



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

Instituto de Ecología

ÁREAS DE DISTRIBUCIÓN Y RIQUEZA
DE TAXA, EL CAMPO DE DIVERSIDAD
EN DIFERENTES NIVELES
TAXONÓMICOS

TESIS

QUE PARA OBTENER EL GRADO ACADÉMICO DE

DOCTOR EN CIENCIAS

P R E S E N T A

CRISÓFORO FABRICIO VILLALOBOS CAMACHO

TUTOR(A) PRINCIPAL DE TESIS: DR. HÉCTOR TAKESHI ARITA
WATANABE

COMITÉ TUTOR: DR. MARK EARL OLSON ZUNICA, DR. CARLOS
MARTORELL DELGADO

MÉXICO, D.F.

SEPTIEMBRE, 2011



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Dr. Isidro Ávila Martínez
Director General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día 27 de junio de 2011, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del alumno **VILLALOBOS CAMACHO CRISOFORO FABRICIO** con número de cuenta **400073011** con la tesis titulada: **"ÁREAS DE DISTRIBUCIÓN Y RIQUEZA DE TAXA, EL CAMPO DE DIVERSIDAD EN DIFERENTES NIVELES TAXONÓMICOS."**, realizada bajo la dirección del **DR. HÉCTOR TAKESHI ARITA WATANABE**:

Presidente:	DR. ALFONSO VALIENTE BANUET
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De acuerdo con lo anterior, el alumno se acogió a la nueva normatividad, con base en el Artículo **QUINTO TRANSITORIO** en apego a lo establecido en el Artículo 31 del Reglamento General de Estudios de Posgrado (29 septiembre de 2006).

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

Atentamente
"POR MI RAZA HABLARA EL ESPIRITU"
Cd. Universitaria, D.F. a 22 de agosto de 2011.

M. del Coro Arizmendi
Dra. María del Coro Arizmendi Arriaga
Coordinadora del Programa

c.c.p. Expediente del interesado.

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In memoriam

Andrés Villalobos Casamadrid
(1934-2000)

Sofía Carolina Villalobos Camacho
(1975-2010)

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RESUMEN

La variación geográfica en el número de especies es uno de los patrones biológicos más interesantes pero aún poco comprendidos. Esta resulta de la coexistencia diferencial de especies en diferentes regiones, a su vez determinada por las propiedades particulares de sus áreas de distribución: tamaño, forma, ubicación y traslape. Los Enfoques correlativos han identificado variables ambientales que describen tales patrones, pero no incorporan mecanismos causales. Las nuevas aproximaciones incluyen procesos que determinan la distribución individual de las especies bajo un enfoque de modelación mecanicista. La variable de respuesta en estos estudios es usualmente la riqueza de especies, pero el uso de otras variables o patrones de respuesta aporta mayor información a la descripción y evaluación de patrones observados al comparar diferentes modelos. En este trabajo se desarrolló y aplicó un marco teórico novedoso que considera simultáneamente diversidad (riqueza de especies) y distribución geográfica para describir y analizar la estructura interna de un área de distribución con base en la riqueza de otras especies (campo de diversidad), las asociaciones geográficas entre especies resultado del traslape de sus áreas de distribución (co-distribución) y la similitud entre sitios basada en especies compartidas (co-diversidad). Asimismo, se desarrollaron diferentes modelos nulos para evaluar la significancia de los patrones estudiados y la contribución relativa de diferentes factores en su determinación. Los objetivos de este estudio fueron describir y analizar 1) la distribución de frecuencias en riqueza de especies y la estructura interna de las áreas de distribución, usando a los murciélagos de hoja nasal (Phyllostomidae, Chiroptera) como caso de estudio; 2) evaluar los patrones de co-distribución y co-diversidad en esta familia de murciélagos mediante la aplicación de modelos nulos y 3) aplicar las herramientas conceptuales y metodológicas desarrolladas en este proyecto al problema de la planeación para la conservación, utilizando la relación diversidad-distribución en la avifauna mexicana como ejemplo particular.

Con base en la distribución continental del grupo de estudio, se construyeron matrices de presencia-ausencia para cada uno (filostómidos y aves mexicanas) y se extrajo información de riquezas dentro de las áreas de distribución individuales (campo de diversidad) y tamaños de área de distribución de las especies presentes en cada sitio (campo de dispersión). Esta información se ilustró mediante gráficas diversidad-distribución que presentan simultáneamente información de riqueza de especies y tamaño de las áreas de distribución, distribución de frecuencias de riqueza de especies (DFRE) y mapas mostrando la estructura interna de las áreas de distribución, así como la variación geográfica en riqueza y rareza (distribución restringida).

En el capítulo 2 se introduce el concepto de 'campo de diversidad' para analizar la estructura interna del área de distribución y se presenta el primer análisis de la DFRE y sus propiedades estadísticas en un taxón mayor (familia Phyllostomidae) y especies particulares. Los murciélagos filostómidos presentaron un patrón de asociación geográfica entre especies altamente positivo y diferente a escenarios modelados, con la mayoría de murciélagos coexistiendo con un mayor número de filostómidos que el promedio de riqueza continental. Una descripción completa de los patrones de co-distribución y co-diversidad en esta familia de murciélagos se realizó en el capítulo 3, bajo un enfoque de modelación nula y

utilizando coeficientes de la varianza para analizar la magnitud general de dichos patrones. Se identificó el efecto que tienen la cohesión de las áreas de distribución y la similitud de nicho entre especies, además de factores de tipo geométrico (límites del dominio geográfico) y geográfico (tamaño y forma del continente), en la generación de señales estadísticas análogas entre patrones modelados y observados (variación en riqueza, co-distribución y co-diversidad positivas). Las desviaciones significativas entre patrones observados y escenarios modelados sugieren la acción de mecanismos históricos y adaptativos (especiación, extinción, dispersión) adicionales que contribuyen fuertemente a una mayor asociación geográfica entre especies y una concomitante similitud entre los sitios ocupados por los murciélagos filostómidos.

Las gráficas diversidad-distribución y los conceptos de 'campo de diversidad' y 'campo de dispersión' pueden ser aplicados en la identificación de patrones geográficos de biodiversidad relevantes para la planeación de la conservación biológica. Evaluando la relación diversidad-distribución en la avifauna mexicana, se reconoció una relación negativa entre riqueza de especies y tamaño promedio del área de distribución. Esto indica que sitios más ricos en especies de aves tienden a estar ocupados por aves que en promedio tienen distribuciones restringidas (raras), principalmente en el caso de la avifauna total. El patrón para las aves endémicas es similar aunque se reconocieron sitios con baja riqueza ocupados por aves de distribución restringida. Se identificó un conjunto de sitios con estas características (riqueza-rareza) cuya representatividad en la red de áreas naturales protegidas a nivel federal es muy baja. Igualmente, se identificó un conjunto de aves con distribución restringidas que coexisten en promedio con muy pocas aves. Estas especies raras, junto con los sitios antes mencionados para aves endémicas, podrían quedar fuera de planes de conservación enfocados únicamente en patrones de riqueza de especies (los llamados hotspots). Lo anterior resalta la importancia de considerar diferentes aspectos de la biodiversidad (riqueza y rareza) en la planeación para la conservación.

Finalmente, este estudio demuestra que el uso de información biogeográfica básica (presencia-ausencia) y la consideración simultánea de la riqueza de especies y distribución geográfica permiten analizar patrones más informativos acerca de la relación diversidad-distribución que pueden ser extendidos a otros grupos taxonómicos y regiones geográficas, facilitando la comparación entre diferentes conjuntos de datos bajo el marco analítico desarrollado en este proyecto doctoral y así avanzar en la comprensión de los patrones geográficos de biodiversidad.

ABSTRACT

Geographic variation in species richness is one of the most important biodiversity patterns but the explanation of its causes remains elusive. This pattern results from the differential coexistence of species in different regions, in turn determined by the properties of the species' geographic ranges such as size, shape, location and overlap. Correlative approaches have identified environmental variables describing such patterns, but do not include causal mechanisms. Recent approaches favor the inclusion of processes determining the individual distribution of species under a mechanistic modeling framework. Species richness is the sole response variable in most of studies, but using other response variables or patterns can provide more information on the description and evaluation of such patterns when comparing different models. In this dissertation, a novel theoretical framework linking diversity (species richness) and distribution (geographic range) simultaneously was applied to study the range's internal structure based on species richness (diversity field), geographic associations among species due to range overlap (co-distribution) and similitude among sites determined by shared species (co-diversity). Also, null models were developed to evaluate the pattern's significance and the relative contribution of different factors in shaping them. The main goals of this work were to describe and analyze 1) the species richness frequency distribution and internal structure of geographic ranges, using the New World leaf-nosed bats (Phyllostomidae) as case study; 2) to evaluate co-distribution and co-diversity patterns in this bat family under a null modeling approach, and 3) apply the conceptual and analytical tools developed in this project to conservation planning, using the diversity-distribution relationship of the Mexican avifauna as an example.

Presence-absence matrices based on the continental distribution of species were built and used to extract information on richness within individual ranges (diversity field) and range sizes of each species present at each site (dispersion field). This information was depicted using range-diversity plots, which simultaneously show both types of information (diversity and distribution), species richness frequency distributions (SRFDs) and maps showing the range's internal structure, and the geographic variation in species richness and rarity (range restrictedness).

Chapter two introduces the concept of 'diversity field' to analyze the internal structure of species' geographic ranges and represents the first analysis of SRFD and its statistical properties in a major taxon (Phyllostomidae) and individual species. Phyllostomid bats showed a strong pattern of positive geographic association among species that differs from that expected under null models. Most of these bats coexist with a higher number of other phyllostomid species than the overall mean for the continent. A detailed description of co-distribution and co-diversity patterns for these leaf-nosed bats was done in Chapter three, under a null modeling approach and using variance-ratios to investigate the pattern's total magnitude. The effect of range cohesion and niche similarity among species was identified, as well as the influence of other factors such as geometric (domain boundaries) and geographic (size and shape of the continent) in creating analogue statistical signals between observed and modeled patterns (richness variation, positive co-distribution and co-diversity). Significant deviations from expected patterns suggest the influence of additional historic and adaptive mechanisms (speciation, extinction, dispersal) contributing to a stronger geographic association

among species and a resulting similarity among sites occupied by phyllostomid bats.

Range-diversity plots and the 'diversity' and 'dispersion field' concepts can be readily applied in the identification of geographic patterns of biodiversity relevant to biological conservation planning. Studying the diversity-distribution relationship in the Mexican avifauna, a negative relationship between species richness and mean per-site range size was discovered. Hence, species-rich sites tend to be occupied by birds averaging restricted ranges (rare species), especially in the total avifauna. A similar pattern was found for endemic birds, although species-poor sites occupied by geographically restricted birds were also identified. A set of sites with both attributes (high richness and restricted ranges: richness and rarity) was recognized and whose representation within the federal protected area network turned out to be low. Also, a set of restricted bird species coexisting with few other birds was also documented. These species, and the aforementioned sites for endemic birds, could be left out of any conservation plan focused on richness patterns only (so-called hotspots), which highlights the relevance of considering both aspects of biodiversity (richness and rarity) when planning for conservation.

To conclude, this study shows how the use of primary biogeographic information (presence-absence) and the simultaneous consideration of species richness and geographical distribution, allow describing and analyzing informative patterns regarding the relationship between diversity and distribution. Moreover, these patterns can be easily extended to other taxonomic groups and geographic regions, facilitating the comparison among different data sets under the analytical framework developed in this dissertation and a comprehensive understanding of geographic patterns of biodiversity.

INTRODUCCIÓN

Una de las metas de la ecología en la actualidad es la comprensión y predicción de fenómenos que caracterizan sistemas ecológicos completos. Esto es posible mediante la identificación de patrones comunes que puedan indicar mecanismos subyacentes o principios generales (Brown 1995, Marquet 2009). El estudio de los sistemas ecológicos ha mostrado la existencia de regularidades, observaciones repetidas de un fenómeno, que sugieren causas comunes entre diferentes sistemas (Gaston 2000). La existencia de estos patrones de organización ecológica, a pesar de la gran diversidad física y biológica del planeta, sugiere la acción de procesos físicos, químicos y biológicos generales que representan las bases mecanicistas de dichos patrones (Brown et al. 2002). Una vez identificados, la comprensión de esos patrones requiere de su explicación basada en los mecanismos potencialmente responsables. Sin embargo, aún no se conocen cuáles son los mecanismos y cómo funcionan individualmente e interactúan entre sí para generar diversos patrones ecológicos. Un enfoque basado en la identificación de patrones biológicos provee un marco conceptual para la discusión de amplias clases de fenómenos y así dilucidar la organización, funcionamiento y relaciones entre los componentes que dan origen a los sistemas ecológicos. Dicho programa de estudio es una de las bases de la investigación macroecológica (Marquet 2009).

Este trabajo de tesis se inserta dentro del programa de investigación de la macroecología, teniendo como objetivo general la descripción y explicación de patrones de biodiversidad en escalas geográficas, y como objetivos particulares evaluar la estructura interna de las áreas de distribución con base en la riqueza de especies (campo de diversidad), la asociación geográfica entre especies resultado del traslape de sus áreas de distribución (co-distribución) y la similitud entre sitios basada en especies compartidas (co-diversidad), así como aplicar las herramientas y teoría generada al problema de la planeación para la conservación (priorización de sitios biológicamente relevantes).

Uno de los patrones más interesantes e intrigantes de la biodiversidad es su distribución heterogénea. Es decir, no todas las especies están en todos lados y,

por tanto, no todas las regiones son similares. Por ejemplo, existe un gradiente muy marcado en el que los trópicos concentran la mayor diversidad de especies en el planeta. Este tipo de patrones básicamente están determinados por la distribución geográfica de cada una de las especies presentes en el planeta. De esta manera, para comprender estos patrones es necesario estudiar las áreas de distribución de las especies.

La distribución geográfica de los organismos está determinada por diferentes factores que interactúan entre sí y operan diferencialmente en distintas escalas. Estos factores incluyen: (a) las condiciones abióticas (e.g. clima, ambiente físico), que imponen límites fisiológicos en la capacidad de un taxón para permanecer en cierta área, (b) las interacciones bióticas, que pueden limitar o favorecer procesos poblacionales, (c) la accesibilidad a ciertas áreas a partir de un área original dependiendo de la configuración del paisaje y la capacidad de dispersión del taxón, y (d) la capacidad evolutiva de los taxa para adaptarse a nuevas condiciones (Pulliam 2000, Soberón y Peterson 2005). En la naturaleza se observa una gran variación con respecto a las características de las áreas de distribución de las especies (e.g. límites, tamaños, ubicación, formas y traslapes) como reflejo de la diversidad de procesos involucrados en la determinación de la distribución de los organismos sobre el planeta (e.g. factores abióticos, bióticos, demográficos y genéticos) y la influencia diferencial que estos pueden tener sobre cada una de las especies. Como consecuencia de la interacción entre estos procesos, el área de distribución resulta en una entidad con variación temporal (dinámica) y difícil de definir sin ambigüedad (Zunino y Zullini 2003). No obstante, las áreas de distribución no se encuentran aleatoriamente distribuidas sobre el espacio geográfico y presentan algunos patrones interesantes, principalmente en relación a su estructura general (e.g. tamaño y forma; Maurer 1999).

El área de distribución de las especies se puede describir con diferentes atributos: forma, tamaño, estructura y posición (entre otros). El tamaño ha sido el atributo más estudiado (Gaston 2003), principalmente la variación latitudinal en el tamaño del área de distribución ha recibido mucha atención debido a sus posibles implicaciones en la determinación de procesos que subyacen la variación geográfica en riqueza de especies, particularmente la mayor riqueza en los trópicos (Orme et al. 2006). La estructura interna, principalmente en términos de la

variación en abundancia, también ha sido estudiada (Brown et al. 1995). No obstante, todos estos atributos son los que finalmente subyacen a los patrones de riqueza de especies como resultado del traslape entre las distintas áreas de distribución. Por esta razón, el estudio de las propiedades geométricas de las áreas de distribución puede contribuir sustancialmente a la comprensión de los patrones geográficos de biodiversidad (Arita y Rodríguez 2002, Villalobos y Arita 2010. Capítulo 2).

La riqueza de especies en escalas continentales es usualmente medida como el traslape entre las áreas de distribución de la especie (Simpson 1964). La metodología estándar para describir dichos patrones es la cuantificación del número de especies que coinciden (sus áreas de distribución se traslapan) en diferentes sitios de la región estudiada, definidos con base en retículas o gradillas conformadas por celdas de igual tamaño (estrictamente, esta es una medida de densidad de especies; Gotelli et al. 2009, Simpson 1964, Rosenzweig 1995, Willig y Gannon 1997). La representación básica de esta metodología es una matriz de presencia-ausencia (PAM) compuesta por sitios (columnas) y especies (filas), en donde los elementos de la matriz son binarios representando la presencia (1) o ausencia (0) de una especie dada en un sitio dado (Gotelli 2000). Este enfoque evidencia la relación intrínseca existente entre la diversidad (número de especies) y la distribución (sitios ocupados). Sin embargo, en la práctica esta relación ha sido desatendida, resultando en análisis independientes de la riqueza o de la distribución (Arita et al. 2008, Villalobos et al. Capítulo 3). Como consecuencia, el estudio de patrones geográficos de biodiversidad se ha enfocado principalmente en analizar ya sea la riqueza de especies (análisis Q, por columnas en la PAM) o el tamaño de su distribución geográfica (análisis R, por filas en la PAM), dejando a un lado un análisis particular de las áreas de distribución individuales y de la relación inherente que existe entre diversidad y distribución.

Los patrones de biodiversidad hacen referencia casi exclusivamente (al menos en escalas geográficas) a estas dos variables fundamentales; principalmente describiendo la variación geográfica en riqueza de especies (Hillebrand 2004) y en el tamaño de sus áreas de distribución (Hawkins y Diniz-Filho 2006). Dicha

descripción, a su vez, usualmente se hace con relación a variables climáticas considerando correlaciones entre diversidad y condiciones ecológicas locales (e.g. temperatura, precipitación o productividad primaria neta) (Rahbek et al. 2007). Este procedimiento invoca el supuesto que dichas correlaciones son consistentes con la idea de que las interacciones (negativas) locales restringen la diversidad (Ricklefs 2004). No obstante, las asociaciones entre variables no revelan los procesos que finalmente influyen sobre los patrones de biodiversidad. Estos deben ser explicados en términos de procesos que directamente cambian el número de especies en una región y el tamaño y forma de sus áreas de distribución, procesos históricos tales como especiación, extinción y dispersión de taxa entre regiones (Wiens et al. 2006). Otros factores como el ambiente biótico (e.g. interacciones ecológicas) y abiótico (e.g. clima) también juegan un papel importante pero actúan finalmente sobre dichos procesos históricos para modificar el número de especies en una región (Wiens et al. 2007). Además, dichos enfoques de correlación describen los patrones geográficos de biodiversidad sin modelar explícitamente el tamaño, forma y posición de las áreas de distribución que se traslapan entre especies de una región. Estos atributos de las áreas de distribución son los que finalmente subyacen a los patrones geográficos de riqueza de especies. De esta forma, con la representación y estudio de las áreas de distribución es posible estudiar la manera en que se organizan las especies en el espacio y así responder varias de las preguntas básicas de la ecología y de la evolución.

Recientemente, se ha propuesto un enfoque alternativo basado en la modelación mecanicista de las distribuciones geográficas particulares de las especies para determinar las causas potenciales de los patrones macroecológicos (Gotelli et al. 2009). La idea general consiste en modelar la conformación de las áreas de distribución bajo diferentes supuestos biológicos (simplificaciones acerca de cómo se construye el área de distribución: aleatoria, dispersa, cohesiva geográfica y/o ambientalmente) y consideraciones geométricas (e.g. extensión y límites geográficos del dominio estudiado). Una primera aproximación para evaluar patrones observados en ausencia de capacidad de experimentación, es la construcción de modelos nulos. Esta aproximación tiene como objetivo poner a prueba hipótesis específicas acerca de patrones ecológicos con base en contrastar patrones observados con aquellos generados por aleatorización de los

datos (bajo ciertas restricciones) y excluyendo procesos de interés (e.g. interacciones bióticas) (Gotelli y Graves 1996). Los modelos nulos generan patrones con base en información biológica mínima (e.g. estructura de los datos), pero permitiendo la variación aleatoria de otros elementos en los datos (Gotelli y McGill 2006). Dichos modelos se basan en simulaciones probabilísticas y estocásticas de los datos, de manera que iteraciones múltiples del mismo modelo pueden utilizarse para estimar las variables de respuesta (i.e. estructura de los datos, distribución de probabilidad del estadístico descriptivo, e.g. riqueza de especies, coeficiente de asociación, etc.) bajo las condiciones del modelo (Gotelli et al. 2009).

Los modelos nulos pueden incluir procesos específicos (modelos dinámicos) o simplemente basarse en la información observada sin suponer mecanismos específicos (modelos estáticos). Estos últimos generan hipótesis estadísticas nulas acerca de cómo podrían ser los patrones en ausencia de procesos biológicos importantes, con las cuáles se pueden contrastar los patrones observados (e.g. estructura aleatoria de comunidades vs. estructura mediada por competencia interespecífica). Por otro lado, los modelos dinámicos usualmente generan predicciones específicas (numéricas), pues suponen que los procesos incorporados al modelo son los verdaderos mecanismos causales del patrón estudiado (e.g. modelos basados en teoría neutral; Bell 2001, Gotelli y McGill 2006). No obstante, ambos enfoques pueden combinarse.

Por ejemplo, es posible considerar cierta estructura realista de los datos (e.g. mantener los tamaños de área de distribución observados) y al mismo tiempo incorporar un proceso particular de conformación de las áreas de distribución (e.g. expansión cohesiva determinada por el ambiente; Connolly 2005, Storch et al. 2006, Villalobos et al. Capítulo 3). Estrictamente, la incorporación de un proceso o mecanismo específico convertiría a los modelos en dinámicos (Gotelli y McGill 2006). Sin embargo, extender los modelos nulos para que incorporen supuestos mecanicistas (e.g. la conformación de las áreas de distribución) no necesariamente implica una dinámica temporal dentro de los modelos ni, mucho menos, la predicción numérica de las variables de interés. En efecto, se pueden acomodar diferentes mecanismos en un modelo único, proporcionando un marco teórico común para poner a prueba hipótesis acerca de la influencia relativa de

diferentes procesos en la determinación de patrones de biodiversidad (Gotelli et al. 2009). Así, es posible evaluar nuestro entendimiento de los patrones de biodiversidad y sus potenciales causas (Hillborn y Mangel 1997). De esta manera, la inclusión de procesos mecanicistas en modelos basados en aleatorizaciones puede entenderse como una extensión de los modelos nulos, sirviendo como hipótesis estadísticas nulas para contrastar patrones observados e investigar la influencia relativa de dichos procesos (Villalobos et al. Capítulo 3).

En este proyecto abordo el estudio de las áreas de distribución de las especies desde una perspectiva novedosa para evaluar la estructura interna de áreas de distribución individuales y los patrones de riqueza de especies, ambos generados por el traslape de las áreas de distribución. La cuantificación de la riqueza como resultado del traslape de áreas de distribución indica una relación intrínseca entre diversidad y distribución. Pero, dado que estas dos propiedades fundamentales de la biodiversidad han sido comúnmente estudiadas por separado, la forma de esta relación es desconocida. Esto no se debe a la falta de reconocimiento o incluso intento de definirla (Rosenzweig 1975), sino por la falta de un marco teórico que relacione explícitamente ambas propiedades y establezca formalmente (matemáticamente) las posibilidades de dicha relación considerando la existencia de límites biológicos y matemáticos. Dicho marco teórico fue introducido por Arita y colaboradores en 2008. En esta tesis desarrollo este marco teórico y los conceptos asociados, describiendo las propiedades estadísticas de dicha relación en función de las especies (Villalobos & Arita 2010. Capítulo 2) y los sitios donde estas se distribuyen (Villalobos et al. Capítulo 3) y proponiendo una aplicación directa del conocimiento adquirido con la exploración de este tipo de patrones (Villalobos et al. Capítulo 4). En particular, introduzco un marco analítico novedoso para (i) describir e interpretar la estructura interna de las áreas de distribución, (ii) la variación geográfica en diversidad y (iii) los patrones de co-distribución y co-diversidad. Asimismo, (iv) aplico la teoría y herramientas generadas en este proyecto al contexto de la planeación y priorización para la conservación biológica. Además, demuestro la utilidad de los enfoques de modelación para evaluar patrones macroecológicos, especialmente cuando se conoce la estructura que pueden tomar los datos (i.e. posibilidades teóricas del patrón estudiado).

En la Parte 2 presento la publicación resultado del proyecto (Villalobos y Arita, 2010. Capítulo 2) y dos manuscritos más (en proceso de ser enviados Capítulos 3 y 4) producto del proyecto doctoral. El capítulo dos representa el primer análisis completo de las propiedades estadísticas del 'campo de diversidad' en un taxón mayor (Phyllostomidae, Chiroptera). En este capítulo exploro la distribución de frecuencias en riqueza de especies para toda la región ocupada por la familia Phyllostomidae y el patrón general de asociación geográfica entre especies a través de las gráficas diversidad-distribución y pruebas del cociente de la varianza. Además, investigo los patrones individuales de campo de diversidad en cada una de las especies de esta familia de murciélagos. Demuestro la utilidad del concepto de campo de diversidad y su importancia para la interpretación de patrones geográficos de biodiversidad. Específicamente, encontré que los murciélagos filostómidos presentan un fuerte patrón de asociación entre especies (co-distribución), mayor al esperado bajo escenarios particulares desarrollados con pocos supuestos biológicos (modelos nulos). Individualmente, los patrones de campo de diversidad de las especies de esta familia son resultado del tamaño, forma y ubicación de sus áreas de distribución, pero también del patrón general de riqueza de especies para toda la familia (la relación entre diversidad y distribución) influenciada por factores geométricos (cohesión de la áreas de distribución, efecto del dominio medio), geográficos (forma y tamaño del continente), climáticos y características idiosincráticas de las especies (historia, interacciones potenciales). En el capítulo tres extiendo este enfoque para incluir la versión por sitios de los análisis basados en la relación diversidad-distribución y evaluar la influencia de otros factores (heterogeneidad ambiental y similitud de nicho) en la conformación de los patrones observados. En este capítulo, bajo el mismo marco conceptual y analítico, confirmo el efecto dominante de la cohesión de las áreas de distribución, especialmente cuando la conformación de éstas es influenciada por la heterogeneidad ambiental, y de factores históricos (contingentes) como la similitud en los nichos ecológicos (grinnellianos) entre las especies en la determinación de patrones de co-distribución y co-diversidad positivas en la familia Phyllostomidae.

Una extensión hacia la aplicación de las herramientas y análisis desarrollados en los capítulos anteriores y del marco teórico general con respecto a la relación diversidad-distribución es presentada en el capítulo cuatro. En este

capítulo, aplico la teoría generada para evaluar los patrones de variación geográfica en diversidad y de la distribución promedio por sitio ('campo de dispersión'); además de los patrones de asociación geográfica entre especies y de campo de diversidad de las especies individuales, en un grupo taxonómico diferente que cuenta con información más detallada acerca de la distribución de especies: las aves mexicanas. Particularmente, encontré una relación negativa entre la riqueza de especies y el tamaño de área de distribución promedio por sitio. Esto es, sitios más ricos contienen, en general, especies con distribuciones restringidas tanto para el conjunto total de aves en México como para las aves endémicas (con distribución exclusiva dentro de México). Finalmente, demuestro cómo las gráficas diversidad-distribución (así como la teoría y parámetros asociadas a éstas) pueden ser utilizadas con relativa facilidad en la priorización de sitios bajo esquemas de planeación para la conservación biológica.

RESEARCH
PAPERThe diversity field of New World
leaf-nosed bats (Phyllostomidae)

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ABSTRACT

Aim To analyse how the patterns of species richness for the whole family Phyllostomidae determine the structure of diversity fields (sets of species–richness values) within the ranges of individual bat species.

Location The range of the family Phyllostomidae in North and South America.

Methods We generated a database of the occurrence of 143 phyllostomid bat species in 6794 quadrats, analysing the species–richness frequency distribution for all sites, and for subsets of sites defined by the geographic ranges of species. Range–diversity plots, depicting simultaneously the size and the mean species richness of ranges, were built to explore the patterns of co-occurrence in widespread and restricted species. We compared the empirical patterns against two null models: (1) with scattered (non-cohesive) ranges, and (2) with cohesive ranges modelled with the spreading-dye algorithm. Diversity fields were analysed with richness maps for individual species and with comparisons of species–richness frequency distributions.

Results Overall richness frequency distribution showed a multimodal pattern, whereas simulated distributions showed lower values of variance, and were unimodal (for model 1) and bimodal (for model 2). Range–diversity plots for the empirical data and for the cohesive–ranges simulation showed a strong tendency of species to co-occur in high-diversity sites. The scattered–ranges simulation showed no such tendency. Diversity fields varied according to idiosyncratic features of species generating particular geographic patterns and richness frequency distributions.

Main conclusions Phyllostomid bats show a higher level of co-occurrence than expected from null models. That tendency in turn implies a higher variance in species richness among sites, generating a wider species–richness frequency distribution. The diversity field of individual species results from the size, shape and location of ranges, but also depends on the general pattern of richness for the whole family.

Keywords

Bats, distribution, diversity, diversity field, geographic range, Neotropics, Phyllostomidae, species richness.

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INTRODUCTION

The geographic variation in species richness across continents remains one of the most enigmatic patterns in biogeography and evolutionary biology (Rosenzweig, 1995; Mittelbach *et al.*, 2007). Despite years of investigation, there is no consensus on the underlying causes of such an obvious pattern, although recent research shows that species richness correlates closely

with environmental variables, especially those related to productivity and energy availability (Hawkins *et al.*, 2003; Field *et al.*, 2009). As a complement to correlative studies, other lines of research have focused on the mechanisms that determine the distribution of individual species to understand the aggregate pattern of species richness (Gotelli *et al.*, 2009). Modelling the dynamics of geographic ranges has already yielded intriguing insights into the processes that shape geographic gradients

Table 1 Equivalence of terms and variables of the dispersion and diversity fields. Mathematical notation follows Arita *et al.* (2008). δ_{ij} is the element of the presence-absence matrix corresponding to site i and species j ($\delta_{ij} = 1$ if species i is present in site j , $\delta_{ij} = 0$ otherwise).

	Analysis by species	Analysis by sites
Type of analysis	By rows (R and Rg)	By columns (Q and Qr)
Total number of rows or columns	Number of species (S). Continental (gamma) diversity or number of species in group under study	Number of sites (N); Size of continent or of combined range of all species
Summation along a row or column	Range size of species i : $n_i = \sum_{j=1}^N \delta_{ij}$	Species richness of site j : $s_j = \sum_{i=1}^S \delta_{ij}$
Field	Diversity field	Dispersion field
Definition	Set of species assemblages of the sites forming the range of a given species	Set of the ranges of species occurring in a given site
Statistical definition	Set of species-richness values of sites within the range of a given species	Set of range-size values of species occurring in a given site
Frequency distribution	Species-richness frequency distribution	Range-size frequency distribution
Sample size	Range size of species i (n_i)	Species richness of site j (s_j)
Mean	Average richness of sites within the range of species i : $\bar{x}_i = \frac{1}{n_i} \sum_{j=1}^N s_j \delta_{ij}$	Average range size of species occurring in site j : $\bar{n}_j = \frac{1}{s_j} \sum_{i=1}^S n_i \delta_{ij}$
Volume	Summation of richness values of sites containing a given species: $D_i = \sum_{j=1}^N s_j \delta_{ij} = n_i \bar{x}_i$	Summation of range-size values of species occurring in a given site: $R_j = \sum_{i=1}^S n_i \delta_{ij} = s_j \bar{n}_j$

of species richness (Rangel *et al.*, 2007; Roy & Goldberg, 2007; Arita & Vázquez-Domínguez, 2008).

Species richness at the continental level is generally measured with the overlap of the geographic ranges of species (Simpson, 1964). Because the overlap is determined by the size, shape and location of individual ranges, studies of their geometric properties can lead to an understanding of large-scale patterns of diversity (Arita & Rodríguez, 2002). The study of geographic ranges is further enhanced when considering their internal structure, which has been described for example in terms of variation in abundance (Brown *et al.*, 1996; Sagarin *et al.*, 2006) or genetic composition (Eckert *et al.*, 2008; Barbour *et al.*, 2009). Here we examine the internal structure of ranges in terms of geographic variation in the number of overlaps with other species. In doing so, we measure the species richness in different parts of the range of a species. The pattern is ultimately determined by the overall variation in species richness across the continent, but also depends on the location and geometric properties of the range of individual species. The internal structure of the range as measured here is a reflection of the tendency of species to occur in species-rich or species-poor locations.

We take advantage of recent analytical developments in extracting information from presence-absence matrices to link diversity and distribution. In particular, we explore the properties of the 'diversity field', the set of species-richness values of sites that are within the range of a given species (Arita *et al.*, 2008). Graves & Rahbek (2005) analysed the distribution patterns of South American birds, and visualized the 'dispersion field' of the set of species occurring in a site by overlaying their continental ranges. They also computed the dispersion field volume as the product of the mean range size and the richness of the set of species; thus, the dispersion field volume equals the summation of all range-size

values of species occurring in a given site. As shown by Arita *et al.* (2008), the diversity field volume of a species is computationally equivalent to the dispersion field volume of a site, given the mathematical properties of presence-absence matrices, and equals the summation of all species-richness values of sites that are within the range of a given species (Table 1).

Because the diversity field of a species is a set of species-richness values, it can be described and analysed with the standard statistical descriptors of central tendency and variation. However, species-richness frequency distributions (FDs) are surprisingly absent from the literature, and their statistical properties remain largely unknown. This is in sharp contrast with the attention that the FD of other macroecological variables, such as abundance, range size and body mass, has received (Brown, 1995; Graves & Rahbek, 2005; McGill *et al.*, 2007; Nekola & Brown, 2007).

We use the family Phyllostomidae of New World leaf-nosed bats as a study case. The family is a diverse group of 160 species distributed in tropical and subtropical areas of the Americas (Simmons, 2005). The group originated approximately 38 Myr BP (Jones *et al.*, 2005; Teeling *et al.*, 2005) and radiated to include a wide gamut of feeding strategies, including insectivory, carnivory, frugivory, nectar feeding and even blood feeding. Because the group is monophyletic, widespread but endemic to a single land mass, and because species show a great deal of variation in range size, Phyllostomidae represents an ideal clade for large-scale studies of diversity and distribution (Stevens, 2006).

METHODS

We constructed a database of the continental (non-insular) distribution of phyllostomid bats, following the current taxonomic

arrangement (Simmons, 2005). Distributional maps were built using ArcGIS with data from the primary literature up to 2004 and from the Nature Serve database (Patterson *et al.*, 2007). The final set included a total of $S = 143$ species with distribution in continental America. A grid of $N = 6794$ equal-area quadrats (2500 km², corresponding to approximately $0.5^\circ \times 0.5^\circ$ latitude and longitude near the Equator) was overlaid on the distributional maps to generate a 143 species \times 6794 sites presence-absence matrix. The sum of elements along rows of the matrix yielded the range size of species (n_i), measured as the number of quadrats that are overlapped by the distributional map of each species. The number of distributional maps that overlapped a given site was defined as the species richness of that site (s_j), which equals the sum of elements of the column of the presence-absence matrix corresponding to that site.

For analytical convenience, all richness and range size variables can be converted to proportional values by dividing them by the corresponding total of species or quadrats for the whole system (Arita *et al.*, 2008). Thus, any richness value divided by S and any range size value divided by N are proportional variables and are denoted by adding an asterisk to their symbols. For example, n_i^* is the proportional range size of species i , and is equal to n_i/N ; equivalently, $s_j^* = s_j/S$ is the proportional species richness of site j .

We computed the diversity field for each species with the set of species-richness values of quadrats in which the focal species occurs. This was done with an Rq analysis whereby information was extracted from the presence-absence matrix row by row, but incorporating data calculated by columns (Arita *et al.*, 2008; Table 1). Thus, diversity fields were samples, of size equal to the range size of species, taken from the pool of richness values of the whole assemblage. The composition and statistical parameters of such samples depend on the size, shape and location of the species' geographic range. We described and examined the statistical characteristics and the spatial variation of diversity fields with three complementary approaches: (1) the analysis of species-richness FDs, (2) the examination of maps showing the internal structure of the range in terms of species richness, and (3) the construction of range-diversity plots (Arita *et al.*, 2008).

Preliminary analyses showed a tendency of richness FDs to be much less skewed than range-size FDs, so we opted not to use the logarithmic transformations routinely employed to deal with continental range size FDs and other highly skewed FDs (Graves & Rahbek, 2005; Nekola & Brown, 2007). To describe and compare richness FDs, we used the standard statistical parameters of central tendency, deviation and shape, that is, the first (mean), second (variance) and third (skewness) moments. In particular, we defined \bar{s} as the mean species richness of sites in which species i occurs, and $\bar{s}^* = \bar{s}/S$ as its proportional equivalent. Also, we computed the diversity field volume of a species as $D_i = n_i \bar{s}$, that is, the summation of species-richness values of sites within the range of species i . We associated the histogram of the richness FD for each species with a range map showing the variation in species richness among the sites forming that range. Maps allowed the visualization of the structure of ranges as spatial patterns of co-occurrence with other species.

Range-diversity plots are visual analytical tools that allow the simultaneous depiction of diversity and distributional data (Arita *et al.*, 2008). In such plots, ordinates are proportional range sizes (n_i^*) and abscissas are mean proportional richness values of sites within the range of species, that is, proportional averages of the diversity field (\bar{s}^*). Mathematical properties of presence-absence matrices impose constraints on the possible combinations of values in such a way that the interval of possible values of \bar{s}^* for species with small ranges is always wider than for widespread species (Arita *et al.*, 2008). Range-diversity plots also allow the interpretation of richness patterns in terms of the association (covariance) among the species, whose statistical significance can be assessed using Schluter's variance ratio test (Schluter, 1984; Gotelli, 2000). For example, if a vertical line is drawn where $\bar{s}^* = \bar{s}$, then points to the right of this line (that is, those for which $\bar{s}^* > \bar{s}$) will correspond to species with positive average covariance with the rest of the species (Arita *et al.*, 2008). It can be shown that, if species arrange along the vertical line (that is, if for all species $\bar{s}^* = \bar{s}$), then

$$V = \text{var}(s) / \sum \text{var}(n_i),$$

which is the ratio of the variance in species richness and the summation of range-size variances, should be close to 1.0. A value of $V > 1.0$ would indicate a positive overall association among species (Schluter, 1984) and would imply that most points in a range range-diversity plot are to the right of the vertical line (that is, that for most species $\bar{s}^* > \bar{s}$).

We developed null models to envision scenarios under which the distribution patterns of species were independent of each other. As in all null models (Gotelli & Graves, 1996), we retained some part of the empirical information and allowed other parameters to vary. We maintained the range size of species and randomized their shape and location, so the row sums of the presence-absence matrix, that is, the empirical range size FD remained intact in all models. We examined models with and without cohesion of ranges, as this factor has been shown to exert an important influence on the outcomes of models of continental diversity and distribution (Jetz & Rahbek, 2001; Rahbek *et al.*, 2007; Arita & Rodríguez-Tapia, 2009).

In our first model, we built the simulated range of a given species by sequentially selecting quadrats, randomly without replacement, until the empirical range size of that species was reached. Thus, sites had equal probabilities of being included in a range (SIM2 case, Gotelli, 2000). Notice that under this model, the geographic location of the selected sites is ignored, so quadrats are scattered all over the continent, forming non-cohesive geographic ranges. In our second model, we used the spreading-dye algorithm (Jetz & Rahbek, 2001) to generate the simulated ranges. For each species, we started by selecting a single quadrat from the pool of sites of the combined distribution of the whole family. Then, in each step, a new quadrat was added in a random position at the periphery of the growing range, with the restriction that new quadrats could be added only within the original area occupied by the family. Consequently, limits to the distribution of phyllostomids, as well as sea borders, constituted hard boundaries to the spreading ranges. The process was iterated

until the simulated range reached the size of the empirical area of distribution. This second model generated random, cohesive ranges that were equal in size to the empirical ranges, but that were different in shape and location.

For both models, we built species-richness FDs for the whole assemblage and for the resulting diversity fields by species. Unless otherwise stated, all statistical inferences were made contrasting the empirical data against FDs of variables generated by 100 repetitions of the models. Simulations were performed using R software (R Development Core Team, 2008).

RESULTS

Empirical data

The family Phyllostomidae distributes over an area of approximately 17 million km² from the south-western United States to northern Argentina and Chile (Fig. 1a). Within that area, the number of ranges overlapping our 6794-quadrat grid varied from 1 to 73, peaking in the tropical part of the Andes in South America and declining towards the northern and southern extremes, following the strong latitudinal gradient of species richness that has been documented for New World bats (Willig & Bloch, 2006). The geographic pattern of richness generated a multimodal FD (Fig. 2a) with an over-representation of quadrats with very low richness (fewer than five species) but that was much less skewed than other macroecological FDs (Brown, 1995; Nekola & Brown, 2007). Mean species richness was $\bar{x} = 33.96$ species ($\bar{x}^* = 0.237$), but figures varied widely (SD = 21.86) and showed a significant negative skew ($g_1 = -0.133$, $P[g_1 = 0] < 0.001$), indicating that in most sites the number of species was higher than the average.

Geographic ranges of species varied in size from $n_i = 1$ quadrat (2500 km²; $n_i^* = 1.5 \times 10^{-4}$) to 6223 quadrats (15.6×10^6 km²; $n_i^* = 0.92$, see Appendix S1 in Supporting Information). The range size FD followed the highly skewed shape typical of continental assemblages (Brown *et al.*, 1996; Nekola & Brown, 2007) (Fig. 3, right-hand panels). As expected from theory (Arita *et al.*, 2008), average richness within the ranges varied widely among species with small ranges ($\bar{x}_i = 3.2 - 70.8$ species; $\bar{x}_i^* = 0.022 - 0.495$, bottom of the range-diversity plot in Fig. 3a), but was constrained to average values for the most widespread species, such as the common vampire bat (*Desmodus rotundus* $\bar{x}_i = 36.82$; $\bar{x}_i^* = 0.257$). One hundred and twenty species (84%) had an average species richness within their ranges higher than the overall mean ($\bar{x}_i^* > 0.237$), corresponding to points to the right of the vertical dashed line in Fig. 3(a). Only five species, all occurring in the northern extreme of the area of distribution of the family, coexisted on average with 20 or fewer species ($\bar{x}_i^* \leq 0.140$; Fig. 3a, lower left corner of the plot). These patterns generated a very high value of Schluter (1984) variance ratio ($V = 26.99$), indicating a high degree of association among species.

The FDs of diversity fields showed a great deal of variation (Fig. 4, see Appendix S1). Small ranges coincided with species-poor or species-rich areas, but they tended to show little varia-

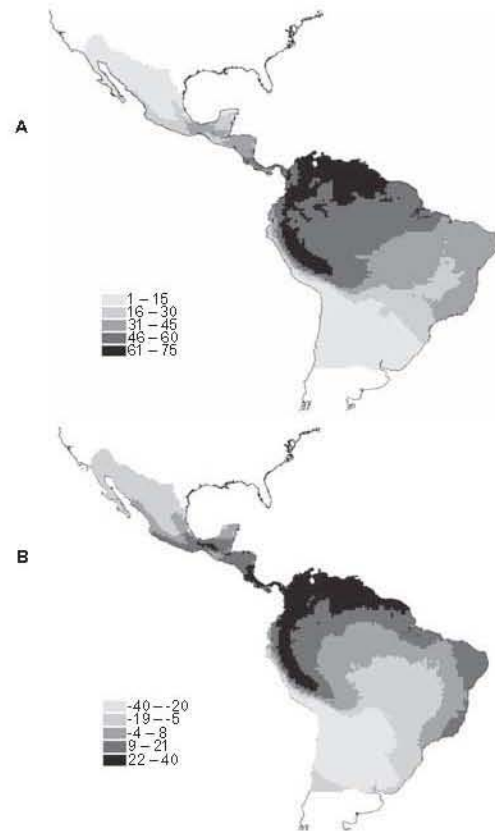


Figure 1 Geographic pattern of species richness of New World leaf-nosed bats (Phyllostomidae). (a) Empirical pattern. (b) Residual values calculated by subtracting, quadrat by quadrat, the average richness of 100 runs of the spreading-dye model from the observed species richness values.

tion in within-species richness values (Fig. 4a-c). The Mexican long-nosed bat (*Leptonycteris nivalis*), for example, occurs over areas of south-western United States and northern Mexico that represent about 6% of the range of the whole family ($n_i = 0.99 \times 10^6$ km², $n_i^* = 0.058$), sharing quadrats with few other phyllostomids ($\bar{x}_i = 7.98$ species), but also occurs also in tropical and subtropical sites of central Mexico, where diversity is intermediate (up to 28 species). Consequently, the FD of its diversity field showed a positive skew ($g_1 = +1.21$) determined by a conspicuous peak of sites with very low species richness and a shallow right-hand tail that ends below 30 species (Fig. 4a). Bokermann's nectar bat (*Lonchophylla bokermanni*) is endemic to a small area of south-eastern Brazil with intermediate species richness ($n_i = 152,000$ km², $n_i^* = 0.009$, $\bar{x}_i = 34.23$ species; $g_1 = 0.08$; Fig. 4b). Species that are endemic to areas of the Andes, such as the tailless bat (*Anoura luismanueli*) occur only in a few

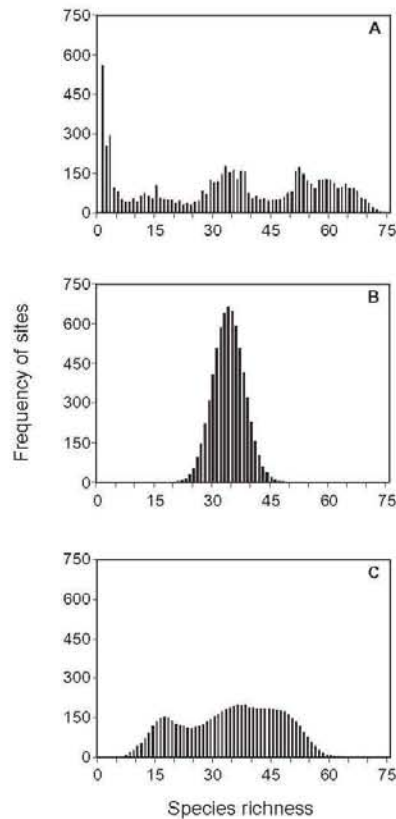


Figure 2 Species-richness frequency distributions of 143 phyllostomid bat species in 6794 quadrats. (a) Empirical data. (b) Result of simulations using scattered (non-cohesive) ranges, as described in the main text. (c) Result of simulations using cohesive ranges, applying the spreading-dye algorithm. To allow comparisons with (a), histograms in (b) and (c) show the cumulative frequency of 100 simulations, adjusting the ordinates scale to correspond to a single assemblage.

sites that are consistently very rich in species ($n_i = 40,000 \text{ km}^2$, $n_i^* = 0.002$, $\bar{s}_i = 70.81$ species, $g_i = -0.39$; Fig. 4c).

The diversity fields of large ranges tended to resemble the pattern for the whole assemblage. In the limit, a species occurring in all quadrats would have, by definition, a diversity field identical to the richness FD of the whole family. Palla's long-tongued bat (*Glossophaga soricina*), for instance, has a wide distribution ($n_i = 13.9 \times 10^6 \text{ km}^2$, $n_i^* = 0.818$) encompassing moderate- to high-richness areas ($\bar{s}_i = 40.85$ species). The FD of its diversity field showed a multimodal pattern that is negatively skewed ($g_i = -0.291$), indicating that most sites within the range have richness values above the average (Fig. 4d). There were several species with ranges encompassing between 30% and 60% of the extent of the whole family that tended to concentrate

on the most species-rich areas. The false vampire (*Vampyrum spectrum*) belongs to this group, distributing over a wide area ($n_i = 5.1 \times 10^6 \text{ km}^2$, $n_i^* = 0.300$) of high richness ($\bar{s}_i = 53.57$ species; $g_i = -0.093$; Fig. 4e).

There was a strong positive correlation between the diversity field volume and the size of the range of a species ($r = 0.986$, Fig. 5). In a plot of volume versus range size, points aggregated close to the line of maximum volumes that is constructed by plotting the cumulative species richness of the sites ordered from the richest to the least rich (Fig. 5). For a given number of sites, the line shows the highest possible number of cumulative overlaps, that is, the maximum value that the diversity field volume can attain.

Null models

By design, our null models retained the empirical range size FD. As a consequence, the average richness of sites was exactly equal to the empirical value in all simulations ($\bar{s} = 33.96$ species, $\bar{s}^* = 0.237$). The richness FD generated by scattered ranges followed a normal distribution (Fig. 2b) with $SD = 4.18$ species (mean for the 100 simulations). The interval of actual values was $15 \leq s_i \leq 53$ species. The geographic distribution of species richness was homogeneous, with sites presenting random noise variation from the mean richness independently of their geographic location.

With cohesive ranges, the richness FD was bimodal, with peaks near the mean and at approximately 18 species (Fig. 2c). Variation in richness was higher than in the first model, but still much lower than with the empirical data ($SD = 12.52$ species, average of the 100 simulations). Ninety-five per cent of observed richness values were within the interval $10 \leq s_i \leq 60$ species. Drawn on a map, results of the spreading-dye simulations showed the typical mid-domain effect pattern whereby species richness peaks near the centre of the continent (Colwell & Lees, 2000; Jetz & Rahbek, 2001; Colwell *et al.*, 2009). A map of residual species richness (empirical minus simulated number of species) still shows the signature of the mid-domain effect as a series of concentric semicircles, but also highlights areas where biological processes determine deviations from expected richness (Fig. 1b).

Simulations using scattered ranges generated range–diversity plots with points arranged along the vertical dashed line and, consequently, with a very narrow FD of mean range richness (Fig. 3b). The mean value of V for our 100 simulations was $V = 0.946$ (interval, $0.85 \leq V \leq 1.12$). Simulations using cohesive ranges generated range–diversity plots with a pattern similar to that of the empirical data, in which most species tended to arrange to the right of the central dashed line, but the deviations from the mean were not as pronounced as with the empirical data ($0.08 \leq \bar{s}_i^* \leq 0.4$, Fig. 3c). The histogram of range richness values showed a distinctive peak located to the right of \bar{s}^* (Fig. 3c top). The value of V in this case was significantly higher than that of the scattered-range simulations, but significantly lower than that of the empirical data (100 simulations, mean $V = 8.60$, interval $5.07 \leq V \leq 12.54$).

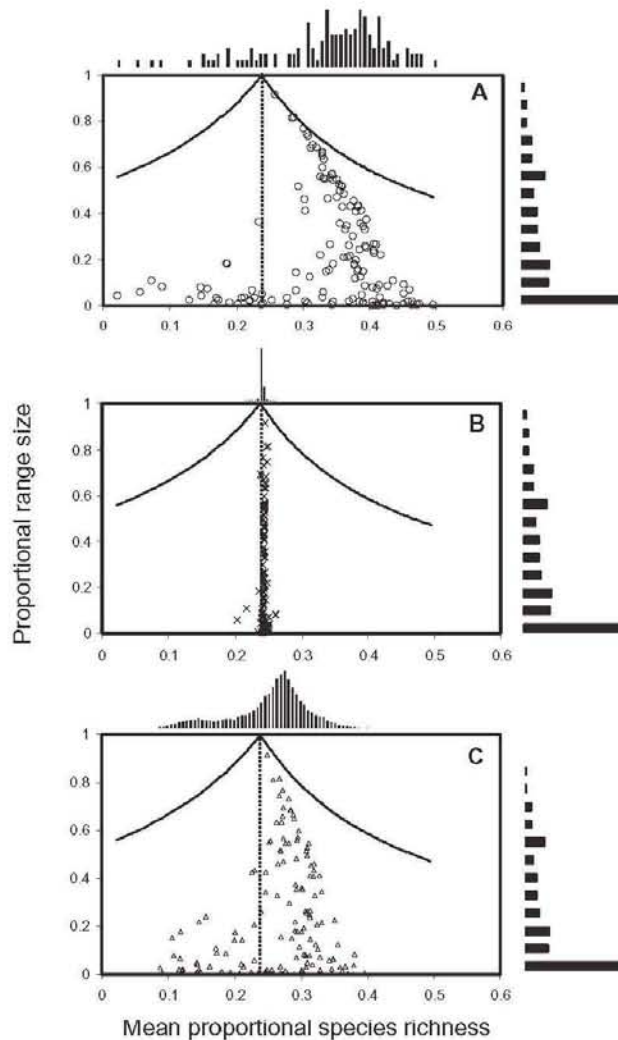


Figure 3 Range-diversity plots for 143 bat species of the family Phyllostomidae. (a) Empirical values. Range size and mean species richness within the ranges are proportional to the total number of quadrats (6794) and species (143), respectively. The vertical dashed line marks the average proportional species richness for all quadrats, and the curved lines are the absolute upper limits determined by mathematical constraints. The histogram in the right panel shows the range-size frequency distribution of the 143 species, and the histogram in the top panel depicts the frequency distribution of mean values of richness within the 143 ranges. (b) Results of the simulation using scattered (non-cohesive) ranges. (c) Results of the simulation with cohesive ranges, using the spreading-dye algorithm. In (b) and (c) points show the results of one simulation in each case; histograms on top of the plots depict the frequency distribution of mean species within the 143 ranges, summarizing the cumulative frequency of 100 simulations in each case. In both simulations the empirical range-size frequency distribution (right panel) was retained.

In the simulation using scattered ranges, the linear fit between diversity field volume and range size was perfect when the intercept was forced to be equal to zero ($r^2 = 1.0$, slope $m = 34.38$, average for the 100 repetitions; Fig. 5). Points for the simulation using the spreading-dye algorithm also showed a very strong positive correlation, but were more scattered than in the first model ($r^2 = 0.984$, $m = 38.82$, average for 100 runs).

DISCUSSION

Patterns for the whole family

Traditionally, continental patterns of species richness have been examined with maps (Simpson, 1964; Terribile *et al.*,

2009), through correlations with environmental variables (Hawkins *et al.*, 2003; Field *et al.*, 2009), or by exploring the properties of the species-area relationship (Rosenzweig, 1995; Nekola & Brown, 2007). Species-richness FDs, on the other hand, have been largely ignored, despite their potential importance in understanding the relationship between species richness and distribution (Arita *et al.*, 2008; Šizling *et al.*, 2009). The richness FD is an aggregate pattern that results from tallying the number of overlapping ranges in several sites. Thus, richness patterns can be interpreted as a measure of association (co-occurrence) among individual species and are ultimately determined by the size, shape and location of the geographic ranges of species (Arita & Rodríguez, 2002; Gotelli *et al.*, 2009).

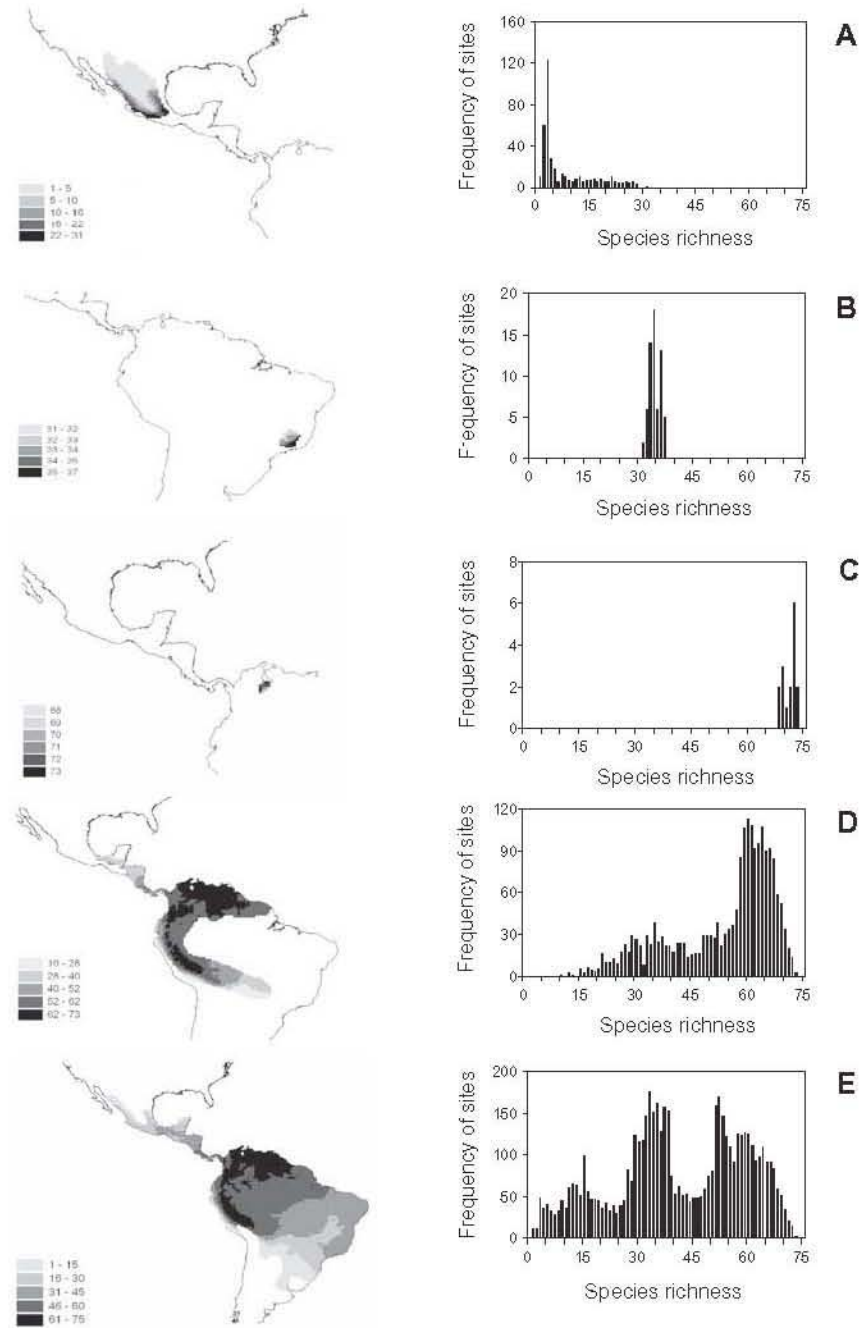


Figure 4 Diversity fields of five species of phyllostomid bats: (a) *Leptonycteris nivalis*, (b) *Lonchophylla bokermanni*, (c) *Anoura luismanueli*, (d) *Vampyrum spectrum*, (e) *Glossophaga soricina*. Maps show the species-richness values of sites within the range of each species, and histograms show the frequency distribution of such richness values.

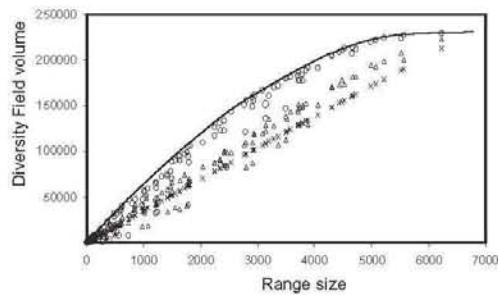


Figure 5 Volume of the diversity field of phyllostomid bats as a function of range size: circles, empirical data; crosses, result of one run of the simulation with scattered (non-cohesive) ranges; triangles, result of one run of the simulation with cohesive ranges, using the spreading-dye algorithm. The line representing the maximum values of the diversity field is built by plotting the cumulative species-richness values of sites ordered from the richest to the least rich.

Results of our first null model (Fig. 2b) show the expected richness FD if the ranges of species were sets of sites randomly scattered all over the continent. Thus, this model excluded all kinds of geographic, geometric and biological determinants of richness, except for the empirical range size FD. Under these circumstances, the map of species richness is homogeneous, with variation limited to random statistical error around the mean and the FD is simply a normal curve with mean equal to the empirical \bar{s} (33.96 species, Fig. 2b). Because in this first model the distribution of each species was independent of the rest, the diversity field volume (that is, the total number of co-occurrences within a given range) increased linearly with range size (Fig. 5).

The variance of any richness FD is determined by two components: one defined by the sum of the binary variances generated by individual ranges and one equalling the sum of pairwise covariances between species (Schluter, 1984). Randomly placed scattered ranges are independent of each other, so the covariance is null, as shown by the points arranged vertically in the range-diversity plot (Fig. 3b) and by Schluter's $V = 1.0$. Because the sum of covariances is close to zero, the variance of the richness FD has to be equal to the summation of the variances of individual ranges, which for phyllostomids is

$$\sum \text{var}(n_i) = \sum n_i^*(1 - n_i^*) = 17.7.$$

This is the 'background' variance generated by range size variation that will appear even in the most unrealistic null models, except the trivial cases in which all species occur in all sites or all species occur nowhere.

Simulations using the spreading-dye algorithm added the effects of geometric constraints and range cohesion (Colwell & Lees, 2000; Arita & Rodríguez-Tapia, 2009; Colwell *et al.*, 2009). In dynamic models, cohesive ranges imply a spatial limitation to

the distance to which a species can expand its range from already occupied sites (Rangel *et al.*, 2007; Gotelli *et al.*, 2009). In non-dynamic null models, cohesive ranges capture the spatial constraints determined by the size and shape of the continent, ignoring the effect of physical heterogeneity and biological processes. Drawn on a map, the typical result of spreading-dye models is a series of concentric circles of increasing richness peaking near the centre of the continent (Colwell & Lees, 2000; Jetz & Rahbek, 2001). For phyllostomid bats that general pattern was modified by the Central American land constriction, and resulted in a latitudinal pattern in which North American sites contained the fewest species (Fig. 1b). This land-constraint effect also explains the left-side peak in species richness of the richness FD, which corresponds to North American sites (Fig. 2c).

Our simulations confirmed the fact that range cohesiveness generates a positive association between species (Arita & Rodríguez-Tapia, 2009), and a concomitant increase in variance of the richness FD. The general positive association between species is shown in the range-diversity plot by the concentration of points to the right of the vertical line (Fig. 3c) and is confirmed by the value of Schluter's ratio ($V = 8.60$) being significantly different from 1.0. Due to the generalized positive association among species, the relationship between diversity field volume and range size showed a steeper slope than in the first model (Fig. 5).

The empirical richness FD of phyllostomids (Fig. 2a) shows the effects on the distribution of species of the shape, topographic elements and environmental features of the continent, but also of some idiosyncratic traits of the clade. The first peak, formed by low-richness quadrats, corresponded to sites in the south-western United States, northern Mexico and northern Argentina and Chile, where a small number of species distribute over large areas that encompass the subtropical and temperate limits of the distribution of phyllostomids. In comparison, the peak of quadrats with approximately 34 species corresponds to sites in south-eastern Brazil, where extensive areas support an intermediate number of species. Similarly, the peak of quadrats with approximately 50–60 species corresponds to areas within the Amazon basin that support a very high, but not the highest, number of phyllostomids. Finally, sites supporting the highest phyllostomid richness (> 65 species) are spread over a comparatively small area of the tropical Andes (Fig. 1a), accounting for the gentle negative slope at the right-hand end of the richness FD (Fig. 2a). The empirical richness FD (Fig. 2a) shows a high variance that cannot be explained solely by the effects of variation in range sizes (shown by the first model, Fig. 2b) and of range cohesion and geometric constraints (shown by the second model, Fig. 2c). This high variance can be also seen in the range-diversity plot, in which most points are to the right of the vertical line for which $\bar{s}^* = \bar{s}^*$ (Fig. 3a) and is confirmed by Schluter's variance ratio being significantly higher than in any of the two null models ($V = 26.99$, $P < 0.01$). The relationship between diversity field volume and range size for empirical data was less linear than with the null models, with points tending to aggregate to the line of maximum volume (Fig. 5). This pattern

also demonstrates the high degree of positive association in the distribution of species.

The empirical richness FD differs from the predictions of the two models mostly in the extremes of the distribution, that is, for sites with $s_i < 10$ species or $s_i > 60$ species. These differences are due to the combined effect of physical heterogeneity and the evolutionary history of the clade. Sites of extremely high bat diversity in the Andes contain a combination of widespread and endemic species that determine patterns of diversity similar to those documented for birds (Graves & Rahbek, 2005; Rahbek *et al.*, 2007). A combination of historical factors and diversity of environments is possibly responsible for such repetitive patterns. Sites with extreme low diversity differ in composition between North and South America. Phyllostomids that occur beyond the tropic of Capricorn are bats with very large ranges (e.g. the woolly false vampire *Chrotopterus auritus*, *G. soricina*, and *D. rotundus*). Species that occur beyond the tropic of Cancer, in contrast, are typically North American endemics with comparatively small ranges (the Californian leaf-nosed bat *Macrotus californicus*, *L. nivalis* and the Mexican long-tongued bat *Choeronycteris mexicana*) that tend to be taxa of recent origin (Stevens, 2006). This pattern suggests that different mechanisms have shaped the composition of bat faunas in the extremes of the range of phyllostomids.

Diversity fields of species

The variation in species richness within the range of a given species can be visualized with a range map showing the geographic pattern of overall species richness, or with an FD plot built by tallying the number of overlapping ranges in each quadrat in which the focal species occurs (Fig. 4). Incidence functions, depicting the presence or absence of species from islands of different levels of species richness (Diamond, 1975), are analogous to our diversity field FD plots. However, analyses for continental and insular faunas require different conceptual frameworks and analytical tools. Most analyses of insular faunas do not include the whole range of all species, and it is normally assumed that any species can potentially colonize any island. Observed patterns of co-occurrence were originally interpreted in terms of competitive exclusion (Diamond, 1975; Gotelli & McCabe, 2002), but can also be understood in terms of similarity in habitat preferences (Wiens, 1989). In most analyses of continental assemblages, ranges are assumed to show spatial cohesiveness, so dispersal to different sites has different probabilities depending on the location of those sites. Under this perspective, the presence of a species in a site is probably determined by the combined effects of evolutionary processes (speciation and extinction) and present-day environmental conditions and species interactions (Wiens & Donoghue, 2004; Ricklefs, 2007; Field *et al.*, 2009).

The distribution of species such as *L. nivalis* (Fig. 4a) is analogous to the Diamond (1975) 'super-tramp' category of species occurring only in the most species-poor sites. Diamond interpreted this pattern by likening it to an *r*-strategy, so super-tramps are species that are excluded through competition from

sites of high species richness. For phyllostomids, the pattern is explained by the group of North American endemics already discussed in the previous section, a set of a few species that have recently invaded the extratropical part of northern Mexico and the south-western United States. The diversity field pattern for Andean endemics, such as *A. luismanueli* is analogous to the Diamond (1975) 'high-S strategy', corresponding to species that occur only in the most species-rich islands (Fig. 4c). Diamond considered high-S species as highly competitive forms capable of co-occurring with many other species, that is, as *K*-strategists. For continental assemblages, the pattern is better explained by observing that these species are restricted to small areas of very high richness where the net diversification rate (speciation minus extinction) is high.

A pattern that does not fit any of Diamond (1975) categories is shown by species such as *L. bokermanni*, which are endemic to areas in south-eastern Brazil and whose diversity field includes only sites of moderate richness, generating a pattern that is intermediate between that of super-tramp and high-S species (Fig. 4b). In fact, as expected by theory (Arita *et al.*, 2008), mean species richness for the diversity fields of small-ranged phyllostomids varies widely along the continuum from super-tramp to high-S species (from the lower left to the lower right sectors of the range-diversity plot, Fig. 3a). The diversity field FD for widespread species resembles Diamond (1975) 'tramp' categories. For example, *V. spectrum* (Fig. 4d) corresponds roughly to a B- or C-tramp strategist and *G. soricina* (Fig. 4e) to a D-tramp. All tramp species aggregate in the right side of the range-diversity plot (Fig. 3a), forming a gradient from A-tramps in the lower sector to D-tramps in the upper part of the graph.

The diversity field of a species can be envisioned as a map of possible interactions with other species. Assuming that the number of populations of a species is proportional to its range size (Hughes *et al.*, 1997), the diversity field volume of any given species should be proportional to the total number of populations of all species potentially interacting with it. Parameters of the diversity field allow an analysis of the geographic distribution of these populations, thus contributing to a better understanding of the internal structure of ranges. From this perspective, the diversity field of a species is a geographic template of possible interactions and is closely related to the concept of the geographic mosaic of coevolution (Thompson, 2005). Given that the theory of the geographic mosaic of coevolution provides specific predictions of the possible outcomes of ecological interactions based on large-scale evolutionary processes (Gomulkiewicz *et al.*, 2007; Thompson, 2009), the concept of the diversity field can provide important elements to test such predictions through the analysis of continental patterns of co-occurrence.

From a different perspective, overlaps of species ranges can be interpreted as the result of species having similar large-scale environmental requirements, with no need to invoke any kind of ecological interaction. The existence of many species with similar Grinnellian environmental niches (Soberón, 2007), for example, would inevitably lead to a large number of overlaps in many sites of high species richness. At the other extreme, the

existence of taxa specialized to particular environments would tend to lower the species richness of sites. These factors can explain the peaks of phyllostomid diversity in the Amazon Basin and in south-eastern Brazil, where there are very large extents that support large assemblages of bat species with similar environmental requirements.

A third approach to explaining diversity fields is to envision present-day patterns of continental co-occurrence of species as the result of evolutionary processes over geological time. As discussed by Stevens (2006), latitudinal patterns of phyllostomid species richness are probably the result of historical processes that reflect the origin of the family in the tropics of the New World and its posterior diversification and dispersal to subtropical and temperate regions. In particular, the geographic pattern of species richness of phyllostomid bats is consistent with the niche conservatism hypothesis (Wiens & Donoghue, 2004; Losos, 2008) that has been posed to explain the origin and diversification patterns of some clades (Wiens *et al.*, 2006; Hawkins *et al.*, 2007). As pointed out by Stevens (2006), the average age of phyllostomid species is negatively correlated with latitude. This means that species that occur in the species-poor areas of northern Mexico and south-western United States are relatively young, just as predicted by the niche conservatism hypothesis.

CONCLUSIONS

We have shown that the diversity field is a versatile and powerful concept that allows the interpretation of diversity and distribution data from different ecological and evolutionary perspectives. It can help in identifying patterns for individual species as well as trends for whole assemblages. For phyllostomid bats, the strong latitudinal gradient of species richness that had been documented in previous papers can be better understood by analysing the patterns of overlap of species as part of the internal structure of geographic ranges. In particular, we have shown that present-day patterns of leaf-nosed bat species richness result from the interaction of different factors, including geometric ones (effect of range cohesion, including mid-domain effects); geographic, including the size and shape of the continent, in particular the Central American land constriction; climatic; and even some idiosyncratic traits of species, including their potential ecological interactions.

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SUPPORTING INFORMATION

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

Appendix S1 Parameters of the diversity field of 143 species of phyllostomid bats

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**Linking patterns of diversity and distribution at continental scales:
the role of environment and niche similarity**

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ABSTRACT

Explaining the causes of the geographic variation in species richness remains an elusive task. Traditional methodologies use a “curve-fitting” approach to relate species richness with contemporary climate variables, without actually explaining the causal factors. Recent approaches propose mechanistic models as more appropriate tools in assessing potential causes of macroecological patterns. Here, we develop different models to assess the relative contribution of regional factors, namely environmental heterogeneity and niche similarity, to the determination of co-diversity and co-distribution patterns in the bat family Phyllostomidae. We extract information from presence-absence data on the continental distribution of phyllostomid bats and use range-diversity plots and variance-ratio tests to describe and evaluate such patterns. Our results confirm the pervasive effect of range cohesion on generating positive association among species and similitude among sites. We also support a strong effect of environmental heterogeneity, when modeling cohesive ranges, in determining stronger positive covariances. Finally, we demonstrate the importance of contingency factors, such as niche similarity among species, in shaping patterns of positive co-distribution and co-diversity for these bats. Our study highlights the importance of regional factors and provides a novel analytical framework to test hypothesis on causal mechanisms determining the relationship between diversity and distribution.

The role of ecological and evolutionary processes in determining geographic patterns of biological diversity is widely acknowledged, but the relative importance of each of these factors is rarely tested. One way to evaluate the effect of those factors is by quantifying the residual variation of linear models relating species richness to variables measuring contemporary climate (Hawkins et al. 2003). However, this widely used “curve-fitting” approach neither considers evolutionary processes that in fact change the number of species (speciation and extinction) nor identifies alternative underlying mechanistic causes of the patterns under study (Willig et al. 2003, Ricklefs 2004). Recently, an alternative mechanistic modeling approach has been proposed to assess the potential causes of observed macroecological patterns (Gotelli et al. 2009). This is based on the assumption that most large-scale patterns of diversity result from the overlap of the ranges of individual species, which is in turn determined by the size, shape and location of those ranges (Arita and Rodriguez 2002, Gaston 2003, Colwell et al. 2009). Consequently, geographic patterns of diversity can be modeled by simulating the dynamics of ranges under different combinations of the underlying variables (Gotelli et al. 2009).

Early studies using that approach examined the effect of geometric constraints with simulations in which ranges were placed randomly within a homogeneous, regular shaped domain (Colwell and Lees 2000, Davies et al. 2005) or in one still showing no environmental heterogeneity but resembling an actual continent in shape (Bokma et al. 2001, Jetz and Rahbek 2001). Other models incorporated topographic and climatic gradients or specific environmental variables to predict the shape and location of ranges with pre-defined sizes (Storch et al. 2006, Rahbek et al. 2007), while others have modeled the dynamics of ranges by

simulating the evolutionary processes of speciation, extinction, and range shifts in individual-based or biogeographic models (Rangel and Diniz-Filho 2005, Rangel et al. 2007).

In most of these studies, species richness has been the sole response variable and the predictive power of different models have been assessed with various goodness-of-fit statistics that compare observed versus expected richness values (Gotelli et al. 2009). In some cases, however, these comparisons are not reliable because similar results can be obtained under completely different combinations of predictive variables; hence, other macroecological parameters are needed to evaluate the performance of different models. For instance, patterns such as the range-size frequency distribution of species (Rangel et al. 2007), the mean range-size of species assemblages (Hawkins and Diniz-Filho 2006), the “dispersion field” of species assemblages (Graves and Rahbek 2005), the degree of nestedness (Ulrich et al. 2009), or the variation in beta diversity (Tuomisto 2010) can be used to compare the predictions of different models.

Most of these response variables are based either on patterns of species richness of sites or on patterns of range size of species. As an alternative, Arita *et al.* (2008) have advocated a more comprehensive approach through the use of range-diversity plots, which are graphical tools that allow the simultaneous depiction of data on diversity and distribution. The output of each run of any model can be conveniently summarized in a presence-absence matrix in which columns represent sites, rows represent species, and the elements are binary entries showing the presence (1) or absence (0) of a given species in a given site (Arita et al. 2008, Gotelli et al. 2009). Range size values are easily calculated in presence-absence matrices as row sums, and, equivalently, species richness values can be

calculated as column sums. The use of a “common currency” (the number of occurrences) for species richness and range size allows the development of response variables that incorporate both diversity and distribution. Moreover, it can be shown that the relationship between diversity and distribution is dependent on the degree of statistical covariation among species or among sites. These mathematical relationships enable researchers to link patterns of diversity and distribution when testing biogeographic hypotheses (Arita et al. 2008, Borregaard and Rahbek 2010).

Using this approach, we have explored the properties of the diversity fields of New World leaf-nosed bats of the family Phyllostomidae (Villalobos and Arita 2010). A diversity field is defined as the set of species richness values of the sites that comprise the range of a given species. Using range-diversity plots, we examined the relationship between range size (a distribution variable) and the mean of the diversity field (a diversity parameter) with individual species as analytical units. We demonstrated the role of the empirical range size frequency distribution (RSFD) and of geometric constraints in shaping the species richness frequency distribution (SRFD) at different scales, from the whole continent to the extent of individual ranges. Variation not explained by the models suggested the possible effect of additional factors that we speculated could be related to spatial heterogeneity, to a lack of independence in the distribution of species due to similar environmental requirements, or to a combination of both factors. Herein we examine the effect of environmental heterogeneity and niche similarity on the linked patterns of diversity and distribution. We use range diversity plots, both by species and by sites to analyze the mathematical and biological relationships between range size and species richness and incorporate the use of two types of

variance-ratio tests to assess the degree to which statistical association among species (co-distribution) and among sites (co-diversity) influence overall patterns of diversity and distribution.

Methods

Database and analytical procedures

We constructed a database of the continental distribution of phyllostomid bats and built range maps for each of the species using ArcGIS software. Phyllostomidae is a diverse family of 160 species with distribution in the tropical and subtropical areas of the New World that has radiated to include a wide range of morphological, functional, and ecological forms (Simmons 2005). Being a monophyletic group restricted to a single continental mass, New World leaf-nosed bats also show a considerable variation in range size, so they constitute an ideal clade for continental analyses of diversity (Stevens et al. 2006, Villalobos and Arita 2010). Because we excluded insular species, our sample consisted of 143 species with continental distribution. Distributional maps were overlaid by a grid of equal-area quadrats (2500 km², equivalent to approximately 0.5° x 0.5° latitude and longitude near the equator) that defined the sites for a $S = 143$ species by $N = 6794$ sites presence-absence matrix.

To characterize the environmental space occupied by Phyllostomidae, we used the 19 bioclimatic variables from the WorldClim database at a resolution of ten min of arc (Hijmans et al. 2005) and upscaled their values to the resolution of our grid cells (2500 km²) by averaging all pixels within each of the 6794 quadrats. To deal with the multicollinearity of environmental variables, we conducted a principal component analysis using a correlation matrix and retained the first four

components, which altogether accounted for 89% of the total variance of the original variables.

We extracted information on distribution and diversity from the presence-absence matrix by calculating four basic parameters: (1) the range size of species, represented by the vector of 143 row sums, (2) the species richness of sites, corresponding to the vector of 6794 column sums, (3) the average specific richness, which is a vector of 143 values of a variable defined as the mean of the species richness values of the sites that form the range of a given species, (4) the average per-site range size, which is a vector of 6794 values of a variable corresponding to the average size of the ranges of the species that occur in a given site. For analytical convenience, variables (1) and (4) were divided by N and variables (2) and (3) were divided by S to yield proportional values that allow comparisons between methods by retaining the “common currency” principle.

We drew two kinds of range-diversity plots, one by species, which is a range size versus specific richness graph (vector 1 vs vector 3), and one by sites, resulting from plotting species richness against per-site range size (vector 2 vs vector 4). In all four cases, proportional values were used. The plot by species depicts simultaneously a diversity variable (the mean richness of sites within the range of species) and a distribution parameter (the range size of species). Equivalently, the plot by sites shows a distribution variable (the mean range size of species occurring in a site) and a diversity parameter (the species richness of sites). Moreover, it can be shown that the relative position of points in range-diversity plots is determined by the degree of statistical association among species (a pattern of co-distribution) or among sites (a pattern of co-diversity). Theoretical aspects of range-diversity plots have been examined elsewhere (Arita et al. 2008,

Christen and Soberon 2009), and a step by step guide to build and interpret them can be found in Arita et al. (submitted).

Range size frequency distributions (RSFD) and species richness frequency distributions (SRFD) were examined visually with the corresponding histograms derived from empirical or modeled data, and the association among species and among sites were assessed with variance-ratio tests (Schluter 1984). In any presence-absence matrix the variance in species richness among sites equals the sum of the binary variances of the range of each species plus twice the sum of covariances among species (Schluter 1984, Bell 2005). Therefore, if the sum of covariances equals zero (meaning that there is no overall association among species), the two variance terms (one of species richness among sites and the other the sum of binary variances generated by the range of each species) must be equal and the ratio $V_{sp} = (\text{variance in species richness}) / (\text{sum of binary range variance})$ must be equal to one. V_{sp} is, then, a convenient measure of covariation (association or co-distribution) of species (Schluter 1984). With exactly the same reasoning, the ratio $V_{si} = (\text{variance in range size}) / (\text{sum of binary richness variances})$ can be used as a measure of covariation (similitude or co-diversity) among sites (Arita et al. submitted).

Models

To evaluate the relative contribution of different factors in shaping continental patterns of diversity, we ran three models that simulated contrasting ways in which the ranges of species can be built. In all three models we retained some basic traits from the empirical data: the area and shape of the combined distributional

range of the family Phyllostomidae (that is, the number of sites), the total species richness, and the range size frequency distribution. Model I (“Scattered ranges with environmental control”) generated scattered (non-cohesive) ranges with this sequence: (1) select a random seed cell, (2) select a new cell randomly, assigning each cell a probability defined by the climatic similarity of that site with the seed cell, (3) repeat the procedure, choosing a site from the set of non-occupied sites, until completing the number of sites forming the range of the simulated species. Environmental similitude between sites was measured with the Mahalanobis distance between them in the four-dimensional space defined by the principal components computed from the environmental variables.

Model II (“Cohesive ranges with environmental control”) was based on the spreading-dye algorithm (Jetz and Rahbek 2001) but modified to account for environmental conditions as follows: (1) select a random seed site, (2) select, among the eight adjacent cells the one with the highest environmental similitude with the seed cell and add it to the range, (3) repeat until the number of cells equals the corresponding range size. In this model, a cell within a short distance from the seed in environmental space had a high probability to be chosen as the next cell of the growing range. Therefore, this model generated locally random, cohesive ranges that tracked the environmental conditions most similar to the ones where the “virtual species” originated. This model is analogous to the Rahbek et al. (2007) “range cohesion” model, but instead of using a single probability map for all the simulated ranges, it requires a different set of probabilities for each unoccupied cell every time a new seed is generated.

In Model III (“Cohesive ranges with niche similarity”) the growth of ranges followed the same rules as in Model II, but the seed cell of each new range was

selected at random from within any of the previously simulated ranges. This rule incorporated an element of biological dependence to the model because new ranges were forced to resemble, to an extent, both the geographic location and environmental preferences of previously simulated species, making them contingent to the existing conditions, but the stochastic nature of the simulations was retained. In models that incorporate phylogenetic information, “niche preferences” or “niche conservatism” has been included to account for the aggregated pattern in the distribution of species (Wiens and Donoghue 2004, Davies et al. 2005, Rangel et al. 2007). Our models did not include speciation or extinction, so the third model did not simulate a process of niche heritability; it did, however, incorporate the more general concept of niche similarity among existing species. Statistical analyses and simulations were written and conducted using the R programming environment (R Development Core Team, 2009).

Results

Empirical patterns

The empirical range size frequency distribution (RSFD) for Phyllostomidae shows the typical hollow-curve pattern described for other continental assemblages of species (Gaston 2003, Nekola and Brown 2007). The histogram is shown in the right-hand panel of Fig. 1A. The combined range of the 143 species encompassed approximately 17 million km², and individual ranges varied from one to 6223 quadrats (2500 to 15.6 x 10⁶ km²) with a mean of 4.024 x 10⁶ km² (Villalobos and Arita 2010). The species richness frequency distribution (SRFD) is multimodal with a high variance and a significant negative skew (mean species richness $\bar{s} = 33.96$, interval $1 \leq s_i \leq 73$, SD = 21.86, $g_1 = -0.133$), indicating that the majority of sites

have richness values higher than the average value for the complete region (Fig. 1C and see Villalobos and Arita 2010).

Range diversity plots are shown in Fig. 1A (by species) and 1B (by sites). The majority of points corresponding to species are located in the right sector of the plot, demonstrating a general tendency to positive average covariance, that is, a tendency of species to co-occur more frequently than expected by chance. This trend is corroborated by a very high variance-ratio value ($V_{sp} = 26.99$) that indicates a strongly positive overall covariance among species. Points corresponding to sites in Fig. 1B also tend to fall on the right sector of the range-diversity plot, indicating an overall positive covariance demonstrated by the variance ratio ($V_{si} = 2470.4$).

Simulations

Range diversity plots by species show contrasting patterns for Model I and Models II and III (Fig. 2 A, C, and E). Notice that the histograms in the right-hand panels are identical in the three cases and identical to the one in Fig. 1A, since the original RSFD was retained in the simulations. Model I, which generated random scattered ranges, produced a pattern in which the average covariance of each species was close to 0.0, so the corresponding points arranged along the vertical line marking the overall average richness; consequently, the histogram of range-richness values showed a single peak (Fig. 2A, top panel). By contrast, Models II and III, which modeled cohesive ranges, generated RD plots in which points were more scattered along the abscissas, producing wider histograms of range-richness values (Fig. 2C and E). Species points in Models II and III tended to lie on the right sector of the

graph, showing a propensity of species to have positive average covariances, that is, to co-occur with other species more frequently than in the scattered ranges model. This overall positive covariance was corroborated by the variance ratio test (Model II: $V_{sp} = 16.35$, average of 100 runs; interval $12.98 < V_{sp} < 20.54$. Model III: $V_{sp} = 17.72$, average of 100 runs; interval $13.57 < V_{sp} < 23.44$). V_{sp} values for models II and III were higher than the one for a simple spreading-dye model with no spatial heterogeneity ($V_{sp} = 8.60$; data from Villalobos and Arita 2010) and closer to, but significantly different from the empirical figure, which was higher than both Models II and III ($V_{sp} = 26.99$, Figure 3A).

Range diversity plots by sites show differences between the results of Model I and Models II and III, but also demonstrate some common patterns resulting from the simulations (Figs. 2B, D, and F). In the three models, the vast majority of points locate to the right of the vertical line, indicating an overall positive covariance (similitude in species composition) of sites. Model I, however, generated a denser cloud of points with less dispersion along both axes, a pattern also seen in the top and side histograms in Fig. 2B. The use of cohesive ranges (Models II and III) generated patterns more similar to the empirical case (Fig. 1B), but showing less dispersion along the abscissas (less variation in average per-site range size) than with real world data. The overall positive covariance was corroborated by the variance ratios (Model II: $V_{si} = 2281.94$, average for 100 runs, interval $2243.95 < V_{si} < 2331.76$. Model III: $V_{si} = 2289.28$, average for 100 runs, interval $2239.23 < V_{si} < 2348.12$). V_{si} values for both models were higher than the

one corresponding to a simple spreading-dye model with no spatial heterogeneity ($V_{si} = 2247.22$) but lower than the empirical value ($V_{si} = 2470.40$, Fig. 3B).

The species richness frequency distribution (SRFD) generated by the overlap of scattered ranges in Model I was unimodal with a mean equal to the empirical one (33.96 species), similar to the distribution that is theoretically predicted for these cases (Fig. 4A; see Arita et al. submitted). Models II and III generated SRFDs that were slightly bimodal and showed higher dispersion than with Model I (Figs. 4B and C). In fact, both distributions showed intervals of richness values larger than the empirical distribution (from 1 to 76 species for Model II and from 1 to 79 species for Model III); although standard deviations were lower than the empirical one (SD = 16.97 for Model II, SD = 17.67 for Model III).

Discussion

Although continental patterns of species richness are commonly measured by the number of ranges overlapping in a given region, the close link between diversity and distribution is seldom analyzed explicitly. Given the mathematical relationships that arise from the structure of presence-absence matrices, a series of constraints are expected on the range of species richness and range size values that are possible in real world systems and in null and predictive models (Arita et al. 2008, Borregaard and Rahbek 2010). When examining patterns of co-distribution of species, ecologists realized that expected patterns resulting from some null models showed intrinsic positive associations among species, so an assessment of the so-called assembly rules (Diamond 1975) implied a consideration of this tendency (Gotelli and McCabe 2002). More recently, neutral

models of species distribution have demonstrated that the “null” expectation in such models is not a lack of association among species, but a pattern of positive co-distribution that needs to be incorporated in any mechanistic explanation of diversity patterns (Ulrich 2004, Bell 2005).

Our results corroborate those observations in the case of Models II and III, that is, when using cohesive ranges. Species in our Model I (with non-cohesive ranges) showed a near zero average covariance despite the incorporation of environmental conditions (Fig. 2A). The modeling of cohesive ranges, by contrast, produced systems in which species, especially those with large ranges, tended to show positive average covariance with other species, that is, they tended to co-occur more frequently than in the scattered ranges case (Fig. 2C and E). The positive covariance was higher in Model III than in Model II, showing an effect of niche similarity on the patterns of co-distribution of species. Our results also show a related pattern that had not been examined in studies before the development of range diversity plots: the positive association among sites that arises even in the simplest model with scattered ranges but that is more pronounced in the models with cohesive ranges (Fig. 2B, D, and F). Range diversity plots and the variance ratio test by sites demonstrate that the null expectation in distribution models is a pattern in which sites show a strong positive covariance, that is, a pattern of positive co-diversity of sites that mirrors the positive co-distribution shown in previous studies. Again, this positive association among sites was stronger in Model III (cohesive ranges with niche similarity) than in Model II (cohesive ranges) and Model I (scattered ranges) and very similar to the empirical pattern.

Our results show the strong effect that range cohesion has on continental patterns of diversity and distribution (Jetz and Rahbek 2002, Rahbek et al. 2007,

Arita and Rodríguez-Tapia 2009). In particular, an overall covariance among species close to zero can be obtained only when modeling scattered ranges, an approach that is appropriate for discrete ecological communities or island assemblages, but that has serious limitations in continental analyses. In any case, even when ranges are simulated as randomly located scattered units there is a general positive covariance among sites (co-diversity), a tendency that is stronger and more similar to empirical patterns when using cohesive ranges.

We also demonstrated the effect of introducing environmental data into the models, simulating non homogeneous continental landscapes, as has been done when examining patterns of species richness (Storch et al. 2006, Rahbek et al. 2007). Our results show that the improved fit that models considering spatial heterogeneity provide is reflected also in our response variables by species and by sites. This effect is noticeable only in the simulations using cohesive ranges, as results for scattered ranges in a heterogeneous environment (Model I) are indistinguishable from those of similar models in an idealized homogeneous continent (Villalobos and Arita 2010). By contrast, results of the simulations that incorporated cohesive ranges into a heterogeneous continent (Model II) differed from similar models on a homogeneous domain (see results in Villalobos and Arita 2010), showing stronger overall covariances and wider spreads of species richness values across the continent. The strength of this effect depends on the particular spatial distribution of environmental factors in the real world continent, but the way in which the randomly located ranges are accommodated to generate overlaps and the concomitant pattern of species richness also shapes the resultant pattern.

A closer approximation to real world patterns can be achieved by models that incorporate niche similarities. This effect arises because species showing

similar environmental preferences will co-occur more frequently, increasing the average covariance among species and among sites, leading in turn to a wider gamut of species richness values, similar to that found in real continents.

Similarities in environmental preferences are generally explained with mechanisms such as niche conservatism (Wiens and Donoghue 2004) that, when incorporated into predictive models of species richness that include evolutionary processes (Rangel et al. 2007), can account for real world patterns of species co-distribution. Species are not fully independent from their evolutionary past, and one consequence is that phylogenetically related species tend to have similar niches, a fact of paramount importance in evolutionary models of diversity and distribution (Buckley et al. 2010, Davies et al. 2005, Wiens and Graham 2005).

We approached niche similarity with a different strategy. Since the number of species was fixed, we could not incorporate the evolutionary processes of speciation and extinction. Instead, we simulated similarities of niche characteristics by limiting the origin of new ranges to previously occupied sites. This procedure does not generate a true phylogenetic relationship between species, but it does incorporate biological contingency through a stochastic procedure determined by existing conditions. In fact, the algorithm of Model III implicitly incorporates a density-dependent factor because when choosing the seed for a new range, richer sites have higher probabilities of being selected. This factor allows the generation of sites with very high diversity, especially in the center of the continent (e.g., the Amazon basin) as dictated by geometric constraints.

As results of our Model III show, niche similarities can have a noticeable effect on patterns of distribution and diversity, particularly in terms of the co-distribution of species and the co-diversity of sites. Our results also point to the

fact that these effects are not necessarily the result of evolutionary processes involving niche conservatism, a circumstance that needs to be considered when testing hypotheses based on phylogenetic relationships. Increased rates of speciation, for example, have been proposed as an explanation for the very high species richness in the Andes region in South America, because of the topographic complexity that characterizes the area (Graves 1985, Fjeldsa 1995). The same patterns can arise, however, from null or neutral models of range expansion and contraction that include density-dependent speciation and extinction, even on homogeneous continents, with no a priori invocation to niche heritability or geographic variation in speciation rates (Waldron 2007, Arita and Vázquez-Domínguez 2008). Our Model III shows not only the effect of niche similarity on patterns of diversity and distribution, but also demonstrates that a simple contingent rule can generate those patterns.

Conclusions

Our study shows the usefulness of range-diversity plots in interpreting potential mechanisms that determine the relationship between distribution and diversity. We have shown that co-distribution and co-diversity patterns in phyllostomid bats arise from the statistical covariation among species and among sites determined by a combination of factors. In addition to geometric constraints and range contiguity, which together can produce positive average covariance among species and among sites, we demonstrated the effect of environmental heterogeneity, especially through its influence on range contiguity, in producing stronger positive covariances among species and among sites. We found that a simple process of biological contingency represented by niche similarities among species can

produce even stronger positive association among species and similitude among sites, implying that initial conditions strongly influence biodiversity patterns. Our analyses suggest that, at continental scales, factors such as range cohesion, environmental heterogeneity and niche similarities shape the linked patterns of distribution and diversity in phyllostomid bats. Evaluating response patterns, such as those depicted in range-diversity plots, under a mechanistic modeling framework constitutes a promising research avenue for testing hypothesis on large-scale biodiversity patterns.

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Figure legends

Figure 1. Range-diversity plots for Phyllostomid bats, by species (A) and by sites (B). Values of range size and mean species richness within ranges are proportional to the total number of quadrats (6794) and species (143), respectively. The vertical dashed line marks the average proportional range size and species richness, and the curved lines are the absolute upper limits determined by mathematical constraints. (C) The species richness frequency distribution (SRFD) of empirical data.

Figure 2. Range-diversity plots for Phyllostomid bats. Left column: plots by species. Results from one run of (A) Model I (“Scattered ranges with environmental control”), (C) Model II (“Cohesive ranges with environmental control”), and (E) Model III (“Cohesive ranges with niche similarity”). Histograms on top of the plots by species depict the frequency distribution of mean species richness within the 143 ranges, summarizing the cumulative frequency of 100 simulations in each case. The observed frequency distribution of range sizes was retained in all models (right panel of plots by species).

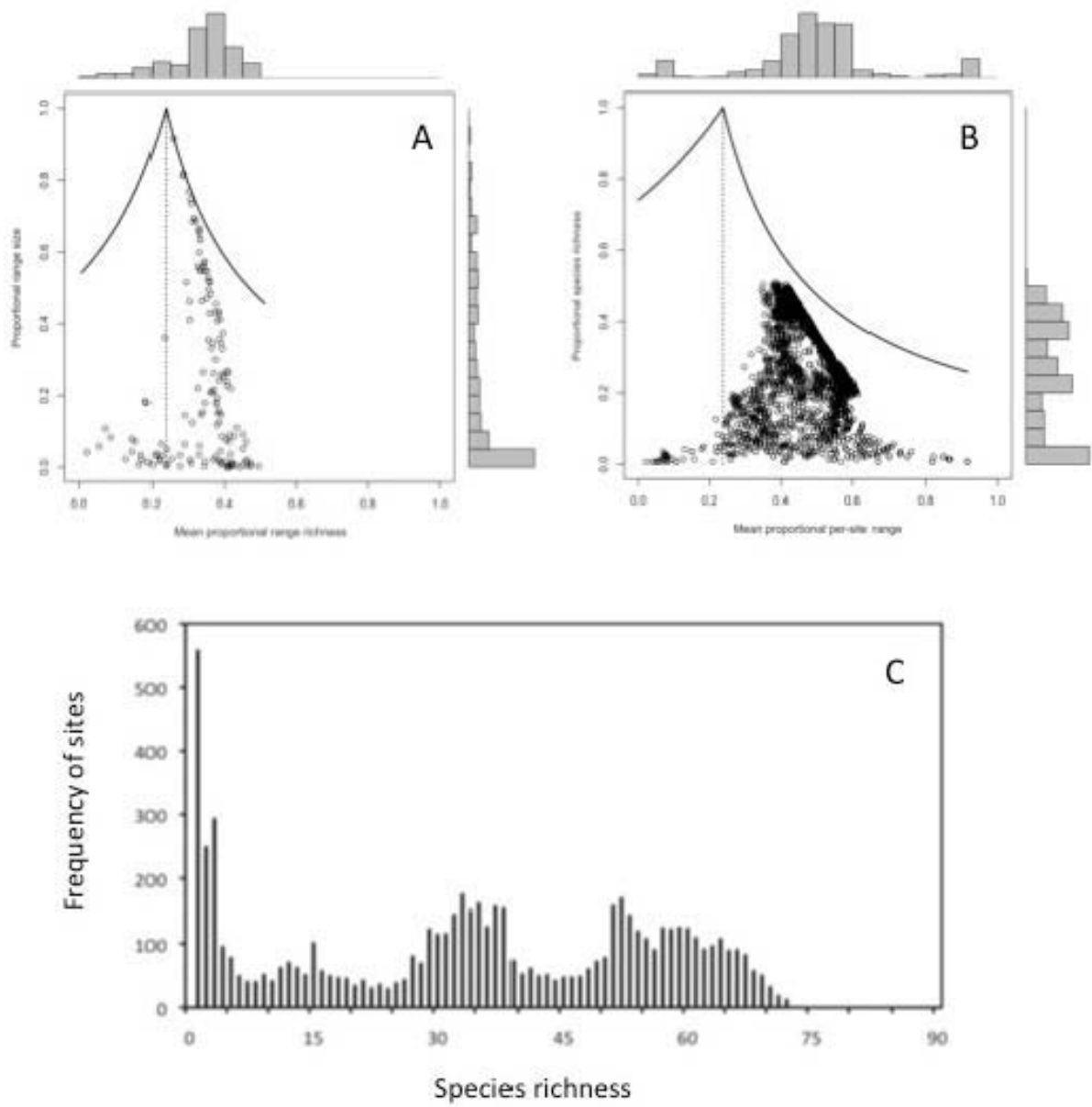
Right column: plots by sites. Results from one run of (B) Model I, (D) Model II, and (F) Model III. Histograms on top of the plots by sites depict the frequency distribution of mean range size within the 6794 sites, results from 100 simulations. Right panel histograms depict the species richness frequency distribution for the 6794 sites.

Figure 3. Histograms showing the cumulative frequency of variance-ratio values. (A) Variance-ratio by species. (B) Variance-ratio by sites. In all cases, *black bars*

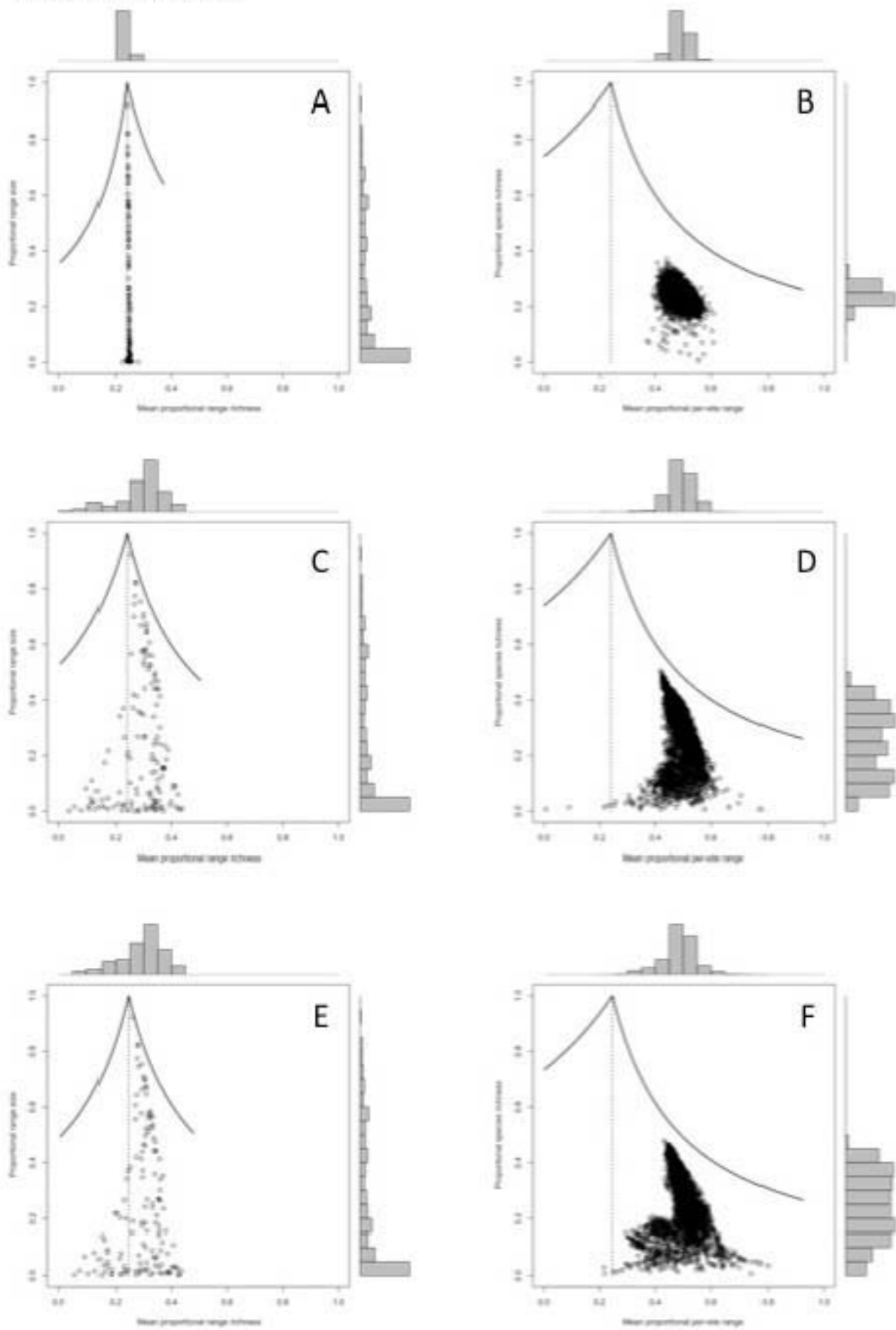
correspond to results from a simple “spreading-dye” model with cohesive ranges, *light grey bars* are for results of Model II (“Cohesive ranges with environmental control”), and *grey bars* represent results of Model III (“Cohesive ranges with niche similarity”). The thick arrows show the actual figures for the observed data.

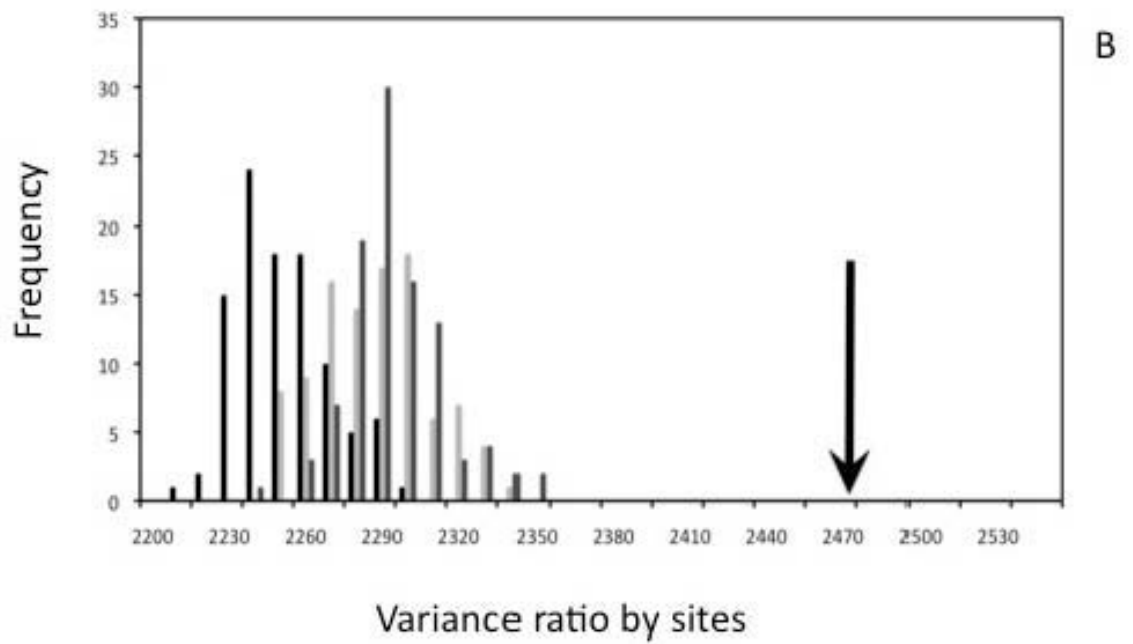
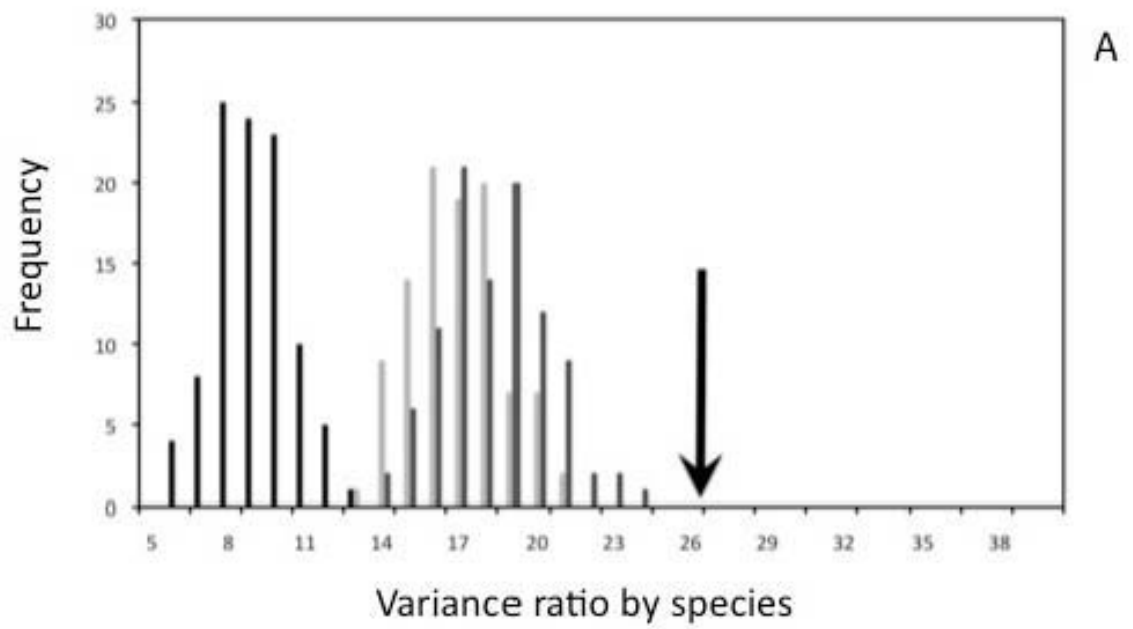
Figure 4. Species richness frequency distributions of 143 phyllostomid bat species in 6794 quadrats. Results from (A) Model I, (B) Model II, and (C) Model III. Histograms show the cumulative frequency of 100 simulations, adjusting the ordinates scale to correspond to a single assemblage and allow comparisons with Figure 1C.

Villalobos et al. Fig. 1

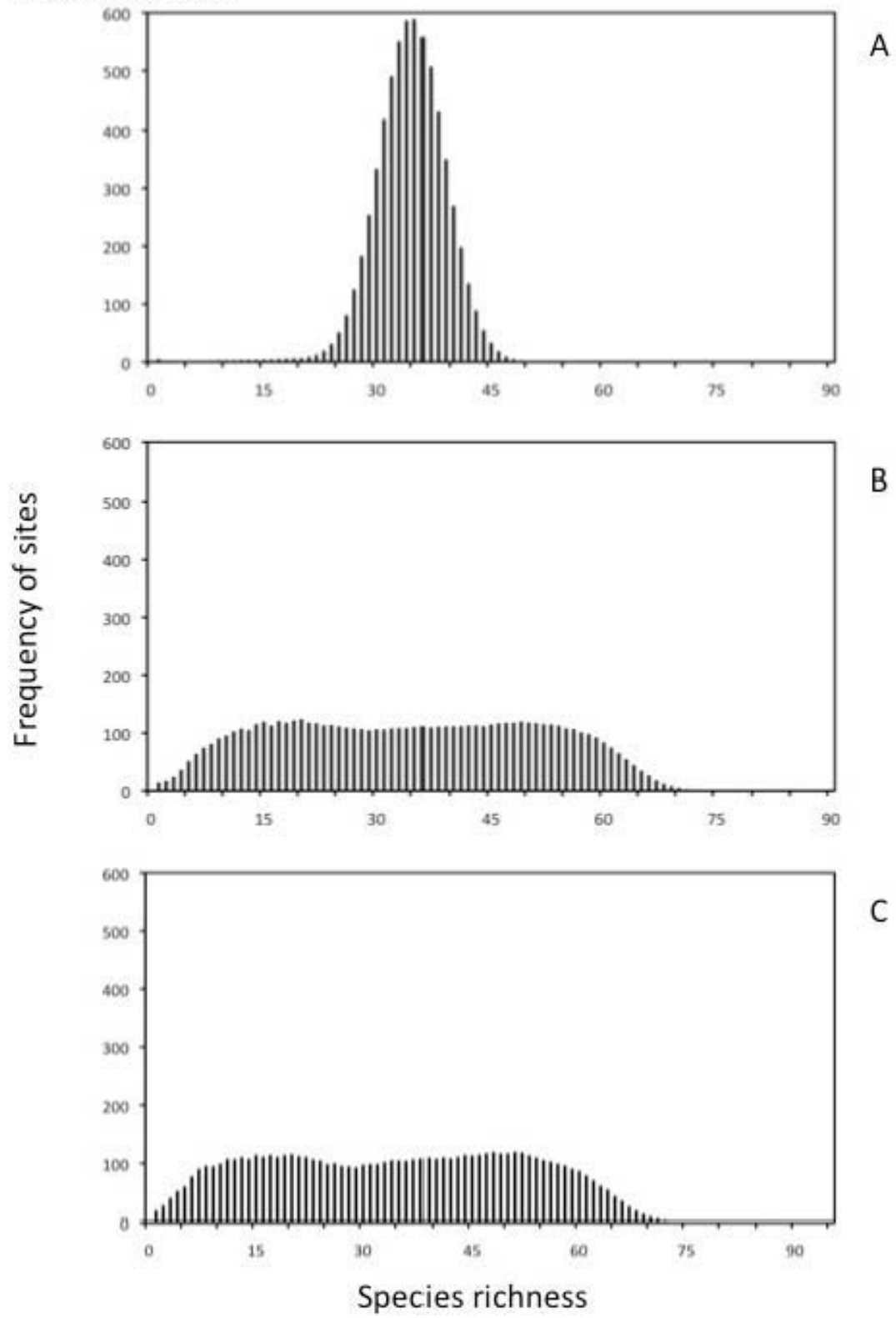


Villalobos et al. Fig. 2





Villalobos et al. Fig. 4



**Range-diversity plots for conservation planning: Using richness and rarity in
priority setting, the case of Mexican avifauna.**

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Manuscrito preparado para someterse a BIOLOGICAL CONSERVATION

Abstract

Current claims of biodiversity crisis call for immediate conservation actions. These require the identification of priority sites for conservation. Patterns of species richness are crucial in such endeavor. Rarity, measured by the size of species' geographical ranges, is often used as a single or complementary criterion. For instance, hotspots for conservation have been defined using either one or the other criterion. We introduce a new tool, range-diversity plots, which simultaneously analyze species richness and range size identifying distinctive types of species assemblages. We applied this tool to the Mexican avifauna and show how it can be readily used to inform conservation practices. Also, we evaluated the representation of different assemblages in the national reserve system. We built a presence-absence matrix from the birds range maps overlaid by an equal-area grid and recorded the number of species and the average range size for assemblages present at each site within Mexico. Mexican birds show congruent patterns between richness and range size, richer sites harbor small-ranged species. These sites are poorly represented in the national reserve system. We show that patterns of congruence between diversity and distribution can be easily identified and interpreted using range-diversity plots based solely on a presence-absence matrix, providing a transparent, robust and explicit application for conservation planning.

Keywords: diversity, distribution, hotspots, range-diversity plots, birds, Mexico, conservation planning

1. Introduction

Current claims of an unprecedented biodiversity crisis, namely species extinctions, call for immediate conservation actions (Ehrlich & Pringle 2008, Pimm et al. 2006). Species richness is the facet of biodiversity that has received most of the attention, because of its relatively easy way to monitor in comparison to other facets of biodiversity. At global and local scales, regions with the highest number of species have attracted the attention as particularly important targets for conservation. These so-called “hotspots” (Myers 1988, 1990, Myers et al. 2000) and their identification have been embraced as the best possible strategy to preserve most species at the least cost (e.g. Conservation International, Jepson & Canney 2001). This is mainly due to competing land interests, since preserving all the places relevant for biodiversity conservation would imply protecting the whole planet. In practice, nevertheless, there is a need to prioritize land for conservation practice (Pressey 1994, Williams et al. 1996). Hotspots can help in this endeavor, by pointing out places with exceptional taxonomic richness. Nonetheless, the identification of such hotspots is not free of difficulties, especially in terms of criteria used to define them.

Hotspots can be defined using different criteria (Orme et al. 2005). Three of the most commonly used criteria are: species richness (Myers et al. 2000), presence of threatened species (Dobson et al. 1997, Troumbis & Panayotis 1998), and number of endemic or narrow-ranged species (Arita et al. 1997, Balmford & Long 1994, Sankaran 1997). The first criterion, number of species, represents an obvious target of any conservation effort. Often, however, not all species are considered in need of conservation depending on the level of threat or relevance in

ecosystem functioning. Threatened species, in turn, would be considered by definition as the most immediate targets for conservation, according to previous evaluations on the level of threat faced by different species (e.g. IUCN's RedList). This approach requires a case-by-case evaluation of threats, implying huge amounts of data and time. A common feature used to defined threatened species in a relatively fast and straightforward manner is to consider the size of their geographical ranges (Gaston 1994). Species with restricted geographical distributions are considered either rare or endemic if restricted to a particular political unit. Such restrictedness can be defined either by using political units or biomes to delimit the domain of interest (Bonn et al. 2002) or, more broadly, as the lower percentiles of a frequency distribution of range sizes (Roberts et al. 2002, Jetz et al. 2004, Orme et al. 2005).

Another source of contention around the hotspots approach is the possible coincidence in location of priority sites defined by different criteria (Orme et al. 2005). Although the issue remains controversial, several lines of evidence suggest that there is little congruence for at least two of the criteria: species richness and rarity/endemism. First, empirical data show that hotspots of richness and endemism do not have the same spatial distribution (Ceballos & Ehrlich 2006, Grenyer et al. 2006, Orme et al. 2005). Second, widespread species seem to exert a disproportional effect on patterns of species richness, as compared with restricted taxa (Jetz & Rahbek 2002, Lennon et al. 2004, Rahbek et al. 2007, but see Arita & Rodríguez-Tapia 2009 for a critic on this effect).

Herein we introduce a methodological framework and a visual analytical tool, called the Range-Diversity plot, to identify particular sites and species that could be relevant for conservation priority setting. Its use of primary information

relating the two most basic attributes of biodiversity at geographic scales: species richness and geographical distribution of species, allows a straightforward description and interpretation of biodiversity patterns (Soberón & Ceballos 2011). Our purpose is to show how the patterns of congruence between species richness and range size, examined from two perspectives (by sites and by species) based on biological and mathematical constraints, can be readily used to inform conservation planning. We used Mexican birds as case study to exemplify the use and interpretation of range-diversity plots (RD plots). We show that patterns of congruence between diversity and distribution can be easily depicted and identified using RD plots based solely on a presence-absence matrix, providing a transparent, robust and explicit application for conservation planning. Finally, we illustrate how well the protected area network established in Mexico represents both restrictedness and richness of breeding birds, demonstrating the importance of considering diversity and distribution simultaneously in conservation priority setting.

2. METHODS

2.1. Study area

Decisions on conservation actions are taken at local and regional scales where actual implementation can take place. Therefore, political units are commonly used as study sites (Bonn et al. 2002, Vazquez et al. 2008, Warman et al. 2004). We focus our study in the avifauna of mainland Mexico, hence considered Mexico as our study unit for reasons of conservation pragmatism (Arita et al. 1997). This

allowed us to make comparisons possible in a national scale and evaluate the validity of our approach against existing conservation actions within the country.

2.2. Distribution data

We used the “Atlas of the Birds of Mexico” database (Navarro-Sigüenza et al. 2003), which is a detailed compendium of geographic information for Mexican birds including > 400,000 specimen records, > 90% of all bird specimens from Mexico, representing the holdings of > 70 natural history museums worldwide. We restricted our analyses to 655 terrestrial and resident species to generate distribution maps representing their breeding ranges at a resolution of 1 km². These ranges were generated using ecological niche modeling techniques and edited on the basis of experts’ knowledge on the distribution of each species (see Lira-Noriega et al. 2007 for details on this process). We overlaid an equal-area hexagonal grid (256 km² per cell) onto the distribution maps and constructed a presence-absence matrix of 7887 sites x 655 species. We repeated the analyses including only those species entirely restricted to Mexico, hereafter endemics. In this case, we considered 98 species generating a presence-absence matrix of 7834 sites x 98 species. Each presence-absence matrix (PAM) represents the distributional information for each subset (total and endemic species) of the Mexican avifauna throughout the whole country.

2.3. Analytical framework

Each type of information, distribution and diversity, is usually treated separately to describe and analyze patterns of either range size (Arita et al. 1997, Gaston 1998, Stevens 1989) or species richness variation (Hillebrand 2004, Willig et al. 2003). Here we simultaneously obtained information from both variables using alternative approaches to the traditional by row (R-mode) and by column (Q mode) counts in PAMs (Connor & Simberloff 1979). Following Arita et al. (2008, in press.) we used the Rq-mode (row by column) and Qr-mode (column by row) to extract more complex—but still very easy to obtain—quantities: the mean richness within species ranges and the per-site mean range size. The Rq-mode takes into account not only the range size of a species but also the richness of each site where that species occurs, its “diversity field” (Arita et al. 2008, Villalobos & Arita 2010). The Qr-mode considers the range sizes of all the species occurring in a particular site. This latter quantity has been dubbed the “dispersion field” (Graves & Rahbek 2005) and used in the examination of continental variation in species’ geographic range sizes (Hawkins & Diniz-Filho 2006, Orme et al. 2006) and the geometry of biotic source pools for local assemblages (Graves & Rahbek 2005).

RD plots are scatter-plots that can be built by species or by sites to explore the properties of diversity or dispersion fields, respectively, by depicting information on range size and species richness simultaneously. In RD plots by species, axes correspond to the mean proportional range richness and the proportional range sizes of species, in the abscissas and ordinates, respectively. In RD plots by sites, axes represent the mean proportional per-site range size and the proportional species richness of sites, in the abscissas and ordinates, respectively. In both plots, a vertical line is drawn to coincide, along the x-axis, with the proportional fill of the PAM, which represents the average proportional richness and average

proportional range size of the system in RD plot by species and sites, respectively (Arita et al. in press). The location of points within these plots is limited by biological and mathematical constraints determined by the minimum and maximum richness and range size values, while the central tendency is determined by Whittaker's beta diversity of the system (i.e. the proportional fill of the PAM; Arita et al. 2008, in press.). Furthermore, the detailed dispersion of points within those limits depends on the overall covariance among species or sites, which is ultimately determined by the patterns of co-occurrence. Specifically, the covariance of a species with the rest depends on the number of species with which it shares its distribution, and the covariance of a site on the number of sites with which it shares species (Arita et al. 2008). In general, points arranging to the left side of the plot's vertical line represent negative covariances whereas points to the right correspond to positive covariances (see Fig. 1 for a simplified version of RD plots).

2.4. Congruence between diversity and distribution

We explored the congruence between species richness and range size for Mexican birds using a RD plot by sites to describe the types of assemblages (in terms of per-site range size) present in each site and determine if sites harboring a high number of species are inhabited by restricted or more widespread species. To investigate the relationship between richness and rarity in the Mexican avifauna, we focused our exploration on the extreme values for both variables species richness (i.e. higher) and range size (i.e. smaller). To do this, we divided the RD plot axes in quartiles defining regions representing distinct type of per-site assemblages. For example, we can define a region where sites harbor species

assemblages of high richness and small ranges (i.e. fourth quartile in richness and first quartile in range size, hereafter “richness-rarity” quartile) or low richness and large ranges (i.e. richness’ first quartile and range size’s fourth quartile). This quartile approach has been commonly used as a pragmatic criterion to define hotspots of richness or rarity of species (e.g. Jetz et al. 2004, Orme et al. 2005). On a more general approach, we also explored the correspondence of such “richness-rarity” quartile with geographical regions within Mexico in order to trace the spatial distribution of these types of assemblages. Additionally, considering the overall covariances of sites, that is, the similitude among sites (Arita et al. 2008), we explored the location of sites with low covariance within Mexico to determine the spatial distribution of sites that, on average, are more dissimilar to the rest of sites. This endeavor has been favored to improve the interpretation of broad-scale biodiversity patterns (Soberón & Ceballos 2011).

In addition, we explored the ‘by species’ case. Using a RD plot by species, we examined the species’ co-distribution patterns, that is, the geographic association among species in terms of their co-occurrence (Villalobos & Arita 2010). In this case, we were interested in describing the diversity field (set of species richness values of sites where a focal species occurs) of restricted species in order to describe their tendency to coexist with either low or high numbers of species. Following Villalobos & Arita (2010), we present distribution maps of four example species along with their correspondent species richness frequency distribution (SRFD) within the individual ranges. This SRFD and its skew value ($g1$) describe the variation of species richness within the geographic range and with the aid of range maps they help inspect what kind of assemblages (in terms of richness) are inhabited by the focal species in different parts of its range,

representing the species' distributional footprint (analogous to Diamond's incidence functions, Villalobos & Arita 2010).

2.4. Protected areas and priority sites

To evaluate the types of bird assemblages represented in the protected area (PA) network and proposed conservation priority sites (PS) of Mexico, we explored the position within the RD plot by sites of grid cells belonging to those areas. We used the federal protected areas and priority sites defined by the Mexican Commissions on Natural Protected Areas (CONANP) and on Biodiversity (CONABIO), respectively. The membership of sites to a particular PA was simply identified if 50% of the site's surface were included in the PA. Since we used the same grid resolution of the PS, site overlap within a PS determined its membership. Overall representation of different assemblages within PA or PS can be determined by counting the number and proportion of sites within each distinct region of the RD plot (defined by quartiles, see above). For instance, on one extreme a PA or PS could harbor site(s) rich in species averaging restricted ranges or, on the other extreme, sites with low numbers of widespread species. We focused on the upper-left corner of the point cloud within the RD plot by sites and defined a "richness-rarity" quartile, representing the possibility of sites with both high numbers of species and populated mostly by restricted species since these, when existing, could be considered crucial for conservation practice (Orme et al. 2005, Prendergast et al. 1993, Williams et al. 1996). Mapping of sites within both the geography and the RD plot was done using ArcGIS 9 (ESRI 2009).

3. Results

3.1. Distribution of bird diversity and 'range-size assemblages'

3.1.1. Total bird species

Spatial variation of breeding bird species richness within Mexico follows the ubiquitous latitudinal gradient, with more species towards the southern parts of the country (Fig. 2A). The largest concentration of species occurs from the lowlands of the Gulf of Mexico through the Isthmus of Tehuantepec to the highlands of Chiapas, with some grid cells occupied by as many as 354 of the species (54.05%). On the other hand, the lowest concentration of species is at the central-northern regions of the country that are characterized by the presence of large desert areas harboring widespread species (Fig. 2B) (Koleff et al. 2008, Navarro-Sigüenza et al. 2009). The range-size frequency distribution (RSFD) for Mexican birds showed the common right-skewed pattern observed in regional/continental assemblages (Gaston 2003), with many narrow-ranged species, most of which occupied less than 20% of all grid cells, and some widespread species with at least one of them occupying the totality of the territory (Fig. 4B, right-hand histogram). The geographical pattern is reversed when looking at the type of species assemblages present at each site in terms of their per-site mean range size. Sites harboring, on average, widespread species locate at central-northern parts of the country whereas sites inhabited by more restricted species, on average, are located towards southeastern parts of Mexico (Fig. 2B). Altogether, the bird fauna of Mexico had a Whittaker's beta of 4.97, which is equal to the inverse of the

PAM's proportional fill (0.2013), in turn equal to the average proportional species richness or the average proportional range size in the system (Arita et al. 2008) ($\bar{s}^* = 0.2013$, $\bar{s} = 131.87$; $\bar{n}^* = 0.2013$, $\bar{n} = 1587.89$), meaning that sites contain, on average, 20.13% of the species and that the average bird species occurs in 20.13% of the sites.

3.1.2. Endemic birds

The geographical patterning of endemic birds in Mexico is known to differ from that of the total bird richness (Escalante et al. 1993, Navarro-Sigüenza et al. 2009, Peterson et al. 2003). Endemic species richness is highest in the western, central and southern highlands of Mexico and lower in regions like the lowlands of Tabasco, northern Chiapas, both peninsulas (Yucatan and Baja California), and the Chihuahuan desert (Escalante et al. 1993, Koleff et al. 2008) (Fig. 3A). The richest sites in endemics hold almost 50% of these species (47 species, 48%), while there are a few sites within the country that are not occupied by any endemic species (53 sites, 0.67% of the total domain of 7887 sites). RSFD for endemic birds is also highly right-skewed with 83% (81 species) of endemics being restricted to less than 20% of the territory and only three species present in more than half of it. Regarding assemblages formed by endemic birds in different parts of the country, sites occupied mostly by restricted species are distributed in the western, central and southern highlands whereas sites harboring mostly widespread endemic species are located in the north-central, northeastern and some parts of the gulf lowlands (Fig. 3B). Spatial turnover of endemic species, measured by Whittaker's beta, is greater than the value for the full set of species

($\beta_w = 7.95$). In this case, an average site contains 12.58% of endemic species and an average endemic bird occurs on 12.58% of the territory ($\bar{s}^* = 0.1258$, $\bar{s} = 12.33$; $\bar{n}^* = 0.1258$, $\bar{n} = 985.89$).

3.2. Range-diversity plot by sites

3.2.1 Total bird species

Since the central tendency of points within the RD plot is determined by the proportional fill value (i.e. the inverse of Whittaker's beta or the average proportional per-site range size; represented by the vertical dashed line), which was low (0.2013), the points arranged to the left of the plot with a right-side tail (Fig. 4A). In fact, all of the points fell to the right side of that value indicating that, on average, all sites covary positively with the rest of sites. As expected from theory, there can be no sites with both high richness and high mean range sizes, but sites with low richness can attain a variety of per-site range size values (Arita et al. 2008). Nonetheless, in this case, sites with low richness only had high mean per-site range size values whereas richer sites had low mean per-site range size values (Fig. 4A). Actually, the vast majority of sites within the lowest range size quartile (1st) are included in the richest quartile (4th) (1674 of 1972 sites, 84.88%) while the few sites left within this quartile are part of the third richness quartile. Hence, there is an overall correspondence between high species numbers and low mean per-site range sizes, confirmed by a negative linear correlation between species richness and per-site range size (-0.928). Consequently, the spatial

distribution of different types of 'range-size assemblages' basically follows the patterns of geographic variation in species richness described above.

Detailed spatial structuring can be found when looking at different regions within the RD plot and choosing sites with contrasting overall covariances. For instance, sites in the upper-most left corner of the point cloud within the RD plot (i.e. those with the highest richness and lowest mean per-site range size) followed clear regions in the southern parts of the country comprising a region from central Veracruz to the north east of Chiapas, crossing the Isthmus of Tehuantepec (Figs. 2A, 4A), while sites in the lower-right corner (those with the lowest richness and highest mean per-site range size) showed a clear pattern at the north central part of the country (Fig. 2B, 4A). Regarding the covariances, all of the sites covariate positively with the rest of sites. Sites with the lowest covariances (i.e. most distinct sites) are located in the southernmost part of the country at the northern and eastern parts of Chiapas, whereas those sites with the highest covariances were distributed over the central and northern parts of both Sierra Madre Occidental and Oriental.

3.2.2. *Endemic birds*

In general, the point dispersion in the RD plot by sites follows a similar structure in the endemic avifauna to that of the total bird species. There is a negative linear correlation between richness and per-site range size (-0.582). The difference between these two sets of species relies on those sites with low species richness. There is a more dispersed pattern for those sites in the lower part of the RD plot. Sites with low richness attained both low and high values of per-site range size,

arranging on both sides of the plot's vertical dashed line (i.e. average proportional range-size value) (Fig. 6A), as expected from theory (Arita et al. 2008). Hence, some sites had negative overall covariances with the rest (349 sites, 4.45%) but still most of the sites covariate positively among them. Almost all sites within the lowest range size quartile (1st) are included either in the 4th (richest) or 1st (poorest) richness quartiles (1779 of 1959 sites, 90.81%). In this case, the correspondence between sites with high richness and low per-site range size values was lower than the one for the total avifauna. However, the richer sites did attained low, but not the lowest, range size values (Fig. 6A).

Geographical patterning of endemic site assemblages is highly structured. For instance, sites in the lower-left corner (low richness and range size) of the RD plot arranged at the eastern part of the Yucatan peninsula and northeast Chiapas (Figs. 3B, 6A), while those sites in the lower-right corner (low richness and high range size) were located at the north central (following the same pattern of the total avifauna) and northwestern parts of the country (Figs. 3B, 6A). The structure regarding the sites' covariances showed an overall geographic patterning similar to that of the total bird species. Those sites with lowest covariances corresponded to those in the lower-left corner of the RD plot (see above), overlapping in some regions with the pattern for the total avifauna (northeast Chiapas and southeast Tabasco). Sites with highest covariances followed a similar pattern to the one of the total avifauna, at least on the west. These sites located at the central and northern parts of Sierra Madre Occidental and were absent from the Sierra Madre Oriental.

3.3. Range-diversity plot by species

3.3.1. Total bird species

Species were arranged in both sides of the vertical dashed line (in this case representing the average proportional range-richness), but tended to clump towards the right side of the plot (Fig. 4B). The vast majority of species (559, 85.3%) had average species richness within their ranges equal or higher than the overall mean (131.87 species), implying a positive covariance with the rest of species (Villalobos & Arita 2010). Only 96 species (14.7%) had mean range-richness lower than the overall mean, in this case implying a negative covariance with the rest of species. Again, as expected from theory, species with large ranges are bound to be closer to the vertical line whereas restricted species can attain a wide variety of mean range-richness values (Arita et al. 2008). In fact, most of species in the lowest (1st) range size quartile (110 species, 67% of 164 species) also belong to both first and fourth quartiles of range-richness, with most of them belonging to the latter quartile (84 out of 110 species).

Species with contrasting diversity field patterns are located in different parts of the country, as would be expected. For example, the two species with the highest mean range-richness (Nava's wren, *Hylorchilus navai* and Sumichrast's wren, *H. sumichrasti*) are geographically restricted and distribute over the richest regions of the country (250-350 species) (Figs. 8A, B). On the other hand, the two species with the lowest average range-richness (Belding's yellowthroat, *Geothlypis beldingi* and Xantus's humminbird, *Hylocharis xantusii*) are also restricted and distribute in the southern Baja California where only a few other bird species occur (30-70 species) (Fig. 8C, D).

3.3.2. Endemic birds

Endemic bird species followed a similar pattern to that of the total avifauna. Species arranged in both sides of the vertical dashed line (i.e. mean proportional range-richness), with most of the species (80, 81.63%) clumping towards the right side of the RD plot (i.e. mean range-richness higher than the overall mean: 12.33 species) and a few species (18, 18.37%) to the left (Fig. 6B). That is, most endemic species have a positive covariance with the rest of endemics while only a few species covariate negatively with the rest. Again, most endemic species in the first (lowest) range size quartile are also included in both first (poorest) and fourth (richest) range-richness quartiles (18 out of 25 species) with most of them belonging to the former quartile (11 out of 18 species).

As with the total avifauna, endemic birds with contrasting diversity field patterns occur in different parts of the country. For instance, the two species with the highest mean range-richness are restricted (White-tailed hummingbird, *Eupherusa poliocerca* and Short-crested coquette, *Lophornis brachylophus*) and locate over the western-central regions where most of the endemics occur (30-46 species) (Fig. 9A, B). The two species with the lowest mean range-richness (Yucatan wren, *Campylorhynchus yucatanicus* and Belding's yellowthroat, *Geothlypis beldingi*) are also restricted and each one distributes at one of the two peninsulas in the country, Yucatan and Baja California (Fig. 9C, D).

3.4. Protected areas, priority sites and 'richness-rarity' hotspots

A total of 699 cells in the total avifauna domain (8.86%, 7887 cells) had at least 50% of their surface within a protected area and were considered to analyze the representation of sites within the richness-rarity quartile. Likewise, 1321 priority sites were considered to compare their potential coverage of such richness-rarity sites (figures for the endemics data set are similar, Table 1). Richness-rarity quartile comprised 1674 sites in the total avifauna set and 1397 in the endemics set (21.22% and 17.83% of domains, respectively). The geographic location of these sites consistently followed regions of high richness and restricted range-size assemblages. As if virtually overlapping both richness and per-site range size maps (Figs. 2A, B), sites within these quartiles are located mainly to the southeast and along both coasts into central Mexico for the total bird species and to the west central and western regions along the pacific coast for the endemic birds (Fig. 5). Representation within the federal protected area network covered 9.26% and 3.86% of these sites for total bird and endemic species, respectively. Consideration of priority sites increased the representation of these sites to 25.75% and 18.47% for total bird and endemic species, respectively (Table 1).

4. Discussion

4.1 Range-diversity plots for conservation planning

Our approach, simultaneously analyzing diversity (species richness) and distribution (range sizes) with range-diversity plots, provides a useful and explicit application for conservation planning. By using primary biogeographic information (i.e. presence-absence data), it allows straightforward identification of sites and

species with characteristics of conservation interest. For instance, in the 'by sites' approach, sites harboring high number of species averaging restricted geographic ranges can be recognized. On the other hand, the 'by species' approach allows the identification of restricted-ranged species occurring in species-poor regions. Both aspects are relevant in conservation priority setting. Furthermore, the spatially explicit component of this approach allows a quick geographic assessment of its results (e.g. identified richness-rarity hotspots) by coupling RD plots and maps within a GIS. In addition, results from this approach could be also used as input for other prioritization procedures. For example, ranking those sites within richness-rarity quartile enabling their addition into multicriteria prioritization algorithms such as those used in systematic conservation planning (Sarkar et al. 2006). Moreover, it enables critical readings of common conservation practices (e.g. Protected Area Networks, Priority Sites) regarding their representation of different aspects of biodiversity (e.g. richness vs. rarity). Finally, the use of primary biodiversity data renders a broad applicability to our approach, being easily extended to any region and taxa, and allowing for comparisons among different data sets.

4.2. 'By sites' approach

4.2.1. Geographic patterns of Mexican avifauna

Spatial variation of bird diversity is highly structured within Mexico. Detailed spatial structuring differs considerably between total bird species and those species entirely restricted to Mexico. The majority of species occur in the south and southeast parts of the country, mostly over lowland areas of the Gulf of Mexico but

also throughout mountainous regions like the east part of the Transvolcanic Belt, Sierra de Oaxaca and the Chimalapas (Fig. 2A), mainly following the distribution of humid montane forests (Challenger 1998). These forests are one of the most diverse habitats in the Neotropics (Brown & Kappelle 2001, Stotz et al. 1996), as exemplified by the birds inhabiting these habitats in Mexico (Hernandez-Baños et al. 1995). For instance, the Chimalapas region has been considered the richest region for Mexican birds due to the co-occurrence along its altitudinal gradient of widespread species over lowlands, and endemic and narrow-range species restricted to mountains (Peterson et al. 1993, 2003). Hence, it has been suggested as a high-priority region for bird conservation in Mesoamerica because of its very high richness (~44% of species known to occur in Mexico) mediated by its large and well-preserved tropical rain and cloud forests, and river basins throughout its entire lowland-to-highland continuum (Peterson et al. 2003). This same pattern likely holds for the mountainous regions mentioned above. For instance, the richest site in our study (354 species) is located at the western part of the state of Veracruz where two important mountain chains meet, the Transvolcanic belt and the Sierra Madre Oriental (Navarro-Sigüenza et al. 2007).

Conversely, in the case of endemic birds most species are found over the highlands of western-central and southern Mexico (Fig. 3A). Again, these regions represent steep altitudinal gradients in which high numbers of endemic species co-occur, both widespread and restricted. Highlands regions, in general, have been suggested as important centers of diversification (Fjeldsa 1995, Graves 1985) because their topographic complexity is thought to facilitate speciation by creating spatial and ecological conditions promoting divergence such as geographic barriers or environmentally induced differences (Fitzpatrick et al. 2009). Regions

such like the Sierra Madre Occidental and Transvolcanic belt in Mexico could be acting as such centers of diversification (Navarro-Sigüenza et al. 2007), adding substantial diversity to the country's biota in general and the Mexican avifauna in particular (García-Trejo & Navarro 2004). Actually, these regions are thought to represent one of the main centers of bird endemism throughout all Mesoamerica, turning these regions into conservation priorities (Hernandez-Baños et al. 1995, Peterson & Navarro 2000).

Although the contrasting pattern between total and endemic species richness of Mexican birds has been widely acknowledged (e.g. Escalante et al. 1993, Koleff et al. 2008, Navarro-Sigüenza et al. 2009), a thorough inspection of such patterns had been surprisingly lacking from the literature (Sánchez-González et al. 2008). This is true especially for 'range-size assemblages' (Figs. 2A, 3A), a site's property just recently being considered in continental analyses (e.g. Hawkins & Diniz-Filho 2006, Graves & Rahbek 2005) and implemented in our 'by sites' approach of range-diversity plots. In this case, for both total bird species and endemics, sites mostly inhabited by widespread species are found in the northern-central parts of the country while sites occupied mostly by restricted species are located towards the south and southeastern regions of Mexico. These kinds of patterns, considering other aspects of biodiversity such as range-restrictedness of species inhabiting different sites, could reveal patterns hidden when just looking at richness. For instance, sites poor in species may not be considered as conservation targets (e.g. "Coldspots", see Kareiva & Marvier 2003 for a thoughtful comment on this topic) even if those sites are inhabited mostly by restricted species. For the total Mexican avifauna, however, this may not be a serious issue.

There is a clear overall positive relationship between richness and rarity (range-restrictedness) for both total bird species and endemics, implying a redundancy in the selection of rich sites or sites with low mean per-site range size. That is, in general, species-rich sites are also sites that harbor restricted species. As stated above, this pattern is a consequence of confluence between widespread and restricted bird species chiefly in highlands regions. Moreover, this pattern is characteristic of nested assemblages in which if a species occurs in only a few sites, these sites tend to be areas of high species richness, whereas low richness sites are occupied by widespread species (Arita et al. in press). While nestedness has been mostly studied in species occurrences and species interactions patterns (Ulrich et al. 2009), it also has direct implications for conservation actions based on the identification of low-richness sites as non-random nested subsets of the species set present at high-richness sites (Patterson 1987). Consequently, an observed positive relationship between richness and rarity in fact could optimize site selection (in terms of pattern description) since either one of these attributes, richness or rarity, can be used to identify priority sites with much the same results. More interesting, in cases where the relationship is clear but not complete (i.e. not all sites with restricted species are also rich in species), like in the endemic birds of Mexico, the existence of sites with low numbers of mostly restricted species highlights the usefulness of a range-diversity plot approach. These sites could be difficult to identify when considering a whole set of species and paying no attention to either restricted species in particular or the per-site mean range size pattern of the study region. Such sites are the most unique and unrelated in terms of species composition to the rest of sites (i.e. lower overall covariances), which means that conservation actions should consider these idiosyncratic sites in order to reach an

inclusive conservation of a region's biota. Still, this richness-rarity relationship could be missed, or at least prove difficult to infer, from a one-dimensional view of biodiversity like mere species numbers.

4.3. Total species richness vs. Endemism

The striking difference in the geographic patterning of total bird species vs. endemic richness highlights the importance of considering different measures of biodiversity when setting conservation priorities (aside from the inherent evolutionary insights of such patterns). Endemic taxa are potentially more sensitive to habitat perturbation, thus especially vulnerable to extinction and regarded as critical for conservation actions (Gaston 1994, Peterson & Watson 1998). Specifically, on a national scale these taxa represent a unique fauna that depends primarily on the conservation actions taken within the country (Stotz et al. 1996). A national conservation strategy aimed towards endemics will ultimately add more species to the preservation of global biodiversity. Furthermore, this distinction allows focusing and exploring specific patterns within different sets of species such as the identification of restricted species within them. Restrictedness, unlike endemism, does not depend on areal definition of particular regions (e.g. natural or political boundaries) but on species' geographic distributions *per se* (Peterson & Watson 1998). Hence, attention to range-restricted species can be further refined by looking at these within an already unique fauna such as national endemics, resulting in a detailed inspection of conservation relevant features.

4.4. 'By species' approach

4.4.1 Species geographic associations

Species' tendencies to occur in species-rich or species-poor regions can be investigated with the 'by species' approach of range-diversity plots and the 'diversity field' concept, studying the range-richness structure of species (Villalobos & Arita 2010). Our study of Mexican avifauna shows that co-occurrence among bird species in general and endemic birds in particular, is very high since most of the species share at least part of their geographic distribution with many other species. Thus, there is an elevated level of overall association among species resulting from the aggregation of high numbers of them in specific regions. Again, this pattern would suggest that conservation of species-rich regions could potentially ensure the conservation of widespread, restricted and endemic species altogether. However, not all bird species tend to occur in species-rich regions. In fact, for both total and endemic birds there are a few restricted species that occur exclusively on species-poor regions sharing their geographic distribution with only a few other birds. These idiosyncratic species (Atmar & Patterson 1993) can be considered analogous to 'super-tramp' species (*sensu* Diamond 1975) showing negative average covariance with the rest of species (Villalobos & Arita 2010). Ulrich et al. (2009) argued that these species run counter to ecological and geographic gradients of species occurrence. However, the mechanisms underlying these patterns, especially at geographic scales, have remained elusive resulting in a poor understanding of such patterns and a limited capability to inform process-based conservation planning.

Diversity field patterns (i.e. set and frequency of richness values within a species' range) have been explained by the action of combined factors such as historic (speciation and extinction), geometric (domain size, mid-domain effect), climatic, geographic (domain shape), and idiosyncratic traits of species (potential ecological interactions) (Villalobos & Arita 2010). These factors are suggested to apply mainly to monophyletic clades and not necessarily to a collection of taxonomically defined species, like the Mexican birds. Nonetheless, they could point towards potential explanations of such patterns. For example, if similar climatic preferences drive the high geographic association among Mexican birds then idiosyncratic species would be regarded as species with different climatic preferences occupying particular habitats devoid of most other bird species. Under this scenario, the consideration of such species in conservation planning could indirectly assist the conservation of those habitats that most likely are also geographically restricted in size or location, or both. Such is the case for Mexican avifauna, where the least associated species (i.e. lower mean range-richness and covariance), among total birds and endemics, were restricted endemics located at the extremes of the country over both peninsulas, Baja California and Yucatan. As mention above, species-poor regions like these may not score high under a common prioritization procedure based on species numbers even though they harbor bird species not present in any other part of Mexico, leaving these idiosyncratic species out of any conservation action focused on richness patterns only. Also, the fact that these idiosyncratic species are all true endemics stresses the importance some "coldspots" (i.e. species-poor regions) can have in the conservation of particular species (Kareiva & Marvier 2003). On the other hand, bird species with high mean range-richness were also restricted endemics

distributed over species-rich regions. Although restricted species are expected by theory to potentially attain any range-richness value (Arita et al. 2008), the recognition of endemics within the total avifauna requires attention to this particular, geographically defined, subset of species. Altogether, these findings highlight the usefulness of range-diversity analyses both 'by sites' and 'by species' in interpreting the diversity-distribution relationship and describing spatial patterns that can help guiding conservation prioritization.

4.5. Protected areas, richness-rarity quartiles and conservation priorities

Protected areas are established for varying reasons such as aesthetics or resource management, and may not always have strong value for biodiversity conservation (Gaston et al. 2008). Consequently, effectiveness of such areas in representing different geophysical and biodiversity features is highly variable (Cantú et al. 2004). This is particularly true in Mexico, where critical evaluations of protected area effectiveness are just starting to appear (Aguirre & Duivenvoorden 2010, Cantú et al. 2004, Ceballos 2002, 2007, Figueroa & Sánchez-Cordero 2008, Vázquez & Valenzuela 2009). Our purpose, however, was not to evaluate the effectiveness of these areas in protecting bird species but the representation of sites with combined characteristics deemed relevant for conservation, namely species richness and range rarity. We identified a "richness-rarity" quartile containing sites with high values of both attributes (richness and rarity), encompassing around 9% of the domain (for both total bird and endemic species). While defined pragmatically, the spatial location of the richness-rarity quartiles reveals the concentration of those attributes over clearly defined regions within the country resulting from the strong

intrinsic relationship between diversity and distribution observed in the Mexican avifauna. Protected area coverage of such regions favors bird species richness over endemism, probably as a consequence of bird diversity (as a whole) being a common surrogate included in many prioritization procedures (Navarro-Sigüenza et al. In press). Hence, being one of the best-known groups of the country's biota, the fairly good representation of Mexican avifauna in protected areas comes as no surprise (Ceballos 2002). Nonetheless, features of bird biodiversity such as types of species assemblages formed in different sites are less known and virtually lacking from conservation priority setting. This community approach to prioritization enhances the goal of a more comprehensive conservation of biological diversity, providing new information for such endeavor. For instance, although in this case restrictedness can be predicted by richness, unique sites can still be identified even if not harboring high numbers of species by their assemblages' degree of restrictedness that could be considered in future conservation goals (e.g. for endemic birds). Furthermore, a closer inspection of the geographic distribution of protected areas shows the scatter pattern over the richness-rarity quartile sites leaving the richest and most restricted bird assemblages (lower per-site mean range size) out of this scheme (Figs. 5, 7). Interestingly, most of these sites tend to follow highland regions in the southeast and west central parts of Mexico. Therefore, our findings echoed previous claims regarding the importance of Mexican highlands as conservation priorities for both global and in-country biodiversity conservation, especially for birds (Garcia-Trejo & Navarro 2004, Hernandez-Baños et al. 1995, Peterson et al. 1993, Sánchez-Gonzalez & Navarro-Sigüenza 2009, Stotz et al. 1996) but also for other animal and plant taxa (Luna-Vega et al. 2000, Urbina-Cardona & Flores-Villela 2010, Sánchez-Cordero 2001).

5. Conclusions

Richness and rarity are positively related in the Mexican avifauna. The relationship is similar for the total bird species set and the endemics although with different detailed structure, richer sites tend to have assemblages of species averaging restricted ranges. Such relationship can be readily depicted and analyze using range-diversity plots, which can be used in the identification of priority sites for conservation of particular assemblages or individual species. While we do not undermine the importance of natural and anthropogenic dynamics, including social, political and economical factors in conservation (Pressey et al. 2007, Wilson et al. 2007), we also acknowledge the need for more transparent, fast, and robust ways to inform conservation planning with primary biodiversity data. We envision our approach as both a rapid assessment of biodiversity patterns to guide initial stages of conservation planning and as a supplemental method to support the inclusion of relevant sites to a network of already protected areas. Ours is a quantitatively rigorous approach that requires only species-occurrence data of the study group, which nowadays is easily obtainable from different free sources (e.g. NatureServe, GBIF), to directly identify the existence of sites harboring both richness and rarity making it easy to adopt and implement in a variety of cases. Such sites, once identified, could be given priority over others and considered or even add to existing protected areas. We hope that our approach and methodology will help in this endeavor.

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Figure legends

Figure 1. Range-diversity plots (a) by sites and (b) by species. In both plots, the solid curved lines mark the upper theoretical limit for points; the vertical dashed line corresponds to the mean proportional species richness.

Figure 2. Mexican avifauna species richness (A) and per-site range size (B) maps.

Figure 3. Endemic birds species richness (A) and per-site range size (B) maps.

Figure 4. Mexican avifauna range-diversity plots by sites (A) and by species (B). Histograms on top and on the right-hand side show the frequency distribution of those variables; the solid curved line marks the upper theoretical limit for points; the vertical dashed line corresponds to the mean proportional species richness.

Figure 5. Map depicting the geographic locations of the 'richness-rarity' ("hotspots") quartile, sites within protected areas, priority sites and "hottest hotspots". Inset: RD plot by sites with "hotspots quartile" highlighted.

Figure 6. Endemic birds range-diversity plot by sites (A) and by species (B). Histograms on top and on the right-hand side show the frequency distribution of those variables; the solid curved line marks the upper theoretical limit for points; the vertical dashed line corresponds to the mean proportional species richness.

Figure 7. Map depicting the geographic locations of the 'richness-rarity' ("hotspots") quartile, sites within protected areas, priority sites and "hottest hotspots". Inset: RD plot by sites with "hotspots quartile" highlighted.

Figure 8. Diversity field of four bird species. (A) *Hylorchilus navai*, (B) *Hylorchilus sumichrasti*, (C) *Geothlypis beldingi*, (D) *Hylocharis xantusii*. Maps show the species-richness values of sites within the range of each species, and histograms show the frequency distribution of such richness values.

Figure 9. Diversity field of four endemic bird species. (A) *Eupherusa poliocerca*, (B) *Lophornis brachylophus*, (C) *Campylorhynchus yucatanicus*, (D) *Geothlypis beldingi*. Maps show the species-richness values of sites within the range of each species, and histograms show the frequency distribution of such richness values.

Table 1. Total number of sites (domain) occupied by the total avifauna and endemic birds in Mexico, showing the total number of sites within protected areas or proposed as priority sites and the percentage (in parentheses) of these with 50% of their surface within it or coinciding in each category (domain and 'hotspots' quartile)

Fig.1

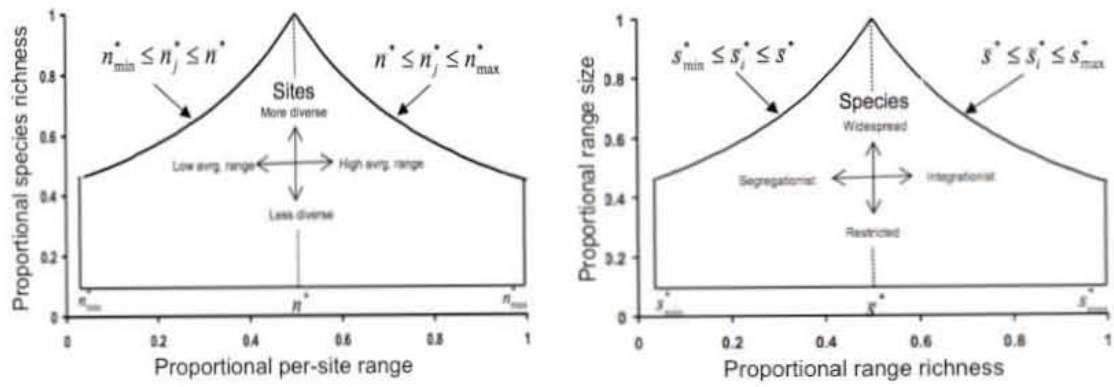
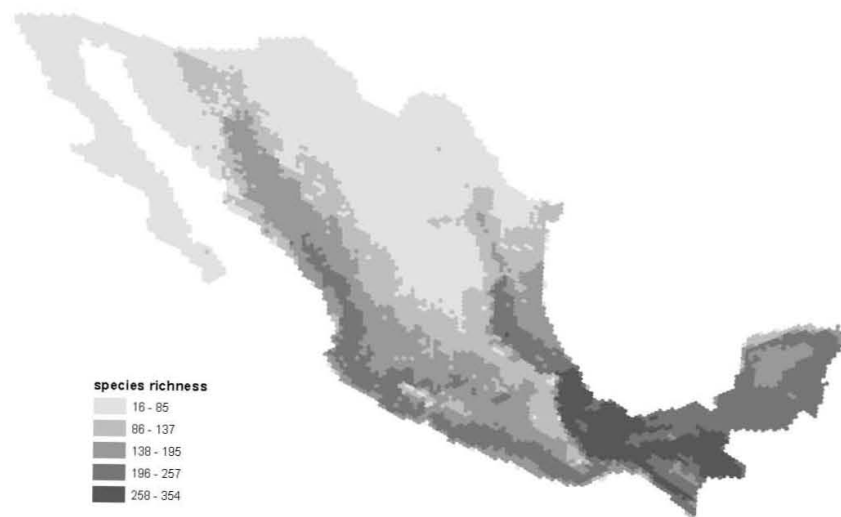


Fig. 2

A



B

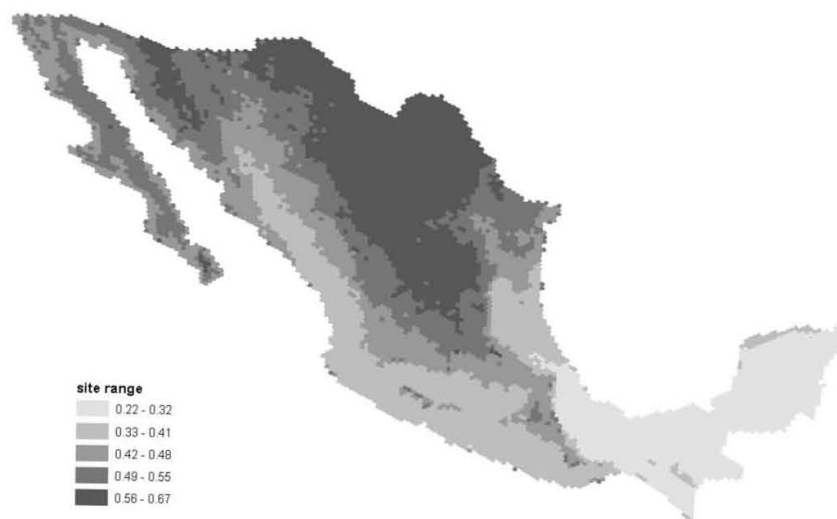
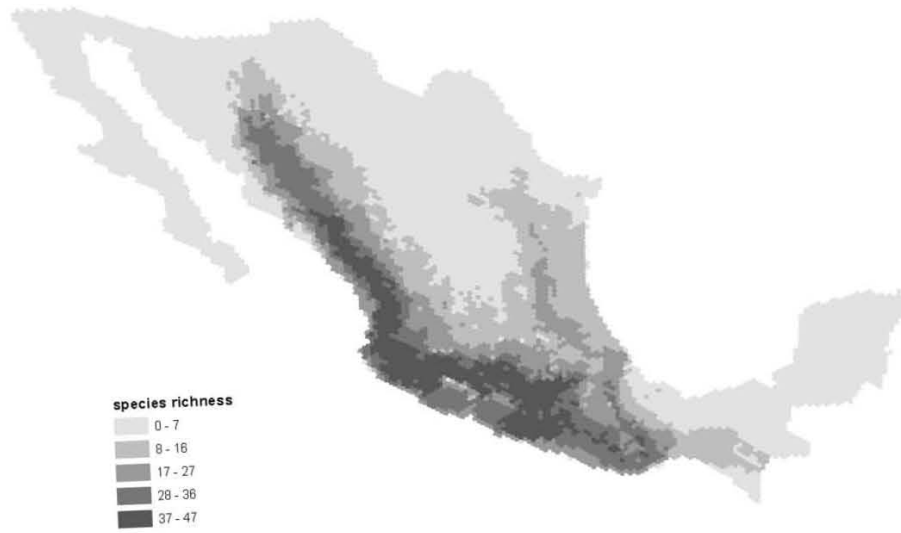


Fig. 3

A



B

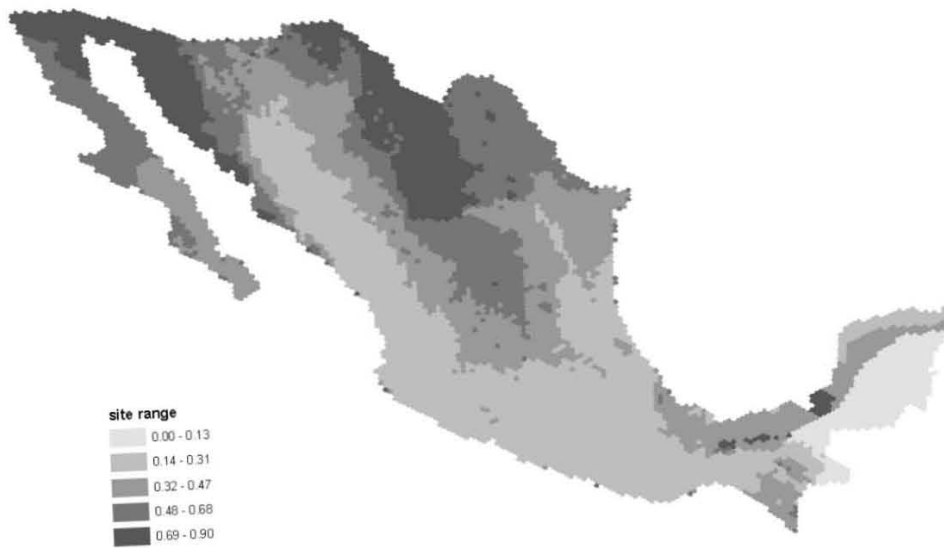


Fig. 4

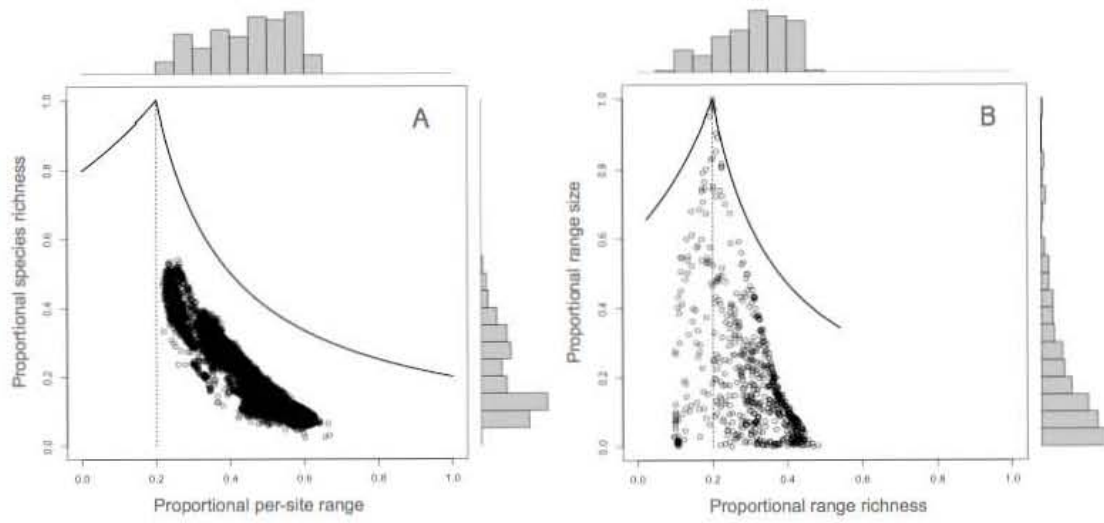


Fig. 5

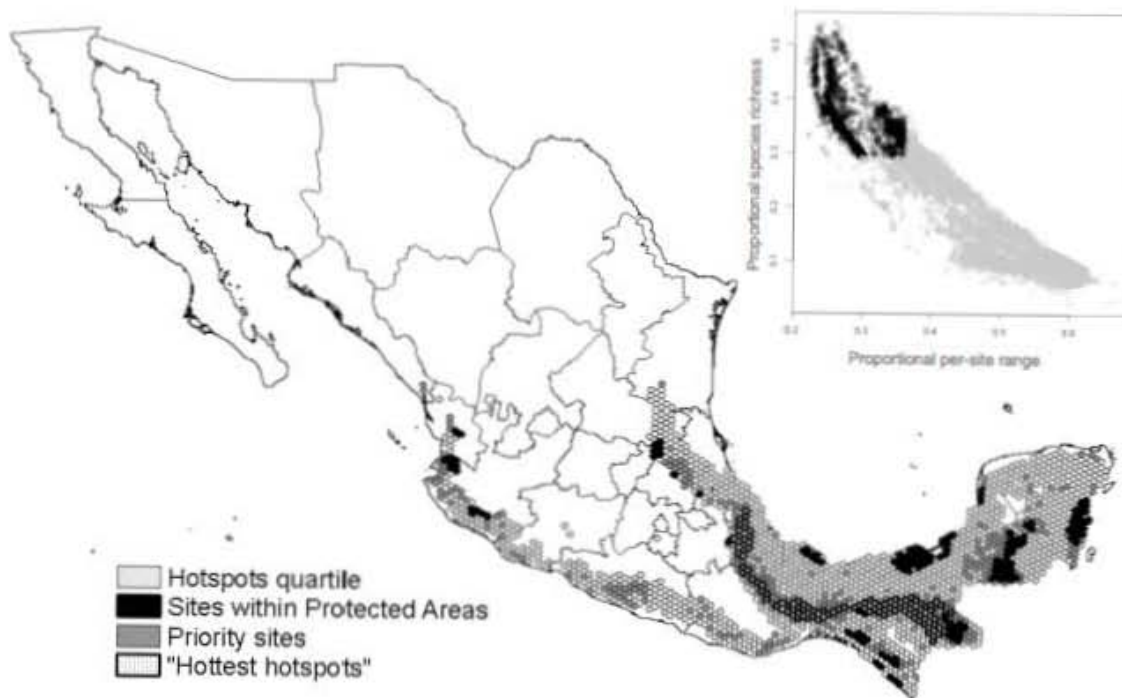


Fig. 6

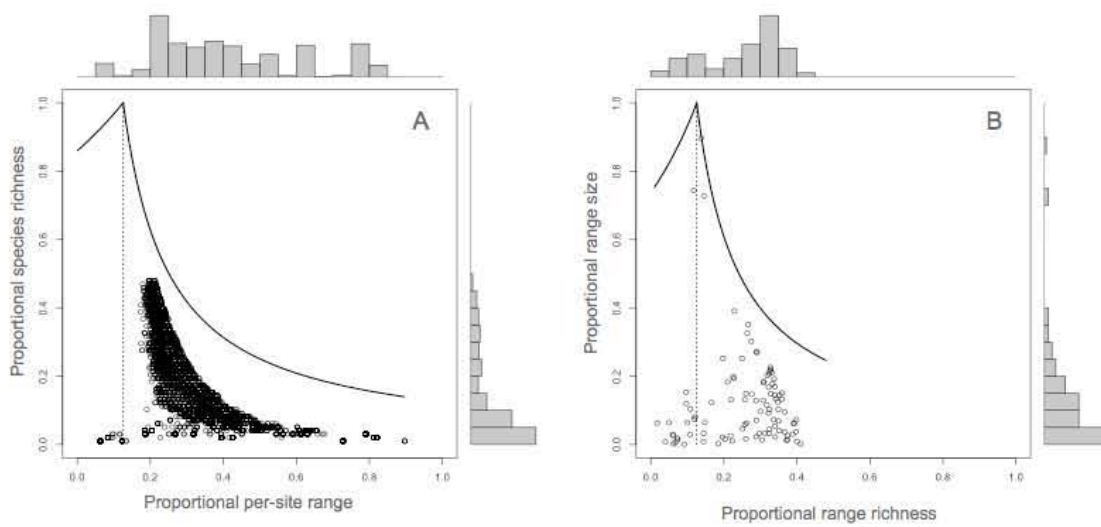


Fig. 7

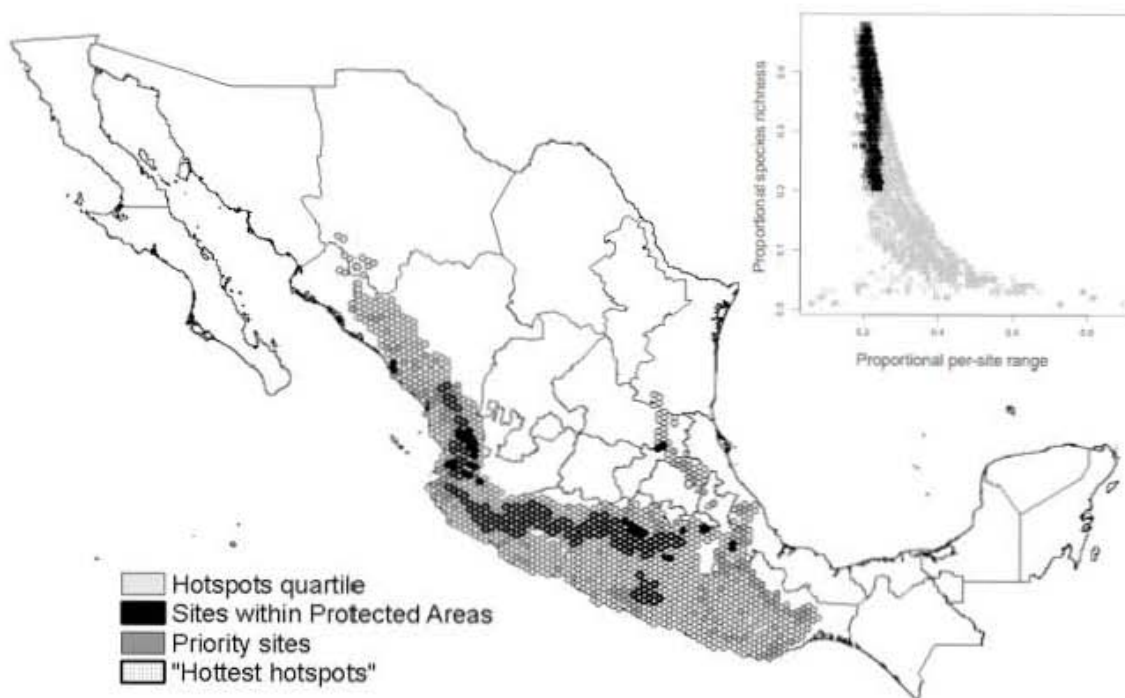


Fig. 8

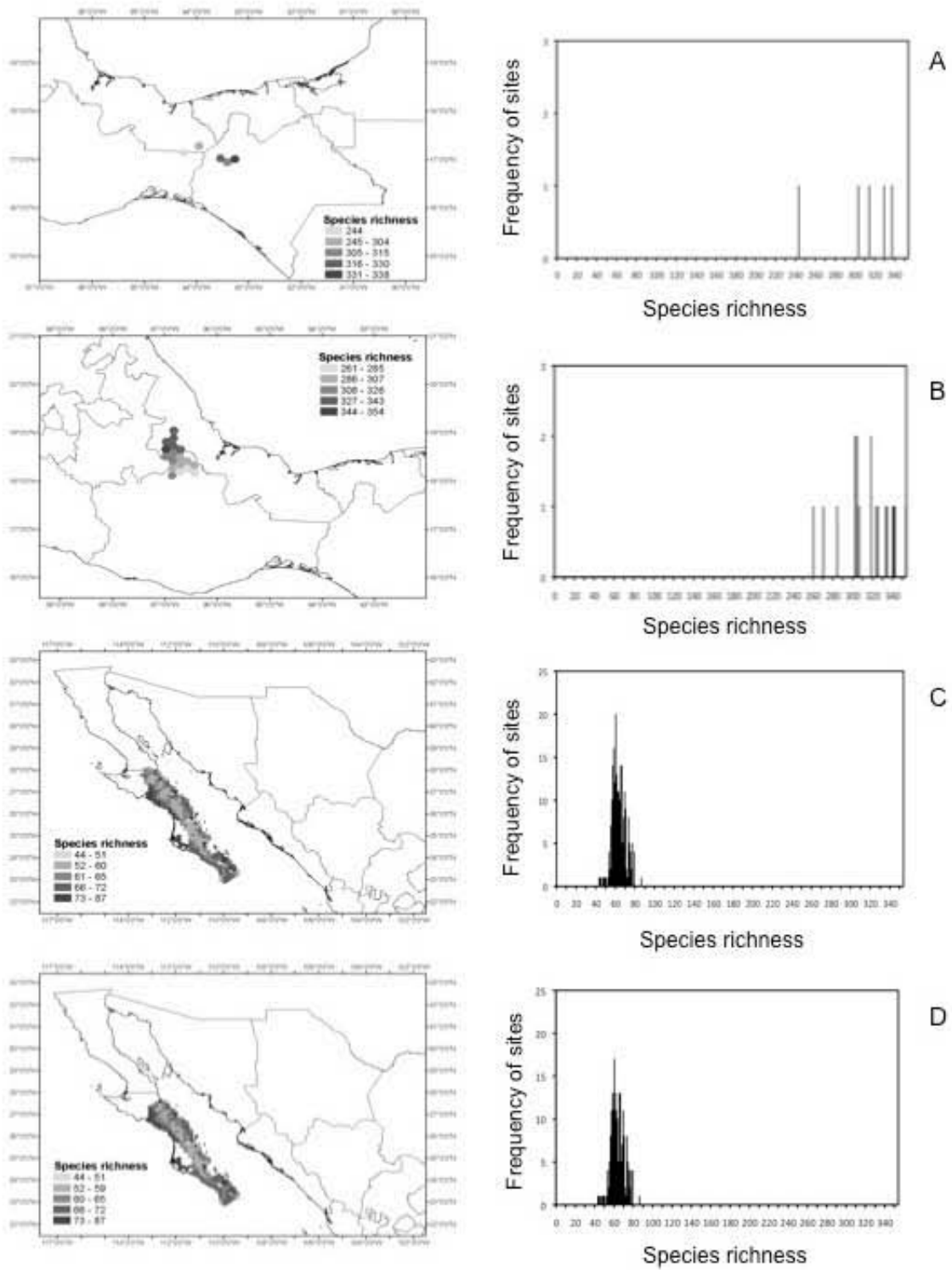


Fig. 9

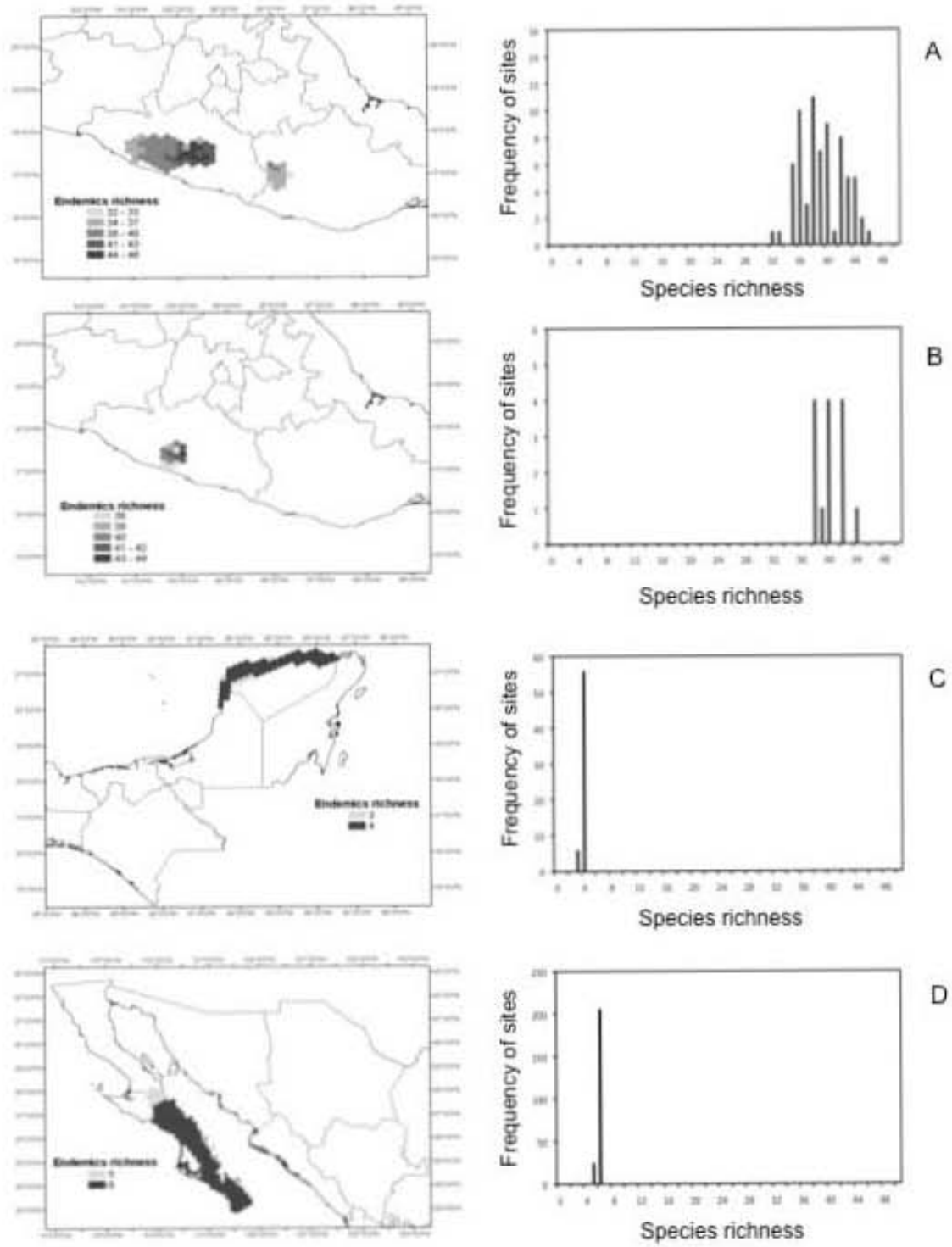


Table 1.

	Total sites	Protected (%)	Priority sites (%)
<i>Total avifauna</i>			
Domain	7887	699 (8.86)	1321 (16.75)
Hotspots quartile	1674	155 (9.26)	431 (25.75)
<i>Endemics</i>			
Domain	7834	686 (8.77)	1321 (16.86)
Hotspots quartile	1397	54 (3.86)	258 (18.47)

DISCUSIÓN GENERAL

El patrón heterogéneo en la distribución geográfica de la biodiversidad es resultado de la distribución individual de las especies presentes en el planeta. Por tanto, existe una relación intrínseca entre diversidad (número de especies) y distribución que subyace a los diferentes patrones de asociación entre especies (co-distribución) y similitud entre sitios (co-diversidad). Dichos patrones, a su vez, son el resultado de procesos que actúan en diferentes escalas de tiempo y espacio. La evaluación de estos procesos y su importancia relativa en la determinación de patrones geográficos es, sin embargo, una tarea complicada. Las escalas de tiempo y espacio en que ejercen su acción impide una aproximación controlada (e.g. experimentación). Una manera de acercarnos al estudio de tales patrones es mediante un enfoque de modelación, en donde se simulan escenarios posibles basados en la aleatorización de los datos observados excluyendo el proceso de interés (modelación nula) o se incorporan mecanismos específicos considerados importantes para el ensamblaje de las comunidades o la distribución de las especies (Gotelli y McGill 2006, Gotelli et al. 2009).

En esta disertación desarrollo y aplico un enfoque novedoso para investigar los patrones geográficos de biodiversidad, basándome en la relación diversidad-distribución evaluada bajo una perspectiva de modelación nula. La exploración de dichos patrones me permitió identificar huecos en el conocimiento de los mismos y demostrar la utilidad de los conceptos y herramientas desarrolladas en este proyecto doctoral para cubrirlos. Las contribuciones de este trabajo de tesis, aunque bajo el mismo marco teórico y metodológico (interrelacionadas), pueden entenderse como contribuciones individuales y ser discutidas en relación al contexto particular en el que se inserta cada una. Por ejemplo, en el capítulo dos, investigué un patrón macroecológico anteriormente desatendido: la distribución de frecuencias de riqueza de especies (DFRE). Este patrón prácticamente no ha sido estudiado en el contexto macroecológico (con una excepción reciente: Sizling et al. 2009) y rara vez en el contexto ecológico (e.g. Van der Maarel et al. 1995, Wilson et al. 1995; aunque estos no consideran la distribución completa de las especies). Como consecuencia, no conocemos sus propiedades estadísticas aún cuando representa la imagen especular (en términos de información) del patrón

geográfico de biodiversidad más evidente: la variación geográfica en riqueza de especies. En los capítulos tres y cuatro exploré los patrones de co-distribución y co-diversidad, permitiendo una descripción completa del sistema bajo estudio (murciélagos y aves, respectivamente) así como una comprensión teórica y aplicación práctica de los patrones interrelacionados de diversidad y distribución causados por el traslape de las áreas de distribución. Asimismo, en los capítulos dos y tres demuestro la utilidad de los enfoques de modelación para evaluar los patrones estudiados. De manera que, es posible identificar tres contribuciones principales de este proyecto doctoral: 1) identificación y estudio de la distribución de frecuencias de riqueza de especies, 2) evaluación teórica y aplicada de patrones de co-distribución y co-diversidad y 3) utilidad de los enfoques de modelación en el estudio de patrones macroecológicos. A continuación discuto cada una de estas.

Distribución de frecuencias de riqueza de especies, el ‘*campo de diversidad*’ y la estructura interna de las áreas de distribución

“Las áreas de distribución son las sombras chinescas producidas por los taxones sobre la pantalla terrestre: estudiarlas es medir, pesar y estudiar el comportamiento de fantasmas”

Eduardo H. Rapoport (1975)

La variación geográfica en riqueza de especies es usualmente representada en un mapa que muestra detalladamente su estructura geográfica (Ruggiero y Hawkins 2006). Aunque dicha representación puede contener mucha más información que cualquier gráfica bivariada (e.g. variación geográfica en características de los ensamblajes formados por especies en diferentes sitios, Villalobos et al. Capítulos 3 y 4), estos mapas son tan sólo uno de los pasos hacia la comprensión de patrones geográficos de biodiversidad. Por ejemplo, la aplicación de enfoques estadísticos a los datos que subyacen tales mapas permite una evaluación rigurosa de los procesos involucrados en la determinación de dichos patrones (Blackburn y Gaston 2006). En la investigación macroecológica, ambos enfoques (i.e. mapas y propiedades estadísticas de los datos) han sido aplicados conjunta o independientemente, con mayor énfasis en la estadística que en la geografía (Ruggiero y Hawkins 2006). No obstante, las variables o relaciones estadísticas

analizadas han sido limitadas (e.g. relación latitud/ambiente-riqueza/tamaño del área de distribución) e incluso han dejado fuera la evaluación de características básicas (propiedades estadísticas) en variables relevantes. Tal es el caso de la riqueza de especies, una variable fundamental de expresión de la biodiversidad.

El patrón geográfico de riqueza de especies puede estudiarse como el conjunto de valores de riqueza (distribución de frecuencias) en los diferentes sitios del dominio estudiado (i.e. región geográfica de interés) y ser descrito y analizado con descriptores estadísticos estándares de tendencia central y variación (Villalobos y Arita 2010, Capítulo 2). Sin embargo, estos estudios no se han llevado a cabo y las propiedades estadísticas de dicho patrón siguen sin conocerse, contrastando con la atención que han recibido las distribuciones de frecuencias de otras variables macroecológicas tales como abundancia, tamaño corporal y de área de distribución.

La distribución de frecuencias de riqueza de especies (DFRE o SRFD, por sus siglas en inglés) es un patrón agregado que resulta de sumar el número de áreas de distribución que se traslapan en diferentes sitios. Esto permite, a su vez, que los patrones de riqueza de especies sean interpretados en términos de asociación (co-existencia) entre especies, demostrando la relevancia de este enfoque para evaluar la relación inherente entre diversidad y distribución. Asimismo, esta distribución de frecuencias puede analizarse desde la perspectiva de las especies individuales. Esto es, la variación en riqueza de especies dentro del área de distribución de una especie focal. El ‘campo de diversidad’ de una especie hace referencia al conjunto de valores de riqueza de especies en los diferentes sitios que conforman la distribución geográfica de esta (Arita et al. 2008, Villalobos y Arita 2010). En el capítulo dos, exploré la distribución de frecuencias de riqueza de especies en la familia Phyllostomidae (Chiroptera) y los patrones de campo de diversidad de cada una de las especies en esta familia de murciélagos.

El patrón observado de DFRE en la familia Phyllostomidae muestra los efectos de la forma, tamaño y ambiente del continente en la distribución de las especies, así como algunas características idiosincráticas de este clado. La DFRE de los filostómidos es multimodal, con distintos “picos” (i.e. frecuencia alta) de sitios con diferentes valores de riqueza. Por ejemplo, hay zonas extensas al norte (norte de México y suroeste de EUA) y sur (norte de Argentina) de la distribución

que cuentan con pocas especies, así como zonas amplias de riqueza intermedia (cuenca del Amazonas) y zonas restringidas con muy alta riqueza (Andes tropicales). Igualmente, la DFRE presenta un sesgo negativo, demostrando que la mayoría de los sitios tienen más especies que la media general y la variación entre estos es alta. Este patrón difiere significativamente de los escenarios generados por modelos nulos. Es decir, no puede ser explicado únicamente por la variación en los tamaños de área de distribución de las especies individuales, la cohesión de estas y los efectos geométricos (e.g. tamaño y forma del continente). No obstante, el efecto de la cohesión en las áreas de distribución es suficiente (aunque no para explicar el patrón observado) para incrementar la varianza en la DFRE como resultado de asociaciones geográficas positivas (co-existencia) entre especies. En particular, las diferencias entre las simulaciones y el patrón observado son más evidentes en los extremos de la DFRE (i.e. sitios con riqueza menor a 10 especies y mayor a 60), indicando el efecto combinado de la historia evolutiva del clado y la heterogeneidad física del continente. Más interesante aún, la composición de los sitios con los números más bajos en riqueza de especies difiere entre los límites norte y sur de la distribución geográfica de la familia, con especies comparativamente más restringidas (geográficamente) y de origen reciente en el norte y especies más ampliamente distribuidas y antiguas en el sur. Esto sugiere, a su vez, que los mecanismos que determinan la composición de la quiroptero fauna en cada uno de los extremos geográficos de la familia difieren entre sí. Por ejemplo, en el límite norte, la presencia de especies restringidas y de reciente origen apoya la idea de una expansión de la familia Phyllostomidae resultado de diversificación y dispersión hacia regiones subtropicales y templadas del norte (Stevens 2006, Villalobos y Arita 2010). En el límite sur, por el contrario, la coexistencia de unas pocas especies de amplia distribución y origen más antiguo podría sugerir una baja diversificación (no especiación y/o mayor extinción) en condiciones ambientales menos heterogéneas.

El campo de diversidad de cada una de las especies de filostómidos es un reflejo de la tendencia individual de estos murciélagos a distribuirse en zonas geográficas con pocas o muchas especies, expresando la asociación que forma cada especie con el resto de estas. De esta manera, las DFRE's de cada especie pueden analogarse con las funciones de incidencia de Diamond (1975), aunque

con interpretaciones diferentes acorde con la escala de análisis (e.g. competencia vs. procesos evolutivos como diversificación o similitud en preferencias ambientales). En la familia Phyllostomidae hay murciélagos que se encuentran exclusivamente en zonas pobres en especies y otros en zonas de alta diversidad, con la mayoría de murciélagos existiendo entre ambas zonas pero preferentemente hacia regiones con mayor número de especies (i.e. asociaciones geográficas positivas, DFRE's de especies individuales con sesgo negativo). Asimismo, el campo de diversidad de una especie puede ser visto como un mapa de las interacciones potenciales con otras especies, relacionándose cercanamente con la teoría del mosaico geográfico de coevolución (Thompson 2005) al proveer un marco geográfico para evaluar predicciones de esta teoría y comprender la estructura interna de las áreas de distribución individuales a través del estudio de patrones de co-existencia continental entre especies.

Patrones de co-distribución y co-diversidad: teoría y aplicaciones

El patrón geográfico de biodiversidad más evidente es la variación en riqueza de especies. En consecuencia, la riqueza de especies es la variable más atendida en el estudio de este tipo de patrones (Rosenzweig 1995). Los enfoques correlativos tanto como de modelación nula/neutral utilizan dicha variable para evaluar la capacidad de predicción (i.e. ajuste, "goodness of fit" en inglés) de los modelos utilizados (e.g. relación riqueza-ambiente). Sin embargo, por la complejidad de los sistemas ecológicos, las relaciones observadas pueden deberse a múltiples factores y es posible obtener resultados similares con diferentes combinaciones de variables predictivas (Gotelli et al. 2009). Entonces, la comparación unidimensional (i.e. una sola variable de respuesta) entre datos observados y esperados puede limitar la interpretación de los modelos y la potencial comprensión de los patrones observados. Por lo tanto, para evaluar el desempeño de los modelos es necesario usar otros parámetros que describan la estructura interna de los datos. Es decir, considerar variables de respuesta o patrones secundarios (Gotelli et al. 2009) que contengan mayor información en diferentes niveles estructurales y permitan validar dichos modelos (Grimm et al. 2005).

Los análisis desarrollados en este proyecto (gráficas diversidad-distribución, campo de diversidad, campo de dispersión) permiten la construcción de variables de respuesta que incorporan simultáneamente diversidad y distribución. Esto obedece al uso de información común en la cuantificación de riqueza de especies y distribución geográfica: el número de presencias dentro de una matriz de presencia-ausencia (i.e. número de 1's, Villalobos et al. Capítulo 3). Además, el reconocimiento de límites teóricos en la estructura de los datos (i.e. restricciones matemáticas y/o biológicas, como los límites para la dispersión de datos dentro de las gráficas diversidad-distribución) permite, a su vez, poner a prueba hipótesis biogeográficas y macroecológicas evaluando patrones más informativos como son la asociación geográfica entre especies (co-distribución) y la similitud entre sitios en términos de especies compartidas (co-diversidad) (Arita et al. 2008, Borregaard y Rahbek 2010).

Murciélagos filostómidos: asociación entre especies y similitud entre sitios.

El estudio de la relación diversidad-distribución y análisis de los campos de diversidad y dispersión de la familia Phyllostomidae (Chiroptera) mostró patrones de co-distribución y co-diversidad positivos. La gran mayoría de estos murciélagos (84% de 143 especies) co-existen, en promedio, con un gran número de otras especies a lo largo de sus distribuciones geográficas. Asimismo, esta asociación positiva entre especies genera una concomitante similitud entre los diferentes sitios ocupados por la familia. La mayoría de sitios comparten especies y están compuestos por ensamblajes de especies que, en promedio, se distribuyen más ampliamente que el promedio de estos murciélagos. Sin embargo, hay algunas especies (16%) que se desvían del patrón general al asociarse negativamente, en promedio, con el resto de las especies (i.e. coexisten únicamente con unas pocas especies). Igualmente, al norte de la distribución de la familia existen unos cuantos sitios con pocas especies que no son compartidas con otros sitios, generando una asociación negativa promedio entre éstos y el resto de sitios dentro de la distribución geográfica de los filostómidos. La construcción de modelos nulos me permitió evaluar los patrones observados bajo diferentes escenarios alternativos en cuanto a la conformación de las áreas de distribución (e.g. área dispersa vs.

ambiental y geográficamente cohesiva) y bajo el supuesto de independencia entre estas.

Los patrones de co-distribución y co-diversidad positivos mostrados por los murciélagos filostómidos difieren (i.e. son más positivos) de los esperados por los modelos nulos. La asociación positiva entre especies y similitud entre sitios no puede ser explicada únicamente por la variación en tamaños de área de distribución ni por el efecto de factores geográficos (tamaño y forma del dominio geográfico), geométricos (cohesión de las áreas de distribución) o ambientales en la conformación de las áreas de distribución. No obstante, la incorporación de estos factores dentro de los modelos demostró su efecto y la influencia que tienen en la determinación de patrones continentales de diversidad y distribución (e.g. co-distribución y co-diversidad positivas), además de su relevancia en la generación de hipótesis nulas apropiadas para la evaluación de este tipo de patrones. Estos resultados sugieren que, además de los factores mencionados, procesos no considerados directamente en los modelos, principalmente aquellos de tipo histórico como especiación (origen evolutivo no independiente en geografía y/o ambiente), extinción (dinámica estocástica de las distribuciones geográficas) y la historia particular de las especies (características intrínsecas del clado estudiado y contingencia histórica) pueden estar actuando y ejerciendo mayor efecto en la determinación de los patrones de diversidad y distribución.

Avifauna mexicana y la aplicación de las gráficas diversidad-distribución.

La exploración de los patrones anteriores en un grupo bien conocido como son las aves mexicanas bajo un enfoque de conservación biológica, me permitió evaluar tanto la aplicación como la utilidad del marco teórico (herramientas y conceptos) desarrollado en este proyecto. Mediante el análisis de la relación diversidad-distribución desde la perspectiva de las especies y de los sitios, demostré cómo las gráficas diversidad-distribución pueden ser fácilmente extendidas para informar prácticas de conservación, particularmente las fases iniciales de planeación y priorización de sitios y especies para conservar. Por ejemplo, desde la perspectiva de los sitios, es posible reconocer sitios que contienen un alto número de especies que promedian áreas de distribución restringidas (e.g. sitios en la región este de la faja volcánica transmexicana). Por otro lado, desde la perspectiva de las especies,

se pueden identificar especies con distribuciones restringidas y que se localizan en zonas de baja riqueza de otras especies (e.g. las penínsulas de Yucatán y Baja California. Ambos aspectos son relevantes para la planeación y el establecimiento de prioridades de conservación.

Encontré una relación significativamente negativa entre diversidad y distribución en las aves mexicanas, totales y endémicas. Es decir, en general, los sitios más ricos en especies contienen especies con distribución geográfica restringida. Lo cual implica una redundancia entre estas dos medidas de biodiversidad: riqueza y rareza (distribución geográfica restringida), que podría facilitar la selección de sitios para la conservación utilizando solo una de estas medidas. Sin embargo, este descubrimiento no sería posible con una visión unidimensional de la biodiversidad (e.g. evaluando sólo riqueza de especies o sólo restricción geográfica). Se necesita, entonces, poner atención a ambos aspectos y esto es posible con las gráficas diversidad-distribución.

La riqueza de especies de aves y el tipo de ensamblajes formados por estas en cada sitio dentro de México presentan una detallada estructura geográfica. Hay diferencias relevantes entre los patrones observados para la totalidad de las aves mexicanas y aquellas con distribución exclusiva dentro de nuestro país (endémicas), principalmente en términos de riqueza, confirmando lo encontrado en otros estudios menos detallados (Escalante et al. 1993, Navarro-Sigüenza et al. 2009). De hecho, este estudio representa el primer análisis detallado de la diversidad y distribución de la avifauna mexicana que sorprendentemente estaba faltando en la literatura científica (Sánchez-González et al. 2008, con la notable excepción de Koleff et al. 2008 en el estudio del capital natural de México realizado por la comisión nacional para el conocimiento y uso de la biodiversidad, CONABIO, www.conabio.gob.mx). La avifauna total se concentra hacia los estados del sureste del país, siguiendo principalmente zonas montañosas. Por el contrario, las aves endémicas se concentran primordialmente hacia regiones del centro-oeste del país. Estas diferencias entre la totalidad de aves presentes en México y solamente las endémicas, enfatizan la importancia de considerar diferentes medidas de biodiversidad no solo en la descripción de patrones sino también en el establecimiento de prioridades para la conservación. Por ejemplo, una estrategia nacional enfocada en especies endémicas contribuiría

más especies a la conservación global de biodiversidad en comparación con un enfoque de riqueza total simple. Con respecto a los ensamblajes formados por las aves en diferentes sitios, en términos del tamaño promedio de sus áreas de distribución (campo de dispersión promedio, Graves y Rahbek 2005), el patrón geográfico es similar entre todas las aves y las endémicas. Los sitios ocupados por especies que, en promedio, se distribuyen ampliamente están ubicados desde el altiplano mexicano y hacia la frontera norte del país; mientras que aquellos sitios con especies restringidas, en promedio, se ubican hacia el sur y sureste de México.

En ambos grupos de especies, todas las aves y sólo endémicas, la mayoría de estas coexiste (en promedio) con un mayor número de especies que el promedio de riqueza en todo México. Esto confirma que la conservación de regiones ricas en especies podría asegurar la protección de especies ampliamente distribuidas, restringidas y endémicas de manera conjunta. Pero, los patrones también muestran la presencia de aves con distribución restringida ocupando zonas pobres en especies (co-distribución negativa) y que por tanto pueden quedar fuera de acciones de conservación enfocadas únicamente en riqueza de especies. Otra vez, esta información resalta la importancia de un enfoque bidimensional de la biodiversidad en donde se consideren simultáneamente la riqueza y rareza de los sitios y especies, respectivamente. Esfuerzo que es posible llevar a cabo de manera relativamente sencilla con la aplicación de las gráficas diversidad-distribución.

Gráficas diversidad-distribución y parámetros asociados

Las gráficas diversidad-distribución pueden construirse con base en especies o sitios para explorar las propiedades de los campos de diversidad y dispersión, respectivamente, mediante el despliegue de información de riqueza y distribución simultáneamente (Arita et al. 2011, Villalobos et al. Capítulo 3). La dispersión de los datos dentro de estas gráficas está limitada por restricciones biológicas y matemáticas definidas por los valores mínimo y máximo de riqueza y área de distribución, mientras que la tendencia central está determinada por el inverso del valor de diversidad beta de Whittaker en el sistema estudiado (i.e. la “densidad” de la matriz, Christen y Soberón 2009; riqueza proporcional promedio o distribución

proporcional promedio, todos valores equivalentes en una matriz de presencia-ausencia; Arita et al. 2008, 2011). Específicamente, la dispersión detallada de los puntos dentro de estos límites depende de la covarianza estadística entre especies o sitios, a su vez determinada por la co-existencia entre especies (Arita et al. 2011).

La principal ventaja de este tipo de gráficas es el despliegue de toda la información contenida en una matriz de presencia-ausencia (PAM), la unidad básica en análisis biogeográficos y macroecológicos, facilitando la visualización y análisis de la conexión entre riqueza de especies y área de distribución (Borregaard y Rahbek 2010). Así, la información contenida en dichas gráficas puede ser interpretada en términos de procesos que determinan la estructura de los ensamblajes de especies (Arita et al. 2008). Además, permiten la evaluación de diferentes tipos de modelos que intentan recuperar (predecir o explicar) la estructura de los datos (Villalobos y Arita 2010). Por ejemplo, resultados de modelos estocásticos de ubicación y conformación de las áreas de distribución individuales pueden ser resumidos en una PAM e ilustrados en las gráficas diversidad-distribución. Adicionalmente, el patrón agregado de covarianza entre especies o sitios representado en estas gráficas puede resumirse a través de pruebas del cociente de la varianza. Este parámetro fue inicialmente propuesto por Schluter (1984) para analizar patrones de co-existencia (co-distribución) entre especies, pero puede ser fácilmente extendido para analizar la co-diversidad entre sitios (Arita et al. 2011, Villalobos et al. Capítulo 3). El cociente observado se puede utilizar para contrastar con la distribución de cocientes generados a través de los modelos y así evaluar la significancia de los patrones observados, permitiendo poner a prueba hipótesis biogeográficas y macroecológicas que nos acerquen hacia una mejor comprensión de los patrones geográficos de biodiversidad. Finalmente, el uso de información básica de biodiversidad (i.e. presencia-ausencia de especies en un dominio geográfico) confiere una amplia aplicabilidad al marco teórico desarrollado en este proyecto, facilitando su extensión a otros dominios geográficos y taxa y, por tanto, la comparación entre diferentes conjuntos de datos.

Modelos nulos y la comprensión de patrones de biodiversidad

“... for unless they could help us do something in the task of investigating natural phenomena, there would be no reason for choosing model building over astrology or mystic revelation as a source of knowledge of the natural world.”

William C. Wimsatt (1987)

Un componente importante de este proyecto doctoral fue la aplicación de modelos nulos para analizar los patrones de biodiversidad aquí descritos. Tanto la relevancia como la controversia alrededor de este enfoque de modelación como estrategia de investigación en ecología, sugieren una discusión acerca de su significado, uso, interpretación y alcances. Esto es lo que intento hacer en esta última parte de mi disertación.

Los modelos son representaciones o descripciones generalizadas de un fenómeno (Hilburn y Mangel 1997). La aplicación de un enfoque de modelación (construcción y evaluación de modelos) en ecología responde a dos razones principales: el reconocimiento de la complejidad en sistemas ecológicos y el objetivo de identificar generalidades en estos sistemas (Taylor 2005). Cualquier modelo es una idealización del fenómeno estudiado y, explícita o implícitamente, implica simplificar e ignorar variables o interacciones entre estas. Esta simplificación permite, a su vez, evaluar la validez de los supuestos biológicos incluidos en el modelo (en caso de tenerlos) y dirigir la atención hacia donde los modelos se desvían de la realidad. En este sentido, los modelos se consideran “falsos” o “nulos”, con el fin explícito de evaluar la eficacia de las variables no incluidas en éstos y contribuir al conocimiento de los fenómenos estudiados a través de la evaluación de los supuestos y la generación de teoría (Wimsatt 1987).

La importancia de los modelos nulos en ecología de comunidades y recientemente en macroecología, radica en la posibilidad de poner a prueba hipótesis específicas y evaluar nuestra comprensión acerca de los patrones observados cuando no podemos llevar a cabo experimentación controlada. Una de las principales ventajas de los modelos nulos es la generación de hipótesis nulas. Es decir, permiten explorar las posibilidades de un patrón (i.e. cuáles son los escenarios posibles) en caso de que no estén actuando ciertos mecanismos (excluidos del modelo). Esto incluye la acción de efectos estocásticos y la

posibilidad de que no haya ningún efecto (Gotelli y Graves 1996) y, por tanto, que los patrones observados terminen siendo “aparentes” y no “reales” (*sensu* May 1984). Básicamente, los modelos nulos permiten construir distribuciones estadísticas de las variables de interés (i.e. estadísticos descriptivos o índices utilizados para describir el patrón observado, e.g. cocientes taxonómicos, medidas de coexistencia) a partir de modelos estocásticos basados en teoría biológica y métodos Monte Carlo (Slobodkin 1987) (i.e. mantienen cierta información biológica básica, e.g. riqueza de especies, distribución de las especies, mientras aleatorizan otros elementos [Gotelli y McGill 2006]).

Es importante resaltar la manera en que podemos utilizar e interpretar modelos nulos, como los que aquí presenté, en la comprensión de patrones geográficos de biodiversidad. Usualmente, la interpretación de modelos nulos es hecha con relación a su “falsedad” y, por tanto, la importancia de variables excluidas. Por ejemplo, desviaciones entre patrones generados por modelos y el patrón observado pueden utilizarse como evidencia indirecta del efecto de dichos mecanismos excluidos. Por el contrario, si el patrón observado no difiere de los generados por modelación nula, los mecanismos excluidos pueden considerarse aleatorios en relación a los supuestos del modelo y, por tanto, no ser necesarios para explicar el patrón observado (Gotelli y Graves 1996). Esta interpretación clásica sigue vigente. Sin embargo, su creciente aplicación y la actual capacidad tecnológica (e.g. programación y cómputo) para resolver modelos complejos e incorporar mecanismos específicos más allá de la aleatorización de datos observados, ha generado confusión con respecto a la aplicación e interpretación de modelos en general.

En primer lugar, existe una ambigüedad terminológica con respecto a lo que es un modelo nulo, neutral, aleatorio, base, referencia o estocástico (Wimsatt 1987). Segundo, y quizás más relevante, es el uso de modelos como herramientas heurísticas, explicativas o predictivas. Todos los modelos pueden considerarse herramientas heurísticas, pues contribuyen al objetivo de comprender los fenómenos estudiados. Sin embargo, hay una diferencia fundamental entre explicar y predecir fenómenos (Epstein 2008). Por un lado, un modelo puede intentar explicar un fenómeno con base en los supuestos considerados en el

modelo. Es decir, evalúa si los supuestos considerados son suficientes para explicar el comportamiento del fenómeno observado e identificar procesos o parámetros importantes en la conformación de un patrón biológico y poner a prueba nuestro conocimiento de dichos fenómenos (Hilborn y Mangel 1997). Por otro lado, la intención de un modelo puede ser predecir un resultado numérico particular para lo cual es necesario considerar los supuestos como verdaderos mecanismos causales del fenómeno y definir sus valores o magnitud (Gotelli y McGill 2006). Esta diferencia tiene relación con la interpretación “débil” o “fuerte” de modelos generales para explicar patrones macroecológicos (*sensu* Bell 2001). Una interpretación “débil” implica considerar al modelo como generador de hipótesis nulas con las cuales deben contrastarse los patrones observados, sin reconocer que los procesos dentro del modelo son necesariamente los mecanismos causales del patrón observado. La interpretación “dura” implica, por el contrario, que los procesos o supuestos del modelo son efectivamente aquellos responsables del patrón observado (Arita y Vázquez-Domínguez 2008, Bell 2001).

Otro aspecto importante en esta dicotomía entre modelos explicativos y predictivos es la incorporación de procesos mecanísticos y dinámicos. Los modelos nulos tradicionales generan ‘hipótesis nulas estadísticas’ a través de la aleatorización de datos existentes. Cuando esta aleatorización incluye un proceso específico (e.g. reglas particulares de dispersión o colonización, Barve et al. 2011), los modelos generan ‘hipótesis nulas dinámicas’ (Gotelli y McGill 2006). En consecuencia, modelos basados en procesos pueden considerarse predictivos (e.g. modelos neutrales). La diferencia entre ambos tipos de modelos parece sencilla. Sin embargo, es posible construir modelos dinámicos que no buscan ser predictivos sino explicativos (e.g. Arita y Vázquez-Domínguez 2008) y modelos ‘estáticos’ que incorporan procesos biológicos con el fin de evaluar nuestro conocimiento de los patrones naturales (e.g. Villalobos et al. Capítulo 3). La pregunta obvia es, entonces, ¿a qué tipo de modelos corresponden los desarrollados en esta tesis?

En este trabajo de tesis desarrollé diferentes modelos para evaluar cómo las áreas de distribución individuales de las especies influyen en los patrones de asociación entre estas y, consecuentemente, en la variación en riqueza de especies y la

relación entre ambas propiedades (distribución y riqueza) de la biodiversidad. En particular, los modelos que construí para este proyecto suponen distribución geográfica independiente entre especies y diferentes maneras en que las áreas de distribución individuales pueden construirse, manteniendo los tamaños de área de distribución y el número de especies observados. De manera que, estrictamente pueden considerarse como modelos nulos generadores de hipótesis nulas estadísticas y ser interpretados desde una perspectiva “débil” con base en los supuestos considerados. No obstante, es importante aclarar la implicación que tiene combinar la aleatorización de datos observados y la incorporación de procesos específicos, además de la necesidad de construir diferentes modelos.

La simplicidad de los modelos nulos me permitió reconocer principios fundamentales de cómo la distribución de las especies (diferentes factores modelados: cohesión ambiental, similitud de nicho) influye en los patrones de asociación entre especies, así como factores geométricos y estocásticos. Específicamente, identifiqué el efecto de la cohesión de las áreas de distribución, principalmente cuando es mediada por el ambiente, en la generación de asociaciones positivas entre las especies y una mayor variación en los valores de riqueza dentro del dominio geográfico. Asimismo, comprobé que la similitud de nicho entre especies, representada por una similitud contingente en las preferencias ambientales para distribuirse geográficamente, contribuye positivamente a la asociación entre especies. Un resultado importante de la aplicación de estos modelos al estudio de patrones de co-distribución y co-diversidad es que el escenario esperado, bajo los supuestos de dichos modelos, es una inherente asociación positiva entre especies y una similitud entre sitios (Villalobos et al. Capítulo 3). Este resultado anteriormente sólo había sido reconocido para el caso de co-distribución entre especies (Bell 2005, Ulrich 2004; aunque usando modelos neutrales). Esto sugiere que dichos patrones positivos deben ser incorporados en las explicaciones de patrones geográficos de biodiversidad. Sin embargo, las desviaciones encontradas entre el patrón observado y aquellos generados por estos modelos nulos sugieren el efecto de otros mecanismos no considerados en dichos modelos.

El efecto de procesos específicos, como cohesión y similitud de nicho, se incorporó a las restricciones ya consideradas (geométricas: dominio geográfico

limitado, geográficas: tamaño y forma del dominio geográfico) en los modelos con el objetivo de “informarlos biológicamente” bajo el supuesto que dichos procesos efectivamente influyen en la distribución geográfica de las especies y así evaluar los patrones observados con base en nuestro conocimiento actual de dichos patrones. Esto implicó la construcción de diferentes modelos que fueron comparados entre sí y con respecto a los patrones observados. En este sentido, son útiles en la discriminación de hipótesis alternativas mediante la construcción y evaluación de modelos cada vez más completos. La flexibilidad del enfoque de modelación aquí presentado evita la limitación de poner a prueba una sola hipótesis (i.e. prueba de hipótesis clásica, en donde una hipótesis nula es contrastada contra una sola hipótesis alternativa, Slobodkin 1987), permitiendo evaluar diferentes hipótesis nulas (Chamberlain 1890, Elliot y Brook 2007) bajo un marco teórico unificado (Harte 2004). Finalmente, permite identificar la potencial importancia de diferentes factores en la determinación de los patrones observados y el reconocimiento de características emergentes, necesarias y suficientes para entender dichos patrones (Hilborn y Mangel 1997).

En suma, los resultados de comparar estos modelos nulos contra los patrones observados indican que, en la escala de análisis de mi estudio, los factores mecanicistas, reproducibles, de cohesión en la distribución geográfica y preferencias ambientales similares son capaces de reproducir aspectos importantes de la señal estadística en la distribución de la biodiversidad. No obstante, los mecanismos restantes, principalmente históricos (e.g. especiación, extinción, dispersión) y adaptativos (e.g. dinámica de las áreas de distribución, evolución de nicho) pueden estar contribuyendo sustancialmente a las contingencias históricas que conllevan al patrón detallado de biodiversidad. Poner a prueba el efecto de estos factores implica un cambio en la manera de hacer investigación macroecológica. Específicamente, implica la construcción de modelos dinámicos basados en procesos específicos, así como la parametrización de dichos procesos responsables y la disponibilidad de información detallada acerca de las relaciones filogenéticas entre especies y los ambientes históricos (Gotelli et al. 2009). Para evaluar la generalidad de dichos modelos, y por tanto de nuestra comprensión de los patrones biológicos, es necesario extender su aplicación a grupos taxonómicos con diferentes características biológicas (grupos

monofiléticos, preferentemente) y considerar diferentes variables de respuesta, así como la generación de medidas de comparación entre modelos y ajuste entre modelos y datos observados (Gotelli et al. 2009). Esta es la frontera de investigación macroecológica actual y este trabajo de tesis doctoral representa un avance en esta dirección.

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