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IMPLICACIONES EN LA DISTRIBUCIÓN GEOGRÁFICA DE LOS
VERTEBRADOS TERRESTRES

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P R E S E N T A

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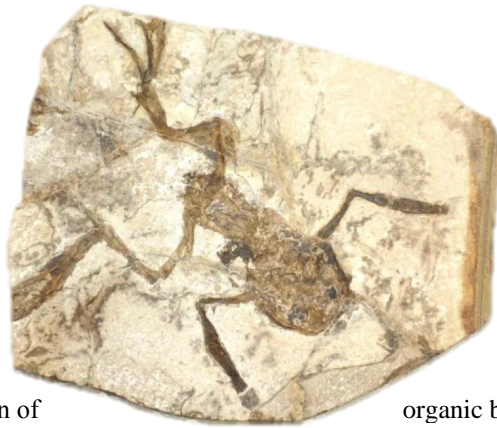
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‘In considering the distribution of organic beings over the face of the globe, the first great fact which strikes us is, that neither the similarity nor the dissimilarity of the inhabitants of various regions can be accounted for by their climatal and other physical conditions ... A second great fact which strikes us in our general review is, that barriers of any kind, or obstacles to free migration, are related in a close and important manner to differences between the productions of various regions.’

Ch.Darwin 1859

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RESUMEN

El clima juega un papel central en la fisiología de las especies que se refleja en sus áreas de distribución a escalas geográficas. Al respecto, es bien conocido desde los primeros estudios de Humbolt, Buffon y Wallace en los siglos XVIII y XIX, que no todos los sitios que son climáticamente similares presentan el mismo ensamblaje de especies; sin embargo, la falta de información sobre las especies y los ambientes no había permitido profundizar en el análisis de este tipo de preguntas, hasta ahora. Mediante el análisis de las condiciones climáticas de las áreas que habita una especie y cómo éstas cambian en el tiempo, se pueden explorar diversos temas biogeográficos; por ejemplo, el grado de equilibrio climático que tienen las especies en la actualidad, o cuántas regiones climáticamente similares a las áreas de distribución de una especie hay en otros lugares y por qué no está presente allá; o si son los factores históricos, como la deriva continental o qué tipo de barreras geográficas delimitan las áreas de distribución de las especies. En general, entender el papel que ha jugado y juega el clima en los procesos de las poblaciones y las especies que repercuten en su distribución geográfica es de interés teórico y aplicado, dado el presente cambio climático y la actual crisis de biodiversidad. Este estudio pretende presentar una visión de amplia escala espacial y temporal acerca de la influencia que tiene el clima en la organización de las comunidades bióticas. En particular, se evaluó (1) la diferencia entre las áreas de distribución actual de los anfibios y la distribución global de las condiciones climáticas favorables en diferentes regiones, escalas y niveles taxonómicos; (2) el rol del clima en la invasión intercontinental de 33 géneros de mamíferos terrestres entre el Mioceno y el Presente, *i.e.*, antes y después de surgimiento del Istmo de Panamá que produjo el Gran Intercambio Biótico Americano (GIBA); y (3) el análisis climático dentro de un contexto filogenético para entender los patrones de parapatría presente en cuatro especies de aves del género *Toxostoma* en las zonas áridas del suroeste de Estados Unidos de América y la Península de Baja California. Los resultados demuestran que a una escala global, el grado de ocupación de las áreas climáticamente favorables de los anfibios depende de la provincia biogeográfica que habitan y no del orden al que pertenecen. Las especies de la región Neártica estuvieron en mayor equilibrio climático que las especies de la región Paleártica, aunque las regiones biogeográficas tropicales mostraron una tendencia a estar en menor equilibrio que las no tropicales. Con respecto al rol del clima en el GIBA, los resultados mostraron que la presencia y la extensión de condiciones climáticas favorables, en particular el aumento de dichas áreas del pasado hacia el presente, favorecieron la dispersión de los mamíferos norteamericanos y su colonización en Sudamérica de manera asimétrica, con respecto a sus contrapartes sudamericanas. En particular, los mamíferos norteamericanos presentaron un incremento de su área potencial en Sudamérica del Mioceno al Plioceno (entre los 8 y los 2.95 millones de años) y durante el Pleistoceno (entre los 115 mil y 21 mil años); en contraste, los mamíferos sudamericanos presentaron una disminución del área potencial en los mismos periodos. La diferencia en el grado de conectividad en Centroamérica entre dispersores y no dispersores determinó el éxito en el movimiento de los dispersores en distancias cortas. Finalmente, el análisis del equilibrio climático en las especies de *Toxostoma* permitió proponer una hipótesis sobre el proceso de especiación y actual ocupación de estas aves en Baja California, que se basa en una probable exclusión competitiva en el pasado, con un consecuente proceso de especiación alopátrica asociado a la presencia de una barreras bióticas. Este resultado apoya la teoría de exclusión filogenética en etapas tempranas de especiación con una posterior diferenciación y puede constituir una relación importante con la teoría de ensamblaje de comunidades. Los

resultados y conclusiones de los capítulos de este trabajo muestran el papel central del clima en los procesos biogeográficos. Considero que es fundamental continuar profundizando en este tema con el fin de entender de mejor manera cómo el clima pasado y actual, en escalas temporales cortas y amplias, influye en la distribución geográfica de las especies, para con ello poder anticipar los efectos del episodio actual de cambio climático.

ABSTRACT

Climate has a central role in the physiology of species, which in turn, determine their geographic distributions. It is well known, since the biogeographical works of Buffon, Humbolt and Wallace, during the XVIII and XIX century, that sites climatically similar do not necessarily hold the same species assemblage. However, the scarce information available regarding the relationship between species and the environment has prevented scientists from addressing these issues thoroughly, until recent times. It is possible to explore diverse biogeographic issues from the currently occupancy of species and its relation to climatic patterns; for example, the current degree of species' equilibrium with climate, or why some regions that are climatically similar to those occupied by a species remain unoccupied by it. Furthermore, understanding the role that climate plays in population processes that influence the geographic range of species is not only of mere academic interest, but given the current climatic change it has profound implications. In this work, I present a large-scale view of the influence of climate in the organization of biotic communities. In particular, I assessed: (1) the difference between the current geographic distribution of all amphibians and their areas of suitable climatic conditions (potential distribution) in different biogeographic regions, taxonomic levels, and scales; (2) the role of climate in the intercontinental colonization of 33 terrestrial mammalian genera from the Miocene to the Present, before and during the Great American Biotic Interchange (GABI); and (3) the climatic and genetic differences among four *Toxostoma* bird species in the Baja California Peninsula, to understand their current geographic patterns. For the first case, results demonstrate that the degree of occupation of climatic suitable areas of amphibians depend on the biogeographical region they inhabit, where species from the Nearctic region held higher equilibrium than the Palearic ones, but in general, species from tropical regions showed lower equilibrium than the non-tropical ones. For the second case, results indicated that the extent of suitable climatic conditions along time was greater for North American mammals in South America than the reverse; also, connectivity of suitable areas in Central America was greater for successful dispersal mammals than those who did not disperse. Finally, the analysis of equilibrium with climate of the *Toxostoma* species suggested that the speciation process and current occupation in Baja California might have been driven by competitive exclusion in the past with a consequent allopatric speciation associated with the presence of a biotic barrier. In sum, results from the chapters of this work demonstrate the central role of climate in diverse biogeographic processes. It is necessary to continue with this research line in order to get a better understanding of species' responses to climate in the past and present, both at small and large spatial and temporal scales, with the aim to anticipating the possible biotic aftermath of the current climate change episode.

INTRODUCCIÓN

La importancia del clima para explicar la distribución geográfica de los seres vivos ha sido reconocida desde hace siglos (Humboldt & Aimé 1807; De Candolle 1855). Sin embargo, hasta hace poco más de una década se ha retomado el concepto de equilibrio de las especies con el clima, también conocido como “ocupación del rango”, *sensu* Svenning y Skov (2004), refiriéndose a la situación donde el ámbito geográfico de las especies está completamente determinado por el conjunto de condiciones climáticas presentes, *i.e.* las especies están presentes en todas las áreas favorables y están ausentes en todas las no favorables (Araújo & Pearson 2005). No obstante, se han identificado también otros factores que determinan la ocurrencia de las especies, como la capacidad de dispersión, las barreras geográficas y las interacciones bióticas (Soberón & Peterson 2005), por lo que, en general, las especies no ocupan toda su área climática favorable. A grandes escalas, el grado de equilibrio climático de la especie es un importante aspecto en el estudio de la ecología (Davis 1986; Gaston 2003) y, distinguir el rol relativo del clima en la determinación del área de distribución de las especies, tiene no sólo un interés teórico sino que es también clave en el entendimiento de las respuestas de las especies ante los cambios climáticos, así como en la dinámica de invasión de nuevas áreas (Araújo & Pearson 2005) y para el mejor entendimiento de la crisis actual de la biodiversidad (Avisé *et al.* 2008).

Los primeros trabajos al respecto han propuesto que el grado de equilibrio climático varía en las especies de plantas, aves, anfibios y reptiles (Svenning & Skov 2004; Araújo & Pearson 2005) en Europa y en mamíferos en México (Munguía *et al.* 2008). Estas diferencias entre taxones son atribuidas a su distinto modo de *dispersión*. Por ejemplo, en Europa el clima es un predictor más débil para anfibios y reptiles que para aves y plantas (Araújo & Pearson 2005), por lo que las especies no ocupan toda su área potencial. Se ha propuesto que especies de plantas, árboles y hierbas de Europa aún se encuentran expandiéndose hacia altas latitudes a partir de sus refugios pleistocénicos, por lo que presentan distribuciones limitadas fuertemente por la dispersión (Skov & Svenning 2004; Svenning & Skov 2004, 2005, 2007).

Así, la habilidad de dispersión y posterior colonización de las especies no sólo depende de que la especie llegue o pueda acceder a nuevas regiones, sino también de la presencia de sitios favorables. Muestra de ello son las especies invasoras introducidas por

el hombre accidental o intencionalmente que han logrado colonizar dichas áreas (Peterson *et al.* 2008). Por un lado, la inaccesibilidad y la baja habilidad de dispersión es entonces clave para entender porqué las especies no ocupan todas las áreas climáticamente adecuadas y por el otro, la ausencia de dichas condiciones en regiones accesibles determina su presencia.

Desde hace tiempo se ha reconocido que las áreas de distribución son dinámicas. Al respecto, el contexto temporal con el que contribuye la paleontología juega un papel clave en el conocimiento de cómo las comunidades han cambiado en la historia de la Tierra. Recientemente ha habido un rápido incremento de los registros paleoclimáticos que van desde el Cretácico hasta el presente (Bradley *et al.* 1999) y, debido a que ha mejorado la datación de las rocas portadoras y la bioestratigrafía, se incrementa la oportunidad de asociar las diferentes localidades fósiles de un mismo taxón, sobre escenarios ambientales, de periodos pasados (paleoautoecología) y dar seguimiento a la dinámica de las comunidades completas en respuesta al medio ambiente a gran escala (paleosinecología). Esto abre una oportunidad de analizar procesos de invasión pasadas, ya que al conocer la localización de diferentes taxones en diferentes tiempos, es posible asociar el paleoclima con las ocurrencias fósiles y fortalecer las inferencias de los procesos biogeográficos, como son los de vicarianza y dispersión. Los predictores que presentan restricciones ante una dispersión geográfica han sido escasamente estudiados e implementados en aplicaciones paleobiológicas (Svenning *et al.* 2008; Blach-Overgaard *et al.* 2010; Svenning *et al.* 2011). El entendimiento de dichos procesos incrementa además el conocimiento sobre las especies contemporáneas, su respuesta ante las variaciones climáticas, y evidencian las condiciones ambientales previas favorables al éxito de la invasión de especies no nativas.

Aunque es indiscutible que las interacciones bióticas (como competencia, depredación, parasitismo, herbivoría, etc.) tienen un papel importante en el establecimiento de los individuos de una especie en las comunidades, existe un escaso conocimiento de cómo estas interacciones actúan a escalas geográficas. Al respecto ha sido de particular interés entender cómo las interacciones pueden moldear las distribuciones geográficas (Terborgh 1985; Haffer 1989; Sánchez-Cordero *et al.* 2008). Asociado a este fenómeno, la similitud ecológica de diferentes especies ha sido asociada con su historia evolutiva; i.e. especies cercanas filogenéticamente presentan conservadurismo de nicho ecológico, es decir son parecidas en sus requerimientos ambientales (Peterson *et al.* 1999). En este sentido se esperaría que especies similares

ecológicamente y cercanas filogenéticamente no coincidan geográficamente para evitar la competencia, por lo tanto la estructura geográfica de las especies tendería a ser parapátrica. Dicha similitud ecológica hace referencia al parecido en las variables ambientales que definen la distribución de una especie con respecto a otra y la parapatría hace referencia a la situación geográfica de especies con áreas contiguas. En particular, en la presente disertación, se analiza cómo la similitud ecológica juega un rol en el establecimiento de barreras bióticas entre especies hermanas y además promueve la parapatría entre especies no hermanas.

La alta congruencia de los cambios y fluctuaciones climáticos con la presencia y la dinámica del área de distribución de las especies ha sido reconocida. Sin embargo, el grado en el que las especies están en equilibrio con el clima, no ha sido explorado actualmente a escalas espaciales globales, ni para evaluar procesos de colonización a lo largo de grandes escalas de tiempo (Svenning *et al.* 2008; Blach-Overgaard *et al.* 2010; Svenning *et al.* 2011) o asociar los procesos de especiación (Svenning & Skov 2004, 2007; Munguía *et al.* 2008; Hof *et al.* 2012; Sánchez *et al.* 2012). Si se estima el área potencial de las especies con las variables climáticas, es posible evaluar dicho grado de equilibrio y contextualizarlo en patrones y procesos biogeográficos. Así, el Capítulo I se desarrolló bajo la hipótesis en la que si existe influencia en el grado de ocupación del área potencial de las especies (equilibrio climático), éste debe estar asociado a la geografía-gradiente latitudinal y deriva continental –y, a las adaptaciones de las especies como la habilidad de dispersión, por lo que el equilibrio climático presenta una diferencia tanto en el patrón espacial como en el taxonómico. El principal objetivo para este capítulo es contrastar las diferencias tanto entre taxones como entre provincias mediante la diferencia existente entre el área geográfica potencial (P) y observada en el presente (O) de los anfibios a escala mundial.

El entendimiento de la dispersión de las especies a escalas continentales o geo-dispersión (Lieberman 2003) son el principal foco de atención en el Capítulo II dónde la hipótesis plantea que la accesibilidad de las especies a un nuevo continente, ante la desaparición de una barrera geográfica, depende de la presencia de áreas climáticas favorables y la distancia, las cuales son resultado de la determinación de las áreas potenciales de distribución de los mamíferos en América durante el GIBA (desde el Mioceno al Holoceno) y son la principal causa del desbalance en el número de especies que

colonizaron los subcontinentes alternos. Así el objetivo general en este apartado es determinar la diferencia en áreas potenciales y conectividad de áreas entre subcontinentes tanto en taxones dispersores como en los no dispersores participantes del GIBA.

Finalmente la hipótesis a probar en el Capítulo III es que los procesos de especiación y geografía de las especies de aves del género *Toxostoma* en las zonas áridas del suroeste de Estados Unidos y la Península de Baja California están asociados con la evolución del nicho ecológico. En particular, el objetivo es evaluar la similitud ecológica de estas aves en un contexto filogenético para explicar las causas del aislamiento de las especies hermanas por la presencia de especies no hermanas, que las separan geográficamente (barreras bióticas). Al concluir los tres capítulos mencionados se desarrolla una discusión general de los resultados, problemas de los métodos y alternativas futuras.

Capítulo I

El equilibrio climático de la distribución global de los anfibios

Equilibrium of Global Amphibian Species Distributions with Climate

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Abstract

A common assumption in bioclimatic envelope modeling is that species distributions are in equilibrium with contemporary climate. A number of studies have measured departures from equilibrium in species distributions in particular regions, but such investigations were never carried out for a complete lineage across its entire distribution. We measure departures of equilibrium with contemporary climate for the distributions of the world amphibian species. Specifically, we fitted bioclimatic envelopes for 5544 species using three presence-only models. We then measured the proportion of the modeled envelope that is currently occupied by the species, as a metric of equilibrium of species distributions with climate. The assumption was that the greater the difference between modeled bioclimatic envelope and the occupied distribution, the greater the likelihood that species distribution would not be at equilibrium with contemporary climate. On average, amphibians occupied 30% to 57% of their potential distributions. Although patterns differed across regions, there were no significant differences among lineages. Species in the Neotropic, Afrotropics, Indo-Malay, and Palaearctic occupied a smaller proportion of their potential distributions than species in the Nearctic, Madagascar, and Australasia. We acknowledge that our models underestimate non equilibrium, and discuss potential reasons for the observed patterns. From a modeling perspective our results support the view that at global scale bioclimatic envelope models might perform similarly across lineages but differently across regions.

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Introduction

A common assumption underlying several large-scale ecological models is that species distributions are in equilibrium with contemporary climate; in other words, that species are generally present in climatically suitable areas while being absent from unsuitable ones [1]. Obviously, this construct is a simplification because species distributions are rarely, if ever, in full equilibrium with contemporary climate. The question is how far species distributions are from climatic equilibrium and, more specifically, how equilibrium varies across taxa and regions. Addressing these questions is not only of theoretical interest. It is also important for understanding the limits to predicting climate change impacts on biodiversity [2,3]. Even though the assumption of equilibrium underpins all models that empirically estimate species-climate relationships, only a few studies have quantified the departure of observed distributions from potential ones. Existing studies were restricted to Europe [1,4] and Mexico [5]. In the case of the European analyses, equilibrium was estimated using a small

proportion of the total extent of species distributions, thus leading to an underestimation of the realized niches.

Another study that overcomes the circularity of quantifying species-climate equilibrium using range filling of potential distributions (which themselves are constrained by biotic interactions and dispersal limitation), used physiologically-derived estimates of the fundamental niche for a small number of bird species in North and South America, and compared them with estimates of the realized niche [6]. Unfortunately, such approach is unfeasible for all amphibians of the world.

Generally, studies investigating species-climate equilibrium with correlative approaches found high levels of non equilibrium, particularly among species with poor dispersal abilities [7]. However, given the small number of studies addressing this question, it is difficult to generalize. Questions such as 'are patterns of non-equilibrium geographically or taxonomically structured?' remain unanswered. Furthermore, any bias introduced by measuring degrees of equilibrium using incomplete species distributions has not been quantified.

Here, we seek to contribute to this debate by providing the first global analysis of equilibrium patterns for an entire class of organisms. We estimated climate envelopes for the world amphibian species using familiar bioclimatic envelope techniques. We then measured the proportion of each species' potential climatic distribution that is currently occupied. The underlying assumption of our test is that the greater the difference between potential and occupied distributions, the greater the likelihood that species distributions would not be at equilibrium with contemporary climate [4]. We then explored how equilibrium of species distributions varies across taxa and regions.

Methods

Data

Distributions of 5544 amphibian species were extracted from the Global Amphibian Assessment database (IUCN 2004). Polygons of species ranges were resampled at a 2-degree latitude-longitude grid cell resolution. Species that occurred in two ($N=235$) or more biogeographical regions ($N=7$) were not modeled to ensure comparability between the global and regional analysis (see description below). Restricted range sized species are known to cause statistical problems for fitting of bioclimatic envelope models [8–10]. We quantified this problem and found that the median range size of amphibians of the world at a 2-degree resolution is equal to three pixels. So, imposing a rule of exclusion for restricted range species would drastically limit the number of species that could be modeled. To deal with the problem, we split the species data by range sizes and analyzed results for sets of species with >0 cells ($N_{\text{Global}}=5544$, $N_{\text{Regional}}=5309$), >5 cells ($N_{\text{Global}}=2005$, $N_{\text{Regional}}=1816$), >10 cells ($N_{\text{Global}}=1321$, $N_{\text{Regional}}=1163$), and >15 cells ($N_{\text{Global}}=1021$, $N_{\text{Regional}}=886$). Although the quality of the models for the data sets including the rarest species is reduced, we assumed that if the patterns emerging are qualitatively similar across the different subsets of species, then the conclusions should be relatively insensitive to the problem of modeling species with restricted ranges. Bioclimatic envelope models were then fitted for the amphibian species using five climate variables selected among those previously reported to be important for hylids (tree frogs) [11] and salamanders [12]: (1) the minimum temperature of the coldest month; (2) the maximum temperature of the warmest month; (3) the annual mean temperature; (4) annual precipitation; and (5) temperature seasonality (standard deviation * 100). Climate data were extracted from the WorldClim database [13].

Climate envelopes

In order to assess inter-model variability [14–16], species potential climatic distributions were calculated with BIOCLIM [17], Euclidian (ED), and Mahalanobis distances [18], using a combination of climate variables and observed species occurrences. BIOCLIM estimates species envelopes by defining the bounding hyper-box that encloses all records of the species in the climatic space. To characterize the hyper-box, it creates a rectilinear envelope in the climatic space, defined by the most extreme records of the species on each axis. To minimize the effect of outliers, species records are sorted along each variable, and the records that lie within a certain percentile range of the data are used for characterizing the envelopes. In this study, we applied a percentile range of 95%, the default option in most studies using this approach [19]. BIOCLIM tends to overestimate species potential distributions slightly more than other presence-only models [20] and significantly more than presence/absence methods [21]. This overestimation of observed ranges leads to

an inflation of false positives (i.e., a species predicted to occur where it has not been recorded), a tendency that contributes to the low-ranking of BIOCLIM when compared with methods that fit more-complex response curves and that adjust projections to balance false positives and false negatives equally. However, if the purpose of the model is to estimate the climatic envelope, then BIOCLIM is potentially as good as many of the concurrent methods available [4].

Euclidian and Mahalanobis distances are conceptually similar to BIOCLIM, but instead of generating a squared hyper-volume, they define circular or elliptical shapes in climatic hyperspace. The idea is to measure the similarity of each occurrence to the mean (or centre) of the ecological space. In Euclidian distances, the distance (D_E) between each occurrence, or grid cell, to the species' centroid is given by:

$$D_E = \sum_i (y_i - y_{b_i})^2$$

Where y_i is the value of the i -th environmental variable and y_{b_i} is the mean of the variable. For the Mahalanobis distance, the distance D_M is given by

$$D_M = (Y - YB)V^{-1}(Y - YB)$$

Where \mathbf{Y} is the vector containing the values of the environmental variables in a cell and \mathbf{YB} is the mean vector across all cells, and \mathbf{V} is the covariance matrix among these variables. Thus, geometrically, whereas BIOCLIM defines the surface range envelope in environmental space as a square (or rectangle), the distances will allow circles, in the case of Euclidian distances (assuming independence effects of the variables) or ellipses in the case of Mahalanobis distances (taking into account the correlation among variables).

Only BIOCLIM was able to characterise climate envelopes for species with <15 records of occurrence. The full set of analysis included: $>0B$ (species with at least 1 record using BIOCLIM), $>5B$, $>10B$, $>15B$, $>15MD$ (from Mahalanobis), and $>15ED$ (from Euclidian Distance). The options for parameterisation of these two methods were the same as defined for BIOCLIM. All models were implemented with BIOENSEMBLES [22,23] software for computer intensive ensemble forecasting.

Equilibrium

For each species, we calculated the potential climate envelope (P) and compared it with its observed distribution (O) (Figure 1). The ratio between O and P O/P was interpreted as a measure of the equilibrium of species distributions with contemporary climate (see also [4,5]); measurements of O/P values closer to 1 were considered to approach equilibrium. We then calculated the mean geographic position (GP) of each species' centroid by matrix multiplication: $GP = AB$, where \mathbf{A} was a transposed matrix of species presence/absence within each grid cell and \mathbf{B} was a matrix with latitude and longitude coordinates for grid cells [24]. The degree of equilibrium of species distributions with climate O/P was then associated with each species' GP and compared across space and taxa. Kruskal-Wallis tests (i.e., a non-parametric test identical to one-way analysis of variance with the data replaced by ranks) were used to test the equality of median O/P values between groups.

Global and Regional analysis

Projections of climatic envelopes were initially made for the entire world, but a regional analysis was also obtained by masking

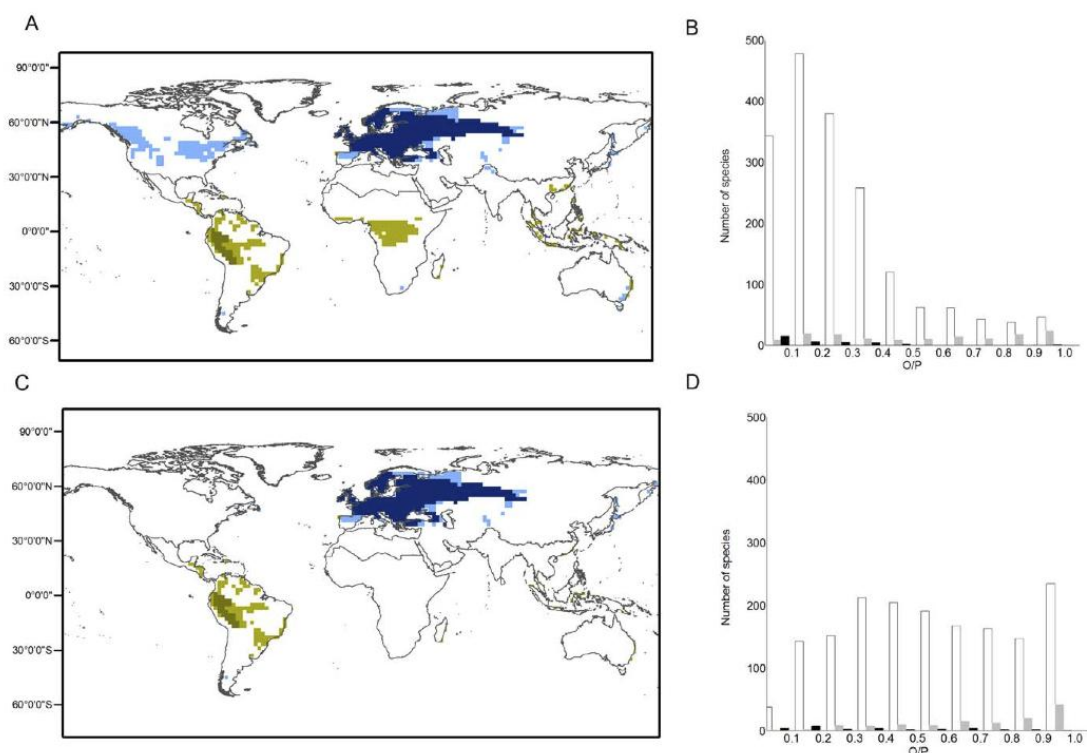


Figure 1. Observed and modeled potential distributions for two selected species: *Lissotriton vulgaris* (Salamandridae, Caudata) in the Palearctic region (Blue) and *Chiasmocleis ventrimaculata* (Microhylidae, Anura) (Green) in the Neotropic region. Dark colors are observed distributions and light colors are potential distributions; the smaller the difference between observed and potential distributions, the greater the expected equilibrium of species with climate. (A) Global analysis, in which models calibrated for species occurring in a particular biogeographical region are allowed to project climate space globally; (C) regional analysis, in which models are not allowed to project climate space beyond the biogeographical region in which the species occurs. Frequency distribution of equilibrium values (O/P) at the (B) global and (D) regional scales. White bars represent Anura, shaded represent Caudata, and black represent Gymnophiona. doi:10.1371/journal.pone.0034420.g001

out climate envelopes occurring outside the biogeographical region where the species occurs (Figure 1). The global analysis was expected to provide quantification of the degree of global equilibrium of species distributions, i.e., discounting for the effects of limited dispersal across biogeographical regions and providing an estimate expected to be closer to the 'abiotically suitable area' available for the species [25]. In contrast, the regional analysis accounted for cross-regional dispersal limitation and other biome-level biotic contingencies [26], thus providing a more rigorous estimate of the potential distribution of species that implicitly accounts for the effects of dispersal and biotic interactions in reducing the abiotically suitable area for the species (Figure 1). Biogeographical regions, or biomes, were classified following the divisions of Selater [27] and Wallace [28], later renamed by Olson *et al.* [29]: Nearctic, Palearctic, Indo-Malay, Australasia, Afrotropics, and Neotropic. We added an additional region, Madagascar, because it is now widely accepted that this region holds a markedly distinct and more diverse biota than anticipated, particularly among amphibian species [30] (Table 1).

For both the global and the regional analyses, comparisons of O/P were made across biogeographical realms and taxonomic groupings at the level of Order: Anura (frogs and toads), Caudata

(newts and salamanders), and Gymnophiona (caecilians). The regional comparison was necessary to tease apart signals that might arise because of the different biogeographical histories of the regions. The taxonomic comparison was undertaken to investigate whether the ecological properties of the groups affected their levels of equilibrium with contemporary climate. Differences in O/P values in regional and global analyses were compared with U-Mann Whitney, which is a non-parametric test of whether two independent samples of observations have equally large values [31]. Results of the analysis are reported for species with >5 cells ($>5B$), since they are qualitatively similar to the patterns obtained with species with broader ranges ($>10B$ and $15B$) and among different bioclimatic models ($15B$, $15MH$ and $15ED$; see full set of results in Table S1, S2 and Figure S1).

Results

We found 1) significant differences in equilibrium (i.e., O/P) among species both when analysis were made including the global potential distributions of the species, which is an attempt to estimate abiotically suitable area for them, and when potential distributions were restricted to the biogeographical region where

Table 1. Geography, richness and equilibrium descriptions across biogeographical regions.

	Afrotropic (without islands)	Australasia (without islands)	Indo-Malay (without islands)	Madagascar	Nearctic (without islands)	Neotropic (without islands)	Palaearctic (without islands)
Area (number of 2decimal degrees cells)	513	488	187	28	1212	559	2041
Maximum and Minimum Latitude	21° HN 35° HS	3° HN 47° HS	33° HN 3° HN	11° HS 25° HS	83° HN 21° HN	27° HN 55° HS	81° HN 17° HN
Number of total latitude geographic coordinates	56°	50°	30°	14°	62°	77°	64°
Percentage in Tropic-Subtropic/Temperate regions	100/0	96.5/3.5	100/0	100/0	30.6/69.4	80.5/19.5	35.9/64.1
Longitudinal wider extent	17° W 51° E	113° E 179° E	67° E 21° E	41° E 51° E	179° W 13° W	109° W 35° W	17° W 179° E
Number of longitude geographic coordinates	68	66	54	10	166	74	196
Number of Biomes	9	9	10	5	11	12	10
Species richness (% total amphibians)	686 (12.9)	516 (9.7)	661 (12.4)	218 (4.1)	249(4.7)	2684 (50.6)	295(5.6)
O/P	0.55	0.70	0.48	0.89	0.83	0.45	0.55

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the species occurs, thus accounting for limited dispersal preventing cross-continent colonization for most amphibians; 2) higher equilibrium among amphibian faunas in Madagascar, Nearctic and Australasian regions compared to the faunas in the Neotropic, Indo-Malayan, Afrotropics, and Palaearctic regions; and 3) that

equilibrium values were not significantly different among amphibian orders (Figure 2).

Global and Regional analysis

Amphibians occupy 30% (Median = 23%) of their potential distribution at global scale. The frequency distribution of

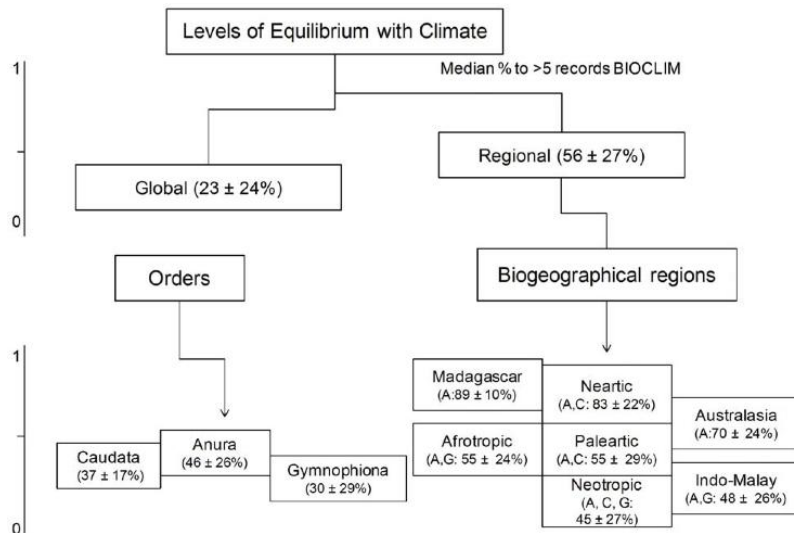


Figure 2. Diagram of climate equilibrium levels at global and regional scales, biogeographical regions and orders. We only show Neotropical orders in the diagram because that show all orders: Caudata (C = salamanders), Anura (A = frogs and toads) and Gymnophiona (G = caecilians), however all regions were analyzed by region (see text).
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equilibrium (O/P ; Figure 1) value is positive skewed (1.34), i.e., most species tend towards low O/P values, and displays positive kurtosis (1.19; Table 2), i.e., with heavy tail and an overly peaked with regards to a normal distribution. In contrast, amphibians were found to occupy 57% of their potential range when analysis were performed at regional scale (Median = 56%; Table 2). The frequency distribution of the equilibrium (O/P ; Figure 1) value is slightly skewed to the right (positive skewness = 0.024) and peaked (low kurtosis = -1.11; Table 2). The frequency distributions of equilibrium values in the global vs. regional analysis were significantly different (U-Mann Whithney = 8098757; $z = 29.68$, $N = 1816$, $P < 0.001$). Orders showed greater median values of O/P in the regional analysis when compared with the global analysis. This outcome is to be expected because the global analysis involves an inflation of the estimated distribution.

Results with the >5B dataset were generally consistent with >10B, >15B, >15MH and >15ED, and are shown in the supplementary material. But the data with >0 records showed discrepant results, particular regarding the frequency distribution of O/P values, which were negatively skewed for the full set of species (see Table S1). In contrast a positively skewed for the subsets of species with larger range sizes and among different bioclimatic models (>5B, >10B, and 15B, 15MH and 15ED; see Table S1) except 15B at regional scale, but the value was almost zero (15B skewness = -0.03). The interpretation of the results for the full set of species (>0B) is therefore driven by the smallest range size species for which models provide less reliable projections of the potential distribution of species.

The greater difference among bioclimatic models was observed in ED model which showed the lowest values of equilibrium because they showed larger P areas than the other models.

However, the relative difference among regions and orders was similar to those observed for the other bioclimatic models.

Regional differences

In the Nearctic, Madagascar and Australasian regions amphibian species showed significantly higher equilibrium with climate ($H_{1817,6} = 288.49$, $P < 0.0001$; Median = 83.88 and 70% respectively) than amphibians inhabiting the other regions (Median = Neotropic 45%, Palearctic 55%, Afrotropics 55%, Indo-Malay 48%; Figure 3, Table 1, see Table S1, S2 and Figure S1). It is noteworthy that amphibians in the Nearctic show higher levels of O/P than the climatically similar Palearctic. When looking at the results by Order, similar patterns emerge. Unsurprisingly, Anurans showed a similar pattern to all amphibians combined as they represent the majority of amphibians ($H_{1655,6} = 220.52$, $P < 0.0001$; Figure 3, Figure 4, Table 3, see Figure S1). But Caudata only occurs in three biogeographical regions, and showed the same patters as observed with Anuran, i.e., greater equilibrium in the Nearctic, followed by the Palearctic and the Neotropic ($H_{29,2} = 24.28$, $P < 0.0001$; Figure 4). In contrast, equilibrium values for Gymnophiona, were not significantly significant across regions ($H_{33,2} = 0.74$, $P = 0.69$; Figure 4).

Taxonomic differences

The three amphibian Orders did not show significant differences in equilibrium within regions ($P > 0.01$). Because not all orders are present in every region, we compared Anura vs. Caudata in the Nearctic ($H_{137,1} = 1.07$, $P = 0.30$) and in the Palearctic ($H_{138,1} = 2.12$, $P = 0.15$) and the Anura vs. Gymnophiona in the Afrotropics ($H_{328,1} = 0.72$, $P = 0.4$) and in the Indo-Malay region (here Gymnophiona showed only 2 species with more than 5 cells, so we did not report the results). Anura is the

Table 2. Descriptive statistics of the level of equilibrium among world.

Scale	Biogeographical region	Order	Mean	Median	Standard deviation	Skewness	Kurtosis	N
Global		All Orders	0.30	0.23	0.24	1.34	1.19	2005
Regional	Neotropic	All Orders	0.57	0.56	0.27	0.02	-1.11	1816
		Anura	0.48	0.45	0.27	0.26	-0.97	729
		Caudata	0.48	0.46	0.27	0.25	-0.97	695
	Palearctic	Gymnophiona	0.33	0.37	0.17	-0.31	-1.47	8
		All Orders	0.38	0.30	0.29	0.67	-1.01	27
		Anura	0.58	0.55	0.29	0.03	-1.32	138
	Nearctic	Anura	0.56	0.50	0.29	0.09	-1.27	97
		Caudata	0.64	0.63	0.28	-0.08	-1.51	41
		All Orders	0.78	0.83	0.22	-0.83	-0.31	137
	Afrotropic	Anura	0.75	0.79	0.24	-0.63	-0.89	57
		Caudata	0.81	0.83	0.20	-0.95	0.29	80
		All Orders	0.55	0.55	0.24	0.11	-0.80	328
Indo-Malay	Anura	0.56	0.55	0.24	0.10	-0.81	325	
	Gymnophiona	0.43	0.54	0.23	-1.68	-----	3	
	All Orders	0.55	0.48	0.26	0.57	-0.86	229	
Madagascar	Anura	0.55	0.49	0.27	0.56	-0.88	226	
	Gymnophiona	0.45	0.42	0.15	0.87	-----	3	
	Anura	0.88	0.89	0.1	-0.88	1.07	72	
Australasia	Anura	0.69	0.70	0.24	-0.24	-1.11	183	

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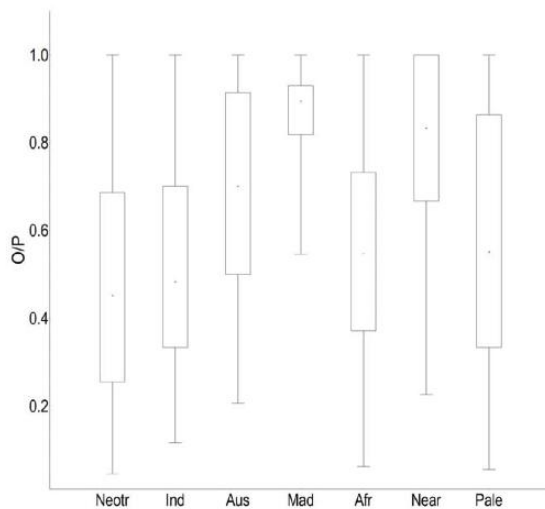


Figure 3. Degree of climatic equilibrium for amphibians within the seven biogeographical regions. Boxes are the percentiles from 25 to 75% around O/P medians, lines indicate the standard deviation. doi:10.1371/journal.pone.0034420.g003

only order present in Madagascar and Australasia. Finally were compared the three orders in the Neotropic ($H_{730,2} = 7.03$, $P = 0.03$).

Discussion

The proportion of the estimated climate envelopes of species that are currently occupied does not differ significantly among amphibian orders. In contrast, significant differences were found among biogeographical regions. Overall, amphibians occupied between 30%–57% (global versus regional analysis) of their potential distributions. Differences between equilibrium at global versus regional levels, highlight the importance of carefully considering the appropriate scale of analysis [25]. Nevertheless, the range of values in our study match those recorded elsewhere with other organisms. For example, Svenning & Skov [4] found that a sample of European temperate tree species occupied 38.3% of their potential distributions, whereas Munguía *et al.* [5] found that this proportion was about 50% for Mexican mammals. Finding the appropriate geographical extent for analysis is not trivial, but we generally recommend that in studies using the O/P ratio as a measure of range filling or equilibrium, the minimum study area should be as large as the largest geographical range of species in the analysis to control for the geographical range [5]. In practice, this strategy involves running the analysis using coherent biogeographical units, with common evolutionary histories, such as the regions used herein.

Fundamentally, though, the levels of range filling among amphibian species are typically low. Our measurement of equilibrium is probably inflated because we measure equilibrium as range filling of potential distributions rather than that of abiotically suitable areas or fundamental niches, which is the quantity of interest. The true level of equilibrium is thus likely to be lower than estimated. Nevertheless, measured low equilibrium among amphibians is unsurprising since the species in the group have generally low dispersal abilities, are often being unable to track suitable climate as it changes through time [32]. However,

significant differences in the degree of range filling among regions indicate that the ability of species to track climate changes varies regionally. According to our models, amphibians in the Nearctic, Madagascar, and Australasia have greater levels of equilibrium with contemporary climate than amphibians in the Neotropic, Afrotropics, Indo-Malay, and the Palearctic. It follows, that the ability to model species distributions, particularly when models are used for transferability [33,34] or extrapolation [35], is greatest in the regions where species have higher levels of equilibrium with climate.

Our study, being based on correlations and on a rather coarse resolution data for species distributions and climate, does not illuminate as to the reasons why range filling varies among amphibians in different parts of the world. Speculations can be offered and some might provide inspiration for future studies. For example, it is noteworthy that two of the biogeographical regions with higher equilibrium are also among the smaller, i.e., Madagascar and Australasia. Just because these regions are small, compared to biogeographical regions that span across vast continents, it is more likely that species inhabiting them can colonize a greater proportion of suitable areas. Another region that is small but has amphibian faunas with low equilibrium with climate is the Indo-Malayan region (Table 2). However, this region comprises an archipelago, so dispersal into suitable sites in unoccupied islands is very unlikely.

Another noteworthy pattern is the difference in equilibrium between amphibian species in the Nearctic and the Palearctic. The former has much higher levels of equilibrium than the latter. Both regions are large and both are exposed to temperate conditions with marked seasonality. Species being exposed to such climate conditions are expected to have evolved thermoregulatory strategies that facilitate adaptation to a wider range of conditions than, for example, tropical species [36–39]. Wider tolerances to climate favor, all other things being equal, dispersal. Several authors have noted that post-glacial colonization in the Palearctic and the Nearctic were different and that such differences might explain why Quaternary extinctions were greater in the western Palearctic than in the Nearctic [40]. To put it simply, the argument goes that the longitudinal orientation of mountain ranges in Europe prevented effective colonization of southern refugia (and back) of some species, while the latitudinal orientation of the major mountains in north American acted as continental-wide corridor easing dispersal [41,42].

Another possibility to explain differences between equilibrium patterns between the Nearctic and Palearctic is that the extent and position of deserts in Palearctic could act as strong physical barriers to dispersal. Amphibians require water or humidity to live and reproduce and they cannot disperse through wide arid lands; estimates are that 37% of Caudata are strictly aquatic, whereas the figure is 75% for Anurans [43]. Deserts occupy 10.4% of the Palearctic and they are generally present in the central and the southern fringes of the region. So, they are likely to play an important role as barriers. In contrast, deserts in Nearctic are in the south-west and account for only 3% of the region.

The description of patterns of equilibrium in species distributions with climate is just beginning. Understanding of the mechanisms determining the geographical variation in equilibrium is still limited. Our study provides the first description of such patterns, for an entire clade of organisms across their global distribution. Alternative studies with other groups, with different ecologies and dispersal abilities, and with data at different spatial scales of resolution, will help provide a broader and more complete picture. Progress will also require that inferences about equilibrium with bioclimatic models are compared with other

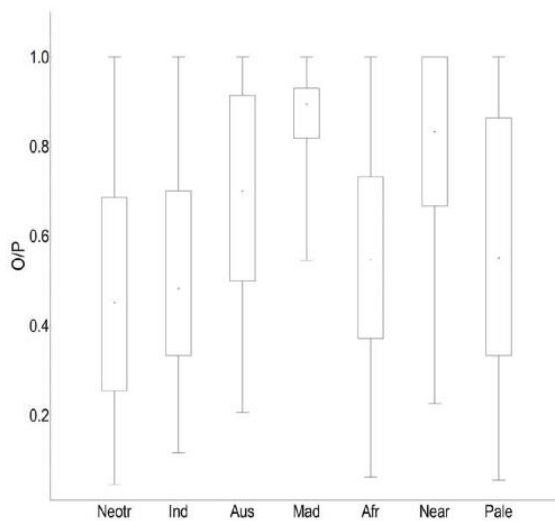


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significant differences in the degree of range filling among regions indicate that the ability of species to track climate changes varies regionally. According to our models, amphibians in the Nearctic, Madagascar, and Australasia have greater levels of equilibrium with contemporary climate than amphibians in the Neotropic, Afrotropics, Indo-Malay, and the Palearctic. It follows, that the ability to model species distributions, particularly when models are used for transferability [33,34] or extrapolation [35], is greatest in the regions where species have higher levels of equilibrium with climate.

Our study, being based on correlations and on a rather coarse resolution data for species distributions and climate, does not illuminate as to the reasons why range filling varies among amphibians in different parts of the world. Speculations can be offered and some might provide inspiration for future studies. For example, it is noteworthy that two of the biogeographical regions with higher equilibrium are also among the smaller, i.e., Madagascar and Australasia. Just because these regions are small, compared to biogeographical regions that span across vast continents, it is more likely that species inhabiting them can colonize a greater proportion of suitable areas. Another region that is small but has amphibian faunas with low equilibrium with climate is the Indo-Malay region (Table 2). However, this region comprises an archipelago, so dispersal into suitable sites in unoccupied islands is very unlikely.

Another noteworthy pattern is the difference in equilibrium between amphibian species in the Nearctic and the Palearctic. The former has much higher levels of equilibrium than the latter. Both regions are large and both are exposed to temperate conditions with marked seasonality. Species being exposed to such climate conditions are expected to have evolved thermoregulatory strategies that facilitate adaptation to a wider range of conditions than, for example, tropical species [36–39]. Wider tolerances to climate favor, all other things being equal, dispersal. Several authors have noted that post-glacial colonization in the Palearctic and the Nearctic were different and that such differences might explain why Quaternary extinctions were greater in the western Palearctic than in the Nearctic [40]. To put it simply, the argument goes that the longitudinal orientation of mountain ranges in Europe prevented effective colonization of southern refugia (and back) of some species, while the latitudinal orientation of the major mountains in north American acted as continental-wide corridor easing dispersal [41,42].

Another possibility to explain differences between equilibrium patterns between the Nearctic and Palearctic is that the extent and position of deserts in Palearctic could act as strong physical barriers to dispersal. Amphibians require water or humidity to live and reproduce and they cannot disperse through wide arid lands; estimates are that 37% of Caudata are strictly aquatic, whereas the figure is 75% for Anurans [43]. Deserts occupy 10.4% of the Palearctic and they are generally present in the central and the southern fringes of the region. So, they are likely to play an important role as barriers. In contrast, deserts in Nearctic are in the south-west and account for only 3% of the region.

The description of patterns of equilibrium in species distributions with climate is just beginning. Understanding of the mechanisms determining the geographical variation in equilibrium is still limited. Our study provides the first description of such patterns, for an entire clade of organisms across their global distribution. Alternative studies with other groups, with different ecologies and dispersal abilities, and with data at different spatial scales of resolution, will help provide a broader and more complete picture. Progress will also require that inferences about equilibrium with bioclimatic models are compared with other

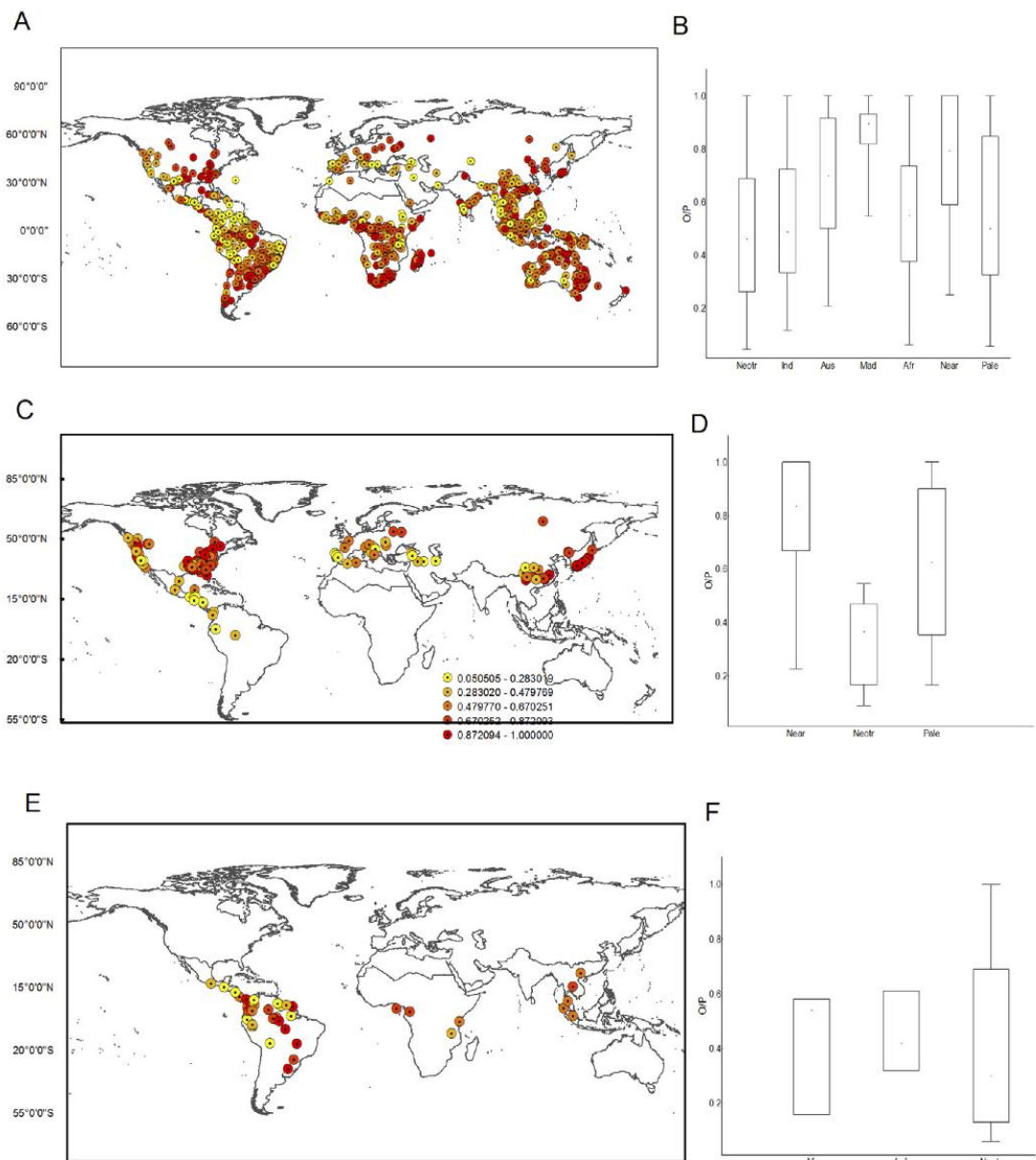


Figure 4. Distribution of the centroids of species geographical distributions and their respective level of equilibrium (O/P): (A) Anura, (C) Caudata, and (E) Gymnophiona. Differences among regions in each order (B) Anura ($N = 1655$) (D) Caudata ($N = 129$) (F) Gymnophiona ($N = 33$). doi:10.1371/journal.pone.0034420.g004

approaches, such that provided with eco-physiologically driven measurements of species niches [44,45] that allow comparisons between species observed distributions versus the abiotically suitable areas or fundamental niche (instead of the provided comparison with species potential distributions or realized niches)

[6]. The latter approach is not practical when analyzing large number of species for which eco-physiological data is unavailable and alternatives might involve running and macroecological analysis of diversity and assemblage composition against contemporary climate [1,32,41,46]. Improved understanding of how and

Table 3. Degree of climatic equilibrium for amphibians within the seven biogeographical regions.

	Afrotropic	Australasian	Indo-Malay	Madagascar	Nearctic	Neotropics	Palaearctics
Afrotropic	—	5.33***	0.54NS	8.95***	8.07***	4.17**	0.78NS
Australasian		—	5.43***	4.84***	2.91NS	9.31***	3.66*
Indo-Malay			—	8.97***	8.03***	3.05*	1.17NS
Madagascar				—	2.36NS	11.68***	7.47***
Nearctic					—	11.80***	6.15***
Neotropics						—	3.85*
Palaearctics							—

*** $P < 0.0001$,** $P < 0.001$,* $P < 0.05$,

NS = Non significant.

Kruskal Wallis test between pairs of regions differences.

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how much species tracked past climate changes, and how they occupy current suitable climates is critical to understand and forecast the potential responses of species to ongoing climate changes.

Supporting Information

Figure S1 Degree of equilibrium of climate for amphibians at regional scale in the seven biogeographical regions. >0B set of species with O equal to more or equal than 1 cell, >10B more than 10 cells, >15B more than 15 cells using BIOCLIM, >15MD more than 15 using Mahalanobis, and >15ED more than 15 using Euclidian Distance. Boxes are the percentiles from 25 to 75% around O/P medians, and lines indicate the standard deviation. (A) All orders; (B) Anura; (C) Caudata; (D) Gymnophiona. Neotropic (Neotr), Indo-Malay (Ind), Australasia (Aus), Madagascar (Mad), Afrotropic (Afr), Nearctic (Near), Palaearctic (Pale). (TIF)

Table S1 Descriptive statistics of the level of equilibrium among the amphibian species at global and regional scales. (DOCX)

Table S2 Test of the differences in the degree of climatic equilibrium between pairs of regions. The

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Capítulo II

El clima promovió la dispersión diferencial en el
Gran Intercambio Biótico Americano

Climate promoted differential mammalian dispersal during the Great American Biotic Interchange

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Abstract

Although the Panamanian Isthmus, in Central America, was established more than 3.5 million years ago (Ma), and an active mixture of biota took place – process known as the Great American Biotic Interchange (GABI)- the mammalian movement started from 6.8 Ma. A question that remains unsolved is why more mammal genera from North America colonized the south than the reverse. We examined if the distribution of suitable climatic conditions for 33 mammal genera before, during, and after the land bridge formation could explain their migratory patterns. We found that suitable climatic conditions for North American mammals expanded in South America during the Miocene, Pliocene and Pleistocene, which was not the case for the South American mammals in North America. Furthermore, suitable areas for North American dispersers increased from the Miocene to the Pliocene, but it did not for North American non-dispersers or South American dispersers and non-dispersers. Finally, connectivity of suitable areas in Central America was higher for successful dispersers from both subcontinents. Body mass was not related to degree of dispersal. Our results support the view that the spatio-temporal dynamics of climatic suitability are a likely explanation for the asymmetry in colonization of mammals during the GABI. More specifically, climatic area of suitability is positively related to time, and that time is associated with the capacity of taxa to invade and with connectivity in pathways. Therefore, these are relevant factors for the detection of species that are potentially successful invaders under current and future climatic change.

Introduction

The Great American Biotic Interchange (GABI) was the result of the formation of the Panamian Isthmus in Central America (Stehli & Webb 1985). Around 2 to 3.5 Ma geological activity of the Pacific tectonic plates caused Central and South America to be linked (Duque-Caro 1990; Coates & Obando 1996; Iturralde-Vinent & MacPhee 1999; Coates *et al.* 2004), providing a path for species migration bringing together otherwise isolated faunas (Ackerly *et al.* 2006).

The equilibrium theory predicts that over time a region such as a continent will become saturated with taxa, reaching a level of diversity where rates of turnover are stochastically constant (MacArthur & Wilson 1967). Equilibrium will then persist until it is disrupted by the appearance of new taxa, a change in physical environment, or a combination of both (MacArthur & Wilson 1967; Webb 1969; Schopf 1974; Simberloff 1974; Webb 1976; Marshall *et al.* 1982). The sudden possibility of interchange between north and south offered an unprecedented opportunity to create novel communities after almost 65 Ma of isolation.

This relatively recent biogeographic event is recognized because a great amount of fossil records and taxonomic work has been widely studied in America from Wallace in 1852. Fossils can provide both a time control for historical biogeography and localities which can provide past biogeographic range of a taxa in both continents, as well as they can help establish a minimum age for a taxon (Grande 1985). Both fossil and also recent records (Webb 1991) in North and South America show a consistent pattern until today: the biotic interchange was asymmetrical, similarly to several biota interchanges in the past (Vermeij 1991), in particular with significantly greater number of species moving from the north to the south than the other way around (Webb 1991). The asymmetry in the GABI had important consequences for biogeographic patterns for New World species, especially for mammals from North America which had an explosive speciation in South America and currently conform 50% of the species in that subcontinent (Webb 2006).

Although asymmetry is a common process in the World biotic interchanges (Vermeij 1991) during GABI, before the continental connection was established, there was occasional interamerican exchanges of species through islands and other pathways (Simpson 1940). Evidence seems to suggest that the interchange of faunas was balanced (Woodburne *et al.* 2006) between the late Miocene and early Pleistocene (i.e. 9 to 2 Ma). Symmetry was lost 1 Ma (Webb 1991), with more North American genera and species

successfully colonizing South American habitats than the reverse (Marshall 1985; Ackerly *et al.* 2006).

The simplest explanation for the observed asymmetry was that northern migrants outnumbered southern migrants, because the temperate area in North America was six times larger than its equivalent in South America (Webb 1991). However, should this explanation be true, migrants from South America that lived in the large tropical areas would have been expected to have reached tropical latitudes in North America and there is yet no evidence in the fossil record for such colonization (Webb 1991). As an alternative, the explanation was offered by the 'Two Phases Ecogeographic Model' (TPEM) (Webb 1991) considered that GABI was a more complex, and long-term process. This process may have consisted in a series of pulses, possibly reflecting the impact of glacial-interglacial cycles in the Northern Hemisphere where glacial periods were more dominant than the shorter interglacial phases, resulting advantageous for North American species (Webb 1991; Woodburne 2010). In any case, the interchange scenario never extended far into temperate North America because interspersed Neotropical fauna seemed to have reached only about 9% of the North American area (Webb 1976). The ecogeographic model fails to explain some key aspects of present-day species biogeography. For instance, suitable new habitats for southern species were never colonized in the north or show few fossil records (Webb 1991). This is especially true for southern species that may have been restricted distribution, and may have found similar environmental conditions in North America during the end of glacial periods. Some examples of this could be demonstrated by the endemic South American glyptodonts like the genus *Doedicurus*, *Neuryurus*, *Panochthus*, big size mylodontid ground sloths like *Lestodon*, or the endemic litopterns, *Macrauchenia* and *Neolicaphrium* which were ecologically similar to several North American ungulates and carnivores. However, there are two records of *Myxotoxodon* in Mexico (Polaco *et al.* 2004 ; Rodríguez-de-la-Rosa *et al.* 2011). They seem to have had abundant suitable environmental conditions in North America, but not enough fossil evidence of colonization has been found (Simpson 1950).

We propose that analysis of the changes in climate suitability through time and space might provide insight into the GABI, since climate is one of the key determinants of species distributional dynamics at coarse scales. To reconstruct such past dynamics, a combination of current and fossil records, with paleoclimatic reconstructions, and ecological niche models is required (Svenning *et al.* 2011).

We reconstruct suitable climate area available for ancient mammals through ecological niche models. Even when most of these reconstructions do not use biological inferences, they still allow for an independent testing of mammals and climate associations, incorporating the role of climatic changes in the definition of suitable habitat (Fig.1A, B). Particularly, a comparison of suitable habitat for mammal species, before, during, and after land bridge formation, may offer valuable information to understand the characteristics that control migration intensity and the role of the mammals origin, since time and space play a major role in dispersal of individuals and populations (Hanski 1999; Hanski & Ovaskainen 2000).

The main hypothesis in this paper is that natural range expansions or contractions in species might be accelerating in response of global climate changes (Thomas & Lennon 1999; Perry *et al.* 2005), so that intercontinental migration asymmetry is the result of historical variations of climatic suitability area. Specifically, we anticipate that at larger (spatio-temporal) scales, there are three main aspects that may control migration success: subcontinent of origin, amount of suitable habitat in the colonizing continent, and connectivity along the migration path. As a result, for a successful migration between the two continents, suitable continuous habitat would be available along Central America. Then, on the long term, larger suitable areas should be available in the target continent for true dispersers than for the non-dispersers (Fig.1A). Furthermore North American mammals showed a great dispersal ability and we would expect they show a greater climatic equilibrium, i.e., geographic range of taxa that geographically fulfilled suitable areas (Svenning & Skov 2004; Araújo & Pearson 2005; Svenning & Skov 2007; Munguía *et al.* 2008) than the South Americans (Fig.1A). Specially because it has been suggested that more environmental variability in the area occupied by species —like we observe in current climate in North America— would select for stronger dispersal abilities (Ribera & Vogler 2000; Hof *et al.* 2006; Hof *et al.* 2012). We finally include body size because it shows a positive relationship with dispersal ability of active dispersers while no such relationship existed for passive dispersers (Jenkins *et al.* 2007).

Because process in the paleontological past has been associated with the size of the geographic range of genus-level clade, like mass extinction or expansions, spatial considerations are fundamental to understand the evolutionary dynamics of biodiversity. These findings have ramifications for the current biodiversity crisis because human activities are altering the geographic distributions of many taxa around the world (Avisé *et al.* 2008).

One of the main challenges identified in macroecology that will probably play a major role in the future, is the integration of the past conditions into macroecological analyses, e.g. by using paleontological or phylogenetic data or by applying methods from historical biogeography, they will strength our understanding of the underlying reasons for contemporary patterns (Beck *et al.* 2012). This study increases the understanding of biological invasions in Neotropics which may reveal that the impact of exotic taxa is more ubiquitous than is reflected in current literature (Rodríguez 2001). In summary, we tested whether: (1) suitable habitats occurred and were larger in North American mammals showing less connectivity than South American mammals; (2) dispersers hold larger suitable areas and shorter connectivity than non-dispersers; and (3) whether the degree of climate equilibrium of genera in the present time is a trait that is related to dispersal attributes of the participants in the GABI.

Results

Migration pulses from Miocene to the Present are associated with the variation of suitable areas for both subcontinents (Fig.1A) in 33 mammal genera (APPENDIX S1). The suitable areas variation can be described: a) by comparing simultaneously the differences in area for both subcontinents at each geological period; and b) as the difference in areas between migration pulses, i.e. through the *rate of change of suitable areas* in each subcontinent. There were differences in the way that suitable areas covaried with time for North and South America ($P < 0.001$). When analyzing differences in suitable areas for geological time, a significant interaction between origin, and dispersal response was $P = 0.005$. However, body size ($P = 0.32$) and their interactions were not different throughout geological time ($P = 0.85$). Throughout the Miocene to the Pleistocene, suitable areas for North America migrants (i.e. suitable areas in the South America subcontinent) were greater than those for South American migrants. Conversely, suitable areas in North America were only greater than those in South America through the Pleistocene to recent times (Table 1a). Mammals showed spatio-temporal heterogeneity during geological time (Fig.2, Fig.3).

Not only there were suitable areas greater in South America within the geological period analyzed, but they also increased more than in North America during each migration pulse. The *rate of change of suitable areas* for North American migrants into South America showed an increasing trend from the Miocene-Pliocene, and from Pliocene-Pleistocene, with no observable changes during Pleistocene-Recent time migration pulse

(Table 1b, Fig.2C). Conversely, no changes or trends were observed in suitable areas for South American emigrants during the same period (Table 1c). Moreover, *suitable area rate of change* for North Americans decreased only in recent times (since 21,000 years ago) in South America in relation with South Americans.

Along with the temporal pattern of suitable areas, dispersal response seemed to play an important role in colonizing a subcontinent. Notably, dispersal responses through all migration pulses were significantly different for both, North and South American immigrants (Table 1d). This difference was particularly clear for true-dispersers. The increase of suitable area rate of change in South America for North American true-dispersers mammals was greater than in North America for South Americans. When comparing the trends of variation in suitable areas (*suitable area rate of change*) for both, North and South American non-dispersers, no significant differences were found. When focusing on the dispersal response pattern for North American mammals, there were significant differences between true-dispersers and non-dispersers only for the Miocene to Pliocene (Table 2a). During this migration pulse, suitable areas in South America were greater for true-dispersers than for non-dispersers (44% greater during Miocene to 18% greater during Pliocene).

Dispersal response for South American migrants showed no differences in any period (Table 2b). Furthermore, there were neither differences in suitable areas for true dispersers through geological time, except for a decrease in the suitable area rate of change from the Pleistocene to recent times (Table 2c). This trend suggests that true-dispersers from South America suffered a reduction of suitable areas in North America during the glacial period (during 21kya-Pleistocene). After that, suitable areas have not changed since the Pleistocene.

In addition to suitable area variation and dispersal response, connectivity along the “bridge” had an additional effect on GABI asymmetry. *Dispersal path length* differences among genera were used as an indirect measure of connectivity (Fig.A). Unexpectedly, dispersal path length covaried with the migration origin ($P=0.002$). In spite of the corridor through Central America is more similar to the North American environment (Woodburne *et al.* 2006), dispersal path length was greater for North American than for South American migrants. Variations in dispersal path length were not correlated with body size ($P=0.98$) evidencing no difference in size between North American and South American mammals, despite our sample included species with body masses spanning several orders of magnitude (from 0.01kg [*Cryptotis*] to 218.82 kg [*Tapirus*]) (Appendix S1).

Non-disperser mammals had longer dispersal *path length* than true-dispersers for both, North and South American mammals ($P < 0.001$). In particular, South American mammals showed shorter distances of suitable areas between subcontinents than North American ones ($P = 0.002$). Also, non-disperser mammals showed greater distances than dispersers ($P < 0.001$). The highest connectivity (continuous suitable areas through Central America) was tested for all niche models. It was present in ~24% of the genera analyzed (both North and South Americans). Nine genera out of 33 analyzed in at least one period of time showed continuity of the suitable areas (i.e., *Heteromys*, *Microsciurus*, *Myrmecophaga*, *Priodontes*, *Tamandua*, *Nasua*, *Bradypus*, *Choloepus*, and *Eira*); from these, 8 genera dispersed and one did not (i.e., *Priodontes*, giant armadillo). Connectivity varied among models, but at least two models were consistent with these results. For instance, *Tamandua* (anteater) showed full connectivity in the three models during present time and all remnant genera models indicated full connectivity with two models. High connectivity was common in Recent, unlike previous periods, where full connectivity was hardly ever observed.

Finally *climatic equilibrium* degree in this analysis refers to the similarity between the current and potential distributions (Fig.1A). A low equilibrium in non-dispersal genera would suggest non-climatic causes of their limited distribution. We did not find differences in both groups dispersers vs. non dispersers ($P = 0.39$). Additionally whether a higher environmental fluctuation of habitat is associated with species with higher ability to disperse, then we would have expected that NA's showed higher equilibrium than SA's. Indeed, higher equilibrium was found in North Americans ($P = 0.03$), an observation particularly supported by the higher variability in temperature of North America than to South America.

Discussion

The climatic factor is here stressed as a selective influence on North America-South American migration. Taxa colonization and settlement not only depend on the suitable climatic areas presence, but also on the permanence of that stage throughout long periods of time. In particular, using an integrative approach involving merging fossil records with paleoclimatic reconstructions and bioclimatic envelope models, we found that: 1) suitable areas for colonization of North American mammals increased in South America until the Present, at a faster rate than suitable areas increased for the colonization of South American mammals in North America; 2) connectivity between areas of suitable habitat

was important to explain the dispersion success, but does not appear to support the asymmetry in GABI, and 3) The dispersal capacity, measured as the amount of current occupancy of potential suitable areas (equilibrium degree with current climate) was an additional factor that controlled GABI asymmetry, and unveiled the *climate equilibrium* as an important taxa attribute in order to evaluate mammals migration (Svenning & Skov 2004; Araújo & Pearson 2005; Svenning & Skov 2007; Munguía *et al.* 2008).

Suitable areas in South America for North American mammals increased consistently until recent times; therefore variations in climate during *geological time* played an important role in the dispersion process of North American mammals in South America, showing an asymmetrical movement at continental level. Most cooling periods occurred mainly in North America (Webb 1991; Woodburne *et al.* 2006; Woodburne 2010) with strong differences in temperature between the two subcontinents (Appendix S5c, d). Those variations in climate affected or modified dispersion performance in a spatio-temporal dynamic factor mainly by the variation of suitable areas.

According with the results presented here, connectivity stemmed as another major contributing factor to dispersion success. Then it would be reasonable to think that species with wide geographic ranges in their native region were more likely to survive in a new region, as a result of broader climatic tolerances (Goodwin *et al.* 1999). Stability and smaller suitable areas in North America available to South American mammals appear to be a reasonable cause of their failure to promote a major northward movement, contrasting with the temporal increment of suitable areas (from the past to the present) for the North Americans. Before interchange, South American mammalian composition was dominated by marsupials. They apparently were less competitive than placental and probably more environmentally sensible (Simpson 1940; Webb 1976). Before interchange, South American mammalian composition was dominated by marsupials however only few of them crossed to North America. They apparently were less competitive than placental and probably more environmental sensible taxa (Simpson 1940; Webb 1976). Even when connectivity was high for dispersers, as observed in their shorter *dispersal path length*, it had an opposite effect for North American mammals, since these appeared to be more successful colonizers. Therefore connectivity apparently is a factor associated with the ability of species to be good dispersers, but not necessarily it is a good explanation for understanding the asymmetry in GABI. Despite their higher connectivity (as compared with the North American dispersers), tropical species seemed to have low dispersal abilities within unsuitable areas. It has been documented that low temperatures and

topographical heterogeneity may limit the dispersion potential of tropical species. For example, the current distribution of South American species (such as *Bradypus*, *Choloepus*, *Myrmecophaga* and *Tamandua*) remains constrained to tropical or subtropical regions whereas only a restricted number of species (e.g. *Dasypus* and *Didelphis*) have been able to reach temperate regions (but the anteater *Myrmecophaga* reached El Golfo, Sonora, in Pleistocene times) North American species exhibit wider physiological tolerances because they have been exposed to broader thermal fluctuations through time, which in turn make them more tolerant to wider areas (Ghalambor *et al.* 2006) , see Appendix S2. With this new evidence, it can be assumed that GABI asymmetry was mainly determined by a North American origin, as well as the spatio-temporal pattern of suitable areas in South America, especially for mammal dispersers.

The shape of subcontinents may have had additional effects for a better successful colonization of North American mammals. For instance, larger suitable areas for North American species in the northern region of South America may have promoted a greater speciation. The current mammalian fauna in South America have a 50% of mammalian species with North American affinities because they have had more speciation events than the South American representatives in North America (only 10%). Great speciation in South America, especially in places where species richness proved to be sensitive to niche dynamics processes, reveal the enormous potential of the link between ecology and historical biogeography under integrated theoretical and methodological frameworks (Rangel *et al.* 2007).

Although prehistoric invasions occurred during thousands or millions of years through adjacent regions and for short distances, they could not be compared or treated similarly with the current human assisted invasions (Ricciardi 2007). However, processes observed through large time-scales that characterize the dynamics of suitable areas for successful dispersers, could draw a picture that shows how taxa respond to environmental changes, as well as to provide a higher predictive power for future climate changes. As observed here, taxa that tend to increase their area and have a current large climatic equilibrium are likely to be potential good dispersers.

Our results showed that higher climate equilibrium was characteristic for North American-dispersers. Apparently, a higher historical variability in their corresponding suitable areas let North American taxa show greater affinities with climate. Consequently, a wide range of climate conditions (as observed for North America) can maintain a pool of potential invasive species more so than those with narrow conditions (i.e., South America). Then it

could be plausible that the invasive power of North American dispersers depended upon the conditions prevailing in the continent of origin. This may be supported by the fact that some empirical studies of the latitudinal extent of invading species showed that the continental tropics have accumulated fewer non-native species than temperate areas have (Rejmanek 1996; Lonsdale 1999), but it could also depend of economic development. In addition, the species' potential of being good dispersers in future scenarios (such as the current climate change), can be predicted for those species that currently fulfill their potential suitable climatic areas, as shown by the North American dispersers during GABI. The potential of using distribution models to predict the dynamic of the species' distribution on future scenarios will be enhanced when predictions will focus on these species (i.e., those that almost entirely occupy the area of distribution) than those species showing low climatic equilibrium.

Although most of taxa showed good performance for niche models (see methods), there was few fossil data that were present outside the suitable area (e.g. Fig.2a, b *Tapirus* during 115kya and *Dasytus* during 2.95 Ma). Some reasons that are in relation to this phenomenon could be associated with the current climate conditions which could not have been represented in the past. Past no-analog communities appear to be climatically driven and linked to climates that are also without modern analogs (Williams & Jackson 2007). Furthermore, fossil data could not represent the niche of the taxa because fossils were vagrant individuals or they belong to a sink population in a metapopulation, they did not live where the deposit or accumulation or fossilization occurred therefore they could be outside their niche (Peterson *et al.* 2011). Finally, fossil radiometry dating commonly show a wide interval of the age uncertainty (Pol & Norell 2006); most of the times relative or stratigraphic dates are given, because radiometric techniques are expensive and not all the cases are suitable for this kind of dating method.

Current invasion species show commonly differential movement. The proportion of exotic species successfully established in recipient communities is not uniformly distributed across the globe (Rodríguez 2001). Therefore, the differential movement also observed in GABI could help to understand the current causes of distribution expansions of some species. The dynamics of suitable climatic areas can help to understand the potential of a species to be a good disperser and invade other geographical areas, but it is not supposed that it acted alone or that it provides a complete explanation of the screening of migrants in this case. The process was complex, and no single or simple explanation could be expected. Although, nowadays movement of species by human causes could play an

additional cause of new species arrivals among continents, the successfulness in their settlement appear to be determined by the persistence through the time by maintaining viable populations in suitable areas as they occurred in the successful North American migrants.

As analyzed here, abiotic events were therefore important factors affecting the evolution of mammalian communities. Although modern biological invasions are an unprecedented form of global change, and are dissimilar in frequency, magnitude and impact to those that occurred in the distant past (Ricciardi 2007), we consider that the behavior observed during past invasions confronting climate changes, should be more frequently assessed in order to understand the invasive potential of the species during future climate changes. Opportunely detecting species with an invasive potential would lead to better decision-making (politically and economically) in some countries.

Materials and Methods

North and South American genera

Mammalian occurrences during the GABI have been described at the genus level via fossil records. Thus, their presences before, during and after the land bridge connection at the continental scale and their dispersal response have been well identified elsewhere (Woodburne *et al.* 2006). Consequently, the asymmetrical dispersal through time has also been analysed at this taxonomic level, based on the most recent revisions (Woodburne *et al.* 2006) for both extant and extinct genera (Fig.1) from the Miocene to Recent times. Fossil data hold an intrinsic bias towards sites in which fossilization took place and the outcrops are available, as well as specialists to study them, underestimating the distribution of species; nonetheless, given that this bias occurs for extinct and extant genera, we consider that this issue does not invalidate our analyses with the extant genera, which were classified as “true dispersal” (Woodburne *et al.* 2006) and “non-dispersal” identifying the subcontinental origin (i.e., North or South American).

Our sample included 33 mammalian genera, 22 from North America and 11 from South America, representing 11 orders (i.e., Artiodactyla, Carnivora, Pacituberculata, Pilosa, Rodentia, Soricomorpha, Cingulata, Didelphimorphia, Microbiotheria, Lagomorpha, and Perissodactyla). We identified 23 true-dispersal (D) and 10 non-dispersal genera (ND). Current occurrence data points were obtained from the Global Biodiversity Information Facility (www.gbif.org). Localities were collapsed in unique occurrences at 1 degree

resolution, to match climatic layers, resulting in 5,753 unique localities ranging from 807 to 6 across genera (Table 1). Finally, we compared our occurrence data against the geographical ranges reported in the International Union Conservation Nature database (IUCN 2009), which is the most updated version, and with a subsequent review outliers were discarded.

Models were calibrated on data for a present period and used to predict the range in the same time period and the preceding 4 periods (i.e. hind-casting; (Svenning *et al.* 2011). To validate retrojections to different past climatic conditions, dated fossil data drawn from the Paleobiology database (<http://paleodb.science.mq.edu.au>) were overlaid with their correspondent time period, estimating the omission error with fossil localities (a minimum of 5 unique records). Because age estimation is not accurate, we considered the maximum, mean and minimum age estimations to associate with the four paleoclimate scenarios and assigned each fossil record to a climate scenario as follows: ‘Recent’ (age estimated between 14 to 0 ka), ‘Pleistocene’, (age estimated between 781 to 100 ka), ‘Pliocene’ (age estimated between 2.58 to 5.33 Ma), ‘Miocene’ (age estimated between 5.33 to 11.61 Ma). This assignment resulted in 11 fossil records for North American and 2 for South American mammals. The genera with fossil records used for analysis were (Appendix S1): *Antilocapra* ($N_f = 8$), *Dasybus* ($N_f = 25$; Figure 2B), *Didelphis* ($N_f = 14$), *Cryptotis* ($N_f = 10$), *Erethizon* ($N_f = 11$), *Geomys* ($N_f = 37$), *Lama* ($N_f = 12$), *Ochotona* ($N_f = 5$), *Canis* ($N_f = 58$), *Pecari* ($N_f = 8$), *Silvilagus* ($N_f = 52$), *Tapirus* ($N_f = 28$; Fig.2A), *Castor* ($N_f = 23$).

There is an evident bias in the fossil record caused not only by the sampling effort, but also by unevenly distributed geomorphological conditions affecting the fossilization and persistence of remains through time. Nevertheless, we mainly based the model’s validation on fossil records, because they are valuable independent data contrasting with the commonly used records from the same period of time.

Climatic Equilibrium for dispersal and non-dispersal genera

We tested the degree of taxa equilibrium with climate for present conditions in order to know whether the no capacity of colonizing the opposite subcontinent by non-dispersal taxa is related to their dispersal capacity or simply to the absence of suitable climatic conditions. This “niche filling” or climate equilibrium has been useful to associate the species dispersal ability through the proportional occupation in the potential climatic area

(Svenning & Skov 2004, 2007; Munguía *et al.* 2008). Here, the R/P ratio (where *R* is the geographic range, and *P* is the potential area) let us discriminate both possibilities. So, a low equilibrium in non-dispersal genera would suggest non-climatic causes of their limited distribution. Climate equilibrium is possible to assess only for the Recent period conditions because of the incompleteness of fossil record. To compare dispersal response and origin we applied a U-Mann Whitney test to find possible differences in equilibrium degree within two groups: Origin and Dispersal responses.

Bioclimate modelling

We hindcasted bioclimate envelopes using three presence-only modelling algorithms: BIOCLIM, GARP, Mahalanobis Distance (MD) to test the robustness of the results (Svenning *et al.* 2008; Flojgaard *et al.* 2009; Nogués-Bravo 2009; Vega *et al.* 2010), models were applied to each extant genus of American mammals in relation to five paleoclimatic projections between Miocene and Present: 8 Ma, 2.95 Ma, 115 ka, 21 ka, and 0 ka (Fig.1A).

While a variety of methods are available for modeling species distributions, certain considerations were used to narrow down the range of algorithms from which to select. First, mammalians records provide information about the presence of species, but not about their absence, and so presence-absence algorithms must be discarded. Complex algorithms such as GARP (Anderson *et al.* 2003) proved to be successful in anticipating most of the species' distributional potential (Peterson *et al.* 2007); furthermore they generate pseudo-absences against which to test the models (Lobo *et al.* 2010; Lobo & Tognelli 2011).

MD models have been shown to perform better than other presence-only methods in a recent comparative study (Tsoar *et al.* 2007). It has been successfully used for palaeobiology studies (Nogués-Bravo *et al.* 2008; Varela *et al.* 2009; Varela *et al.* 2010) and is specifically recommended for modeling species potential distributions using the fossil record (Varela *et al.* 2010).

Finally the basic BIOCLIM algorithm finds the climatic range of the points for each climatic variable (Nix 1986; Busby 1991). It has been successfully applied to a wide range of plant and animals species in particular, it has been suggested be useful to highly mobile species and their spatio-temporal variations (Doran & Olsen 2001).

Periods of time

The oldest climate period analysed was before the bridge formation and was selected considering the first genera recognized to have crossed to any of the subcontinent, namely

Pliometanastes (Xenarthra: Megalonychidae) and *Thinobadistes* (Xenarthra: Mylodontidae), whose fossils in North America have been estimated around 8 to 9 Ma (Woodburne *et al.* 2006). In addition, first occurrences of gomphotheres, peccaries, and tapirs in South America were estimated during the late Miocene (Campbell Jr *et al.* 2010). This record is quite controversial because of the dating of the sediments. Most of the authors considered that the oldest presence of North American taxa in South America is that of procyonid (of 6 Ma) sigmodontine rodents (5-6Ma), peccaries (4 Ma) (Woodburne *et al.* 2006; Prevosti *et al.* 2006). They are, in fact, recognized as the first pulse of the Great American Faunal Interchange.

Paleoclimate scenarios were generated with a GCM coupled with a Q-flux ocean model extracted from Haywood *et al.* (Araújo *et al.* 2008) database (see Appendix S5). Miocene (8 Ma), Pliocene (2.95 Ma), Pleistocene (115 ka, 21 ka), and the Recent climate data hold a 1° cell size.

When generating our bioclimatic envelopes, we selected five climatic variables relevant for the distribution of mammals (Nogués-Bravo 2009): (1) Annual mean precipitation (mm/year), (2) Annual mean temperature (°C), (3) the difference between mean temperature of the warmest month (WMM) and the mean temperature of the coldest month (CMM), and (4) Mean precipitation of the dry season (mm/day) (Appendix S5). We calculated the suitable area, and the distance between suitable areas from one subcontinent to the other in each time period as our response variables.

Distances were calculated for each genus between the southern limit of its suitable predicted area in North America to its northern border in South America. When prediction in one of the subcontinents was null, we recorded *not available* distance, and when the area predicted was continuous through Central America, the distance value was recorded as zero, representing full connectivity. This procedure was followed for each period.

Statistical Analyses

General linear models, as implemented in STATISTICA 8.0, were used to fit data and investigate effects of interest: disperser response, origin and body mass. Because data structure consisted of response variables (area, and distance) measured for the same genus through time, specific package options invoked repeated measures ANCOVA. Two subject effects (bioclimatic models and time) and three factors (origin, dispersal response and body size) were incorporated as explanatory variables. In all, our analyses considered different categorical and continuous datasets, 3 bioclimatic models (B, MD and GARP), 5 Periods of time (8 Ma, 2.95 Ma, 115 ka, 21 ka and 0 ka) as repeated measures and 2 origin

categories (NA and SA), 2 dispersal responses (D and ND), and body size (average in kilograms).

Basic diagnostics were performed for checking model assumptions prior to taking for granted statistical estimates and tests. In particular, homogeneity of variance and normality of residual terms in the linear models were both induced by applying a square root transformation of area and distance. This was checked by graphical residual analysis methods and goodness of fit tests (Appendix S3). Another critical issue for correct repeated measures analysis is the so-called sphericity assumption. To verify this, STATISTICA 8.0 provides the Greenhouse-Geisser (G-G) test, and because sphericity was generally rejected, we opted for using the pertinent statistical corrections in all tests we have reported. We tested both main effects and interactions among variables, searching for a parsimonious model in stages (Appendix S2). To begin, because area and distance variables did not covariate significantly with bioclimatic models, bioclimatic models were used as independent replicates. These procedures demonstrated that our results and the patterns observed were very similar even using different methods of niche estimation; the interpretation is that different bioclimatic models are indeed all unbiased measurements (with error) of the same physical quantity, namely the distributional area of the species. Furthermore, because body size resulted non-significant it was excluded from further analyses, thus simplifying a final tentative model. Likewise, interactions among explanatory variables, when tested under the G-G correction, resulted non-significant. A working model was thus obtained that contained only main effects. This final model was subject to diagnostic tests for assumptions, and deemed a good fit to data and having clear interpretation of its components. All above reported computations of *P*-values for testing effects are thus regarded as justifiably correct.

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Figure legends

Figure 1. Procedure followed to perform the Spatial and Statistical Analysis.

Figure 2. Bioclimatic projections in 5 different times (right to left 8 Ma, 2.95 Ma, 115 ka, 21 ka, 10 ka) in America for two current genera that participated in the Great American Biotic Interchange: (a) *Tapirus* (tapirs) of North American origin. Fossil localities (minimum age estimate) ($N = 28$) projected to Holocene (10 ka), 115 ka and 8 Ma. (b) *Dasypus* (armadillo) of South American origin. Fossil localities (minimum age estimate) ($N = 25$) projected to 10 ka, 115 ka and 2.95 Ma times. (c) Projection of areas of all 34 genera of South American mammals in North America (NA) and vice versa. Graduated colors (green to red) indicate the number of species overlaid. For North America there is a maximum number of 13 genera from South American and a maximum of 21 North American mammals in South America; the diagonal line indicates the Panamanian Isthmus.

Figure 3. Plot designed to display relevant variables comprehensively: Climatic suitable Area and Dispersal path length (square root Distance) through geologic time for 33 mammalian genera; N= North Americans, S = South Americans, Disp = Dispersal and NonDisp = Non dispersal mammals. Because geologic time is discrete, the graphical resource called *jittering* (randomly displacing plotted symbols by a small amount) is applied so that symbols do not overlay and that underlying structure can be effectively visualized.

Tables Legends

Table 1. Suitable area rate of change for North Americans (NA) in South America and South Americans (SA) in North America and individual effects in each origin group. Arrows indicate whether suitable area increase (\uparrow) or decrease (\downarrow) between previous period to the next one in each time pulse (e.g. first pulse: Mioc.-Plioc. where. Mioc= Miocene and Pliocene=Pliocene). Pleis¹ = 115 kya; Pleis² = 21kya and Rec= Recent.

Table 2. Suitable area rate of change for Dispersers (D) and Non Dispersers (ND) and individual effects in each origin group North Americans (NA) and South Americans (SA)

Table 1.

	Mioc.- Plioc.		Plioc.-Pleis ¹		Pleis ¹ -Pleis ²		Pleis ² -Rec.	
	NA	SA	NA	SA	NA	SA	NA	SA
a. Suitable area between both origin	↑*	↓*	↑*	↓*	↑*	↓*	↓*	↑*
b. Area between NA	↑*	---	↑*	---	NS	---	NS	---
c. Area between SA	---	↓*	---	NS	---	↓*	---	↑*
d. Area between both origin dispersers	↑*	↓*	↑*	↓*	↑*	↓*	↑*	↓*

Table 2.

	Mioc.-Plioc.		Plioc.-Pleis		Pleis ¹ -Pleis ²		Pleis ² -Rec.	
	D	ND	D	ND	D	ND	D	ND
a. NA's	↑*	↓*	NS	NS	NS	NS	NS	NS
b. SA's	NS	NS	NS	NS	NS	NS	NS	NS
c. SA's Dispersers	NS	---	NS	---	↓*	---	↓*	---

Supplementary Material

Additional Supporting information is found in the online version of this article:

APPENDIX S1 Table of data. Disperser (D) and non-disperser (ND) genera and their continental origin: North America (NA) or South America (SA). Number of fossil data available in the Paleobiology database (Woodburne *et al.* 2006).

Appendix S2. Model Repeated Measures Area (Square root transformed)

Appendix S3. Chi Square test in Dependent Variables Area (square root) and Distance (square root).

APPENDIX S4 Suitable areas overlapped for: (a) Disperser North American genera. Maximum number of genera (darker orange) for 8 Ma (12), 2.95 Ma (12), 115 ka (12), 21 ka (12), and present (12), Total: 15 genera. (b) Dispersal South Americans, 8 Ma (6), 2.95 Ma (6), 115 ka (6), 21 ka (6), and Present (6), Total: 6 genera. (c) Non-Dispersal North Americans, 8 Ma (5), 2.95 Ma (4), 115 ka (5), 21 ka (5), and Present (5), Total: 5 genera. (d) Non-dispersal South Americans, 8 Ma (4), 2.95 Ma (4), 115 ka (4), 21 ka (4), and Present (4), Total: 6 genera.

APPENDIX S5 Histograms of environmental variables used for modeling in each time period: (a) Annual Precipitation, (b) Minimum precipitation, (c) Mean annual temperature, and (d) Temperature. BLACK: North America; GREY: South America.

Appendix S1.

Family	Genera	Localities	Fossil records*	Dispersor	Body size	Origin	Literature
Antilocapridae	Antilocapra	70	8	ND	46.08	NA	(Woodburne <i>et al.</i> 2006)
Bradypodidae	Bradypus	53	–	D	3.45	SA	(Delsuc <i>et al.</i> 2002; Delsuc <i>et al.</i> 2004)
Caenostalidae	Caenolestes	13	–	ND	0.03	SA	(Woodburne <i>et al.</i> 2006)
Camelidae	Lama	38	12	D	120	NA	(Menegaz <i>et al.</i> 1989; Woodburne <i>et al.</i> 2006)
Canidae	Canis	807	58	D	28.08	NA	(Bardeleben <i>et al.</i> 2005)
Castoridae	Castor	284	23	ND	21.82	NA	(Woodburne <i>et al.</i> 2006)
Chinchillidae	Lagostomus	16	–	ND	6.17	SA	(Woodburne <i>et al.</i> 2006)
Chinchillidae	Chinchilla	12	–	ND	0.49	SA	(Woodburne <i>et al.</i> 2006)
Dasypodidae	Dasypus	214	25	D	3.72	SA	(Woodburne <i>et al.</i> 2006)
Dasypodidae	Priodontes	13	–	ND	50	SA	(Woodburne <i>et al.</i> 2006)
Didelphidae	Didelphis	536	14	D	1.34	SA	(Woodburne <i>et al.</i> 2006)
Erethizontidae	Erethizon	369	11	D	7.09	NA	(Woodburne <i>et al.</i> 2006)
Felidae	Panthera	220	–	D	100	NA	(Woodburne <i>et al.</i> 2006)
Geomyidae	Geomys	246	37	ND	0.23	NA	(Woodburne <i>et al.</i> 2006)
Geomyidae	Orthogeomys	51	–	D	0.5	NA	(Woodburne <i>et al.</i> 2006)
Geomyidae	Pappogeomys	66	–	ND	0.25	NA	(Woodburne <i>et al.</i> 2006)
Heteromyidae	Heteromys	71	–	D	0.1	NA	(Woodburne <i>et al.</i> 2006)
Leporidae	Sylvilagus	765	52	D	1.42	NA	(Woodburne <i>et al.</i> 2006)
Megalonychidae	Choloepus	46	–	D	5.52	SA	(Delsuc <i>et al.</i> 2002; Delsuc <i>et al.</i> 2004)
Microbiotheridae	Dromiciops	12	–	ND	0.02	SA	(Woodburne <i>et al.</i> 2006)
Mustelidae	Conepatus	157	–	D	1.79	NA	(Woodburne <i>et al.</i> 2006)
Mustelidae	Eira	107	–	D	3.91	NA	(Woodburne <i>et al.</i> 2006)
Mustelidae	Lontra	94	–	D	7.62	NA	(Woodburne <i>et al.</i> 2006)
Myrmecophagidae	Myrmecophaga	34	–	D	22.33	SA	(Delsuc <i>et al.</i> 2002; Delsuc <i>et al.</i> 2004)
Myrmecophagidae	Tamandua	114	–	D	5.52	SA	(Delsuc <i>et al.</i> 2002; Delsuc <i>et al.</i> 2004)
Ochotonidae	Ochotona	165	5	ND	0.14	NA	(Woodburne <i>et al.</i> 2006)
Procyonidae	Nasua	151	–	D	3.91	NA	(Woodburne <i>et al.</i> 2006)
Procyonidae	Procyon	445	–	D	5.83	NA	(Woodburne <i>et al.</i> 2006)
Sciuridae	Microsciurus	53	–	D	0.1	NA	(Mercer & Roth 2003; Woodburne <i>et al.</i> 2006)
Sciuridae	Sciurillus	6	–	D	0.04	NA	(Woodburne <i>et al.</i> 2006)
Soricidae	Cryptotis	213	10	D	0.01	NA	(Woodburne <i>et al.</i> 2006)
Tapiridae	Tapirus	127	28	D	218.82	NA	(Holanda & Cozzuol 2006)
Tayassuidae	Pecari	150	8	D	21.27	NA	(Woodburne <i>et al.</i> 2006)

*Source: Paleobiology database. Total number of fossil records in all periods of time.

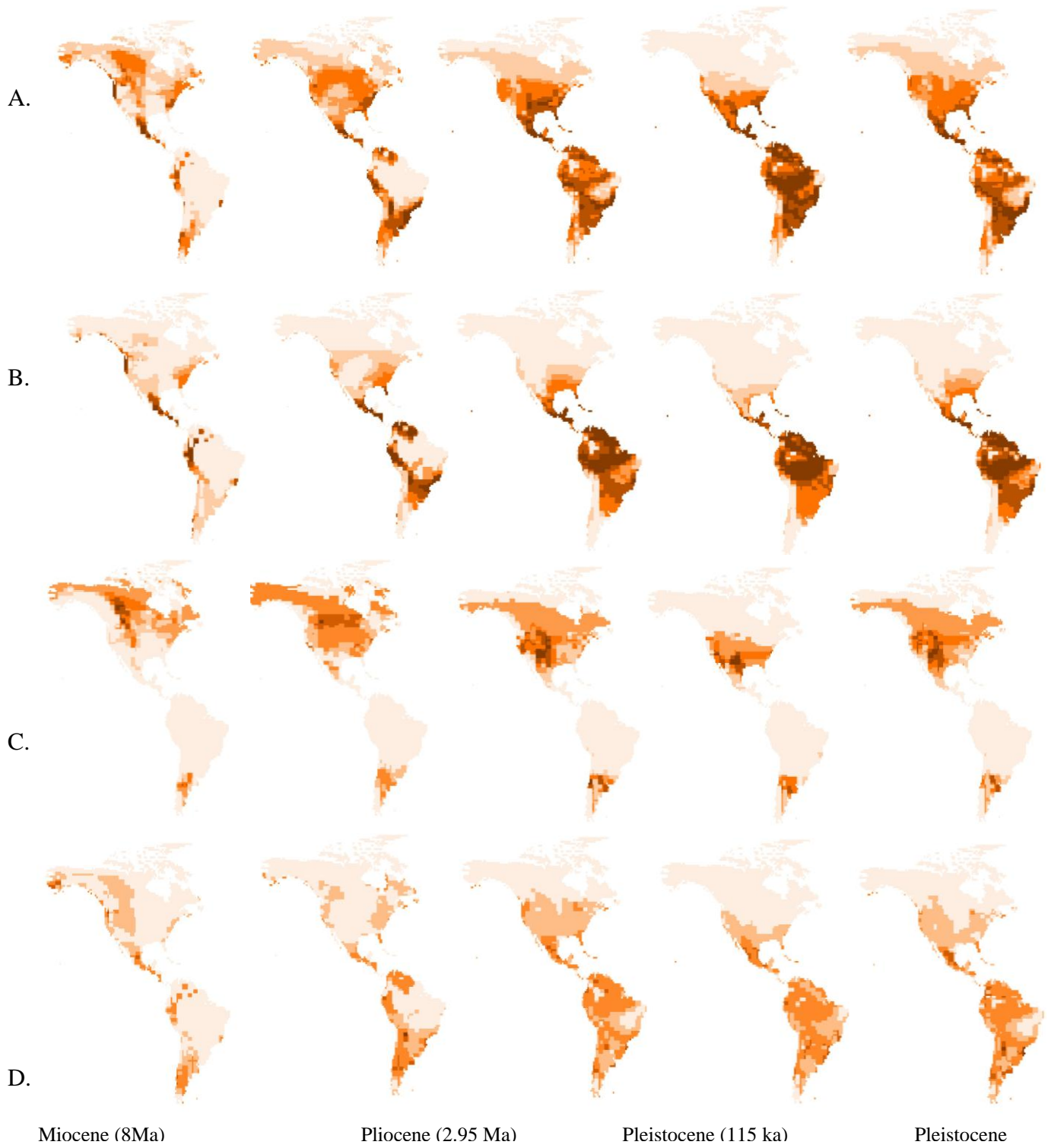
Appendix S2

	SS	Degr. of Freedom	MS	F	P
rs(Area)					
Intercept	68879.98	1	68879.98	189.5299	0.000000
Or	531.15	1	531.15	1.4615	0.230123
D	3793.30	1	3793.30	10.4376	0.001771
Or*D	3065.06	1	3065.06	8.4338	0.004718
Error	30164.31	83	363.43		
T	345.08	4	86.27	6.5462	0.000044
t*Or	1041.05	4	260.26	19.7489	0.000000
t*D	212.90	4	53.22	4.0387	0.003269
t*Or*D	197.64	4	49.41	3.7493	0.005337
Error	4375.31	332	13.18		
rs(Distance)					
Intercept	556592.9	1	556592.9	265.3500	0.000000
Or	21501.4	1	21501.4	10.2506	0.002236
D	75519.8	1	75519.8	36.0033	0.000000
Error	119562.1	57	2097.6		
t	6240.7	4	1560.2	15.3559	0.000000
t*Or	102.7	4	25.7	0.2526	0.907887
t*D	475.3	4	118.8	1.1696	0.324990
Error	23165.3	228	101.6		

Appendix S3

Period of time	Sqrt(Area)		Sqrt(Distance)	
	Chi square	P	Chi square	P
Miocene	3.48998	0.32206	5.97209	0.30894
Pliocene	2.50138,	0.47504	3.16860	0.36635
Pleistocene ¹	6.59907	0.08584	6.43185	0.09239
Pleistocene ²	4.76472	0.18986	0.36152	0.94807
Recent	4.81719	0.18568	2.56514	0.76665

APPENDIX S4.



APPENDIX S5

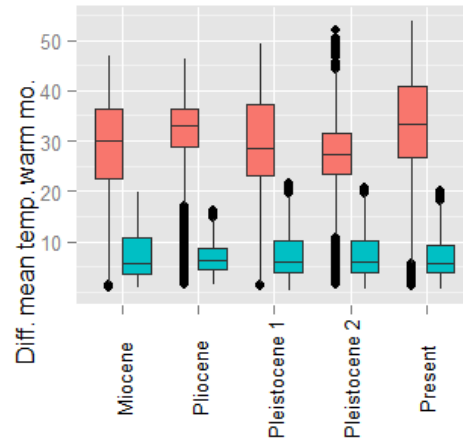
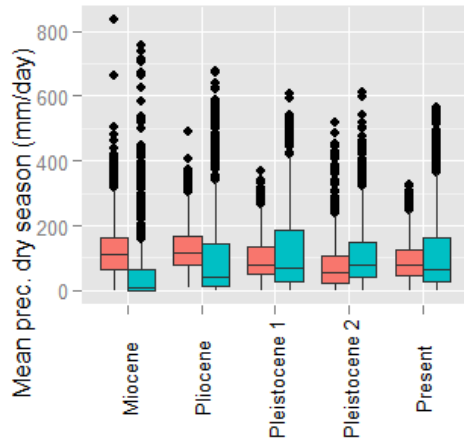
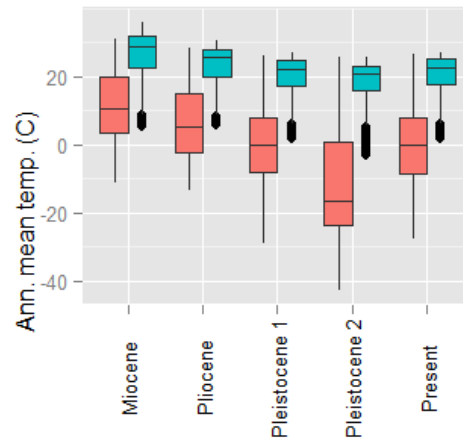
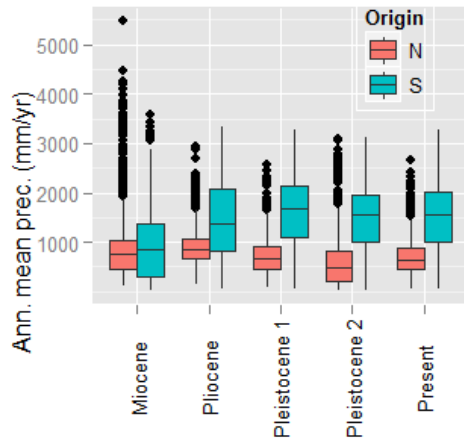


Figure 1.

A

Glossary	
<i>Subcontinents:</i>	North America and South America.
<i>True disperser:</i>	Mammal species that crossed the bridge, and have the potential to originate new species and genera in the opposite continent.
<i>Non Disperser:</i>	mammal species and genera endemic to one subcontinent.
<i>Dispersal path length:</i>	An indirect measure of connectivity calculated as the distance between north and south borders of suitable areas of each genera. When this is equal to zero the connectivity was considered maximum.
<i>Migration pulse:</i>	Each of the 2 consecutive time-periods where both suitable area and dispersal path length is measured (e.g. Miocene-Pliocene, Pliocene-Pleistocene, Pleistocene-Recent time) that conform the "geological time".
<i>Geological time:</i>	Period from Miocene to recent-time
<i>Suitable area:</i>	Potential ecological niche projection into the continent to be colonized (non native continent).
<i>Suitable area rate of change:</i>	Changes in suitable area between pulses.
<i>Dispersal response:</i>	Migratory strategy for mammals between subcontinents (i.e., true-dispersers and non-dispersers).
<i>Climate equilibrium degree:</i>	Refers to the similarity between the current and potential distributions

. B.

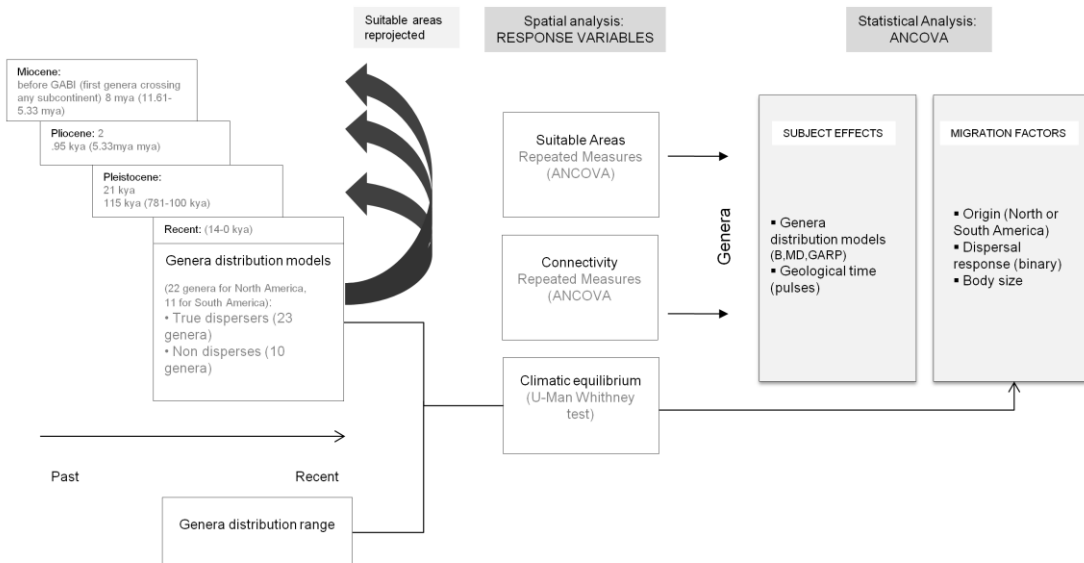


Figure 2.

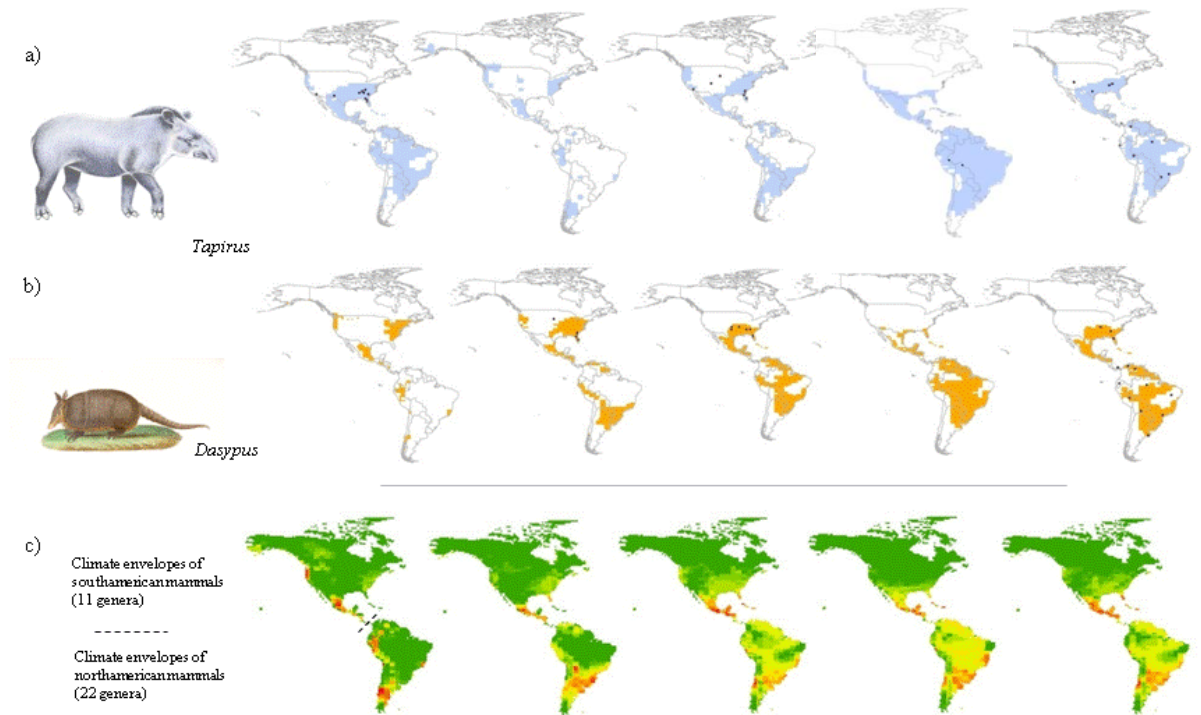
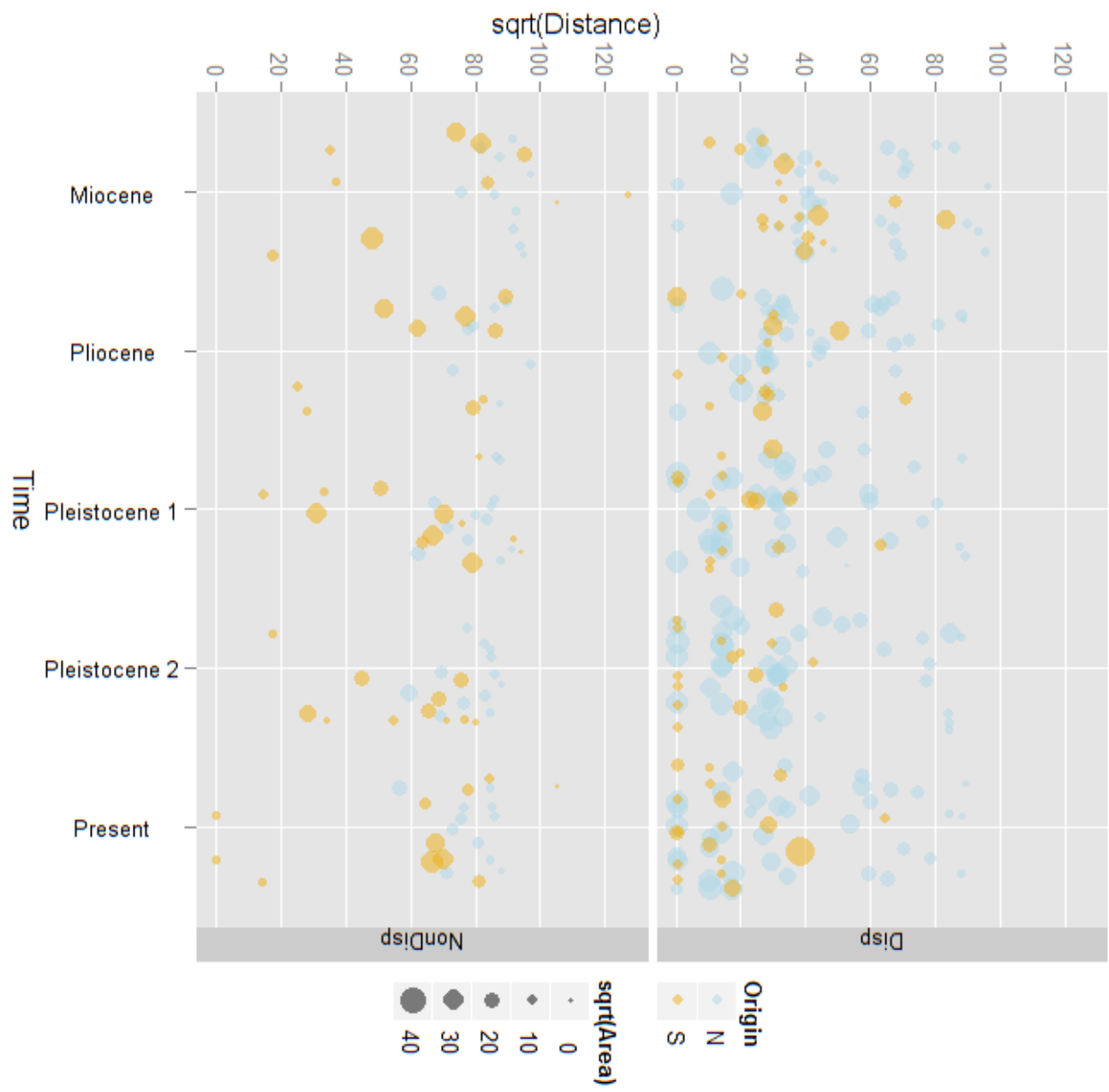


Figure 3



Supplementary Material

Method. Niche models.

There are known differences between Bioclimatic models: BIOCLIM (Nix 1986) tends to overestimate species potential distributions slightly more than other presence-only models (Tsoar *et al.* 2007), and significantly more than presence-absence methods (Elith *et al.* 2006). MD produces predictions significantly more accurate than those produced by corresponding rectilinear models (elliptic shape), with the advantage of its ability to cope with autocorrelations among climatic variables (Farber & Kadmon 2003). Finally the Genetic Algorithm for Rule-set Production (GARP (Grinnell 1917); <http://www.nhm.ku.edu/desktopgarp/>) relates ecological characteristics of known occurrence points to those of points sampled randomly from the rest of the study region to develop a series of decision rules that summarize factors associated with the potential for presence (Stockwell & Noble 1992; Peterson & Cohoon 1999). These are considered more complex algorithms because they generate pseudoabsences against which to test the models. The final ecological niche model is a set of if–then statements used to determine whether a particular pixel will be predicted as present or absent (Peterson & Cohoon 1999). All Bioclimatic models were then projected to all climatic scenarios to produce digital maps in raster format of areas with environmental characteristics suitable for the species (Anderson *et al.* 2002).

After genera were bioclimatically modelled, the geographic information system (GIS) ArcView Ver. 3.2 (ESRI 1999) and Microsoft Office ACCESS were used to process and edit maps and to calculate the potential distribution areas (Figure 1C).

Distances between predicted suitable areas were calculated in Arc View 3.2 (ESRI 1999) with the *Measure tool*, which calculates distance avoiding crossing outside the continental land surface.

Capítulo III

¿Puede la similitud ecológica promover la parapatría?

Evidencia en las aves de zonas áridas (Género *Toxostoma*)

Can ecological similarity promote parapatry? Evidence from aridland birds (Genus *Toxostoma*)

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ABSTRACT

Aim To analyze the degree of ecological similitude among four closely-related birds, in order to explain their current parapatric and allopatric ranges and to explore the role of ecological replacements in species differentiation.

Location Peninsula of Baja California and adjacent arid lands of southwestern United States and northwestern Mexico.

Methods Using the locality records of the four historically related species (*Toxostoma bendirei*, *T. arenicola*, *T. cinereum*, and *T. lecontei*) and 22 environmental variables, we modelled the ecological niches. To test whether the species pairs (sister and non-sister) showed a conservative or an evolutionary niche scenario, we measured the ecological differentiation among species based on the distance between their niche centroids. We then correlated it to the known mtDNA genetic distances. To test the niche' similarity between species pairs we analysed the overlapping potential areas and finally, we applied a randomization test to explore whether the four parapatric and allopatric groups, were different from what was expected by chance, given the underlying environmental differences between the regions in which they occur.

Results According with patterns of niche evolution, sister species were more differentiated ecologically, showing higher ecological niche centroid's distances where non-sister species showed the opposite patterns. In some pair of species the background test did not distinguish whether the pattern was due to evolution, conservation or random, but in a majority of the cases, parapatric non-sister species were ecologically more similar (showing conservative niche patterns) than allopatric sisters species (showing evolution niche patterns).

Main conclusions The four species analyzed are geographically confined by non sister species, but adjacent species share similar ecological conditions. These patterns suggest an ecological replacement of species that could have acted as biotic barriers, where patterns of parapatry maintain the isolation between sister species.

Keywords Allopatry, biotic barriers, ecological niche modeling, ecological similarity, niche conservatism, niche evolution, parapatry, Thrashers

INTRODUCTION

Each taxon has a particular geographical range which varies in extent and shape in response to its particular history and ecological requirements. The role of abiotic conditions over short evolutionary time scales has been well established as a common phenomenon, often driving vicariance as a result of the inability of species to adapt to novel ecological conditions or to low dispersal abilities (e.g. Svenning & Skov, 2004; Kozak et al., 2006; Munguía et al., 2008). However, biotic factors (e.g., competition with closely-related species) are also important because morphologically similar species commonly share ecological requirements that can prevent their coexistence, often replacing one another ecologically (Jaeger, 1970; MacArthur, 1972; Anderson et al., 2002a). For instance, sympatrically closely related mammals, when present, often display behavioral, microhabitat or macrohabitat segregation (Emmons, 1980; Anderson et al., 2002a). A specific example is the case of the widely distributed terrestrial salamanders of the genus *Plethodon* in North America, where interspecific competition promotes ecological replacements which appear to have restricted the geographic range of potential competitors for resources (Hairston, 1980a; Hairston, 1980b; Adams & Rohlf, 2000; Adams, 2007). Some authors (e.g. Soberón, 2007) have suggested that biotic factors present themselves at finer scales.

Most explanations of parapatric distribution assume that competitive interactions and species similarity can cause interspecific exclusion upon geographic contact (Terborgh, 1985; Haffer, 1989; García-Ramos et al., 2000; Sánchez-Cordero et al., 2008). A species' potential range may therefore be restricted by the presence of interacting species (i.e. competitors, predators, or parasites) reducing its fundamental niche to a fraction or subset that can actually be exploited, the realized niche (Hutchinson, 1957). Sometimes these intermediate steps, which occur during the process of exclusion, are

difficult to test because they occurred in the past (Keast, 1968). However, the detected parapatry could be a response to gradients in elevation, climate, soil structure, and vegetation (Terborgh, 1985; Bull, 1991; Bull & Possingham, 1995). Separating the relative ecological and historical determinants of individual species' distribution has proven difficult from a geographic perspective (Endler, 1982). Therefore, the question of how interactions between species help in the molding of individual geographic distributions remains unsolved.

The parapatric distribution is a spatial contiguous segregation of species separated by sharp boundary ranges without any clear physical barriers between them (García-Ramos et al., 2000). It is relatively common between closely-related species (King, 1993) although spatial segregation also occurs in less related species but with similar ecological requirements (García-Ramos et al., 2000; Anderson et al., 2002a). Recent studies have emphasized the importance of ecological niches in allopatric speciation (Peterson & Holt, 2003; Wiens, 2004; Weaver et al., 2006) suggesting that the analysis of ecological data gives a more robust framework for interpreting speciation patterns, particularly within geographical and phylogenetic context (Rice et al., 2003; Graham et al., 2004; Weaver et al., 2006). In addition, it has been suggested that there is a tendency for species to retain similar ecological niches over evolutionary time scales in closely-related species; although diverse exploration of the conservative aspects of ecological niches across evolutionary time scales (Peterson et al., 1999; Graham et al., 2004; Martínez-Meyer et al., 2004; Knouft et al., 2006; Yesson & Culham, 2006) has shown that ecological niche conservatism is common, but far from universal (Wiens, 2004). Furthermore the possibility of misunderstandings in the interpretations of ecological similarity in niche conservatism is frequent (Losos, 2008; Warren et al., 2008; Peterson, 2011).

The overlapping of ecological niches among closely-related species suggests their potential capability to occupy the same geographical areas (Anderson et al., 2002a). Thus, special attention should be paid to parapatric boundaries between closely-related species along a continuum of environments, where ecological exclusion could explain the lack of coexistence in similar ecological species. In the particular species of Thrashers that we analyzed, current distribution shows that species are limited by each other, creating an incredibly rare correspondence between geographical boundaries (i.e., parapatry). We hypothesized that such geographical patterns could be explained by ecological exclusions that occupy the same geographical areas.

The goal of this article is to analyze the degree of ecological similarity amongst four closely-related birds, in order to explain their current parapatric and allopatric ranges and also to explore the possible role of ecological replacement in species differentiation.

Biogeographic scenario and bird taxa

The geographical and ecological distributions of groups that have evolved in regions with geological complex origins and dynamic environments, such as the Baja California Peninsula and adjacent desert areas, offer the opportunity to study niche interactions. The analyzed taxa are morphologically similar and possess a credible hypothesis of close phylogenetic relationship (Zink et al., 1997; Zink et al., 1999). This group is formed by two complexes with non-overlapping geographical ranges. The Le Conte's complex has two allopatric but sister forms: *Toxostoma lecontei* and *T. arenicola* (Zink et al., 1997). *T. lecontei* inhabits southeastern California, southern Nevada, south-central Arizona, south to northeastern Baja California; *T. arenicola* is restricted to west-central Baja California (Zink et al., 1997; AOU, 1998; Fig. 1). Similarly, the *cinereum* complex includes two

allopatric, sister forms: *T. cinereum* and *T. bendirei* (Engels, 1940; Zink et al., 1999).

Toxostoma cinereum inhabits Baja California from lat. 31.7° N on the Pacific coast and Animas Bay on the southeast coast to Cape San Lucas. *Toxostoma bendirei* breeds from southeastern California, southern Nevada, southern Utah, south-central Colorado, western and central New Mexico, south to central Sonora, and winters from southern Arizona and extreme southwestern New Mexico south through Sonora to northern Sinaloa (AOU 1998, Fig. 1) although few winter records exist from Baja California (Wilbur, 1987; Erickson & Howell, 2001).

These four taxa have apparently evolved as a result of the same historical event in the Peninsula of Baja California and adjacent areas: All speciation events within these four species occurred at least one million years ago, when Baja California was fragmented by trans-peninsular seaways (into one or more islands and on several occasions) connecting the Pacific Ocean and Sea of Cortés (Murphy, 1983; Grismer, 1994; Riddle et al., 2000a; Riddle et al., 2000b). After Baja California returned to a peninsular stage, it is possible that isolated populations expanded into their ancestral ranges, promoting secondary contact, and therefore possible ecological exclusion amongst groups that could have maintained the same or similar ecological niches. Such exclusions could have bound the current geographical distributions acting as biotic barriers, preventing introgressions among sister species and maintaining the genetic and morphological differentiations. Furthermore, Hubbard (1973) advocates that the climatic cycles of the late Pleistocene glaciations led to speciation and that parallels in the distribution of groups resulted from independent evolutionary responses to a common set of isolating events. However, Zink et al. (1997) and Zink et al. (1999) advocated that an intra-peninsular seaway could explain the speciation patterns within these complexes, as it has been suggested in relation to other taxa (e.g. Riddle et al., 2000a). This discrepancy might be a result of the complexity on the

origin of Baja California peninsula, one of the most geologically dynamic areas on Earth (Grismer, 2000; Bernardi et al., 2003), where both geology and climate have affected the biogeography of the regional biota (Lindell et al., 2006).

METHODS

In spite of encompassing only a few of the possible niche dimensions (*sensu* Hutchinson, 1957), currently available digital maps provide environmental information for many major physical variables that commonly influence species' macro-distributions (Anderson et al., 2002a). Ecological niches can then be estimated by the use of computational algorithms that correlate precise locality records with environmental layers, such as climate and topography (Peterson & Cohoon, 1999) therefore generating a hypothesis of the potential distribution of the species (Cowley et al., 2000). Models are developed based on large regions with varying biotic contexts and so the respective models then approximate the species' fundamental niches (Hutchinson, 1957; Anderson et al., 2002a). Nevertheless, similarities in niche characteristics can be visualized and analyzed statistically with methods from ecological niche modeling (Guisan & Thuiller, 2005; Wiens & Graham, 2005; Warren et al., 2008).

Occurrence and environmental data

We compiled a database with the records of the four species of *Toxostoma* including a refined distribution obtained from the Atlas of Mexican Birds (Navarro et al., 2002), the Museum of Vertebrate Zoology web database (<http://www.mip.berkeley.edu/mvz/collections/index.html>), and The Field Museum web database (<http://fm1.fieldmuseum.org/collections/search.cgi?dest=birds>). Some additional records were obtained from literature (Wilbur, 1987; Zink et al., 1997; Erickson &

Howell, 2001; Rojas-Soto et al., 2002). They were processed to remove conspicuous errors, and exhaustively cross-checked against auxiliary information and spatial datasets to validate positional accuracy.

We gathered the following unique occurrence data points by species: *T. bendirei* (only year-round records) N=47, *T. arenicola* N= 15, *T. cinereum* N= 129, *T. lecontei* N= 64 (Fig. 1).

To characterize environments, we used 30” resolution (~1 km² cell size) interpolated climate data summarizing 19 ‘bioclimatic’ variables —Bio 1 (mean annual temperature); Bio 2 (mean diurnal range); Bio 3 (isothermality); Bio 4 (temperature seasonality); Bio 5 (maximum temperature of the warmest month); Bio 6 (minimum temperature of the coldest month), Bio 7 (annual temperature range); Bio 8 (mean temperature of the wettest month); Bio 9 (mean temperature of the driest month); Bio 10 (mean temperature of the hottest month); Bio 11 (mean temperature of the coldest month); Bio 12 (mean annual precipitation); Bio 13 (mean precipitation of the wettest month); Bio 14 (mean precipitation of the driest month); Bio 15 (precipitation seasonality); Bio 16 (total precipitation of the wettest quarter); Bio 17 (total precipitation of the driest quarter); Bio 18 (total precipitation of the hottest quarter); and Bio 19 (total precipitation of the coldest quarter of the year)— from the WorldClim project (Hijmans et al., 2005). In combination with the bioclimatic variables, we used elevation, slope, and the compound topographic index (CTI; a function of the upstream contributing area and the slope that reflects tendency to pool water), all from the Hydro-1K dataset (USGS, 2001).

Ecological niche modeling

Although ecological differentiation has been analyzed using different algorithms and methods (e.g. Peterson et al., 1999; Elith et al., 2006; Hawkins et al., 2007; Warren et al.,

2008), MaxEnt is one of the most widely used algorithms (Phillips et al., 2006). MaxEnt's predictive performance is consistently competitive with the highest performing methods (Elith et al., 2006). Since becoming available in 2004, it has been utilized extensively for modeling species distributions. Published examples cover diverse aims (finding correlates of species occurrences, mapping current distributions, and predicting to new times and places) across many ecological, evolutionary, conservation and biosecurity applications (Elith et al., 2010). We used MaxEnt version 3.3.3e and the default settings were used during the run, except that we used 25% presence records for testing and 75% for training. Niche models were tested by their AUC performance.

We calculated the overlapping potential geographic area between pairs of species (sister and non-sister species inter-prediction). A geographic information system, GIS ArcView Ver. 3.2 (ESRI 1999) was used during the maps editing process.

Ecological and genetic distances

The ecological differentiation between species was estimated using the five most important environmental variables (Bio14, precipitation of driest month; Bio18, precipitation of warmest quarter; Bio8 mean temperature of wettest quarter; Bio9, mean temperature of driest quarter; Bio3, isothermality) in order to better explain each of the potential distribution models for each species. These were obtained through a Jackknife test performed in Maxent (Phillips et al., 2006). Then we estimated niche centroids in ecological distances by calculating the weighted mean of the standardized values ($x=0$, $s^2=1$) in which the taxon was predicted present for each environmental parameter (following Rice et al., 2003). Then, the Euclidian distance among centroids was calculated for every pair of taxa using the formula:

$$\sqrt{\sum(X1a-X2a)}$$

where X_{1a} is the weighted mean of variable a in species 1, and X_{2a} is the weighted mean of the same variable in species 2, and the total is over all variables. Then, the square root of the total of the square is the difference between the means of each species to each variable (i.e., square root $[(\text{var}_{1\text{sp}1} - \text{var}_{1\text{sp}2})^2 + (\text{var}_{2\text{sp}1} - \text{var}_{2\text{sp}2})^2 + (\text{var}_{3\text{sp}1} - \text{var}_{3\text{sp}2})^2 + (\text{var}_{4\text{sp}1} - \text{var}_{4\text{sp}2})^2 + (\text{var}_{5\text{sp}1} - \text{var}_{5\text{sp}2})^2 + (\text{var}_{6\text{sp}1} - \text{var}_{6\text{sp}2})^2]$). This was calculated by species pairs.

Genetic distances were obtained from the published data on mtDNA by Zink et al. (1997) and Zink et al. (1999). We used the Nei's genetic distances based on the number of pair bases that differ among species (mutations) in percentage (Table 1), which we assumed would be sufficient to show the magnitude of differentiation among species, although alternative methods exist (e.g. Eaton et al., 2008).

Considering that the more common patterns of speciation (i.e. allopatry, parapatry and peripatry) resulted in the occupation of different areas, the degree of niche ecological similitude would depend on the proximity among such areas, or in the geographical coincidence of ecological conditions, independently of the geographic distances. Under a conservative niche scenario we predicted that ecological similarity between niches would be maintained long after the process of speciation (Fig. 2A). In contrast, under an evolution niche scenario, ecological differences would increase starting with the initiation of the speciation process (Fig. 2B). To test the association with either scenario we compared the ecological distances among species pairs (sister and non-sister) and we applied a Spearman Correlation Test to the genetic and ecological distances of each species pairs.

Ecological similarity among species' predicted areas

We also measured the overlap of the predicted area (considering the numbers of pixels) by pairs of species, which represented the proportion of niche geographic coincidence among species.

Finally, we applied a randomization test proposed by Warren et al. (2008) named “background test” (ENMTools; <http://purl.oclc.org/enmtools>) to explore whether or not the four parapatric and allopatric groups were more different than would be expected given the underlying environmental differences between the regions in which they occur (i.e. whether one species’ ENM predicts that of a second species better than expected by chance). This technique makes comparisons based on the geographical regions (background area) in which a species resides instead of where the species was registered (for detailed methods see Warren et al., 2008, 2010). We used the polygons delimited around the occurrence data of each species as background areas.

RESULTS

The Spearman Test showed no correlation between genetic and ecological distances ($N=6$, $r_s=-0.06$, $p=0.9$). Sister species (AL and BC) were more differentiated ecologically than non-sister species (AC, BL, and CL). The non-sister species pair AB was the more genetic and ecologically differentiated (Fig. 3).

Geographic overlapping of the four species’ models (Fig. 4A,B) showed over predicted areas based on the current known species’ distribution (Fig. 1) that also revealed potential areas that share the same ecological conditions amongst species pairs (Fig. 4A-D). The analysis based on the overlap of predicted area by species pairs (considering the numbers of pixels) showed that for the non-sister species *T. arenicola* – *T. cinereum* (Fig. 4C), showed the highest values of similarity according to their inter-prediction, as opposed to *T. lecontei* – *T. arenicola* (Fig. 4 A), *T. cinereum*– *T. bendirei* (Fig. 4 B), and *T. lecontei*

– *T. bendirei* (Fig. 4D) where there was almost no similarity between them. Although not shown, the other combinations of species pairs (*T. arenicola* – *T. bendirei* and *T. cinereum* – *T. lecontei*) showed the lowest values of inter-prediction among each other.

The background test suggested that parapatric non-sister species *T. bendirei* and *T. lecontei* were ecologically similar (Fig. 5a); on the contrary the allopatric sister species *T. arenicola* and *T. lecontei* showed no evidence for niche similitude (Fig. 5b). Comparisons between the other allopatric non-sister species *T. cinereum* and *T. bendirei* (Fig. 5c) suggests that the former is more similar ecologically based on the niche available to *T. bendirei*; however, *T. bendirei* in relation with *T. cinereum* does not allow the distinction with the expected by chance. Similarly, the comparison between the allopatric non-sister species *T. arenicola* and *T. bendirei* (Fig. 5d) does not allow the distinction with the expected by chance. Considering the parapatric non-sister species *T. lecontei* and *T. cinereum* (Fig. 5e) the background test suggests that *T. cinereum* in relation with *T. lecontei* does not allow the distinction with the expected by chance; however, *T. lecontei* is more divergent than expected based on the niche available to *T. cinereum*. The background test for the parapatric non-sister species *T. arenicola* and *T. cinereum* suggested that comparisons showed no evidence for niche similitude (Fig. 5f).

DISCUSSION

According to ecological similarity, the distributional pattern of parapatry and the consequent differentiation among taxa could be explained if there were similarities in ecological niches. Sister species showed greater ecological distances than non-sister' species as we expected (AL, BC in Fig. 3) which, combined with the genetic distances, correspond with patterns of niche evolution. In contrast, the non-sister species (AC, BL and CL in Fig. 3) showed patterns of niche conservatism. In the former cases we

suggested that the ecological differentiation could be the result of their isolation (allopatry) influenced by the geographical presence of a non-sister species in between the two. Alternatively, the ecological resemblance shown by non-sister species could be explained by ecological convergence associated with the occupied areas, which tend to be geographically closer, but also by dispersion after an ecological release. Thus, the availability of areas represented by the Sonoran desert might have facilitated the geographic expansion for *T. bendirei*, and *T. lecontei*, allowing their niche conservatism. In contrast, *T. arenicola* and *T. cinereum* might have had more ecological pressures, considering the forced coexistence in the limited area of Baja California (sometimes as an island and at others as a peninsula depending on the geological stage) promoting their niche differentiation with low possibility of dispersion. Although both sister and non-sister pair species could have been affected by themselves acting as biotic barriers, their niches have not had the same evolutionary history, resulting in niche evolution in sister species and niche conservatism in non-sister species (Fig. 2). This is similar of many species in *Eleutherodactylus* genera within the wet forest restricted in the upper Amazon Basin, where for example the nearest relative of *E. nigrovittatus*, live in mountain environment in the Andes at elevations above 1000 meters (Lynch 1990).

The analyses of inter-prediction suggest two ecological patterns: sister species (*T. arenicola* – *T. lecontei* and *T. bendirei* – *T. cinereum*) showed a lack of inter-prediction in both directions (Fig. 4A, B). For non-sister species, the values of similarity varied from low to high (Fig. 4C, D), suggesting some degree of niche differentiation; however, these values were not much different from those of the sister species. *T. arenicola* – *T. bendirei* were the only pair of non-sister species that presented patterns of niche evolution (Fig. 3) with high values of inter-prediction (not shown). In this case, as has been suggested, the most isolated and range restricted species (*T. arenicola*) could have been affected by

climate changes and by the coexistence with *T. cinereum* within a limited area, promoting its niche evolution.

Species with high values of ecological similarity (the non-sister species *T. arenicola* – *T. cinereum*) indicate that although ecological niches expand further geographically over the predicted areas, species do not. This fact suggests that species could be limited by each other acting as biotic barriers and resulting in the observed parapatry pattern.

The background test showed contrasting results; in some cases, similar results occurred as observed in previous analyses, but in others it was impossible to observe any niche pattern; and in some cases the reverse pattern resulted. For instance, we can confirm that an ecological similitude occurred between *T. bendirei* and *T. lecontei* and that according to the ecological replacement hypothesis, such similitude might have formed this pattern of parapatry. Another expected pattern was displayed by the sister species *T. arenicola* and *T. lecontei*, which did not share similar ecological niches and based on the hypothesis of ecological replacement, the existence of an intermediate species (*T. cinereum*) could have promoted the niche evolution of *T. arenicola* (Table 2, Figs. 4 and 5). *T. bendirei* and *T. cinereum* are additional parapatric species that were in line with the replacement hypothesis. They showed significant ecological similitude according to the background test (although the relation between *T. cinereum* and *T. bendirei* was not possible to separate from the expected by chance).

In contrast, *T. arenicola* and *T. bendirei* are non-sister species distributed much too far geographically from each other and separated by two other parapatric species (*T. cinereum* and *T. lecontei*). These species are the most differentiated genetically and ecologically (Fig. 3) and should correspond with the pattern of niche evolution (Fig. 2); however, the background test did not allow for distinguishing neither similarity nor

divergence. Surprisingly, the background test suggested niche evolution between *T. lecontei* in relation to *T. cinereum*; therefore, this is a case in which there is no support for ecological replacement due to the lack of a similar ecological niche; except in the case of *T. cinereum* which did not present differences from those expected by chance in relation to *T. lecontei*. In contrast, the analysis of ecological distances suggested to be shorter than in the two sister species (Fig. 3).

The most unexpected response in the background test was the relation between *T. arenicola* and *T. cinereum*, because in spite of their parapatry, they didn't show similar ecological niches. This contradicts the suggestions of previous analyses where these species in fact showed an ecological similitude (Table 2, Figs. 4 and 5). However, this could be the only case where the parapatry is the result of a local adaptation to dunes in the Midwestern region of Baja California, where *T. arenicola* inhabits and is restricted; although this could also be promoted by an ancient ecological exclusion by the widespread *T. cinereum*, whose distribution range currently excludes such dune areas. On the other hand, the analysis of ecological distances (Fig. 3) for this pair species showed the lowest values in relation with other non-sister species.

In spite of some divergence and discrepancy amongst the analyses, we propose that measuring ecological distances, based on the species' niche centroids, is the most reliable approach to test for niche similarity. In contrast, the background test is based on ecological space but confined to a particular geographical space.

Geological events could have been the primary cause of species geographic isolation, with a secondary genetic differentiation. However, the climate-driven habitat fragmentation (Grismer, 2002) in combination with biotic factors, could have promoted the diverse degrees of ecological differentiation as well as the current parapatric distributions of the species. We advocate that after 'isolation' (i.e., the formation of the sea

of Cortés and the mid-Penninsular seaway) the niche overlap of ecologically similar taxa drove the degree of differentiation amongst species. This, in combination with the continuous and sometimes abrupt changes in weather patterns particularly during the dry periods of the Pleistocene, dramatically affected the distribution of these four species.

A stage of dispersion was also included in the process of shaping the current parapatry, at least in the case of the non-sister species. Although dispersion events are difficult to prove, there are some well documented examples in Baja California when it was no longer geographically isolated and had returned to a peninsular stage, diverse species of birds spread out into their ancestral ranges, such as the California Gnatcatcher (*Polioptila californica*), the Cactus Wren (*Campylorhynchus brunneicapillus*) and the Verdin (*Auriparus flaviceps*) (Zink et al. 2000; Zink et al. 2001). There are other non-avian examples of dispersion along the Peninsula, for instance the North American Side-blotched lizard (genus *Uta*; Upton & Murphy, 1997). Therefore, it's probable that more vagile species such as Thrashers could have spread out along seemingly continuous environments and have been limited by biotic barriers, as represented in these cases by ecologically similar species. Although *T. bendirei* is a partially migratory species that can coexist during the summer with *T. lecontei*, they do not coexist during the winter, probably because they share the same ecological conditions (see Nakazawa et al., 2004).

Wiens & Graham (2005) have argued that differences in niche characteristics are important for speciation if a set of populations are geographically separated from closely related species by areas that are outside of the climatic niche envelope. However, the gene flow between two related populations would be unlikely if another, less related taxa exists and occupies intermediate geographical areas that share a similar ecological niche. Niche conservatism between sister species, as a common phenomenon, has been proposed (Peterson et al., 1999; Wiens & Graham, 2005). However we suggest that interactions

between ecologically similar species could have also played an important role in the genetic and ecological divergence and isolation.

Four factors have been proposed to maintain the ancestral niche and limit local adaptation during vicariance: lack of variability, natural selection, pleiotropy, and gene flow (Wiens, 2004). These factors both separately or in conjunction, will prevent local adaptation to conditions at the geographic barrier, and form the microevolutionary basis for phylogenetic niche conservatism and vicariance (Peterson & Holt, 2003; Wiens, 2004). However the maintenance, or lack therefore, of the niche will depend on the capability or failure of populations to adapt to new environmental conditions, as has been analyzed for allopatric populations (Mc Cormack et al., 2010); the tendency of species to retain similar ecological niches (phylogenetic niche conservatism) in the absence of physical barriers and particularly when other closely-related taxa are part of such “new available conditions” has been underestimated. Therefore, if parapatric distributed taxa occupy similar niches, it might be an additional extrinsic factor that could promote niche evolution.

We identified extrinsic ecological factors (i.e., climatic and topographical) in a coarse scale throughout the documentation of possible ecological and geographical displacement, however more detailed factors that are associated with a finer scale explanation (i.e. realized niche or “Eltonian” niche sensu Soberón 2007) could include similarities or differences among range sizes, growth rates, spatial segregation, density, mating systems, dispersal and even intra-specific competition (e.g., Kildaw, 1999; García-Ramos et al., 2000; Cooper et al., 2007; Gurd, 2008). Although our analyses do not conclusively demonstrate ecological replacement as the cause of parapatry, it could strongly suggest ecological niche similarity as an important factor in establishing a biotic barrier and drawing the current distributions. Further theoretical and empirical research on

these topics is needed to improve our understanding of ecological niches and their interactions in parapatric species at finer scales.

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Tables

Table 1. Nei's genetic distance among species. Taken from Zink et al. (1997) and Zink et al. (Zink et al., 1999). Numbers in bold indicate the genetic distance among sister species.

	<i>T. bedirei</i>	<i>T. cinereum</i>	<i>T. lecontei</i>
<i>T. cinereum</i>	0.015	0	-
<i>T. lecontei</i>	0.092	0.088	0
<i>T. arenicola</i>	0.096	0.092	0.026

Appendix 1.

Collections included in the Bird Atlases: Moore Laboratory of Zoology, Occidental College; Museum of Comparative Zoology, Harvard University; Instituto de Biología, Universidad Nacional Autónoma de México Mexico n/a; Louisiana State University Museum of Natural Science; American Museum of Natural History; Western Foundation of Vertebrate Zoology; Field Museum of Natural History; Bell Museum of Natural History, University of Minnesota; Museo de Zoología, Facultad de Ciencias, UNAM; Museum of Vertebrate Zoology, University of California; United States National Museum of Natural History; Carnegie Museum of Natural History; San Diego Natural History Museum; University of California, Los Angeles; Cornell University Laboratory of Ornithology; Los Angeles County Museum of Natural History; Denver Museum of Natural History.

Figure legends

Figure 1. Geographic distribution ranges (represented by different grey polygons) and locality records of: *T. arenicola* (A- black triangles), *T. cinereum* (C- white dots), *T. lecontei* (L- white triangles) and *T. bendirei* (B- black dots are year-round records; black and white dots are summer records not used for modeling). Phylogenetic relationships come from Zink et al. (1999). Letters in the phylogeny correspond as follows: L = *T. lecontei*, A = *T. arenicola*, C = *T. cinereum* and B = *T. bendirei*.

Figure 2. Expected relationships between genetic and ecological distances by pair species, according to the expected patterns of niche conservatism (A) and niche evolution (B) scenarios.

Figure 3. Genetic and ecological distances by pair species (L = *T. lecontei*, A = *T. arenicola*, C = *T. cinereum* and B = *T. bendirei*). An asterisk indicates sister species and the grey line defines scenarios described in Figure 2.

Figure 4. Predicted geographical distribution based on ecological niche modeling by pair species: (A) sisters' species *T. arenicola* (dark grey) and *T. lecontei* (light grey), (B) sisters' species *T. cinereum* (dark grey) and *T. bendirei* (light grey), (C) non-sisters' species *T. arenicola* (black) and *T. cinereum* (light grey), and (D) non-sisters' species *T. lecontei* (light grey) and *T. bendirei* (dark grey). In all cases black represents the overlapping among potential areas of presence. Bars on the top of each map show the degree of inter-predictability among species based on the percentage of total predicted pixels as described in methods.

Figure 5. Background tests of niche similarity. The niche-overlap values (arrows) are compared to a null distribution of background divergence, where each pairwise comparison produces two reciprocal analyses, one in which the niche model for group A is compared to a niche model generated from random points from the group B's geographic range and vice versa (hence, the two distributions in each plot; grey correspond to the first written species and black to the other, and indicate the lineage for which the actual niche model is compared to the null model to generate the null distribution; see Warren et al. 2008 for details). Overlap values smaller than the null distribution support niche divergence (D), whereas larger values indicate niche conservatism (C).

Fig. 1

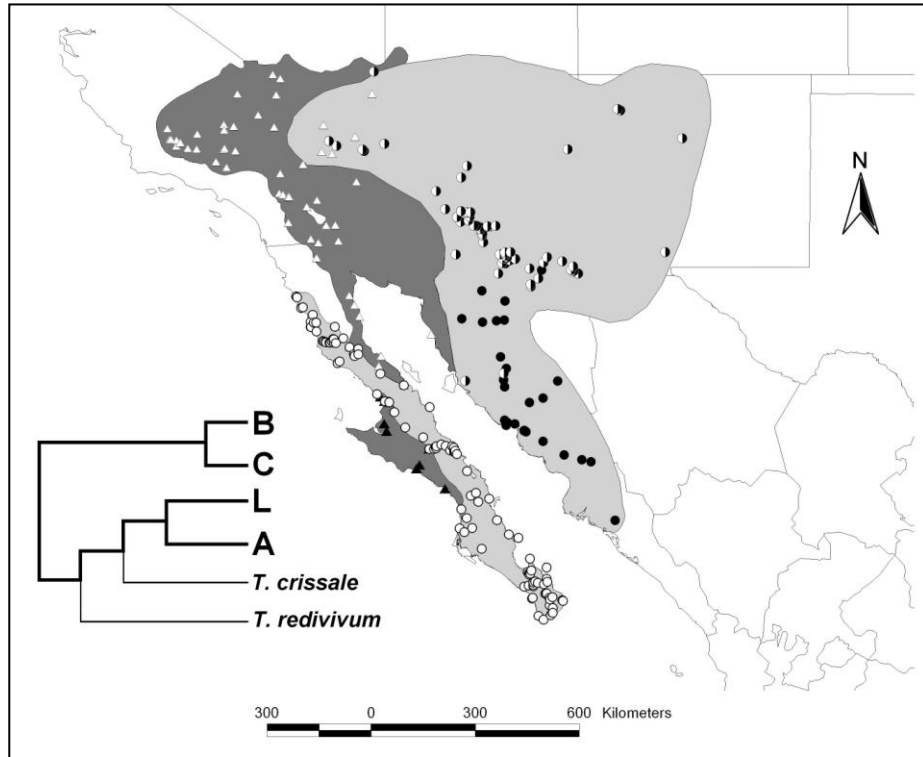


Fig. 2

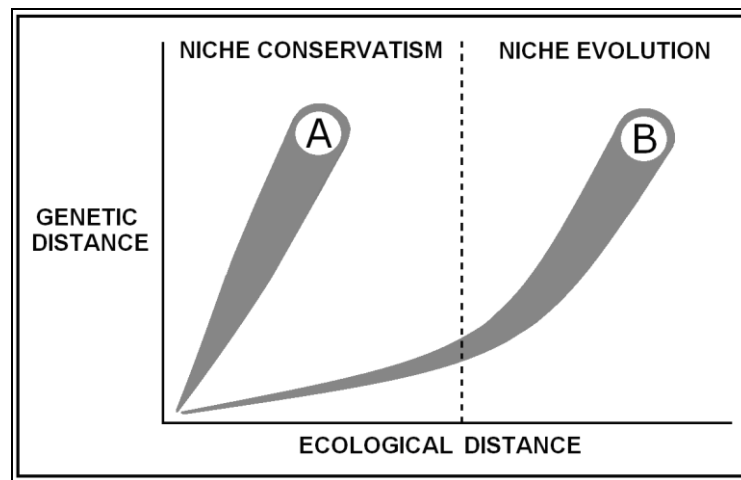


Fig. 3

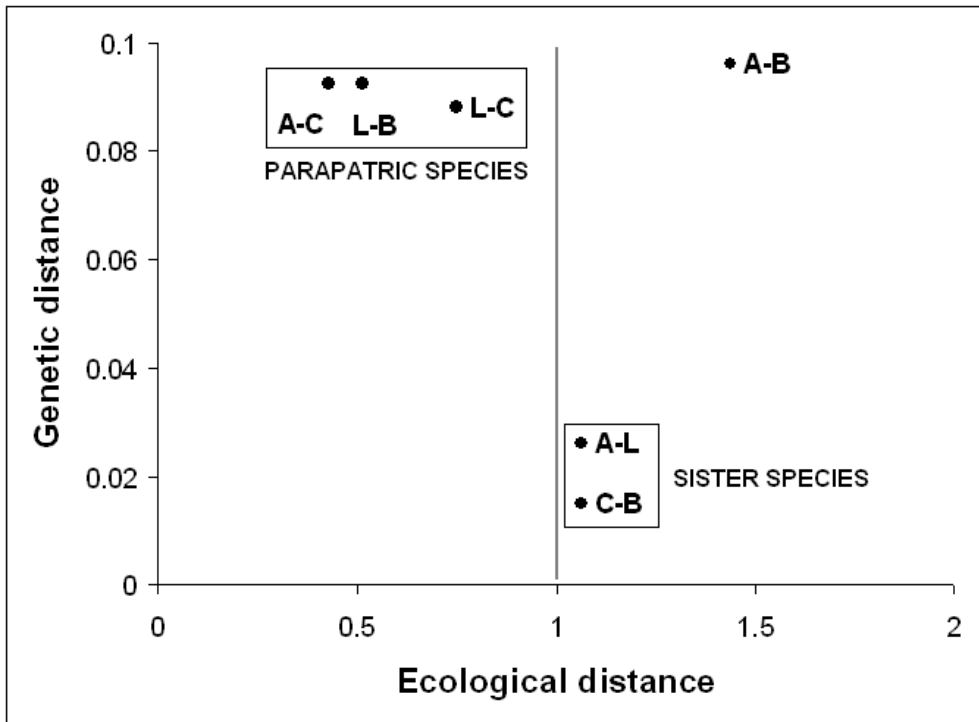


Fig. 4

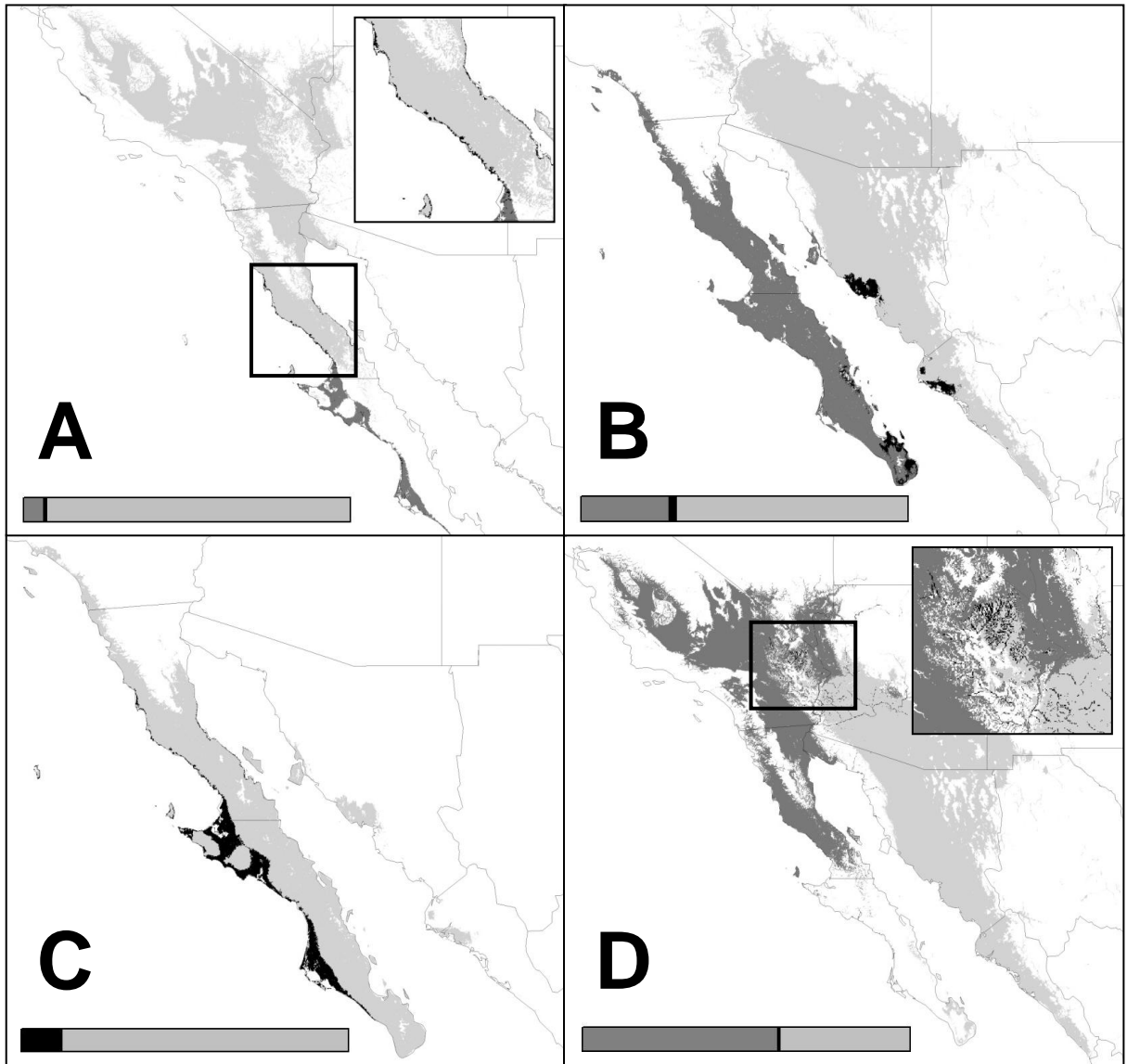
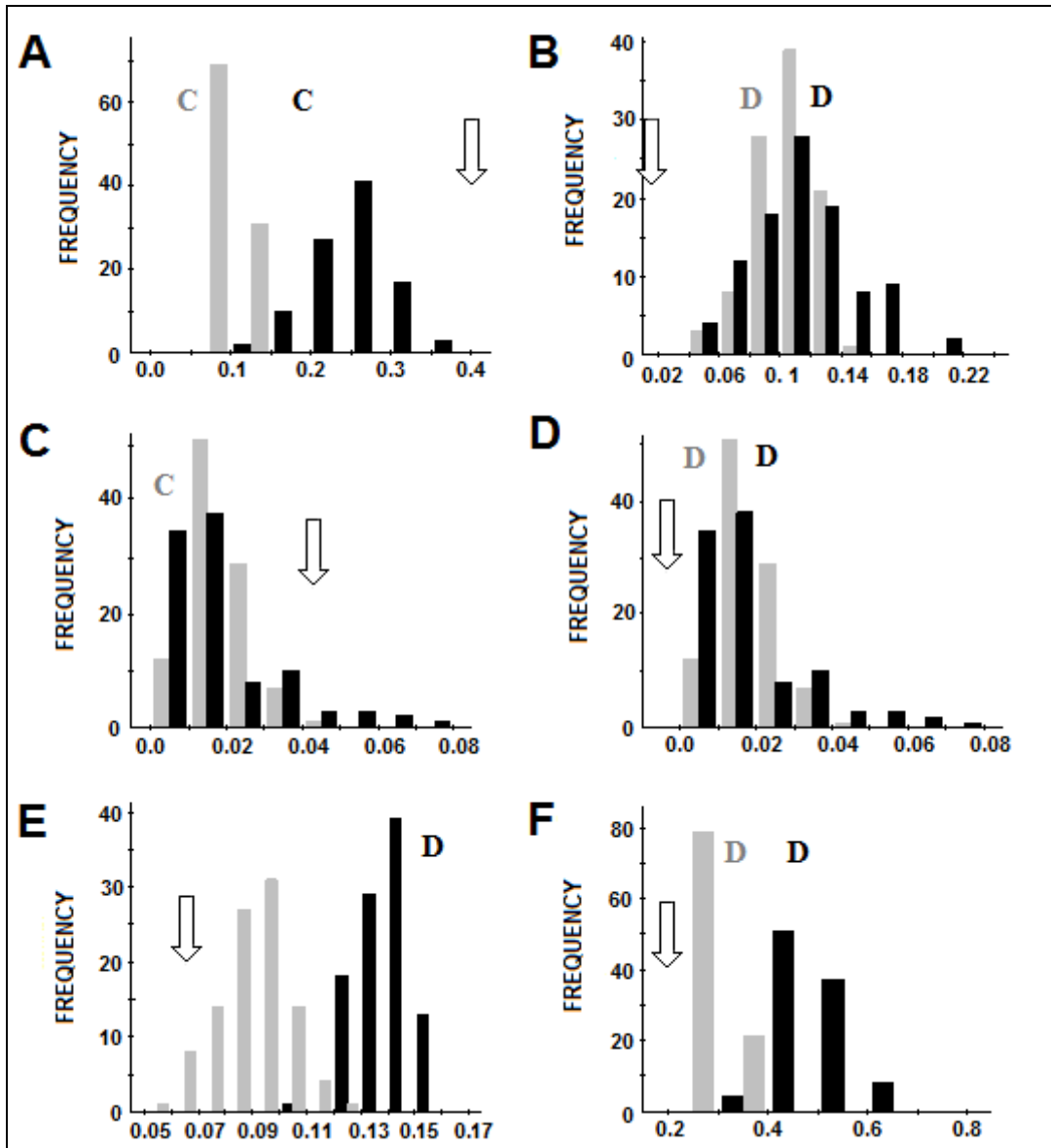


Fig. 5



DISCUSIÓN GENERAL

Entender la relación que existe entre las especies y el ambiente es el objeto central de estudio de la Ecología y es de particular interés en el área de la biogeografía ecológica, al relacionar la distribución geográfica de las especies con las variables del ambiente (Cox & Moore 2010). En la presente disertación se desarrolló un enfoque analítico para investigar el papel que juega el clima tanto en los patrones geográficos de las especies, como en sus procesos de dispersión y de especiación. Este enfoque tiene como base el análisis de la relación que existe entre la distribución de las especies y las variables abióticas.

En años recientes, esta relación ha sido evaluada con base en los registros de presencia de las especies y un conjunto de variables ambientales usando herramientas de modelado, con lo cual ha sido posible determinar el área de distribución potencial de las especies (Franklin 2009). Los métodos aplicados en los diferentes apartados de este trabajo se sustentó en el uso de herramientas de modelación ecológica que permitieron realizar el análisis de las áreas potenciales de distribución en contextos específicos. Así, cada uno de los capítulos se desarrolló dentro del mismo marco teórico y metodológico, aportando una contribución a diferentes aspectos centrales en el área de la biogeografía ecológica, como los patrones de equilibrio climático, la dispersión y la especiación.

De esta forma, el primer capítulo fue producto del interés en el estudio global sobre el equilibrio de las especies con el clima. Se tenía como referencia una serie de estudios previos a escala regional, que carecía de la representación del área geográfica de distribución de las especies estudiadas, lo que es una clara limitante metodológica. Por esta razón, en el presente trabajo se evaluó el grado de equilibrio con el clima de los anfibios; comparando entre las provincias biogeográficas, los órdenes taxonómicos y las implicaciones del uso de diferentes escalas espaciales. En el segundo capítulo se evaluó la asociación de la presencia de los mamíferos con el clima a través del tiempo para entender la asimetría del proceso de dispersión intercontinental, bajo un marco de variabilidad climática espacio-temporal entre Norte y Sudamérica. A partir de este análisis, se logró generar inferencias sobre los factores que llegaron a determinar una migración y posterior colonización diferencial. Finalmente, en el capítulo tercero, se analiza la asociación especies-ambiente en un contexto filogenético, en donde se propone una hipótesis del

papel que juegan las especies parapátricas como barrera biótica en un marco de discusión entre evolución y conservadurismo de nicho. Al respecto y, contrario a lo esperado, se encontró ausencia de conservadurismo en especies filogenéticamente cercanas y similitud ecológica entre especies lejanas.

Consecuentemente, como resultado de este proyecto doctoral, se generaron tres aportaciones importantes al área de la biogeografía ecológica y el uso de herramientas de modelación climática. La primera es una descripción de patrones del equilibrio global de las especies de todo un clado (anfibios) con el clima. La segunda es el desarrollo de un marco metodológico para evaluar la dispersión intercontinental con base en datos paleobiológicos y paleoclimáticos en un evento masivo de Intercambio Biótico y la dinámica de las áreas potenciales de distribución delimitadas por el clima. Finalmente, resultó cuestionable la hipótesis del conservadurismo de nicho ecológico en una situación particular: cuando las especies no hermanas pero parapátricas son similares ecológicamente, pueden actuar de barrera entre especies hermanas, propiciando la divergencia ecológica entre ellas, inclusive mayor que entre especies no hermanas.

Equilibrio climático de las especies

La proporción ocupada climáticamente en el área de distribución de las especies de anfibios no difiere entre los diferentes órdenes. En contraste, existieron diferencias entre las diferentes provincias biogeográficas. Los anfibios ocupan entre el 30 al 57% de su área potencial (análisis global vs regional) como parte de su área de distribución. Las diferencias entre los valores de equilibrio global y regional destacan por la importancia de considerar la escala apropiada de análisis (Peterson *et al.* 2011). Sin embargo, el rango de valores en este estudio coincide con otros organismos. De hecho, Svenning & Skov (2004) encontraron en una muestra de árboles de zonas templadas en Europa que ocupan el 38.3% de la distribución potencial, mientras que Munguía *et al.* (2008) encontraron una ocupación del 50% de los mamíferos de México. Utilizar la extensión geográfica apropiada es clave en este tipo de análisis, por lo que es recomendable que para aquellos estudios en los que se use la relación O/P como una medida de equilibrio, el área mínima de estudio debería de ser tan grande como el área de distribución más grande de las especies en estudio y así, tener representada la totalidad de dicha unidad de estudio (Munguía *et al.* 2008). En la práctica, esta estrategia propone utilizar unidades

biogeográficas coherentes con la historia común de las especies, como las provincias biogeográficas utilizadas aquí.

En general el grado de equilibrio encontrado entre los anfibios fue bajo. La medida de equilibrio obtenida está probablemente inflada porque se basó en el área potencial de ocupación y no del nicho fundamental. Sin embargo, el bajo equilibrio climático no es una sorpresa debido a que el grupo en general tiene baja habilidad de dispersión, que lo limita a seguir sitios con clima favorable a través del tiempo (Araújo *et al.* 2008). Sin embargo, las diferencias observadas en el grado de ocupación de las áreas potenciales entre las diferentes regiones sugieren que la habilidad de las especies de seguir los cambios climáticos depende de la región. De acuerdo a los modelos, los anfibios en el Neártico, Madagascar y Australasia tienen niveles mayores de equilibrio con el clima contemporáneo que los anfibios en el Neotrópico, el Afrotrópico, el Indo-Malayo y el Paleártico. Las implicaciones de estos resultados son importantes, porque indican que la efectividad de los modelos de distribución de las especies es mayor en las regiones donde tienen mayores niveles de equilibrio con el clima; esto es especialmente importante cuando son usados para transferibilidad (Bonn & Schröder 2001; Araújo & Rahbek 2006) o extrapolación (Thuiller *et al.* 2004).

Los análisis aquí desarrollados, al ser correlaciones sobre escalas globales de distribución y clima, no ofrecen información sobre los mecanismos que determinan el tamaño de las distribuciones o el nivel de equilibrio con el clima del área de distribución de los anfibios entre las diferentes regiones del mundo. Sin embargo, surgen algunas hipótesis que valdría la pena explorar en futuros estudios. Por ejemplo, llama la atención que dos de las regiones biogeográficas con más alto nivel de equilibrio también son de las regiones más pequeñas, *i.e.*, Madagascar y Australasia. Es posible que las especies que ahí habitan han podido colonizar una alta proporción de áreas favorables porque el área potencial es relativamente menor que la mayoría de las regiones. Sin embargo, la región Indo-Malaya también es relativamente pequeña pero contienen una fauna anfibia con bajo equilibrio climático; no obstante, esta región está conformada en gran parte por un archipiélago y esto seguramente ha limitado la dispersión de especies hacia islas no ocupadas con sitios favorables.

Otro patrón interesante es la diferencia en equilibrio entre los anfibios del Neártico y del Paleártico. Los primeros tienen mucho más alto nivel de equilibrio que los últimos. Ambas regiones presentan grandes extensiones y son expuestas a condiciones templadas con marcada estacionalidad. Se esperaría que las especies que han sido expuestas a dichas

condiciones hayan evolucionado estrategias de termorregulación que faciliten la adaptación a intervalos más amplios de condiciones que, por ejemplo, las especies tropicales (Feder 1976; Feder 1977; Martin & McKay 2004; Bernardo & Spotila 2006), las tolerancias más altas a los factores del clima favorecen la dispersión. Muchos autores han notado que la colonización postglacial en el Paleártico y en el Neártico fueron diferentes y que estas diferencias pueden explicar porque las extinciones del Cuaternario fueron mayores en el oeste del Paleártico que en el Neártico (Botkin *et al.* 2007). Su argumento es que la orientación longitudinal de las cadenas montañosas en Europa pudo haber prevenido una colonización efectiva de los refugios del sur (y regreso) de algunas especies, mientras que la orientación latitudinal de las montañas más prominentes en Norteamérica actúan como un corredor continental que facilitó la dispersión (Brown JH 1989; Baselga *et al.* 2011). Otra posibilidad para explicar las diferencias de los patrones de equilibrio entre el Neártico y el Paleártico es que la extensión y la posición de los desiertos en el Paleártico podrían actuar como fuertes barreras de dispersión. Los anfibios requieren de agua o humedad para vivir y reproducirse y ellos no pueden dispersarse a través de grandes extensiones áridas; los datos indican que el 37% de los Caudata son estrictamente acuáticos, mientras que los Anura son el 75% (Vences & Köhler 2008). Los desiertos están presentes en el centro y sur de la región Paleártica y ocupan 10.4% del área, mientras que los desiertos del Neártico se restringen al suroeste de la región y únicamente abarcan el 3% del área.

La descripción de los patrones de equilibrio en la distribución de las especies está en su inicio y, por ello, el entendimiento de los mecanismos que determinan la variación geográfica en el equilibrio con el clima es todavía limitado. Este estudio provee de las primeras descripciones de estos patrones en una Clase completa a nivel global. El desarrollo de más estudios de este tipo con otros grupos taxonómicos con diferente ecología y capacidades de dispersión, así como la disponibilidad de datos con diferente resolución espacial, ayudarán a tener una visión más amplia y completa de dichos patrones. Sin duda, existen alternativas para mejorar el enfoque metodológico propuesto en este trabajo, como la posibilidad de incluir información eco-fisiológica de las especies en la modelación (Morin & Chuine 2006; Kearney *et al.* 2010) para tener un mejor entendimiento de los mecanismos que determinan los patrones observados (Monahan 2009); sin embargo, este enfoque es limitado cuando se analizan un gran número de especies para los cuales no existen datos eco-fisiológicos. Otras alternativas que se han explorado incluyen análisis macroecológico de diversidad y ensamblaje de especies en

relación al clima contemporáneo (Araújo & Pearson 2005; Araújo *et al.* 2008; Baselga & MB 2010; Baselga *et al.* 2011). Finalmente, el avance en el conocimiento de la evolución del clima y cómo las especies han respondido a estos cambios para llegar a los patrones geográficos actuales, es necesario no sólo para comprender el equilibrio de las especies con el clima, sino también para entender y anticipar las respuestas de las especies al cambio climático actual.

Disponibilidad climática y dispersión de las especies en el Gran Intercambio Biótico Americano (GIBA)

Los resultados más importantes obtenidos en este análisis para entender los procesos de dispersión intercontinental de los mamíferos y en particular para explicar la asimetría observada durante el GIBA, en la que existe un mayor número de géneros de mamíferos de origen norteamericano en Sudamérica que lo opuesto, fueron que: (1) las áreas potenciales climáticamente favorables para los mamíferos norteamericanos en Sudamérica fueron incrementando a una tasa mayor hacia el presente que para los sudamericanos en Norteamérica; (2) existió una mayor conectividad en Centroamérica entre las áreas potenciales de los mamíferos que colonizaron el continente contrario, independientemente de su continente de origen; y (3) los mamíferos norteamericanos presentan un mayor grado de equilibrio climático en el presente que los sudamericanos, sugiriendo que los primeros tienen una mayor capacidad de dispersión (Svenning & Skov 2004; Araújo & Pearson 2005; Svenning & Skov 2007; Munguía *et al.* 2008).

Aunque desde Simpson (1940; 1947) se sugiere que la historia ha favorecido selectivamente a los mamíferos norteamericanos porque fueron capaces de enfrentar previamente cambios en las condiciones ambientales por su habilidad migratoria y movimiento hacia nuevos ambientes, así como alta sobrevivencia desde el intercambio previo ocurrido con Eurasia (Simpson 1947). Nosotros discordamos con la idea de que los norteamericanos fueron buenos en enfrentar estas nuevas condiciones. Siguiendo la teoría de conservadurismo de nicho y que las especies tienden a mantener condiciones similares a lo largo del tiempo, sería entonces más bien probable el establecimiento de las especies y su éxito en la colonización si encuentran en nuevas regiones las condiciones similares a las que ocupaban previamente, como lo observamos en nuestros resultados. En particular el

patrón asimétrico en el GIBA favoreció a los norteamericanos no sólo por la presencia de condiciones favorables, si no por su extensión y prevalencia a lo largo del tiempo.

Bajo el supuesto de que las áreas climáticas representan zonas favorables a colonizar, en este trabajo demostramos que tanto su extensión geográfica como su disposición espacial a través del tiempo han jugado un papel crucial en los procesos de dispersión de los mamíferos en América. Se encontró una mayor variabilidad ambiental ya que hay una mayor diferencia entre las temperaturas más cálidas y más frías en Norteamérica que en Sudamérica y con temperaturas mínimas menores en todos los periodos con respecto a Sudamérica; así como una tendencia general del descenso de temperaturas del Mioceno al Pleistoceno en Norteamérica (Webb 1991; Woodburne *et al.* 2006; Woodburne 2010). Al respecto podemos destacar dos puntos: El mayor intervalo de valores ambientales disponibles en el subcontinente norteamericano representa una mayor probabilidad de encontrar condiciones parecidas en Sudamérica por lo que especies norteamericanas resultarían beneficiadas por tal situación. Por otro lado, los mamíferos de Norteamérica, al estar expuestos a una mayor variabilidad climática, presentan mayores tolerancias fisiológicas lo que probablemente favoreció su dispersión a Sudamérica (Goodwin *et al.* 1999). La mayoría de los marsupiales presentan una tasa metabólica promedio inferior a la de los placentados, además de una baja temperatura corporal las cuales son por ejemplo una ventaja en lugares secos y calientes ya que tienen menos calor metabólico que pueda disiparse en el ambiente (Tyndal-Biscoe 2005). En general, estos primeros resultados contribuyen con la explicación de las causas clave de la asimetría que caracteriza al GIBA.

En otro resultado, la alta conectividad en Centroamérica estuvo más bien asociada con el éxito en la colonización y la dispersión, sin importar el origen de los mamíferos, ya que ambos conjuntos de especies presentaron niveles de conectividad similares de sus áreas potenciales en el área de contacto inicial (Istmo de Panamá), mientras que la conectividad más alta la presentaron los géneros tropicales. Al respecto, se ha reconocido que las bajas temperaturas y la heterogeneidad topográfica limita la dispersión de las especies tropicales (Ghalambor *et al.* 2006). Por ejemplo, la distribución actual de los géneros sudamericanos, como *Bradypus*, *Choloepus* y *Tamandua*, aunque cruzaron a Norteamérica, permanecen restringidos a regiones tropicales y subtropicales y sólo un número restringido de especies (*e.g.*, *Myrmecophaga*, *Dasybus novemcinctus* y *Didelphis virginiana*) han sido capaces de alcanzar áreas en la región Neártica. Si suponemos que los géneros norteamericanos exhiben tolerancias fisiológicas más amplias por ser placentados

y han estado expuestos a fluctuaciones térmicas más amplias, es posible pensar que a pesar de presentar menos conectividad en el Istmo, pudieron cruzar áreas poco favorables en ciertos periodos. Lo más importante aquí es reconocer que la conectividad es un atributo que favorece la dispersión y que esta conectividad fue dinámica durante cientos o millones de años, acercando y separando zonas climáticamente viables, un fenómeno que no es directamente comparable con la actual invasión asistida (Lonsdale 1999; Ricciardi 2007).

La forma de los subcontinentes pudo también favorecer a los mamíferos norteamericanos. Las áreas más grandes al norte del cono sudamericano pudieron haber significado una mayor extensión, lo que promovió el establecimiento de los norteamericanos e inclusive una alta especiación después de su establecimiento. En contraste, el área de contacto de los sudamericanos en Norteamérica es substancialmente más reducida. De hecho, la fauna actual de los mamíferos de Sudamérica tiene un 50% de especies con ancestría norteamericana, indicando que tuvieron más eventos de especiación que los sudamericanos en Norteamérica, los cuales únicamente representan el 10% de la biota de Norteamérica.

En la mayoría de los intercambios, las especies invasoras han representado sólo una pequeña proporción de la biota donante (Vermeij 1991). Únicamente del 2 al 11% de los géneros norteamericanos y 2 al 7% de la contraparte sudamericana, tomó parte en el GIBA (Marshall *et al.* 1982). Debido a esto podría ser más fácil alcanzar pronto un mayor conocimiento del comportamiento de dispersión de las especies invasoras y cada vez conseguir una mejor precisión sobre su comportamiento geográfico. Además los taxa que han migrado en algún evento, tienden a hacerlo de nuevo en posteriores eventos (Simpson 1947). Sería de especial interés conocer si las especies de los géneros que tuvieron éxito en la expansión de su área de distribución, son también más propensas a ser especies invasoras en la actualidad.

Finalmente, el análisis del movimiento diferencial observado durante el GIBA aunque no es directamente comparable, puede aportar elementos útiles para comprender los mecanismos de las actuales invasiones bióticas. Es cierto que las invasiones actuales no tienen precedente y son diferentes en frecuencia, magnitud e impacto de aquellas que ocurrieron en el pasado (Ricciardi 2007), sin embargo, considero que el estudio de las invasiones pasadas en el contexto de los cambios climáticos debería de ser analizada profundamente con el fin de entender el potencial invasivo de las especies durante futuros cambios climáticos.

El Contexto Geográfico y Ecológico de la Especiación

En el tercer capítulo de esta tesis, analicé la hipótesis de evolución y conservadurismo del nicho ecológico en un grupo de dos pares de especies del género *Toxostoma* en Baja California, cuya distribución geográfica muestra un patrón claro de parapatría. Los resultados obtenidos del análisis de interpredicción mostraron que es posible la evolución de nicho en especies hermanas (*T.arenicola-T.lecontei*, *T.benderei-T.cinereum*) y el conservadurismo de nicho en especies no hermanas (*T. arenicola - T.cinereum*, *T. benderei- T.lecontei*, *T.cinereum-T.lecontei*). Para las especies no hermanas, los valores de similitud variaron de bajo a alto, sugiriendo algún grado de diferenciación de nicho. Sin embargo, estos valores no fueron muy diferentes de los pares de especies hermanas. *T. arenicola-T. benderei* que fue el único par de especies no hermanas que presentó altos valores de interpredicción, sugiriendo un fuerte conservadurismo de nicho. Las especies parapátricas con altos valores de similitud ecológica (*T.arenicola* y *T. cinereum*) indican que aunque los nichos se extienden sobre las áreas predichas, las especies no están presentes, lo que sugiere que una especie podría estar limitada por la otra, cada una actuando como la barrera biótica.

La prueba del entorno (“background”) realizada presentó resultados contrastantes. En algunos casos se obtuvieron resultados similares a los observados en los análisis previos, en otros casos se obtuvo el patrón contrario, y en otros fue imposible observar algún patrón. Por ejemplo, se pudo confirmar que hay similitud ecológica entre las especies parapátricas *T. benderei* y *T. Lecontei*, que de acuerdo con la hipótesis de remplazo ecológico, esta similitud pudo haber causado la separación geográfica.

Otro patrón observado fue en las especies hermanas *T. arenicola* y *T. lecontei*, las cuales no compartieron nichos ecológicos. De acuerdo a la hipótesis de remplazo ecológico, la existencia de una especie intermedia entre sus áreas de distribución (en este caso *T. cinereum*) pudo haber promovido la evolución del nicho de *T. arenicola*. Asimismo, *T. benderei* y *T. cinereum* son especies parapátricas que también se comportan de acuerdo a la hipótesis de remplazo.

En contraste, *T. arenicola* y *T. benderei* son especies no hermanas, geográficamente lejanas y separadas por otras dos especies parapátricas (*T. cinereum* y *T. lecontei*). Estas especies son las más diferenciadas genéticamente y ecológicamente, por lo que deberían observar patrones de evolución de nicho. Sorpresivamente, la prueba del entorno sugiere diferenciación del nicho entre *T. lecontei* y *T. cinereum*, aunque el

resultado más inesperado en la prueba del entorno fue la relación entre *T. arenicola* y *T. cinereum*, porque pese a ser parapatricas sus nichos ecológicos no fueron similares. Este resultado contradujo los análisis previos donde estas especies presentaron similitud ecológica. Sin embargo, podría ser que el único caso en donde la parapatría es el resultado de la adaptación local a dunas en la región centro-oeste de Baja California, que es donde habita *T. arenicolai*. Por otro lado, el análisis de distancia ecológica para estos pares de especies presentó el más bajo valor en relación con otras especies no hermanas.

Los eventos geológicos podrían haber sido una causa primaria del aislamiento geográfico, con una diferenciación genética secundaria. Sin embargo, la fragmentación del hábitat debido al clima (Grismer 2002) en combinación con los factores bióticos, pudieron haber promovido los diversos grados de diferenciación ecológica, así como los actuales distribuciones de las especies. Es posible que después del aislamiento (*i.e.*, la formación del Mar de Cortés y el mar intra-peninsular), el traslape de nicho ecológico en los taxa los dirigiera a un grado de diferenciación entre especies. Esto, en combinación con los cambios abruptos continuos en los patrones del clima, particularmente durante el periodo seco del Pleistoceno, que si bien aún en esta región no han sido detalladamente estimadas dichas fluctuaciones, si ocurrieron como en el área continental pudieron haber afectado dramáticamente la distribución de estas cuatro especies.

Aunque los eventos de dispersión son difíciles de probar, hay algunos ejemplos bien documentados en Baja California. Cuando Baja California se separó, diversas especies de aves se dispersaron a sus rangos ancestrales, como la perla de California (*Polioptila californica*), el cactus *Campylorhynchus brunneicapillus*, el cuitlacoche (*Auriparus flaviceps*) (Zink *et al.* 2000; Zink *et al.* 2001) y las lagartijas del género *Uta* (Upton & Murphy 1997). Por lo tanto, es posible que especies más vágiles, como los *Toxostoma*, pudieron haberse dispersado en ambientes continuos y haber sido limitados por barreras bióticas, como se ha presentado en este estudio en el caso de las especies ecológicamente similares. Cabe mencionar que aunque *T. benderei* es parcialmente migratorio y puede coexistir durante el verano con *T. lecontei*, no pueden coexistir durante el invierno, probablemente porque comparten las mismas condiciones ecológicas (Nakazawa *et al.* 2004). Wiens & Graham (2005) han argumentado que las diferencias en las características de los nichos son importantes para la especiación cuando un conjunto de poblaciones de especies filogenéticamente cercanas está geográficamente separadas por áreas que están fuera la envoltura climática. Sin embargo, el flujo genético entre dos poblaciones sería poco probable si otro taxa menos relacionado ocupara áreas geográficas

intermedias que comparten un nicho ecológico similar. El conservadurismo de nicho entre especies hermanas ha sido propuesto como un fenómeno común (Peterson *et al.* 1999; Wiens & Graham 2005); no obstante, este estudio sugiere que las interacciones entre especies ecológicamente similares podría también haber jugado un papel importante tanto en la divergencia genética y ecológica como en el aislamiento.

Los cuatro factores que se han propuesto para mantener el nicho ancestral y la adaptación local durante la vicarianza son: la falta de variabilidad genética, la selección natural, pleiotropía y el flujo genético (Wiens & Donoghue 2004). Estos factores separados o en conjunto prevendrán una adaptación local a condiciones en la barrera geográfica y forman las bases de microevolución para el conservadurismo filogenético de nicho ecológico y vicarianza (Peterson & Holt 2003; Wiens 2004). Sin embargo, el mantenimiento del nicho dependerá de la capacidad de las poblaciones para adaptarse a nuevas condiciones ambientales, como ha sido analizado para poblaciones alopátricas (McCormack *et al.* 2010); la tendencia de las especies de retener nichos ecológicos similares (conservadurismo de nicho filogenético) en la ausencia de barreras físicas y particularmente cuando otros taxa cercanamente relacionados son parte de las nuevas condiciones, ha sido subestimado. Por lo tanto, si los taxa distribuidos parapátricamente ocupan nichos similares, este puede ser un factor extrínseco adicional que podría promover la evolución de nicho.

En el análisis desarrollado se identificaron los valores ecológicos extrínsecos (climáticos y topográficos) en una escala amplia a través de la documentación posible desplazamiento ecológico y geográfico; sin embargo, existen factores asociados con procesos ecológicos a una escala más fina i.e., el nicho “Eltoniano” (Soberón 2007) que no se evaluaron, diferencias en los tamaños de rangos, tasas de crecimiento, segregación espacial, densidad, sistemas reproductivos, dispersión y competencia intraespecífica (Kildaw 1999; García-Ramos *et al.* 2000; Cooper *et al.* 2007; Gurd 2008). No obstante, nuestros análisis sugieren que la similitud ecológica como barrera biótica puede ser la causa de la parapatría.

En resumen, los resultados sugieren que la diferenciación ecológica podría ser el resultado del aislamiento (alopatría) influenciado por la presencia de una especie no hermana entre las dos. Además, el resultado entre las especies no hermanas resultó en una convergencia ecológica asociada con las áreas ocupadas, la cual tiende a estar geográficamente más cercana. Así, la disponibilidad de áreas desérticas pudieron haber facilitado la expansión geográfica de *T. benderei* y de *T. lecontei*, permitiendo la

conservación del nicho. En contraste, *T. arenicola* y *T. cinereum* pudieron haber tenido mayores presiones ecológicas, considerando la coexistencia forzada por el área de Baja California (algunas veces siendo isla y otras península), promoviendo la diferenciación de nichos con baja posibilidad de dispersión. Sin embargo, es necesario considerar que la causa más plausible de la divergencia inicial de las especies hermanas fueron los eventos tectónicos que produjeron el aislamiento de la Península y posiblemente las variaciones climáticas asociadas a éste. Aunque por desgracia no hay evidencias robustas al respecto, se puede inferir que hubo actividad tectónica por su carácter peninsular y variación climática durante el Pleistoceno como sucedió en el continente. Por lo tanto, la diferenciación de las especies hermanas pudo haber sido favorecido por la interrupción del flujo génico a causa de la presencia de especies no hermanas pero parapátricas, las cuales muestran un patrón de convergencia ecológica a condiciones locales. Así, los patrones de evolución de nicho en especies genéticamente cercanas y el conservadurismo de nicho en especies no hermanas pero parapátricas fueron el patrón resultante.

CONCLUSIONES GENERALES

Este trabajo da muestra del papel del clima en la determinación de patrones y procesos biogeográficos y evolutivos. La distribución geográfica de las especies está además restringida por barreras geográficas que limitan su ocupación a lo largo de toda su extensión climáticamente favorable en la Tierra. Un factor clave identificado para entender la dinámica de las áreas de distribución fue la evaluación espacio-temporal de las invasiones biológicas, determinadas a su vez por el clima. Finalmente, la evaluación de la similitud ecológica de las especies demostró que el clima juega un papel preponderante en los procesos de aislamiento de las especies y posterior especiación.

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