a few clades have a distribution in several islands.

Clades	Number of species
clade *Dactyloa* in Southern Lesser Antilles	8
clade *Deiroptyx* in Cuba	7
Clade *Deiroptyx* in Hispaniola	9
clade *Chamaelinorops* in Hispaniola	8
clade *Xiphosurus* in Cuba	5
clade *Xiphosurus* in Hispaniola	5
clade *Audantia* in Hispaniola	9
clade *Anolis* in Cuba	32
clade *Ctenonotus* in Northern Lesser Antilles	13
clade *Ctenonotus* in Puerto Rico	12
clade *Ctenonotus* in Hispaniola	6
clade *Norops* in Cuba	18
clade *Norops* in Jamaica	7

* Anole species were assigned following to Nicholson et al. (2012) with slight modifications.

Appendix S2. Performance and validation metrics for ecological niche models for Caribbean anole species.

Figure S1. Comparison of validation metrics (Kappa, ROC, TSS) for three niche modeling algorithms (GAM, MaxEnt, SRE) for Caribben *Anolis* species (80 species). Ecological niche models were generated using the Biomod2 library in R (Thuiller et al. 2009) (See main text for details).
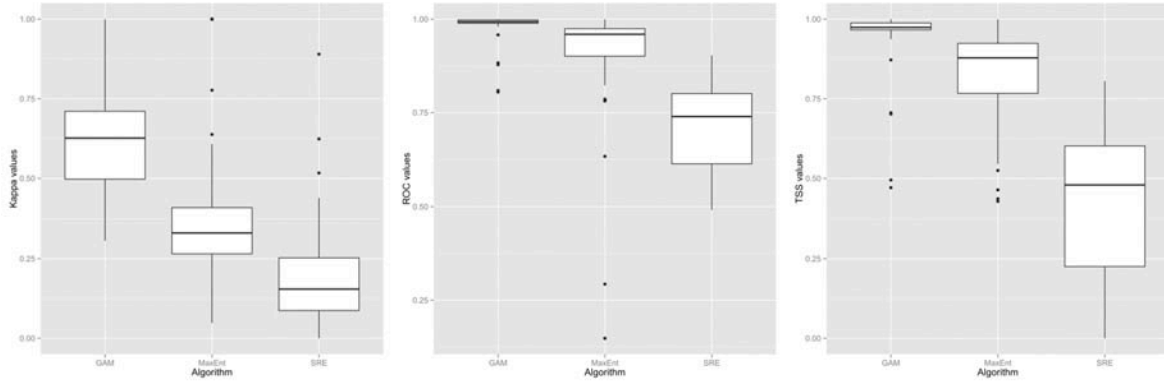

Figure S2. Comparison of AUC values between different regularization values for niche models of Caribbean *Anolis* lizards (80 species) implemented in Maxent software (Phillips et al. 2006).
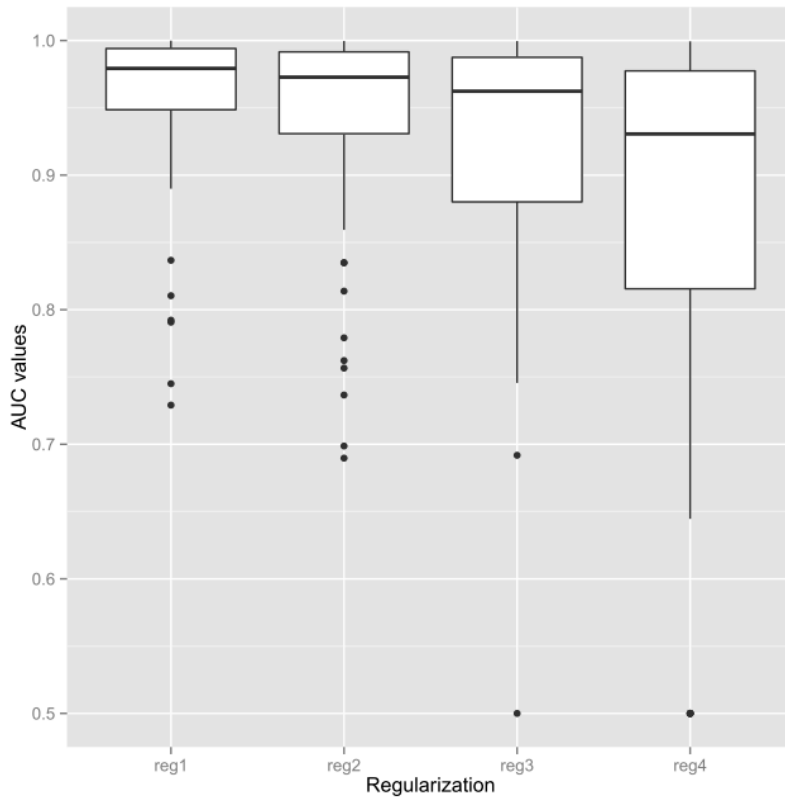
Figure S3. Comparisons of climatic niche overlap between Caribbean anole species from a single island vs. other islands. Niche overlap was measured using Schoener index (D; Schoener 1968) and values close to 1 indicate high niche similarity and values close to 0 indicate very low niche similarity.
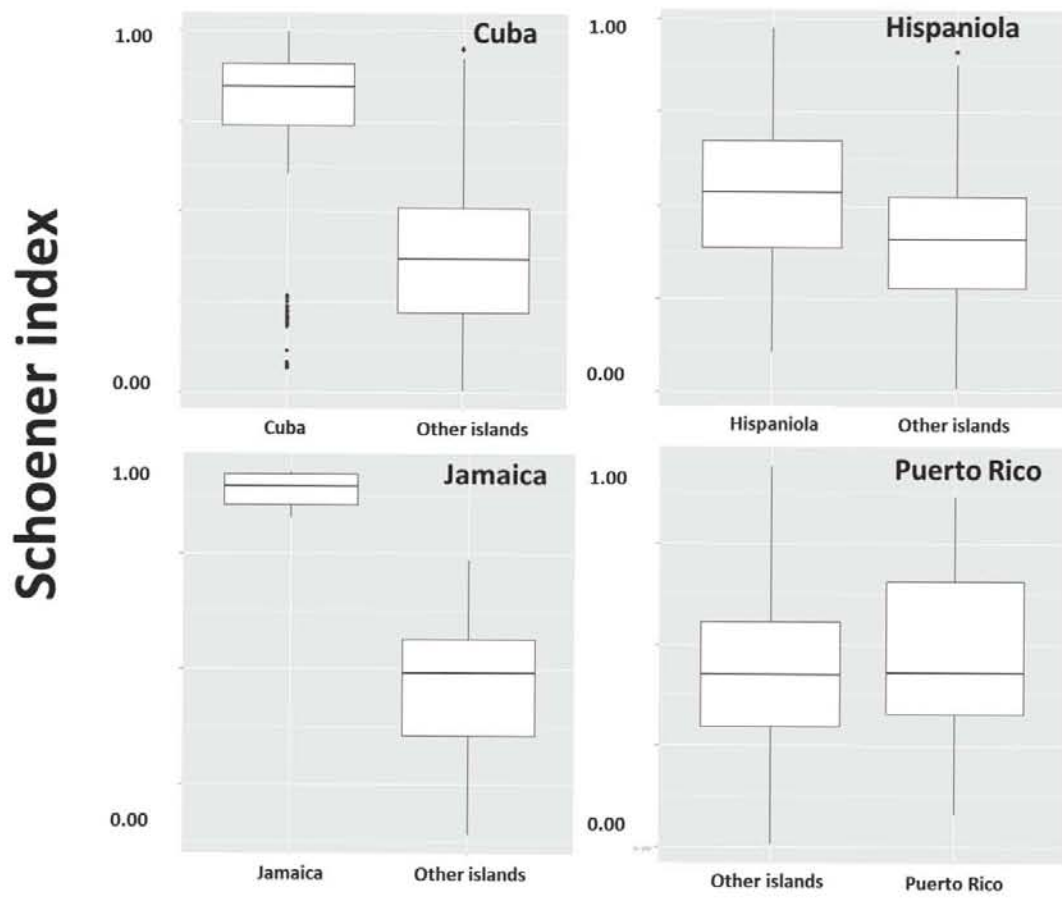
Figure S4. Average climatic suitability estimated from Maxent models for endemic species to each Greater Antillean islands. We calculated an average for logistic raster from Maxent models for all species endemic to each island.