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Macroecological and macroevolutionary factors related to vertebrate diversity

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Macroecological and macroevolutionary factors related to vertebrate diversity

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Resumo

Esta tese céntrase na análise de patróns ecolóxicos e evolutivos a escala continental e mundial en mamíferos e aves. Este tipo de análises son fundamentais na bioxeografía, a ciencia que se encarga de describir e explicar os patróns espaciais da biodiversidade estudando as distribucións presentes e pasadas das especies (Brown & Lomolino 1998), ou a macroecoloxía, o campo da ecoloxía que estuda a relación entre os organismos e o ambiente para analizar a abundancia e distribución das especies a escalas (espaciais e temporais) grandes (Gaston & Blackburn 2000).

Profundar na comprensión dos procesos a grande escala é importante porque ter en conta só os procesos a pequena escala non é suficiente para explicar totalmente os patróns de distribución e abundancia das especies (Keith et al. 2012). En concreto, a composición de especies dunha comunidade local está limitada ao conxunto de especies da rexión na que se encontra, e este depende de procesos que actúan en áreas grandes (ex. especiación, extinción ou migración; Ricklefs 1987). Isto non exclúe que os procesos que acontecen a pequena escala (ex. interaccións bióticas) poidan influír nos patróns a grande escala (revisión en Wisz et al. 2013).

Dos patróns que se examinan en disciplinas como a bioxeografía ou a macroecoloxía, o máis estudado (e seguramente o máis coñecido) é o gradiente latitudinal de riqueza de especies, isto é, o descenso do número de especies do ecuador aos polos (Willig et al. 2003). Unha das principais explicacións para a existencia deste patrón é a influencia das condicións climáticas actuais (Hawkins et al. 2003; Currie et al. 2004), dado que as variábeis climáticas están fortemente relacionadas coa latitude, e ademais existe unha forte correlación entre a riqueza de especies e as condicións climáticas. Porén, existen outras hipóteses non necesariamente relacionadas coas condicións climáticas. Algúns traballos mostran que as taxas de especiación e extinción varían coa latitude, e que isto podería contribuír ao gradiente latitudinal de riqueza. No entanto, non está completamente

claro como é esta variación, habendo estudos que suxiren que as taxas de extinción e especiación son maiores en zonas temperadas ca nos trópicos (Weir & Schluter 2007), e outros cuxos resultados apoian que nos trópicos as taxas de especiación son maiores e as de extinción menores (Rolland et al. 2014).

A riqueza de especies, a pesar de ser unha medida de diversidade comunmente examinada, non ten en conta a identidade das especies dunha comunidade, é dicir, non inclúe información sobre que especies a conforman. Ter en conta esta información é importante na análise dos patróns de diversidade porque unha maior substitución de especies entre comunidades (isto é, comunidades con composicións de especies máis distintas) a pequena ou mediana escala resulta nunha maior riqueza de especies a escalas maiores (Koleff et al. 2003). Esta relación entre a diversidade a pequena escala (diversidade local ou diversidade alfa) e a diversidade a unha escala maior (diversidade rexional ou gamma) é a diversidade beta. Polo tanto, a diversidade beta (Whittaker 1960) é unha medida da variación na composición de especies entre localidades. Existe un número importante de medidas da diversidade beta ou medidas de disimilitude (Koleff et al. 2003), e é posíbel calculala entre pares de localidades ou entre múltiples localidades (Baselga 2013).

É importante sinalar que a variación na composición de especies (diversidade beta) entre dous ou máis sitios pode ser debida a dous tipos de procesos antagónicos: perda ou substitución de especies (Baselga 2010). No primeiro caso, as diferenzas de composición son debidas a que as especies presentes nos sitios con menor riqueza de especies son un subconxunto das especies presentes na localidade con maior riqueza de especies. No segundo caso, as diferenzas entre localidades son debidas a que certas especies son exclusivas de determinados sitios, e son substituídas por diferentes especies nos outros sitios. É fundamental separar estes dous tipos de diferenzas de composición se se quere valorar a relevancia relativa de procesos que son antagónicos. Por exemplo, se a maior parte da diversidade beta entre varias localidades se debese á perda de especies, pódese inferir que os procesos como a extinción ou a diferente capacidade de dispersión das especies teñen un peso importante, porén, se se debese principalmente á substitución de especies, poderíase considerar que outros procesos como a especiación son máis relevantes. Existen métodos para separar os compoñentes de aniñamento (perda de especies) e substitución da diversidade beta (Baselga 2010), que permiten discernir estes procesos de natureza oposta.

É habitual que, como no caso do gradiente latitudinal de riqueza, os estudos a grande escala se centren en explicar patróns bióticos tendo en conta as condicións ambientais actuais (Beck et al. 2012). Porén, é posíbel que a correlación entre biodiversidade e clima non sexa causal, porque as condicións climáticas teñen unha clara estrutura espacial, e entón a relación entre diversidade (ou abundancia) e clima pode ser debida a outros procesos estruturados espacialmente (autocorrelación espacial, Currie 2007). Polo tanto, tamén é importante ter en conta outros factores con estrutura espacial, como certos acontecementos no pasado (ex. mudanzas do clima e glaciacións no Pleistoceno) que poden ter un papel fundamental na distribución das especies (Svenning & Skov 2007b; Hortal et al. 2011). A separación dos compoñentes da diversidade beta mencionada antes resulta útil para estudar a influencia destes factores, xa que permite observar en que zonas predominan os patróns de substitución ou aniñamento, e revela que, en xeral, os patróns de aniñamento (perda de especies) predominan nas rexións máis afectadas polas glaciacións no Pleistoceno, debido a que estas son recolonizadas após a retirada do xeo por especies con alta capacidade de dispersión que viron reducida a súa área de distribución a rexións con climas máis estábeis durante a glaciación, e nas cales se observan patróns de substitución na actualidade (ex. Leprieur et al. 2011 en peixes de auga doce; Hortal et al. 2011 en escarabeíneos; Baselga et al. 2012a en anfibios), debido a que nelas están presentes especies con áreas de distribución máis restrinxidas. Estes patróns diferentes non se poden detectar ao considerar a diversidade beta total, sen separar os compoñentes.

Outra cuestión común nos estudos macroecolóxicos é valorar a importancia relativa de factores como as barreiras á dispersión, as capacidades de dispersión intrínsecas das especies ou as limitacións do nicho climático na determinación dos límites das distribucións das especies (Baselga et al. 2012c). Unha maneira pouco explorada de abordar este problema é examinar as formas das distribucións das especies: se se supoñen dinámicas ecolóxicas neutrais (Hubbell 2001), a expansión do rango dunha especie a partir da súa localización orixinal despois dun evento de especiación sería igual de probábel en todas as direccións (isotrópica), por tanto os rangos tenderían a ter forma circular, e o tamaño destes círculos estaría determinado pola capacidade de dispersión da especie en particular. Dito doutro xeito, os límites dos rangos de distribución estarían determinados esencialmente pola capacidade de dispersión das especies. Polo contrario, as limitacións extrínsecas á dispersión (ex. barreiras xeográficas) ou as limitacións producidas polo nicho (ex. requisitos climáticos das especies) farían que os rangos se desviasen da circularidade. Observar as formas das distribucións non é unha aproximación frecuentemente usada: non existe un grande número de estudos que cuantifiquen a forma das distribucións e analicen a súa variación entre especies (mais véxase Brown & Maurer 1989; Rosenfield 2002; Pigot et al. 2010; Baselga et al. 2012c), a pesar de que xa se suxire estudar a forma dos rangos de distribución das especies desde que se formaliza o concepto de «Macroecoloxía» (Brown & Maurer 1989).

Tendo en conta o exposto anteriormente, no primeiro capítulo presentado nesta tese analizáronse os patróns latitudinais de diversidade beta en mamíferos e aves. En particular, ponse a proba a hipótese de que nas rexións máis afectadas polas glaciacións do Pleistoceno a diversidade beta de aniñamento (que reflicte perda de especies) é predominante, mentres que en latitudes máis baixas predomina o compoñente de substitución. Estes patróns observáronse previamente noutras clases de vertebrados ectotermos (Leprieur et al. 2011 en peixes, Baselga et al. 2012a en anfibios). Dado que as aves e os mamíferos son clases de vertebrados endotermos, estes patróns poderían diferir con respecto aos ectotermos. Para comprobar esta hipótese, examinouse a variación latitudinal da diversidade beta de aves e mamíferos en América (calculada como a diversidade beta rexional entre múltiples sitios de 100 km × 100 km contidos en celdas rexionais de 500 km × 500 km) usando regresións por partes (Crawley 2007). Este tipo de regresión consiste en axustar dous modelos lineais procurando un punto de inflexión na variábel explicativa (neste caso, a latitude) de forma que se minimicen os residuos, e permiten así detectar (no caso de que as pendentes dos modelos lineais axustados sexan significativamente diferentes) puntos nos que hai unha mudanza na tendencia. Isto, en combinación coa partición da diversidade beta (en compoñentes de substitución e aniñamento), permitiu identificar rexións diferenciadas nas que distintos tipos de procesos (causantes de eventos de especiación ou extinción) poden estar determinando os patróns de variación espacial da diversidade beta. Un dos obxectivos principais deste estudo foi determinar se estes puntos de inflexión son comúns a varias clases de vertebrados e examinar se están relacionados cos puntos de inflexión observados en variábeis ambientais. En aves e mamíferos (voadores e non voadores) encontrouse que os patróns son moi similares, co compoñente de substitución da diversidade beta presentando un máximo en latitudes medias e descendendo cara os polos, e co compoñente de aniñamento sendo predominante en latitudes altas en todos os grupos examinados, discriminándose así dúas rexións nas que os principais procesos que determinan a biodiversidade parecen ser diferentes. A diversidade beta de aniñamento está relacionada sobre todo coas condicións de temperatura actuais, e a de substitución presenta unha débil relación coa altitude media da rexión. Porén, só aparecen puntos de inflexión similares aos observados na variación latitudinal dos compoñentes da diversidade beta na variación latitudinal da altitude media e nas diferenzas entre as condicións de temperatura actuais e as do último máximo glacial.

Unha das aplicacións da diversidade beta como medida das diferenzas de composición de especies entre localidades é a definición de rexións bioxeográficas mediante métodos cuantitativos e replicábeis. Estas rexións proporcionan unha base para investigar cuestións relacionadas coa bioxeografía, a bioloxía evolutiva, a sistemática ou a conservación (Kreft & Jetz 2010). Para definir rexións bioxeográficas, a escolla da medida de disimilitude (diversidade beta) é fundamental, e, neste contexto, é necesario usar unha medida que non teña en conta os gradientes de riqueza (véxase, por exemplo, Kreft & Jetz 2010; Holt et al. 2013). Se a medida de disimilitude ten en conta os gradientes de riqueza (por exemplo, a disimilitude de Jaccard, Koleff et al. 2003), as localidades con fauna ou flora empobrecida son consideradas disimilares ás localidades con maior riqueza de especies, aínda que as especies que as primeiras conteñen sexan simplemente un subconxunto das especies nas segundas (patróns de aniñamento). Isto é problemático para a definición de rexións bioxeográficas, onde se pretende clasificar rexións que conteñen especies diferentes, particularmente se a mostraxe nalgúns lugares é relativamente baixa (deste xeito, poderíanse considerar dúas localidades como disimilares, e ser clasificadas en rexións bioxeográficas diferentes, aínda que tivesen exactamente as mesmas especies se unha delas ten menor mostraxe). Nun traballo recente sobre a definición de rexións bioxeográficas mariñas (Costello et al. 2017), no que se usaron datos de distribución de milleiros de especies mariñas de animais e plantas, basean o seu resultado principal en rexionalizacións que usan a disimilitude de Jaccard (que está afectada polas diferenzas de riqueza). No segundo capítulo desta tese, exploráronse as consecuencias que pode ter a escolla da medida de disimilitude no proceso de rexionalización, usando a base de datos de distribucións de especies proporcionada por Costello et al. (2017). Para iso, comparouse a rexionalización obtida usando medidas de disimilitude que teñen en conta os gradientes de riqueza coa obtida con medidas independentes das diferenzas de riqueza entre localidades (disimilitude de Simpson, Simpson 1960). Os resultados obtidos usando os mesmos datos son moi diferentes aos presentados por Costello et al. (2017). Cando se definen 30 rexións (igual que no estudo citado), obsérvase que a maioría delas son bastante discontinuas (tanto ao usar Jaccard como ao usar Simpson), ao contrario dos mapas presentados por Costello et al. (2017)., que non foi posíbel reproducir usando os métodos que describen. Isto suxire que as diferenzas de mostraxe son unha fonte de erro importante a estes niveis de disimilitude. As rexións son algo máis cohesivas se se define un número menor delas. Neste capítulo tamén se examinou a importancia doutras decisións metodolóxicas na rexionalización, nomeadamente o algoritmo para agrupar as localidades xerarquicamente en rexións cada vez máis inclusivas e o número de rexións definidas. Observouse que, neste caso, o método de Ward produce rexións máis equilibradas e cohesivas que o método UPGMA que se usa xeralmente, posibelmente debido a que nos datos proporcionados por Costello et al. (2017) o esforzo de mostraxe é moi heteroxéneo.

O foco do terceiro capítulo é examinar os factores que poden determinar os límites dos rangos de distribución das especies e, en particular, a relevancia das limitacións producidas polo nicho climático das especies por un lado, e de factores bióticos ou estocásticos por outro. Debido a que a maiores latitudes as condicións climáticas son máis diferentes do clima nos trópicos, onde a maioría de clados se orixinaron (Wiens & Donoghue 2004), pódese esperar que as limitacións debidas ao nicho climático sexan máis importantes nestas rexións máis afastadas do ecuador, porque en xeral son necesarias novas adaptacións fisiolóxicas para sobrevivir nestas condicións. Por outro lado, os factores bióticos e estocásticos gañarían relevancia nos trópicos, debido a que aquí as condicións climáticas non serían limitantes. Para comprobar esta posibilidade, examinouse a variación espacial (latitudinal) da forma dos rangos de distribución de mamíferos e aves. Aínda que existen traballos previos que estudan a forma dos rangos das especies (ex. Brown & Maurer 1989; Rosenfield 2002; Baselga et al. 2012c), neles non se explora a variación espacial da forma dos rangos de distribución (polo menos de maneira explícita). Analizar a variación espacial pode dar novas pistas sobre os factores que determinan os límites das distribucións das especies. En concreto, considerando que (1) a maiores latitudes o efecto das condicións climáticas é máis importante, xa que as especies que habitan estas latitudes teñen que ter unha fisioloxía adaptada a condicións máis frías e unha grande capacidade de dispersión para recolonizar as áreas que fican libres despois da retirada das glaciacións do Pleistoceno (Svenning & Skov 2007a,b), e (2) que as zonas climáticas a grande escala tenden a estar estruturadas en bandas latitudinais (Peel et al. 2007), pódese predicir que en latitudes altas os rangos tenderán a estar alongados en dirección leste-oeste. Neste terceiro capítulo fíxose unha análise adicional para avaliar se os límites dos rangos de distribución son máis estocásticos (e, polo tanto, máis retortos e longos) na porción do rango máis próxima ao ecuador que na porción máis próxima aos polos. Isto sería esperábel se os límites a maiores latitudes estivesen máis determinados por factores climáticos (máis estruturados espacialmente), e se os límites a menores latitudes estivesen máis determinados por factores bióticos, que son máis estocásticos (Normand et al. 2009). Observouse que, tanto en mamíferos como en aves de todo o mundo, existe unha tendencia a que os rangos de distribución estean alongados en dirección leste-oeste en latitudes altas do hemisferio norte, máis do que se esperaría se os rangos se expandisen isotropicamente. Non se encontraron diferenzas significativas no perímetro das porcións dos rangos de distribución máis próximas aos polos e máis próximas ao ecuador. Nos rangos de distribución máis extensos das especies localizadas no hemisferio sur os perímetros da porción máis próxima aos polos si son significativamente máis curtos que os da porción máis próxima ao ecuador, pero isto pode atribuírse á forma dos continentes, que en xeral se estreitan cara o polo sur.

Para estudar os procesos que inflúen na variación da biodiversidade, ademais de analizar a variación espacial desta (ex. diferenzas de composición de especies ou de riqueza entre distintos lugares), pódense examinar tamén as diferenzas de diversidade entre clados. Este é o tema principal do cuarto capítulo, que se centra na cuestión de por que certos clados teñen máis especies ca outros. Nel, explóranse os factores que inflúen na taxa de diversificación (isto é, o balance entre a taxa de especiación e a taxa de extinción) das familias de mamíferos e, polo tanto, nas diferenzas de riqueza de especies entre elas. Un dos principais factores que poden provocar as diferenzas de riqueza (ou taxa de diversificación) entre clados é o nicho climático das especies, isto é, as condicións climáticas dos lugares onde viven (Soberón 2007), porque o nicho climático podería determinar onde poden estar presentes as especies e, polo tanto, influír fortemente nos procesos de especiación (ex. especiación ecolóxica por diverxencia de nicho, Hua & Wiens 2013) ou extinción (ex. a consecuencia de mudanzas importantes no clima ás que unha especie non pode responder). Deste xeito, pódese esperar que existirá unha relación entre os patróns de variación no nicho climático entre clados e as súas taxas de diversificación. Moitos estudos previos xa comprobaron a relación entre a evolución do nicho climático e a diversificación, encontrando en xeral unha relación positiva (véxase, por exemplo, Schnitzler et al. 2012; Lawson & Weir 2014; Moen & Wiens 2017), e outros observaron que unha maior diverxencia de nicho climático absoluta (isto é, as diferenzas de nicho entre as especies dunha familia ou clado) está asociada a unha maior taxa de diversificación (Gómez-Rodríguez et al. 2015). Neste cuarto capítulo analizouse a importancia relativa da diverxencia de nicho absoluta e a taxa de evolución do nicho para explicar a variación da taxa de diversificación entre clados de mamíferos, xa que non existen traballos previos que o fagan. Os resultados mostraron que estas dúas variábeis explican unha porcentaxe de variación grande (>50 %) e similar da taxa de diversificación das familias de mamíferos, aínda que a contribución única da diverxencia de nicho absoluta foi algo maior. Estas variábeis explican porcentaxes moito maiores de variación que outras como a amplitude de nicho das familias (20 %) e o tamaño da área que ocupan

(19 %). A variación na taxa de diversificación explicada pola posición de nicho (variábel que está asociada ao réxime climático predominante, ex. tropical ou temperado), por outro lado, é moi baixa (7 %).

Os resultados presentados nos distintos capítulos mostran regularidades en patróns bioxeográficos ou macroecolóxicos en distintos grupos de vertebrados. Por exemplo, no primeiro capítulo desta disertación, mostrouse por primeira vez que a variación latitudinal dos compoñentes da diversidade beta é moi similar en grupos de vertebrados con capacidades de dispersión e formas de termorregulación moi distintas. Obsérvase que a variación latitudinal é análoga en aves e mamíferos voadores e non voadores. No terceiro capítulo, as aves e os mamíferos presentan tamén patróns latitudinais moi parecidos na forma dos rangos, que tenden a ser máis alongados en dirección leste-oeste en latitudes altas do hemisferio norte.

O punto de inflexión encontrado no primeiro capítulo delimita dúas grandes rexións no mundo nas que predominan compoñentes distintos da diversidade beta: en latitudes inferiores á marcada polo punto de inflexión, predomina o compoñente de substitución, e en latitudes superiores á de aniñamento. Os patróns que se observan en aves e mamíferos en América son comparábeis aos que aparecen noutras clases de vertebrados, como peixes de auga doce (Leprieur et al. 2011) ou anfibios a escala mundial (Baselga et al. 2012a). O máis rechamante destes patróns é que os puntos de inflexión que se encontraron na variación latitudinal dos compoñentes da diversidade beta son consistentes entre grupos, e só aparecen puntos de inflexión análogos na variación latitudinal da altitude media das celas rexionais ou nas diferenzas entre as condicións climáticas actuais e as do último máximo glacial (hai aproximadamente 21 000 anos), pero non na variación latitudinal das condicións climáticas actuais. Isto fai pensar que tanto a presenza de montañas como as glaciacións do Pleistoceno tiveron algún papel na formación dos patróns na diversidade observados actualmente. As montañas poden actuar como centros de diversificación (Rahbek & Graves 2001) xerando así patróns de substitución a escalas rexionais. As glaciacións cubriron grandes extensións con xeo e desprazaron a distribución da maioría de especies a menores latitudes (Hewitt 1999), e após a súa retirada estas rexións foron recolonizadas primeiro polas especies con maior capacidade de dispersión, o que resultaría nos patróns espaciais de perda de especies (aniñamento) observados aquí. Móstrase neste capítulo que a aproximación de procurar puntos de inflexión nos patróns de diversidade en lugar de consideralos como algo continuo pode ser útil de forma xeral para comprender os procesos que os determinan.

No segundo capítulo móstrase que as medidas de diversidade beta que non discriminan o compoñente de substitución do de aniñamento non son apropiadas para usar como medida de disimilitude en estudos de rexionalización bioxeográfica, xa que, como se indica no capítulo 1, os dous compoñentes da diversidade beta poden presentar patróns espaciais distintos e opostos, co que poden cancelarse mutuamente (isto é, dúas rexións poden ter a mesma diversidade beta total, pero un caso pode estar dominado polos procesos de substitución e o outro polos de aniñamento, Baselga 2010). Neste segundo capítulo, reanalizouse unha recente proposta de clasificación bioxeográfica das biotas mariñas (Costello et al. 2017) baseada nunha medida da diversidade beta que está afectada polos gradientes de riqueza, xa que tamén ten en conta as diferenzas de composición provocadas por patróns de aniñamento (disimilitude de Jaccard). Os resultados que se obteñen ao usar unha medida de disimilitude non afectada pola riqueza (Simpson) son distintos. Por exemplo, cando se define un número pequeno de rexións, coa disimilitude de Simpson, obsérvase que varias das rexións se corresponden aproximadamente cos océanos Atlántico, Pacífico ou Índico. Porén, ao usar a disimilitude de Jaccard, unha das rexións ocupa case todo o mundo e divídese o Océano Atlántico en dúas rexións, probabelmente porque se discriminan rexións tendo en conta gradientes de riqueza. Neste caso concreto, as rexións mariñas son máis equilibradas e compactas se se usa o método de Ward para agrupar as localidades en rexións que se se usa o frecuentemente utilizado método da media (UPGMA). Polo tanto, cando as bases de datos analizadas se obteñen cun esforzo de mostraxe moi heteroxéneo, pode ser apropiado considerar métodos de agrupación alternativos ao UPGMA para clasificar rexións.

No terceiro capítulo analizouse a variación espacial (latitudinal) na forma do rango das especies de aves e mamíferos a escala mundial. No hemisferio norte, en latitudes superiores a 30°–40°, obsérvase unha tendencia a que os rangos estean alongados en dirección leste-oeste. En latitudes inferiores, non hai unha tendencia tan clara a estar alongados nunha dirección en particular. No hemisferio sur hai unha leve tendencia a unha elongación norte-sur, que se pode deber á forma dos continentes. Esta elongación non se pode atribuír exclusivamente á forma dos continentes no hemisferio norte, xa que un modelo nulo no que os rangos se expanden con igual probabilidade en todas as direccións non predí rangos tan alongados (si predí a leve tendencia a unha elongación norte-sur no hemisferio sur). Dado que a grande escala as condicións climáticas están máis ou menos estruturadas en bandas latitudinais (Peel et al. 2007), esta maior desviación con respecto aos modelos nulos suxire que a influencia das condicións climáticas na determinación dos límites dos rangos de distribución en latitudes altas do hemisferio norte é maior. Estas limitarían a expansión latitudinal dos rangos, resultando en formas alongadas en dirección leste-oeste.

En latitudes menores e nas especies con rangos de distribución pequenos, non hai tendencia á elongación nunha dirección en particular, e ademais teñen extensións latitudinais e lonxitudinais máis parecidas en comparación ás especies presentes en latitudes maiores. Isto concorda coa hipótese de que en latitudes baixas a expansión dos rangos de moitas especies estaría determinada principalmente por procesos isotrópicos (coa mesma influencia en todas as direccións) ou por outros procesos independentes do nicho climático das especies (factores bióticos ou estocásticos, Normand et al. 2009). Por outro lado, isto non é o que se esperaría observar se o nicho fose o principal limitante da expansión, excepto se os gradientes ambientais fosen equivalentes en dirección latitudinal e lonxitudinal. Porén, esperaríase que a influencia predominante de procesos neutrais resultase en rangos de distribución con extensións latitudinal e lonxitudinal similares (Baselga et al. 2012c).

A interpretación dos resultados neste terceiro capítulo é complexa, e a grande variación na forma dos rangos en latitudes baixas pode ser causada por moitos procesos diferentes. Coas análises realizadas, non se pode descartar que nalgúns casos a variación climática a escalas máis pequenas ou a heteroxeneidade espacial de factores abióticos puidesen ser os principais determinantes da forma dos rangos. En concreto, ao haber unha variación climática máis limitada e tolerancias fisiolóxicas restrinxidas, as barreiras topográficas serían máis efectivas (Ghalambor et al. 2006), e se a orientación destas barreiras é variada, as desviacións da isotropía nos trópicos causadas por factores abióticos serían máis irregulares. Sería interesante comprobar esta posibilidade en futuros estudos, aínda que probabelmente se necesitarían datos adicionais. De todas formas, como nestas análises se incluíu un número de especies considerábel, espérase que a influencia dalgúns casos particulares no patrón xeral sexa baixa.

No cuarto capítulo exploráronse os factores que potencialmente inflúen na diversificación das familias de mamíferos. Das variábeis examinadas, as máis fortemente relacionadas coa taxa de diversificación (e a riqueza de especies) das familias foron a taxa de evolución do nicho climático e a diverxencia de nicho absoluta. En mamíferos, esta relación é comparábel á que se pode encontrar noutras clases de vertebrados, como aves (Cooney et al. 2016) e anfibios (Gómez-Rodríguez et al. 2015; Moen & Wiens 2017). Todos estes resultados suxiren que a variación nos nichos climáticos é imporante para explicar as diferenzas de diversificación entre clados. A importante relación que se encontra entre a taxa de evolución do nicho climático é coherente coa idea de que as familias con maiores taxas de evolución se diversifican máis rápido debido a que a diverxencia de nicho favorece a especiación ou a que a labilidade no nicho climático diminúe a taxa de extinción (ao permitir unha mellor adaptación a flutuacións climáticas, por exemplo). Así, cos resultados das análises realizadas aquí, a hipótese máis apoiada é a de que a especiación por diverxencia de nicho é común e importante (Hua & Wiens 2013).

Os estudos presentados nesta tese analizan os factores e procesos que inflúen na diversidade de aves e mamíferos a escala mundial. Un dos principais obxectivos das análises realizadas foi estimar a relevancia de procesos neutrais e de nicho. Parece que hai unha influencia importante da diverxencia de nicho ou da taxa de evolución do nicho climático nas taxas de diversificación das familias de mamíferos (capítulo 4). Por outro lado, os procesos neutrais poderían ser máis relevantes na determinación dos límites dos rangos das especies que habitan latitudes baixas, aínda que o nicho climático tamén parece un factor importante dando forma aos rangos de distribución en latitudes altas do hemisferio norte (capítulo 3). Algúns dos patróns examinados mostran un comportamento análogo bastante interesante. Concretamente, o compoñente de aniñamento da diversidade beta é predominante en latitudes por encima de 30° en varios grupos de vertebrados (capítulo 1), e por encima dunha latitude similar os rangos de distribución mostran unha maior tendencia a estar alongados en dirección leste-oeste. Aínda que estas semellanzas poden chamar a atención, coas análises feitas aquí non se pode tirar unha conclusión delas, xa que poden ser simplemente superficiais. De todas formas, dan pé a preguntarse se o mesmo proceso ou conxunto de procesos deu forma a estes dous patróns, e poderían ser unha base prometedora para estudos posteriores.

As análises realizadas nos estudos presentados nesta tese permitiron explorar algunhas cuestións básicas na bioxeografía e a macroecoloxía. No primeiro capítulo, observáronse patróns análogos na variación latitudinal dos compoñentes da diversidade beta en varios grupos de vertebrados (aves e mamíferos voadores e non voadores) con capacidades de dispersión e termorregulación moi distintas, que presentan puntos de inflexión que só se observan na variación latitudinal da altitude media e as diferenzas de temperatura con respecto ao último máximo glacial (que indican o impacto das glaciacións), suxerindo a importancia de procesos históricos na formación destes patróns de diversidade. No segundo capítulo, mostrouse que as medidas de disimilitude (diversidade beta) afectadas polos gradientes de riqueza non son adecuadas para estudos de rexionalización bioxeográfica, porque tenden a separar localidades ricas en especies e localidades con menos especies que son un subconxunto das que se encontran nos lugares con máis especies. Ademais, sinalouse a importancia da escolla do método de agrupación de localidades dependendo da calidade dos datos dispoñíbeis. No terceiro capítulo describiuse o patrón latitudinal que existe na forma dos rangos das especies, con rangos máis alongados en dirección leste-oeste en latitudes altas do hemisferio norte debido posibelmente a limitacións climáticas, mentres que no hemisferio sur hai unha certa tendencia a unha elongación norte-sur causada probabelmente pola forma dos continentes. Finalmente, no cuarto capítulo analizouse que factores poden explicar as diferenzas na taxa de diversificación (e na riqueza de especies) das familias de mamíferos, sendo a diverxencia de nicho climático absoluta (entre as especies dentro dunha familia) e a taxa de evolución de nicho as variábeis máis relacionadas coa taxa de diversificación. Estes resultados son consistentes coa hipótese de que a diverxencia de nicho climático é un factor importante nos procesos de especiación.

Introduction

This dissertation is focused on the analysis of ecological and evolutionary patterns at continental and global scales in birds and mammals. This sort of analyses are fundamental in biogeography, the science that describes and tries to explain spatial patterns in biodiversity by studying past and present distributions of species (Brown & Lomolino 1998), or in macroecology, the field of ecology that studies the relationships between organisms and environment to determine the abundance and distribution of species at large (spatial and temporal) scales (Gaston & Blackburn 2000).

Understanding large-scale processes is important because only accounting for small-scale processes is not sufficient to fully explain the distribution and abundance patterns of species (Keith et al. 2012). In particular, the species composition of a local community is limited to the set of species that are present in the corresponding region, and this set of species depends on large-scale processes, such as speciation, extinction or migration (Ricklefs 1987). This does not preclude that small-scale processes (e.g., biotic interactions) could influence large-scale patterns (review in Wisz et al. 2013).

Of all the patterns that are examined in subjects such as biogeography or macroecology, probably the most studied (and possibly the most well-known) is the latitudinal gradient in species richness, that is, the decrease in the number of species that is observed from the equator to the poles (Willig et al. 2003). A common explanation for the existence of this pattern is the influence of current climatic conditions (Hawkins et al. 2003; Currie et al. 2004), as climatic variables are strongly correlated with latitude, and in addition there is a strong correlation between species richness and climatic conditions. There are several hypotheses that try to explain this relationship between current climate and species richness. One of them is the physiological tolerance hypothesis, which proposes that the number of species in a region depends on the tolerance of species to different climatic conditions, and that there are more possibilities of surviving in warm or wet conditions than in cold or dry conditions (Currie et al. 2004). Another hypothesis, the species-energy hypothesis (Wright 1983), suggests that the available energy in an ecosystem regulates species richness through food chains and the number of individuals that can be supported. For example, plant species richness would be determined mainly by solar energy and water availability, and it would in turn limit herbivore richness which would limit carnivore richness (Hawkins et al. 2003). There are alternative hypotheses that are not necessarily related to climatic conditions. Some studies show that speciation and extinction rates vary with latitude, and this could contribute to the latitudinal gradient in species richness. However, the nature of this variation is not completely clear, with some studies suggesting that extinction and speciation rates are higher in temperate zones than in the tropics (Weir & Schluter 2007), and others whose results support that speciation rates are higher and extinction rates lower in the tropics (Rolland et al. 2014).

Although species richness is the most commonly used measure of diversity, it does not take into account the identity of species in a community or, in other words, it does not include information about which species constitute that community. Taking this information into consideration can be important because higher species turnover between communities (that is, communities with largely different species composition) at medium or small scales causes higher species richness at larger scales (Koleff et al. 2003). Beta diversity (Whittaker 1960) is a measure of the variation in species composition between localities. There is a relatively large number of beta diversity (or biological dissimilarity) measures (Koleff et al. 2003), but one of the most simple definitions, and also one of the most frequently used, is the ratio between regional diversity (i.e., total number of species in the studied region, or gamma diversity) and local diversity (i.e., the mean number of species in each of the sampled locations in that region, or alpha diversity). The value of this ratio is the number of distinct compositional units ("communities") in that region (Tuomisto 2010). This ratio has a maximum value that depends on the number of localities in the region, so it has to be standardised: depending on the standardisation, different dissimilarity indices are obtained (Chao et al. 2012). There are indices to calculate beta diversity between pairs of localities or between multiple localities. When calculating the overall beta diversity between multiple sites, it is preferable to use these multiple site dissimilarity measures than taking the average of pairwise measures between all possible pairs of sites (Baselga 2013). This is because pairwise measures only consider the information of shared or unique species in one pair in particular, but not in the set of localities. In contrast, this information is incorporated when using multiple site dissimilarity measures.

It is important to note that the variation in species composition between two or more sites could be generated by two antagonistic processes: species losses or species turnover (Baselga 2010). In the first case, compositional differences are due to species present in sites with lower richness being a subset of the species present in the locality with the highest species richness. In the second case, the differences are caused by certain species that are exclusive of particular sites, and are substituted by different species in other places. It is crucial to separate these two types of compositional differences if we are to assess the relative importance of these antagonistic processes. For example, if most beta diversity between multiple localities were due to species losses, it could be inferred that processes such as extinction or the different dispersal capabilities of species have an important role. However, if species turnover predominated, some other processes such as speciation might be more relevant. There are methods that allow to calculate the nestedness (species losses) and turnover components of beta diversity (Baselga 2010), and thus make possible to discern these processes of opposite nature.

In most cases, such as in the study of the latitudinal richness gradient, studies at large scales try to explain biotic patterns taking current environmental conditions into account (Beck et al. 2012). However, it is possible that the correlation between biodiversity and climate is not causal, because climatic conditions have a clear spatial structure, and therefore the relationship between diversity (or abundance) and climate could be caused by other spatially structured processes (spatial autocorrelation, Currie 2007). Consequently, it is also important to consider other factors with spatial structure, such as some past events (e.g., Pleistocene climate change and glaciations) that could play an essential role in species distribution (Svenning & Skov 2007b; Hortal et al. 2011). The aforementioned partitioning of the components of beta diversity is useful to analyse the influence of these factors, because it allows to observe if turnover or nestedness patterns are predominant in certain zones. For example, some studies have revealed that, in general, nestedness patterns (species losses) are more important in regions that were affected by Pleistocene glaciations, because these are recolonised after the retreat of ice sheets by species with high dispersal capabilities that had inhabited more stable climatic areas during the glaciation period (e.g., Leprieur et al. 2011 in freshwater fishes; Hortal et al. 2011 in Scarabaeineae; Baselga et al. 2012a in amphibians). On the contrary, in the more climatically stable zones, turnover patterns are generally dominant. These constrasting patterns cannot be detected when considering the overall beta diversity, without partitioning its components.

Another important question in macroecological studies is to assess the relative importance of factors such as dispersal barriers, the intrinsic dispersal capabilities of species or climatic niche constraints in the determination of species distribution limits (Baselga et al. 2012c). One way of addressing this problem that is not frequently used is to examine the shape of species distributions: under neutral ecological dynamics (Hubbell 2001), the expansion of a species range after a speciation event would be equally probable in all directions (isotropic), and thus ranges would tend to have a circular shape, with range size being determined by the dispersal capability of that particular species. In other words, range limits would be exclusively determined by dispersal capabilities. In contrast, extrinsic dispersal limitations (e.g., geographic barriers) or niche constraints (e.g., climatic requirements of species) would cause a deviation of ranges from circularity. Not many studies have tried to quantify range shape and analyse its variation among species (but see Brown & Maurer 1989; Rosenfield 2002; Pigot et al. 2010; Baselga et al. 2012c), despite the fact that it was suggested that the study of range shape could provide an insight on large scale ecological processes when the concept "Macroecology" was formalised (Brown & Maurer 1989).

Currently, the availability of large datasets and the increase of computational capacity to process them make easier to carry out studies which use information on thousands of species to delve into the previously formulated questions. In particular, there are available datasets with distribution maps of many vertebrate species (e.g., International Union for Conservation of Nature [IUCN], 2013, for mammals; and BirdLife International and NatureServe, 2013, for birds), as well as information on current and past climatic conditions (Hijmans et al. 2005). These types of data are frequently used to perform biogeographic or ecological analyses at large scales (which might include a large number of species) or to fit models that allow to predict the spatial distribution of species (species distribution modelling, Peterson et al. 2011). Additionally, there are currently methods for producing large size phylogenies (by aggregating the information of many phylogenies of more restricted groups) that make the inference of the evolutionary relationships between the majority of species in a class possible (e.g., Bininda-Emonds et al. 2007; Jetz et al. 2012). These phylogenies allow integrating evolutionary hypotheses in macroecological analyses, such as examining the variation in climatic niche between species through time and exploring its relationship with clade diversification (e.g., Kozak & Wiens 2010; Cooney et al. 2016), thus considering the historical dimension in the diversity and distribution of species. In summary, the availability of these kinds of data makes possible to ask new questions concerning biogeography and macroecology and to progress in their knowledge.

Having some of the previously aforementioned topics in mind, the patterns in beta diversity of birds and mammals are analysed in the first chapter of this dissertation. In particular, I tested the hypothesis that in the regions that were more affected by Pleistocene glaciations, the nestedness component of beta diversity (that reflects species losses) is predominant, as it happens in other ectotherm vertebrate classes (Leprieur et al. 2011 in freshwater fishes, Baselga et al. 2012a in amphibians). If this were true, a breakpoint (a change of tendency) might appear in the latitudinal patterns of the components of beta diversity at the latitude above which the impact of glaciations was higher, because in those regions the nestedness component would be predominant, and at lower latitudes this component would not be so important. Since birds and mammals are endotherm vertebrate classes, these patterns could be different to those that appear in ectotherms. To test this hypothesis, the latitudinal variation in beta diversity of birds and mammals in the New World was examined by using piecewise regressions (Crawley 2007), which allow to find the presence of breakpoints. The regional beta diversity was calculated as the multiple-site dissimilarity between 100 km × 100 km cells in regional cells of 500 km × 500 km. In piecewise regressions, two linear models are fitted to the data, searching for a breakpoint in the explanatory variable (latitude, in this case) which minimises residuals, and thus allow detecting (in the case that the slopes of the fitted linear models are significantly different) points in which there is a change in the general trend. This, in combination with the partitioning of beta diversity, makes possible to identify distinct regions in which different types of processes (that cause speciation or extinction events) might be determining patterns of spatial variation in beta diversity. One of the main objectives of this study is to determine if these breakpoints are related to the breakpoints observed in environmental variables. More generally, it is explored if analysing macroecological patterns considering the possibility of the existence of some kind of discontinuity (by searching for breakpoints) instead of assuming that they are continuous can reveal more information about the processes that determine those patterns.

One of the applications of beta diversity as a measure of differences in species composition between localities is the definition of biogeographic regions through quantitative and replicable methods. These regions provide a basis to address questions related to biogeography, evolutionary biology, systematics, or conservation (Kreft & Jetz 2010). In order to define biogeographic regions, the choice of the dissimilarity measure between localities and regions is fundamental: it is necessary to use a measure that is not affected by richness gradients (see, for example, Kreft & Jetz 2010; Holt et al. 2013). If the dissimilarity measure accounts for richness gradients (for example, Jaccard dissimilarity, Koleff et al. 2003), localities with impoverished fauna or flora would be considered dissimilar to sites with higher species richness, even when the species in the former localities are simply a subset of the species in the latter. This is problematic for the definition of biogeographic regions, where the goal is to classify regions that contain different species, particularly if the sampling effort in some localities or regions is relatively low (two localities could be considered dissimilar even if they had the same set of species, if they were sampled differently). In a recent study that addressed the regionalisation of marine realms (Costello et al. 2017), which used distribution data of thousands of marine species of animals and plants, the main result is based on regionalisations that use Jaccard dissimilarity (which is affected by richness differences). In the second chapter of this dissertation, the consequences of the choice of a dissimilarity measure in the process of regionalisation are explored, using the dataset provided by Costello et al. (2017). With this aim, the regionalisation obtained using dissimilarity measures that are affected by richness gradients and the one obtained with measures that are independent of richness differences between localities (Simpson's dissimilarity index, Simpson 1960) are compared. In this chapter, an assessment of potential methodological biases in biogeographic regionalisations is performed. Thus, the effect of algorithm choice to hierarchically cluster localities in more inclusive regions and of the number of defined regions in the regionalisation of marine realms is evaluated.

The third chapter examines the factors that might determine species distribution range limits, and, in particular, the relevance of constraints caused by the climatic niche of species on one side, and the relevance of biotic or stochastic factors on the other. Since at higher latitudes climatic conditions are generally different to the climatic regimes found in the tropics, where most clades originated (Wiens & Donoghue 2004), it can be expected that climatic niche constraints are more important in regions distant from the equator, because some physiological adaptations are generally needed to survive in these conditions. In contrast, stochastic and biotic factors would be more relevant in the tropics, since here climatic conditions would not be limiting in general. In order to test this possibility, the spatial (latitudinal) variation of distribution range shape of mammals and birds was examined. In most previous studies that analyse species range shape (e.g., Brown & Maurer 1989; Rosenfield 2002; Baselga et al. 2012c) it is observed that the longitudinal and latitudinal extents of distribution ranges are strongly correlated. Still, this does not mean that all ranges are isotropic (equal dispersal in all directions) and that, therefore, its shape is exclusively controlled by dispersal. In some cases, the observed patterns in range shape are intermediate between what would be expected if they were solely controlled by dispersal or solely controlled by climatic conditions (Baselga et al. 2012c). Interestingly, when the species with the largest distribution ranges are excluded, the patterns that appear in small ranges (which correspond to the majority of species) do not differ from what neutral mechanisms predict, which suggests that range shape is determined by mechanisms that are associated to range size, with species with small ranges being more limited by dispersal and species with large ranges being more constrained by climate (Brown & Maurer 1989). It is important to note that the previously cited studies do not explore the spatial variation in range shape (at least in an explicit manner). Taking into account that distribution ranges tend to show different shapes depending on their extent, analysing its spatial variation could give some clues about which factors determine the range limits of species distributions. Specifically, considering that (1) at higher latitudes the effect of climatic conditions is more important, because species living there have to be physiologically adapted to colder conditions and have to be good dispersers to recolonise the areas that become available after the retreat of Pleistocene glaciations (Svenning & Skov 2007a,b), and (2) that climatic zones at large scales tend to be structured in latitudinal bands (Peel et al. 2007), it could be predicted that distribution ranges would be elongated in an east–west direction at high latitudes. In this third chapter an additional analysis is performed to evaluate if distribution range limits are more stochastic (and, therefore, more twisted and longer) in the equatorward portion of the range than in the poleward portion. This is what would be expected if at higher latitudes range limits were more determined by climatic factors (which are more spatially structured), and if limits at lower latitudes were determined by more stochastic biotic factors (Normand et al. 2009).

To study the processes that influence the variation in biodiversity, besides analysing its spatial variation (e.g., differences in species composition or species richness between different places), it is possible to examine differences in diversity among clades. This is the main topic of the fourth chapter, which is focused on the question of why some clades have more species than others. In this chapter, we explore the factors that have an influence in diversification rate (that is, the balance between speciation and extinction rate) of mammal families, and, therefore, in the difference in species richness among them. Estimated diversification rates reflect the result of processes such as speciation and extinction through time, and consequently investigating which ecological and evolutionary processes determine these rates is key to understand richness differences between clades. One of the main factors that can be behind these differences is the climatic niche of species, that is, the climatic conditions of the sites in which they live (Soberón 2007), because climatic niche might determine where species are present, and thus it can have a strong influence in speciation processes (e.g., ecological speciation by niche divergence, Hua & Wiens 2013) or extinction (e.g., due to substantial climatic change to which species cannot respond).

Therefore, the existence of a relationship between the patterns of climatic niche variation between clades and their diversification rates could be expected, and there are several studies that show that diversification could be faster in the tropics (e.g., Rolland et al. 2014) or that a higher rate of variation in climatic niche through time is associated to higher diversification (e.g., Kozak & Wiens 2010; Title & Burns 2015). There are also studies that observed a positive relationship between the climatic niche width of clades (here, the width is the difference between the maximum and minimum value of a climatic variable) and diversification rate, and, in particular, families with more niche divergence among their species tend to have higher diversification rates (Gómez-Rodríguez et al. 2015). This has been observed using an absolute measure of current niche divergence (that is, the differences between the climatic niches of species). However, further insight can be gained if the evolutionary rate of variation (temporal variation) is also analysed. If niche divergence is related to speciation (and, therefore, to diversification rate), the rate of climatic niche evolution would also be related to diversification rate, and this association could be even stronger than that found with absolute niche divergence, since the latter does not take temporal variation into account. Thus, it would be interesting to test the relative importance of absolute niche divergence and niche evolution rate in explaining the variation of diversification rate between clades. This is a novel approach compared to previous studies addressing that question, which mostly explore the relationship between the rate of climatic niche and diversification, and in general they find that there is a positive relationship (see, for example, Schnitzler et al. 2012; Lawson & Weir 2014; Moen & Wiens 2017). In the fourth chapter of this dissertation, the relationship between the diversification rate of mammal families and niche divergence among the species within each family was analysed. Its relationship with the rate of climatic niche evolution of each family was assessed as well. To estimate the climatic niche of species, families, and clades, the distribution maps of mammal species that are provided by the IUCN and climatic data at a global scale from WorldClim (Hijmans et al. 2005) were used. Family (or clade) diversification rates are calculated using the species richness of the families and its age (see Magallón & Sanderson 2001). Family age is extracted from the estimations of a published phylogeny comprising most mammal families (Meredith et al. 2011). The rate of climatic niche evolution was calculated using another published phylogeny that includes most described mammal species (Bininda-Emonds et al. 2007). This latter phylogeny could not be used for analyses at the family level because many mammal families were paraphyletic in this tree, so estimating their age from it would be less reliable.

These four chapters build on some fundamental topics in biogeography and macroecology, using two vertebrate classes (birds and mammals) as study models, since their species distributions are reasonably well-known compared with other groups of animals. I hope that these contributions might be useful to further delve into these issues, or, better yet, to perhaps inspire new questions.

Objectives

The general objective that unifies this dissertation is to gain insight about the processes that determine biological diversity in terrestrial vertebrates. In order to do that, the following specific objectives will be addressed:

1. To identify potential latitudinal patterns of beta diversity in groups of terrestrial vertebrates with different dispersal capacity and thermal regulation.
2. To assess the relationship between these latitudinal beta diversity patterns, if they exist, and current and historical climatic conditions.
3. To evaluate potential biases in biogeographic regionalisation, mainly the ones associated to the choice of beta diversity measures, clustering algorithm and number of regions.
4. To assess the relationship between climatic niche width, rate of climatic niche evolution, and diversification rate in mammal families worldwide.
5. To analyse the latitudinal variation in range shape in birds and mammals worldwide.
6. To assess the role of climatic niche constraints and neutral processes in the determination of distribution range limits.


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Breakpoints in the latitudinal variation of beta diversity in New World vertebrates

Multiple abiotic factors can potentially have effects on patterns of compositional variation (beta diversity; Whittaker 1960). Assessing their relative contributions is necessary to unveil why regional diversity changes across latitudes. Beta diversity comprises two components (Baselga 2010): turnover (compositional variation due to species replacement) and nestedness-resultant dissimilarity (variation due to species loss). Both components can be caused by different processes and might show contrasting latitudinal patterns (Leprieur et al. 2011; Dobrovolski et al. 2012). Baselga et al. (2012a) hypothesized the existence of a latitudinal breakpoint defining two world regions where the variation in amphibian species composition is dominated by turnover or nestedness, respectively. If changes in the regime of latitudinal patterns of variation in species composition are general across other biological groups, it might be justified to adopt a general two-step analytical strategy in global analyses of beta diversity (and more generally in the analysis of global macroecological patterns). First, it would be necessary to search for the existence of breakpoints, and then for the potential predictors of beta-diversity patterns. Here we assess if such a breakpoint can be found for New World mammals and birds. Considering that these groups are endotherms and have better dispersal capabilities than amphibians (in particular, flying animals could track suitable environments more quickly; Harrison et al. 1992), it is possible that the effects of past climate on these groups are less clear than in amphibians (as the climatic constraints experienced by endothermic animals are different; Buckley & Jetz 2007). If endotherms are more capable of tracking suitable climatic conditions in a scenario of climate change, the proportion of beta diversity due to species loss could be lower (Dobrovolski et al. 2012); therefore, for these groups, different patterns of beta diversity could be expected. Specifically, we predict that, in endotherms, the latitudinal breakpoint at which the differences in species composition due to species losses start to be more important should be located at latitudes higher than those observed for ectotherms. In turn, species turnover should decrease less sharply at higher latitudes compared with ectotherms.

We measured multiple-site dissimilarity in regional cells of 500 km × 500 km, partitioning overall dissimilarity into two components due to spatial turnover (β_{SIM}) and due to nestedness (β_{SNE}) following a similar approach to that described by Baselga et al. (2012a). The distribution ranges of 4265 species of New World birds and 1728 New World mammals were derived from expert-drawn range maps (Patterson et al. 2007; Ridgely et al. 2007). Bats (322 species) and non-volant mammals (1406 species) were split into independent datasets in order to assess the relevance of flight ability. We also independently analysed two avian and three non-volant mammalian orders that differ considerably in dispersal capabilities (see Appendix S1.6 in the Supplementary Material): rodents (937 species), carnivores (80 species), even-toed ungulates (29 species), Passeriformes (2387 species) and Anseriformes (97 species). Body size is generally related to range size (Gaston & Blackburn 1996), so we can assume that rodents tend to disperse less than carnivores or even-toed ungulates, or that Passeriformes generally disperse less than Anseriformes. Polygonal range maps were converted into presence–absence matrices of 1° × 1° cells. Environmental variables for those cells were obtained from WorldClim (Hijmans et al. 2005), both for present conditions and for the Last Glacial Maximum (about 21 000 years ago). The study area was divided in 500 km × 500 km regional cells (Sastre et al. 2009) superimposed over the aforementioned grid of 1° × 1° cells, and, within these regional cells, multiple-site dissimilarity due to spatial turnover (β_{SIM}) and due to nestedness (β_{SNE}) was calculated among 1° × 1° cells using the `betapart` package (Baselga & Orme 2012) in R (R Core Team 2016). Only regional cells with more than 15 terrestrial 1° × 1° cells and more than five species of each one of the studied groups were used in the calculations (the number of regional cells used in the analyses was 115 for bats, 158 for non-volant mammals and 159 for birds). Due to the fact that each regional cell might contain a different number of 1° × 1° cells, beta diversity was computed in 10 random samples of 15 1° × 1° cells, calculating the arithmetic mean of β_{SNE} and β_{SIM} in each regional cell.

Using simple linear regressions (Appendix S1.1), we found that mean elevation was the variable that showed the strongest positive relationship with spatial turnover (albeit this relationship was somewhat weak: $r^2 = 0.14$ for bats, $r^2 = 0.20$ for non-volant mammals, $r^2 = 0.21$ for birds, all $P < 0.01$), suggesting that the presence of mountains creates barriers that promote speciation processes, or that the spatial heterogeneity allows the existence of diverse environments with different faunal composition (see also Melo et al. 2009). For nestedness-resultant dissimilarity, the best predictors are current temperature variables (maximum temperature of warmest month, $r^2 = 0.44$ for bats, $r^2 = 0.55$ for non-volant mammals, $r^2 = 0.37$ for birds, all $P < 0.01$). This could suggest that current temperatures determine species distributions, so that the species assemblages of colder regional cells tend to include nested patterns of species losses among their constituent 1° × 1° cells.

Besides testing linear relationships, we also checked for the existence of breakpoints in the latitudinal patterns of both beta diversity components. To do this, we implemented piecewise regressions (Crawley 2007), testing all possible breakpoints at 1° intervals and selecting the breakpoint with the lowest residual standard error. In addition, we fitted cubic polynomial regressions and compared them with piecewise regressions using the Akaike information criterion (AIC, Appendix S1.5). In general, the AIC of piecewise regressions was lower than that of cubic polynomial regressions, and in the only case where the AIC of the polynomial regression was lower (nestedness-resultant dissimilarity of non-volant mammals), the point of inflection of this model did not differ substantially from that of a piecewise regression and thus does not alter our interpretation of the results. The fit of piecewise regressions (Fig. 1.1) was significantly better than that of simple linear regressions in all cases (the reduction in residual standard error was compared by an ANOVA analysis; see Appendix S1.2).

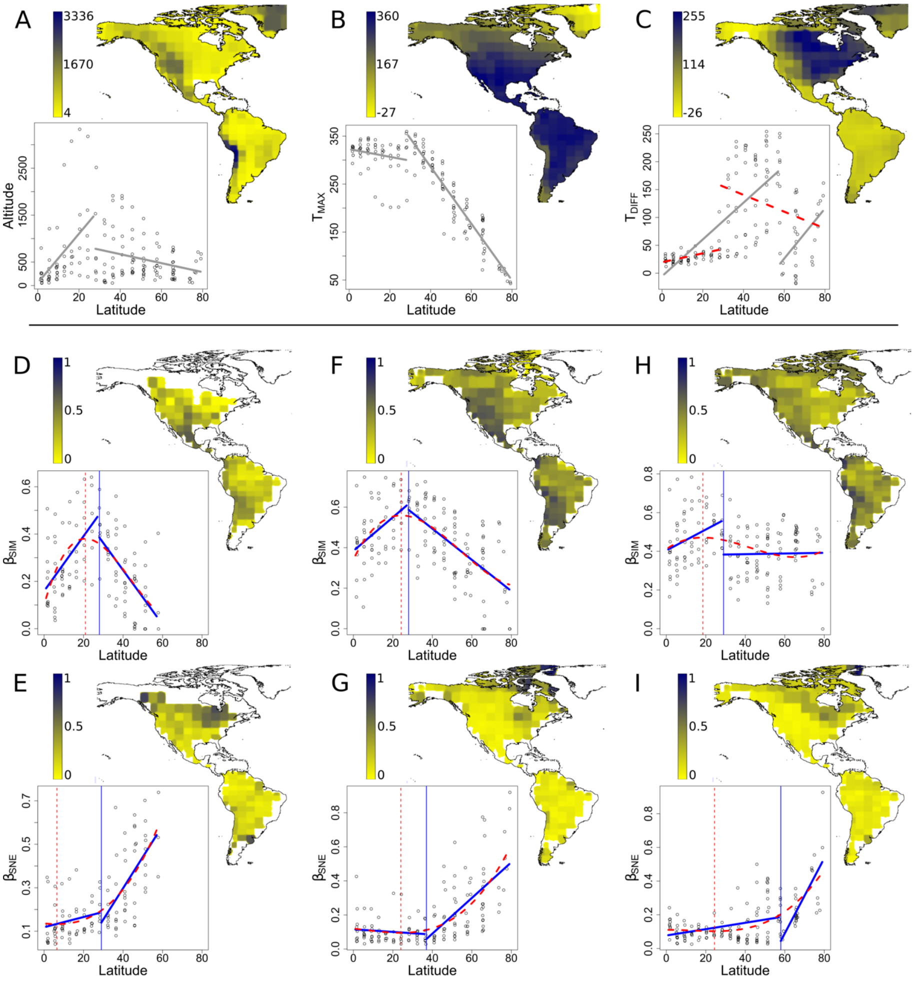

Figure 1.1: Patterns of latitudinal variation in (a) mean elevation (in metres), (b) maximum temperature of the warmest month, (c) annual mean temperature difference since the Last Glacial Maximum (*c.* 21 000 years ago, temperature in °C × 10), and, additionally, in the turnover (β_{SIM}) and nestedness (β_{SNE}) components of beta diversity for bats (d, e), non-volant mammals (f, g) and birds (h, i), with corresponding maps showing their spatial variation. In the plot for climate change (c), the breakpoint which minimizes the residual standard error is at 58° (continuous line), but the scatter of this variable dramatically increases above 29° (dashed line). In the plots for beta diversity (d–i), piecewise regressions are superimposed as a continuous line and cubic polynomial regressions as a dashed line. The vertical lines mark the breakpoint in piecewise regressions and the inflection point in polynomial regressions.

The turnover (species replacement) component of dissimilarity increased from the equator to the breakpoint (located at 28° for bats and non-volant mammals and 29° for birds), and decreased from the breakpoint towards higher latitudes (except in the case of birds, where the slope was not significantly different from zero above the breakpoint). Similar patterns of turnover were found in rodents and carnivores, with a peak at 29°, but not for even-toed ungulates, where piecewise regressions did not improve the fit of simple linear models (ΔAIC < 2; Appendix S1.6. In Passeriformes, the patterns observed are similar to those of birds in general (Fig. S1.6.2), which is consistent with the fact that they comprise a large proportion of bird species. In Anseriformes, which disperse more, this peak in turnover does not appear (in agreement with our prediction that in very mobile organisms species turnover should decrease less sharply with latitude). Nestedness-resultant dissimilarity showed a flat relationship with latitude between the equator and the breakpoint, and increased steadily above the respective breakpoints. In mammals, the breakpoint was located at 29° for bats, 37° for non-volant mammals, and the same latitude for rodents and carnivores considered separately. In birds, the breakpoint was found at 58°, a latitude very similar to that of Anseriformes (56°) but higher than that of Passeriformes (42°), in agreement with the prediction that the greater the dispersal ability, the higher the latitude at which nestedness-resultant dissimilarity dominates beta-diversity patterns. The quantitative differences among groups in the breakpoints for the nestedness-resultant component might partially be an outcome of the extreme sensitivity of the method (i.e. minimizing standard error above and below the breakpoint). In fact, AIC values and the amount of variation explained are very similar when forcing the breakpoint at 29° in non-volant mammals (Appendices S1.2 & S1.3). This was not the case of birds, suggesting a more relevant difference in the nestedness component patterns of this group (likely related to their physiological traits rather than their dispersal ability, given the contrast with bats). Moreover, cubic polynomial regressions have inflection points that in most cases are located around 20°–25° (see Fig. 1.1), except for nestedness-resultant dissimilarity of bats (at 6°). We note that in this particular case the nestedness component of beta diversity increases constantly with latitude (the sign of the slope does not change), and the inflection point of a polynomial relationship does not capture the abrupt increase in the slope of the relationship above *c.* 30° of latitude that is detected with piecewise regressions. A visual inspection of the scatterplots reveals that the nestedness components of all groups are very low below 30° and show a flat relationship with latitude, while the scatter is very large above 30°. This was also observed for climate change since the Last Glacial Maximum (calculated as the difference in annual mean temperature between the present time and Last Glacial Maximum conditions; see Fig. 1.1c, Appendix S1.4) but not for elevation or current climate variables.

Taken together, our results unveil the existence of a latitudinal breakpoint that separates two distinct regions in the globe. This pattern seems common to all terrestrial vertebrates. When we looked for correlations with environmental variables, we only found a strong relationship between nestedness-resultant dissimilarity and current temperature conditions, which might be explained by mammals and birds being more at equilibrium with current temperature conditions than amphibians because of their endothermy and better dispersal capabilities (Araújo & Pearson 2005; Dobrovolski et al. 2012). However, elevation and the historical change in temperature conditions show interesting latitudinal breakpoints (which are not observed in current temperature conditions) parallel to those found in the components of beta diversity. This might suggest that historical processes have imprinted the beta-diversity patterns of all groups regardless of their life histories. First, mountains (acting as refuges and sources of diversification) are responsible for higher levels of species replacement at a regional scale (500 km squares). Second, glaciations would have wiped out the vertebrate assemblages independently of temperature regulation capabilities, and these regions had to be recolonized after the retreat of the ice (e.g. Sommer & Zachos 2009; Alexandri et al. 2012; Dufresnes & Perrin 2015), driving ordered patterns of species losses to higher latitudes. The quantitative differences in latitudinal thresholds of the nestedness component could, in turn, reflect the different dispersal or, most likely, temperature requirements of different groups.

The existence of breakpoints is not exclusive of beta diversity patterns, as some other macroecological studies have also found thresholds which define changes in the tendencies of biodiversity patterns, or zones where different factors might determine these patterns. For example, Kerr & Packer (1997) found that potential evapotranspiration (PET) below values of 1000 mm year^{-1} was an important predictor of mammalian species richness in North America, but not in high-energy regions (PET $\geq$ 1000 mm year^{-1}), where habitat heterogeneity (variation in topography and local variation in energy availability) explains more variation in species richness, as energy does not seem to be a limiting factor in these high-energy areas at lower latitudes. Consistent with this idea that energy might be limiting species richness mainly at higher latitudes, Hawkins et al. (2003), in a review of studies on the relationship between climate and species richness, observed that water variables seem to be stronger predictors below a given latitudinal threshold with energy variables being more determinant at latitudes above that threshold. Whittaker et al. (2007) tested this hypothesis for several taxa in Europe, and found some evidence that water variables could be more important at lower latitudes and energy variables could be the limiting factor at higher latitudes (although their results were not consistent across taxa). There are some other examples of breakpoints, such as the one Zagmajster et al. (2014) found for the range size of groundwater crustaceans in Europe, which starts to increase markedly with latitude only above 43° N. This pattern is mainly associated with long-term climatic variability. Taking into account that these sorts of breakpoints can be important for explaining or clarifying some patterns in ecology, we encourage macroecologists to consider threshold-based exploration of their data, as it can give additional insight compared with analyses that consider biodiversity to vary spatially in a smooth manner.


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Dissimilarity measures affected by richness differences yield biased delimitations of biogeographic realms

Recently, Costello et al. (2017) established 30 marine biogeographic realms using the distributions of thousands of species of marine animals and plants. This contribution is key to complement similar work on the terrestrial realm (Holt et al. 2013). However, in our opinion, their methodological approach is not the best. First, based on the methods they report, reproducing their results was not possible to us. Second, for their main result they defined regions using Jaccard similarity between sites, but it is well established that Jaccard's similarity index is not the most appropriate for the delimitation of biogeographic regions (Kreft & Jetz 2010; Holt et al. 2013), because it is affected by differences in richness (Lennon et al. 2001; Koleff et al. 2003; Baselga 2010, 2012). As a result, cells with impoverished fauna or flora, whose species composition is a subset of that of richer cells, are considered dissimilar and thus can be clustered in different regions, even if no species has been replaced from cell to cell. This behaviour is completely undesired for delimiting biogeographic regions, particularly when sampling effort is uneven, which Costello et al. (2017) acknowledge to be the case in their dataset. The reason is that two cells with exactly the same composition can be considered as very different and thus assigned to different regions if one is well sampled (high observed richness) and the other is poorly sampled (low observed richness).

Costello et al. (2017) also analyse their data using dissimilarity indices that are not influenced by gradients in species richness (e.g., Simpson's dissimilarity index, β_{sim}, Simpson 1960), and they argue that their results are robust to these alternative measures. However, we observe important discrepancies between their Fig. 2 (their main result based on Jaccard) and their Fig. 3c (realms based on β_{sim}). For instance, in their Fig. 2, the Atlantic Ocean is divided in two regions (northern and southern), and there is a separate region in the Indian Ocean. However, in their Fig. 3c, all these regions seem to be lumped into one.

Costello et al. (2017) initially use predefined regions (i.e. seas) as units for regionalisation, but this introduces a priori constraints in the regionalisation that should be avoided. We thus used the dataset they provide in their Supplementary Material (a presence-absence table of species in $5^\circ \times 5^\circ$ cells) to test if we could define similar marine biogeographic regions by using Simpson dissimilarity between cells (an index which is appropriate for regionalisation, because it is not affected by gradients in species richness) and well established procedures for delineating biogeographic regions (Kreft & Jetz 2010; Holt et al. 2013). We also used Jaccard's dissimilarity index with the aim to reproduce the results of the authors. All analyses were conducted in R (R Core Team 2016). From the presence-absence matrix we obtained a matrix of dissimilarities between cells using function `beta.pair` in package `betapart` (Baselga & Orme 2012). We then performed a hierarchical cluster analysis on this matrix of dissimilarities, using function `hclust` in R. When we used the average clustering method, as Costello et al. (2017) did, we found that it yielded very unbalanced dendrograms, and as a result, most newly defined clusters consisted of only one cell (or very few cells, see Appendix S2.1). Therefore, in order to obtain a more appropriate regionalisation, we used Ward clustering as the agglomeration method to minimise the distances within clusters and maximise the distances between them. This is one of the most relevant clustering criteria for regionalisation (Holt et al. 2013), as the objective is to maximise the internal coherence of realms, and the differences between them. Another critical step is defining the number of clusters (regions). For this, we assessed the significance of cutting the dendrogram resulting from the hierarchical cluster analysis into n clusters (n ranging from 2 to 50 clusters) by performing ANOSIM tests (Clarke 1993) with command `anosim` in package `vegan` (Oksanen

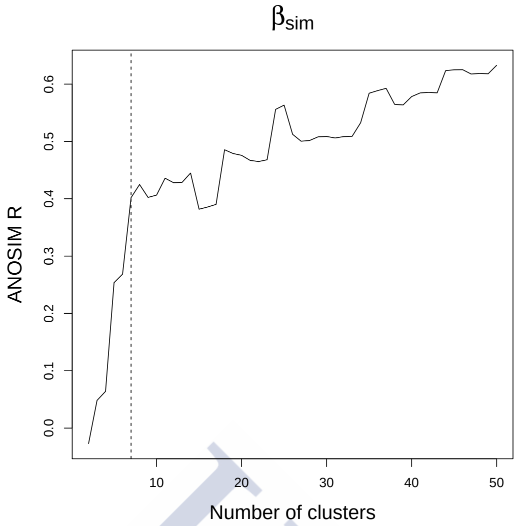

Figure 2.1: ANOSIM R values against the number of clusters in which the dendrogram is cut. The dendrogram was built using Simpson dissimilarity (β_{sim}) between cells and Ward clustering. Above the vertical dashed line (7 clusters), the ANOSIM R statistic raises more slowly with an increasing number of clusters

et al. 2017). In the β_{sim} dendrograms, we selected a value of $n = 7$ as the minimum value for which $n + 1$ did not cause a relevant increment in the ANOSIM R statistic (see Fig. 2.1). Therefore, we defined 7 biogeographic regions. Since Costello et al. (2017) define 30 regions, we also delimited 30 clusters for comparison with their results.

When defining 7 regions, we found some important differences between using β_{sim} (Fig. 2.2a) or Jaccard (Fig. 2.2c) as a measure of differences in species composition between sites. Using β_{sim} rendered three large regions that correspond roughly with the Atlantic, Pacific, and Indian Ocean, and the Antarctic Ocean is divided into two regions (one roughly south to the Pacific Ocean, another south to Atlantic and Indian oceans). Interestingly, the North Pacific and parts of the North Atlantic and the Arctic Ocean are grouped together. However, when using Jaccard, a widespread region occupies the Pacific Ocean, an important part of the Atlantic Ocean and some parts of the Arctic. When defining 30 regions

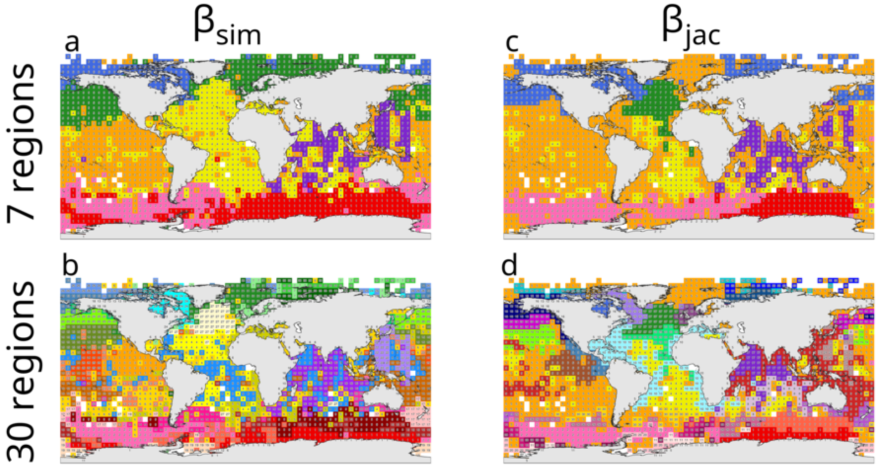

Figure 2.2: Regionalisation of marine assemblages using Simpson (β_{sim}) or Jaccard (β_{jac}) dissimilarity indices and Ward clustering, defining 7 or 30 regions.

(Fig. 2.2b,d), most of them are not very continuous (both in the case of β_{sim} and Jaccard), suggesting that the sampling noise is a relevant source of error at this level of similarity. Importantly, we find very few similarities between these maps and those presented by Costello et al. (2017), which we were unable to reproduce.

When defining biogeographic regions, the choice of the measure of dissimilarity between cells is fundamental. As we argued before, indices that account only for the replacement component of assemblage dissimilarity and are independent of richness differences, as Simpson dissimilarity, are the most appropriate ones (Lennon et al. 2001; Baselga 2010, 2012; Baselga & Leprieur 2015). If richness gradients exist, regionalisations based on indices that account for richness differences (as Jaccard) are biased because those indices reflect these gradients (Svenning et al. 2011), even in the absence of species replacement (i.e., the pattern that should determine the regionalisation). When richness differences are caused by sampling biases, the differences between indices can be marked, as Jaccard accounts for the sampling biases, while Simpson's dissimilarity is quite robust. For example, when we excluded cells with less than five species, which can affect dissimilarity analyses considerably (Kreft & Jetz 2010), the main difference we observed in the case of β_{sim} was that the region near the Arctic became more coherent (i.e., not associated with the North Pacific, Appendix S2.2a). However, in the case of Jaccard, we observed that the North Atlantic region expanded to the Eastern Pacific and some parts of the coasts of South America and Africa when excluding those cells (Appendix S2.2c).

Finally, we note that when dealing with unevenly sampled data, the choice of the clustering method has to be carefully considered as well. In this particular case, the widely used average method seemed inappropriate, because the resulting dendrogram was very unbalanced, and consequently many of the defined regions consist of only one cell (Appendices S2.1, S2.3). By contrast, Ward's method gives a more balanced dendrogram (Fig. 2.2, Appendix S2.2), and might perform better for less well-sampled datasets (Dapporto et al. 2015).

In conclusion, we show that three major methodological decisions are critical for biogeographic regionalisation: dissimilarity index, clustering algorithm and number of clusters. Objective criteria are available to optimise the selection of clustering algorithms and number of clusters (Kreft & Jetz 2010; Holt et al. 2013; Dapporto et al. 2015) depending on the characteristics of the dataset. Regarding the selection of dissimilarity measures, a clear consensus has been recently reached about the need to use indices not affected by richness gradients (Kreft & Jetz 2010; Baselga 2010; Svenning et al. 2011; Holt et al. 2013; Dapporto et al. 2015). If these methodological guidelines are not followed, biotic regionalisations will not reflect the patterns we are aiming to capture (i.e., regions with different biotas), but richness gradients and sampling biases.


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Latitudinal variation in species range shape

Introduction

Understanding the factors determining the limits of species distribution ranges and unveiling global regularities across biological groups is crucial for discovering the mechanisms behind the distribution of biodiversity and predicting how species will respond to global change. The geometry of species distributions can be characterised by their size and shape. Range size has received comparatively more attention (Gaston 2003), e.g. with studies showing that larger range sizes are associated with climatic instability (Morueta-Holme et al. 2013) and revealing similar range size–latitude patterns among different classes of vertebrates (Orme et al. 2006; Davies et al. 2009; Whitton et al. 2012). By contrast, little is known about the factors influencing the shape of species ranges and its geographic variation (but see Brown & Maurer 1989; Rosenfield 2002; Pigot et al. 2010; Baselga et al. 2012c), which is surprising given that range shape reflects the relative roles of niche limitation, dispersal barriers, and intrinsic dispersal limitation (Baselga et al. 2012c). In fact, here we show that unique predictions for range shape patterns can be derived from these alternative mechanisms, opening new avenues for assessing what determines species' range limits.

If species distributions were mainly under the control of neutral ecological processes (Hubbell 2001), after speciation takes place, the spread of a species distribution range would be equiprobable in all directions (i.e., isotropic) and, therefore, species distributions would tend to be circular. In this situation, the intrinsic dispersal capability of species would control the size of isotropic ranges (Cain 1944; Rapoport 1975). Instead, extrinsic dispersal constraints (e.g., topographic barriers) or niche limitation (e.g., climatic requirements) would cause ranges to deviate from isotropy by determining differential probabilities for range expansion in different directions. Of course, in reality, all mechanisms could be acting simultaneously with different relative relevance. A previous study on global range shape patterns of multiple taxa (plants, amphibians, birds, and mammals) found that range shape patterns were intermediate between the predictions from either pure climatic or pure dispersal control (Baselga et al. 2012c). However, when large-ranged species were removed, the observed ranges of small-ranged species (the vast majority of species) did not differ from neutral predictions, suggesting that range shapes might be determined by processes linked to range size, with small-ranged species more limited by dispersal and large-ranged species more limited by climate (Brown & Maurer 1989).

Baselga et al. (2012c) analysed how continental patterns of range size deviated from neutral and niche predictions, but not how range shape varies spatially (e.g., with latitude). Here, building on the finding that small- and large-ranged species have different range shapes, we assess whether variation in species range shape with latitude can provide new insights on the processes limiting species distributions. The motivation for such an analysis lies in five major sources of information:

1. Climatic zones at large scales are generally structured in latitudinal bands (Brown & Maurer 1989; Peel et al. 2007), particularly in the Northern Hemisphere.

2. Most clades have tropical origins (i.e., in warm climates), with niche conservatism being an important mechanism behind the maintenance of the latitudinal richness gradient (Wiens & Donoghue 2004; Smith et al. 2012; Qian & Ricklefs 2016).

3. Tolerance to heat is largely conserved across lineages, while tolerance to cold varies between and within species (Araújo et al. 2013). This suggests the existence of hard physiological boundaries constraining the evolution of tolerances to high temperatures, while evolution of tolerances to cold would be relatively more frequent

(but still not very frequent, due to niche conservatism, as stated above).

4. Distribution range size tends to increase with latitude (Rapoport 1975; Ruggiero & Werenkraut 2007), although there are many exceptions to this pattern (see, for example, Stevens 1989) and some authors suggest that it might be a local phenomenon (Gaston et al. 1998).

5. Dispersal limitation has strong effects on large-scale species distributions (e.g., Baselga et al. 2012b). Notably, dispersal has limited postglacial re-colonisation, with only good dispersers reaching high latitudes (e.g., Alsos et al. 2007), and poor dispersers remaining limited to relatively low latitudes (Svenning & Skov 2007a,b; Baselga et al. 2012b).

The above propositions allow us to derive the following hypotheses. First, we hypothesise (H1) that because at higher latitudes climate is in general more different from the ancestral tropical conditions of most lineages (point 2) and closer to their species-specific lower thermal limits (in contrast to the hard-boundary upper thermal limits, point 3), the effect of niche constraints should be stronger at higher latitudes. In addition, species living there have to be good dispersers able to quickly recolonise large areas after the retreat of Pleistocene glaciations (points 4–5), hence occupying most suitable areas (i.e., distributions relatively close to equilibrium with current climatic conditions). This leads to the prediction that species ranges at higher latitudes should be elongated in east–west direction, mirroring the geographic structure of climatic zones (particularly in the Northern Hemisphere, cf. point 1). Second, we hypothesise (H2) that the poleward limits of species ranges (associated with tolerance to cold) are likely to be more determined by climatic requirements (because, at higher latitudes, climatic conditions differ more from the ancestral tropical conditions of most lineages, cf. point 2), while equatorward limits are likely to be more determined by stochastic biotic processes (Normand et al. 2009), rather than to thermal niche constraints (as tolerance to heat is determined by hard boundaries with smaller variation across lineages, cf. point 3). This leads to the prediction that poleward range limits should be more compact (i.e., less convoluted and hence shorter).

The aim of this chapter is to asses the aforementioned hypotheses, using two clades of terrestrial mammals as model taxa, birds and mammals. To do this, we quantified the shape of the breeding ranges of 10 057 species of birds and 5411 species of mammals worldwide. Specifically, to test H1 we assessed whether species at higher latitudes or with larger ranges are more elongated in an east–west direction by evaluating relationships between range shape and latitude and range extent, and whether the observed patterns could be accounted for by a null model in which species ranges are solely constrained by the shape of land masses. To test H2, we assessed whether the poleward semi-perimeters of the ranges are shorter than the equatorward semi-perimeters.

Methods

Latitudinal and longitudinal ranges

Range maps of 5411 mammal species (including 127 marine species) were downloaded from the IUCN (2013) database, and range maps of the breeding distributions of 10 057 bird species (including 332 marine species) were downloaded from the BirdLife International & NatureServe (2013) database. We analysed marine species separately, and the main results refer only to terrestrial species. We excluded non-native range polygons, i.e., zones where a species has been introduced. We calculated the maximum longitudinal and latitudinal extents of each polygon as the difference between their maximum and minimum longitude and latitude, respectively. The coordinates in these range maps were specified in degrees, and we transformed the maximum longitudinal and latitudinal extents in degrees to kilometres. One degree of latitude is equivalent to approximately 110.6 km at the equator, and this length does not vary much at higher latitudes. However, the length of one degree of longitude varies significantly with latitude, so we estimated the longitudinal span in kilometres at the lowest latitude (closer to the equator) of the distribution, or at the mean latitude, in the cases in which this latitude was closer to the equator than the latitudinal extremes of the distribution range.

For details in the calculations used to estimate the longitudinal range (in kilometres), see Appendix S3.1 in the Supplementary Material.

Range shape

An isotropic distribution range has equal latitudinal and longitudinal extents. Based on this, we followed two approaches to characterise the shape of distribution ranges. First, in the relationship between latitudinal and longitudinal ranges, we measured the minimum distance between each point and the 1:1 line (in which latitudinal and longitudinal range are equal). Distribution ranges that are closer to this line should, in general, be more isotropic. This measure does not capture in the directionality of deviations from isotropy or the proportion between latitudinal and longitudinal ranges, but it reflects the absolute magnitude of the deviation from exactly equal latitudinal and longitudinal ranges. Second, we calculated the scaled difference between latitudinal and longitudinal ranges: (Lat−Lon)/(Lat+Lon), with "Lat" being the latitudinal range and "Lon" being the longitudinal range. When the latitudinal and longitudinal range are the same, this difference is equal to zero; when the latitudinal range is greater than the longitudinal one (the range is elongated in a north–south direction), this difference is positive; and when the range is elongated in an east–west direction, it is negative. Thus, this measure informs about the direction of the elongation of the shape.

Univariate generalised additive models (GAM), with a normal error structure and identity link function, were used to assess the relationship of these measures of range shape (distance to the 1:1 line and latitude–longitude scaled difference as response variables) with latitude and with geographic range size as explanatory variables. This analysis was performed for terrestrial and marine species separately. In addition, we performed a variance partitioning analysis of the full models (i.e., latitude and range size as predictors) to partial out the effect of each variable.

Null models

We built null models to assess the potential influence of geometric constraints on distribution range shapes. This is particularly relevant because the shape of the continents might be important in determining range shape at large spatial scales. To account for these geometric constraints, we compared the observed patterns in range shape with the patterns arising from a simple null model in which species expand their ranges randomly from a starting cell. Each species starts in a random 50 km × 50 km cell (similar to those of Sastre et al. 2009) and is allowed to occupy any of the cells neighbouring the already occupied cells, one at a time, until it reaches an area similar to its observed range size. If the species was not able to expand until reaching that area (e.g., because the starting cell was in an island smaller than the species' range size), we selected a different random starting cell.

To compare the observed latitudinal patterns in range shape with those predicted by the null models, we plotted the kernel density distribution of the latitude–longitude scaled difference of all species with their latitudinal midpoint falling in 10° latitudinal windows, both for the null model and for the real distributions. Then, we calculated the overlap between the observed distribution and the null model distribution.

Range semi-perimeters

As climatic conditions at higher latitudes differ more, in general, from the ancestral tropical conditions of most lineages, it could be expected that the limits of species ranges are more constrained by climate there and, thus, less stochastic than at lower latitudes (Normand et al. 2009; Pellissier et al. 2013). To assess this we compared the poleward and equatorward semi-perimeters (that is, the perimeters of the poleward and equatorward portions of a polygon) of species ranges, predicting that the equatorward semi-perimeter of a polygon should be more stochastic (i.e., with a more uneven edge) if it is significantly longer than the poleward semi-perimeter.

Poleward and equatorward semi-perimeters were quantified by dividing each distribution range into two polygons by the latitudinal line that passed through the centroid of the range, and estimating the perimeter (in km) of the resulting polygons (one to the north and the other to the south of the centroid). This estimation was done using the package `geosphere` (Hijmans 2016) in R, which allows to compute distances between angular coordinates (i.e., expressed in latitude/longitude). We tested if the perimeter of the polygon closer to the equator (the equatorward semi-perimeter, ES) is longer than the perimeter of the polygon at a higher latitude (the poleward semi-perimeter, PS) for each species, by using a one-sided paired *t* test (that is, we tested if ES > PS). For this comparison, we standardised the semi-perimeters by dividing them by the sum of the semi-perimeters of both polygons for each species (thus, we compared ES/(PS + ES) and PS/(PS + ES)). The poleward polygon is the one above the centroid in the Northern Hemisphere and the one below the centroid in the Southern Hemisphere.

Because the shape of land masses systematically differs between the Southern and Northern hemispheres (i.e., the continents generally taper to the pole in the Southern Hemisphere but to the equator in the Northern Hemisphere), we performed this analysis separately for each hemisphere in order to assess the influence of the shape of land masses on the lengths of range semi-perimeters. This geometric constraint could create an artefactual pattern, confounding the effect of the shape of the continents with that of the different climatic determinism between poleward and equatorward semi-perimeters. Thus, separating both hemispheres should allow identifying whether such a confounding effect is taking place. We assigned each species to the Northern or Southern Hemisphere (2905 and 2379 species of mammals and 4717 and 5008 species of birds in the Northern and Southern Hemisphere, respectively). If the range of the species crossed the equator, we used its mean latitude to assign it to one of the hemispheres. Additionally, in order to assess if these differences depend on range size, we also conducted this analysis using only the species with the smallest and largest range sizes (first and fourth range size quartiles, respectively), as species with small ranges are more likely limited by dispersal, and the main factors that determine their range shape might differ from more widely distributed species. Note that, as the semi-perimeters were standardised, range size should not influence the magnitude of the difference between semi-perimeters.

Since the area of latitudinal belts (i.e., stripes with the same latitudinal extent) decreases towards the poles, this approach presents an important problem, as it would be possible to find that the lower-latitude portions have longer perimeters simply because these halves occupy latitudinal belts with larger areas. To account for this, we flipped the polygons on their east–west axis and repeated the same measures described above. If the lower-latitude portions of the original polygons have effectively longer perimeters, we should find that after flipping them, the upper-latitude polygons have longer perimeters. However, if the perimeters of lower-latitude portions remain longer in the flipped polygons, we cannot conclude that there are any significant differences between perimeters.

All GIS and statistical analyses were conducted in R (R Core Team 2016, version 3.2.4) using the package `maptools` (Bivand & Lewin-Koh 2016, package version 0.8-39) to read shapefiles, the package `rgeos` (Bivand & Rundel 2016, package version 0.3-17) to manipulate polygons, and the package `geosphere` (Hijmans 2016, package version 1.5-1) to estimate the geographic range size (in km^2) and to measure the perimeters (in km) of each species. GAMs were fitted with package `mgcv` (Wood 2011, package version 1.8-12), using penalised cubic regression splines. The R code for manipulating range polygons (with an example polygon included) and the C++ code we used to implement the null model are available in Appendix S7 in the online version of this manuscript.

Results

The species distribution ranges of birds and mammals present latitudinal and longitudinal extents that are positively correlated (Spearman's $\rho = 0.90$, $P < 0.001$ in mammals and $\rho = 0.87$, $P < 0.001$ in birds, Fig. 3.1), with species deviating more from the 1:1 line with increasing longitudinal extent in both mammals and birds. Moreover, there is a triangular pattern in the relationship between mean latitude of the distributions and distance to the 1:1 line (Fig. 3.2A–B). In other words, most of the species have range shapes that are isotropic or close to isotropy (closer to the 1:1 line), but the species that deviate the most from isotropy occur, in general, at higher latitudes in the Northern Hemisphere. Similarly, the species with the largest geographic extents tend to deviate more from the 1:1 line (Fig. 3.2C–D); and there is a strong positive correlation between distance to the 1:1 line and range area (Pearson's $r = 0.75$ in mammals and $r = 0.70$ in birds, all $P < 0.001$, both variables ln-transformed).

Hence, species with large range sizes deviate more from equal latitudinal and longitudinal ranges. A GAM including mean absolute latitude and range size explains about half of the variability in the distance to the 1:1 line ($r^2 = 0.50$ for mammals, $r^2 = 0.61$ for birds, all $P < 0.001$). Most of this variation is explained uniquely by range size (unique contribution of range size = 34% [mammals] and 32% [birds]; unique contribution of mean absolute latitude = 7% [mammals] and 14% [birds]), and only a small proportion of this explained variation is shared between both variables.

Shape directionality, estimated by the latitude–longitude scaled difference, shows no marked latitudinal patterns from the equator to a point around 30°–40° N. Above these latitudes, the latitude–longitude scaled difference decreases with latitude, such that at high latitudes ranges tend to be elongated in an east–west direction (Fig. 3.3A–B). Near the equator most species ranges tend to have similar latitudinal and longitudinal ranges (the local central tendency of the scaled difference is negative, but close to zero), as it is evidenced by the high density of points. At high latitudes in the Southern Hemisphere, species tend to have north–south elongated ranges. This latitudinal pattern also appears if we plot the mean of the latitude–longitude scaled difference in of all species present in 100 km × 100 km cells against latitude (see figures in Appendix S3.3 and Fig. 3.4). The latitude–longitude scaled difference also varies with range size, with ranges being isotropic on average when geographic range size is small, but tending to be elongated in an east–west direction when it is large (Fig. 3.3C–D). Remarkably, only a low proportion of variance of the latitude–longitude scaled difference is explained by a GAM including mean absolute latitude and range size ($r^2 = 0.16$ in mammals, $r^2 = 0.21$ in birds, all $P < 0.001$). This implies that, although these variables largely explain deviations from isotropy (see above), these predictors do not explain the direction of these deviations (i.e., north–south or east–west elongation). The fact that there are not systematic range shape deviations associated with these predictors would be in accordance with the hypothesis that only a small fraction of the species (widespread or high-latitude species) would be constrained by their niche requirements. Again, a variance partitioning analysis shows that most of the variance is explained uniquely by either mean latitude or area

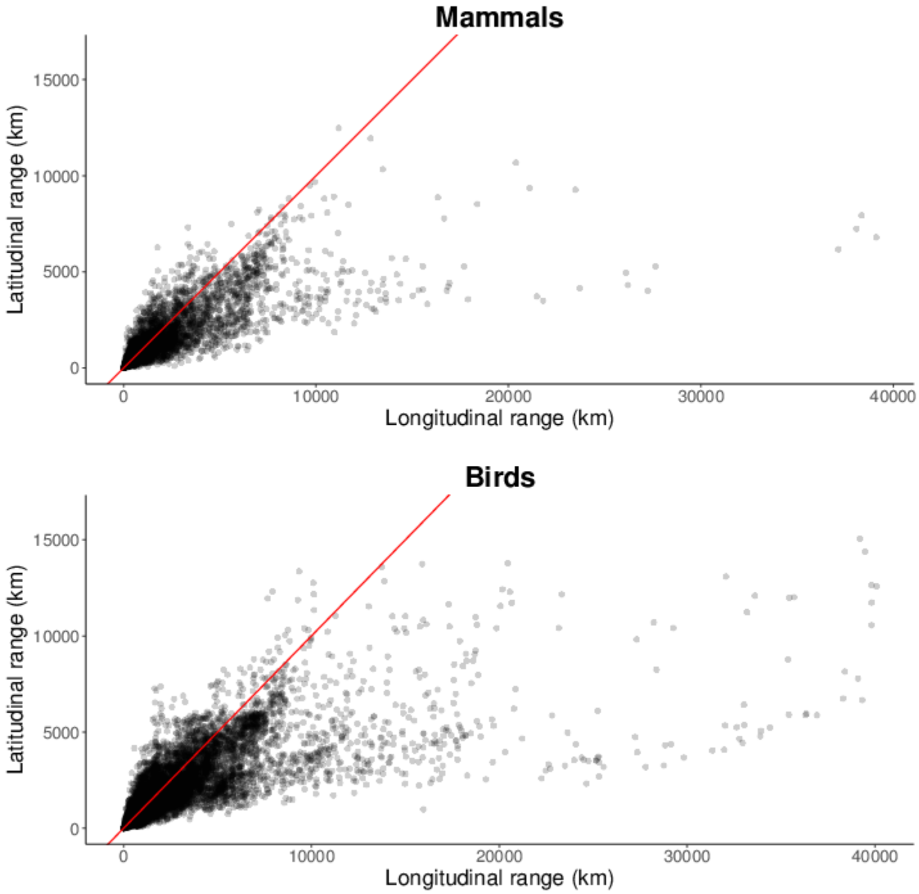

Figure 3.1: Relationship between the extent of longitudinal and latitudinal ranges in birds and mammals. The 1:1 line is shown in red.

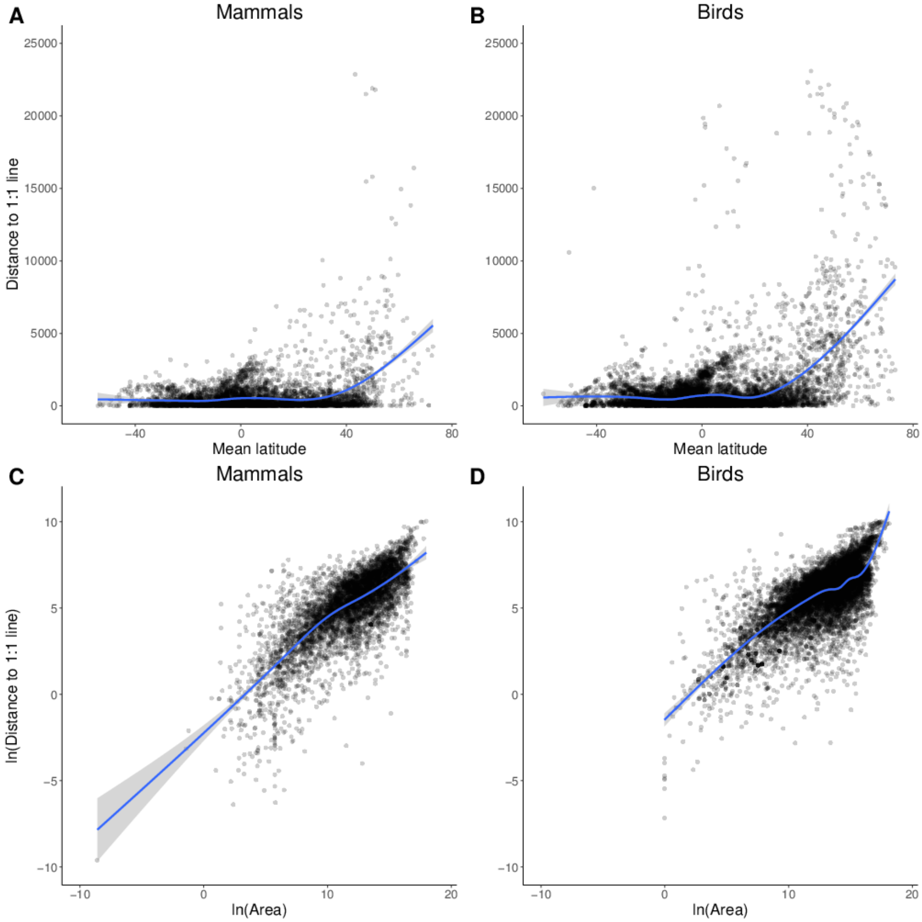

Figure 3.2: Relationship between the distance to the 1:1 line of Fig. 3.1 and the mean latitude of the range (A–B) or range extent (C–D, in km^2), for birds and mammals. Note that ranges with more similar latitudinal and longitudinal ranges are closer to the 1:1 line of Fig. 3.1. In the scatterplots against range extent, both variables are ln-transformed. The fitted single-term GAM is superimposed, with a 95% confidence interval.

(unique contribution of mean absolute latitude = 8% [mammals] and 11% [birds]; unique contribution of range size = 5% [mammals and birds]). While at low latitudes no pattern is observed for the direction of the deviation from isotropy, it should be noted that the shape of the continents and regional topography seem to influence the latitude–longitude scaled difference in particular cases. For example, ranges are generally north–south elongated in southern South America (where the Andes likely act as both a climatic constraint and a dispersal barrier), as well as in Madagascar (where the shape of the island is likely the factor behind this elongation) or eastern Australia for mammals (probably due to climatic constraints, in this case, see Fig. 3.4).

We also performed the same analyses using a more conservative estimate of longitudinal range (calculating longitudinal span in kilometres at the mean latitude of the distribution), finding similar patterns to those described above (see Appendix S3.2).

The observed maps of mean range shape elongation were broadly similar to those predicted by the null models (Fig. 3.4). For example, the null models predict north–south elongated ranges in the southern end of South America or Madagascar, and east–west elongated ranges at high latitudes in the Northern Hemisphere. However, the null models do not show the same latitudinal pattern in range shape (Fig. S3.4.1), that is, we do not find strong deviations from isotropy at high latitudes in the Northern Hemisphere. There is a slight tendency at the highest latitudes towards east–west elongated ranges in the Northern Hemisphere and towards north–south elongated ranges in the Southern Hemisphere. This tendency might be explained in part by the shape of the continents, particularly in the Southern Hemisphere. However, the tendency towards east–west elongated ranges in the Northern Hemisphere is much stronger in the empirical patterns (they are more elongated than predicted by the null model, see Fig. 3.3A–B), as the difference between the observed pattern and the null model is greater at high latitudes (less overlap in the distributions) in the Northern Hemisphere (see Fig. 3.5).

Regarding range edge evenness, the observed species distribution showed equatorward semi-perimeters that tended to be longer than poleward semi-perimeters in both hemispheres, with a greater difference in the Southern Hemisphere (mean of the differences 0.008 ± 0.006 in

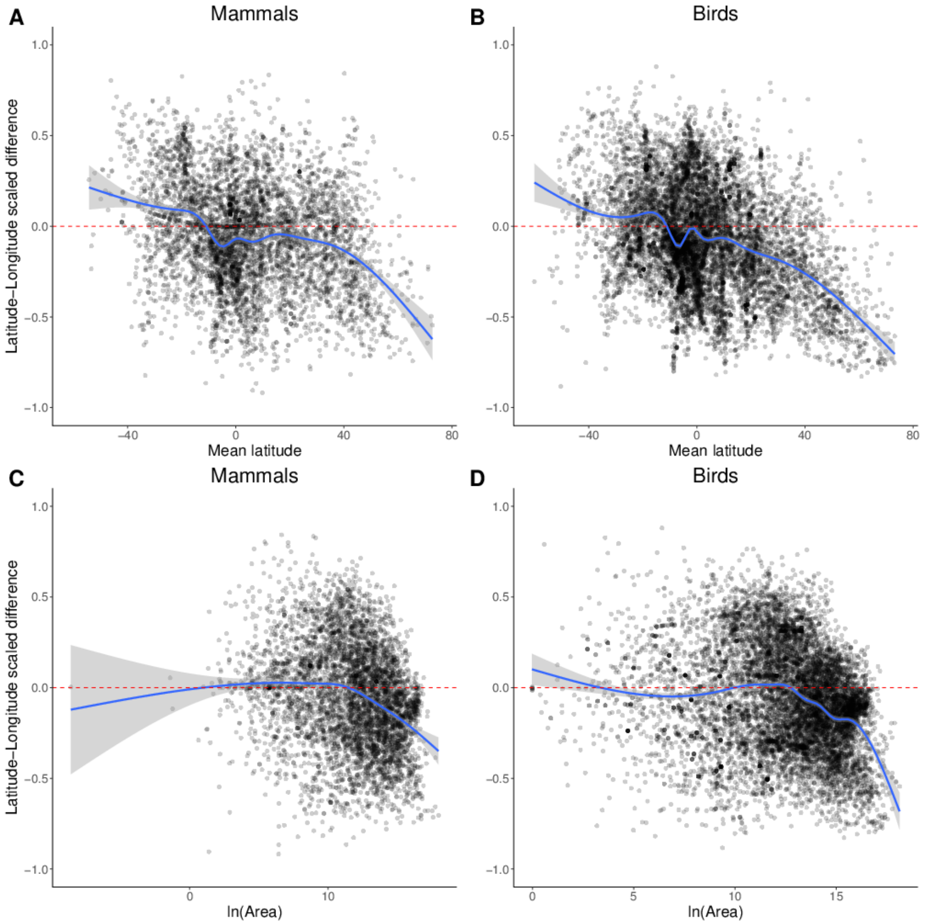

Figure 3.3: Relationship between latitude–longitude scaled difference and mean latitude of the ranges (A–B) or range extent (C–D, in km^2, ln-transformed), for birds and mammals. Note that ranges with more similar latitudinal and longitudinal ranges are closer to zero, indicated by a dashed red line. The fitted single-term GAM is shown, with a 95% confidence interval.

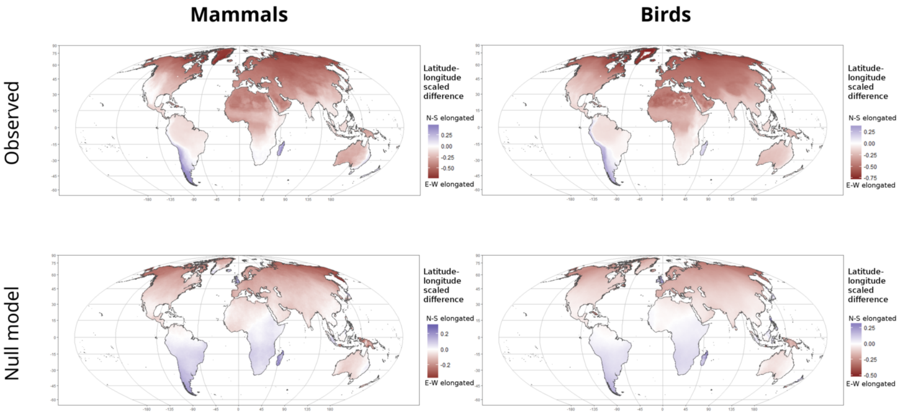

Figure 3.4: Maps for the average range shape (i.e., latitude–longitude scaled difference) of all species present in each 100 × 100 km cell. Blue indicates that the mean is positive (i.e., many species in those cells have ranges elongated north–south) and red indicates that the mean is negative (i.e., ranges are generally elongated east–west). The maps of the first row are those of the observed distribution ranges, and the maps of the second row correspond to the null model distribution ranges.

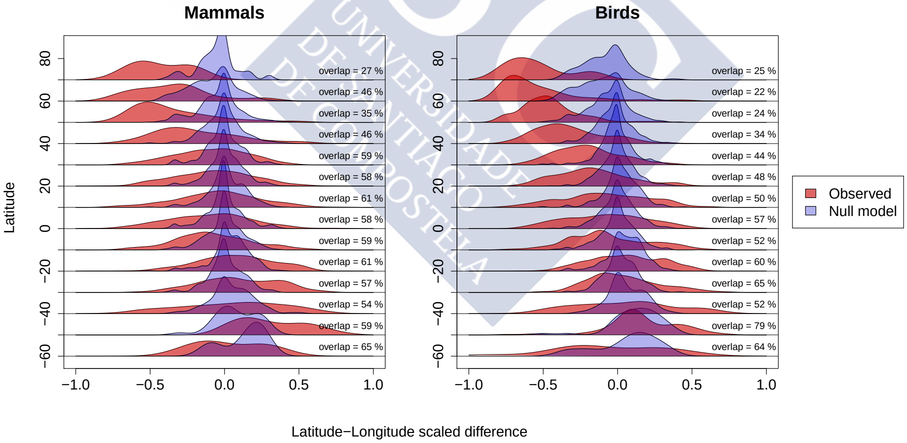

Figure 3.5: Comparison between the observed and null distributions of range shapes. For each 10° latitudinal band, we show the observed distribution of range shapes in red and the distribution in the null model in blue of all the species with their distribution centred in that particular latitudinal band. More similar distributions overlap more.

Table 3.1: Results of the paired one-sided t tests comparing the length of the equatorward and poleward semi-perimeters (standardised, see main text) of the ranges. A positive difference (significantly different from zero) means that the poleward semi-perimeters are shorter. We present the results for all species, for the species with larger geographic range extents (4th area quartile), and for the species with smaller geographic range extents (1st area quartile). The last two columns show the mean difference between the equatorward and the poleward semi-perimeter with a 95% confidence interval and a measure of the effect size (r^2) when the difference is statistically significant. Significant values of P (< 0.01) are marked in bold.

		Hemisphere	t	df	P	Mean of the differences	r^2
Mammals	All species	North	2.56	2904	0.010	0.008 ± 0.006	—
		South	9.48	2378	**< 0.001**	0.032 ± 0.007	0.036
	4th area quartile	North	2.76	725	**0.006**	0.021 ± 0.015	0.01
		South	15.31	594	**< 0.001**	0.108 ± 0.014	0.283
	1st area quartile	North	−0.54	725	0.59	−0.003 ± 0.011	—
		South	−0.16	594	0.87	−0.001 ± 0.012	—
Birds	All species	North	4.79	4716	**< 0.001**	0.014 ± 0.006	0.005
		South	24.54	5007	**< 0.001**	0.067 ± 0.005	0.107
	4th area quartile	North	6.24	1178	**< 0.001**	0.045 ± 0.014	0.032
		South	31.08	1251	**< 0.001**	0.182 ± 0.012	0.436
	1st area quartile	North	−0.02	1178	0.98	−0.000 ± 0.009	—
		South	1.15	1251	0.25	0.006 ± 0.010	—

the Northern Hemisphere and 0.032 ± 0.007 in the Southern Hemisphere for mammals; and 0.014 ± 0.006 in the Northern Hemisphere and 0.067 ± 0.005 in the Southern Hemisphere for birds, see Table 3.1). Results are again similar for mammals and birds. These differences are driven by large-ranged species, as they are not significant for species in the first geographic range size quartile and are greater for species in the fourth geographic range size quartile. However, after flipping the polygons on their horizontal axis we found that these differences only seem to be significant in the Southern Hemisphere (see Appendix S3.5), since only in this case poleward semi-perimeters become longer than equatorward semi-perimeters (see the negative mean of the differences).

Discussion

The assessment of how range shape elongation varies with latitude reveals a novel macroecological pattern: distribution ranges of widespread and high-latitude species in the Northern Hemisphere are systematically elongated in an east–west direction. The deviation of observed patterns from null expectations systematically increases to the north. In turn, low-latitude and small-range species do not show any consistent bias towards east–west or north–south elongated ranges. These low-latitude species (below 30 degrees) constitute the vast majority of mammal (83.4%) and bird species (88.7%) and, remarkably, most of them have ranges with similar latitudinal and longitudinal extents (see Fig. 3.2A–B). This is consistent with range expansion of most species at low latitudes being largely driven by isotropic processes not expected under niche control of species distributions (however, note that isotropic ranges could appear under niche constraints if environmental gradients along longitudinal and latitudinal directions were similar). Isotropy would be a macroscopic property of systems under neutral dynamics (i.e., stochastic dispersal equal in latitudinal and longitudinal directions, speciation and extinction). In contrast, niche constraints seem to dominate at higher latitudes, as inferred from the systematic elongation in east–west direction in the small proportion of species centred above 30 degrees in the Northern Hemisphere. The deviation from what is expected from null models simulating isotropic distributions increases towards the North (see Fig. 3.5), suggesting an increasing relevance of climatic forcing when the climatic conditions differ more from the ancestral tropical conditions in which most clades have originated (Wiens & Donoghue 2004). Thus, although climate is structured in latitudinal belts all across the globe, these belts only force species ranges to be elongated in east–west direction when they occur at high latitudes. In other words, only species in colder regions would reach their climatic niche limits, and thus their range limits would be mostly niche-driven. In turn, the low-latitude species would not reach their upper thermal limits, because these are a hard boundary (Araújo et al. 2013). As a consequence, differences across species in upper thermal limits are less likely to be responsible for differences in species distributions. Thus, the ranges of low-latitude species are probably less constrained by thermal niches, but are likely subject to other processes; probably stochastic or biotic processes (Normand et al. 2009), given the lack of any systematic deviation from isotropic ranges. These results are also consistent with the findings of previous studies that show that the thermal tolerance limits of species predict their latitudinal range limits well in many cases (particularly in ectotherms, e.g. Sunday et al. 2012).

Another important result is that range shape patterns are markedly different in the Northern and Southern hemispheres, as the distribution ranges in the Southern Hemisphere tend to be elongated in a north–south direction, particularly at higher latitudes. The most probable explanation for this is that the shape of the continents constrains ranges to be elongated in this direction, as the null models do predict north–south elongation. In turn, in marine species, which mostly have ranges elongated in an east–west direction, we find the same tendencies in elongation in both hemispheres, with ranges being more elongated in an east–west direction at higher latitudes, also in the Southern Hemisphere (see Appendix S3.6). This is what would be expected when continent shape does not influence range shape elongation, further supporting the idea that the gradient in range shapes reflects the increasing relevance of climatic niches towards the poles in constraining species ranges. The general result we found does not preclude that climate might be one of the main factors determining local range limits in some small range, low-latitude species (Morueta-Holme et al. 2010), while historical range constraints might be more important for the broad-scale distribution (e.g., Araújo et al. 2008). Likewise, specific lineages of organisms might show patterns that differ from the general one (Pfrender et al. 1998).

A tendency for species with larger range sizes having east–west elongated ranges was also observed (Fig. 3.3C–D). This could be consistent with the proposition that the variation of climate at larger scales (continental or regional) is a more important determinant of range limits in those species that are more widely distributed (Pearson & Dawson 2003). The patterns of variation of range shape with latitude and with range size might be related, since species of birds and mammals at high latitudes tend to have larger range sizes and latitudinal ranges (Orme et al. 2006; Davies et al. 2009; Tomašových et al. 2016). However, the variance partitioning analysis we performed shows that most of the variance in latitude–longitude scaled difference (proxy for shape directionality and relative elongation) explained by the GAM is not jointly explained by latitude and range size, and that the unique contribution of latitude to the explained variance is slightly larger.

The differences between equatorward and poleward semi-perimeters were generally not large, with small effect sizes in most cases (see Table 3.1). After flipping the polygons on their horizontal axis, we would expect that poleward semi-perimeters become longer, but this is not the case. The only exception are the species with the largest range sizes (4th quartile) in the Southern Hemisphere (in this case, the mean of the differences becomes negative, see Table S3.5.1). This suggests that, in most cases, the reason why we find that equatorward semi-perimeters are longer is that, because the Earth is a sphere, latitudinal bands near the equator are larger, and thus we find that equatorward semi-perimeters are longer. However, in the species with large range sizes in the Southern Hemisphere, the shorter poleward semi-perimeters cannot be solely explained by the shape of the Earth. Here, the shape of the continents is the most plausible explanation, given that in the Southern Hemisphere they taper toward the poles, enforcing smaller poleward range limits. In any case, with this approach our results do not support previous suggestions that biotic interactions are more important at lower latitudes, where abiotic conditions are less stressful (Brown et al. 1996; Loehle 1998; Pellissier et al. 2013).

Unavoidably, our results are subject to several limitations. First, estimating longitudinal extents of species ranges is not straightforward. The method that we used (measuring the longitudinal range at lowest latitude of the distribution) may overestimate longitudinal span consistently, particularly at higher latitudes, but when we used a more conservative estimate (calculating the longitudinal span at the mean latitude of the distribution) we found the same patterns (see Appendix S3.2). Second, we used simple measures of range shape based on the difference between latitudinal and longitudinal range extents instead of more complex measures (see, for example, Pigot et al. 2010). However, we did this because fixed longitudinal and latitudinal axes allow direct comparison of the direction of elongation of the ranges between species and, since climatic variation is generally more marked across latitudes, the patterns of elongation can be interpreted in relation to unique predictions (Baselga et al. 2012c). Third, we are aware that the high variation in range shape at low latitudes might be caused by many different processes, and our analyses do not rule out that, in some cases, small-scale variation in climate or high spatial heterogeneity of abiotic factors at low latitudes could be among the main determinants of range shape in these regions. For instance, lower climatic variability and narrower physiological tolerances would make topographical barriers more effective at low latitudes (Janzen 1967; Ghalambor et al. 2006). This being true, the variation in the orientation of mountain ranges would cause more irregular deviations from isotropy in low latitudes compared to high latitudes. This is difficult to assess because disentangling the effects of climatic variation and topography is problematic, but future studies should try to address this question. In any case, we are assessing macroscopic patterns arising from variation across a high number of species and regions, so these particular cases are expected to have little weight in the results.

To conclude, a novel macroecological pattern was unveiled by assessing the latitudinal variation in the shape of species ranges: isotropic ranges are more frequent at the tropics, while anisotropic ranges are the rule at high latitudes. This pattern is consistent with stochastic processes being more important in driving species ranges at low latitudes, and deterministic processes (related to latitudinal climatic variation) being stronger at higher latitudes. One plausible explanation for this is that the majority of species living at high latitudes must unavoidably have high dispersal ability (because they have re-colonised those regions in a short period of time, i.e., since Last Glacial Maximum), allowing them to reach their physiological limits. At lower latitudes, most distributions have similar latitudinal and longitudinal ranges, an isotropic pattern expected if species distributions are predominantly controlled by intrinsic dispersal limitation, which probably does not allow most of these species to reach their physiological limits.


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Niche divergence and diversification in mammal families

Introduction

A fundamental goal of evolutionary biology and related disciplines is to understand why some clades have more species than others (Futuyma 2013). In general, differences in current species richness between clades will be explained by either their age (e.g., older clades with more species) or by differences in how quickly they have accumulated species (i.e., net diversification rate). The net diversification rate of a clade is the outcome of speciation and extinction over time (e.g., Nee et al. 1992; Ricklefs 2007; Wiens 2011). Differences in species richness among clades of the same rank (e.g., families, phyla) seem to be explained largely by differences in these net diversification rates (Scholl & Wiens 2016). Therefore, to understand richness patterns among clades, it is essential to uncover the ecological and evolutionary processes that determine differences in diversification rates among clades.

Climatic niches may be one of the key factors that drive variation in diversification rates and species richness among clades. Every terrestrial species has a realized climatic niche, which is the set of large-scale temperature and precipitation conditions where it occurs (Hutchinson 1957; Soberón 2007; Holt 2009). The climatic niche of a species may strongly influence where it can occur over space and time (e.g., Soberón 2007), and thus may be critically important for both speciation (e.g., ecological speciation through climatic niche divergence; Moritz et al.

2000; Hua & Wiens 2013), and extinction (e.g., due to climate change). We can thus expect a relationship between patterns of variation in climatic niches across clades and their net diversification rates. In support of this idea, some studies have shown that the climatic regime where a clade occurs can influence its diversification rate (e.g., faster diversification in tropical clades; Rolland et al. 2014). Similarly, other studies have shown that the rate of change in climatic niches among species within a clade can be positively related to species diversification (e.g., Kozak & Wiens 2010; Schnitzler et al. 2012; Title & Burns 2015; Cooney et al. 2016; Moen & Wiens 2017).

Differences in climatic niche width among species and clades may also influence diversification rates. Climatic niche width is the range of climatic conditions where a species or clade occurs (e.g., maximum yearly temperature – minimum yearly temperature across localities), for one or more climatic niche variables, instead of the values of the variables themselves. Gómez-Rodríguez et al. (2015) developed a framework to understand how climatic niche widths of species and clades might be related to diversification (and why). They outlined five competing hypotheses. First, the null hypothesis (H0) is that faster diversification rates lead to higher richness and higher richness leads to wider clade niches, but only because a clade with more species should span more divergent climatic conditions due to sampling alone, all else being equal. This hypothesis predicts a relationship between diversification rates and family-level niche width, but also predicts that the levels of climatic niche divergence can be explained by greater species sampling alone. Second, if speciation occurs mostly due to climatic niche conservatism, a negative correlation between clade-level diversification rates and niche width is expected (H1). In this scenario, a narrower species niche would lead to more fragmentation of species ranges when barriers of climatically unsuitable habitats appear, and thus more opportunities for allopatric speciation (Wiens & Donoghue 2004). Alternatively, if speciation is predominantly linked to climatic niche divergence (e.g., Moritz et al. 2000; Hua & Wiens 2013), a positive relationship between diversification rate and clade-level niche width is expected (H2). Another hypothesis (H3) suggests that a positive relationship between diversification rate and clade-level niche width could arise from reduced extinction rates in clades with wider species-level niches that buffer them from the negative impacts of climatic fluctuations. This hypothesis minimally predicts a relationship between diversification rates and species-level niche widths. Alternatively (H4), wider family-level niche width could be indirectly related to diversification rate via a positive relationship between family-level niche width and the geographic extent of clades. Under this hypothesis, a larger geographic range area for a clade could lead to a larger range of climatic conditions experienced by its species, and the larger range area could more directly increase diversification rate by increasing the chances of allopatric speciation, or diminishing the probability of extinction (e.g., Rosenzweig 1995; Losos & Schluter 2000; Cardillo et al. 2003; Mittelbach et al. 2007). This hypothesis predicts a relationship between diversification and family-level niche widths, but also predicts that there will be little unique effect of niche width when the area of each clade is accounted for statistically. Finally (H5), a relationship between diversification rate and niche width could also be the result of coincident geographic patterns of clade niche width and diversification rate. For example, tropical clades could be characterized both by narrower species-level niches for temperature-related variables (e.g., Ghalambor et al. 2006; Quintero & Wiens 2013) and faster diversification rates than temperate clades, but with no causal relationship between niche widths and diversification rates.

Gómez-Rodríguez et al. (2015) tested these hypotheses using climatic data from amphibian species and families. They found that diversification rates of families were strongly and positively related to family-level niche widths, but weakly related to mean species niche widths of families. Additionally, the variable that explained the most variance in diversification rates of amphibian families (53%) was an indirect measure of niche divergence (i.e. families with narrow species-level niche widths but wide family-level niche widths). Taken together, the results were consistent with the hypothesis that diversification rates were strongly influenced by speciation linked to climatic niche divergence (H2).

In that study, niche divergence was quantified in absolute terms (i.e. present day differences in climatic niches between species in clades), ignoring the evolutionary rate of change. However, if niche divergence is linked to speciation and hence to diversification rate, then the rate of niche divergence over time should be associated with diversification rate even more strongly than with absolute niche divergence. Previous studies have tested the relationship between rates of climatic-niche evolution and diversification in several groups, including the Cape flora (Schnitzler et al. 2012), plethodontid salamanders (Kozak & Wiens 2010), frogs (Moen & Wiens 2017), all amphibians (Pyron & Wiens 2013), and birds (Lawson & Weir 2014; Title & Burns 2015; Cooney et al. 2016). A positive relationship was generally supported (but not across amphibians; Pyron & Wiens 2013). Likewise, absolute niche divergence was the strongest correlate of variation in diversification rate among amphibian families (Gómez-Rodríguez et al. 2015). However, to our knowledge, no study has assessed the relative importance of absolute niche divergence and rates of niche evolution in explaining variation in diversification rates among clades.

Here we perform such an analysis across mammals. Our results shed light on the ecological factors linked to patterns of macroevolution and species richness in a major clade of vertebrates. They also address whether clade diversification is more strongly related to the absolute range of environmental conditions a clade occupies or to the velocity with which they occupy different environmental conditions, and how these latter two variables are related.

We analyze diversification rates in mammal families (dependent variable), and their relationship to climatic niche width, niche divergence, and rate of niche evolution (independent variables). Previous studies have addressed some related issues in mammals, but not the specific questions we address here. For example, Cooper et al. (2011) examined patterns of climatic-niche evolution in mammals, and found that tropical, small-ranged, and specialized mammals tended to have slower rates of thermal-niche evolution than temperate, large-ranged, and generalist mammals (see also Cadena et al. 2012). However, they did not relate climatic-niche evolution to patterns of diversification. Past studies showed that diversification rates in mammals are related to geographic or life-history factors (e.g., Cardillo et al. 2003 in Australian mammals), trophic strategy (Price et al. 2012), and climatic niche width (Rolland & Salamin 2016), but did not address how much variation in diversification rates across mammals is explained by these variables. Latitudinal patterns in diversification rates among mammalian species and clades were also assessed in previous analyses, with the goal of explaining higher tropical species richness. These studies found higher diversification rates in tropical lineages at broad phylogenetic scales (Rolland et al. 2014), but not among genera (Soria-Carrasco & Castresana 2012) or species (Weir & Schluter 2007). However, they did not test if tropical distribution helps explain patterns of diversification and richness among mammalian families. Other studies have addressed patterns of diversification over time across all mammals (e.g., Bininda-Emonds et al. 2007; Meredith et al. 2011; Stadler 2011) or at lower taxonomic levels (e.g., Fabre et al. 2012; Schenk et al. 2013; Jansa et al. 2014; Shi & Rabosky 2015), but did not focus on the correlates of diversification rates or richness among clades.

Here we test the relationships between niche evolution and diversification using climatic, distributional, and phylogenetic data for 3335 terrestrial mammal species in 92 families. We explore the relationships between diversification rates and: (i) average species niche widths within clades (families), (ii) clade-level niche widths (range of climatic conditions across all species within a family), (iii) absolute niche divergence among species within clades, (iv) rates of niche evolution within clades, (v) the mean position of the clade's niche (e.g., tropical vs. temperate), and (vi) the geographic range area of the clade. Note that we treat diversification rate as the dependent variable, and therefore describe how much variation in diversification rate is explained by other variables (following standard statistical terminology). Nevertheless, we are initially neutral about the direction of causality underlying the relationship between niche divergence and diversification. However, by testing these alternate hypotheses we can gain insights on the causality and mechanisms involved (see Discussion in this chapter).

Materials and Methods

Climatic niche width

All range maps for terrestrial mammal species available from the IUCN (2013) database were downloaded ($n = 5285$). This GIS database basically covers all described mammal species (5488 known species, including marine species). By "terrestrial" we mean non-marine, and thus marine species and families were excluded (given that we lack climatic data for these species). Species climatic niches were estimated from their distributions, as the climatic conditions in which each species live (a Grinnellian niche operationally estimated following Peterson et al. 2011). Specifically, climatic data at 2.5 arc-minutes (or approximately 4.5 km) resolution were downloaded from the WorldClim database (Hijmans et al. 2005), by extracting the climatic values in the geographic range of a species or clade using the package `raster` (Hijmans 2014) in R (R Core Team 2016). Details on the functions used are given in Appendix S4.1 in the Supplementary Material. Six variables were selected to represent the climatic niche of mammal species, following standard practice in similar studies (e.g., Quintero & Wiens 2013; Gómez-Rodríguez et al. 2015): annual mean temperature (BIO1), maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), annual precipitation (BIO12), precipitation of the wettest quarter (BIO16), and precipitation of the driest quarter (BIO17). These variables represent annual means and extreme values of temperature and precipitation, so it is assumed that they can give a robust description of species' climatic niches. Other climatic variables in the WorldClim dataset generally represent minor variations on these six.

For each species, the climatic niche width was calculated following Gómez-Rodríguez et al. (2015). The niche width for each variable and species was defined as the difference between the minimum and maximum values across the species' geographic range (extracted for each grid cell). The overall climatic-niche width for each species was then the product of the species' climatic ranges (niche widths) multiplied across the six variables. The climatic niche could not be estimated for three species having very small geographic ranges in areas with no climatic data available. To allow the inclusion of variables in different units (temperature and precipitation) in niche-width estimation, niche widths for each species for each climatic niche variable were standardized considering the maximum and minimum values for that variable across all species. Thus, for each species i in a set of j species, the standardized climatic range (niche width) is:

$$\mathrm{StRg}_i = [\mathrm{Rg}_i - \min(\mathrm{Rg}_1 : \mathrm{Rg}_j)]/[\max(\mathrm{Rg}_1 : \mathrm{Rg}_j) - \min(\mathrm{Rg}_1 : \mathrm{Rg}_j)],$$

with Rg_i being the range of species i and $\max(\mathrm{Rg}_1 : \mathrm{Rg}_j)$ and $\min(\mathrm{Rg}_1 : \mathrm{Rg}_j)$ being the maximum and minimum values of the ranges in the set of j species, respectively. Additionally, for each species and each climatic variable, the average of all observed values across all the grid cells of the species geographic range was calculated. These mean values were used to define the species' niche position. The niche width and niche position of each family were computed following the same protocol as above, considering the distribution area occupied by all the species in the family as the family's distribution range.

We also explored an alternative approach, computing family niche width after summarizing the six climatic variables through a principal components analysis (PCA). This yielded equivalent results. Specifically, the first two PCA axes accounted for 97% of the variance among the climatic variables, and family niche widths based on these two PCA axes were highly correlated (Pearson's $r = 0.937$) with niche widths computed as described above (Appendix S4.12).

The mean species niche width for a family was computed as the average value of all the species' climatic niche widths in that family. Finally, the geographic extent (in km^2) of each family was also computed, again considering the union of the ranges of all the species in the family as the range. All GIS analyses were conducted in R using the packages `rgdal` (Bivand et al. 2014), `geosphere` (Hijmans 2016), `maptools` (Bivand & Lewin-Koh 2016), and `raster` (Hijmans 2014). Details on R functions are provided in the Supplementary Material (Appendix S4.1).

We acknowledge that outliers or erroneous localities could cause errors in our estimates of climatic niche width. However, this should be a source of random error, and not bias. Further, our use of range maps (rather than point localities) to estimate climate niche values should tend to ameliorate rather than exacerbate such effects.

Diversification rates

The net diversification rate for each family was estimated given the species richness and age of each family. The species richness of each family was based on the number of species in each family for which climatic niche data were obtained. These data include all species included in the IUCN (2013) database (with exception of three species for which the niche could not be computed) and guarantees that both family species richness and niche width are computed for exactly the same set of species. Ages of families were estimated from a time-calibrated phylogeny of mammals (Meredith et al. 2011). The phylogeny is based on a concatenated analysis of 26 genes, and the divergence dates were estimated incorporating autocorrelated evolutionary rates and hard-bounded age constraints. Although other mammal phylogenies are available, this phylogeny is based on extensive molecular data and is well-resolved at the family level. This phylogeny includes 164 mammal species, representing 147 terrestrial and marine families. Four terrestrial families (i.e. Aotidae, Lepilemuridae, Pitheciidae, and Platacanthomyidae) were not included in this phylogeny and were therefore excluded here. However, these four families collectively include only 80 species, and so their exclusion should have limited impact on the results. Diversification rates could be computed for all the terrestrial families included in the tree.

Family diversification rates were estimated following the method-of-moments estimator for stem groups described in Magallón & Sanderson (2001, their equation 6). This method typically incorporates an assumed value of the relative extinction rate (ε = extinction rate / speciation rate) for calculating diversification rates:

$$\hat{r}_\varepsilon = \frac{1}{t} \ln[n(1-\varepsilon)+\varepsilon].$$

$\hat{r}_\varepsilon$ represents diversification rate under a certain relative extinction fraction (ε), which accounts for the fact that only clades that survive to the present day are included (and thus might lead to bias in estimating rates). t is the family stem group age (i.e. the time of divergence between a family and its sister clade, so that the stem group age of two sister families is the same). n is the number of extant species in the family. Following standard practice, three different values for the relative extinction fraction were assumed ($\varepsilon = 0$, no extinction; $\varepsilon = 0.45$, intermediate rate; and $\varepsilon = 0.9$, high rate). Results were similar using all three values. Therefore, for brevity, only the results for $\varepsilon = 0.45$ are presented in the main text (see Appendix S4.3 for analyses using $\varepsilon = 0$ and $\varepsilon = 0.9$). We used the stem-group estimator because it is more accurate in simulations than the crown-group estimator and (unlike the crown-group estimator) is not affected by incomplete taxon sampling within clades (Meyer & Wiens 2017).

Some authors have claimed that the net diversification rate estimator requires that diversification rates must be constant within clades (Rabosky 2009; Rabosky & Adams 2012), and that they should therefore only be used if there is a positive relationship between clade age and richness among clades. However, these authors did not actually address the accuracy of this estimator. Simulations that did address its accuracy show that it yields strong relationships between true and estimated diversification rates, regardless of the relationship between clade ages and richness (Kozak & Wiens 2016) and regardless of whether rates are homogeneous or heterogeneous within clades (Meyer & Wiens 2017). Furthermore, this estimator will correctly reflect that young clades with many species have high net diversification rates (and older clades with fewer species have lower rates), regardless of variation in instantaneous diversification rates within clades over time. Simulations also show that diversification rates (speciation – extinction) can be informative for predicting richness patterns even when there are strong ecological limits on richness (Pontarp & Wiens 2017). However, variation in diversification rates over time could potentially uncouple net diversification rates from clade richness (Wiens 2011; Kozak & Wiens 2016), for example, if fast rates in young clades fail to generate high richness due to declining diversification rates over time. Therefore, the relationship between diversification rate and species richness was assessed (see Appendix S4.5) in order to test if the differences in diversification rates between families are relevant to explaining richness patterns (Wiens 2011). We also conducted analyses using ln-richness instead of diversification rates as the dependent variable, as recommended by authors who argue that net diversification rates require constant rates within clades (e.g., Rabosky 2009; Rabosky & Adams 2012; Title & Burns 2015).

We note that many possible approaches are available to analyzing diversification. The approach that we use here focuses on estimating net rates for individual clades, which is our main focus. Therefore, the estimator that we used here should be the most appropriate for our research question. This is also the same estimator used in previous studies on this topic (e.g., Kozak & Wiens 2010; Gómez-Rodríguez et al.

2015; Cooney et al. 2016; Moen & Wiens 2017), which allows our results to be directly compared to earlier studies.

Rates of niche evolution

Rates of niche evolution were calculated separately for each family and for both temperature and precipitation. Rates were calculated based on the phylogeny of species within each family, using species values for annual mean temperature (BIO1) and annual mean precipitation (BIO12), using average values across the range of each species. We focused on these two variables because they should reflect the most important aspects of the species climatic distribution (e.g., BIO1: tropical vs. temperate; BIO12: arid vs. mesic), and more so than short-term, extreme values (BIO5, BIO6, BIO16, BIO17). For the phylogeny within each family, we used the species-level tree of mammals from Rolland et al. (2014, their maximum clade credibility consensus tree). These authors generated this tree by redating the species-level tree of Bininda-Emonds et al. (2007, as modified by Fritz et al. 2009) using dates from Meredith et al. (2011). They also randomly resolved polytomies in this tree using the method of Kuhn et al. (2011) to generate 100 trees, and then obtained a consensus tree from those 100 trees. We conducted analyses on this consensus tree. Only one terrestrial family (Diatomyidae) was not represented in this phylogeny. This tree includes 5020 terrestrial and marine mammal species.

The rate of niche evolution was estimated as the sigma parameter of a Brownian-motion model of evolution (for details see O'Meara et al. 2006). The lambda model of evolution (Pagel 1999) actually showed a better fit both for BIO1 and BIO12 than the Brownian-motion model (or than the Ornstein-Uhlenbeck [OU] model, see Table S4.6.1 in Supplementary Material), but the sigma parameter of a lambda or a OU model could only be computed for families with three or more species in the tree (76 families), which would further reduce the dataset. However, sigma values calculated using the lambda and Brownian-motion models have a strong, positive correlation (Pearson's $r = 0.90$ for BIO1 and $r = 0.80$ for BIO12, see Fig. S4.6.1 in Supplementary Material), as expected given the close relationship between these models when lambda is high (i.e. fitted lambda = 0.89 for both BIO1 and BIO12, and lambda = 1 is the Brownian-motion model). Therefore, the sigma values for the Brownian-motion model were used, as they could be computed for more families. Furthermore, using the same set of families in all phylogenetic regressions is necessary in order to partition the variance among competing models. The sigma parameter was computed for all monophyletic families with two or more species in the tree with the command `fitContinuous` in the R package `geiger` (Harmon et al. 2008). All families that were monospecific ($n = 20$) or paraphyletic ($n = 17$) in the tree of Rolland et al. (2014) were excluded, since estimation of ages, richness, and rates of niche evolution and diversification would be problematic for these families. We also excluded two families that each had two species in the IUCN database but with only one of those species in the tree (Mystacinidae and Myzopodidae). Therefore, in all subsequent analyses, the dataset was composed of 92 families (spanning 3335 species).

We also performed alternative analyses to address whether our estimates of rates of niche evolution, were affected by the algorithms used to resolve polytomies (Rabosky 2015). We tested the correlation between our niche evolution rates (from the tree of Rolland et al. 2014) and an alternative set of rates for 18 mammal families computed from alternative trees. These trees were from Arnold et al. (2010), and included version 3 of the primates dataset (based on sequences from 17 genes) and version 1 of the Perissodactyla (15 genes), Cetartiodactyla (20 genes), and Carnivora (29 genes) datasets (see Appendix S4.7). The niche evolution rates computed for these families from these two sources were strongly correlated (Pearson's $r = 0.91$, $P < 0.001$ for temperature niche rate, and $r = 0.70$, $P = 0.001$ for precipitation niche rate). Therefore, we considered the estimates of niche evolution rate derived from the tree of Rolland et al. (2014) to be robust and used them in subsequent analyses. We also note that the strong phylogenetic signal in the temperature and precipitation variables (see above) suggests that random resolution of polytomies within families has not strongly influenced our inferences of evolutionary patterns in these variables (i.e. if random resolutions had a strong effect, there should be limited phylogenetic signal instead of lambda values close to 1). Furthermore, random resolution of polytomies should have no impact on our estimates of diversification rates.

Phylogenetic regression

Regression analyses were conducted using phylogenetic methods to control for the effect of shared phylogenetic history on diversification rates and niche attributes among families (Grafen 1989). We conducted phylogenetic generalized least-squares regressions (PGLS, Freckleton et al. 2002) using the R package `caper` (Orme et al. 2013). We used lambda values estimated by maximum likelihood to transform branch lengths and with kappa and delta values both set to 1.

The relationship between family niche width and mean species niche width can indicate levels of niche divergence among species within a family (Gómez-Rodríguez et al. 2015). A PGLS between family niche width and mean species niche width was fitted and the residuals of this relationship were used as a proxy for niche divergence. With perfect niche conservatism among the species in a family, mean species niche width and family niche width would be the same, with the residuals of the relationship close to zero. Therefore, residuals reflect non-overlap of species niches within families (i.e. niche divergence; Gómez-Rodríguez et al. 2015). However, we acknowledge that this index may not be as informative as using direct estimates of rates of niche evolution, and comparing these indices is one of our goals here. For example, niche divergence ignores the phylogeny within clades, whereas rates of niche change incorporate this information.

Five linear regression analyses were conducted to evaluate the hypotheses presented in Gómez-Rodríguez et al. (2015). Specifically, we assessed the relationships between diversification rate and (i) family niche width, (ii) mean species niche width, (iii) family niche divergence, (iv) family niche position for each individual climatic variable (i.e. defined as the mean climatic conditions across the geographic range of the family), and (v) family geographic extent. Given that niche position was defined by six variables, a forward stepwise procedure was used to select the most parsimonious model (based on F-statistic) explaining diversification rate.

We also compared the explanatory power of niche divergence (the aforementioned residuals of family vs. mean species niche width) relative to the rate of niche evolution. First, a bivariate linear regression was conducted to assess the relationships between niche divergence and niche evolution rate for BIO1 (hereafter "temperature niche evolution rate") and niche evolution rate for BIO12 (hereafter "precipitation niche evolution rate"). Second, two linear regressions were conducted to test the relationships between diversification rate and temperature niche evolution rate and precipitation niche evolution rate. Third, we performed a multiple regression analysis including both temperate and precipitation niche rates as independent variables (this should be more comparable to niche divergence, which combines both temperature and precipitation). Finally, to partition the unique contribution of those models explaining an important portion of the variance in diversification rate (i.e. ~20% or more), four models (i.e. family niche width, geographic extent, niche divergence, and niche evolution rate) were combined in a full model and variance partitioning was used to compute their unique and shared contributions to the explained variance.

We performed null models in order to assess if the observed relationships between niche width and diversification rate appear because families with more species span more divergent climatic conditions due to sampling alone (H0). We tested the relationship between (a) family niche width vs. mean species niche width, (b) diversification rate vs. family niche width, (c) diversification rate vs. mean species niche width, and (d) diversification rate vs. niche divergence (residuals of regression "a") using PGLS in the null families. We sampled with replacement 92 null families with the same species richness as the original ones. Three different null models were considered: (1) species sampled from the pool of all mammal species (unconstrained model), (2) species sampled from the pool of species within the latitudinal and longitudinal range of the original family (spatially constrained model), and (3) species sampled from the pool of species within the original family climatic niche (climatically constrained model). We took 1000 samples of 92 null families and compared the distribution of the r^2 of the aforementioned PGLS among these 1000 replicates with the observed r^2 in the original families.

An additional robustness test was performed to ensure that results were not influenced by the different ages of clades. We defined major clades of similar age in the species-level tree of Bininda-Emonds et al. (2007) with dates from Meredith et al. (2011), regardless of whether they corresponded to a named higher taxon or not Specifically, we went through the tree and identified the clades with stem ages that were closest to the average stem age of all families (41.65 Mya), but with the restriction that the clades selected were older than that mean age. We then computed climatic niches and niche evolution rates for these clades, excluding those that were monospecific (86 clades were used in these analyses). We conducted the same regression analyses and variance partitioning described before, with the richness of these clades as the dependent variable.

All variables (unless otherwise noted in the Results) were logarithmically transformed (natural logarithm) to improve the normality of model residuals. All analyses were conducted in R. Raw data (e.g., diversification rates, niche widths, niche evolution rates) used for statistical analyses are provided in Appendix S4.2.

Results

A positive and strong relationship was observed between family niche width and mean species niche width ($r^2 = 0.73$, $F_{1,90} = 243.8$, $P < 0.001$, $n = 92$ families, Fig. 4.1A). The relationship between diversification rate and family niche width was positive and significant ($r^2 = 0.20$, $F_{1,90} = 22.92$, $P < 0.001$, Table 4.1, Fig. 4.2A). In contrast, there was not a significant relationship between diversification rate and mean species niche width ($r^2 < 0.001$, $F_{1,90} < 0.001$, $P = 0.99$; Table 4.1, Fig. 4.2B). A strong positive relationship ($r^2 = 0.59$, $F_{1,90} = 130$, $P < 0.001$; Table 4.1, Fig. 4.2C) was observed between diversification rate and absolute niche divergence (i.e. the residuals of the family niche width vs. mean species niche width relationship). A significant, positive relationship was also observed between diversification rate and geographic extent ($r^2 = 0.19$, $F_{1,90} = 21.65$, $P < 0.001$; Table 4.1, Fig. 4.2E) and a weak negative one with niche position ($r^2 = 0.07$, $F_{1,90} = 6.341$, $P = 0.014$; Table 4.1, Fig. 4.2D). Niche position was defined by the minimum temperature of the coldest month (BIO6) after a forward stepwise procedure to select the most parsimonious model (see Appendix S4.8). However, both geographic range area and niche position explained little variation in diversification

Table 4.1: Results from univariate phylogenetic generalized least-squares models testing the relationship between diversification rate ($\varepsilon = 0.45$) and different attributes of the family niche as well as with the geographic extent of the family. Significant P-values are marked in bold. F-values for 1 and 90 degrees of freedom, and the slopes of the relationships with a 95% confidence interval are also provided.

	r^2	F	P	Slope(95% CI)
Family niche width	0.2	22.92	< 0.001	0.129 (± 0.053)
Mean species niche width	< 0.001	< 0.001	0.99	−0.000 (± 0.075)
Niche divergence*	0.59	130	< 0.001	0.384 (± 0.066)
Niche position*	0.07	6.34	0.014	−0.002 (± 0.002)
Geographic extent	0.19	21.65	< 0.001	0.261 (± 0.110)
Temperature niche evolution rate	0.38	55.04	< 0.001	0.204 (± 0.054)
Precipitation niche evolution rate	0.44	69.31	< 0.001	0.253 (± 0.060)

* Variable not ln-transformed

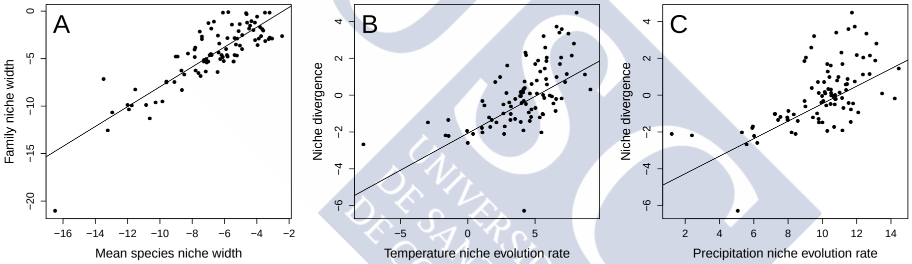

Figure 4.1: Scatterplots of the relationship between family niche width and mean species niche width (A) and between niche divergence and temperature niche evolution rate (B) and precipitation niche evolution rate (C). Note that the residuals of the model represented in Figure A correspond to the variable defined as "niche divergence". Phylogenetic generalized least-squares models are superimposed. All variables (except niche divergence) are ln-transformed.

rates relative to climatic niche divergence. There was a strong positive relationship between diversification rate and species richness of families ($r^2 = 0.79$; $F_{1,90} = 342.7$, $P < 0.001$).

Niche divergence showed a positive relationship with rates of temperature and precipitation niche evolution in a bivariate model ($r^2 = 0.50$,

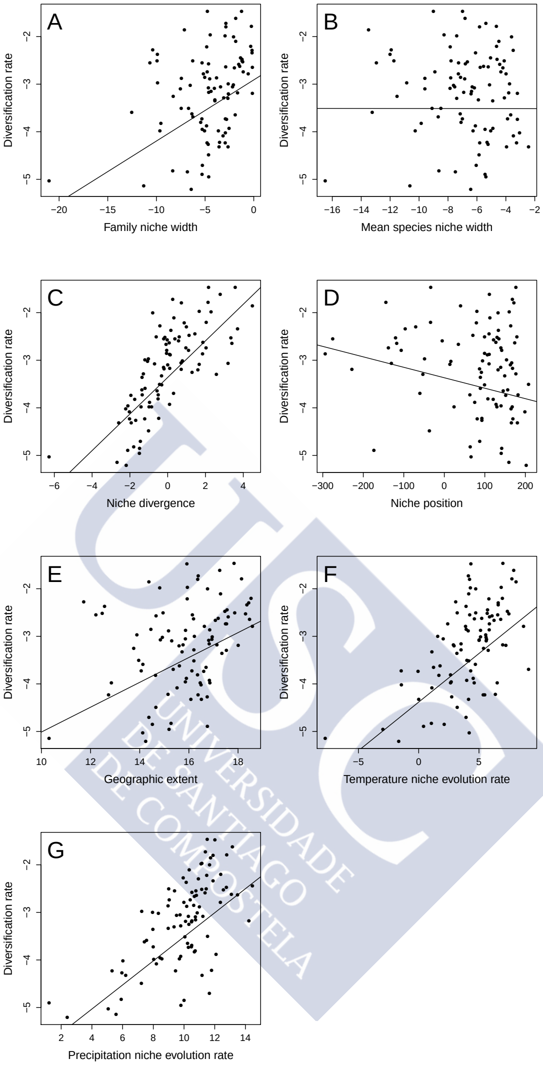

Figure 4.2: Scatterplots showing the relationships between diversification rate and family niche width (A), mean species niche width (B), niche divergence (C), niche position (D), geographic extent (E), temperature niche evolution rate (F) and precipitation niche evolution rate (G). Phylogenetic generalized least-squares regression lines are superimposed. All variables (except niche divergence and niche position) are ln-transformed.

$F_{2,89} = 44.87$, $P < 0.001$). This shows that greater niche divergence among species within a family is generally related to a higher rate of niche evolution in that family. A strong positive relationship was also found between diversification rate and rate of temperature niche evolution ($r^2 = 0.38$, $F_{1,90} = 55.04$, $P < 0.001$; Table 4.1, Fig. 4.2F) and rate of precipitation niche evolution ($r^2 = 0.44$, $F_{1,90} = 69.31$, $P < 0.001$; Table 4.1, Fig. 4.2G). A multiple regression model including rates of both temperature and precipitation niche evolution explained more than half of the variation in diversification rates ($r^2 = 0.51$, $F_{1,89} = 46.73$, $P < 0.001$), similar to the level explained by niche divergence.

A model assessing the relationship between diversification rate and all independent variables explaining an important portion of its variance was also tested. These independent variables included family niche width, geographic extent, rate of niche evolution (with temperature and precipitation rates as independent variables), and niche divergence from the residuals of the regression of family niche width vs. mean species niche width. This model explained a large proportion of the variation in diversification rates ($r^2 = 0.65$, $F_{5,86} = 31.55$, $P < 0.001$). Variance partitioning (Fig. 4.3) showed that most of the variance explained by this model (64.7% explained variance) was shared among the variables (46.3%). The variance explained exclusively by family niche width (0.5%) and geographic extent (0.5%) was negligible, and relatively low for rates of niche evolution (5.1%). Niche divergence was the variable with the largest unique contribution (12.4%). Most of the variance was shared between niche divergence and niche evolution rate (26.4%) and between all variables (14.5%).

To assess the robustness of our results regarding the estimates of diversification rates, the full model was conducted with species richness instead of diversification rate as the dependent variable, and results were similar. Family richness was strongly and positively related to niche divergence ($r^2 = 0.70$, $F_{1,90} = 207.9$, $P < 0.001$), temperature niche evolution rate ($r^2 = 0.34$, $F_{1,90} = 45.47$, $P < 0.001$) and precipitation niche evolution rate ($r^2 = 0.38$, $F_{1,90} = 55.43$, $P < 0.001$). In a variance partitioning of a full model, niche divergence was again the variable with the largest unique contribution (21.9%). Most of the variance was shared between niche divergence and rates of niche evolution (25.4%;

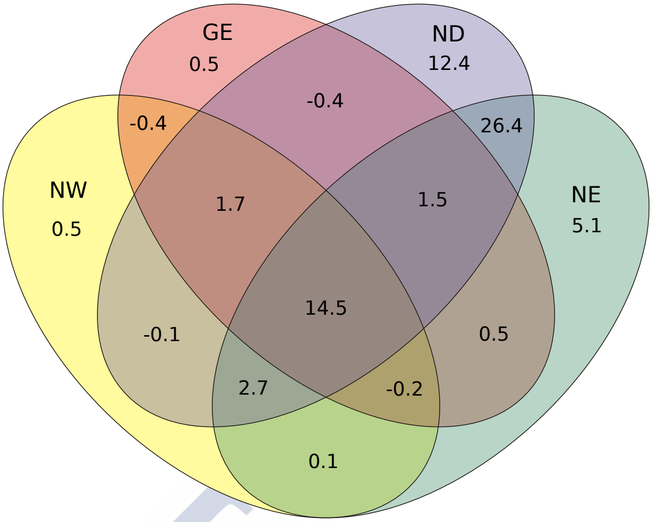

Figure 4.3: Venn diagram showing the results of variance partitioning on a full model of diversification rate with family niche width (NW), geographic extent (GE), niche divergence (ND), and niche evolution rate (NE) as explanatory variables. Results are shown as percentage of explained variance.

see Appendix S4.4).

In the null models (unconstrained, geographically constrained, and climatically constrained) in which we sampled 1000 replicates of 92 null families, the relationship between diversification rate and mean species niche width and between diversification rate and family niche width was generally stronger than the observed relationship (see Appendix S4.11). However, the relationship between diversification rate and niche divergence was comparable to the observed relationship only in the case of the unconstrained model ($P = 0.056$), and was weaker in the spatially and climatically constrained models ($P \leq 0.002$ in both cases). The r^2 in the relationship between family niche width and mean species niche width was higher in the null models ($P \leq 0.011$ in the spatially and climatically constrained models), except in the unconstrained null model ($P = 0.428$). This results suggest that the observed relationship between diversification rate and niche divergence between species within families is comparable to sampling these species from the pool of all mammals, from any biome or world region.

We then used major clades stemming from the nodes closest to (but older than) the average family age (41.65 Mya) instead of families as units of analysis. Using these clades (mean stem age = 54.7 Ma, standard deviation = 20.2, $n = 86$), strong positive relationships were again found between clade richness and niche divergence ($r^2 = 0.58$, $F_{1,84} = 114.9$, $P < 0.001$), rate of temperature niche evolution ($r^2 = 0.46$, $F_{1,84} = 70.47$, $P < 0.001$) and rate of precipitation niche evolution ($r^2 = 0.46$, $F_{1,84} = 72.79$, $P < 0.001$). Partitioning of variance in species richness among all predictors also yielded results similar to those reported above (Appendix S4.9).

Discussion

Overall, our results show that two measures of niche change among species within clades (climatic niche divergence and rates of climatic niche evolution) are each strongly related to diversification rates among mammal clades. In regression models, absolute climatic niche divergence and rates of climatic niche evolution each explain over half of the variation in diversification rates among mammal families. Diversification rates in turn explain most (79%) of the variation in species richness. These results parallel those for amphibians (Gómez-Rodríguez et al. 2015; Moen & Wiens 2017) and birds (Cooney et al. 2016), and together they suggest that changes in climatic niches are broadly important in understanding large-scale patterns of diversification and richness. We also show here that our measures of absolute niche divergence and climatic niche rates are strongly related, and explain similar amounts of variation in diversification rates.

These results are consistent with the hypothesis that speciation by climatic niche divergence is common and important (H2, e.g., Kozak & Wiens 2007; Hua & Wiens 2010). Support was not found for the hypothesis that most speciation is linked to climatic niche conservatism (H1), since that hypothesis predicts a negative relationship between diversification rate and family-level niche width. The hypothesis that families with broader species-level niche widths have lower extinction rates (leading to higher diversification rates, H3) was also not supported, as this hypothesis predicts a strong relationship between diversification rate and mean species niche width (see Gómez-Rodríguez et al. 2015). We found that families containing species with wider niches do not tend to have higher diversification rates (and diversification rates reflect both speciation and extinction). Likewise, the unique contribution of geographic extent was negligible. Thus, even though the variation in diversification rate explained by family niche width and geographic extent was very similar, there was no strong support for geographic extent influencing diversification rates (H4). Surprisingly, only weak support was found for the hypothesis linking diversification rate and climatic regime (e.g., tropical vs. temperate; H5). This lack of a clear relationship is consistent with some previous studies in mammals (e.g., Weir & Schluter 2007; Soria-Carrasco & Castresana 2012), but not others (e.g., Rolland et al. 2014). These discrepancies may be due to the different taxonomic levels at which analyses were performed. For example, our results include most mammal families and disagree with those from mammalian orders (Rolland et al. 2014), but that study only included the eight most species-rich orders, and did not include direct data on climate. We also did not find any evidence of narrower niche widths being associated with higher diversification rates, as previous studies suggested (Rolland & Salamin 2016). In this case, the discrepancies may be due to methodological differences. Specifically, our measure of niche width was continuous and not a binary (i.e. specialist/generalist, as used by Rolland & Salamin 2016) and we analysed data at the level of families and clades, and not at the species level (as in Rolland & Salamin 2016). Overall, given these results, we favour the hypothesis that large-scale patterns of mammalian diversification are strongly influenced by a relationship between climatic niche change and speciation. The role of climatic niche divergence in mammalian speciation could be further explored by more detailed analyses within these families, such as looking for non-overlap in climatic niche models of sister species (e.g., Hua & Wiens 2010). Furthermore, the relative roles of speciation and extinction in driving these overall patterns of diversification could be explored with additional clade-level analyses.

Based on our results, we speculate that it is most likely that climatic niche change drives diversification rather than vice versa. It is very difficult to devise a plausible mechanism whereby diversification drives niche change that is not ruled out by our results. Clades could speciate with little change in their climatic niches, through niche conservatism, divergence on non-climatic niche axes, and/or non-ecological speciation processes. However, such processes should not generate a strong relationship between diversification rate and niche change. In theory, higher species richness of clades could lead to greater climatic niche divergence through geographic spread alone. Thus, the more diversification, the more divergence in climatic niches. But again, this should not increase the rate of climatic niche change (i.e. if niche divergence is a passive byproduct of speciation and range expansion). Furthermore, this scenario should generate a strong relationship between diversification rate, niche divergence, and clade range extent (area). Our results do not support this idea, as niche divergence has a strong relationship with diversification rate that is independent of clade area. In addition, the fact that the relationship between diversification rate and niche divergence is significantly stronger than would be expected under null assumptions (see Appendix S4.11) suggests that there are other mechanisms that link niche divergence and diversification rate other than families with more species having more divergent climatic niches due to sampling alone.

Our study includes two similar measures of climatic niche change within families (climatic niche divergence and climatic niche rates). These measures are significantly related, and explain similar amounts of variation in diversification rates. However, most previous studies have focused on niche rate rather than absolute niche divergence. The positive relationship between diversification rates and rates of climatic-niche evolution has been found in other groups (e.g., Kozak & Wiens 2010 for plethodontid salamanders; Schnitzler et al. 2012 for the plant genus *Babiana* in the Cape flora; Cooney et al. 2016 for birds; Moen & Wiens 2017 for frogs). These results suggest that families with faster rates of climatic-niche evolution might diversify faster due to niche divergence promoting speciation or climatic-niche lability buffering families from extinction (e.g., due to climatic fluctuations; Kozak & Wiens 2010). As mentioned above, we favour the hypothesis that niche divergence drives speciation, but this should be verified with additional species-level and clade-level analyses.

Interestingly, in mammal families, faster rates of climatic-niche evolution are not associated with species having narrower niche widths, as there is no relationship between climatic-niche evolution rate and mean species niche width (see Appendix S4.10). Other studies have found weak or positive relationships between niche width and rates of niche evolution (e.g., in salamanders; Fisher-Reid et al. 2012). They have also found faster rates of temperature niche evolution in temperate species, which typically have wider niche temperature widths (e.g., in mammals: Cooper et al. 2011; birds: Lawson & Weir 2014; across plants and animals: Jezkova & Wiens 2016).

There are several potential sources of error in our study, but none that should overturn our major conclusions. First, climatic niches were estimated using geographic data from species range maps. Range maps are based on interpolations of locality data, and some maps might span grid cells outside the actual species range. On the other hand, use of range maps samples niche variables equally from of all parts of the species range, whereas estimating mean niche variables from locality data alone might over-represent some parts of the range relative to others. Thus, the use of range maps should be less problematic. Second, the climatic variables were measured at a slightly larger spatial grain than in some previous studies (~4.5 km vs. 1 km). This larger grain size might contribute some random error to the climatic data, especially for species that occur in montane tropical regions where climate varies extensively over small spatial scales. However, it seems very unlikely that these errors could introduce a systematic bias that explains the strong relationship between diversification rate and climatic niche divergence reported here. Third, the phylogeny and divergence dates within and between mammalian families may not be fully accurate, leading to potential errors in estimating diversification rates and rates of niche evolution. But again, it is unclear how random errors in clade ages could generate a significant non-random relationship between diversification rates and climatic niche variables. Similarly, even if all the estimated ages were non-randomly biased (e.g., older than the actual ages), this would not necessarily overturn our conclusions (i.e. younger clades with high richness would still have high diversification rates). Furthermore, we used alternative measures of diversification (richness) and niche change that do not depend on the phylogeny or clade ages, and found that they gave similar results to the phylogeny-based measures. Fourth, some authors have claimed that the use of these net diversification rate estimators requires that rates of diversification are constant within clades (e.g., Rabosky 2009). However, the stem-age estimators require only clade age and richness (and yield the same net rate regardless of whether rates are constant or variable within clades over time or among subclades), and the overall accuracy of these estimators is supported by recent simulations (Kozak & Wiens 2016) including ones that incorporate heterogeneous rates within clades (Meyer & Wiens 2017). We also show that diversification rates are strongly linked to richness patterns across mammalian families, and that we obtain similar results using richness instead of diversification rates.

In summary, our results here shed light on patterns of variation in diversification rate in one of the major clades of vertebrates. We find that two related measures of niche change within families (rates of climatic-niche evolution and climatic niche divergence) each explain > 50% of the variation in diversification rates among mammalian families. These results suggest that climatic-niche divergence may be broadly important for speciation in mammals, given that our results are less consistent with alternative hypotheses to explain this relationship. More broadly, our results are similar to those from parallel analyses in plants (Schnitzler et al. 2012), amphibians (Kozak & Wiens 2010; Gómez-Rodríguez et al. 2015; Moen & Wiens 2017) and birds (Cooney et al. 2016). The similarity in results is particularly intriguing given the very different biologies of plants and animals and the very different physiologies and ecologies of amphibians and mammals (i.e. predominantly terrestrial endotherms vs. ectotherms that are typically at least partially aquatic; Pough et al. 2009). Given these results, we speculate that similar processes might explain patterns of diversification and species richness in many other major clades across the Tree of Life.


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General discussion

The overarching aim of this dissertation is to contribute to the understanding of the factors that can determine large-scale patterns of diversity of two vertebrate classes (birds and mammals). With this goal in mind, public databases of species distributions and recently published phylogenies have been analysed using different methodological approaches. In general, the results presented here are consistent with previous studies, and show regularities in biogeographical or macroecological patterns among different vertebrate clades. Some of the analyses performed in this thesis delve into important questions in Biogeography and Macroevolution. In particular, in Chapter 1 it is shown for the first time that the latitudinal variation in the components of beta diversity is very similar in several groups of vertebrates with diverse dispersal abilities and life histories. More strikingly, all the analysed groups present similar latitudinal breakpoints in turnover and nestedness components of beta diversity, pointing to common non-contemporary processes behind present biodiversity patterns. In Chapter 2, the importance of choosing appropriate dissimilarity measures and clustering algorithms for regionalisation studies is stressed. A recent contribution (Costello et al. 2017) has proposed a regionalisation of marine realms based on a wide-sense beta diversity measure that accounts for richness differences. In this chapter, the original data in Costello et al. (2017) is re-analysed using well established methods for biotic regionalisation and, in consequence, providing an alternative regionalisation not biased by richness gradients and, more importantly, minimising sampling effort biases. In Chapter 3, a novel macroecological pattern is unveiled: the latitudinal variation of range shape is explored for the first time, and a general trend of high-latitude species having east–west elongated ranges is described for the first time. This suggests that only boreal species distribution ranges are systematically constrained by climate, whereas species in tropical and temperate regions do not seem to be primarily constrained by climatic latitudinal bands. Finally, in Chapter 4 the relative relevance of absolute niche divergence and niche evolution rate in the diversification rate of mammal families is examined. The results of this analysis show that both the absolute climatic niche divergence and the rate at which this divergence took place are correlated with the rate at which mammal families have diversified.

In the first chapter, a breakpoint is evidenced in the latitudinal patterns of beta diversity components in birds and mammals (volant and non-volant). This breakpoint divides the globe into two regions that differ in their diversity patterns and, therefore, in the processes responsible for them. Above this latitudinal breakpoint, the turnover component of beta diversity (due to the substitution of species between localities) tends be lower and decreases towards the poles. In contrast, the nestedness-resultant component of beta diversity is predominant (and increases towards the poles) in latitudes above this breakpoint, suggesting that species in species-poor localities tend to be a subset of those present in richer localities (within these latitudes). That is, at high latitudes the beta diversity facet associated to processes that involve species losses (and thus generate nestedness patterns) increases. These patterns found in birds and mammals are analogous to the patterns that appear in other vertebrate classes, such as freshwater fishes (Leprieur et al. 2011) or amphibians (Baselga et al. 2012a). When the linear relationship between beta diversity and its possible determinants was examined (e.g., present temperature or precipitation conditions, or climatic conditions in the Last Glacial Maximum), no particularly strong relationships were found, with the exception of that between current temperature variables and the nestedness-resultant component of beta diversity, which could be the result of the influence of current climatic conditions in species distributions. However, what is remarkable about these patterns is that the breakpoints that were found in the latitudinal variation of beta diversity components are quite consistent between groups, and although similar breakpoints in the latitudinal variation of current climatic conditions were not found, an analogous breakpoint is observed in the latitudinal variation of mean elevation in the cells or in the difference between current climatic conditions and Last Glacial Maximum conditions, so both the presence of mountains and the influence of Pleistocene glaciations are potential factors behind these patterns.

Taking this into account, a possible explanation to the existence of two regions delimited by a latitudinal breakpoint is the imprint of historical processes. On the one hand, mountains can act as diversification sources (due to speciation processes, Rahbek & Graves 2001) and are places where glacial microrefugia are likely to occur (e.g., Médail & Diadema 2009), and thus that would generate substitution patterns at regional scales (in 500 km × 500 km cells). In addition, spatial heterogeneity allows the existence of different environments with varying species composition (Melo et al. 2009). On the other hand, Pleistocene glaciations would have covered extensive regions with ice sheets and most species would have changed their distributions to be restricted to lower latitudes (Hewitt 1999), independently of their thermoregulation capabilities. These regions would be recolonised only after the retreat of the ice cover (Hewitt 1999), and this would result in spatially structured patterns of species losses as the ones that are observed in our study. It is interesting that fundamentally similar patterns are observed in different vertebrate classes, even with very different thermoregulation and dispersal capabilities. The particular differences that can be observed in the breakpoints of the latitudinal variation in the nestedness-resultant component of beta diversity could be due to the differences in dispersal capabilities, because species with better dispersal capabilities move faster to the regions that become available after the retreat of the glaciations, hence they occupy higher latitudes earlier. Consequently, species losses patterns would appear only at very high latitudes, and thus the breakpoints in the nestedness-resultant component of beta diversity would be found at higher latitudes when dispersal capabilities are better. However, in volant mammals (Chiroptera), which show high dispersal capabilities, the breakpoint in the latitudinal variation of nestedness-resultant beta diversity is found at relatively low latitudes, possibly due to the fact that they are heterotherms (Hock 1951; McGuire & Guglielmo 2009), that is, their body temperature reduces to the ambient temperature when they are not active, making it difficult to establish at very high latitudes. Thus, in this particular case, the quantitative differences in the latitudinal thresholds of the nestedness component of beta diversity seem to be more related to physiological requirements than to differences in dispersal capability.

It might be relevant to note, however, that when some particular orders of birds or mammals with different dispersal capabilities were examined (it was assumed that orders with larger body sizes have in general higher dispersal capabilities, since species with larger body size tend to have larger range sizes, Gaston & Blackburn 1996), it was found that some of them show latitudinal patterns that are different from the overall pattern of the corresponding class. For example, the pattern in Passeriformes is similar to the overall pattern in birds (which is reasonable given that they comprise a large proportion of bird species), but Anseriformes, which have in general high dispersal capabilities, do not show a peak in turnover at middle latitudes. In groups of organisms that contain species with diverse dispersal capabilities (for example, all birds), it can be expected that only the subset of species with higher dispersal capability would quickly recolonise regions that became available after the retreat of the glaciations (e.g., Svenning & Skov 2007a; Baselga et al. 2012a). Consequently, at higher latitudes, species assemblages would be similar, yielding lower turnover values than regions that were not covered by ice sheets, because in those regions at lower latitudes communities would be composed of both the species with high dispersal ability (that also reached northern latitudes) and the ones with low dispersal ability. In contrast, in groups consisting of generally very mobile organisms (e.g. Anseriformes), turnover does not have to be spatially structured in that way, since most species could rapidly settle in newly unglaciated areas, and thus turnover would be more similar across different latitudes. In summary, the influence of dispersal could be sometimes reflected in the latitudinal patterns of the components of beta diversity in some specific orders.

In Chapter 1, it is shown that the two components of beta diversity (turnover and nestedness) present completely different spatial patterns. These patterns are in many cases opposed, mutually cancelling one another (e.g., two regions might have the same overall beta diversity, but one case might be dominated by turnover and the other by nestedness, Baselga 2010). For this reason, dissimilarity measures that account for both components are not adequate for their use as a distance measure in regionalisation studies, as it is shown in Chapter 2. In that chapter, a recent proposal for the biogeographical regionalisation of marine biota (Costello et al. 2017) is reanalysed, and it is argued that the differences in composition due to richness gradients are not of interest when defining biogeographical regions (because species-rich sites and species-poor sites whose species composition is a subset of the aforementioned richer sites would be classified in different regions, even when they contain no unique species). In an appropriate classification, the defined regions should have some level of endemism (Kreft & Jetz 2010). Moreover, it is discussed how the choice of the dissimilarity index influences regionalisation. Other important methodological choices are the number of defined groups and, particularly, the clustering algorithm for hierarchically grouping sites in more inclusive regions (Kreft & Jetz 2010; Holt et al. 2013). When analysing data where sampling effort is very heterogeneous, as is the case with this particular dataset, the use of the average linkage (UPGMA) clustering method, which is a broadly used method, produces very unbalanced groups (i.e., groups with a very uneven number of sites, defining regions with excessively small or large areas). The use of alternative clustering methods might be more appropriate for this sort of datasets (Dapporto et al. 2015). In this particular case, Ward clustering results in more balanced and cohesive regions. Thus, biogeographic regionalisations should carefully consider these methodological decisions depending on the characteristics of the available data.

In Chapter 3, the latitudinal variation in range shape was examined, and it was observed that species tend to have ranges more elongated in an east–west direction at high latitudes in the Northern Hemisphere, particularly above 30°–40° N, possibly due to the influence of climatic niche constrictions in the limits of distribution ranges. Below these latitudes, ranges are not systematically elongated in one direction or another. The similarity between this breakpoint (situated at 30°–40° N) and those that appear in the latitudinal variation of beta diversity components in birds and mammals is quite striking, and suggests that it could be due to common factors. In the case of range shape, that breakpoint is only clearly observable in the Northern Hemisphere. In the Southern Hemisphere, there is a slight tendency to ranges being elongated in a north–south direction, probably due to the predominant shape of the continents. It is plausible that the breakpoint that appears in the latitudinal variation of beta diversity components is mainly explained by the spatial variation of beta diversity in the Northern Hemisphere, although in this case the analyses considered its variation with absolute latitude, so a distinction cannot be made between hemispheres. However, it can be noted that in the maps that show the spatial variation of beta diversity components (Fig. 1.1), the nestedness component increases exclusively in the Northern Hemisphere (particularly in non-volant mammals and birds, in volant mammals there seems to be some increase in the Southern Hemisphere). This would be consistent with the hypothesis that these breakpoints are a mark on these large-scale patterns caused by the effect of Pleistocene glaciations in species distributions, because in the continental masses of the Northern Hemisphere the impact of the glaciations has been stronger (Ehlers et al. 2018).

At lower latitudes and in species with small distribution ranges, the shape of the distribution ranges does not tend to be elongated in one direction in particular, and remarkably the species in these regions have very similar latitudinal and longitudinal ranges compared to those at high latitudes in the Northern Hemisphere (see Fig. 3.2a,b). This is consistent with the hypothesis that range expansion in many species at low latitudes is mainly determined by isotropic processes, that is, processes which have the same influence in all directions (for more detailed explanations on how isotropic expansion might define distribution range limits, see Chapter 3 in Rapoport 1975). In contrast, this is not what would be expected if niche constraints are the main factor that controls species distributions (although niche constraints could generate isotropic ranges if there were equivalent environmental gradients in latitudinal and longitudinal directions). However, under neutral dynamics it would be expected that most distribution ranges had similar latitudinal and longitudinal extension (Baselga et al. 2012c). Conversely, in the Northern Hemisphere a systematic tendency towards east–west elongated ranges can be observed. This tendency cannot be exclusively attributed to the shape of the continents, because in null models where ranges expand only constrained by continental limits, it is found that the elongation is not so marked. In fact, the deviation in range shape in the observed distributions compared to the null models that simulate isotropic distributions increases to the north, and this suggests that the influence of climatic conditions in determining distribution range limits is greater in these regions, where climate differs more from the tropical climatic conditions where most clades originated (Wiens & Donoghue 2004). At lower latitudes, it is more probable that other processes besides the climatic niche are more relevant in the development of distribution shapes, such as stochastic or biotic factors (Normand et al. 2009), given that the ranges there do not tend to be elongated in any direction in particular.

In the Southern Hemisphere, ranges are generally elongated in a north–south direction, especially at higher latitudes, probably due to the predominant shape of the continents in this region, as the null model predicts that ranges would be elongated in this manner. In marine species, in which the elongation of distribution shapes would not be determined by the shape of terrestrial masses, it is observed that distributions are more elongated in an east–west direction at higher latitudes, similarly in the Northern and the Southern Hemisphere. This is the pattern that would be observed if the shape of the continents did not influence the elongation of range shapes, giving more support to the hypothesis that the latitudinal variation in range shape reflects the greater importance of climatic constrictions at higher latitudes.

A relationship between range size and range shape was also found, with larger ranges tending to be more elongated in an east–west direction. This observation could be explained by the possibly greater influence of large-scale climatic variation in species with broad distributions (Pearson & Dawson 2003). It could be thought that this relationship and that found between latitude and range shape are somehow linked, because bird and mammal species at high latitudes tend to have more extensive latitudinal ranges and larger range sizes (Orme et al. 2006; Davies et al. 2009). However, in the variance partitioning analyses that were performed in the third chapter, most of the variance in range shape that is explained by latitude or range size is not shared between these two explanatory variables, and the unique contribution of latitude is slightly larger.

In order to evaluate the relative influence of less spatially structured stochastic factors (e.g., biotic interactions) and other more spatially structured factors (e.g., variation in climatic conditions) in the determination of distribution range limits at different latitudes, the perimeters of the portions of the ranges at lower and higher latitudes were compared, expecting to find more twisted and longer perimeters if the influence of stochastic or biotic factors is greater (Normand et al. 2009). In general, no significant differences were found between the perimeter of the equatorward portion of the range and the poleward portion. The only significant differences were found in species with the largest ranges in the Southern Hemisphere. Again, the shape of the continents seems the most plausible explanation to this result, because it forces ranges to taper towards the South Pole, thus making the perimeters of this portion shorter.

The interpretation of these results is not straightforward, and the large variation in range shape at low latitudes could be caused by many different processes. With the performed analyses, it is not possible to rule out that, in some cases, climatic variation at small scales or spatial heterogeneity of abiotic factors could be the main determinants of species range shape. In particular, lower climatic variability and more restricted physiological tolerances would result in more effective topographical barriers (Ghalambor et al. 2006), and assuming that the orientation of these barriers is varied, the deviations from isotropy in the tropics caused by abiotic factors would be more irregular. Still, given that a considerable number of species were included in the analyses, the influence of some particular cases in the general patterns is most likely low.

In the fourth chapter, a different point of view is adopted to investigate the causes of biological diversity, analysing its variation between different clades rather than between different regions. With this goal in mind, we explored the factors that might influence diversification in mammal families. It was observed that the variables that are more strongly correlated with diversification rate (and family species richness) were climatic niche evolution and absolute niche divergence. In this study, we examined for the first time the relative importance of absolute niche divergence and niche evolution rate in explaining the variation of diversification rate among clades, and it was found that both are strongly related and explain large and similar proportions (more than 50%) of the variation in diversification rate. In mammals, the relationship between climatic niche and diversification rate is comparable to that found in other vertebrate classes, in particular birds (Cooney et al. 2016) and amphibians (Gómez-Rodríguez et al. 2015; Moen & Wiens 2017). All these results suggest that studying the variation in climatic niches is important to explain differences in diversification or richness between clades.

Most of the previous studies focus on niche evolution rate, and in many cases they find that it is positively related to diversification rate or richness (Kozak & Wiens 2010; Schnitzler et al. 2012; Cooney et al. 2016). This suggests that families with higher niche evolution rates would diversify faster due to niche divergence promoting speciation or climatic niche lability diminishing extinction rates (e.g., allowing to adapt to climatic fluctuations). Therefore, taking into account the analyses performed in this study, the hypothesis that speciation due to niche divergence is common and important (Hua & Wiens 2013) is the most supported.

It seems more probable that climatic niche change drives diversification rather than the other way around, because it is not easy to find a mechanism in which diversification drives niche divergence that is not ruled out by the results of our study. If clades speciated with little or no change in their climatic niches (for example, through niche conservatism [Wiens & Graham 2005], divergence on non-climatic niche axes or non-ecological speciation processes), no relationship should be found between diversification rate and niche change, the opposite of what is observed. Theoretically, niche divergence between species could be higher in clades with higher richness, only because they are more geographically spread (Gómez-Rodríguez et al. 2015), but this would not increase niche evolution rate, and here it is observed that niche evolution rate is positively related to diversification rate. Additionally, this hypothesis predicts that a strong relationship would arise between diversification rate, niche divergence, and clade range extent, but in our study niche divergence explains an important proportion of variation in niche divergence which is not explained by clade range extent. Furthermore, the observed relationship between diversification rate and niche divergence is stronger than expected under null assumptions (Appendix S4.11), suggesting that the hypothesis of species in richer families having more divergent niches due to sampling alone is not sufficient to explain this relationship.

Other hypotheses (reviewed in Gómez-Rodríguez et al. 2015) are not backed up by these results. For example, support was not found for the hypothesis that speciation is mainly linked to climatic niche conservatism (Wiens & Graham 2005), since it predicts that diversification rate and family-level niche width would be negatively related. The hypothesis that families with broader species-level niche widths have lower extinction rates, leading to higher diversification rates, was also not supported, since no relationship was found between mean species niche width and diversification rate. The amount of variation in diversification rates explained by family niche width and geographic extent was very similar, but the unique contribution of geographic extent was very small, so there was no strong support for geographic extent influencing diversification rates. Only a weak relationship was found between diversification rate and niche position (climatic regime). This is consistent with some previous studies in mammals (Weir & Schluter 2007; Soria-Carrasco & Castresana 2012), although others have found that diversification rate is faster in the tropics (e.g., Rolland et al. 2014). The latter study only included the eight most species-rich orders and did not include direct data on climate, which might explain the discrepancies. Finally, narrower niche widths do not seem to be associated with higher diversification rates (but see Rolland & Salamin 2016). The inconsistency between the results presented here and those of Rolland & Salamin (2016) may be due to methodological differences, since our measure of niche width was continuous and not a binary (specialist/generalist), and the data were analysed at the level of families or clades, not species.

Given the importance of climatic niche variation within mammal families in their diversification rate and, consequently, in its species richness; and given that climatic niche seems to be one of the main factors in the determination of distribution range limits in species living at high latitudes in the Northern Hemisphere, it could be interesting to analyse if there is a relationship between the isotropy of distribution ranges within families and their diversification rate, as this could give some hints about common processes that determine clade diversification as well as their geographic distribution, and in addition could serve to verify if diversification is higher when distribution ranges are determined by neutral processes or when they are more influenced by climatic constraints.

This dissertation analyses the factors and processes that influence bird and mammal diversity at continental and global scales. One of the main objectives was to estimate the relevance of neutral and niche processes. For example, there seems to be an important influence of niche divergence or climatic niche evolution through time in the diversification rates of mammal families (Chapter 4). In contrast, neutral processes could be more relevant in the determination of distribution limits of species at low latitudes, although climatic niche also seems to be an important factor in shaping the distribution ranges of species at high latitudes in the Northern Hemisphere (Chapter 3). Some of the examined patterns show quite an interesting analogous behaviour. In particular, the nestedness-resultant component of beta diversity is predominant at high latitudes above approximately 30° of latitude in several groups of vertebrates (Chapter 1), and, above a similar latitude, distribution ranges have a stronger tendency to be elongated in an east–west direction. These similarities are intriguing, but with the analyses performed here it is not possible to draw solid conclusions, because these resemblances could be merely superficial. Nevertheless, they raise the possibility for the existence of a common process or combination of processes behind these two patterns, which could be a promising foundation for later studies.


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Conclusions

1. There are analogous patterns of latitudinal variation in beta diversity in several groups of vertebrates (amphibians, volant and non-volant mammals, birds) with very different dispersal and thermoregulation capabilities.

2. Similar breakpoints (points in which the tendency of a relationship changes) are found in the latitudinal variation of the turnover and nestedness components of beta diversity. Above *c.* 30° of latitude the turnover component decreases and the nestedness component increases, with a peak in turnover at middle latitudes.

3. Current temperature conditions are the best predictor of the nestedness component of beta diversity, while the presence of mountains was the best predictor for the turnover component of beta diversity, although this relationship was still weak. However, the latitudinal variation of elevation and the historical change in temperature conditions show breakpoints which are very similar to those in the latitudinal variation of the components of beta diversity. Notably, a similar breakpoint is not found in current temperature conditions. This suggests that historical processes (in particular, Pleistocene glaciations) have imprinted the current latitudinal patterns of beta diversity of all groups independently of their dispersal or thermoregulation capabilities.

4. A threshold-based analysis of macroecological patterns (i.e., identification of breakpoints) might provide insight into the mechanisms behind such patterns.

5. Dissimilarity measures that are affected by richness gradients are not suitable for biogeographic regionalisation studies, because they tend to separate species-rich localities from species-poor localities

whose species composition is a subset of the species present in species-rich sites.

6. The choice of clustering method in regionalisation studies is critical, in particular when sampling effort is very heterogeneous. Clustering methods such as Ward clustering result in the definition of more balanced and cohesive biogeographic regions, while other broadly used methods (e.g. average linkage/UPGMA) produce undesired results, such as very unbalanced groups.

7. A latitudinal pattern is found in the range shape of birds and mammals, with ranges tending to be more elongated in an east–west direction at high latitudes in the Northern Hemisphere. The existence of this latitudinal gradient suggests a different role of climatic niche constraints, neutral processes, biotic interactions and other stochastic processes at different latitudes.

8. At higher latitudes in the Northern Hemisphere, range shape deviates more from the expectations of a null model in which ranges expand isotropically, suggesting that the influence of climatic conditions in range limits is greater in these regions.

9. Significant differences in the perimeter of range limits in the equatorward and poleward portions of distribution ranges were not found, except in the largest ranges in the Southern Hemisphere, which can be explained by the general shape of the continents at these latitudes, which force ranges to taper towards the South Pole. In other words, no contrasting effects of stochastic and deterministic processes could be detected when comparing the poleward and equatorward limits of species ranges.

10. Two measures of niche change within families or clades explain a large amount of the variation in diversification rate and species richness in mammal families. This is mostly consistent with the hypothesis of climatic-niche divergence being an important factor behind speciation processes. These results are similar to those found in plants, amphibians, or birds, which suggests that common

processes might be behind the patterns of diversification of many clades across the Tree of Life.

11. Only a weak association was found between diversification rate of families and niche position, a proxy for the predominant climatic regime (tropical or temperate).

12. Some macroecological patterns are common to multiple vertebrate classes, such as the latitudinal variation of the turnover and nestedness components of beta diversity or the tendency in the ranges of species inhabiting the highest latitudes in the Northern Hemisphere to be elongated in an east–west direction, which implies that similar processes might be behind these patterns and that they affect a broad range of organisms with very diverse dispersal capabilities and life histories.


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Supplementary Material


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Appendix
S1

Chapter 1 Supplementary Material

Appendix S1.1

Linear relationships between environmental variables and beta-diversity components.

Coefficients of determination (r^2) of ordinary least squares (OLS) regressions between five environmental variables (altitude, mean annual temperature [T_{MEAN}], difference in temperature between current conditions and the Last Glacial Maximum (LGM) [T_{DIFF}], maximum temperature of warmest month [T_{MAX}], annual precipitation [P_{ANN}], actual evapotranspiration [AET], and potential evapotranspiration [PET]) and the turnover (β_{SIM}) and nestedness-resultant (β_{SNE}) components of beta diversity. The sign of the relationship is indicated in parentheses. Non-significant relationships ($P > 0.01$) are marked with the superscript *ns*.

	β_{SIM}			β_{SNE}		
	Bats	Non-volant mammals	Birds	Bats	Non-volant mammals	Birds
Altitude	0.14 (+)	0.20 (+)	0.21 (+)	0.02 (+)^{ns}	0.01 (−)^{ns}	0.06 (−)
T_{MEAN}	0.05 (+)^{ns}	0.18 (+)	0.03 (+)^{ns}	0.50 (−)	0.39 (−)	0.33 (−)
T_{DIFF}	0.07 (−)	0.09 (−)	0.25 (−)	0.24 (+)	0.04 (+)^{ns}	0.09 (+)
T_{MAX}	0.05 (+)^{ns}	0.25 (+)	< 0.01 (+)^{ns}	0.44 (−)	0.55 (−)	0.37 (−)
P_{ANN}	<0.01 (−)^{ns}	<0.01 (+)^{ns}	<0.01 (+)^{ns}	0.17 (−)	0.08 (−)	0.08 (−)
AET	<0.01 (−)^{ns}	0.04 (+)^{ns}	<0.01 (+)^{ns}	0.31 (−)	0.24 (−)	0.18 (−)
PET	0.05 (+)^{ns}	0.15 (+)	0.04 (+)^{ns}	0.49 (−)	0.31 (−)	0.26 (−)

Appendix S1.2

Comparison of piecewise regressions and simple linear regressions.

Results of the ANOVA (presented in the last three columns) comparing the fit of piecewise regressions in relation to simple linear regressions. The variable indicated in the first column of the table is the dependent variable and latitude is the independent variable in all cases. Significant values of *P* are marked in bold. T_{MAX}: maximum temperature of warmest month; T_{DIFF}: difference in mean annual temperature between present time and the Last Glacial Maximum.

	r^2 simple regression	r^2 piecewise regression	Latitudinal breakpoint	*F*	Degrees of freedom	*P*
Altitude	0.005	0.19	28	17.735	2, 155	< 0.001
T_{MAX}	0.71	0.87	29	94.505	2, 155	< 0.001
T_{DIFF}	0.18	0.39	29	27.222	2, 155	< 0.001
β_{SIM} (bats)	0.03	0.35	28	27.21	2, 111	< 0.001
β_{SNE} (bats)	0.41	0.5	29	9.066	2, 111	< 0.001
β_{SIM} (non-volant mammals)	0.14	0.34	28	24.334	2, 154	< 0.001
β_{SNE} (non-volant mammals)	0.31	0.45	37	19.82	2, 154	< 0.001
β_{SNE} (non-volant mammals)	0.31	0.44	29	18.388	2, 154	< 0.001
β_{SIM} (birds)	0.04	0.14	29	8.97	2, 155	< 0.001
β_{SNE} (birds)	0.27	0.43	58	28.477	2, 155	< 0.001
β_{SNE} (birds)	0.27	0.37	29	12.76	2, 155	< 0.001

Appendix S1.3

Comparison of different breakpoints for the nestedness-resultant dissimilarity of non-volant mammals and birds.

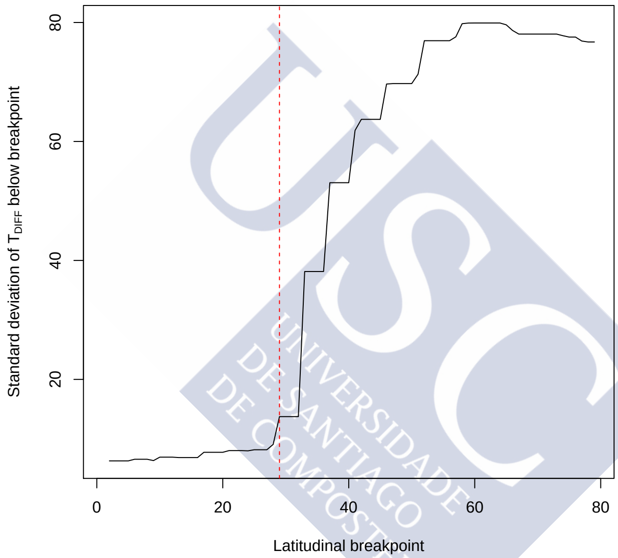
AIC values of different models with β_{SNE} as the dependent variable and latitude as the independent variable.

	Regression type	Breakpoint	AIC
Non-volant mammals	Simple	—	−162.57
	Piecewise	37	−194.76
	Piecewise	29	−192.41
Birds	Simple	—	−238.83
	Piecewise	58	−275.85
	Piecewise	29	−259.06

Appendix S1.4

Standard deviation of climatic change since the Last Glacial Maximum below different latitudinal breakpoints.

Standard deviation of the difference in mean annual temperature between present time and the Last Glacial Maximum (T_{DIFF}) below different latitudinal breakpoints. All possible latitudinal breakpoints were tested at 1° intervals. Note that above 29° (dashed red line) the standard deviation starts to increase markedly (see also Fig. 1.1c in main text).



Appendix S1.5

Results of cubic polynomial models and comparison with piecewise regressions and simple linear regressions.

AIC of three different models to assess the relationship between latitude and beta diversity due to species turnover (β_{SIM}) and due to species losses (β_{SNE}): Ordinary Least Squares (OLS), piecewise regressions, and cubic polynomial regressions. The lowest AIC value is marked in bold. The inflection point of the polynomial regressions (as indicated in Fig. 1.1 in the main text by a dashed red line) is presented in the table as well.

		OLS	Piecewise	Polynomial	Inflection point
Bats	β_{SIM}	−90.77	**−132.65**	−123.65	20.9
	β_{SNE}	−142.50	**155.90**	−155.01	6.5
Non-volant mammals	β_{SIM}	−128.40	**−167.79**	−165.34	24.2
	β_{SNE}	−162.57	−194.76	**−201.08**	24.0
Birds	β_{SIM}	−178.35	**−191.77**	−177.89	18.5
	β_{SNE}	−238.83	**−275.85**	−268.51	24.5

Appendix S1.6

Supplementary results for different orders of non-volant mammals and birds.

Latitudinal variation of turnover and nestedness in different orders of non-volant mammals (rodents, carnivores, and even-toed ungulates) and birds (Passeriformes and Anseriformes).

Table S1.6.1: AIC of three different models to assess the relationship between latitude and beta diversity due to species turnover (β_{SIM}) and due to species losses (β_{SNE}): Ordinary Least Squares (OLS), piecewise regressions, and cubic polynomial regressions. The lowest AIC value is marked in bold. The breakpoint of piecewise regressions and inflection point of cubic polynomial regressions is also indicated.

		OLS	Piecewise	Polynomial	Breakpoint (piecewise)	Inflection point
Rodents	β_{SIM}	−82.85	−104.95	**−110.54**	29	20.2
	β_{SNE}	−204.94	**−214.04**	−212.38	37	18.4
Carnivores	β_{SIM}	−79.39	−115.73	**−116.44**	29	30.8
	β_{SNE}	−118.51	−136.12	**−141.95**	37	*
Even-toed ungulates	β_{SIM}	**−16.67**	−15.90	−14.30	—	—
	β_{SNE}	−102.90	**−103.96**	−100.99	—	—
Passeriformes	β_{SIM}	−141.63	**−164.70**	−161.48	29	16.8
	β_{SNE}	−151.26	**−190.40**	−185.45	42	17.9
Anseriformes	β_{SIM}	−82.76	**−90.15**	−83.60	47	21.9
	β_{SNE}	−212.10	**−232.68**	−224.21	56	46.8

* No inflection point for the fitted cubic polynomial model.

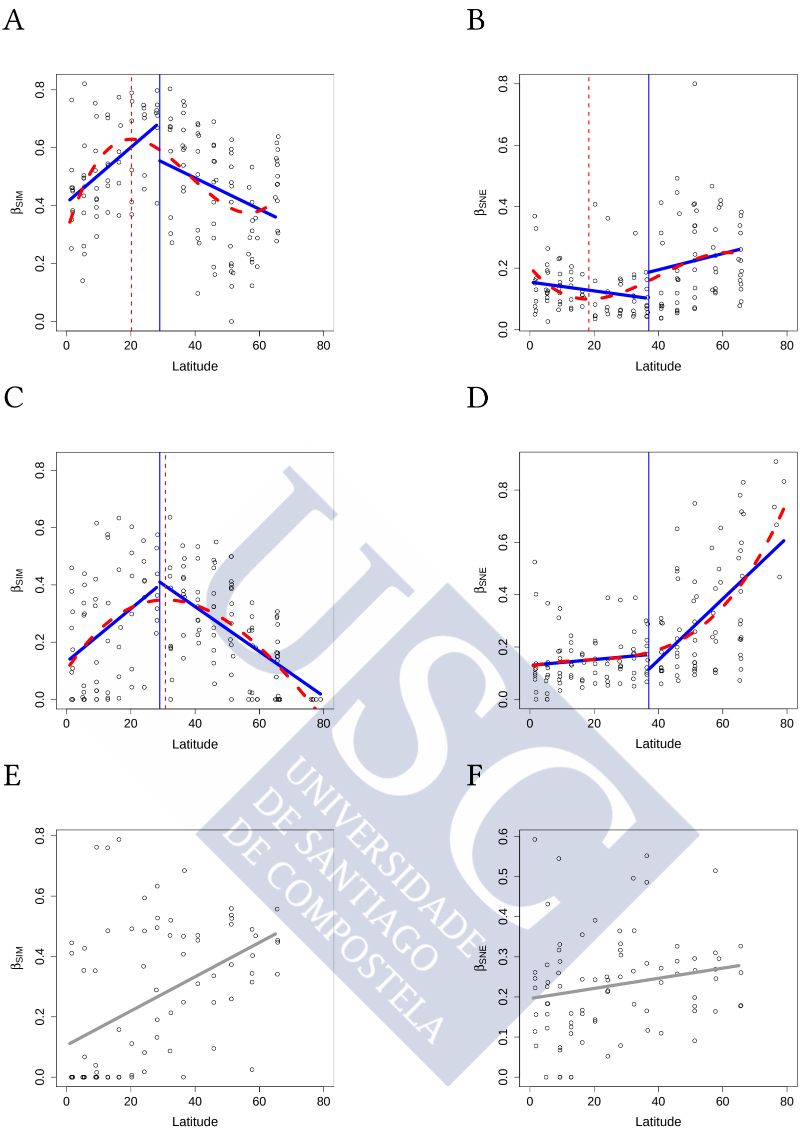


Figure S1.6.1: Scatterplots showing the latitudinal variation in turnover (A, C, E) and nestedness (B, D, F) for rodents (A, B), carnivores (C, D), and even-toed ungulates (E, F). Piecewise regressions are shown with a continuous blue line and cubic polynomial models with a dashed red line. Vertical lines indicate the breakpoint in piecewise regressions and the inflection point in polynomial regressions. In the case of even-toed ungulates, a grey line shows the fitted simple linear model (OLS).

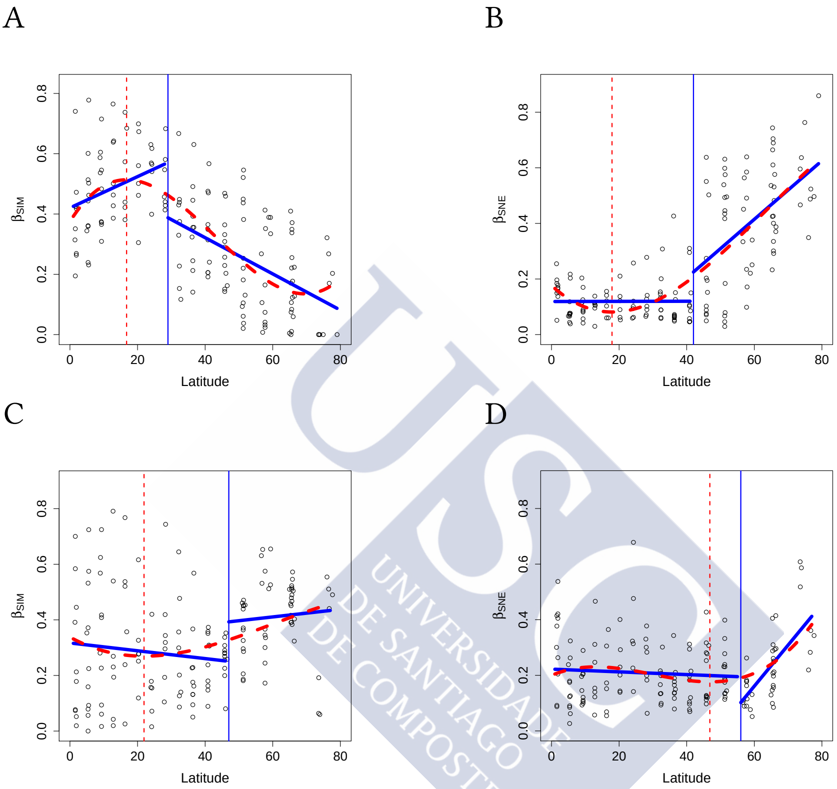


Figure S1.6.2: Scatterplots showing the latitudinal variation in turnover (A, C) and nestedness (B, D) for Passeriformes (A, B) and Anseriformes (C, D). Piecewise regressions are shown with a continuous blue line and cubic polynomial models with a dashed red line. Vertical lines indicate the breakpoint in piecewise regressions and the inflection point in polynomial regressions.

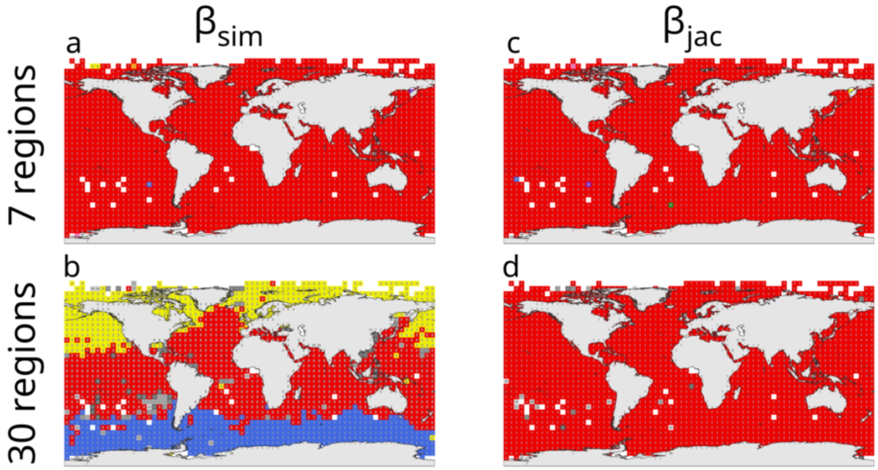
Appendix

S2

Chapter 2 Supplementary Material

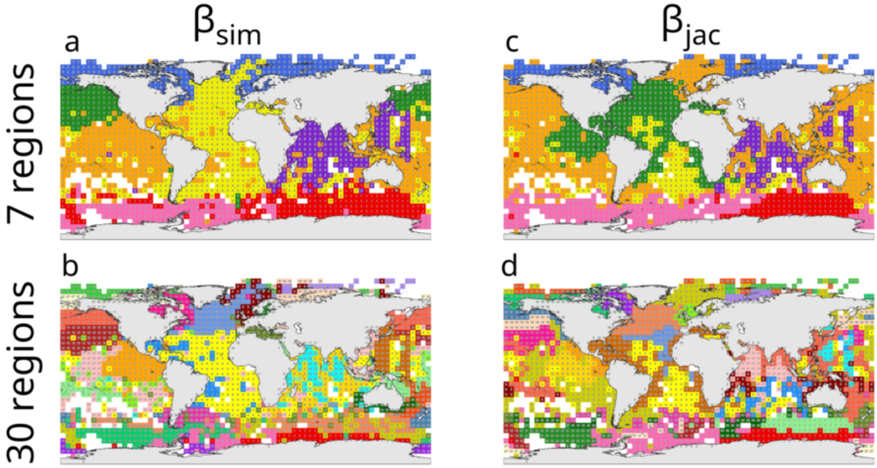
Appendix S2.1

Regionalisation of marine assemblages using Simpson (β_{sim}) or Jaccard (β_{jac}) dissimilarity indices and average clustering, defining 7 or 30 regions. Note that in many cases, regions consist of one or very few cells. When 30 regions are defined, regions comprising very few cells are coloured in grey tones.



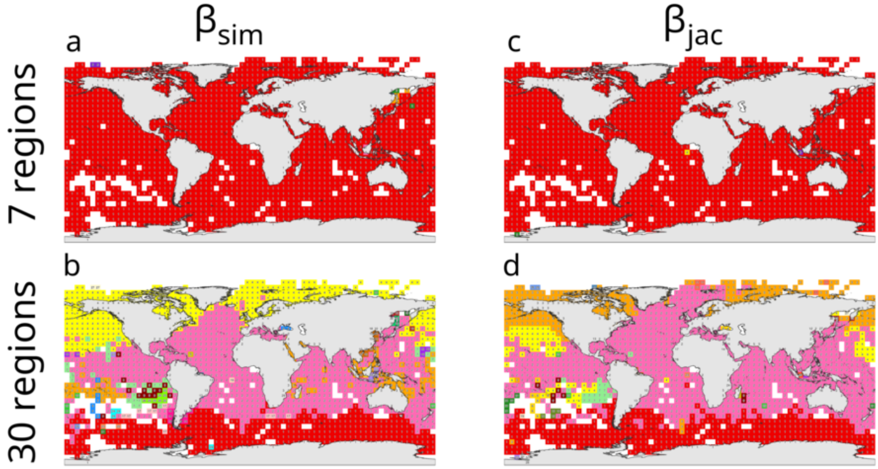
Appendix S2.2

Regionalisation of marine assemblages excluding cells with less than five species, using Simpson (β_{sim}) or Jaccard (β_{jac}) dissimilarity indices and Ward clustering, defining 7 or 30 regions.



Appendix S2.3

Regionalisation of marine assemblages excluding cells with less than five species, using Simpson (β_{sim}) or Jaccard (β_{jac}) dissimilarity indices and average clustering, defining 7 or 30 regions.

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Appendix

S3

Chapter 3 Supplementary Material

Appendix S3.1

Estimation of longitudinal ranges

We estimated longitudinal ranges in kilometres from the longitudinal span in degrees of the distribution ranges. The length of one degree of longitude varies with latitude, so we used the lowest latitude (the closest to the equator) of each distribution range, or the mean latitude, in the cases in which this latitude was closer to the equator than the latitudinal extremes of the distribution range. We used the WGS84 reference ellipsoid to define the shape of the Earth. Following Osborne (2013), we calculated the length of one degree ($\pi/180$ radians) of longitude as

$$\frac{\pi}{180}\frac{a\cos\phi}{\sqrt{(1-e^2\sin^2\phi)}},$$

where ϕ is the latitude of the distribution range, a is the semi-major axis (equatorial radius) of the WGS84 ellipsoid (6378.137 km), and e is the eccentricity of the ellipsoid, which is equal to

$$e^2 = \frac{a^2 - b^2}{a^2},$$

where b is the semi-minor axis (polar radius) of the WGS84 ellipsoid (6356.752 km).

Appendix S3.2

Patterns in the variation of range shapes using more conservative estimates of longitudinal ranges, calculated at the mean latitude of the ranges instead of using the lowest latitude.

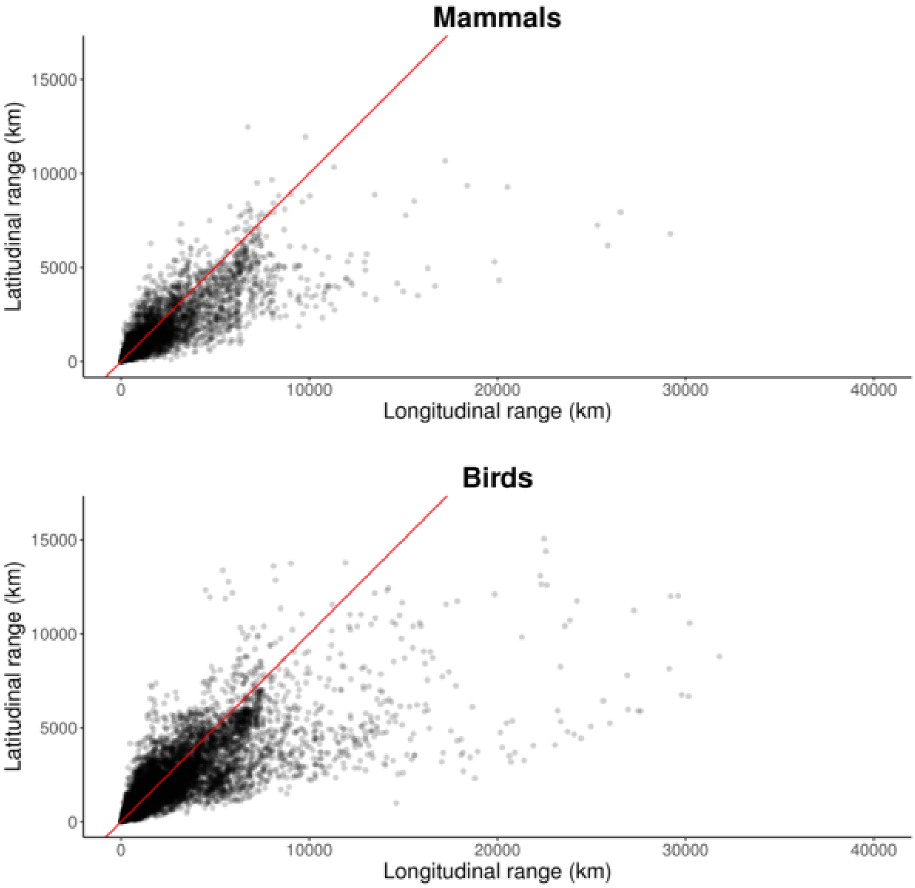

Figure S3.2.1: Longitudinal range plotted against latitudinal range. The 1:1 line is superimposed in red.

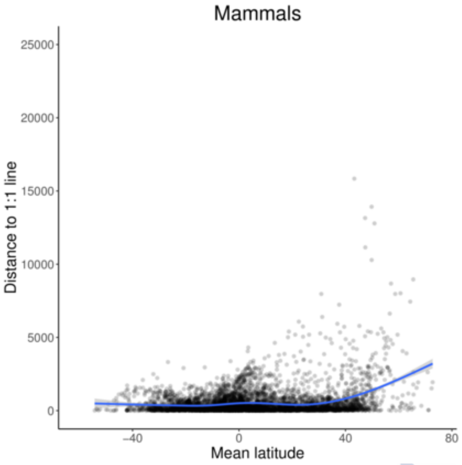

Figure S3.2.2: Relationship between the distance to the 1:1 line in Fig. S3.2.1 (ranges that are more circular are closer to the 1:1 line) and the mean latitude of the range. The fitted GAM is shown.

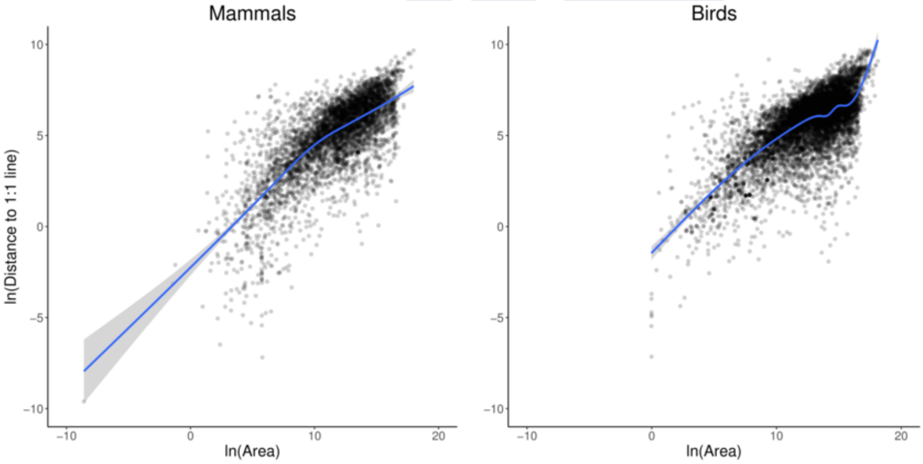

Figure S3.2.3: Relationship between the distance to the 1:1 line in Fig. S3.2.1 (ranges that are more circular are closer to the 1:1 line) and range extent (in km^2). Both variables are ln-transformed. The fitted GAM is shown, with a 95% confidence interval.

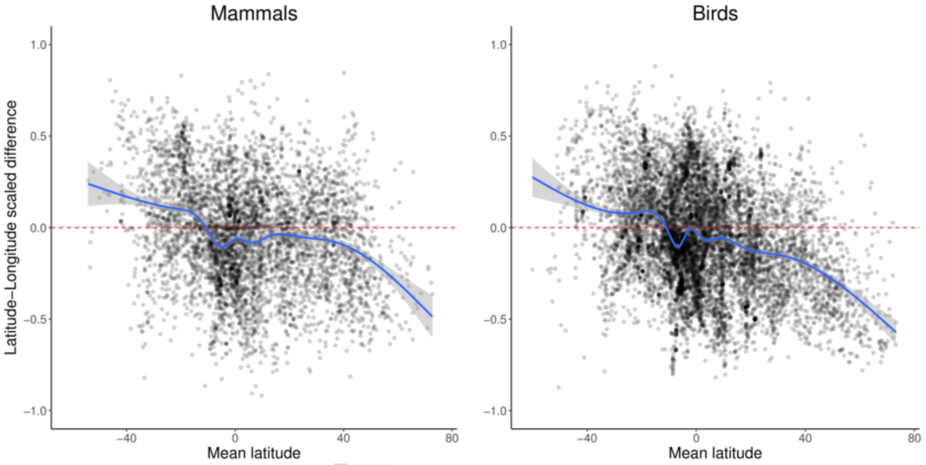

Figure S3.2.4: Relationship between latitude–longitude scaled difference (ranges that are more circular are closer to zero, indicated by a dashed red line) and mean latitude of the ranges. The fitted GAM is shown, with a 95% confidence interval.

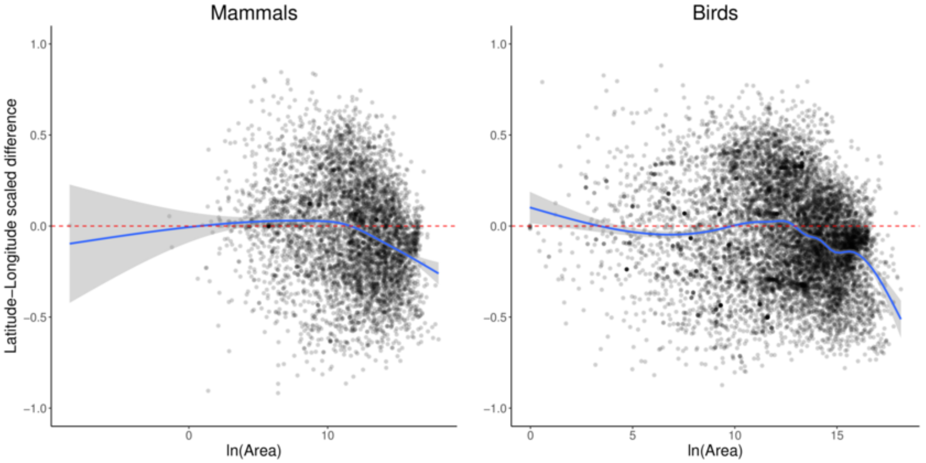

Figure S3.2.5: Relationship between latitude–longitude scaled difference (ranges that are more circular are closer to zero, indicated by a dashed red line) and range extent (in km^2, ln-transformed). The fitted GAM with a 95% confidence interval is shown.

Appendix S3.3

Relationship between the mean of the latitude–longitude scaled difference of all the species falling in a particular 100 km × 100 km cell (see Fig. 3.4 in main text) and latitude. Fitted GAM are superimposed in blue.

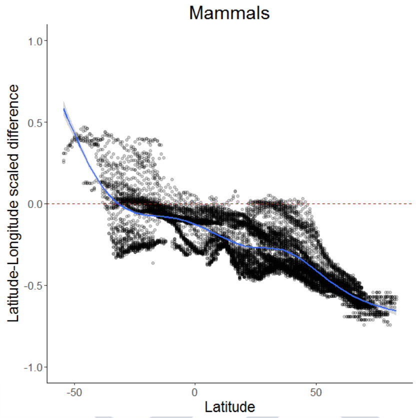

Figure S3.3.1: Latitudinal variation in mean latitude–longitude scaled difference in mammals.

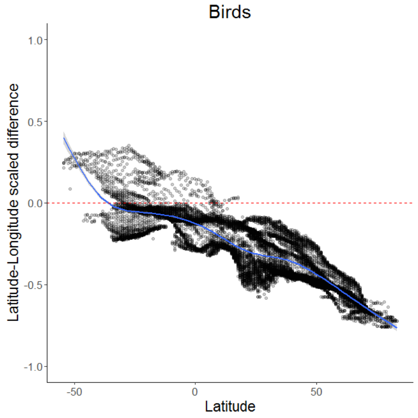

Figure S3.3.2: Latitudinal variation in mean latitude–longitude scaled difference in birds.

Appendix S3.4

Spatial variation of range shape in the null models.

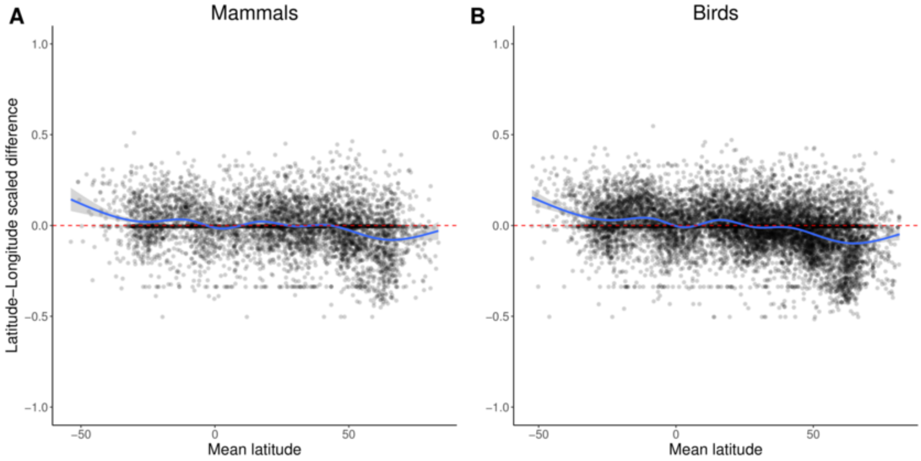

Figure S3.4.1: Relationship between latitude–longitude scaled difference (ranges with more similar latitudinal and longitudinal ranges are closer to zero, indicated by a dashed red line) and mean latitude of the ranges. The fitted GAM is shown, with a 95% confidence interval.

Appendix S3.5

Differences between equatorward and poleward semi-perimeters in the flipped polygons.

Table S3.5.1: Results of the paired t tests comparing the length of the equatorward and poleward semi-perimeters (standardised) of the ranges. A positive difference (significantly different from zero) means that the poleward semi-perimeters are shorter. We present the results for all species, for the species with larger geographic range extents (4th area quartile), and for the species with smaller geographic range extents (1st area quartile). The last two columns show the mean difference between the equatorward and the poleward semi-perimeter with a 95% confidence interval and a measure of the effect size (r^2) when the difference is statistically significant. Significant values of P (< 0.01) are marked in bold. Note that the degrees of freedom are different from the results in the main text, because for some bird species we were not able to flip the range polygons.

		Hemisphere	t	df	P	Mean of the differences	r^2
Mammals	All species	North	4.17	2904	**< 0.001**	0.013 ± 0.006	0.006
		South	−6.55	2378	**< 0.001**	−0.022 ± 0.007	0.018
	4th area quartile	North	4.76	725	**< 0.001**	0.035 ± 0.015	0.03
		South	−11.97	594	**< 0.001**	−0.087 ± 0.014	0.194
	1st area quartile	North	0.95	725	0.34	0.005 ± 0.011	—
		South	0.42	594	0.67	0.003 ± 0.012	—
Birds	All species	North	4.96	4709	**< 0.001**	0.015 ± 0.006	0.005
		South	−19.35	5003	**< 0.001**	−0.054 ± 0.005	0.07
	4th area quartile	North	4.54	1177	**< 0.001**	0.032 ± 0.014	0.017
		South	−25.61	1250	**< 0.001**	−0.157 ± 0.012	0.344
	1st area quartile	North	0.56	1177	0.57	0.003 ± 0.009	—
		South	−0.60	1250	0.55	−0.003 ± 0.010	—

Appendix S3.6

Latitudinal patterns of range shape in marine species.

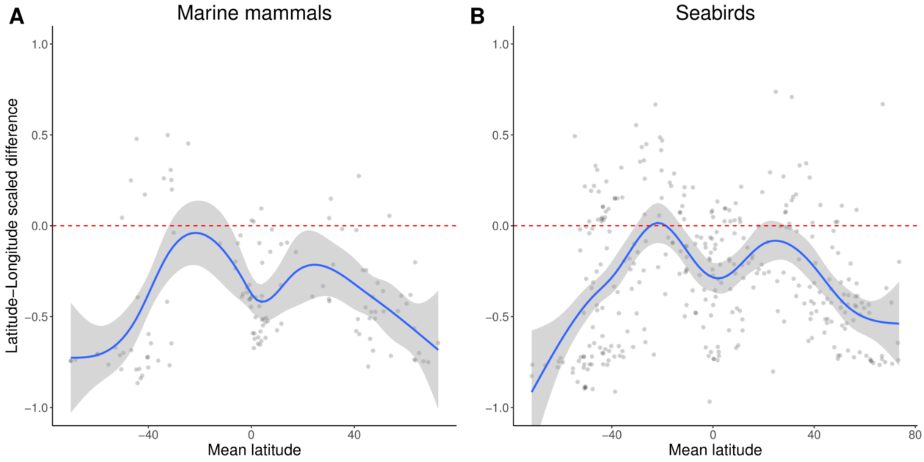

Figure S3.6.1: Relationship between latitude–longitude scaled difference (ranges with more similar latitudinal and longitudinal ranges are closer to zero, indicated by a dashed red line) and mean latitude of the ranges in marine mammals (A) and seabirds (B). Fitted GAM are superimposed in blue.

Appendix
S4

Chapter 4 Supplementary Material

Appendix S4.1

R functions for GIS analyses.

Species niche width and position

```
library(raster)
library(rgdal)
library(maptools)

# Reading raster with climatic data (done for six
# climatic variables described in main text, here
# presented only for BIO1)
bio1 <- raster("./bio1.bil")

# Reading polygons with species distribution
mamm <- readOGR("./All_MAMMALS_NOV2013/",
                "All_MAMMALS_NOV2013")

# For each species
union.poly <- unionSpatialPolygons(sp.polys,
                                   rep(1, length(sp.polys)))
# Extracting values of each climatic variable for
# the species distribution polygon
# (here presented only for BIO1)
bio1.ext <- extract(bio1, union.poly, small = TRUE)[[1]]
# Minimum, maximum, and mean values were obtained
# for each species and climatic variable
```

Family niche width and position

```r
library(raster)

# For each family
# All the polygons of the species of each family are stored
# in the object "fam.polys"
# Convert all the polygons of a family to one raster
# representing its distribution range
fam.rast <- rasterize(fam.polys, bio1, field = 1)

# Extracting values of each climatic variable for the
# family distribution raster (here presented only for BIO1)
bio1.ext <- fam.rast[] * bio1[]
# Minimum, maximum, and mean values were obtained for each family
# and climatic variable
```

Family distribution area

```r
library(geosphere)

# The function gdal_polygonizeR (a function by
# John Baumgartner, available at
# <https://johnbaumgartner.wordpress.com/2012/07/26/
#  getting-rasters-into-shape-from-r/> [accessed 15 February 2014])
# was used in order to convert family rasters to a polygon

gdal_polygonizeR <- function(x, outshape = NULL,
                             gdalformat = ’ESRI Shapefile’,
                             pypath = NULL, readpoly = TRUE,
                             quiet = TRUE) {
  if (isTRUE(readpoly)) {
    require(rgdal)
  }
  if (is.null(pypath)) {
    pypath <- Sys.which("gdal_polygonize")
  }
  if (!file.exists(pypath)) {
    stop("Can’t find gdal_polygonize.py on your system.")
  }
  owd <- getwd()
  on.exit(setwd(owd))
  setwd(dirname(pypath))
  if (!is.null(outshape)) {
```

```
    outshape <- sub('\\.shp$', '', outshape)
    f.exists <- file.exists(paste(outshape, c('shp', 'shx', 'dbf'),
                                  sep = '.'))
    if (any(f.exists)) {
      stop(sprintf('File already exists: %s',
                   toString(paste(outshape, c('shp', 'shx', 'dbf'),
                                  sep = '.')[f.exists])),
           call. = FALSE)
    }
  } else {
    outshape <- tempfile()
  }
  if (is(x, 'Raster')) {
    require(raster)
    writeRaster(x, {f <- tempfile(fileext = '.asc')})
    rastpath <- normalizePath(f)
  } else if (is.character(x)) {
    rastpath <- normalizePath(x)
  } else {
    stop('x must be a file path (character string), or a Raster object
        .')
  }
  system2('python',
          args = (sprintf('"%1$s" "%2$s" -f "%3$s" "%4$s.shp"',
                          pypath, rastpath, gdalformat, outshape)))
  if (isTRUE(readpoly)) {
    shp <- readOGR(dirname(outshape), layer = basename(outshape),
                   verbose = !quiet)
    return(shp)
  }
  return(NULL)
}

# For each family
fam.poly <- gdal_polygonizeR(fam.rast)

# Specify latlong projection to that polygon
fam.poly@proj4string <- CRS("+proj=longlat +datum=WGS84 +no_defs +ellps=
    WGS84 +towgs84=0,0,0")

# Area (in km^2) of the polygon calculated using
# the function areaPolygon() from package "geosphere"
area.km2 <- sum(areaPolygon(fam.poly)) / 1e+6
```

Appendix S4.2

Data for each mammal family, including stem group age (millions of years ago), species richness (S), diversification rate in events per million years (using a relative extinction fraction of ε = 0, ε = 0.45, and ε = 0.9, geographic extent, family niche width (FNW), mean species niche width (MSNW), temperature (BIO1) niche evolution rate (TNE), and precipitation (BIO12) niche evolution rate (PNE). Niche widths are standardized and ln-transformed. Rates of niche evolution were only estimated for monophyletic families with more than one species in the phylogenetic tree used.

			Diversification rate							
Family	Age	S	ε = 0.0	ε = 0.45	ε = 0.9	Area (km^2)	FNW	MSNW	TNE	PNE
Acrobatidae	48.5	2	0.0143	0.009	0.002	1 744 594	−5.27	−6.04	51.3	115 325.7
Anomaluridae	54.7	7	0.0356	0.0267	0.0086	6 036 800	−6.35	−7.15	5.9	1666.3
Atelidae	15.5	28	0.2149	0.1782	0.0844	12 994 908	−2.86	−5.37	62	88 550.7
Bathyergidae	38.4	15	0.0706	0.0564	0.0228	7 789 625	−7.44	−9.59	170.3	26 279.5
Bovidae	18.7	134	0.2622	0.2305	0.1424	56 071 127	−1.24	−6.99	1086.5	100 692.3
Bradypodidae	26	4	0.0533	0.0375	0.0101	10 896 101	−3.07	−4.1	33.8	17 805.8
Burramyidae	48.2	5	0.0334	0.0241	0.007	1 283 808	−5.32	−7	75.4	35 839.9
Caenolestidae	90.8	6	0.0197	0.0146	0.0045	340 216	−4.78	−5.8	211	12 722.1
Callitrichidae	13.8	42	0.2712	0.2293	0.1182	8 211 439	−4.76	−9.01	76.3	165 060.5
Calomyscidae	30.9	8	0.0673	0.0511	0.0172	1 075 536	−9.87	−10.85	260.5	1409.2
Camelidae	66	3	0.0166	0.0112	0.0028	2 323 493	−4.63	−5.85	24.6	1377.3
Canidae	48.4	35	0.0734	0.0615	0.0306	118 204 955	−0.57	−3.98	6068.8	235 383.9
Capromyidae	19.7	13	0.1302	0.1029	0.04	123 282	−10.37	−11.91	21.7	21 016.9
Castoridae	58.7	2	0.0118	0.0075	0.0016	18 975 764	−5.31	−5.43	1.5	3.4
Cebidae	13.8	17	0.2056	0.1656	0.0693	12 758 010	−2.86	−5.82	68.7	146 403.1
Cercopithecidae	21.3	123	0.2261	0.1983	0.1212	31 183 190	−1.85	−6.82	2670.9	518 810
Cervidae	20.3	54	0.196	0.1674	0.0905	76 143 249	−0.23	−4.65	2285.3	354 795.5
Cheirogaleidae	29.9	29	0.1125	0.0934	0.0446	289 204	−9.89	−12	51.3	25 503.8
Chinchillidae	27.2	6	0.066	0.0487	0.0149	3 029 534	−6.52	−7.61	269.2	4175.6
Chrysochloridae	64.5	21	0.0472	0.0385	0.017	946 762	−8.27	−11.52	218.7	30 256.5
Ctenodactylidae	42.2	5	0.0382	0.0276	0.008	1 371 877	−12.54	−13.23	110.3	1919
Ctenomyidae	22.5	60	0.1819	0.1559	0.0858	1 749 335	−7.13	−13.49	3242.8	124 491.7
Cuniculidae	30.1	2	0.023	0.0146	0.0032	12 901 337	−2.92	−3.25	239.2	203.2
Cynocephalidae	80.2	2	0.0086	0.0055	0.0012	1 542 056	−6.42	−6.43	0.2	10.9
Dasyproctidae	28.2	13	0.091	0.0719	0.028	10 754 521	−2.88	−5.22	101.7	719 486.2
Dasyuridae	33.9	72	0.1261	0.1088	0.0617	8 304 427	−4.82	−7.84	337.8	96 656.5
Didelphidae	81	98	0.0566	0.0493	0.0292	23 085 640	−2.09	−5.13	169.8	52 269.2
Dipodidae	51.6	50	0.0758	0.0645	0.0344	39 652 782	−4.78	−8.9	355.1	8447.9
Elephantidae	62	2	0.0112	0.0071	0.0015	3 975 154	−4.62	−5.38	0.1	18 015.9
Emballonuridae	52.2	52	0.0758	0.0646	0.0347	41 156 101	−1.07	−4.33	11.1	33 245.4
Equidae	58.5	7	0.0333	0.0249	0.008	4 695 786	−6.26	−8.67	9117.6	36 471.6
Erinaceidae	70.9	24	0.0448	0.0369	0.0168	41 049 823	−2.66	−7.39	319.4	11 524.9

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			Diversification rate							
Family	Age	S	ε = 0.0	ε = 0.45	ε = 0.9	Area (km^2)	FNW	MSNW	TNE	PNE
Felidae	29.8	36	0.1201	0.1008	0.0504	101 564 537	−0.16	−3.49	738.3	56 164.1
Furipteridae	33	2	0.021	0.0133	0.0029	9 686 263	−3.56	−3.94	62.9	71 473.9
Galagidae	37.9	18	0.0762	0.0616	0.0262	16 749 518	−5.16	−7.27	49.1	21 857.6
Giraffidae	20.1	2	0.0345	0.0218	0.0047	2 294 613	−9.54	−9.84	5.3	43 668.7
Gliridae	60.4	28	0.0552	0.0458	0.0217	19 997 589	−4.04	−7.85	150.4	29 375.1
Herpestidae	24.2	34	0.1455	0.1218	0.0602	32 336 739	−1.85	−4.47	63.4	31 076.4
Hippopotamidae	55.9	2	0.0124	0.0078	0.0017	2 021 067	−6.82	−7.48	8.4	22 232.9
Hipposideridae	44.3	84	0.1	0.0867	0.0503	42 164 259	−1.35	−5.06	304.5	1 902 269.2
Hominidae	16.2	6	0.1107	0.0817	0.0251	3 104 826	−6.26	−7.79	24.7	8209.3
Hyaenidae	27.9	4	0.0497	0.0349	0.0094	34 164 485	−3.99	−4.91	23.8	2916.3
Hylobatidae	16.2	16	0.1713	0.1375	0.0566	2 725 783	−2.94	−7.4	72.9	66 876.2
Hystricidae	45.1	11	0.0532	0.0415	0.0154	27 917 086	−1.66	−3.8	1063.6	1 507 282.9
Indriidae	29.9	18	0.0965	0.0781	0.0332	202 527	−10.66	−12.94	69.4	11 907.2
Lemuridae	30.7	21	0.0991	0.0809	0.0358	262 139	−9.93	−11.74	295.1	69 740.4
Leporidae	49.8	62	0.0829	0.0712	0.0394	105 215 759	−0.13	−5.76	906.5	49 595.8
Lorisidae	37.9	10	0.0607	0.047	0.0169	7 749 835	−3.41	−6.33	7.7	17 017.7
Macropodidae	25.5	63	0.1626	0.1397	0.0775	8 369 975	−4.47	−8.26	939.8	71 100.7
Macroscelididae	76.5	17	0.037	0.0298	0.0125	10 935 530	−6.7	−8.49	64	23 295
Manidae	80.4	8	0.0259	0.0196	0.0066	20 581 970	−2.53	−4.9	54.1	17 854.1
Megadermatidae	44.7	5	0.036	0.026	0.0075	17 962 591	−1.9	−3.66	3.4	27 724.5
Megalonychidae	26	2	0.0267	0.0169	0.0037	5 491 962	−3.16	−3.47	3	3672.9
Molossidae	49.3	100	0.0935	0.0815	0.0485	57 444 294	−1.19	−4.11	114.3	93 905.9
Mormoopidae	33.8	9	0.0651	0.0499	0.0174	11 165 117	−2.61	−3.74	4.9	2858.2
Moschidae	18.7	7	0.1042	0.0781	0.0252	10 302 535	−5.31	−7.27	710.4	48 091.9
Myrmecophagidae	41.3	3	0.0266	0.018	0.0044	14 606 567	−2.91	−3.05	0.2	413.1
Natalidae	52.4	11	0.0458	0.0357	0.0132	6 754 595	−3.99	−5.9	3	7864.6
Noctilionidae	33	2	0.021	0.0133	0.0029	14 859 794	−2.63	−2.43	1	493.7
Notoryctidae	67.1	2	0.0103	0.0065	0.0014	1 360 427	−21.02	−16.49	66.2	158.2
Nycteridae	52.2	16	0.0532	0.0426	0.0176	20 417 544	−4.37	−6.36	34	46 633.3
Ochotonidae	49.8	30	0.0683	0.0569	0.0273	20 744 722	−3.82	−7.8	346.9	7796.7
Pedetidae	54.7	2	0.0127	0.008	0.0017	4 297 716	−8.33	−8.63	2.9	369.2
Peramelidae	30.7	18	0.0942	0.0761	0.0324	2 349 572	−4.64	−6.8	444.1	37 017.6
Petauridae	40.7	11	0.0589	0.046	0.017	2 788 752	−4.65	−6.17	152.9	75 488.5
Phalangeridae	48.2	26	0.0676	0.0558	0.026	3 890 476	−4.52	−6.84	61	60 272.1
Phyllostomidae	33.8	173	0.1526	0.1351	0.0859	19 041 332	−2.06	−3.6	113.2	116 327.1
Prionodontidae	29.8	2	0.0232	0.0147	0.0032	3 805 072	−3.51	−5.29	581.4	133 054.9
Procaviidae	62	5	0.0259	0.0187	0.0054	20 879 586	−5.04	−6.26	14.1	16 314.9
Procyonidae	30	14	0.0879	0.0699	0.0277	26 201 302	−1.98	−4.2	523.3	43 295.2
Pseudocheiridae	40.7	18	0.071	0.0574	0.0244	1 894 912	−5.03	−7.13	51.8	41 528.5
Pteropodidae	63.5	183	0.082	0.0727	0.0465	29 378 339	−1.43	−5.54	187.1	482 020.2
Rhinocerotidae	52.3	5	0.0307	0.0222	0.0064	12 641 510	−5.44	−7.09	14.1	45 733.1
Rhinolophidae	44.3	74	0.0971	0.0839	0.0478	38 478 070	−1.19	−4.6	1575.6	349 130
Rhinopomatidae	53	3	0.0207	0.014	0.0034	18 805 492	−4.67	−5.23	15.7	386.4
Sciuridae	52.4	279	0.1075	0.0961	0.0641	94 058 541	−0.18	−6.09	737.3	145 891.1
Solenodontidae	75	2	0.0092	0.0058	0.0013	30 151	−11.3	−10.63	0	265.2
Soricidae	67	375	0.0885	0.0796	0.0545	89 142 599	−1.12	−6.66	1774.7	288 023
Suidae	31.1	18	0.0929	0.0751	0.0319	44 088 398	−1.55	−4.41	357.9	86 927
Tachyglossidae	47.2	4	0.0294	0.0206	0.0056	8 061 611	−4.84	−6.1	93.1	178 963
Talpidae	67	41	0.0555	0.0468	0.024	22 767 344	−2.18	−7.53	280.1	13 638.8

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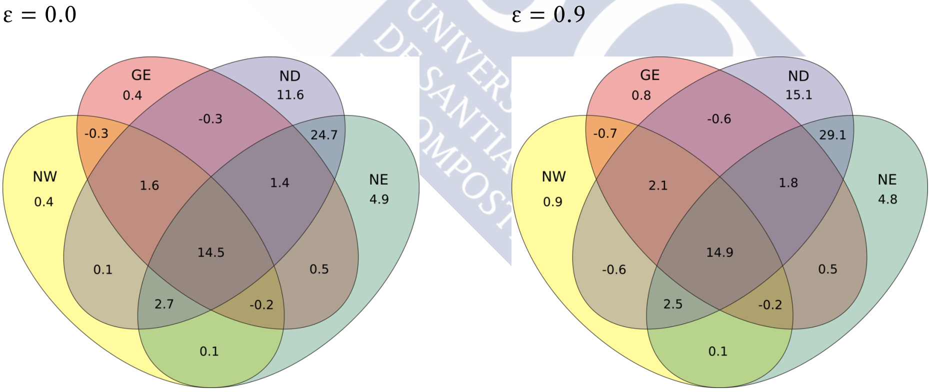
			Diversification rate							
Family	Age	S	ε = 0.0	ε = 0.45	ε = 0.9	Area (km^2)	FNW	MSNW	TNE	PNE
Tapiridae	52.3	4	0.0265	0.0186	0.005	14 096 321	−3.64	−5.05	679.9	3066.1
Tarsiidae	59.3	10	0.0389	0.0301	0.0108	1 157 479	−7.45	−9.1	54.7	102 327.5
Tayassuidae	31.1	3	0.0353	0.0239	0.0059	16 305 276	−2.79	−3.2	0.9	29 505.6
Tenrecidae	64.5	33	0.0542	0.0453	0.0222	4 439 112	−7.54	−9.59	271	46 328.2
Thryonomyidae	22.9	2	0.0303	0.0192	0.0042	7 709 923	−5.29	−5.43	14.9	4658.1
Thyropteridae	40.4	4	0.0343	0.0241	0.0065	10 058 317	−2.91	−3.88	0.2	2960.3
Tragulidae	42.7	10	0.0539	0.0418	0.015	7 020 197	−4.62	−6.91	17.8	36 817.2
Tupaiidae	57.3	18	0.0505	0.0408	0.0173	5 973 476	−2.6	−6.4	18.8	36 091.9
Ursidae	38.4	8	0.0541	0.0411	0.0138	66 363 940	−0.14	−3.2	1388.9	24 523.7
Vespertilionidae	49.3	417	0.1225	0.1104	0.0762	111 856 799	−0.31	−4.63	1035.6	241 300
Vombatidae	39.8	3	0.0276	0.0186	0.0046	379 792	−9.64	−10.26	100.7	5247.1

Appendix S4.3

Complementary analyses done for diversification rates estimated with relative extinction fractions of ε = 0.0 and ε = 0.9.

Table S4.3.1: Results of the phylogenetic generalized least squares (PGLS) regression with diversification rate as the response variable. Results from PGLS models testing the relationship between diversification rate (ε = 0.0 and ε = 0.9) and the variable in the first column as the explanatory variable. Significant P-values are marked in bold. F-values for 1 and 90 degrees of freedom.

	ε = 0.0			ε = 0.9		
	r^2	F	P	r^2	F	P
Family niche width	0.21	23.4	**< 0.001**	0.2	23.05	**< 0.001**
Mean sp. niche width	< 0.01	0.003	0.96	< 0.01	0.11	0.74
Niche divergence	0.57	118.3	**< 0.001**	0.65	164.6	**< 0.001**
Geographic extent	0.19	21.37	**< 0.001**	0.21	23.58	**< 0.001**
Niche position (BIO6)	0.06	6.153	**0.015**	0.07	6.793	**0.011**
Temp. niche evolution rate	0.37	52.06	**< 0.001**	0.4	59.89	**< 0.001**
Prec. niche evolution rate	0.42	65.32	**< 0.001**	0.45	74.41	**< 0.001**


ε = 0.0

ε = 0.9

Full model: $r^2 = 0.62$, $F_{5,86} = 28.16$, $P < 0.001$ (62.1% explained variance)

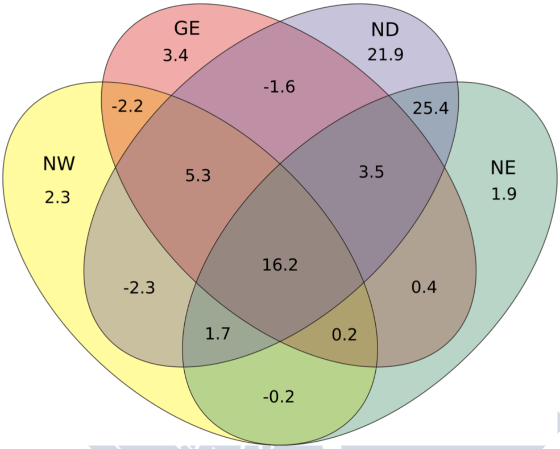
Full model: $r^2 = 0.71$, $F_{5,86} = 41.32$, $P < 0.001$ (70.6% explained variance)

Figure S4.3.1: Variance partitioning of the full model assessing the relationship between diversification rate (response variable) and family niche width (NW), geographic extent (GE), niche divergence (ND), and niche evolution rate (NE) as explanatory variables, with results for diversification rates calculated considering no extinction (ε = 0) and a high relative extinction fraction (ε = 0.9).

Appendix S4.4

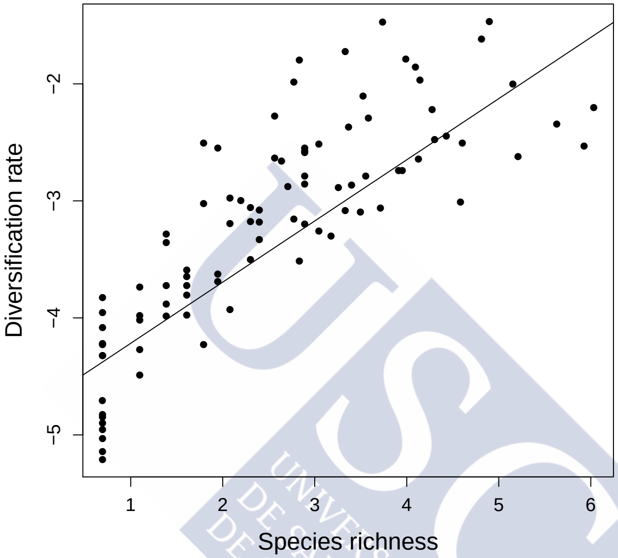
Results of the variance partitioning on a full model of species richness (ln-transformed) as the dependent variable with family niche width (NW), geographic extent (GE), niche divergence (ND), and rate of niche evolution (NE) as explanatory variables. Results are shown as percentage of explained variance.

Full model: $r^2 = 0.76$, $F_{5,86} = 54.18$, $P < 0.001$ (75.9% explained variance)



Appendix S4.5

Scatterplot of the relationship ($r^2 = 0.79$, $F_{1,90} = 342.7$, $P < 0.001$) between diversification rate (ε = 0.45) and species richness (both variables were ln-transformed). The fitted PGLS model is superimposed.

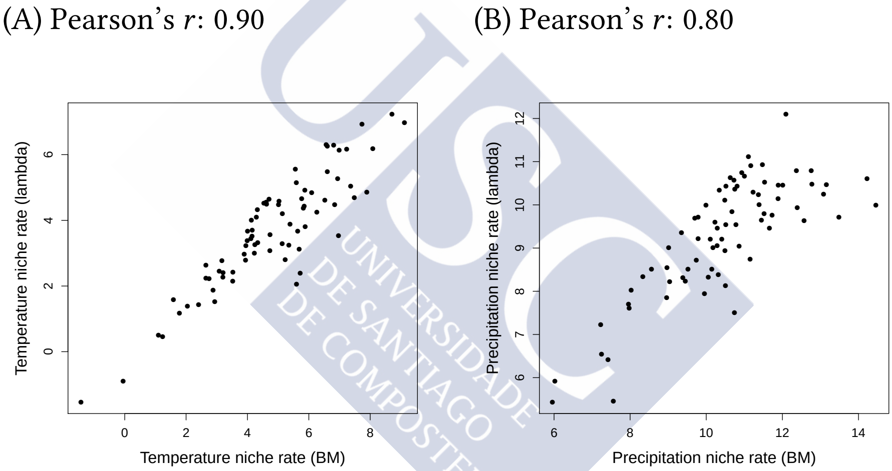


Appendix S4.6

Evolutionary models for the estimation of niche evolution rates.

Table S4.6.1: AIC values of the evolutionary models for rates of change in annual mean temperature (BIO1) and annual mean precipitation (BIO12). The lowest AIC (corresponding to the best-fitting model) is marked in bold.

	BM	OU	Lambda	White
Annual mean temperature (BIO1)	35 315	33 906	**32 585**	34 501
Annual mean precipitation	52 004	49 478	**47 985**	49 468


(A) Pearson's r: 0.90

(B) Pearson's r: 0.80

Figure S4.6.1: Scatterplots showing the relationship between the sigma parameter values computed using a Brownian-motion model of evolution (x-axis) and a lambda model (y-axis) for annual mean temperature (A) and annual mean precipitation (B). Both variables were ln-transformed. Pearson's r values measure the linear correlation between these estimates of niche evolution rate. Both estimates could be computed for 76 families.

Appendix S4.7

Comparison of temperature and precipitation niche evolution rates obtained using phylogenies of 18 mammal families from two different sources. The second to fourth columns show the number of species in the phylogeny used for the results in the main text (from Rolland *et al.* 2014), number of species in alternative phylogenies (from Arnold *et al.* 2010), and the number of shared species between them. The last four columns show the values of niche evolution rates estimated from the phylogenies from both sources.

Family	Species Rolland *et al.* 2014	Species Arnold *et al.* 2010	Shared species	T niche rate Rolland *et al.* 2014	P niche rate Rolland *et al.* 2014	T niche rate Arnold *et al.* 2010	P niche rate Arnold *et al.* 2010
Hominidae	6	6	6	24.7	8209.3	39	8733.9
Atelidae	24	13	13	62	88 550.7	122.9	122 355.7
Callitrichidae	36	25	23	76.3	165 060.5	72.3	108 777.4
Cebidae	12	9	9	68.7	146 403.1	24.5	132 019.3
Tarsiidae	7	4	3	54.7	102 327.5	87.4	8920.4
Indriidae	10	11	9	69.4	11 907.2	105	50 860.4
Lemuridae	19	18	17	295.1	69 740.4	174.2	74 264.9
Lorisidae	8	10	8	7.7	17 017.7	91	220 093.4
Galagidae	18	11	11	49.1	21 857.6	141	32 137
Rhinocerotidae	5	5	5	14.1	45 733.1	7.4	19 291.9
Tapiridae	4	4	4	679.9	3066.1	763.5	3207.1
Canidae	34	32	31	6068.8	235 383.9	1973.7	53 819.9
Procyonidae	14	10	10	523.3	43 295.2	249.2	25 114.8
Ursidae	8	8	8	1388.9	24 523.7	1649.9	30 297
Camelidae	3	3	3	24.6	1377.3	41.5	1571.7
Moschidae	7	5	5	710.4	48 091.9	1179.5	36 488.4
Suidae	18	12	12	357.9	86 927	449	137 591
Tayassuidae	3	3	3	0.9	29 505.6	2.8	34 653

Appendix S4.8

Results of the forward stepwise procedure used to select the most parsimonious model explaining diversification rate (estimated with different relative extinction fractions, ε) using niche position variables. The tables show the results of an ANOVA comparing the models specified in the first two columns.

Table S4.8.1: $\varepsilon = 0.45$

Step	Model	*F*	d.f.	*P*
Step 1:	x = BIO1	5.04	1, 90	0.027
Div. rate ~ 1 (null model)	x = BIO5	0.96	1, 90	0.331
vs.	x = BIO6	6.34	1, 90	0.014
Div. rate ~ x	x = BIO12	3.46	1, 90	0.066
	x = BIO16	2.16	1, 90	0.145
	x = BIO17	3.85	1, 90	0.053
Step 2:	x = BIO1	0.96	1, 89	0.329
Div. rate ~ BIO6	x = BIO5	1.42	1, 89	0.237
vs.	x = BIO12	0.15	1, 89	0.697
Div. rate ~ BIO6 + x	x = BIO16	0.08	1, 89	0.778
	x = BIO17	1.19	1, 89	0.279

Final model: Diversification rate ~ BIO6

Table S4.8.2: $\varepsilon = 0.0$

Step	Model	*F*	d.f.	*P*
Step 1:	x = BIO1	4.84	1, 90	0.03
Div. rate ~ 1 (null model)	x = BIO5	0.85	1, 90	0.359
vs.	x = BIO6	6.15	1, 90	0.015
Div. rate ~ x	x = BIO12	3.53	1, 90	0.064
	x = BIO16	2.21	1, 90	0.14
	x = BIO17	3.97	1, 90	0.049
Step 2:	x = BIO1	1.06	1, 89	0.307
Div. rate ~ BIO6	x = BIO5	1.59	1, 89	0.211
vs.	x = BIO12	0.22	1, 89	0.643
Div. rate ~ BIO6 + x	x = BIO16	0.03	1, 89	0.853
	x = BIO17	1.32	1, 89	0.254

Final model: Diversification rate ~ BIO6

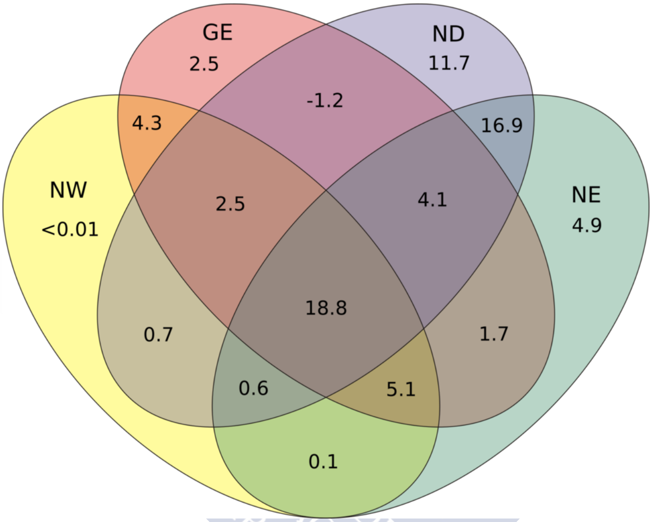
Table S4.8.3: $\varepsilon = 0.9$

Step	Model	F	d.f.	P
Step 1:	x = BIO1	5.53	1, 90	0.021
Div. rate ~ 1 (null model)	x = BIO5	1.24	1, 90	0.268
vs.	x = BIO6	6.79	1, 90	0.011
Div. rate ~ x	x = BIO12	3.33	1, 90	0.071
	x = BIO16	2.06	1, 90	0.155
	x = BIO17	3.54	1, 90	0.063
Step 2:	x = BIO1	0.79	1, 89	0.378
Div. rate ~ BIO6	x = BIO5	1.09	1, 89	0.299
vs.	x = BIO12	0.05	1, 89	0.826
Div. rate ~ BIO6 + x	x = BIO16	0.24	1, 89	0.623
	x = BIO17	0.87	1, 89	0.352

Final model: Diversification rate ~ BIO6

Appendix S4.9

Results of the variance partitioning on a full model of species richness with clade niche width (NW), geographic extent (GE), niche divergence (ND), and niche evolution (NE) as explanatory variables, but using clades defined with an age equal to the mean stem group age of all families (mean stem group age = 41.7 Mya). 86 clades were used in this analysis. Results are shown as percentage of explained variance. Full model: $r^2 = 0.73$, $F_{5,80} = 42.48$, $P < 0.001$.



Appendix S4.10

Results of the PGLS between niche evolution rates and mean species niche width of each family.

Temperature niche evolution rate
$r^2 = 0.006$, $F_{1,90} = 9.061$, $P = 0.48$

Precipitation niche evolution rate
$r^2 = 0.014$, $F_{1,90} = 1.275$, $P = 0.26$

Appendix S4.11

Kernel density plots showing the distribution of r^2 across 1000 replicates of 92 randomly sampled clades of richness equivalent to real families under three different null models (unconstrained, geographically constrained, and climatically constrained). These distributions correspond to the r^2 of PGLS analyses conducted to assess the relationship between (a) family niche width and mean species niche width, (b) diversification rate and family niche width (c) diversification rate and mean species niche width, and (d) diversification rate and niche divergence. The observed r^2 is indicated with a vertical gray line.

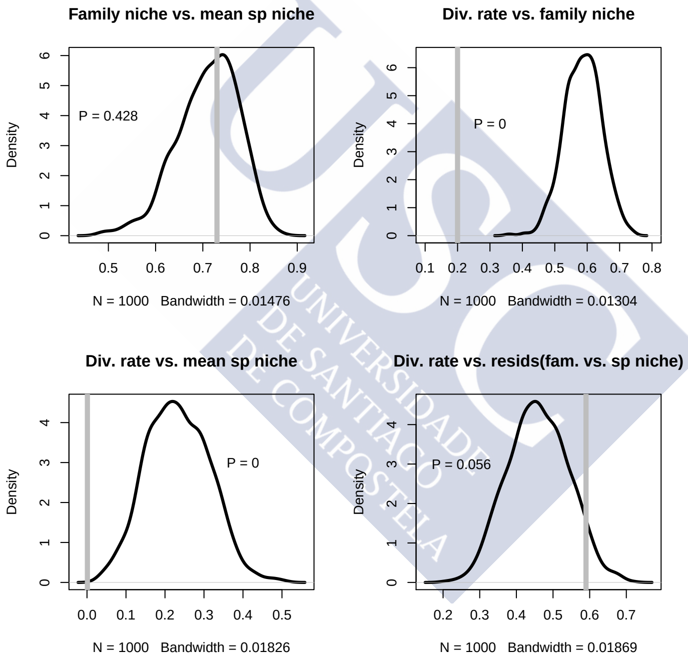


Figure S4.11.1: Distribution of r^2 across 1000 replicates in the unconstrained null model (species from each null clade are sampled from the pool of all mammal species). The observed r^2 is indicated with a vertical gray line.

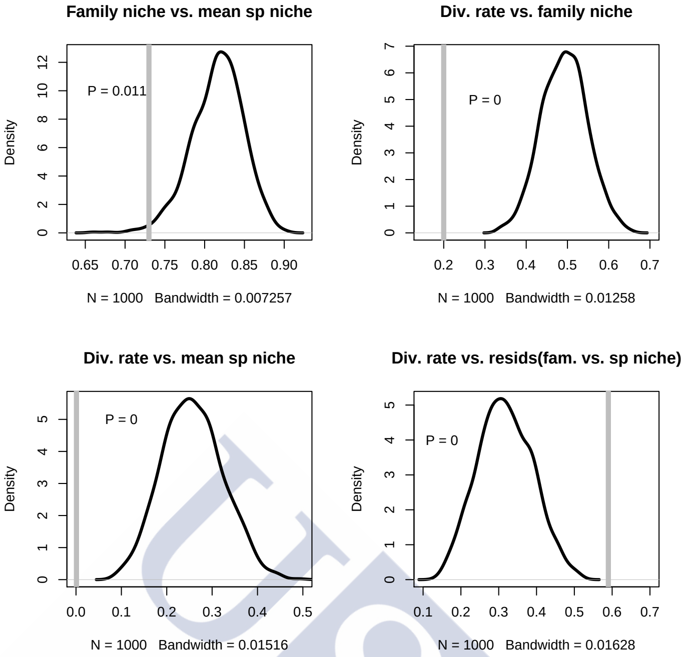


Figure S4.11.2: Distribution of r^2 across 1000 replicates in the geographically constrained null model (species from each null clade are sampled from the pool of species within the latitudinal and longitudinal extent of the corresponding original family). The observed r^2 is indicated with a vertical gray line.

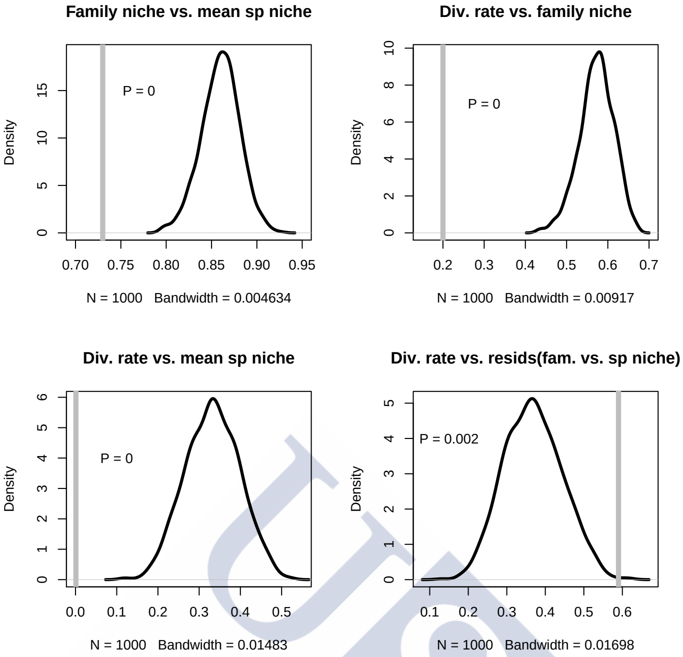
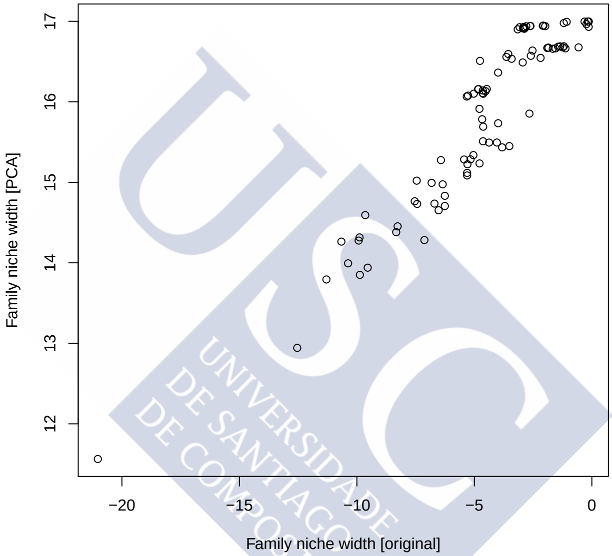


Figure S4.11.3: Distribution of r^2 across 1000 replicates in the climatically constrained null model (species from each null clade are sampled within the original family climatic niche). The observed r^2 is indicated with a vertical gray line.

Appendix S4.12

Comparison of measures of family niche width. Family niche width calculated as the product of the climatic ranges on the six climatic variables (measure used in this study) is very strongly correlated with family niche width calculated multiplying the ranges on the first two principal components (explaining 97.12% of the variance in the original variables) of a PCA on the six climatic variables (Pearson's $r = 0.937$).



Bibliography

Alexandri, P., Triantafyllidis, A., Papakostas, S., Chatzinikos, E., Platis, P., Papageorgiou, N., Larson, G., Abatzopoulos, T. J. & Triantaphyllidis, C. (2012) The Balkans and the colonization of Europe: the post-glacial range expansion of the wild boar, *Sus scrofa*. *Journal of Biogeography*, **39**, 713–723.

Alsos, I. G., Eidesen, P. B., Ehrich, D., Skrede, I., Westergaard, K., Jacobsen, G. H., Landvik, J. Y., Taberlet, P. & Brochmann, C. (2007) Frequent long-distance plant colonization in the changing Arctic. *Science*, **316**, 1606–1609.

Araújo, M. B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P. A., Valladares, F. & Chown, S. L. (2013) Heat freezes niche evolution. *Ecology Letters*, **16**, 1206–1219.

Araújo, M. B., Nogués-Bravo, D., Diniz-Filho, J. A. F., Haywood, A. M., Valdes, P. J. & Rahbek, C. (2008) Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography*, **31**, 8–15.

Araújo, M. B. & Pearson, R. G. (2005) Equilibrium of species' distributions with climate. *Ecography*, **28**, 693–695.

Arnold, C., Matthews, L. J. & Nunn, C. L. (2010) The 10kTrees website: A new online resource for primate phylogeny. *Evolutionary Anthropology: Issues, News, and Reviews*, **19**, 114–118.

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19**, 134–143.

Baselga, A. (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, **21**, 1223–1232.

Baselga, A. (2013) Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. *Ecography*, **36**, 124–128.

Baselga, A., Gómez-Rodríguez, C. & Lobo, J. M. (2012a) Historical legacies in world amphibian diversity revealed by the turnover and nestedness components of beta diversity. *PLoS ONE*, **7**, e32341.

Baselga, A. & Leprieur, F. (2015) Comparing methods to separate components of beta diversity. *Methods in Ecology and Evolution*, **6**, 1069–1079.

Baselga, A., Lobo, J. M., Svenning, J.-C., Aragón, P. & Araújo, M. B. (2012b) Dispersal ability modulates the strength of the latitudinal richness gradient in European beetles. *Global Ecology and Biogeography*, **21**, 1106–1113.

Baselga, A., Lobo, J. M., Svenning, J.-C. & Araújo, M. B. (2012c) Global patterns in the shape of species geographical ranges reveal range determinants. *Journal of Biogeography*, **39**, 760–771.

Baselga, A. & Orme, C. D. L. (2012) betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, **3**, 808–812.

Beck, J., Ballesteros-Mejia, L., Buchmann, C. M., Dengler, J., Fritz, S. A., Gruber, B., Hof, C., Jansen, F., Knapp, S., Kreft, H., Schneider, A.-K., Winter, M. & Dormann, C. F. (2012) What's on the horizon for macroecology? *Ecography*, **35**, 673–683.

Bininda-Emonds, O. R. P., Cardillo, M., Jones, K. E., MacPhee, R. D. E., Beck, R. M. D., Grenyer, R., Price, S. A., Vos, R. A., Gittleman, J. L. & Purvis, A. (2007) The delayed rise of present-day mammals. *Nature*, **446**, 507–512.

BirdLife International & NatureServe (2013) *Bird species distribution maps of the world.* Version 3.0. BirdLife International, Cambridge, UK and NatureServe, Arlington, USA.

Bivand, R., Keitt, T. & Rowlingson, B. (2014) *rgdal: Bindings for the 'Geospatial' Data Abstraction Library.* https://CRAN.R-project.org/package=rgdal.

Bivand, R. & Lewin-Koh, N. (2016) *maptools: Tools for Reading and Handling Spatial Objects.* https://CRAN.R-project.org/package=maptools.

Bivand, R. & Rundel, C. (2016) *rgeos: Interface to Geometry Engine - Open Source ('GEOS').* https://CRAN.R-project.org/package=rgeos.

Brown, J. H. & Maurer, B. A. (1989) Macroecology: the division of food and space among species on continents. *Science*, **243**, 1145–1150.

Brown, J. H. & Lomolino, M. V. (1998) *Biogeography.* 2nd ed., Sinauer Associates Inc, Sunderland, MA, U.S.A.

Brown, J. H., Stevens, G. C. & Kaufman, D. M. (1996) The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, **27**, 597–623.

Buckley, L. B. & Jetz, W. (2007) Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 1167–1173.

Cadena, C. D., Kozak, K. H., Gómez, J. P., Parra, J. L., McCain, C. M., Bowie, R. C. K., Carnaval, A. C., Moritz, C., Rahbek, C., Roberts, T. E., Sanders, N. J., Schneider, C. J., VanDerWal, J., Zamudio, K. R. & Graham, C. H. (2012) Latitude, elevational climatic zonation and speciation in New World vertebrates. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 194–201.

Cain, S. A. (1944) *Foundations of Plant Geography.* Harper & Brothers, New York.

Cardillo, M., Huxtable, J. S. & Bromham, L. (2003) Geographic range size, life history and rates of diversification in Australian mammals. *Journal of Evolutionary Biology*, **16**, 282–288.

Chao, A., Chiu, C.-H. & Hsieh, T. C. (2012) Proposing a resolution to debates on diversity partitioning. *Ecology*, **93**, 2037–2051.

Clarke, K. R. (1993) Non-parametric multivariate analyses of changes in community structure. *Austral Ecology*, **18**, 117–143.

Cooney, C. R., Seddon, N. & Tobias, J. A. (2016) Widespread correlations between climatic niche evolution and species diversification in birds. *Journal of Animal Ecology*, **85**, 869–878.

Cooper, N., Freckleton, R. P. & Jetz, W. (2011) Phylogenetic conservatism of environmental niches in mammals. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 2384–2391.

Costello, M. J., Tsai, P., Wong, P. S., Cheung, A. K. L., Basher, Z. & Chaudhary, C. (2017) Marine biogeographic realms and species endemicity. *Nature Communications*, **8**, 1057.

Crawley, M. J. (2007) *The R Book.* 1st ed., Wiley, Chichester, UK.

Currie, D. J. (2007) Disentangling the roles of environment and space in ecology. *Journal of Biogeography*, **34**, 2009–2011.

Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guegan, J.-F., Hawkins, B. A., Kaufman, D. M., Kerr, J. T., Oberdorff, T., O'Brien, E. & Turner, J. R. G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7**, 1121–1134.

Dapporto, L., Ciolli, G., Dennis, R. L. H., Fox, R. & Shreeve, T. G. (2015) A new procedure for extrapolating turnover regionalization at mid-small spatial scales, tested on British butterflies. *Methods in Ecology and Evolution*, **6**, 1287–1297.

Davies, T. J., Purvis, A. & Gittleman, J. L. (2009) Quaternary climate change and the geographic ranges of mammals. *The American Naturalist*, **174**, 297–307.

Dobrovolski, R., Melo, A. S., Cassemiro, F. A. S. & Diniz-Filho, J. A. F. (2012) Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **21**, 191–197.

Dufresnes, C. & Perrin, N. (2015) Effect of biogeographic history on population vulnerability in European amphibians. *Conservation Biology*, **29**, 1235–1241.

Ehlers, J., Gibbard, P. L. & Hughes, P. D. (2018) Chapter 4 - Quaternary Glaciations and Chronology. *Past Glacial Environments* (ed. by Menzies, J. & van der Meer, J. J. M.), pp. 77–101. 2nd ed., Elsevier.

Fabre, P.-H., Hautier, L., Dimitrov, D. & Douzery, E. J. P. (2012) A glimpse on the pattern of rodent diversification: a phylogenetic approach. *BMC Evolutionary Biology*, **12**, 88.

Fisher-Reid, M. C., Kozak, K. H. & Wiens, J. J. (2012) How is the rate of climatic-niche evolution related to climatic-niche breadth? *Evolution*, **66**, 3836–3851.

Freckleton, R. P., Harvey, P. H. & Pagel, M. (2002) Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist*, **160**, 712–726.

Fritz, S. A., Bininda-Emonds, O. R. P. & Purvis, A. (2009) Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecology Letters*, **12**, 538–549.

Futuyma, D. J. (2013) *Evolution*. 3rd ed., Sinauer Associates, Inc., Sunderland, MA.

Gaston, K. J. (2003) *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, Oxford, UK.

Gaston, K. J. & Blackburn, T. M. (1996) Range size-body size relationships: evidence of scale dependence. *Oikos*, **75**, 479.

Gaston, K. J. & Blackburn, T. M. (2000) *Pattern and Process in Macroecology*. 1st ed., Wiley-Blackwell, Oxford, UK.

Gaston, K. J., Blackburn, T. M. & Spicer, J. I. (1998) Rapoport's rule: time for an epitaph? *Trends in Ecology & Evolution*, **13**, 70–74.

Ghalambor, C. K., Huey, R. B., Martin, P. R., Tewksbury, J. J. & Wang, G. (2006) Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology*, **46**, 5–17.

Gómez-Rodríguez, C., Baselga, A. & Wiens, J. J. (2015) Is diversification rate related to climatic niche width? *Global Ecology and Biogeography*, **24**, 383–395.

Grafen, A. (1989) The Phylogenetic Regression. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **326**, 119–157.

Harmon, L. J., Weir, J. T., Brock, C. D., Glor, R. E. & Challenger, W. (2008) GEIGER: investigating evolutionary radiations. *Bioinformatics*, **24**, 129–131.

Harrison, S., Ross, S. J. & Lawton, J. H. (1992) Beta diversity on geographic gradients in Britain. *The Journal of Animal Ecology*, **61**, 151–158.

Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J.-F., Kaufman, D. M., Kerr, J. T., Mittelbach, G. G., Oberdorff, T., O'Brien, E. M., Porter, E. E. & Turner, J. R. G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.

Hewitt, G. M. (1999) Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society*, **68**, 87–112.

Hijmans, R. J. (2014) *raster: Geographic Data Analysis and Modeling*. R package version 2.2-31. `https://CRAN.R-project.org/package=raster`.

Hijmans, R. J. (2016) *geosphere: Spherical Trigonometry*. R package version 1.5-1. `https://CRAN.R-project.org/package=geosphere`.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**. Available at `http://www.worldclim.org`, 1965–1978.

Hock, R. J. (1951) The metabolic rates and body temperatures of bats. *The Biological Bulletin*, **101**, 289–299.

Holt, B. G., Lessard, J.-P., Borregaard, M. K., Fritz, S. A., Araújo, M. B., Dimitrov, D., Fabre, P.-H., Graham, C. H., Graves, G. R., Jønsson, K. A., Nogués-Bravo, D., Wang, Z., Whittaker, R. J., Fjeldså, J. & Rahbek, C. (2013) An update of Wallace's zoogeographic regions of the world. *Science*, **339**, 74–78.

Holt, R. D. (2009) Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences*, **106**, 19659–19665.

Hortal, J., Diniz-Filho, J. A. F., Bini, L. M., Rodríguez, M. Á., Baselga, A., Nogués-Bravo, D., Rangel, T. F., Hawkins, B. A. & Lobo, J. M. (2011) Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. *Ecology Letters*, **14**, 741–748.

Hua, X. & Wiens, J. J. (2010) Latitudinal variation in speciation mechanisms in frogs. *Evolution*, **64**, 429–443.

Hua, X. & Wiens, J. J. (2013) How does climate influence speciation? *The American Naturalist*, **182**, 1–12.

Hubbell, S. P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ, U.S.A.

Hutchinson, G. E. (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415–427.

IUCN (2013) *IUCN Red List of Threatened Species*. Version 2013.2. http://www.iucnredlist.org/technical-documents/spatial-data.

Jansa, S. A., Barker, F. K. & Voss, R. S. (2014) The early diversification history of didelphid marsupials: a window into South America's "splendid isolation". *Evolution*, **68**, 684–695.

Janzen, D. H. (1967) Why mountain passes are higher in the tropics. *The American Naturalist*, **101**, 233–249.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. (2012) The global diversity of birds in space and time. *Nature*, **491**, 444–448.

Jezkova, T. & Wiens, J. J. (2016) Rates of change in climatic niches in plant and animal populations are much slower than projected climate change. *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20162104.

Keith, S. A., Webb, T. J., Bohning-Gaese, K., Connolly, S. R., Dulvy, N. K., Eigenbrod, F., Jones, K. E., Price, T., Redding, D. W., Owens, I. P. F. & Isaac, N. J. B. (2012) What is macroecology? *Biology Letters*, **8**, 904–906.

Kerr, J. T. & Packer, L. (1997) Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature*, **385**, 252–254.

Koleff, P., Lennon, J. J. & Gaston, K. J. (2003) Are there latitudinal gradients in species turnover? *Global Ecology and Biogeography*, **12**, 483–498.

Kozak, K. H. & Wiens, J. J. (2007) Climatic zonation drives latitudinal variation in speciation mechanisms. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 2995–3003.

Kozak, K. H. & Wiens, J. J. (2010) Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters*, **13**, 1378–1389.

Kozak, K. H. & Wiens, J. J. (2016) Testing the relationships between diversification, species richness, and trait evolution. *Systematic Biology*, **65**, 975–988.

Kreft, H. & Jetz, W. (2010) A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography*, **37**, 2029–2053.

Kuhn, T. S., Mooers, A. Ø. & Thomas, G. H. (2011) A simple polytomy resolver for dated phylogenies. *Methods in Ecology and Evolution*, **2**, 427–436.

Lawson, A. M. & Weir, J. T. (2014) Latitudinal gradients in climatic-niche evolution accelerate trait evolution at high latitudes. *Ecology Letters*, **17**, 1427–1436.

Lennon, J. J., Koleff, P., GreenwooD, J. J. D. & Gaston, K. J. (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology*, **70**, 966–979.

Leprieur, F., Tedesco, P. A., Hugueny, B., Beauchard, O., Dürr, H. H., Brosse, S. & Oberdorff, T. (2011) Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecology Letters*, **14**, 325–334.

Loehle, C. (1998) Height growth rate tradeoffs determine northern and southern range limits for trees. *Journal of Biogeography*, **25**, 735–742.

Losos, J. B. & Schluter, D. (2000) Analysis of an evolutionary species–area relationship. *Nature*, **408**, 847–850.

Magallón, S. & Sanderson, M. J. (2001) Absolute diversification rates in angiosperm clades. *Evolution*, **55**, 1762–1780.

McGuire, L. P. & Guglielmo, C. G. (2009) What can birds tell us about the migration physiology of bats? *Journal of Mammalogy*, **90**, 1290–1297.

Médail, F. & Diadema, K. (2009) Glacial refugia influence plant diversity patterns in the Mediterranean Basin. *Journal of Biogeography*, **36**, 1333–1345.

Melo, A. S., Rangel, T. F. L. V. B. & Diniz-Filho, J. A. F. (2009) Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography*, **32**, 226–236.

Meredith, R. W. et al. (2011) Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science*, **334**, 521–524.

Meyer, A. L. S. & Wiens, J. J. (2017) Estimating diversification rates for higher taxa: BAMM can give problematic estimates of rates and rate shifts. *Evolution*, **72**, 39–53.

Mittelbach, G. G. et al. (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**, 315–331.

Moen, D. S. & Wiens, J. J. (2017) Microhabitat and climatic niche change explain patterns of diversification among frog families. *The American Naturalist*, **190**, 29–44.

Moritz, C., Patton, J. L., Schneider, C. J. & Smith, T. B. (2000) Diversification of rainforest faunas: an integrated molecular approach. *Annual Review of Ecology and Systematics*, **31**, 533–563.

Morueta-Holme, N., Fløjgaard, C. & Svenning, J.-C. (2010) Climate change risks and conservation implications for a threatened small-range mammal species. *PLoS ONE*, **5**, e10360.

Morueta-Holme, N. et al. (2013) Habitat area and climate stability determine geographical variation in plant species range sizes. *Ecology Letters*, **16**, 1446–1454.

Nee, S., Mooers, A. O. & Harvey, P. H. (1992) Tempo and mode of evolution revealed from molecular phylogenies. *Proceedings of the National Academy of Sciences*, **89**, 8322–8326.

Normand, S., Treier, U. A., Randin, C., Vittoz, P., Guisan, A. & Svenning, J.-C. (2009) Importance of abiotic stress as a range-limit determinant for European plants: insights from species responses to climatic gradients. *Global Ecology and Biogeography*, **18**, 437–449.

O'Meara, B. C., Ané, C., Sanderson, M. J. & Wainwright, P. C. (2006) Testing for different rates of continuous trait evolution using likelihood. *Evolution*, **60**, 922–933.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E. & Wagner, H. (2017) *vegan: Community Ecology Package*. R package version 2.4-5. `https://CRAN.R-project.org/package=vegan`.

Orme, C. D. L., Davies, R. G., Olson, V. A., Thomas, G. H., Ding, T.-S., Rasmussen, P. C., Ridgely, R. S., Stattersfield, A. J., Bennett, P. M., Owens, I. P. F., Blackburn, T. M. & Gaston, K. J. (2006) Global patterns of geographic range size in birds. *PLoS Biology*, **4**, e208.

Orme, C. D. L., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N. & Pearse, W. (2013) *caper: Comparative Analyses of Phylogenetics and Evolution in R*. `https://CRAN.R-project.org/package=caper`.

Osborne, P. (2013) The geometry of the ellipsoid. *The Mercator Projections: The Normal and Transverse Mercator Projections on the Sphere and the Ellipsoid with Full Derivations of all Formulae*, Edinburgh.

Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature*, **401**, 877–884.

Patterson, B., Ceballos, G., Sechrest, W., Tognelli, M., Brooks, T., Luna, L., Ortega, P., Salazar, I. & Young, B. (2007) *Digital Distribution Maps of the Mammals of the Western Hemisphere*. Version 3.0. Available at `http://www.natureserve.org` (accessed 5 October 2009). NatureServe, Arlington, VA.

Pearson, R. G. & Dawson, T. P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.

Peel, M. C., Finlayson, B. L. & McMahon, T. A. (2007) Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences Discussions*, **4**, 439–473.

Pellissier, L., Bråthen, K. A., Vittoz, P., Yoccoz, N. G., Dubuis, A., Meier, E. S., Zimmermann, N. E., Randin, C. F., Thuiller, W., Garraud, L., Es, J. V. & Guisan, A. (2013) Thermal niches are more conserved at cold than warm limits in arctic-alpine plant species. *Global Ecology and Biogeography*, **22**, 933–941.

Peterson, A. T., Soberón, J., Pearson, R. G., Anderson, R. P., Martínez-Meyer, E., Nakamura, M. & Araújo, M. B. (2011) *Ecological Niches and Geographic Distributions*. Princeton University Press, Princeton, NJ, U.S.A.

Pfrender, M. E., Bradshaw, W. E. & Kleckner, C. A. (1998) Patterns in the geographical range sizes of ectotherms in North America. *Oecologia*, **115**, 439–444.

Pigot, A. L., Owens, I. P. F. & Orme, C. D. L. (2010) The environmental limits to geographic range expansion in birds. *Ecology Letters*, **13**, 705–715.

Pontarp, M. & Wiens, J. J. (2017) The origin of species richness patterns along environmental gradients: uniting explanations based on time, diversification rate and carrying capacity. *Journal of Biogeography*, **44**, 722–735.

Pough, F. H., Janis, C. M. & Heiser, J. B. (2009) *Vertebrate Life*. 8th ed., Benjamin Cummings, New York.

Price, S. A., Hopkins, S. S. B., Smith, K. K. & Roth, V. L. (2012) Tempo of trophic evolution and its impact on mammalian diversification. *Proceedings of the National Academy of Sciences*, **109**, 7008–7012.

Pyron, R. A. & Wiens, J. J. (2013) Large-scale phylogenetic analyses reveal the causes of high tropical amphibian diversity. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20131622.

Qian, H. & Ricklefs, R. E. (2016) Out of the tropical lowlands: latitude versus elevation. *Trends in Ecology & Evolution*, **31**, 738–741.

Quintero, I. & Wiens, J. J. (2013) What determines the climatic niche width of species? The role of spatial and temporal climatic variation in three vertebrate clades. *Global Ecology and Biogeography*, **22**, 422–432.

R Core Team (2016) *R: A Language and Environment for Statistical Computing*. `https://www.R-project.org/`. R Foundation for Statistical Computing, Vienna, Austria.

Rabosky, D. L. (2009) Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. *Ecology Letters*, **12**, 735–743.

Rabosky, D. L. (2015) No substitute for real data: A cautionary note on the use of phylogenies from birth-death polytomy resolvers for downstream comparative analyses. *Evolution*, **69**, 3207–3216.

Rabosky, D. L. & Adams, D. C. (2012) Rates of morphological evolution are correlated with species richness in salamanders. *Evolution*, **66**, 1807–1818.

Rahbek, C. & Graves, G. R. (2001) Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences*, **98**, 4534–4539.

Rapoport, E. H. (1975) *Areografía: estrategias geográficas de las especies*. Fondo de Cultura Económica, México D.F.

Ricklefs, R. E. (1987) Community diversity: relative roles of local and regional processes. *Science*, **235**, 167–171.

Ricklefs, R. E. (2007) Estimating diversification rates from phylogenetic information. *Trends in Ecology & Evolution*, **22**, 601–610.

Ridgely, R., Allnutt, T., Brooks, T., McNicol, D., Mehlman, D., Young, B. & Zook, J. (2007) *Digital Distribution Maps of the Birds of the Western Hemisphere*. Version 3.0. Available at `http://www.natureserve.org` (accessed 5 October 2009). NatureServe, Arlington, VA.

Rolland, J., Condamine, F. L., Jiguet, F. & Morlon, H. (2014) Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biology*, **12**, e1001775.

Rolland, J. & Salamin, N. (2016) Niche width impacts vertebrate diversification. *Global Ecology and Biogeography*, **25**, 1252–1263.

Rosenfield, J. A. (2002) Pattern and process in the geographical ranges of freshwater fishes. *Global Ecology and Biogeography*, **11**, 323–332.

Rosenzweig, M. L. (1995) *Species Diversity in Space and Time*. Cambridge University Press.

Ruggiero, A. & Werenkraut, V. (2007) One-dimensional analyses of Rapoport's rule reviewed through meta-analysis. *Global Ecology and Biogeography*, **16**, 401–414.

Sastre, P., Roca, P., Lobo, J. M. & EDIT co-workers (2009) A Geoplatform for improving accessibility to environmental cartography. *Journal of Biogeography*, **36**, 568–568.

Schenk, J. J., Rowe, K. C. & Steppan, S. J. (2013) Ecological opportunity and incumbency in the diversification of repeated continental colonizations by muroid rodents. *Systematic Biology*, **62**, 837–864.

Schnitzler, J., Graham, C. H., Dormann, C. F., Schiffers, K. & Linder, H. P. (2012) Climatic niche evolution and species diversification in the Cape flora, South Africa. *Journal of Biogeography*, **39**, 2201–2211.

Scholl, J. P. & Wiens, J. J. (2016) Diversification rates and species richness across the Tree of Life. *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20161334.

Shi, J. J. & Rabosky, D. L. (2015) Speciation dynamics during the global radiation of extant bats. *Evolution*, **69**, 1528–1545.

Simpson, G. G. (1960) Notes on the measurement of faunal resemblance. *American Journal of Science*, **258**, 300–311.

Smith, B. T., Bryson, R. W., Houston, D. D. & Klicka, J. (2012) An asymmetry in niche conservatism contributes to the latitudinal species diversity gradient in New World vertebrates. *Ecology Letters*, **15**, 1318–1325.

Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, **10**, 1115–1123.

Sommer, R. S. & Zachos, F. E. (2009) Fossil evidence and phylogeography of temperate species: ‘glacial refugia’ and post-glacial recolonization. *Journal of Biogeography*, **36**, 2013–2020.

Soria-Carrasco, V. & Castresana, J. (2012) Diversification rates and the latitudinal gradient of diversity in mammals. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4148–4155.

Stadler, T. (2011) Mammalian phylogeny reveals recent diversification rate shifts. *Proceedings of the National Academy of Sciences*, **108**, 6187–6192.

Stevens, G. C. (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *The American Naturalist*, **133**, 240–256.

Sunday, J. M., Bates, A. E. & Dulvy, N. K. (2012) Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, **2**, 686–690.

Svenning, J.-C., Fløjgaard, C. & Baselga, A. (2011) Climate, history and neutrality as drivers of mammal beta diversity in Europe: insights from multiscale deconstruction. *Journal of Animal Ecology*, **80**, 393–402.

Svenning, J.-C. & Skov, F. (2007a) Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecology Letters*, **10**, 453–460.

Svenning, J.-C. & Skov, F. (2007b) Ice age legacies in the geographical distribution of tree species richness in Europe. *Global Ecology and Biogeography*, **16**, 234–245.

Title, P. O. & Burns, K. J. (2015) Rates of climatic niche evolution are correlated with species richness in a large and ecologically diverse radiation of songbirds. *Ecology Letters*, **18**, 433–440.

Tomašových, A., Kennedy, J. D., Betzner, T. J., Kuehnle, N. B., Edie, S., Kim, S., Supriya, K., White, A. E., Rahbek, C., Huang, S., Price, T. D. & Jablonski, D. (2016) Unifying latitudinal gradients in range size and richness across marine and terrestrial systems. *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20153027.

Tuomisto, H. (2010) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, **33**, 2–22.

Weir, J. T. & Schluter, D. (2007) The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science*, **315**, 1574–1576.

Whittaker, R. H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, **30**, 279–338.

Whittaker, R. J., Nogués-Bravo, D. & Araújo, M. B. (2007) Geographical gradients of species richness: a test of the water-energy conjecture of Hawkins *et al.* (2003) using European data for five taxa. *Global Ecology and Biogeography*, **16**, 76–89.

Whitton, F. J. S., Purvis, A., Orme, C. D. L. & Olalla-Tárraga, M. Á. (2012) Understanding global patterns in amphibian geographic range size: does Rapoport rule? *Global Ecology and Biogeography*, **21**, 179–190.

Wiens, J. J. (2011) The causes of species richness patterns across space, time, and clades and the role of “ecological limits”. *The Quarterly Review of Biology*, **86**, 75–96.

Wiens, J. J. & Donoghue, M. J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*, **19**, 639–644.

Wiens, J. J. & Graham, C. H. (2005) Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 519–539.

Willig, M., Kaufman, D. & Stevens, R. (2003) Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 273–309.

Wisz, M. S. et al. (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews*, **88**, 15–30.

Wood, S. N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, **73**, 3–36.

Wright, D. H. (1983) Species-energy theory: An extension of species-area theory. *Oikos*, **41**, 496–506.

Zagmajster, M., Eme, D., Fišer, C., Galassi, D., Marmonier, P., Stoch, F., Cornu, J.-F. & Malard, F. (2014) Geographic variation in range size and beta diversity of groundwater crustaceans: insights from habitats with low thermal seasonality. *Global Ecology and Biogeography*, **23**, 1135–1145.

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