

**Spatial and temporal signatures of ecological
constraints on diversity**

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Abstract

Broad-scale diversity patterns are the outcome of ecological and evolutionary processes that permit different numbers of species to coexist in a region. Many studies have focused on understanding the factors that allow a region to contain more species or a clade to diversify more rapidly. In this thesis, I shift focus to instead explore the constraints that prevent biodiversity increasing unbounded, using a combination of phylogenetic and biogeographical approaches across a range of temporal and spatial scales. In chapter two, I investigate conservatism (i.e., the tendency for more closely related species to be more similar) in the extremes of climate tolerated by a species, assessing the hypothesis that tightly-conserved tolerances are influential in determining the range extents of the species. By using global data from two vertebrate classes and a range of climatic variables, I assess the taxonomic generality of this hypothesis and identify the most strongly conserved variables. In chapters three and four, I develop novel macroecological analyses of factors that may limit the extent of geographic ranges and apply them to Afrotropical birds (chapter three) and all continental mammals (chapter four). Chapter five assesses how the spatial distribution of range limits can be used to compare species' relative abilities to occupy available landscape. In chapter six, I present new methods to detect signals of past changes to diversity limits in phylogenies, using simulations to explore the power of phylogenies to reveal such patterns of diversity-dependent cladogenesis. In addition to the main research chapters, I append a synthetic review, of which I am joint first author, exploring the evolutionary underpinnings of large-scale species-area relationships. This thesis builds links between the macroecology of species' distributions with the dynamics of clades over macroevolutionary timescales to determine how geography, phylogeny and history interact in the generation and maintenance of large-scale biodiversity.

Declaration

All work presented in this thesis is my own, with the following acknowledgements:

Most datasets used in this thesis were compiled by others, and I cite the data sources throughout and reference published software and code where appropriate.

I also made use of some programming code kindly provided by others: Rodolphe Bernard wrote the Python script used to extract the climatic variable summary statistics used in chapter 2. Susanne Fritz and David Orme wrote the ArcInfo macros to extract species' grid cell occurrences and identify range boundary cells for the grid cell analyses of chapters 2-5. Natalie Cooper provided R code used in chapter 4 to optimise the neighbourhood distances used in the simultaneous autoregressive models and in chapter 5 to automate partitioning the spatial and phylogenetic signals in relative occupancy.

Chapter 2 was jointly first-authored with Miguel Á. Olalla-Tárraga and is currently in press at *Journal of Biogeography*. Apart from where noted in the text, I wrote all R code used to analyse the data in this chapter. Miguel was responsible for processing the amphibian data using R code written by me. Because we developed the paper together, I retain 'we' as in the in press manuscript.

Chapters 3 & 6 are both published or in press at *Proceedings of the Royal Society B-Biological Sciences*, and were co-authored with my thesis supervisors, David Orme and Andy Purvis. While the published papers use 'we', I have converted these to 'I' for the thesis chapters.

Appendix 1 was jointly first-authored with Yael Kisel and is currently in press at *Philosophical Transactions of the Royal Society B-Biological Sciences*. I carried out the diversification analyses using R code modified from that provided by Albert Phillimore.

David Orme carried out the remaining analyses and all co-authors contributed to writing the manuscript.

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Table of contents	
Abstract	2
Declaration.....	3
Acknowledgements.....	5
Table of contents.....	7
List of Tables	9
List of Figures.....	10
Chapter 1. Introduction	11
Chapter 2. Climatic niche conservatism and the evolutionary dynamics in species' range boundaries: global congruence across mammals and amphibians.....	24
Abstract	24
Introduction	25
Methods	28
Results	34
Discussion	36
Tables	43
Figures	44
Chapter 3. Where do species' geographic ranges stop and why? Landscape impermeability and the Afrotropical avifauna	47
Abstract	47
Introduction	48
Methods	51
Results	57
Discussion	59
Tables	64
Figures	66
Chapter 4. Global patterns and inter-realm differences in mammalian landscape impermeability	68
Abstract	68
Introduction	69
Methods	71
Results	76
Discussion	78
Tables	85
Figures	88
Chapter 5. Can landscape impermeability be co-opted into a measure of species' relative occupancy?	92
Abstract	92
Introduction	93
Methods	96
Results	102
Discussion	105
Tables	112
Figures	115
Chapter 6. Detecting shifts in diversity limits from molecular phylogenies: what can we know?	123
Abstract	123
Introduction	124
Methods	126
Results	133

Discussion	135
Tables.....	141
Figures	142
Chapter 7. Conclusion.....	146
References	154
Appendix 1. How diversification rates and diversity limits combine to create large-scale species-area relationships	176
Abstract	176
Introduction.....	177
Methods	178
Section 1: A verbal model for clade diversification in space	182
Section 2: Generating SARs in an evolutionary framework.....	184
Section 3: Abiotic factors modulating the species-area relationship	189
Section 4: Clade traits modulating the species-area relationship	190
Section 5: Historical and temporal effects on the species area relationship.....	193
Conclusions.....	195
References.....	197
Tables.....	205
Figures	208
Supporting information for Appendix 1.....	211
<i>Tables</i>	<i>211</i>
<i>Figures.....</i>	<i>214</i>
Appendix 2. Supporting information for chapter 2.....	219
2.1 – Latitude analysis.....	219
2.2 – Range size analysis.....	220
2.3 – Amphibian phylogeny construction	222
2.4 – Character-dependent diversification analyses.....	223
2.5 – Variance components obtained from nested ANOVAS	225
Appendix 3. Supporting information for chapter 3.....	228
3.1 – References used in the construction of the distribution maps	228
3.2 – References used to construct the predictor variables.....	228
3.3 – Preliminary analyses to determine the minimum adequate model.....	229
3.4 – Exploring spatial autocorrelation	235
3.5 – F ratios for each term retained in the (A) non-spatial and (B) spatial models.	239
3.6 – Analysis of species in the largest range size quartile	240
Appendix 4. Supporting information for chapter 4.....	242
4.1 – Distributions of variables included in the models	242
4.2 – The use of spatially-explicit models to control for spatial autocorrelation	243
Appendix 5. Supporting information for chapter 5.....	244
5.1 – Tables for single predictor models of relative occupancy	244
Appendix 6. Supporting information for chapter 6.....	252
6.1 – Assessing alternative diversification scenarios	252
6.2 – Correcting for multiple tests	257
6.3 – Validity testing.....	258
6.4 – Exploring downshifts.....	260
6.5 – Empirical results tables	261
6.6 – Signal from mass extinction	262
Appendix 7. Additional references from appendices 2-6.....	263

List of Tables

Table 2.1. Test statistics indicating whether species are more similar in their climatic requirements within than between genera or families.....	43
Table 3.1. Results of model selection.	64
Table 3.2. Summary of top models.	65
Table 4.1. Summary of results of OLS and SAR model selection.	85
Table 4.2. Results of OLS and SAR model averaging.....	86
Table 4.3. Correlation between mammal and amphibian impermeability.	87
Table 5.1. Possible interpretations of ω_i and ω_e	112
Table 5.2. Correlations among traits	112
Table 5.3. Results of multi predictor models using phylogenetic GLS	113
Table 5.4. Phylogenetic and spatial signal in the measures of relative occupancy	114
Table 6.1. Comparing power to detect rule changes.....	141
Table A1.1. Summary of factors affecting diversification rates and diversity limits.....	205
Table A1.2. Summary of diversification models fitted to mammalian clades.	206
Table A1.3. Multivariate SARs, with mammal species richness regressed against area and other environmental variables.....	207
Table S1.1. Parameters of linear regression models	211
Table S1.2. Slopes of SARs for mammalian orders	212
Table S1.3. Dispersal analysis.	213
Table A2.4. Comparing character-dependent diversification models.....	224
Table A2.5. Variance components obtained from nested ANOVAs.	225
Table A3.3.1. Regression statistics for the single-predictor non-spatial analyses.....	230
Table A3.3.2. Analyses by biome.	231
Table A3.5.1. F ratios for each term retained in the (A) non-spatial and (B) spatial models.	239
Table A3.6.1. F ratios for largest range size quartile.....	240
Table A5.1.1. Results of models predicting ω_i	244
Table A5.1.2. Results of models predicting ω_e	246
Table A5.1.3. Results of models predicting ω_e using all species	248
Table A5.1.4. Results of models predicting ω_e with ω_i as a covariate	250
Table A6.1.1. Type I error rates of diversity-independent null simulations.	256
Table A6.1.2. Power of alternative diversification scenarios to detect rule changes at the end of T1 (55 My ago).....	256
Table A6.3. Validity testing.	258

List of Figures

Figure 2.1. Taxonomic structure of the variance in climatic tolerances for amphibians (A) and mammals (M).....	44
Figure 2.2. Spatial patterning of recent evolution in cold tolerance.....	44
Figure 3.1. Landscape impermeability for Afrotropical birds.....	66
Figure 3.2. Landscape impermeability for subsets of species from the dataset.....	67
Figure 4.1. Mammalian impermeability.....	88
Figure 4.2. Coefficient estimates for the top OLS models.....	89
Figure 4.3. Coefficient estimates for the top SAR models.....	90
Figure 4.4. Amphibian impermeability.....	91
Figure 5.1. The different combinations of ω_e and ω_i possible.....	115
Figure 5.2. Assessing phylogenetic selectivity in range determinants.....	116
Figure 5.3. Relationship between measures of relative occupancy and range size.....	117
Figure 5.4. Results of models predicting ω_i	118
Figure 5.5. Results of models predicting ω_e	119
Figure 5.6. Relationship between ω_i and ω_e	120
Figure 5.7. Results of models predicting ω_e with ω_i fitted as a covariate.....	121
Figure 5.8. Richness of good and poor occupiers.....	122
Figure 6.1. Example lineage-through-time plots.....	142
Figure 6.2. Schematic explaining $\Delta\gamma$	143
Figure 6.3. Contour plots of power to detect the rule change in the specified interval.....	144
Figure 6.4. Diversification bursts in the angiosperm family, mammal and mammalian superorder trees analysed using 2 My intervals.....	145
Figure A1.1. Variation in patterns of clade diversification.....	208
Figure A1.2. Development of the species area relationship.....	208
Figure A1.3. Species area relationships in mammals across scales.....	208
Figure S1.1. Geographic distributions of biotic clusters.....	214
Figure S1.2. Size distributions of geopolitical (TDWG) and clustered biotic regions.....	215
Figure S1.3. Species-area relationships for geopolitical regions.....	216
Figure S1.4. Species-area relationships for clustered biotic regions.....	217
Figure S1.5. Prediction surfaces from models of log species richness.....	218
Figure A2.2. Variance explained at the species level across range-size quartiles.....	221
Figure A2.6. Mean assemblage (grid cell) values for independent evolution in cold tolerance.....	226
Figure A3.3.1. Tree diagram of the seven hypothesised predictor variables.....	233
Figure A3.3.2. Generalised additive models.....	234
Figure A3.4.1. Moran's I correlograms.....	237
Figure A4.2.1. Moran's I correlograms.....	243
Figure A6.1. Example lineage-through-time plots for alternative diversification scenarios.....	255
Figure A6.4. Exploring downshifts.....	260
Figure A6.6. Comparing lineage-through-time plots.....	262

Chapter 1. Introduction

We live in a diverse world, but no species is distributed ubiquitously. Every species is limited by its physiological requirements to specific habitats and prevented from occupying all suitable habitats by biotic interactions, dispersal limitation and landscape features (Gaston, 2003). Likewise, most higher taxa are confined to some subset of the space available, the extent of which is also determined by the traits and history of the clade combined with the nature and history of the region. When the inherently spatial nature of most cladogenesis is taken into account, models wherein clades continue to diversify exponentially lose credibility. Rather, clade growth is expected to slow through time as a region fills with species and competitive interactions increase over the limited niche space available. Nevertheless, the structure of biodiversity is not expected to be static. Biotic interactions and key innovations can promote evolutionary responses that lead to occupation of new eco-space; and external perturbations, major and minor, can alter the areas suitable for species or clades and can lead to range changes, radiations and extinctions. In this thesis, I investigate the spatial and temporal signatures of ecological constraints on diversity focussing exclusively on extant taxa; I quantify when we can and cannot hope to reliably detect these signatures and the conditions under which species, clades and areas overcome these constraints.

Why study biodiversity dynamics?

Human actions, both directly through habitat destruction and overexploitation and indirectly through anthropogenic climate change and land-use transformation, are altering the distribution of biodiversity very rapidly. Understanding how biodiversity is generated and maintained is not only of fundamental interest, but may also help us determine how to optimise biodiversity conservation into the future to ensure human wellbeing through the

preservation of ecosystem functioning and the provision of ecosystem services (e.g., Dawson *et al.*, 2011; Naidoo *et al.*, 2008; Pereira *et al.*, 2010).

Understanding diversity patterns

Our understanding of the broad-scale determinants of diversity gradients has been facilitated in recent years by robust compilations of global environmental data and species' range extents for all species within several major taxa, although debate remains on the relative contributions of ecological and evolutionary processes (e.g., Mittelbach *et al.*, 2007; Ricklefs, 2004). We know that water-energy dynamics explain a substantial amount of spatial variation in species richness across a broad range of taxa (Hawkins *et al.*, 2003). The strength of such correlations between contemporary climate and species richness, combined with the observation that local interactions among coexisting species constrain species numbers (MacArthur & Levins, 1967), initially supported the idea that local determinism controlled species' distributions with little input from regional or historical processes (Currie *et al.*, 1999). Such a model requires that the local physical environment controls community composition and richness, that similar habitats in different regions harbour similarly rich biotas, and thus that local diversity be largely decoupled from regional diversity. However, a significant effect for region is almost always found in tests comparing diversity across comparable habitats (e.g., Latham & Ricklefs, 1993; Qian & Ricklefs, 2000). Furthermore, although strong correlations between contemporary climate and diversity have been used in support of local determinism, they do not imply any specific mechanism and could also come about if historical processes affect spatial patterns of diversity. Because clades start as a single lineage in a single ecological zone, and shifts between zones are difficult and thus rare, if certain areas produce more lineages, diversity gradients will persist among zones through time (Ackerly, 2003). In the past decade, a more balanced view of the generation and

maintenance of biodiversity acknowledges that contemporary, ecological and historical, evolutionary explanations for diversity gradients are not mutually exclusive (Harrison & Cornell, 2008; Ricklefs, 2004) and that many processes can influence the observable patterns (Mittelbach *et al.*, 2007).

Macroecologists typically have access only to contemporary distribution maps and data on current environmental conditions; the emphasis on contemporary processes controlling diversity patterns is therefore unsurprising (Harrison & Cornell, 2008). Ultimately, however, explanations for diversity patterns must include the processes that directly change species numbers and thus must incorporate a temporal perspective. The fossil record, although patchy, has been useful in this regard (Jackson & Erwin, 2006), providing evidence of fluctuating levels of diversity through time (e.g., Sepkoski, 1978), biotic responses to events such as major climatic change (Culver & Rawson, 2000) and macroecological patterns in deep time, such as the latitudinal diversity gradient (Jablonski *et al.*, 2006; Valentine *et al.*, 2008). There is an unprecedented amount of data available for major vertebrate groups such as the mammals, amphibians and birds. In combination with a richer understanding of the complexity of processes contributing to biodiversity patterns, it is possible to use this data sensitively to better understand the factors contributing to the diversification and diversity gradients of entire taxonomic groups. My approach in this thesis, then, is to focus exclusively on extant taxa, but to include a consideration of the impact of historical processes on biodiversity patterns. In my final chapter, I also assess our ability to make inferences on temporal diversity dynamics using only extant taxa.

Defining the niche

Despite the increasing realisation that species' ranges limits are determined by a complex interplay of biotic and abiotic factors, evidence for climatic controls on individual species'

distributions remains strong – many studies have identified climatic thresholds beyond which species do not occur (reviewed in Gaston, 2003). Characterising species' distributions based on the climatic conditions found within them has a long history and was perhaps most clearly expressed by Joseph Grinnell in the 1920s. Grinnell's pioneering work (e.g., Grinnell, 1914; Grinnell, 1917) has led to the term Grinnellian niche being adopted to describe, for each species, that subset of environmental conditions that facilitates population growth rather than population decline (Soberón, 2007). Hutchinson (1957) introduced an elegant way of visualising the link between the Grinnellian niche, in environmental space, and the distribution of a species, in geographic space. If a grid of a certain resolution is visualised over geographic space, each cell of the grid can be uniquely characterised by some combination of environmental variables: all combinations together make up the available environmental, or niche, space. Those cells occupied by a species can also be uniquely characterised and these define the species' niche. The niche is a slippery concept, however, in at least two ways (Colwell & Rangel, 2009; Soberón, 2007). Firstly, while the Grinnellian niche focuses on defining relatively stable conditions that facilitate persistence of the species, the Eltonian niche takes a more dynamic view incorporating both the availability of resources and the impact the focal species has on its environment and is perhaps most relevant to population-level persistence and over the lifetime of individuals (Soberón, 2007).

The second slippery element of the niche is the discrepancy between all the environmental conditions under which a species *could* persist in the absence of dispersal or biotic limitations (the fundamental niche) and those conditions under which the species *is* found (the realised niche). In the absence of expensive translocation or exclusion experiments, we are typically restricted to quantifying the realised niche under the assumption that it is a good reflection of the fundamental niche. Although this is unlikely to always be the case, particularly in species whose ranges are not at equilibrium (e.g., Svenning & Skov, 2004), there exists strong

support for climatic factors shaping the observable, realised niches of many species particularly at the broad scale (Soberón & Nakamura, 2009).

The focus on local determinism in the 1960s meant that the link between the distribution of individual species and those of related species was briefly forgotten. During his travels in the East Indies in the mid-19th century, Alfred Russell Wallace observed that species found west of the Lombok Strait were quite distinct from those found to the east (Wallace, 1869). Later formalised as Wallace's Line, the region separates the ecozones of Asia from that of Wallacea and, further east, Australia. Thus, it has long been known, both that related species occur in close geographic proximity to each other, and that biotic provinces can be delineated and that they correspond to regions that have been separate from neighbouring areas over geological time (in this instance by a deep-water channel between the continental shelves of Asia and Australia). It is only relatively recently, however, with the concomitant development of robust phylogenetic methods and the rejection of local determinism, that there has been a realisation that a consideration of the evolutionary relationships among species can reveal how a biota is structured at large scales (Ackerly, 2003; Wiens & Donoghue, 2004).

Phylogenetic niche conservatism

Phylogenetic niche conservatism (PNC), broadly defined as the tendency for lineages to retain their ancestral niches over evolutionary time (Grafen, 1989), is gaining ground in explaining broad-scale distributions of clades (Wiens & Donoghue, 2004). If niche conservatism is prevalent within a clade, the ancestral niche will determine the regions that new species can occupy and the geographical spread of the clade as a whole. Similarly, it will affect how lineages respond to environmental change (Wiens & Graham, 2005).

There has been substantial debate, however, on both the definition and detection of PNC (Losos, 2008; Wiens, 2008). Some (e.g., Losos, 2008) state that conservatism only occurs when a trait is more similar among related species than expected under a Brownian motion model of trait evolution, others think that this is an unduly strict definition. Rather, it is enough to find some signal of conservatism above the species level in a niche-related trait to think of the trait as conserved and the focus should instead be on the patterns that niche conservatism can help explain (e.g., Cooper *et al.*, 2010; Wiens, 2008; Wiens *et al.*, 2010; Wiens & Graham, 2005). The debate really comes down to whether PNC is a pattern to be explained or a process that can explain additional patterns. I am inclined to agree with the second position: phylogenetic niche conservatism as a concept is almost uninteresting: no two species occupy identical niches, but related species surely occupy similar ones (Harvey & Pagel, 1991). Thus, PNC is most interesting when it is thought of as a process that can help explain a multitude of patterns at both the macroecological (e.g., the latitudinal diversity gradient) and macroevolutionary (e.g., inability of lineages to adapt to cold climates) levels (see also Wiens, 2008; Wiens *et al.*, 2010).

One of the reasons why PNC has provoked such controversy is because, in the absence of clearly defined variables and specific hypotheses to test, the same aspect of a species' niche can be considered conserved or not (Cooper *et al.*, 2010). One of the foremost problems is a lack of consideration of taxonomic or geographic scale. For example, within an exclusively tropical lineage there might be substantial niche lability but, when compared to a sister lineage occurring at higher latitudes, the entire tropical lineage is conserved in its tropicity (Wiens, 2008). Similarly, the niche is multidimensional and conservatism may be stronger along certain axes than others (e.g., the thermal vs. precipitation niche; Bonebrake & Mastrandrea, 2010). Thus, niche conservatism must be studied with scale explicitly stated

and a valuable route, avoiding absolute definitions, is to investigate relative conservatism e.g., among lineages or among variables (e.g., Cooper *et al.*, 2011).

Here, I undertake the first global comparison of niche conservatism across two vertebrate taxa, mammals and amphibians (chapter 2), investigating conservatism across a suite of climatic factors potentially important in determining a species' distribution. Specifically, I investigate conservatism in climatic tolerances - in the extremes of climate experienced by a species – under the hypothesis that climatic factors that exhibit strong conservatism within a taxon are influential in determining the range extents of the species. The chapter has three main aims: to compare and contrast conservatism in the means and extremes of climate found within a species' range, to identify which climatic variables are most conserved and to compare and contrast the strength of conservatism in the two taxa.

Species distribution modelling and climate change

The idea that species' niches are conserved is potentially very important to the growing field of predicting species' responses to climate change (Sinclair *et al.*, 2010). Whether explicitly stated or not, models predicting species' range movements rely on species retaining their present niche dimensions in their new range (Pearman *et al.*, 2008). A veritable plethora of methods for species distribution modelling (outlined in Elith *et al.*, 2006; Thuiller *et al.*, 2009; Zimmermann *et al.*, 2010) have sprung up to quantify the “climatic envelope” in which species now occur. These envelopes are then projected in space to determine where suitable conditions will exist in the future and assess whether species will be able to reach these new habitats in time to resist extinction (recent reviews include Araújo *et al.*, 2005; Elith & Leathwick, 2009; Guisan & Thuiller, 2005).

All such approaches take niche conservatism as a given, at least over short timescales, assuming no possibility for *in situ* adaptive responses despite evidence to the contrary across

a number of species (Gienapp *et al.*, 2008). The approach has been used, for example, to bracket estimates of the expected loss of biodiversity from climate change (e.g., Thomas *et al.*, 2004). It is particularly useful if niche conservatism is prevalent (Pearman *et al.*, 2008) or climatic changes are of such a high magnitude that species are not expected to be able to mount adequate adaptive responses to retain their current range location (e.g., Devictor *et al.*, 2008). In order to provide more robust predictions, however, a number of improvements can be made. So far, most attempts have focused on including additional factors considered important in determining a species' range (e.g., biotic interactions: Araújo & Luoto, 2007; Heikkinen *et al.*, 2007; population dynamics: Keith *et al.*, 2008; topography: Luoto & Heikkinen, 2008, physiology: Kearney & Porter, 2009; history: Svenning & Skov, 2007b). A further shortfall common to most methods of range projection is a limited consideration of both the landscape over which species must travel to reach their new range and the intrinsic capacity of the species to make this journey (but see Engler *et al.*, 2009; Meier *et al.*, in press for some recent examples incorporating migration capacities).

Whereas chapter 2 focuses on unravelling the relative strength of climatic determinants of species' distributions, chapters 3, 4 and 5 explore the insights possible from taking a macroecological perspective of range limits by exploring emergent patterns in co-occurring range limits in geographic space.

Macroecology of range limits

In this time of rapid environmental change, species' responses are going to be apparent first at their range boundary; therefore the importance of studying species' range limits is clear (Gaston, 2009; Sexton *et al.*, 2009). Studies have typically focussed on the range limits of single species. While resource requirements might be the proximate cause of range limits, studies have focussed on what prevents species expanding their range to occupy a broader

niche (reviewed in Sexton *et al.*, 2009). Possible explanations include gene flow from the centre of the range thwarting local adaptation at the range edge (Kirkpatrick & Barton, 1997), unstable population dynamics in depauperate populations (Keitt *et al.*, 2001) as well as competitive exclusion (Case *et al.*, 2005) and dispersal limitation (e.g., out of glacial refugia, Fang & Lechowicz, 2006). Recent research also suggests that borders maintained through competition may be attracted to abiotic dispersal barriers with suture zones formed where multiple species' borders coincide (Goldberg & Lande, 2007).

Although studies investigating the macroecological correlates of species richness and average range size abound (e.g., Orme *et al.*, 2005; Orme *et al.*, 2006), there has been little investigation of the macroecological correlates of high densities of range limits. Phylogenetic niche conservatism would suggest that related species will be limited by similar factors, but this does not necessarily extrapolate to range limits co-occurring in space (Roy *et al.*, 2009). Indeed, correlates of beta diversity in various taxa suggest that species' turnover is highest in areas of steep environmental turnover (e.g., Buckley & Jetz, 2008) indicating that range limits cluster in heterogeneous areas where range expansion is impeded.

Landscape impermeability

To quantify clustering in range limits, I defined and generated a measure of landscape impermeability, namely, the proportion of local species whose ranges end in a certain area, to give an indication of how freely species can move across a landscape. Many factors have been proposed as potentially limiting to species' ranges including physical landscape features, topography, climate, resource availability and competitors, as well as unstable population dynamics and limited genetic variability (Gaston, 2003). Understanding the nature of areas where high proportions of resident species have coincident range edges can help elucidate which factors are generally important in limiting species' ranges.

Chapter 3 presents my first exploration of the macroecology of range limits, exploring spatial patterning and the environmental correlates of landscape impermeability in the Afrotropical avifauna. Chapter 4 extends this analysis to mammals globally, comparing and contrasting patterns and correlates across realms. Both chapters build spatially-explicit multivariate models, using model selection to obtain the most explanatory models.

Although I identify strong correlates of landscape impermeability, it is also clear that some species are not limited in the same places or in the same ways as the majority. For example, some species can span areas of high impermeability and others have seemingly idiosyncratic range barriers within homogeneous habitats. In chapter 5, I investigate whether our measure of landscape impermeability could be co-opted into a species-based measure of relative landscape occupancy. Are there diagnosable traits of good and bad occupiers, or are they a disparate array of species with anomalous distributions due to historical contingencies or strong dispersal or biotic limitations? An understanding of the breadth of possible explanations may be one way in which to inform species distribution modellers on the validity of their models for certain species.

Understanding diversity dynamics of clades

Up to this point, I have focussed on a static world where there is spatial variation in the environment and by extension in species richness, beta diversity, average range size and landscape impermeability. I have identified a suite of factors that might be responsible for this variation and underlined the importance of energy availability and landscape features in determining the distributions of individual species and of clades. Nevertheless, the distribution of diversity has been far from static on ecological (e.g., invasive/introduced species: Jackson & Sax, 2010), evolutionary (e.g., adaptive radiations: Glor, 2010; Schluter, 2000) or geological (e.g., mass extinctions: Erwin, 2001) timescales. How do clades diversify

through time? What are the signatures of temporal diversity dynamics and are they detectable in the present day? In my final chapter, I adopt a model of diversity-dependent cladogenesis and assess our ability to detect the signal of past changes to diversity limits using data from extant species.

In order to make robust inferences about temporal dynamics, it is important to first understand how clades diversify through time and what determines diversity differences among clades. Reconstructed phylogenies that document the evolutionary relationships among extant species of a clade are often used to study these dynamics (e.g., Bininda-Emonds *et al.*, 2007; Magallon & Sanderson, 2001, reviewed in Ricklefs, 2007). Because these phylogenies do not contain extinct taxa they give the potentially false impression that diversity has been continually expanding and that clade diversity is highest in the present day (Ricklefs, 2009). This bias has helped promote the idea that to explain diversity differences between clades we should be looking for traits associated with higher diversification rates, because faster diversification rates will lead more quickly to more species. Despite some successes (reviewed in Coyne & Orr, 2004), few studies have managed to identify strong trait correlates of high diversity (Phillimore *et al.*, 2006).

Like species, most clades are restricted to some subset of available space. Clade richness should depend then on the size and age of the area in which they are found, alongside characteristics of that area and characteristics of the species (Losos & Schluter, 2000; Rabosky, 2009b; Ricklefs, 2006; Ricklefs, 2009). Just as resource-based limits to species coexistence set upper limits on the number of co-occurring species at finer scales (Chesson, 2000), available niches should set upper limits on the number of species possible in a clade occupying a certain area (Rabosky, 2009a). It is only very recently, however, that the contribution of ecological limits to diversification has been investigated (e.g., Rabosky,

2009a, b; Vamosi & Vamosi, 2010) with mounting evidence that diversification slows through time as clades fill available geographic, or niche, space (Phillimore & Price, 2008; Rabosky, 2009a, b). These results suggested that that a failure to consider the possibility that clades are no longer growing might lead to erroneous conclusions on the impact of traits on diversification and that more complex models than the constant-rate birth-death model of macroevolution are necessary to characterise diversification through time (Rabosky, 2010b).

As part of a synthetic account of the macroevolutionary contribution to species-area relationships, I investigated the influence of available area on diversification in mammalian clades (Appendix 1: in press as Kisel *et al.*). We outlined a model of diversity-dependent cladogenesis and reviewed the ways in which area, or its correlates, could influence clade diversification rate and diversity limits to determine the extent to which diversity differences among clades could be due to effects of area. We found a significant effect of area on both the initial diversification rate and rate of decline across a suite of mammalian clades and go on to discuss the ecological and evolutionary factors that contribute to this result.

Shifts in diversity limits

Kisel *et al.* (in press) championed a model of diversification wherein ecological constraints prevent ongoing exponential cladogenesis. In our model, clades diversify up to a limit that depends on the size and the nature of the area that they occupy. Such a model leaves little room either for the replacement of entire clades through time or for the expansion of clades into new ecospace (Simpson, 1953; Valentine *et al.*, 2008). We know that the environment through Earth history has been far from constant: continents moved, temperatures fluctuated, sea levels changed, meteorites landed and volcanoes erupted, all impacting the nature of the surface of the Earth. Diversity limits are thus expected to change through time and there is fossil evidence for such biotic responses in the past (Ezard *et al.*, 2011). As data proliferate

on the evolutionary relationships among extant species, it becomes important to know how much information we can feasibly recover about their past diversification trajectories in the absence of additional data.

In chapter 6, I use a simulation approach to assess the breadth of parameter space under which we can expect to retain the signal of past events in the reconstructed phylogenies of extant species. Extinction throughout the history of the clade will have removed some of the branching relationships, potentially eroding any signal of past events. Specifically, I use a model of logistic diversity-dependent cladogenesis and develop two new methods to detect increases in diversity limits. I alter the timing and magnitude of the shift and the turnover rate at equilibrium diversity to assess how these parameters affect our ability to detect the shift. Ecological constraints are continually operating to limit the spread of species through space, but constraints are not static through time. Chapter 6 investigates our ability to extract the signal of such temporal dynamics in deep time using data on extant species.

Summary of thesis aims

The overarching aim of this thesis is to explore our ability to recover spatial and temporal signatures of ecological constraints on diversity using data from extant species only. I start from the position that such constraints are common and that they produce broad-scale spatial patterns in the distributions of species and clades that are unlikely to remain static through time. My specific aims are:

- To explore the detectability of *past* changes to diversity limits;
- To uncover patterns and correlates of *present* range limits;
- To assess whether present range limits can be used to quantify species' relative ability to overcome landscape constraints with a view to conditioning *future* range projections.

Chapter 2. Climatic niche conservatism and the evolutionary dynamics in species' range boundaries: global congruence across mammals and amphibians¹

Abstract

Comparative evidence for phylogenetic niche conservatism – the tendency for lineages to retain their ancestral niches over long timescales – has so far been mixed, depending on spatial and taxonomic scale. We quantify and compare conservatism in the climatic factors defining range boundaries in extant continental mammals and amphibians in order to identify those factors that are most evolutionarily conserved, and thus hypothesised to have played a major role in determining the geographic distributions of many species. We also test whether amphibians show stronger signals of climatic niche conservatism, as expected from their greater physiological sensitivity and lower dispersal abilities. We use nearly complete global distributional databases to estimate the climatic niche conservatism in extant continental mammals and amphibians. We characterise each species' climatic niche using a suite of variables and separately investigate conservatism in each variable using both taxonomic and phylogenetic approaches. Finally, we explore the spatial, taxonomic and phylogenetic patterns in recent climatic niche evolution. Amphibians and mammals showed congruent patterns of conservatism in cold tolerance, with assemblages of escapee species (i.e., those escaping most from the climatic constraints of their ancestors) aggregated in the North Temperate Zone. The relative strength of climatic niche conservatism varies across the variables tested, but is strongest for cold tolerance in both mammals and amphibians. Despite the apparent conservatism in this variable, there is also a strong signal of recent evolutionary

¹ A version of this chapter is in press as: Olalla-Tárraga, M.A.*, McInnes, L.*, Bini, L.M., Diniz-Filho, J.A.F., Fritz, S.A., Hawkins, B.A., Hortal, J., Orme, C.D.L., Rahbek, C., Rodriguez, M.A. & Purvis, A. (in press) Climatic niche conservatism and the evolutionary dynamics in species' range boundaries: global congruence across mammals and amphibians. *Journal of Biogeography*. *Joint first authors.

shifts in cold tolerance in assemblages inhabiting the North Temperate Zone. Our results thus indicate that distribution patterns of both taxa are influenced by both niche conservatism and niche evolution.

Introduction

Deciphering why species live where they do has long been a central issue in ecology and evolution (Darwin, 1859). A species' geographic range reflects both its environmental tolerances and its geographical opportunities, now and in the past. Accordingly, ranges shift in response to environmental change (Parmesan & Yohe, 2003) and following specific adaptations to cope with conditions beyond the range edge (Holt, 2003). Although some large-scale spatial patterns in geographic ranges have been found (such as a trend of increasing range size northwards: see Stevens, 1989), the biogeographical and historical complexities make it unsurprising that closely-related species often have very different range sizes (e.g., Freckleton *et al.*, 2002). If, however, large-scale range limits are largely governed by slowly-evolving environmental tolerances (Wiens & Donoghue, 2004), then these limits will tend to be more similar among related species than are range sizes (Roy *et al.*, 2009).

Climatic niche conservatism has been defined as the tendency for species to retain aspects of their ecological niche over evolutionary time-scales (Wiens & Graham, 2005). There has been debate recently over what constitutes niche conservatism: whether it is enough for phylogeny or taxonomy to explain significant variation in species' traits or whether trait values specifically need to be more similar in closely-related species than expected under a Brownian motion model of trait evolution (Harvey & Pagel, 1991; Losos, 2008; Wiens, 2008). We use the former, more permissive, definition. Under this view, niche conservatism

is common and research attention switches from demonstrating it to measuring and comparing its strength in different traits, groups or regions. Different ecological characteristics often show widely different degrees of conservatism across the same set of species (Freckleton *et al.*, 2002). Here, we specifically test the strength of conservatism across a suite of potential range-limiting factors across two major vertebrate taxa to investigate which environmental aspects are most conserved within clades and, therefore, implicated in having played the most important roles in limiting and structuring distributions at a broad scale (Soberón, 2007).

Detection of climatic niche conservatism (Harvey & Pagel, 1991; Wiens & Graham, 2005) depends on both taxonomic resolution and spatial scale (Cooper *et al.*, 2010; Losos, 2008; Wiens, 2008). Many genera and families are geographically restricted and so experience a limited range of environmental variation, making climatic niche conservatism harder to detect (Wiens & Graham, 2005). As an emergent species-level property, the range boundaries of species distributions are determined by biotic interactions, abiotic constraints or a combination of both. Hutchinson's (1978) niche concept provides a clear link between a species' observed geographical distribution and the multiple biotic and abiotic dimensions limiting where a species can persist. While the fundamental niche represents all regions where a species could maintain a positive growth rate in the absence of biotic or dispersal limitation, observed species' ranges correspond to realised niches, a subset of the fundamental niche (Soberón, 2007). Despite the difficulties involved in disentangling the relative contribution of biotic and abiotic factors in shaping observed range edges, there is strong support for climate as a major driver at continental and global scales (i.e., the Grinnellian niche, Soberón & Nakamura, 2009). Detection of conservatism in specific climatic requirements therefore suggests that those variables influence the broad-scale

distribution of species and can be termed range-limiting factors (see also Cooper *et al.*, 2011 who made similar assumptions).

Despite the awareness that climatic niche conservatism may only become apparent at these broad spatial scales and higher phylogenetic levels, few phylogenetically inclusive global studies have been conducted to date. Hof *et al.* (2010) and Buckley *et al.* (2010) provide two exceptions. However, rather than investigate potentially important factors individually, Hof *et al.* (2010) instead used ordination techniques to derive single niche values for amphibians and Buckley *et al.* (2010) only investigated two climatic variables for continental mammals. Here, we use nearly complete global distributional databases to estimate conservatism in the climatic tolerances of two vertebrate taxa: continental mammals and amphibians. For each taxon, we compare the relative conservatism across a suite of potentially important variables to address the idea that different aspects of the niche may evolve independently (Cooper *et al.*, 2010; Freckleton *et al.*, 2002; Losos, 2008). We characterise each species' climatic niche using the suite of variables and separately investigate conservatism in each. Our goal is to identify those climatic factors that are most conserved within clades (and thus hypothesised to influence the distributions of many species in the clade) and those factors for which related species' tolerances are more idiosyncratic. We also test whether the greater physiological sensitivity and lower dispersal abilities of amphibians compared to mammals have produced a stronger signal of conservatism in climatic range limits. Furthermore, we explore whether conservatism is stronger in the extreme values (minima or maxima) of environmental factors experienced by species in any part of their range than in whole-range averages. Finally, we map inferred recent changes in climatic tolerances to investigate spatial patterning in lineages that have escaped conservatism.

Methods

Geographic distribution data for mammals and amphibians

Polygon shapefiles of the geographic ranges of each mammal and amphibian species were taken from the Global Mammal and Amphibian Assessments (GMA:

www.iucnredlist.org/mammals; Schipper *et al.*, 2008 and GAA:

www.iucnredlist.org/amphibians; Stuart *et al.*, 2004). Because islands may be subject to different evolutionary processes, we excluded island endemics and any parts of species' ranges that fell on islands. We also excluded wholly marine mammalian families within Cetartiodactyla, Carnivora and Sirenia, as well as the polar bear (*Ursus maritimus*) and the sea otter (*Enhydra lutris*). We matched the GMA species with the taxonomy of Wilson & Reeder (2005) as in Fritz & Purvis (2010a), and the GAA with the taxonomy of Frost *et al.* (2006). The final data set contained 3878 mammal and 4165 amphibian species.

Environmental variables

Environmental variables came from the WorldClim database (Hijmans *et al.*, 2005; <http://www.worldclim.org/current.htm>) at 5 arc-min (=0.083°) resolution and EDIT Geoplatform (<http://edit.csic.es>) at a resolution of 0.1°. Environmental factors thought to limit ranges of terrestrial vertebrates include ambient energy, primary productivity, water availability and their seasonal variation (Hawkins *et al.*, 2003). We chose four of the 19 BioClim variables available from WorldClim as well as Normalized Difference Vegetation Index (NDVI) remote-sensing data to address our hypotheses, on the basis of their importance for the ecology and distribution of vertebrates (see e.g., Aragón *et al.*, 2010). We used mean temperature of the warmest quarter (Bio10) and mean temperature of the coldest quarter (Bio11) to represent heat- and cold-tolerance and, together, tolerance to seasonal temperature variation. Similar alternative measurements such as maximum temperature of the

warmest period or minimum temperature of the coldest period are probably too extreme and mostly capture outlier conditions unlikely to influence the long-term viability of all populations of each species. We used annual precipitation (Bio12) to capture cumulative water availability through a year, and precipitation seasonality (Bio15) to capture its seasonality, measured as the coefficient of variation of the weekly mean values. Finally, we used mean annual NDVI, calculated from monthly values for the period 1982-2000 (see EDIT Geoplatform, <http://edit.csic.es> for details on data processing), to reflect primary productivity. We also calculated a measure of seasonality (coefficient of within-year variation) in NDVI, but it provided no additional information and was omitted from the final analyses. By using these fine-grain climatic datasets, we aim to characterize species climatic niches in a way that not only incorporates broad-scale macroclimatic effects, but also mesoscale climatic variation associated with elevational gradients. Note, however, that we do not attempt to characterise microclimatic factors that may be relevant for the habitat suitability of species at more local scales (e.g., microclimatic variation in water availability for amphibians: Hillmann *et al.*, 2009).

We used the environmental variation within each species' geographic range as a proxy of its realised niche (e.g., Cooper *et al.*, 2011; Hof *et al.*, 2010), under the assumption that species' distributions, at the coarse scale of our data, are primarily set by their environmental tolerances (Pearson & Dawson, 2003; but see Soberón & Nakamura, 2009). For each environmental variable, we characterised each species' tolerance by calculating the mean, maximum and minimum values within its continental range (hereafter termed climatic niche measurements). At the coarse resolution of our analysis, our polygon-based range data (i.e., extent of occurrence) is congruent with survey-based data (see Hawkins *et al.*, 2008 and references therein) and, hence, consistent with those that may be obtained from species distribution modelling approaches. We recognise that biotic interactions and different kinds

of historical effects can also limit distributions, so our measurements correspond to the realised rather than the fundamental niche (Soberón & Nakamura, 2009). However, quantitative genetic models (Case & Taper, 2000) suggest that even competitive limits may be strongest along steep environment gradients. Therefore, we assume that if we detect conservatism in any climatic extreme, it is in spite of any idiosyncratic effects.

We analyse these environmental variables separately, rather than processing them through a principal components analysis (as in, e.g., Hof *et al.*, 2010), to preserve their interpretability and evaluate their individual importance. As expected, mean temperature of the warmest and coldest quarters are strongly correlated. This is, however, not a problem because we test each variable individually and are primarily interested in identifying which climatic variables are the most strongly conserved among species, with the aim of identifying that climatic factor along which related species diverge least. Finally, we also tested the absolute latitude of the centroid of each 0.1° grid cell, because latitude could be a proxy for as-yet-unidentified environmental factors (Hawkins & Diniz-Filho, 2004, see Appendix 2.1).

Data processing and statistical analyses

We first used a nested ANOVA to examine how variance in species' climatic tolerances is partitioned among taxonomic levels (Hof *et al.*, 2010). Species were assigned to genera and families and these taxonomic levels were treated as random effects in a linear mixed-effects model fitted using restricted maximum likelihood with the R package nlme (Pinheiro & Bates, 2000). Variance components were scaled to sum one. We tested the significance of each taxonomic level in two ways. First, we used likelihood ratio tests and Akaike's information criterion (AIC) to compare the full model to models omitting a level. Second, we tested whether the 95% confidence intervals of each level's variance estimate included zero. We interpret greater than 50% variance explained above the species level as indicative of

niche conservatism. To check whether the selection of this threshold may affect our perceptions on the existence of niche conservatism we additionally used more liberal (40%) and conservative (60%) thresholds for comparison. Very wide-ranging or narrowly-distributed species can sometimes drive macroecological patterns (Jetz & Rahbek, 2002). Accordingly, we split species according to range size quartile and repeated the linear mixed-effects model within quartiles to test whether the taxonomic structure of niche conservatism varies with range size (see Appendix 2.2).

To complement the nested ANOVA analysis, we followed the approach of Roy *et al.* (2009) and quantified the tendency for tolerances to be more similar within than among genera, in units of the variable in question (rather than proportion of variance explained at higher taxonomic levels). For each climate niche measurement, the differences between pairs of species are calculated first for species within each genus and second for species across all genera. The test statistic is then calculated as the median difference between these two distributions, and expresses the absolute magnitude of within-group similarity in the correct units. Differences were calculated separately for the three climate niche measurements (maximum, minimum and mean). We repeated this analysis at the family level (within- and between family comparisons). Significance was assessed by randomly assigning taxonomic affinities across genera and families (depending on the level of analysis) while keeping the original number of species in each clade (1000 permutations).

Results of the analyses above could differ between mammals and amphibians simply if taxonomic levels are not comparable between the two groups. To assess the influence of family age on our results, we used Mann-Whitney U tests to compare crown group ages of mammalian families (taken from the mammal supertree, Fritz *et al.*, 2009) with amphibian family ages from each of two sources (Frost *et al.*, 2006; Roelants *et al.*, 2007). We also

calculated ratios of genus-to-family ages (i.e. the average age of genera relative to their family age). Low values of this ratio indicate that genera are young relative to families. In two families of comparable age and conservatism, more variance would be attributed to genus level in the family with the lower ratio because the component genera have had less time for trait divergence. In the absence of a dated phylogeny, these results help indicate the extent to which our taxonomic results are truly comparable among the two taxa.

The validity of analyses of taxonomic structure, such as nested ANOVAs, depends on the extent to which taxonomic clustering directly reflects evolutionary relationships. We therefore also calculated Pagel's λ (1999), a measure of phylogenetic signal strength in comparative data, for our mammalian climatic niche measurements using the best available phylogeny (Fritz *et al.*, 2009) under the assumption that finding significant phylogenetic signal bolsters our inferences based on taxonomy (see also Roy *et al.*, 2009). We did not repeat this analysis for amphibians because Pagel's λ is a branch length transformation and dating is not complete in the best-available amphibian phylogeny (see below).

Even if environmental tolerances are usually strongly conserved through evolutionary history, there will have been exceptions. Identifying lineages along which tolerances have shifted, and assemblages where many species show a change from ancestral environmental limits, may highlight the importance of adaptive innovations in structuring present-day assemblages. Mean temperature in the coldest quarter showed the strongest conservatism across both groups (see results); ideally, we would assess divergent lineages by estimating ancestral states for this variable and calculating the magnitude of species' deviations from these to quantify independent evolution. However, currently available phylogenies may not be sufficiently resolved to permit these analyses; while the mammal supertree we use (Fritz *et al.*, 2009) is nearly complete, some parts of the tree are highly polytomous, and there is no

well-resolved species-level amphibian phylogeny. Instead, we use the residuals from the nested ANOVA as a coarse proxy of intra-generic evolution with negative values indicating an increased ability to tolerate cold.

For comparison, we also conducted phylogenetically-explicit analyses using the mammal supertree (Fritz *et al.*, 2009) and a newly-constructed genus-level amphibian supertree with all the species within each genus included as polytomies (Fritz & Rahbek, unpublished manuscript and see Appendix 2.3) and with all branch lengths set equal. We estimated ancestral states using a one-parameter maximum likelihood (Brownian motion) model (Maddison, 1991) and estimated each species' change in cold tolerance as the change in mean temperature of the coldest quarter along the terminal branch of the phylogeny leading to it. In well-resolved sections of the mammal tree, these changes estimate species-level change. In the amphibian tree, and within internally unresolved mammalian genera, they reflect deviations from the genus mean, as in the earlier analysis, but accounting for evolutionary relationships among genera. Given the reservations outlined above, these results must be interpreted with caution, but are still useful as an examination of the consistency of taxonomy and phylogeny-based approaches.

For both methods, we combined these results with each species' occurrences in the cells of a 96.5 x 96.5 km Behrmann projection global grid to calculate and map the mean inferred amount of recent evolution in cold tolerance within each grid cell, for amphibians and mammals separately. We also calculated cell-average differences between amphibians and mammals to map cross-taxon congruence.

We classified cells according to whether or not mean temperature in the coldest quarter dropped below 5° Celsius and defined species as escapees if any part of their range fell within these cold cells or as non-escapees if they were restricted to warmer climates. This threshold

was defined on the basis of the relationship between temperature and plant growth (as measured by NDVI), following the procedure described in Olalla-Tárraga *et al.* (2006). We wished to test whether release from conservatism has impacted clade diversification by comparing the diversities of sister clades where one clade was exclusively composed of escapees and the other of non-escapees. However, because of polytomies in both the mammal and amphibian trees, only three valid phylogenetically independent contrasts were possible in each group precluding formal analysis.

Ideally, we would also have liked to estimate the effect of our binary character (escapee vs. non-escapee) on diversification using a maximum likelihood-based model such as BiSSE (binary-state speciation and extinction, Maddison *et al.*, 2007). However, when we carried out this analysis on the dated mammal supertree (see Appendix 2.4), maximum likelihood extinction rates were estimated as zero for both character states calling into question the validity of these results and suggesting that the lack of resolution or heterogeneity in rates across the phylogeny prevents robust conclusions being made at this time.

Results

Nested ANOVAs show substantial variation in conservatism across climatic variables (figure 2.1, table A2.5). Mean temperature in the coldest quarter was strongly conserved in both vertebrate classes: the proportion of variance explained above the species level across the three summary statistics (maximum, minimum and mean) ranged from 63.8% to 73.4% in amphibians and 50.3 to 65.8% in mammals (i.e., the sum of family and genus values in table A2.5). In amphibians, the highest proportion of variance for this variable was attributed to the family level, ranging from 40.0 to 48.5% across the three summary statistics. In mammals, however, although a similar amount of variance was explained above the species level, more

of it was attributable to genera rather than families (figure 2.1). As for the consistency across climatic niche measurements, mean values generally showed as strong as or stronger taxonomic structure than did the minimum or maximum values.

Comparing within- and between-genus differences in climatic preferences to null expectations (Roy *et al.*, 2009) also indicated marked conservatism of mean temperature in the coldest quarter (table 2.1). Results remained qualitatively the same after excluding monotypic genera (data not shown). Pagel's λ also indicates significant phylogenetic conservatism for the same set of variables in mammals (table 2.1).

The observed signal in our nested ANOVAs was not an artefact of amphibian families being younger than those of mammals: they are older, whichever amphibian phylogeny is used (amphibians - Roelants: median = 66.1 mya, Frost: 66.0 mya, n = 54; mammals: median = 24.7 mya, n = 101, Mann-Whitney U test: U = 325 and U = 316 respectively, P<0.0001).

The average ratio for genus-to-family ages was higher for amphibians (0.46) than mammals (0.33) (Mann-Whitney U test: U = 6546, P<0.0001) which, even though ages were available for only 17% of amphibian genera, suggests that mammalian genera are relatively as well as absolutely younger than amphibian genera. This non-comparability of taxa between the two groups weakens comparisons of the depth of conservatism, but indicates that when conservatism is found to be stronger in amphibians, this conclusion is robust to taxonomic artefacts.

For both taxa, latitude (in absolute degrees) gave similar results to mean temperature in the coldest quarter (figure 2.1 and table 2.1). We investigated whether the latitudinal signal was anything more than a proxy for climatic signal, but found no independent contribution of latitude (Appendix 2.1).

Global maps of the mean residuals from our nested ANOVA models highlighted regions where many of the species have recently shifted their tolerance to cold climates (figure 2.2). Results were qualitatively similar using ancestral trait reconstructions on phylogenies (Appendix 2.6), supporting the validity of our taxonomy-based analyses. As indicated by the strongly negative mean deviations (dark blue), mammal and amphibian assemblages inhabiting the northern Nearctic and Palearctic regions can cope with much lower minimum temperatures in the coldest quarter than expected compared to their relatives (figures 2.2a and b, see also figure A2.6). On the contrary, few assemblages contained species whose cold tolerance is strongly under-predicted by phylogeny (red and orange cells in figures 2.2a and b). For both vertebrate classes, these under-predictions are clustered in northern Australia, Malaysia and the Ethiopian Highlands as well as in the Nubian Desert and southern parts of the Arabian Peninsula and Atlas Mountains for amphibians (see also figure A2.6). Our cross-taxon congruence map (figure 2.2c) picked out the latter regions, together with the Iberian and Italian peninsulas, as places where the mammals have evolved relatively greater cold tolerance than amphibians. Conversely, amphibian faunas of Canada, northern India and Patagonia have recently evolved greater cold tolerance than mammalian faunas there.

Discussion

Our findings suggest that cold tolerance is a major limiting factor for the geographic distributions of both amphibians and mammals, apparently with broadly similar levels of conservatism in the two groups. Strong phylogenetic conservatism in cold tolerance has previously been reported for hyloid frogs (Smith *et al.*, 2005, Wiens *et al.*, 2006); our results show that the phenomenon is much more general, but that there are exceptions within each taxon – ‘escapee’ lineages that have shifted their cold tolerance. These expansions are

associated with colonisation of the North Temperate Zone, leading to the spatial aggregation of assemblages dominated by escapee species. Our results agree with a recent meta-analysis of experimental evidence (Sunday *et al.*, 2011) showing that thermal tolerance breadth in terrestrial ectotherms – including amphibians – indeed changes latitudinally, mostly as a result of increasing cold tolerance in northern temperate regions. They also reflect those of Cooper *et al.* (2011), who found greater conservatism of the thermal niche in tropical than temperate mammals.

Signals of conservatism in mammals and amphibians

While amphibians showed slightly stronger climatic niche conservatism than mammals for the most conserved variable, for other variables showing strong conservatism (e.g., annual precipitation), this conservatism was stronger in mammals than amphibians. These results also remained consistent under a more restrictive threshold for conservatism (60% variance accounted for above the species level). The variation in precipitation requirements across all amphibians is much more restricted than in mammals and the absence of strong phylogenetic signal in these variables may be due to this low variation and so a simple reflection of amphibians' strict minimum water requirements. Above this minimum, precipitation is no longer a limiting factor. Conversely, mammals are capable of persisting under a wider range of precipitation regimes, with conservatism for particular regimes apparent above the species level.

Our results must be interpreted bearing in mind that amphibian and mammalian taxonomists may or may not be acting equivalently. Mammalian families are younger than amphibian families and, on average, mammalian genera are also younger relative to the age of their family than is the case for amphibians. This indicates that, for a given proportion of variance explained at the genus or family level, the variable in question is more conserved in

amphibians than in mammals, as amphibians have more time for divergence. This does not mean that the mammalian signal is not real; simply that it is less “impressive” than the amphibian one. The absence of a dated phylogeny for amphibians prevents more formal analyses of the rate of evolution of the climatic tolerances of this group (Ackerly, 2009). However, our observation that amphibians, with, on average, older families and older genera than mammals, have more limited variation and similarly strong levels of conservatism in cold tolerance, strongly suggests they must have evolved more slowly along this niche axis. Indeed, the younger average age of mammalian genera and families may partly be a reflection of this faster rate of evolution (Simpson, 1953). It is possible that differences in the branching patterns within clades may be contributing to the observed differences between the two groups (O’Meara *et al.*, 2006).

That most of the variation in amphibians was strongly structured at the family level for cold tolerance, but not for the remaining variables, may be due to the ectothermicity of this group. That is, even though many amphibian species (especially anurans) can regulate their body temperatures within narrow ranges through behavioural and physiological adjustments (see e.g., Hillmann *et al.*, 2009), as ectothermic organisms they rely on external sources for heat gain and are unable to produce metabolic heat to the levels of mammals. In colder environments, amphibian heating rates are lower and thermoregulation is severely limited, which, in turn, affects their operative temperatures and activity times. Under prolonged cold conditions, amphibians survive by decreasing metabolic rates and resorting to overwintering strategies (i.e., spending most of the year inactive in burrows or under logs). These responses appear to have been established early in the evolutionary history of the clade and are consistent with a recent interpretation of the amphibian fossil record. Sahney *et al.* (2010) have suggested that climate aridification through the later Paleozoic, which eventually led to the collapse of Carboniferous Coal Forests, favoured the ecological diversification of

amniotes (reptiles) but had devastating effects on amphibian faunas. Mainly as a result of their limitations to adapt to the drier conditions that dominated Permian environments, many amphibian families failed to occupy new ecological niches (in terms of climate preference, body size or diet) and went extinct. A more nuanced understanding of the temporal dynamics of niche evolution and clade diversification in amphibians must await a well-resolved and dated amphibian phylogeny (e.g., Kozak & Wiens, 2006, 2010 for plethodontid salamanders).

Recent evolution of cold tolerance

Our map comparing the changes in cold tolerance of amphibians and mammals suggests that the amphibian species inhabiting the northern-most latitudes show more pronounced shifts in cold tolerance than mammals do. Amphibian species able to survive in northern parts of the Nearctic, Western Palearctic and Siberia (seven anurans and the Siberian salamander) have evolved to tolerate freezing: they are able to convert 50% or more of their total body water into extracellular ice (Hillmann *et al.*, 2009). Conversely, mammals in the Iberian and Italian peninsulas have shifted their cold tolerance more than amphibians have. These mammalian faunas consist of species whose ranges stretch northwards into much colder areas, whereas the amphibian faunas are largely endemic to the peninsulas themselves so their cold tolerances reflect only Mediterranean minimum temperatures. This result may echo the two groups' different rates of emergence from southern refugia following the retreat of the Pleistocene glaciers: while many mammal species have been able to expand out of these refugia, most amphibians have shown more limited recolonisation abilities or greater specialisation to Mediterranean habitats. Araújo *et al.* (2008) argue that the scarcity of amphibian species further north may result from either dispersal limitation or stronger physiological constraints stemming from their being ectotherms. It remains unresolved which hypothesis is more important; however, the facts that even wide-ranging European

amphibians are limited by climate (Araújo *et al.*, 2008) and the successful dispersal of other 'poor' dispersers out of glacial refugia (e.g., some European trees: Svenning & Skov, 2007a) suggest that physiological limitations may be more important in constraining amphibian rather than mammalian diversity at least in Europe. Further research is needed to determine whether this limitation is due to the basic ecophysiological organisation of the clade (as we suggest above) or to difficulties in evolving new adaptations to cold environments for particular subclades only.

We wanted to test whether the hypothesis that species currently occupying northern latitudes are members of a relatively small number of 'escapee' clades nested within tropical clades (Buckley *et al.*, 2010; Jablonski *et al.*, 2006; Wiens *et al.*, 2006) and whether escape from conservatism has led to rapid diversification following entry into new niche space (Simpson, 1953). Due to the lack of resolution in both the mammal and amphibian phylogenies, we could identify few valid sister-clade contrasts precluding formal analyses. If diversity only needs time and space to accumulate, diversification since the appearance of large geographical areas of new temperate and boreal environments in the Miocene should have produced many new species. However, other factors are likely necessary to build up diversity, in particular habitat heterogeneity, climatic stability and consistent energy (Kisel *et al.*, in press; Mittelbach *et al.*, 2007; Stephens & Wiens, 2003). Escapee clades may then be depauperate, due to higher rates of extinction during glacial cycles, or due to selection for generalists or large-range species better able to cope with fluctuating climates (over geological time) and strong annual seasonality (Davies *et al.*, in press).

Niche conservatism in means versus extremes

We had hypothesised that the extreme values of environmental variables that species experience would relate most closely to the phylogenetically conserved physiological traits

underlying species' tolerances (Soberón & Nakamura, 2009), so would show stronger conservatism than average values of environmental variables across species' ranges. However, mean values of climatic variables had similar amounts of taxonomic structure as minima or maxima. These findings concur with Wiens *et al.*'s (2006) and Martin & Husband's (2009) results for mean and extreme values in hylid frogs and North American angiosperms, respectively. Given the broad-scale spatial autocorrelation in climatic variables, it is unlikely that slight discrepancies between actual and modelled distributions would cause grossly incorrect estimates of climatic requirements. Nevertheless, one possible explanation for the strong signals found for mean values is that they correlate better with actual tolerances than extreme values do simply because centres of distributions are easier to characterise than are extremes. Part of our signal strength could also stem from the spatial autocorrelation in climatic variation: related species may have similar climatic tolerances due to their geographic proximity (despite having very different range sizes if, for instance, one is a peripheral isolate of the other). Indeed, Cooper *et al.* (2011) found that the spatial component of various aspects of the mammalian climatic niche was significant for that reason. However, the congruence in conservatism for mean and extreme values suggests that our results are not driven purely by spatial proximity in range edges (e.g., abutting sister species) but rather reflect conserved climatic tolerances across the range.

Concluding remarks

All our environmental variables showed conservatism that was stronger than or similar to that for geographic range size itself, suggesting that much of the interspecific variation in range size might reflect that simple 'rules' such as threshold tolerances and dispersal limitation are being played out on a complex surface. Most vertebrate speciation is allopatric, contingent on the location and timing of range-splitting barriers (Coyne & Orr, 2004). We here show that

among related species and for certain climatic factors – cold tolerance in particular – climatic requirements remain similar following speciation events while range sizes may be very different. With better-resolved phylogenies it will also become possible to explore how niche conservatism and evolution have affected diversification within these two groups.

Tables

Table 2.1. Test statistics indicating whether species are more similar in their climatic requirements within than between genera or families.

Taxon		Temp Warm (°C)	Temp Cold (°C)	Annual Precipitation (mm)	Precipitation Seasonality	NDVI	Absolute Latitude (°)
<i>Genus level comparisons</i>							
Amphibians	Max.	0.3*	1.6	-48.0*	6.0	0.0	4.1
	Min.	0.3*	1.8	48.0	6.0	2.0	4.4
	Mean.	0.1	1.7	31.8*	5.5	0.0	4.4
Mammals	Max.	0.6	2.0	659.0	6.0	3.0	5.9
	Min.	1.7	3.2	86.0	2.0*	3.0	5.6
	Mean.	1.1	3.1	258.1	2.9	5.6	6.2
<i>Family level comparisons</i>							
Amphibians	Max.	0.5	1.3	25.0*	4.0	1.0	3.0
	Min.	0.4	1.3	33.0	3.0	1.0*	3.0
	Mean.	0.4	1.3	48.5	3.5	1.0	3.0
Mammals	Max.	0.2*	0.2	293.0	4.0	1.0	0.5*
	Min.	0.9	0.8	33.0	-1.0*	2.0	0.9
	Mean.	-0.4	0.5	83.5	0.3	1.0	0.9
<i>Pagel's λ</i>							
Mammals	Max.	0.68	0.86	0.77	0.63	0.74	0.88
	Min.	0.64	0.80	0.79	0.54	0.62	0.84
	Mean.	0.84	0.88	0.71	0.88	0.90	0.86

Bold values are significant at $P < 0.001$, except values followed by * (significant at $P < 0.05$).

Negative values indicate that closely related species are less similar than more distantly related species. Pagel's λ is 0 if there is no phylogenetic signal and 1 if the signal corresponds to expectation from Brownian motion; all values here are significantly different from 0 and 1 according to likelihood ratio tests. Abbreviations: Temp warm/cold: mean temperature of the warmest/coldest quarter; NDVI: Normalized Difference Vegetation Index.

Figures

Figure 2.1. Taxonomic structure of the variance in climatic tolerances for amphibians (A) and mammals (M).

The main bars show the proportion of variance attributed to families (darkest grey), genera and species (lightest grey) by nested ANOVA. For each variable, the smaller bars show the relative sizes of the total variance associated with amphibians (left of the tick) and mammals (right of the tick).

Figure 2.2. Spatial patterning of recent evolution in cold tolerance for mammals and amphibians

Mean assemblage (grid cell) values for recent evolution in cold tolerance calculated as the average residuals from a nested ANOVA (see main text) for the species occurring in each cell. (a) Mammals; (b) amphibians and (equal-intervals above and below zero are used in the colour scale); (c) their difference (amphibians minus mammals). Only extreme differences are coloured; white cells are unoccupied by amphibians; grey cells are those where the difference is small.

Figure 2.1

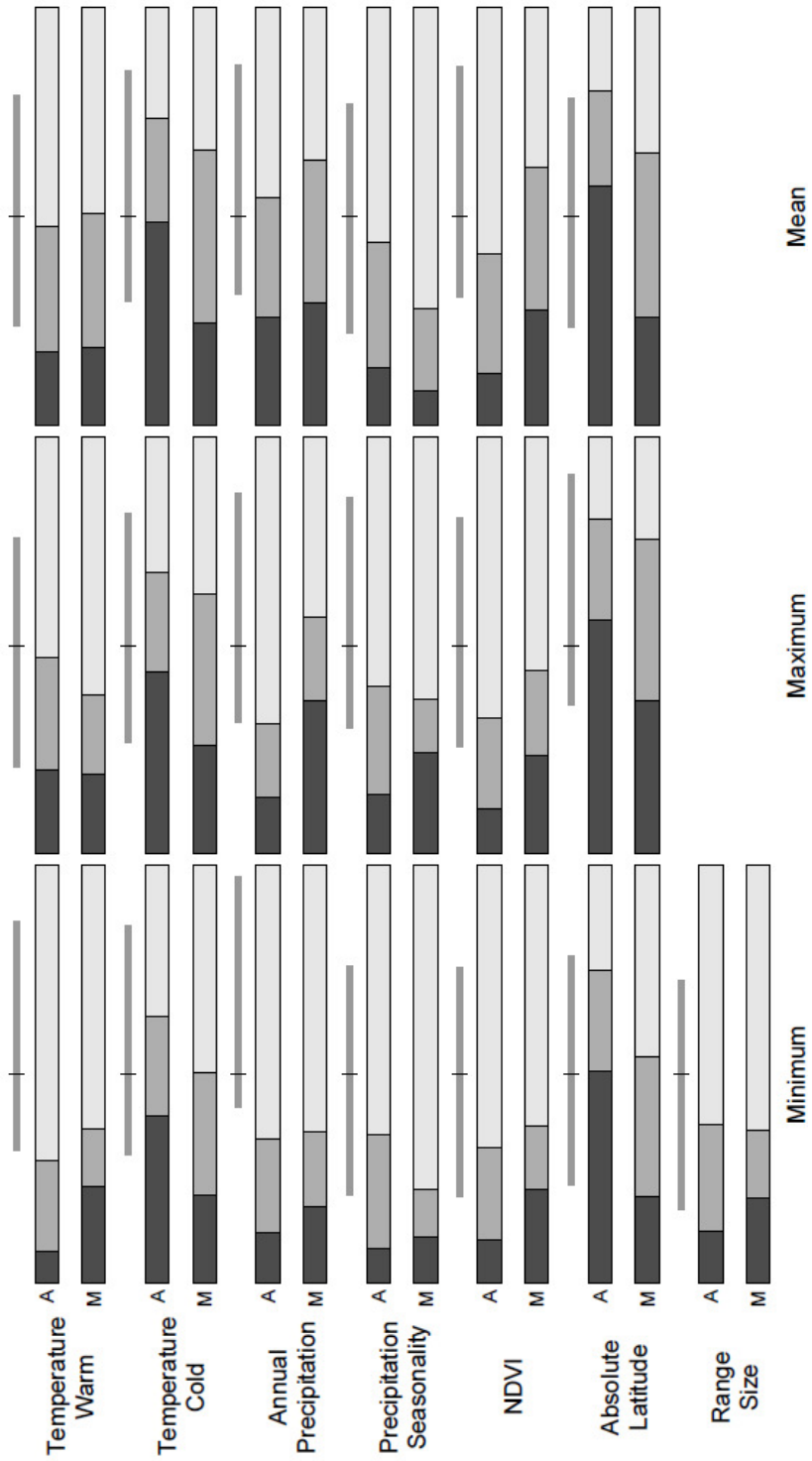
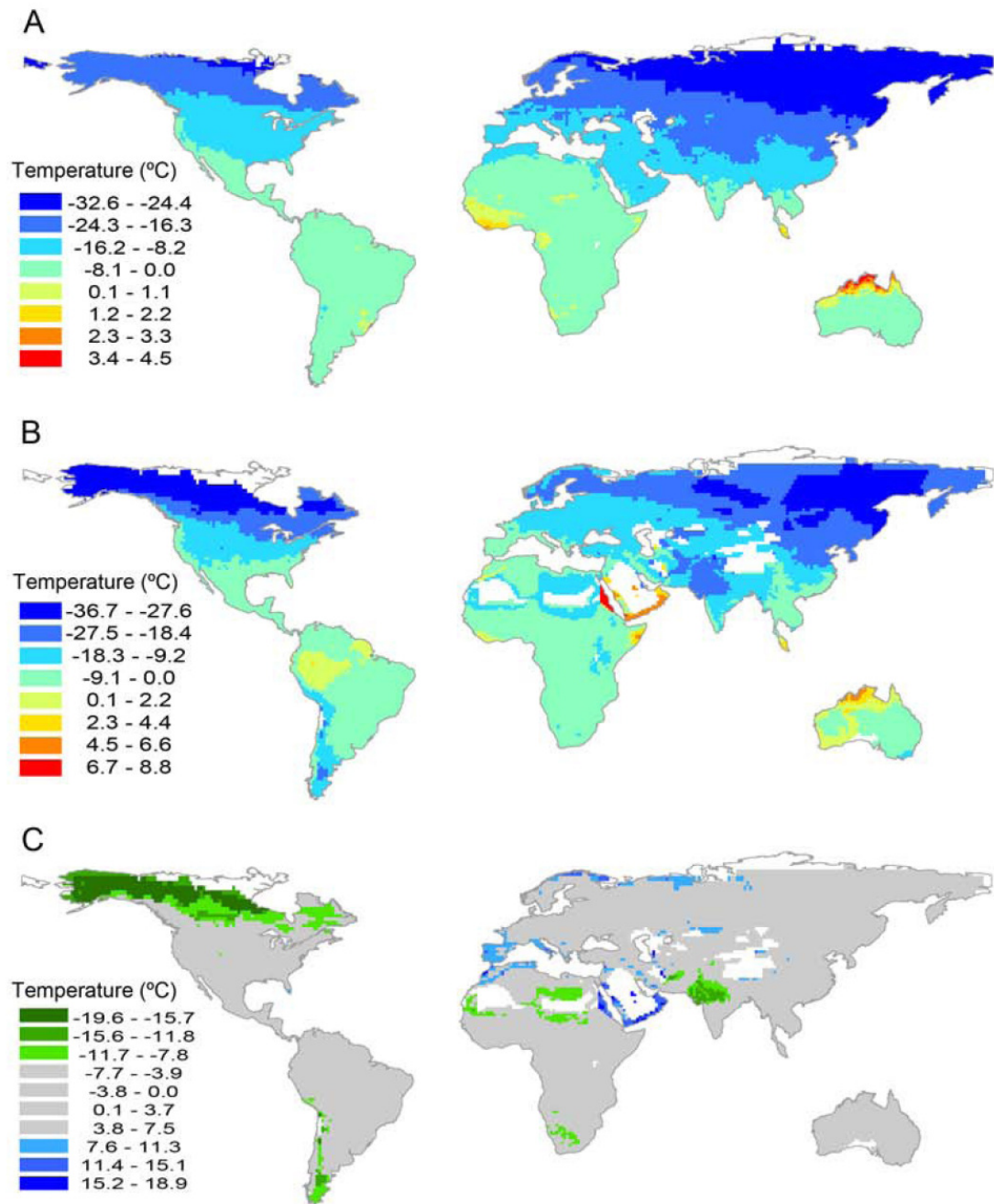


Figure 2.2



Chapter 3. Where do species' geographic ranges stop and why? Landscape impermeability and the Afrotropical avifauna²

Abstract

Although understanding large-scale spatial variation in species' distributions is a major goal in macroecology, relatively little attention has been paid to the factors limiting species' ranges. An understanding of these factors may improve predictions of species' movements in response to global change. I present a measure of landscape impermeability, defined as the proportion of resident species whose ranges end in an area. I quantify and map impermeability for Afrotropical birds and use multi-model inference to assess support for a wide suite of hypotheses about its potential environmental correlates. Non-spatial analyses emphasise the importance of broad-scale environmental patterns of energy availability and habitat heterogeneity in limiting species' distributions. Conversely, spatial analyses focus attention on smaller-scale factors of habitat and topographic complexity. These results hold even when only species from the top quartile of range sizes are assessed. All my analyses highlight that range edges are concentrated in heterogeneous habitats. Global change is expected to alter the nature and distribution of such habitats, necessitating range movement by many resident species. Therefore, impermeability provides a simple measure for identifying regions where continuing global change and human encroachment are likely to cause profound changes in regional diversity patterns.

² A version of this chapter is published as: McInnes, L., Purvis, A. & Orme, C.D.L. (2009) Where do species' geographic ranges stop and why? Landscape impermeability and the Afrotropical avifauna. *Proceedings of the Royal Society B-Biological Sciences*, **276**, 3063-3070

Introduction

The geographic ranges of many species are expected to change in response to ongoing global climate change. When trying to predict future ranges, researchers are often forced to make assumptions, e.g., that species will not colonise regions outside their present ranges and that there are no obstacles to colonisation of newly suitable locations (e.g., Thomas *et al.*, 2004). An understanding of current constraints acting at species' range boundaries may therefore make predictions about the future movements of species more accurate.

Range boundaries have often been studied from a single- or two-species perspective (Holt & Keitt, 2005). For example, population genetic models have shown how gene flow from the centre of a species' range may thwart local adaptation at the range edge, which can either promote or disrupt the generation of stable range limits (Kirkpatrick & Barton, 1997).

Interspecific interactions may also stabilise range limits, even in the absence of strong gradients in environmental variables or dispersal barriers (Case *et al.*, 2005; Case & Taper, 2000). While much attention has been given to identifying the patterns and environmental correlates of species richness and range size (e.g., Currie *et al.*, 2004; Hawkins *et al.*, 2003; Jetz & Rahbek, 2002), there have been few large-scale analyses devoted to deciphering patterns in the distribution of range boundaries (Svenning & Condit, 2008; but see Williams *et al.*, 1999). Further, the use of species distribution modelling (SDM), where a species' climatic envelope is inferred from the climatic variables found within its range, under the assumption that this is an adequate description of a species' realised niche (Guisan & Thuiller, 2005), defines edges largely as the location where a variable becomes unsuitable, rather than by modelling the conditions currently constraining range expansion. Here, I identify the areas where high proportions of range boundaries are clustered to provide an ensemble, macroecological perspective on species' limits. I therefore focus on the factors

affecting generalised limits of species' distributions and do not consider temporary, or sink, populations or individuals occurring outside this general limit (Fortin *et al.*, 2005; Gaston, 2003). I do not incorporate the roles of population dynamics (Kirkpatrick & Barton, 1997), genetics (Bridle & Vines, 2007) or biotic interactions (Case *et al.*, 2005; Terborgh, 1985) in limiting individual species' ranges. I locate regions where the range limits of multiple species coincide, and identify the environmental conditions within these areas.

Every species has a unique set of environmental variables under which it can survive and reproduce. Outside this niche space a species is unable to persist in the long-term. While many abiotic and biotic factors have been proposed to limit species' ranges (reviewed by Gaston, 2003), the availability of ambient and productive energy has long been considered the most important factor (Currie *et al.*, 2004). The range edges of many species coincide with climatic thresholds and have been found to change in broad synchrony with changing climate (Gaston, 2003). Consequently, SDMs have been used widely to predict the expected new range of a species under one or more climate change scenarios (Thomas *et al.*, 2004). Recently observed changes in avian community composition suggest, however, that the current pace of climate change may be too rapid, with species' ranges lagging behind their climatic envelopes (Devictor *et al.*, 2008). Furthermore, there is growing evidence that non-climatic factors also limit ranges (e.g., Beale *et al.*, 2008). Habitat heterogeneity has been shown to influence species richness and average range sizes of an area (Davies *et al.*, 2007; Rahbek & Graves, 2001). Complex habitats, or steep altitudinal gradients, often harbour high numbers of endemic species, uniquely adapted to one of the array of narrow niches found there (Terborgh, 1977). Heterogeneous habitats are expected to contain high densities of range edges, from resident endemics and larger-ranged species unable to cross the varied terrain (Kark *et al.*, 2007).

Evolutionary processes of niche conservatism and niche evolution (Hawkins *et al.*, 2007; Rangel *et al.*, 2007), along with Pleistocene glacial cycles and older climate changes (Davies *et al.*, 2007; Hawkins *et al.*, 2007; Rahbek *et al.*, 2007), have also recently been invoked to explain species' distribution patterns and will likely also impact on the patterning of range boundaries. Indeed, evolutionary explanations of high avian species richness in the montane tropics include: climatic stability over time; persistence of old species within refugial environments; and the generation of new species through fine-scale niche partitioning along environmental and topographic gradients (Rahbek & Graves, 2001). In short, where evolutionary and ecological explanations of high species richness converge, for example in the montane tropics, the density of range edges will also be high. Range edges will also cluster at the margin between tropic and temperate zones if it is true that species are generated in the tropics and that their ranges expand out of the tropics only rarely (Hawkins *et al.*, 2007; Rangel *et al.*, 2007).

Here I use the birds of the Afrotropics to conduct the first large-scale taxonomic and spatial analysis of the distribution and environmental correlates of range boundaries. To do so, I develop a measure of landscape impermeability (ω), calculated as the proportion of resident species with range boundaries within an area (e.g., a 1° grid cell). This measure gives an indication of how readily species' ranges have extended through an area and captures factors beyond hard landscape features (e.g., coastline) that prevent high proportions of species from expanding their ranges. My measure is similar to beta-diversity measures (Gaston *et al.*, 2007a; Koleff *et al.*, 2003), and spatial patterning of ω is expected to be similar to that for beta-diversity. However, ω is simpler and easier to interpret because it has relevance within a focal cell. It is therefore not necessary to define the neighbourhood within which turnover is examined, and yet ω captures compositional changes through space when viewed across grid cells.

I test a range of potential predictors of ω in three categories – habitat type, energy availability and habitat heterogeneity – reflecting the identified roles of both average environment (Gaston *et al.*, 2007a) and environmental variability (Buckley & Jetz, 2008; Melo *et al.*, 2009) in explaining patterns of global avian turnover. Whilst I expect the signal of ω to be high in areas rich in restricted-range endemics (e.g., the montane tropics), I am also interested in identifying additional patterns and in capturing the range-limiting factors of species of all range sizes (Jetz & Rahbek, 2002). Finally, I also look at differences in the spatial patterning of ω between passerines and non-passerines to assess whether characteristics of these major groups influences a species' ability to occupy the landscape. This focus on what limits species, rather than on what determines where they are found, sheds new light on the processes governing patterns in the distribution of species diversity and provides information regarding areas where responses to ongoing global change are expected to be most difficult.

Methods

Range data

I used data for all 2075 terrestrial Afrotropical bird species taken from a global database of bird ranges (Orme *et al.*, 2005; 2006). I included all endemic Afrotropical species and the Afrotropical range of non-endemic species. All range maps for this region were digitised from expert-drawn distribution maps from a single source (*'The Birds of Africa'*, references in Appendix 3.1). The distribution data in this source provide consistent, detailed range polygons, constructed without recourse to environmental modelling.

The digitised vector maps were converted into a Behrmann equal area grid containing 2569 land cells at a resolution of 96.5 km. This scale, approximately equivalent to a 1° grid,

minimises the overestimation of species occupancy of cells arising from using broad-scale distribution maps (Hurlbert & Jetz, 2007), especially for species with ragged range edges. The scale is also not so coarse as to obscure patterns in edge distribution, particularly in relation to restricted-range species (Fortin *et al.*, 2005). Species were scored as present in a grid cell if any part of the breeding range fell within the cell. A grid cell was counted as containing a species' range edge if any part of the perimeter of the species' range, including the boundaries of sections of disjunct range, fell within the cell.

Issues of differences in sampling effort across the realm do exist, for example between the well-studied southern African avifauna (Allan *et al.*, 1997) and the under-studied tropical forests of Central Africa. However, *The Birds of Africa* remains the best available source for my analyses and a recent comparison of gridded survey data (Allan *et al.*, 1997) and these range maps for southern Africa concluded that congruence was adequate using grid cells of 1° (my scale of analysis) and larger (Hurlbert & Jetz, 2007).

Calculating impermeability

Impermeability (ω) was calculated as the proportion of resident species that also had a range edge in a cell. As ω is bounded between zero and one, and has non-constant variance and a non-normal error distribution, I used logit-transformed ω [$\log(\omega/1-\omega)$] in all models.

Predictor variables

I identified the biome (Olson *et al.*, 2001) occupying the largest proportion of each cell but restricted analyses to the four biomes represented in at least 50 cells. Mean ω for the cells in discarded biomes (tropical & subtropical dry broadleaf forests (10 cells); temperate grasslands, savannas & shrublands (1); flooded grasslands & savannas (33); mediterranean forests, woodlands & shrubs (3)) did not differ significantly from those in the remaining four

major biomes: tropical & subtropical moist broadleaf forests; tropical & subtropical grasslands, savannas & shrublands; montane grasslands & savannas; and deserts & xeric shrublands (results not shown). In addition, all cells with $\omega > 0.9$ were identified as cells containing ranges with boundaries clipped to lakes or coast and hence where ω was trivially high. In total, 696 cells were discarded from the original dataset, resulting in the removal of 170 species restricted to the omitted cells (163 from coastal cells and seven from minor biomes). All the omitted species are restricted-range species (mean occurrence: 4.2 cells, range: 1 – 45 cells) and, since almost all occur in coastal/lakeside cells which are always completely impermeable, their omission is unlikely to obscure additional patterns in ω at this scale of analysis.

Biome type was used as a predictor variable describing broad-scale habitat type; I also used mean elevation (metres) as a second measure to capture habitat type. As measures of habitat heterogeneity within each cell I used: the number of the four major biomes present, to indicate large-scale habitat heterogeneity; the number of land cover types, to represent small-scale landscape heterogeneity; and \log_{10} elevational range, to capture topographic complexity. To investigate the correlation of climatic factors with ω , I used mean annual temperature ($^{\circ}\text{C}$) as a proxy for ambient energy and mean annual actual evapotranspiration (AET, mm) as a proxy for productive energy (all references in Appendix 3.2). The data for each of these variables was re-sampled from the original resolutions into the equal-area grid.

Anthropogenic impacts are expected to be important in determining the boundaries of ranges, particularly given the changes expected in human population and land use within the region (Millennium Ecosystem Assessment, 2005). However, the absence of estimates of range change resulting from anthropogenic impact, a temporal disassociation between available measures of impact and the avian range data and the known positive correlation between

measures of human impact and biodiversity at coarse spatial scales (Luck, 2007), suggest that establishing cause and effect of any relationship between human impact and ω will be difficult. Therefore I consider only environmental correlates in my reported models. In addition, a correlation test accounting for spatial autocorrelation (Clifford *et al.*, 1989) revealed no correlation between mean human population density and ω ($r=-0.00281$, $n = 2018$, effective sample size (ess) = 61.72, $t = -0.0216$, $p = 0.98$).

Data analysis

Preliminary analyses were performed to limit the scope of the most complex model considered. I calculated ordinary least squares (OLS) univariate regressions of ω against each predictor across the entire dataset and within each biome (details in Appendix 3.3). Significantly different relationships were often found in the biome-specific analyses, indicating that biome type is a key factor affecting landscape impermeability. I then used regression trees to visualise the structure of the data and to identify potential interaction terms (Appendix 3.3). Finally, I used a generalised additive model (GAMs: Wood, 2006) to examine the possibility of significant non-linearity between ω and the predictor variables (Appendix 3.3). All of the main effects showed broadly linear relationships with ω , except for AET and elevational range which approximated quadratic relationships. My most complex model therefore included all main effects and second-order polynomial terms for these two variables. I included first-order interaction terms between each main effect and biome and also between AET and both temperature and elevational range, resulting in a maximal model containing 19 terms. Variance inflation factors between the main effects were all low (≤ 4) indicating that there is no strong collinearity among them (Fox, 2002).

There has been a growing reaction against stepwise model simplification to a single minimum adequate model, particularly for broad-scale analyses where multiple alternative

hypotheses may be relevant (Diniz-Filho *et al.*, 2008; Johnson & Omland, 2004). Here, I fitted all 14,752 valid simplifications of my maximal model and follow a multi-model inference approach (Burnham & Anderson, 2002; Johnson & Omland, 2004). Models were fitted using OLS multiple regression and I obtained AIC_c , the sample size corrected version of AIC, for each model. I then computed the Akaike weights of each model across the full set of models using ΔAIC_c values and identified the set of most highly weighted models with a combined Akaike weight of greater than 0.95 (the 95% confidence set; Burnham & Anderson, 2002).

Spatial modelling

Cells close to one another in space will tend to have more similar values of both response and explanatory variables than cells located further apart (Legendre, 1993). Such spatial autocorrelation can inflate Type I error rates and cause bias in the magnitude of effect of explanatory variables (Davies *et al.*, 2007). Coefficients may also be estimated incorrectly and their variances strongly underestimated. Irrespective of the model selection method used, highly-supported non-spatial models are thus expected to be more inclusive than equivalently supported spatial models (Diniz-Filho *et al.*, 2008). However, OLS models may still be useful, despite their higher Type I error rates, in capturing broad-scale drivers of macroecological patterns (Diniz-Filho *et al.*, 2007). Interpretation of both non-spatial and spatial models and explicit consideration of scale and the hierarchical nature of diversity drivers may generate a more complete picture than one or the other mode of analysis alone (Diniz-Filho *et al.*, 2003; 2007). I follow this course here and present the results of both non-spatial and spatially-explicit regression analyses following exploration of the spatial structure of my data.

Correlograms of Moran's I confirmed the presence of substantial spatial autocorrelation in explanatory and response variables and in the residuals of models in my OLS best-model subset (Appendix 3.4). Following examination of semi-variograms and calculation of AIC values (Rangel *et al.*, 2006; data not shown) to determine the form of the spatial structure in the data, I refitted all models using a generalised least squares (GLS) approach (Pinheiro & Bates, 2000, Beguería & Pueyo, 2009) including an exponential spatial correlation structure. GLS incorporates this spatial structure directly into model residuals and correlograms of normalised residuals from fitted models were used to check that spatial autocorrelation had been adequately accounted for (Appendix 3.4; Pinheiro & Bates, 2000).

When fitting a spatial model using GLS, the range (ρ) over which autocorrelation operates is usually optimised for each set of explanatory variables, as the structure of the autocorrelation will vary with the suite of variables chosen. However, changes in the correlation structure will affect the calculation of AIC_c for a model and so, in order to simplify multi-model inference across models, I used a fixed range ($\rho = 39.095$ km). This value was obtained as the mean of independently estimated ρ from a random subset of 200 models. Pearson's correlation between the AIC_c values of these 200 models calculated using both optimised and fixed ρ is almost perfect ($r = 0.999$, $t_{198} = 29432$, $p < 0.0001$), suggesting that this restriction does not unduly affect subsequent model weighting. In addition, visual inspection of Moran's I correlograms indicated that spatial autocorrelation is similarly accounted for in both model sets (data not shown) and that residual autocorrelation was similarly reduced using the fixed or optimised ρ .

Range size and taxonomic influences

Results from studies of species richness and range size (Jetz & Rahbek, 2002; Orme *et al.*, 2006) suggest that correlates of ω will differ between large- and small-range species.

Following Jetz & Rahbek (2002), the species were divided into range size quartiles based on the number of cells occupied within the truncated dataset and the spatial distribution of ω was calculated for each quartile. The analyses described above were repeated using the species within the top range size quartile to investigate the expected high influence of this quartile on analyses of the dataset as a whole. In addition, I split my dataset into Passeriformes and all remaining birds and recalculated ω for each group. I calculated the correlation between the two subsets to investigate the degree to which taxonomic biogeographic structure is reflected in landscape impermeability.

Results

Spatial distribution of ω

Impermeability (ω) shows strong spatial patterns throughout the Afrotropics (figure 3.1). Permeable regions include the resource-rich Guinean and Congo basin forests and the savannas of the Sahel; ω increases markedly at the boundaries of these productive regions. Impermeability is also high in the montane habitats of northeastern Africa and along the edges of the Sahara desert in the north and the Namib Desert in the south.

Non-spatial OLS analyses

Non-spatial modelling produces a 95% confidence set containing ten models (table 3.1a). As expected, these highly supported models are inclusive (summarised in table 3.2a, see also Appendix 3.5), with the maximal model being the most highly weighted (weight, $w_i = 0.184$) and the remaining nine models including a mean of 16.9 terms. On the basis of F ratios, all models in the top set highlight the importance of available energy (AET, AET²) as well as elevational range, temperature and biome heterogeneity. Interactions with biome typically

have lower explanatory power, but are present in models retained in the preferred model set. Although correlograms of the raw residuals from the top OLS model exhibit reduced spatial autocorrelation compared to those of individual variables, there is still evidence (Appendix 3.4) for substantial short-range autocorrelation (Diniz-Filho *et al.*, 2003).

Spatial GLS analyses

Accounting for spatial autocorrelation using a GLS approach results in a 95% confidence set of two substantially simpler and better-fitting models (table 3.1b) with little remaining autocorrelation (Appendix 3.4). Both models include biome heterogeneity and then landscape heterogeneity as their strongest explanatory variables (table 3.2b), followed by either elevational range or elevational range². Highly spatially-autocorrelated variables such as AET and temperature (Appendix 3.4) are dropped from these models.

Effect of range size and taxonomy on ω

Broad scale patterns in ω vary considerably within range size quartiles (figure 3.2a-d) but are dominated by species in the top range size quartile (figure 3.2d), which inevitably contribute disproportionately to the number of species' presence (73.6%) and edge (54.8%) records in the dataset. Impermeability for this quartile is strongly correlated with overall ω ($r = 0.93$, $n = 2018$, $ess = 16.30$, $t = 13.27$, $p < 0.0001$). Both spatial and non-spatial models (Appendix 3.6) for this quartile mirror those for the whole dataset, with OLS models only suggesting a more significant role for temperature and with GLS models supporting the importance of habitat heterogeneity variables (biome heterogeneity, landscape heterogeneity and elevational range). In addition, mean ω for this quartile is significantly higher in cells where restricted-range species are also found ($F_{1,2016} = 28.50$, $p < 0.0001$), highlighting the congruence in highly impermeable areas for both small- and large-range species. Finally, the correlation between passerine and non-passerine ω was moderately strong and significantly positive ($r = 0.61$, $n =$

2018, $ess = 32.94$, $t = 5.50$, $p < 0.0001$). Given the larger average range size of non-passerines, it is unsurprising that the patterning of ω for this subset (figure 3.2f) mirrors that of the largest range size quartile (figure 3.2d) while that for the passerines (figure 3.2e) is an amalgam of the three smaller quartiles (figures 3.2a-c).

Discussion

I find strong broad-scale patterns of impermeability across Afrotropical birds, despite the idiosyncrasies of survival, reproduction and immigration that inevitably define individual species' range limits. Of the variables assessed, measures of habitat variability (biome and landscape heterogeneity and elevational range) are the most consistent predictors of impermeability (ω). These variables are significant in both non-spatial and spatial analyses (table 3.2) and show that transitional or complex habitats act as barriers for a majority of species, even those with the largest ranges (Appendix 3.6). These results support those of van Rensburg *et al.*, (2004) who found greater avian turnover at biome transitions in South Africa, but differ from the early conclusions of Allan *et al.* (1997) who believed that the botanically-defined biomes of the Afrotropics were not “entirely relevant to [its] avifauna.” Whether the clustering of avian range boundaries at biome edges is due to active habitat selection or enforced limits does not detract from the congruence found between avian and vegetation turnover and that high ω areas are areas where free range expansion is impeded.

I expected impermeability to be high at the transitions between biomes and in topographically complex regions for two reasons. First, such areas act as barriers to the expansion of mid- and large-range species as they reach the limits of their environmental tolerances. Second, they will be rich in restricted-range endemics adapted to niches uniquely found within the transitional habitat. Range edges for these two groups therefore coincide where habitat

heterogeneity is greatest and, indeed, mean ω for the widest-ranging species is significantly higher in cells also occupied by the narrowest-ranging species. Furthermore, only measures of habitat heterogeneity are included in the best supported spatial models for these wide-ranging species (Appendix 3.6).

Landscape heterogeneity, measured as the number of ecosystem types within a grid cell, shows a more complex relationship with ω . My initial single-predictor analyses show that high landscape heterogeneity in tropical & subtropical grasslands, savannas and shrublands is associated with lower impermeability (Appendix 3.3). This, however, is driven by the strong signal arising from the species-poor, highly impermeable boundary of this biome with the Sahara (figure 3.1). In spatial models, which account for the spatial non-independence of this signal, I find a strong positive association between landscape heterogeneity and impermeability across all biomes (table 3.2b, see also Rosenzweig, 1995).

Model choice also affects conclusions on the importance of energy availability. In my non-spatial analyses, ω is low where energy availability (AET, temperature and their interaction) is high. However, the strength of these relationships decreases greatly when spatial structure in these variables is accounted for. The fact that climatic variables drop out in the best spatial models indicates that the matching spatial structures of the explanatory and response variables might be driving the strength of these relationships. Additional analyses in other realms are required to determine if there is a genuine effect of climate on ω that is not simply a function of the broad-scale covariance in these variables.

Macroclimatic variables may be true range-limiting factors, but for large-range species only (Jetz & Rahbek, 2002 Rahbek *et al.*, 2007). Spatially-explicit analyses take account of the same large-range species contributing similar signal in many adjacent cells and change the focus of analysis from long-distance clinal variables, such as temperature and AET, towards

predictors acting at finer geographical scales (Diniz-Filho *et al.*, 2003; 2007). Biome heterogeneity, landscape heterogeneity and elevational range are the only predictors remaining in my best spatial models (table 3.2b, Appendix 3.5) suggesting that spatial analyses permit detection of additional explanatory variables acting at scales where the macroclimate is expected to vary only slightly (Diniz-Filho *et al.*, 2007; Hawkins & Diniz-Filho, 2006). Interestingly, these measures of habitat heterogeneity are also the only variables remaining in the best spatial models for species in the largest range size quartile. This suggests that additional factors beyond climatic isotherms also limit large-range species, and that even species capable of maintaining a large range do not necessarily cross regions of major habitat turnover.

My results complement analyses of beta-diversity in the Afrotropical avifauna (Williams *et al.*, 1999). These found that, at higher latitudes, turnover was dominated by richness gradients associated with the changing climate (at the edge of the Sahara and Kalahari deserts), while at low latitudes most signal was derived from species replacements along complex habitats (along the boundary of the humid equatorial forests and to the north and west of Lake Victoria). Different environmental factors therefore operate at different scales in shaping macroecological patterns (Rahbek & Graves, 2001), and non-spatial and spatial analyses should together explain the wider hierarchy of factors affecting species of all range sizes (Diniz-Filho *et al.*, 2003; 2007).

I do not assess the scale-dependency of my results, because such an assessment would be confounded by the scale limitations of broad-scale distribution maps (Hurlbert & Jetz 2007). My finding of the importance of elevational range and habitat heterogeneity is consistent with the observed fine-scale elevational zonation of avian communities within the tropical forest of the Udzungwa Mountains, Tanzania (Romdal & Rahbek, 2009) and of the earlier results of

Terborgh (1977) for birds along an elevational transect in the Cordillera Vilcabamba, Peru. However, neither scale of analysis directly determines the causal factors limiting species within heterogeneous habitats, and a detailed understanding of such limits is likely to require fine-scale mapping of species' abundances in combination with models of the population dynamics at range edges (Case *et al.*, 2005). Environmental models may also incompletely explain variation in ω if range limits are set primarily by historical factors such as the location of refugia (Davies *et al.*, 2007; Rahbek *et al.*, 2007). This would also help explain the high ω found in montane habitats where ecological factors promoting small ranges and refugial environments are coincident (Kark *et al.*, 2007). It is likely that finer-scale analyses would further emphasise some areas of high impermeability associated with excluded coastal cells (figure 3.1, e.g., in Angola, in Kenya and along the Rift Valley), as these would reintroduce some narrow-ranged species culled from the dataset that are also associated with transitional habitats in these regions.

It is likely that areas of high ω will show early responses to the adverse impacts of global change. I show that the edges of wide-ranging and the entirety of narrow-ranging species' distributions are concentrated in heterogeneous areas. Under global change, it is likely that the nature and location of these habitats will change (e.g., Hannah *et al.*, 2002). Species will respond idiosyncratically to these habitat movements (Davis & Shaw, 2001) and changes in community composition in high ω areas are expected to be common (Devictor *et al.*, 2008). The steepness of the elevational gradient in mountainous areas may allow some species to keep pace with their shifting niches (given the high number of, albeit narrow, niches, that can be packed into a certain area; Luoto & Heikkinen, 2008; Rahbek & Graves, 2001). However, certain habitats are projected to have no analogues in the near future (Williams *et al.*, 2007), and only limited adaptation to changing climates is expected (e.g., Gienapp *et al.*, 2008). Şekercioğlu *et al.* (2008) also highlight the elevated extinction risk of highland birds, with

warming temperatures expected to force species uphill, sometimes resulting in complete range extirpation.

Human presence is known to correlate positively with many biodiversity measures at coarse spatial scales (Luck, 2007), partly because available energy facilitates both dense human populations and diverse natural assemblages, and partly because human settlements in transitional habitats can probably access more diverse resources (Hugo & van Rensburg, 2008). However, in my preliminary analyses, I found no correlation between human population density and ω . While this may be due to the temporal discord between the two datasets, it seems that the areas I identify as particularly vulnerable to disturbance in the face of climate change are not currently facing unusually high human densities.

Previous studies have highlighted transitional habitats as dynamic centres of endemism meriting conservation attention (Kark *et al.*, 2007). I concur with this study, and others, in suggesting that both transition zones and the surrounding areas into which species are likely to “want” to move, alongside montane areas, are important in systematic conservation planning (Luoto & Heikkinen, 2008). My analyses complement others which suggest that climate envelope models do not fully capture species’ distributional limits (Beale *et al.*, 2008) and make a start at answering the call for a more inclusive understanding of range-limiting factors (Gaston, 2009; Svenning & Condit, 2008).

Tables

Table 3.1. Results of model selection. Akaike weights (W_i), AIC_c and the number of terms in each model for all the (a) non-spatial and (b) spatial models in the 95% confidence sets.

	W_i	AIC_c	Terms
(a) Non-spatial	0.18	2578.1	19
	0.17	2578.3	18
	0.17	2578.3	16
	0.16	2578.4	17
	0.09	2579.5	17
	0.09	2579.5	18
	0.03	2581.9	16
	0.03	2582.0	15
	0.02	2582.2	18
	0.02	2582.6	17
(b) Spatial	0.81	-47.2	3
	0.15	-43.8	3

Table 3.2. Summary of top models. (a) The minimum and maximum F ratio and the number of times retained (n) for each term across the 95% confidence set of 10 non-spatial models. (b) F ratios for significant terms in the two models in the 95% confidence set for the spatial models. Superscripts show significance at $p < 0.001$, along with the sign of the coefficient where relevant.

	(a) Non-spatial			(b) Spatial	
	<i>Min F</i>	<i>Max F</i>	<i>n</i>	<i>Model 1</i>	<i>Model 2</i>
<i>Main effects</i>					
Biome	61.17 [*]	61.54 [*]	10		
Mean elevation	0.05	0.05	10		
Mean annual AET	494.79 ⁺	497.82 ⁺	10		
Mean annual temperature	123.66 ⁺	124.42 ⁺	10		
Elevational range	357.10 ⁺	359.28 ⁺	10	33.59 ⁺	
Landscape heterogeneity	0.29	0.30	6	23.86 ⁺	28.58 ⁺
Biome heterogeneity	203.49 ⁺	204.74 ⁺	10	50.61 ⁺	61.74 ⁺
Mean annual AET ²	283.59 ⁻	291.32 ⁻	10		
Elevational range ²	40.51 ⁺	43.92 ⁺	10		19.47 ⁺
<i>Biome interactions</i>					
Mean elevation	15.17 [*]	15.48 [*]	10		
Mean annual AET	25.98 [*]	26.41 [*]	10		
Mean annual temperature	19.03 [*]	19.49 [*]	10		
Elevational range	41.81 [*]	42.93 [*]	10		
Landscape heterogeneity	6.37 [*]	6.48 [*]	4		
Biome heterogeneity	3.85 [*]	3.87 [*]	6		
Mean annual AET ²	17.72 [*]	18.81 [*]	10		
Elevational range ²	8.25 [*]	11.34 [*]	10		
Mean annual AET: Mean annual temperature	16.48 ⁻	21.93 ⁻	10		
Mean annual AET: Elevational range	1.90 ⁺	2.38 ⁺	5		

Figures

Figure 3.1. Landscape impermeability for Afrotropical birds using untransformed ω .

Impermeability increases from 0 to 1. Yellow = high ω ; red = low ω . Grey cells are omitted from all analyses (see text for further justification)

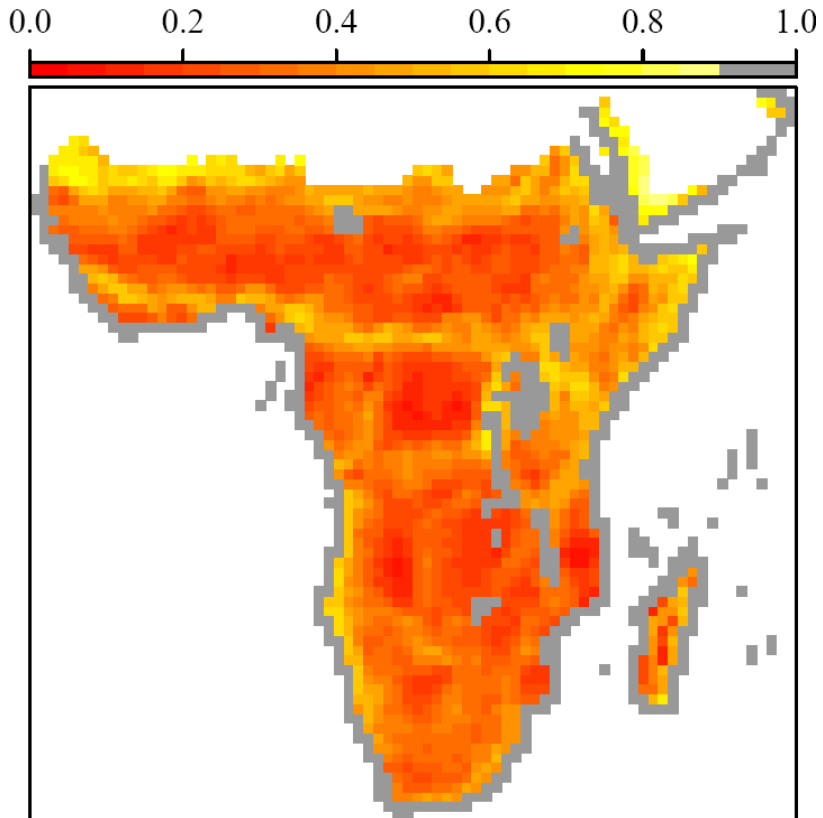
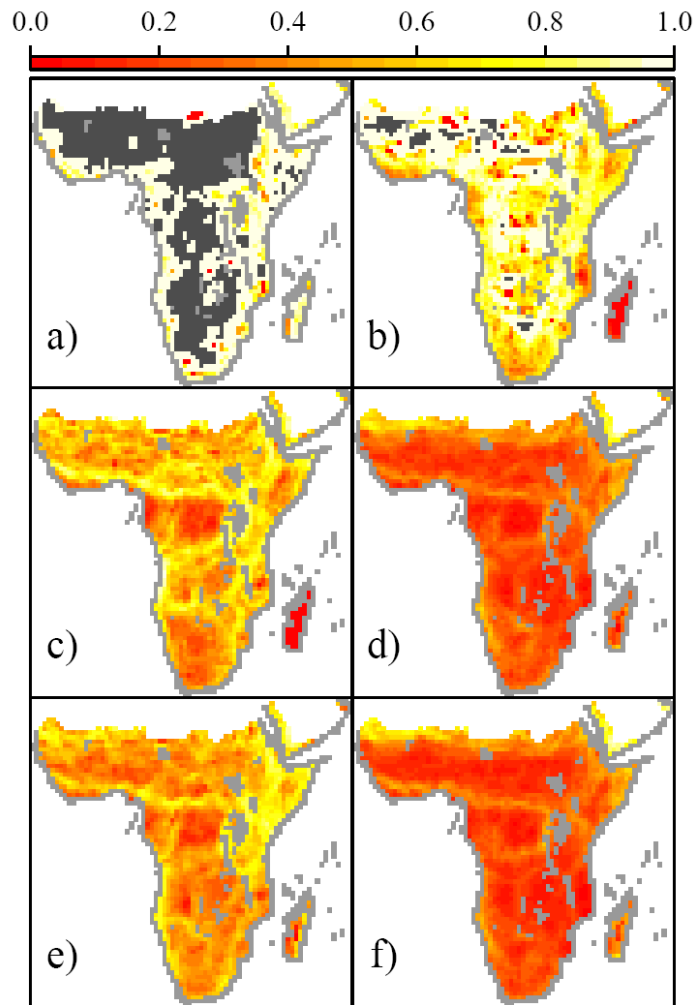


Figure 3.2. Landscape impermeability for subsets of species from the dataset: range size quartiles (a-d) from the narrowest-ranged (a) to the widest-ranged (d) species, (e) passerines and (f) non-passerines. Grey cells as in figure 3.1 with dark grey cells (a-b) showing cells which contain no species from that subset.



Chapter 4. Global patterns and inter-realm differences in mammalian landscape impermeability

Abstract

Advances in data availability have enhanced our understanding of broad-scale diversity gradients by facilitating global scale analyses of patterns in, for example, species richness, range size and body size. Here, I extend my initial exploration of landscape impermeability in the Afrotropical avifauna to mammals globally. Because analyses at the global scale may mask considerable variation stemming from regional effects, I compare and contrast the patterns and correlates of impermeability found for each biogeographic realm. While I find a consistent signal of the most impermeable habitats being concentrated in heterogeneous areas, there are also differences apparent particularly between temperate and tropical realms where characteristic gradients in energy availability modulate landscape impermeability in distinct ways. I also present an initial exploration of spatial patterning in amphibian landscape impermeability and investigate its congruence with that for mammals, globally and within each realm. Species' movements in response to global change will manifest themselves first at range edges, but areas where range edges are currently concentrated represent regions where unimpeded range expansion may be difficult. I discuss how an understanding of the macroecology of range limits may constitute a necessary additional component when forecasting the redistribution of biodiversity under climate change.

Introduction

Much is known of the factors underlying broad scale patterns in species richness and average range size, with a consensus emerging over the importance of climatic drivers (e.g., Hawkins *et al.*, 2003) in combination with region-specific effects (e.g., Hortal *et al.*, 2008; Ricklefs, 2004). While single species studies have identified a multitude of factors influencing species' range limits including hard landscape barriers such as coastline or rivers, climatic thresholds, landscape heterogeneity and biotic interactions (Gaston, 2003; Sexton *et al.*, 2009), broad scale patterns in range limits have, in contrast, been largely ignored (but see McInnes *et al.*, 2009; Pigot *et al.*, 2010).

To this end, we recently published a study of the macroecology of range limits in the Afrotropical avifauna (chapter 3; McInnes *et al.*, 2009). In this study, we mapped the proportion of resident species that have range edges in an area, and termed our new measure landscape impermeability (ω) given that areas where most resident species' ranges end correspond to difficult habitats where easy range expansion is impeded. We tested a range of potential environmental correlates of ω in three categories - habitat type, energy availability and habitat heterogeneity. We found that range limits are clustered in heterogeneous habitats, in areas that both harbour restricted-range species endemic to specialised microhabitats and act as barriers to larger range species inhabiting the surrounding more homogeneous habitats.

Here, I extend our analysis of landscape impermeability to mammals globally using distribution data from the Global Mammal Assessment (GMA, Schipper *et al.*, 2008). I fit models separately within each biogeographic realm under the expectation that their differing historical and current environments may lead to contrasting patterns and correlates of ω (Davies *et al.*, 2007; Hortal *et al.*, 2008). For example, range sizes are typically larger at higher latitudes (Stevens, 1989) and this is commonly attributed to species possessing

generalist adaptations to cope with seasonal climates (Davies *et al.*, 2009). Will ω be lower in temperate realms where there are fewer range edges and by extension less clustering of range edges? Or will correlates of ω in these realms be more strongly biased to climatic thresholds beyond which few species can persist (Olalla-Tárraga *et al.*, in press)?

I also present an initial exploration of amphibian impermeability using data from the Global Amphibian Assessment (GAA, Stuart *et al.*, 2004). With more stringent habitat requirements and lower dispersal capacity, landscape impermeability might be expected to be “higher” for amphibians (Buckley & Jetz, 2008). It is not clear, however, whether amphibians’ more fine-grained landscape experience (Belmaker & Jetz, 2011) will translate into novel patterns in impermeability. As for conservatism in climatic tolerances in the two groups (Olalla-Tárraga *et al.*, in press), the clustering of amphibian range limits in space may be highly congruent with mammalian clustering if the same underlying landscape features limit high proportions of resident species of the two taxa.

Impermeability is related to various measures of beta-diversity (Koleff *et al.*, 2003), but is simpler to calculate and easier to interpret because it has relevance within a focal cell whilst also capturing compositional changes through space when viewed across grid cells. Thus, while both require decisions on the grain size of the grid, because beta-diversity is concerned with compositional and/or richness differences between cells, a suite of further decisions may also be necessary (Tuomisto, 2010a, b). Furthermore, an understanding of the macroecology of beta-diversity requires partitioning variation into that explained by geographic versus environmental distance (e.g., Qian *et al.*, 2009) in order to capture turnover related to dispersal- and niche-limitation (Baselga, 2010; Gaston *et al.*, 2007b). In contrast, ω directly quantifies areas which are traversed by few species and is useful in assessing the nature of such regions.

I find that there is a globally consistent signal of high ω in heterogeneous areas. My results in general concur with recent studies suggesting that climate change responses will be first apparent in montane areas and along major habitat transitions and suggest that ω may be a useful measure to identify areas of high current and future biotic turnover.

Methods

Processing the mammalian range data

I used the polygon shape files of the ranges of all mammals from the Global Mammal Assessment (GMA: www.iucnredlist.org/mammals; Schipper *et al.*, 2008), processed in the same way as detailed in chapter 2 (Olalla-Tárraga *et al.*, in press). Briefly, I excluded ranges of extinct species as well as the parts of ranges classified as introduced, presence uncertain or historical range. I also excluded all marine mammal species. Finally, I matched the GMA species with the species found in Wilson & Reeder (2005). In addition, I retained 103 species not found in the mammal supertree (Fritz *et al.*, 2009), but with distributional data available.

Calculating impermeability

I converted the polygons of each species using a Behrmann equal-area projection; preserving area but not necessarily the shape or distance between cells. I overlaid a 96.5 km² equal-area grid system on the projections and extracted grid cell occurrences for each species. Species were scored as present in a grid cell if any part of the breeding range fell within the cell. A grid cell was counted as containing a species' range edge if any part of the perimeter of the species' range, including the boundaries of sections of disjunct range, fell within the cell. Impermeability (ω) was calculated as the proportion of resident species that also had a range

edge in a cell. As ω is bounded between zero and one, and has non-constant variance and a non-normal error distribution, I used a logit [$\log(\omega/(1-\omega))$] transformation in all analyses.

I obtained ω for 17450 cells globally. I removed all remaining cells with $\omega > 0.9$ (McInnes *et al.*, 2009), as these cells contained ranges with boundaries clipped to lakes or coast and hence were where ω was trivially high. I restricted analyses to continental cells (Kreft *et al.*, 2008) as patterns of ω on islands are hard to interpret. I also excluded biomes that were represented in less than 50 other cells in the same realm, apart from in Australasia where the temperate broadleaf and mixed forests biome (37 cells) was retained as it formed a contiguous region in the south east. Finally, I removed 65 cells with $\omega = 0$ to facilitate the logit transformation. In total, 6044 cells were removed from the dataset, leaving 11406 cells with 3981 species contributing to ω .

Environmental predictor variables

I used the same set of environmental variables as in McInnes *et al.* (2009; chapter 3) to test for significant correlations with mammalian impermeability (variables mapped in Appendix 4.1). Briefly, the variables chosen were: biome type and mean elevation (metres) to represent broad-scale habitat type; the number of co-occurring biomes and the number of land cover types as measures of broad- and small-scale habitat heterogeneity, respectively, and elevational range (metres) as a measure of topographic complexity. Ambient energy availability has been shown to limit species in high latitude environments, while water availability increases in importance in higher energy (i.e., lower latitude) regions (Hawkins *et al.*, 2003; O'Brien, 2006; Whittaker *et al.*, 2007). To represent these two climatic axes, I used mean annual temperature ($^{\circ}\text{C}$) and mean annual actual evapotranspiration (AET, mm) as proxies for ambient and productive energy, or resource, availability. Mean elevation and elevational range were natural-log transformed and AET was square-root transformed to

improve normality. The data for each of these variables was re-sampled from the original resolutions into the equal-area grid (references in Appendix 3.2). I centred and scaled the variables to facilitate comparison of slope estimates both within and between models (Schielzeth, 2010).

Beta-diversity studies commonly include environmental differences between focal cells as a measure of environmental roughness (Buckley & Jetz, 2008; Gaston *et al.*, 2007a; Melo *et al.*, 2009). In this analysis, topographic and habitat complexity variables both capture the degree of such roughness within a given cell precluding the need to include additional roughness measures.

In the original analysis (McInnes *et al.*, 2009; chapter 3), I fitted biome interactions with each of the main effects hypothesising that variables such as elevation might affect ω differently depending on additional features of the landscape. However, to retain tractability among models across realms and because of limits to computing power in the fitting of spatially-explicit models (see below), here I do not fit biome interactions and include biome identity only as a main effect. Thus, while I am still able to assess differences among biomes, I am less able to explore which variables in the model may be contributing to differences in ω between biomes.

Data preparation

I undertook preliminary exploratory analyses to define an adequate maximal model. First, I fitted generalised additive models (Wood, 2006) to characterise the shape of the relationship of each variable with ω . This identified a humped relationship between ω and mean annual temperature, captured here using a squared term. Second, I fitted regression tree models: these revealed associations between values of mean annual temperature and both AET and elevational range, represented here by the use of two-way interaction terms. The first of these

interactions likely reflects how energy and water availability interact to limit ranges (e.g., high temperatures may only be limiting in dry environments, Hawkins *et al.*, 2003). The second captures the contrasting effect of elevational gradients where energy is plentiful versus where it is scarce (e.g., altitudinal change might only be associated with range limits when it is also associated with steep gradients in energy availability, Hawkins & Diniz-Filho, 2006). These additions resulted in a maximal model of 7 main effects, 2 interaction terms and 1 factor (biome) with between 3 (Indomalaya) and 11 (global) levels. For the global dataset, variance inflation factors (all < 2) and condition indices (all < 4) were low indicating there was not a problem of multicollinearity among the main effects (Fox, 2002).

Data analysis – ordinary least squares modelling

I first fitted ordinary least squares (OLS) multiple regression models separately to each realm. Each realm-specific model included all realm endemics and that part of cosmopolitan species' ranges that fell within the focal realm. To best facilitate identification of the most explanatory model and to avoid the subjective process of model simplification (Mundry & Nunn, 2009), I implemented multi-model inference using the R package, MuMIn (Barton, 2011). I ranked models ($n = 416$) according to sample-size corrected AIC (AICc) and identified that set of models within four AICc units of the top-ranked model (Barton, 2011). Having obtained the top model set, I used model averaging to obtain averaged coefficients weighted by the Akaike weights of the set of models each variable occurred in. Note that as model averaging may involve sets of models where some models include only main effects without their interaction terms, the use of standardised coefficients facilitates interpretation of their averaged coefficients (Schielzeth, 2010).

Data analysis – simultaneous autoregressive modelling

I checked for the presence of spatial autocorrelation by plotting correlograms of Moran's I generated from the OLS maximal models using the `correlog()` function in the R library *ncf* (Bjoernstad, 2006). Following evidence of spatial autocorrelation, I then fitted simultaneous autoregressive (SAR) models for each realm using the *spdep* library (Bivand, 2007). I only fitted realm-specific models given that cells in different realms are likely to be spatially independent from one another and the degree of spatial autocorrelation is also expected to differ between realms (see also Davies *et al.*, 2007; Whitton *et al.*, in press).

SAR models (reviewed in Beale *et al.*, 2010; Kissling & Carl, 2008) are faster to fit than including spatial autocorrelation (SA) structures within a generalised least squares framework (McInnes *et al.*, 2009) and can use a single pre-defined spatial weights matrix rather than requiring repeated optimisation of a spatial autocorrelation model. While GLS directly models the spatial covariance structure and extracts this structure to generate spatially-structured residuals, SAR models the way SA is produced and corrects for it using a chosen form of weight matrix that specifies the strength of interaction between neighbouring sites. I followed Kissling & Carl (2008) and fitted SAR_{error} models that assume that autocorrelation is found only in the error term, for example due to a missing explanatory variable or to the inherent SA of the response variable itself. I used the recommended row-standardised weighting scheme which scales covariances based on the number of neighbours in each region and used the method developed by Cooper & Purvis (2010) to find the optimal neighbourhood distance (lowest AIC) for each realm.

Pseudo- R^2 values were calculated for OLS and SAR models as the squared Pearson correlation between fitted and observed values (Kissling & Carl, 2008).

Amphibians

To compare and contrast mammalian impermeability with another vertebrate group with a contrasting ecology, I also calculated impermeability for continental amphibians (ω_A) globally. I used polygon shapefiles of the geographic ranges of each amphibian species taken from the Global Amphibian Assessment (GAA: www.iucnredlist.org/amphibians; Stuart *et al.*, 2004) and processed them as above to obtain ω_A values for 13080 cells globally. Because amphibian ranges are, on average, smaller than mammals' (see also Buckley & Jetz, 2008, Qian, 2009), many amphibian species do not occur in more than one grid cell at the 96.5 km² scale. This also means that many cells have very high ω_A values within the interior of continents (e.g., 1139 non-coastal cells with $\omega_A > 0.9$, 994 of these with $\omega_A = 1$). In contrast to mammals, there are also a large number ($n = 1471$) of cells that have $\omega_A = 0$. Because 0 and 1 are not finite on the logit scale, rather than fit models to such a depauperate dataset, I look only at the congruence between untransformed mammal and amphibian impermeability using correlation tests accounting for spatial autocorrelation (Clifford *et al.*, 1989). I look at congruence in two ways: a. including all cells and b. omitting coastal cells where ω and ω_A are always 1. I repeat analyses at both the global and realm level.

Results

Mammals

Striking spatial patterns of impermeability are visible in each realm (figure 4.1).

Impermeability (ω) varies significantly among realms (one-way ANOVA, $F_{5,11400} = 107.6$, $p < 0.001$) although the interpretation of such a result is complicated by spatial autocorrelation.

OLS model sets by realm all contain few, parameter-rich models (table 4.1). In the case of the Neotropics and Indomalaya, the maximal model is unequivocally superior ($w_i > 0.98$); Australasia shows the most variation with four competing models (highest $w_i = 0.374$). All models show reasonable explanatory power with pseudo- R^2 varying between 0.303 (Afrotropics) to 0.697 (Neotropics) for the top model in each realm. Model-averaged t values suggest a key role of elevational range in increasing impermeability across most realms. Temperature also appears to play a crucial role although this is mitigated in the tropics by interactions with elevational range and accentuated in temperate realms by interactions with AET (table 4.2).

The large confidence limits on the temperature variables for the Afrotropics (figure 4.2) stem from the absence of the polynomial term in one of the models in the top model set (table 4.2). The large absolute values for the temperature variables in Indomalaya and Australasia are a function of the low variation in temperature found in these realms: although ω varies as much as in other realms, the temperature range is much reduced.

Correlograms of the residuals from the most highly-weighted OLS model in each realm confirmed significant positive spatial autocorrelation (SA) at the shortest distance class (100 km) indicating that spatially-explicit models were a necessary addition (plots in Appendix 4.2). Corresponding correlograms for the SAR models indicated that residual SA had been successfully removed to non-significant levels apart from in the Nearctic and Palearctic where SA was still significant at the shortest distance class (plots in Appendix 4.2).

Furthermore, the top SAR model in each realm has consistently lower AICc scores and higher pseudo- R^2 than the corresponding top OLS model with pseudo- R^2 for the SAR models varying between 0.723 (Australia) and 0.918 (Neotropics) (table 4.1).

A greater number of models enter the top model sets for the SAR models in some realms (e.g., 22 models in Indomalaya and 25 in Australia) indicating greater model uncertainty (table 4.1). Nevertheless, measures of habitat heterogeneity are highly-ranked in most realms with elevational range generally remaining one of the highest-ranked variables and biome and landscape heterogeneity increasing in importance as compared with the OLS models. In the Nearctic and Palearctic, the energy interaction term remains highly-ranked and there is an additional signal of a negative relationship between mean elevation and ω in Australia and the Afrotropics (table 4.2). In general, the signs of the relationships between each predictor and ω remain the same, although in some realms the intercept estimated for certain biomes changed considerably (figure 4.3).

Mammalian versus amphibian impermeability

Spatial patterns of amphibian impermeability are similar to those found for mammals (figure 4.4). Using all cells, the Pearson correlation coefficients range between 0.615 (Palearctic) and 0.898 (Indomalaya). Omitting coastal cells, where all species in both taxa must end, the correlation coefficients all decrease and now range between 0.205 (Australasia) and 0.831 (Neotropics). See table 4.3 for full results.

Discussion

Results summary

Across all realms, there is strong spatial patterning in mammalian impermeability (ω). As with Afrotropical birds, the most consistent predictors of ω are measures of habitat heterogeneity, highly ranked in both OLS and SAR models and across all realms. For instance, topographically complex areas along the Pacific coast of the Americas, the

Himalayas in Asia and the African rift mountains all show high ω , patterns also apparent for amphibians. Nevertheless, there are also differences among realms and between the two taxa.

In temperate northern latitudes, there are strong positive correlations between high ω and both elevational range and resource availability (captured in the interaction term of temperature with AET). Much of the temperate realms was under ice as recently as 13,000 years ago (Webb & Bartlein, 1992) and dispersal limitation may mean that species in these regions have yet to reach their equilibrium range limits (Fang & Lechowicz, 2006). If species also vary in their dispersal ability (e.g., Bowman *et al.*, 2002), range limits could then be notably more idiosyncratic in these realms; alternatively they could collect in areas between refugia (e.g., Hewitt, 1996, 1999). Such idiosyncrasy would predict poorer models in these regions whereas, in fact, the models for the Nearctic and Palearctic are highly explanatory with range edges collecting in topographically complex regions (see also Qian *et al.*, 2009). My results generalise those of Swenson & Howard (2005) and Hewitt (1996, 1999) who found that hotspots of mammal contact zones in North America and Europe were often found in mountain ranges. Mountains can act as strong barriers to dispersal and, as species emerged from glacial refugia on either side of mountain chains, contact zones came to cluster within the chains (facilitated by low mountain passes functioning as dispersal corridors: Hewitt, 1996, 1999). The additional strong association of ω with resource availability suggests that fine-scale niche partitioning in resource-rich areas in the south of these realms has led to a proliferation of small-range species (Rahbek & Graves, 2001; Wright, 1983). In sum, ω in temperate realms is highest where the landscape structure is complex, preventing free range expansion and facilitating *in situ* diversification.

In the Afro- and Neotropics, ω is not high where both elevational range and temperature are high. This is perhaps surprising given that tropical montane areas are home to many

restricted-range endemics (Janzen 1967; Ruggiero & Kitzberger, 2004). However, this signal of fine-scale niche partitioning in tropical mountains is still apparent in the positive correlation and high ranking of elevational range as a main effect with the sign of the interaction term a function of each realm's hot and dry desert areas harbouring relatively few species that each occur throughout the region, discernible also from the relatively low intercepts specified for the desert & xeric shrubland biome in these realms (figures 4.2-3).

My exploration of amphibian ω_A remains preliminary in the absence of modelling its environmental correlates. However, I identified substantial congruence in ω and ω_A , indicating similar factors lead to the clustering of range limits across the two taxa, although the strength of this congruence varies among realms (table 4.3). With their stringent water requirements, a major difference for amphibians is the hard landscape barrier represented by the boundaries of desert biomes in north Africa and central Asia. High ω_A in eastern North America stems from the unparalleled diversification of small-range amphibian species in this region (Kozak & Wiens, 2006; Rissler & Smith, 2010, see also Buckley & Jetz, 2007). Conversely, the high ω_A bands visible in the northeastern Palearctic stem from there being very few amphibian species in this region.

Beta-diversity

As expected, my results bear resemblance to recent studies of broad-scale correlates of beta-diversity. For instance, McKnight *et al.* (2007) and Melo *et al.* (2009) found a strong signature of high beta-diversity along altitudinal gradients for New World mammals. Both attributed this to species being adapted to unique niches found there, in combination with histories of vicariant speciation. I would add that both ω and beta-diversity are high in such areas, as the ranges of many large range species occupying, for instance, the Amazon basin end along the slopes of the Andes. Given the variety of ways in which these studies

calculated beta-diversity and the broad congruence between all of their conclusions and mine, it would be of interest to calculate the relationship between beta-diversity measures and ω . Studies have recently focused on partitioning the nestedness and turnover components of beta-diversity (e.g., Baselga, 2010; Svenning *et al.*, 2011). While ω seems closer to the turnover component, how it relates to either component will likely depend on an area's species richness in combination with its underlying environmental gradients.

Impermeability and climate change

Understanding the factors limiting species' ranges has taken on new importance recently as the scale of the threat from climate change becomes apparent (Gaston, 2009; Sexton *et al.*, 2009). We can expect to see substantial range movement as species attempt to track their climatic niche (Parmesan & Yohe, 2003) and this range movement will first become apparent at the range edge (Ackerly, 2003). The range limits of numerous species have already been observed to be moving in the expected direction (e.g., Hill *et al.*, 1999; Parmesan *et al.*, 1999) and this response has been used as evidence that climatic factors are important in determining range limits at the broad scale (Gaston, 2003; Soberón, 2007). My analyses also demonstrate that climatic/energy variables are important factors in determining where the range boundaries of multiple species coincide. I additionally find a strong signal of the most impermeable areas being concentrated in heterogeneous areas such as mountain ranges, in complex habitats and at biome transitions. These results suggest that climate change responses will be visible first in these areas and that high ω areas constitute good conservation targets: a lot is expected to happen in relatively small areas (see also McKnight *et al.* 2007). While the low velocity of climate change expected in mountainous biomes (Loarie *et al.*, 2009) may mean species need to move less far to track their climatic niche, any

lag in the vegetation response at non-mountainous biome transitions may make the consumer species found there particularly vulnerable (e.g., Kissling *et al.*, 2010; Loarie *et al.*, 2009).

Although efforts to generate robust predictions of species' range responses typically focus on individual species, an alternative approach has been to use the parameters estimated from regression models explaining macroecological patterns such as species richness to make ensemble predictions of the likely redistribution of biodiversity under global change (e.g., Algar *et al.*, 2009; Sommer *et al.*, 2010). Exact forecasts of the future ranges of species are implausible – range movements will of course be influenced by unmeasured factors, stochastic events, altered biotic interactions and *in situ* adaptation. Nevertheless, if present day macroecological patterns are driven by true functional relationships between species and their environment, ensemble forecasts are likely to be informative on the future distribution of biodiversity. Mapping the likely redistribution of range limits would provide a complementary perspective on shifting biodiversity to studies focused on richness changes and would constitute a good extension to the analyses presented here.

Spatial modelling

Following evidence of spatial autocorrelation in the residuals of my OLS models, I used SAR models to account for the spatial structure in my data and obtain unbiased parameter estimates. Both GLS and SAR models were judged to have “generally good overall performance” in a recent assessment of the suite of methods now available to account for SA in ecological data (Beale *et al.*, 2010). Both were found to perform well in terms of low absolute bias and high precision of coefficient estimates. It was also noted that GLS is highly computationally intensive and its performance rests on identifying the correct autocorrelation structure, a subjective and time-consuming endeavour especially when fitting large or a large

number of models (Beale *et al.*, 2010). I therefore feel confident that my switch to SAR models has not threatened the legitimacy of my results.

Caveats

I used co-occurrence of a range boundary within a grid cell to capture coincident range limits. Of course, range limits are notoriously difficult to quantify (Gaston, 2003) with species able to persist in sink populations outside their realised niche (Holt, 2009). In using globally consistent sources of expert-drawn range maps (Schipper *et al.*, 2008; Stuart *et al.*, 2004) projected onto a 96.5 km² grid, I have attempted to strike a balance between spurious accuracy and discrimination of local spatial gradients in impermeability. Analyses using a range of grain sizes suggest that a grid of this resolution is appropriate for macroecological analysis (Hurlbert & Jetz, 2007; see also McInnes *et al.*, 2009). Nevertheless, my conclusions are shaped by the relatively coarse scale of my analysis (Belmaker & Jetz, 2011). It is likely that, if range limits were explored within each grid cell, one would find examples of active habitat selection, competitive exclusion and microscale climatic gradients determining the fine-scale distribution of range limits (Sexton *et al.*, 2009). In fact, it is heartening to find that, despite the idiosyncrasies that inevitably contribute to determining the range limits of most species, we are still able to uncover broad-scale spatial patterning in range limits.

Future directions

My initial comparison of mammals and amphibians revealed strong congruence in landscape impermeability for the two groups. Once a suitable transformation is identified, it will be of interest to quantify the similarities and differences between the two groups using equivalent modelling techniques. Buckley & Jetz (2008) found turnover in the most narrowly-distributed birds to closely match amphibian turnover. Similarly, it would be of interest to separate mammals into quartiles by range-size and model ω in each quartile (see also McInnes *et al.*,

2009). Finally, modelling mammalian subclades may reveal idiosyncrasies particular to certain groups that have been masked by modelling all mammals together (e.g., Buckley *et al.*, 2010).

Tables

Table 4.1. Summary of results of OLS and SAR model selection.

	Afrotropics		Australasia		Indomalaya		Nearctic		Neotropics		Palearctic	
	<i>OLS</i>	<i>SAR</i>	<i>OLS</i>	<i>SAR</i>	<i>OLS</i>	<i>SAR</i>	<i>OLS</i>	<i>SAR</i>	<i>OLS</i>	<i>SAR</i>	<i>OLS</i>	<i>SAR</i>
No. of grid cells	2018	2018	710	710	578	578	1558	1558	1714	1714	4828	4828
No. of parameters in full model	13	14	14	15	12	13	15	16	15	16	18	19
No. of models in top model set	3	4	4	25	1	22	2	6	1	7	2	2
<i>Top model statistics</i>												
AICc	3668.6	1560.4	1454.2	1073.0	1222.7	688.0	3002.6	1713.7	3563	2000.5	10817.3	6642.5
No. of parameters	13	11	12	9	12	8	15	15	15	16	18	19
Pseudo R ²	0.303	0.839	0.392	0.723	0.421	0.846	0.503	0.844	0.697	0.918	0.448	0.839
Moran's <i>I</i>	0.654	0.026	0.449	0.025	0.602	0.099	1.816	0.264	0.597	0.038	1.151	0.126
Akaike weight	0.589	0.364	0.374	0.105	0.983	0.132	0.702	0.360	0.988	0.396	0.667	0.633
Autoregressive error	--	0.908	--	0.785	--	0.892	--	0.779	--	0.905	--	0.834

Table 4.2. Results of OLS and SAR model averaging. Model averaged t values (for OLS models) and Z values (for SAR models) are shown. The most significant variable in each model is highlighted in bold. Note that the t and Z values for each biome (apart from the first) refer to the magnitude of the difference between the focal biome and the first biome in each realm (see figures 4.2-3 for actual intercept estimates for each biome). Biome did not feature in any of the top SAR models for Australasia. For this realm, the Z value refers to the intercept estimated for the entire realm. Biomes: 1 (tropical & subtropical moist broadleaf forests); 2 (tropical & subtropical dry broadleaf forests); 4 (temperate broadleaf & mixed forest); 5 (temperate coniferous forests); 6 (boreal forests/taiga); 7 (tropical and subtropical grasslands, savannas and shrublands); 8 (temperate grasslands, savannas and shrublands); 10 (montane grasslands and shrublands); 11 (tundra); 12 (Mediterranean forests, woodlands and scrub); 13 (deserts and xeric shrublands).

	Afrotropics		Australasia		Indomalaya		Nearctic		Neotropics		Palearctic	
<i>Terms</i>	<i>t</i>	<i>Z</i>	<i>t</i>	<i>Z</i>	<i>t</i>	<i>Z</i>	<i>t</i>	<i>Z</i>	<i>t</i>	<i>Z</i>	<i>t</i>	<i>Z</i>
Biomes				3.861								
1	2.083	2.390			-2.153	1.027			0.29	0.955	-2.172	0.814
2					-5.025	-0.332			13.255	2.508		
4			7.697				-2.638	-0.963			-1.176	0.166
5							-0.847	0.250			0.232	0.777
6							-8.023	-2.392			-1.264	-0.110
7	4.307	2.280	9.401						2.549	0.657		
8			6.211				3.217	0.812	3.402	1.831	4.059	0.997
10	3.785	2.016							5.973	2.135	4.407	0.868
11							-8.003	-2.175			3.388	0.022
12			8.991								2.331	0.651
13	1.837	1.489	7.802		1.215	-1.284	-2.720	-0.270	1.359	2.069	5.209	1.425
Mean elevation	-3.397	-4.125	-5.481	-2.843	-6.991	0.228	1.353	1.298	-8.487	-2.334	-9.575	-4.558
Mean annual temperature	-0.788	-0.376	-4.363	-1.083	8.81	-0.241	8.664	5.410	-2.852	-1.391	9.083	3.364
Mean annual temperature ²	1.516	-1.053	4.047	-0.338	-11.903	-0.690	2.643	-0.191	-10.487	-3.772	-6.147	-3.659
Mean annual AET	-4.694	-2.975	2.535	3.017	-6.855	0.266	-5.870	-2.620	2.661	0.449	-1.308	-1.300
Elevational range	12.049	4.983	-2.435	0.428	7.894	5.533	9.236	7.126	15.395	8.777	19.206	12.224
Biome heterogeneity	8.890	3.276	0.225	2.897	3.178	3.954	5.471	3.245	8.083	5.980	15.005	7.681
Landscape heterogeneity	2.892	4.767	2.939	1.519	5.263	4.144	3.889	2.657	10.801	6.661	8.194	6.429
Mean annual temperature: elevational range	-8.112	-3.864	4.680	0.519	-6.535	-0.038	6.908	4.624	-12.125	-5.260	1.230	-1.116
Mean annual temperature:AET	1.799	3.000	-0.590	0.368	6.906	-0.041	9.016	6.554	3.283	1.308	18.304	7.116

Table 4.3. Correlation between mammal and amphibian impermeability. Pearson's correlation coefficient (*Pearson's r*), number of cells compared (*n*), effective sample size after correcting for spatial autocorrelation (*ess*), t-value (*t*) and p-value (*p*) of each correlation are given.

	<i>Pearson's r</i>	<i>n</i>	<i>ess</i>	<i>t</i>	<i>p</i>
<i>All cells</i>					
Afrotropics	0.782	2271	33.5	9.38	0.000
Australasia	0.694	834	18.4	5.08	0.000
Indomalaya	0.898	763	21.3	12.39	0.000
Nearctic	0.703	1890	56.9	9.56	0.000
Neotropics	0.874	2098	12.2	7.87	0.000
Palearctic	0.615	4362	76.0	8.52	0.000
Global	0.714	12218	122.8	14.70	0.000
<i>Omitting coastal cells</i>					
Afrotropics	0.517	2057	91.4	7.04	0.000
Australasia	0.205	694	56.4	1.70	0.095
Indomalaya	0.765	610	15.3	5.75	0.000
Nearctic	0.374	1547	36.7	2.78	0.009
Neotropics	0.831	1789	10.3	5.83	0.000
Palearctic	0.402	3750	28.0	2.65	0.014
Global	0.489	10447	72.4	5.75	0.000

Figures

Figure 4.1. Mammalian impermeability. Grey cells are coastal cells omitted from the analysis because $\omega = 1$. Blue cells are cells in minor biomes not included in the models. Green cells had $\omega = 0$ and were omitted from the models so that a logit transformation could be used. Greenland and Antarctica were omitted from all analyses because of missing environmental data.

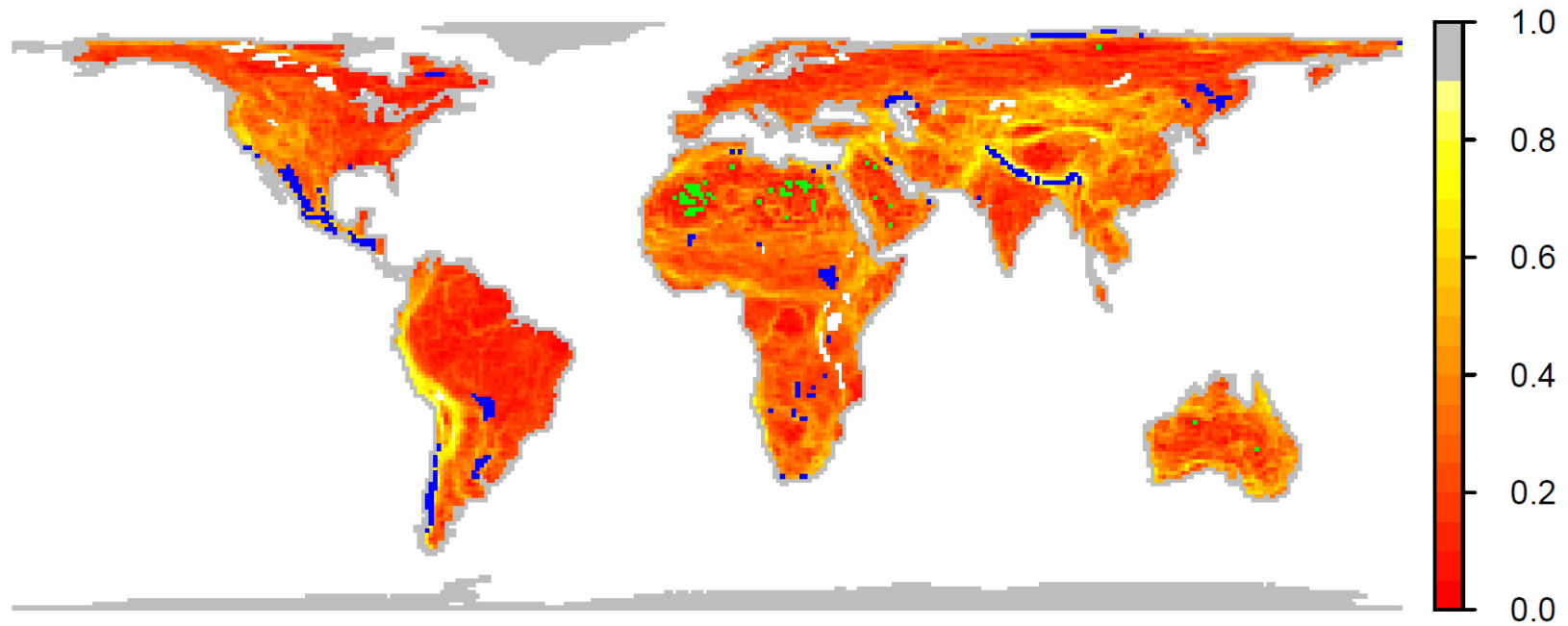


Figure 4.2. Coefficient estimates for the top OLS models. The error bars show the 95% confidence intervals across the averaged estimates. Because only one model entered the top model set for Indomalaya and the Neotropics the error bars in those panels show the 95% confidence intervals of the estimates from that model. Note the different scales on the x axes of each plot. The grey panel highlights the same range (-0.5 – 0.5) on each plot for comparison. The number next to each realm is the number of models that enter into the top model set. Biomes described in table 4.2.

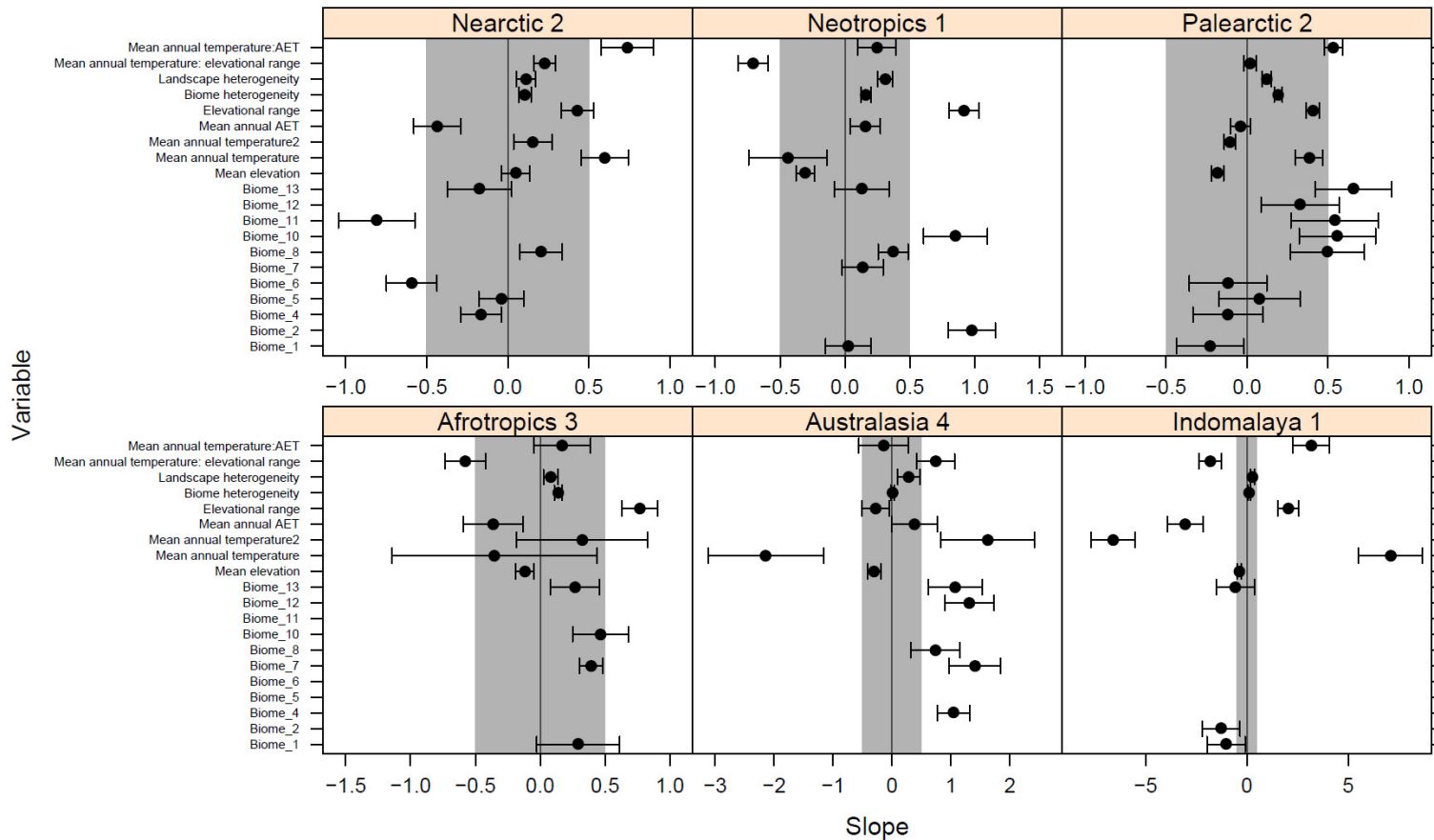


Figure 4.3. Coefficient estimates for the top SAR models. Figure layout as described in figure 4.2. Biome did not feature in any of the top models for Australasia. For this realm, a single intercept was estimated across all biomes (“Biome_all” in the figure).

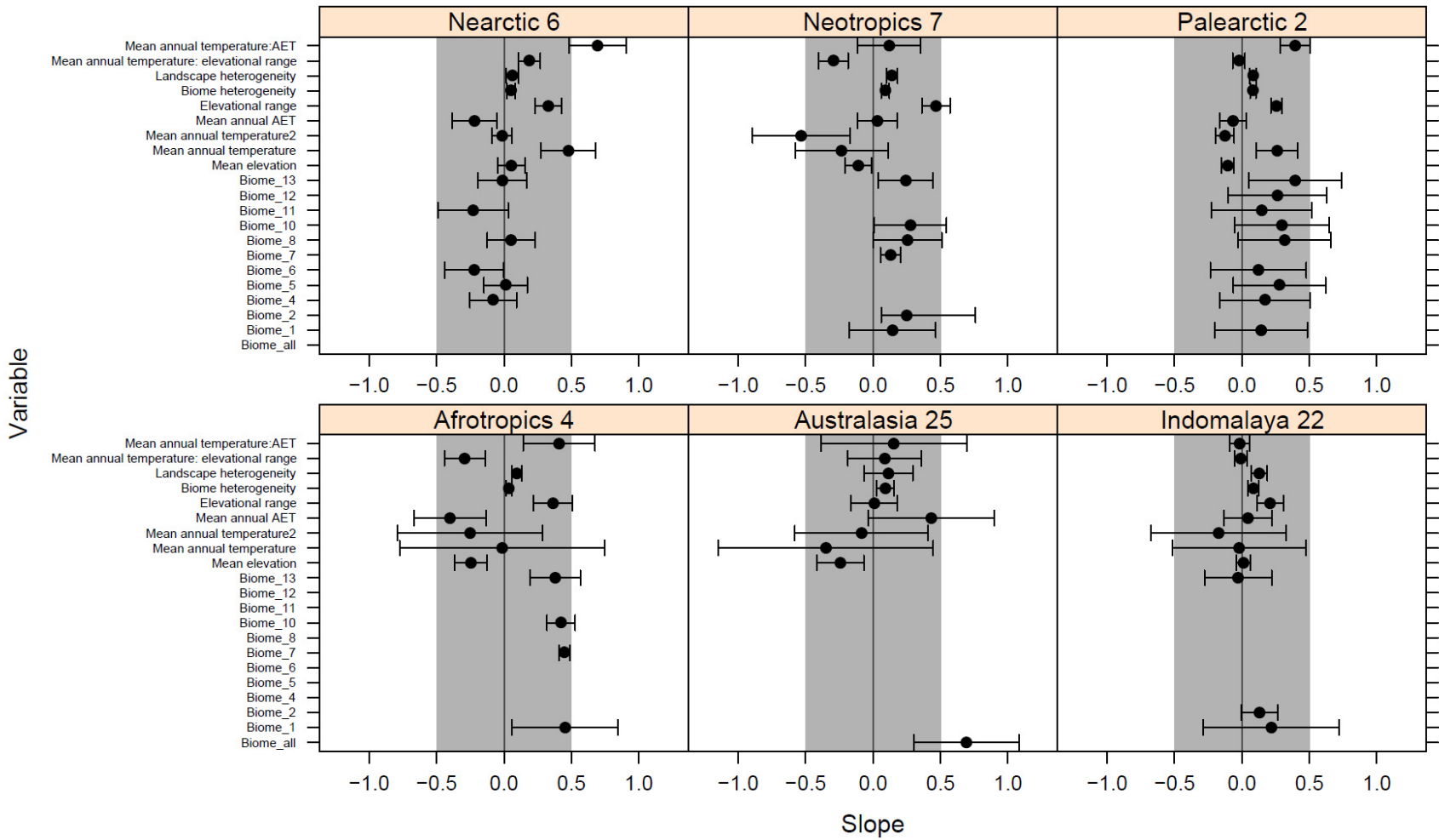
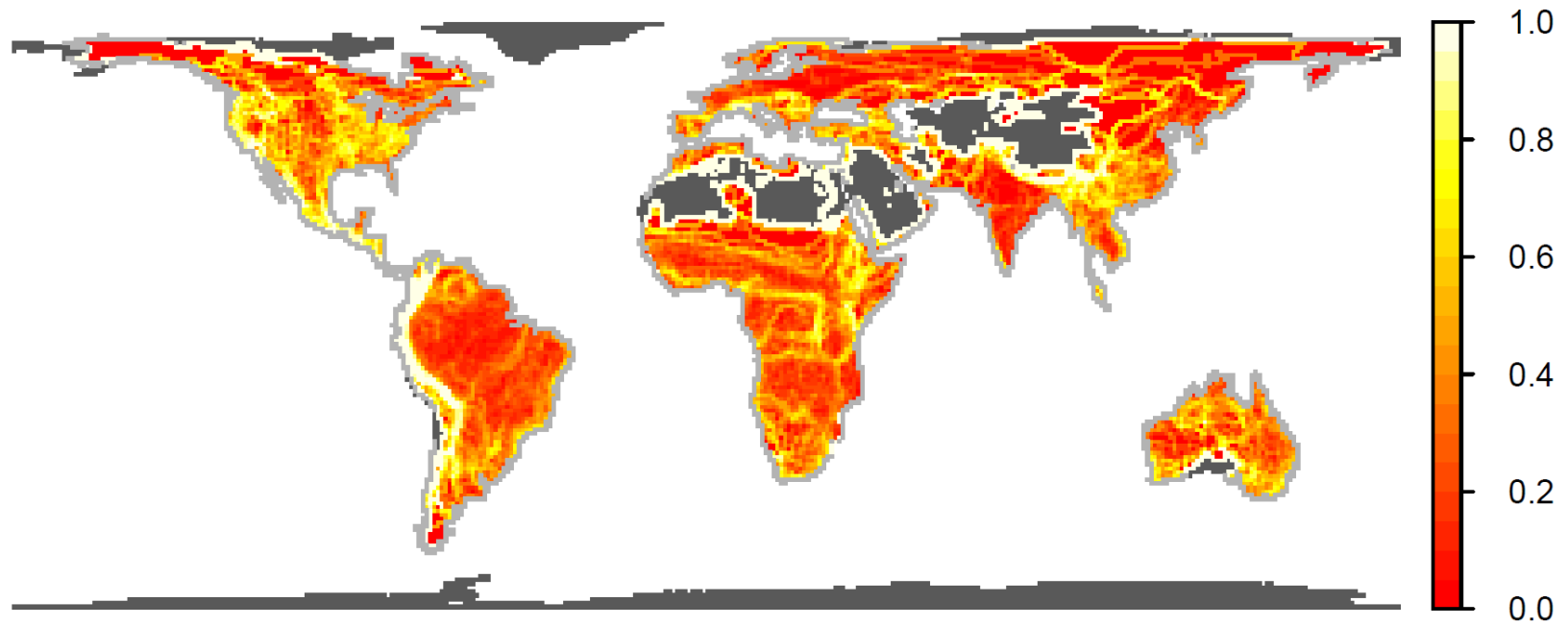


Figure 4.4. Amphibian impermeability. Dark grey cells contain no amphibians. Light grey cells are coastal cells (ω_A all 1). Greenland and Antarctica omitted from all analyses.



Chapter 5. Can landscape impermeability be co-opted into a measure of species' relative occupancy?

Abstract

Predicting species' abilities to respond to climate change is a difficult, but pressingly important, endeavour. It requires knowledge of the intrinsic capacity of the species to respond, as well as the nature of the landscape both where the species is currently found and where it could move to. Measuring the proportion of resident species whose ranges end in an area quantifies landscape impermeability and indicates which regions currently act as barriers to the range expansion of many species. In this study, I investigate whether this spatial measure of landscape structure can be successfully co-opted into species-based measures of relative landscape occupancy. My motivation for doing so is that such measures integrate intrinsic species' traits and extrinsic environmental conditions, which must be combined for robust prediction. I develop two measures of relative occupancy, but, using a phylogenetic generalised least squares approach, I identify few strong trait correlates from a suite of potential predictors including measures of species' dispersal ability, generalism and climatic tolerances. Rather, I find that relative occupancy is more strongly related to where on the globe a species' range is located, underlining that the most effective conservation under climate change may come from targeting vulnerable locations rather than specific species.

Introduction

There is an increasing need to make robust predictions on how species will respond to current rapid global change. Range projection modelling can be a powerful tool in this endeavour, but has low power for species whose distributions do not meet its assumptions (reviewed in Guisan & Thuiller, 2005). Objective criteria to separate those species that can be adequately described by SDMs from those that cannot will increase efficiency in predicting responses to global change by facilitating improved targeting of limited resources (Thuiller *et al.*, 2008).

Quantifying the proportion of resident species that had their range limits within regions, I earlier developed a measure of landscape impermeability (ω : McInnes *et al.*, 2009; chapters 3 & 4), with high values corresponding to areas where range expansion appears impeded. Landscape impermeability is strongly correlated with landscape and topographic complexity, supporting the inclusion of topographic and habitat variables in SDMs (e.g., Luoto & Heikkinen, 2008). However, substantial residual variation in environmental models (McInnes *et al.*, 2009; chapters 3 & 4) indicates that species differ considerably in their ability to overcome barriers and occupy the landscape, with some species having range limits in homogeneous areas easily traversed by other species.

Here, I assess whether impermeability can be used to quantify species' *relative ability to occupy the landscape*, as more able species are expected to be well equipped to change their distribution in the face of rapid climate change. I overlay the geographic distribution of individual species of terrestrial mammals onto a gridded global map of impermeability for all terrestrial mammals. For each species, I separate the overlapping set of grid cells into those that constitute the edge of the species' range (exterior) and those that lie entirely within the distribution (interior). From these two sets of cells, I calculate the mean interior (ω_i) and

exterior (ω_e) impermeability for each species. Since ω is calculated across species, both these new measures assess the strength of the constraints on a given species' distribution relative to other co-occurring species (see also Arita *et al.*, 2008 for a similar approach involving relative range sizes). Since different processes are expected to occur at the core and margin of ranges (Gaston, 2003; Sexton *et al.*, 2009), these two measures provide complementary approximations of relative occupying ability within and at the edge of a species' range. Although these measures do not address intraspecific variation in occupancy across a species' range (beyond the distinction of range exterior and range interior), they are intended to provide an interspecific ranking of relative ability.

Typically, species might be expected to have lower ω_i and higher ω_e , perhaps occupying a homogeneous tract of habitat and limited, in common with other species, by a major habitat transition (see also table 5.1 & figure 5.1 for a graphical representation of these ideas). I am interested in species having unusually high ω_i or low ω_e , respectively considered good and poor "occupiers", and focus on characterising species with these traits. Species with high ω_i are able to occupy regions that act as barriers for most other co-occurring species. Intuitively, high ω_i should correlate positively with traits associated with the ability to reach and persist in a range of habitats, such as indices of habitat generalism, broad climatic tolerances and high dispersal ability. Low ω_e indicates a species whose range is more constrained than those of most co-occurring species. Such species are expected to possess traits such as low dispersal ability and strong specialisation to specific habitats. Species might also have low ω_e if biotic interactions prevent expansion into suitable habitat, resulting in seemingly idiosyncratic range limits. Although both indices are informative on their own, it is also of interest to investigate how ω_i and ω_e are related to each other and to range size. For instance, a species with high ω_i , but occupying only a handful of cells, may not be a particularly good occupier, residing in a high ω area through an accident of history.

I fit a suite of models to test these hypotheses using a database of mammalian traits (PanTHERIA, Jones *et al.*, 2009). While neither measure of a species' ω is directly heritable, similar emergent traits such as range size or extinction risk (e.g., Freckleton *et al.*, 2002; Fritz *et al.*, 2009) often show phylogenetic structure arising from shared ancestry. I therefore use a phylogenetic generalised least squares approach (Freckleton *et al.*, 2002) in combination with a recent mammalian supertree (Fritz *et al.*, 2009). I also assess the relative contributions of space and phylogeny (Freckleton & Jetz, 2009) to the measures, under the hypothesis that a species' occupancy may be better explained by its spatial location, rather than by any intrinsic traits it might possess (see also Gove *et al.*, 2009; Munguía *et al.*, 2008).

Although climate change is widely accepted to be one of the most pressing risks to species' survival, the extinction risk associated with climate change is much less well quantified than the risks associated with other contemporary drivers such as habitat loss or over-exploitation (Dawson *et al.*, 2011). Some of the main insights emerging from recent studies (e.g., Davies *et al.*, 2008; Fritz *et al.*, 2009) include pervasive geographic heterogeneity in the strength of extinction risk drivers and phylogenetic heterogeneity in the lineages most at risk. For example, extinction risk for small-bodied mammals is largely shaped by location whereas risks for large-bodied mammals depend also on their ecology (Cardillo *et al.*, 2005). If I am to use relative occupancy as a proxy for vulnerability to climate change, I must also address geographical heterogeneity in landscape structure and phylogenetic heterogeneity in the responses of species. To tackle these issues I investigate trait correlates at both the global and realm levels.

I find that mammals exhibit a wide diversity of relative occupancies, but that no strong trait correlates emerge. Rather, relative occupancy is intricately linked to the environments species are found in, suggesting that while we may not be able to obtain robust predictions of climate

change responses of particular species, we can nevertheless target attention to specific areas in order to reap the most conservation benefits.

Methods

Dataset

I used the same dataset of mammalian species' ranges as detailed in chapters 2 & 4. Briefly, I extracted polygon shape files of the ranges of all mammals from the Global Mammal Assessment (GMA: www.iucnredlist.org/mammals; Schipper *et al.*, 2008). I converted the polygons of each species into the Behrmann equal-area projection, preserving area but not necessarily the shape or distance between cells. I overlaid an equal-area grid (96.5 km² resolution) on the polygons and extracted grid cell occurrences for each species. Species were scored as present in a grid cell if any part of the breeding range fell within the cell. A grid cell was counted as containing a species' range edge if any part of the perimeter of the species' range, including the boundaries of sections of disjunct range, fell within the cell. As in chapters 2 & 4, I analyse only species whose distributions overlap continental cells. In addition, 178 species were omitted from the analyses as they are not found in the most current version of the mammal supertree (Fritz *et al.*, 2009), leaving 3803 species in the dataset.

Phylogenetic clustering in edges

For each grid cell, I recorded which species present in the cell also had a range edge in the cell. I then used a supertree of mammals (Fritz *et al.*, 2009) to obtain a phylogeny for the species present in the cell and computed D , a measure of the phylogenetic signal strength in binary traits (Fritz & Purvis, 2010b). The parameter D reveals the pattern of dispersion of a

trait on a tree with 0 and 1 as convenient calibration points. Here, D indicates whether species with range edges in the focal cell are phylogenetically clumped ($D \ll 1$), with $D \sim 0$ corresponding to a binary trait underpinned by a trait evolving under Brownian motion and $D \sim 1$ corresponding to a binary trait that is randomly distributed on the tree. Spatial variation in this measure reveals whether there is geographical heterogeneity in the phylogenetic selectivity of impermeable landscapes. As a measure of spatial structure in D within each realm, I plotted Moran's I correlograms and assessed the significance of Moran's I at the shortest distance class (100 km). D is unreliable for small phylogenies (Fritz & Purvis, 2010b) so I did not evaluate it for cells containing fewer than 50 species. I also exclude cells where all resident species, or all but one, have a range edge as D cannot be interpreted unless the less common trait is present in at least two species.

Generating species scores

For each species, I re-calculated impermeability (ω) for the cells occurring in its range, excluding the focal species (for details see McInnes *et al.*, 2009; chapters 3 & 4). I separated the grid cells of each species into interior and exterior cells, where exterior cells contain any part of the perimeter of the species' range, including the boundaries of sections of disjunct range. Coastal cells truncate all species' ranges and always have a ω of one. These cells cannot inform tests of the ecological predictors of relative occupancy and were removed prior to generating species' scores. To preserve the range of ω between 0 and 1 whilst also bringing its distribution closer to normal, I used a square-root transformation; all references to ω and its derivatives henceforth refer to the square-root transformation. I then calculated mean ω separately for interior and exterior cells to give a measure of the central tendency of ω_i and ω_e .

Because a substantial proportion of the range edge for some species may be coastal, I tested whether there was a relationship between the mean ω_e values obtained for each species and whether any of their range edge included coastline. Thirty-six species were excluded from analyses of ω_e because their range margins fell entirely in coastal cells.

Calculation of ω_i requires that species' ranges have interior cells. However, under the scale of grid used, the ranges of 1042 species (27.4%) have no interior cells. These are overwhelmingly small-range species and are not expected to possess traits hypothesised to be associated with high ω_i (e.g., broad climatic tolerance, strong dispersal ability). I tested whether ω_e differed between those species with and without interior cells and repeated the trait correlate analyses for ω_e (see below) including only those species that also had interior cells.

Covariate choices and modelling

I tested the following set of variables hypothesised to predict ω_i and/or ω_e :

- i) The number of cells contributing to ω_i and ω_e to assess how ω_i and ω_e scale with the **range size** of species. One expects that the variance in each measure will decrease as range size increases, from a regression on the mean effect. However, it is unclear what trend to expect in the mean value of each measure as range size increases. Large range species might be expected to be good occupiers based on their range extent, but large ranges are also expected to encompass both high and low ω areas.
- ii) The product of the number of dietary items eaten (range: 1-8) and the number of habitat types occupied (range: 1-4) as a coarse measure of **generalism** (Cooper *et al.*, 2011; Jones *et al.*, 2009).

- iii) The standard deviation of the mean annual temperature across the grid cells in a species' interior or exterior range as a measure of **climatic niche breadth** (Hijmans *et al.*, 2005).
- iv) A suite of variables taken from PanTHERIA (Jones *et al.*, 2009) thought to capture aspects of **dispersal**, given that there are limited data directly quantifying mammalian dispersal (Lester *et al.*, 2007). Successful dispersers need to be able to both colonise new areas and form viable populations upon arrival. Traits that could act as proxies thus include measures of colonisation and competitive abilities (see also Angert *et al.*, in press).
 - a. As a coarse measure of abundance and thus of competitive ability I include **population density** (individuals per km²) (Enfjäll & Leimar, 2009). Across most groups examined, local population density and regional site occupancy are positively correlated: species that are locally common are regionally widespread (Blackburn *et al.*, 2006). Here I use mean population density across a species' range and look to see whether the abundance-occupancy relationship holds when occupancy is measured relative to other co-occurring species.
 - b. Life-history speed also impacts colonisation and competitive abilities (Freckleton *et al.*, 2005) and so I include **gestation length** (days) and **weaning age** (days) to represent two axes of the 'fast-slow' life history continuum: fecundity and timing of reproduction, respectively (Bielby *et al.*, 2007).
 - c. I also investigate whether there is a consistent relationship between the measures and **body mass** (grams): movement is energetically cheaper per unit mass as mass increases so it might be expected that larger-bodied species that typically experience their landscape at a broader scale are also better at occupying their landscape. Body mass is also often used as a proxy for various species' traits

including dispersal ability, life history speed, competitive ability and ecological generalisation (Gaston, 2003). Following Fritz & Purvis (2010a), for species lacking body mass data, I interpolated values as the value of their closest relative (or the mean of all equally close relatives). This action is justified because body mass is strongly phylogenetically patterned in mammals (values of $\lambda = 1$ reported in Freckleton *et al.*, 2002). Following interpolation, data was available for a far larger number of species than for most of the other variables under test; body mass is thus expected to be a useful proxy in my hypothesis testing.

- v) Two further variables are each specific to a single measure. For ω_i , I recorded the **number of subspecies** in each species (Wilson & Reeder, 2005): high ω_i may mask internal subspecies range margins that do coincide with the margins of co-occurring species. For ω_e , I included the **number of congeners** (Wilson & Reeder, 2005), since low ω_e may be associated with biotic constraints such as competition.
- vi) Finally, I modelled ω_e as a function of ω_i to explore how the two measures are related.

Whilst multiple predictor analyses would be preferable (Houle, 2007), missing data for many of the variables ($n = 703 - 2761$) resulted in few species with data available for all traits. I therefore built single predictor models using phylogenetic generalised least squares (Freckleton *et al.*, 2002) to test support for each variable, but include the full multivariate models (ω_e : $n = 301$, ω_i : $n = 303$) for comparison. All variables were log10-transformed, except climatic niche breadth which was square-root transformed so that their distributions better approximated normality. They were then scaled and centred (Schielzeth, 2010). I generated correlation matrices of the variables entering the two multiple predictor models (table 5.2) and calculated variance inflation factors (VIFs) which were all below 3. Although the VIFs indicated that multicollinearity was not a problem, the correlation matrices indicated that weaning age, gestation length and population density were substantially collinear with

body mass. Therefore, I fitted additional models for these variables with body mass as a covariate: these models assess the importance of the variables while controlling for body mass effects. Finally, I repeated the analyses of ω_e including ω_i as an additional predictor variable to address the hypothesis that relative occupancy in the range core may dictate the nature of a species' range margin. I repeated all analyses at a global scale and within biogeographic realms. Within realms, I calculated ω_i and ω_e using only that portion of a species' range that occurred in the focal realm.

The phylogenetic signal in variables associated with species niches has recently come under scrutiny (Cooper *et al.*, 2011; Dormann *et al.*, 2010), particularly since biogeographic patterns in species' ranges may confound phylogenetic and spatial structure. Indeed, a recent study has identified a strong spatial signal in the climatic niche similarity of related mammalian species (Cooper *et al.*, 2011). I therefore used Freckleton & Jetz's (2009) method to estimate the relative contributions of space and phylogeny to ω_e or ω_i . This method quantifies the proportion of variance attributable to space (ϕ) and phylogeny accounting for space (λ') and the residual variation unexplained by either (γ). λ' equates to $(1 - \phi) \lambda$ and would be equivalent to λ in the absence of effects that are attributed to space.

Finally, for each measure, I ranked species. For ω_i , I generated species richness maps of the highest scoring 25% of species to investigate the spatial distribution of species with high relative landscape occupancy. For ω_e , I mapped the lowest scoring 25% of species to investigate the spatial distribution of poor occupiers.

Results

Figure 5.2 shows the global distribution of the phylogenetic signal (D) in the species whose ranges end in each cell. The D values in the majority of cells ($n = 4708$) are not statistically distinguishable from a random distribution on the phylogeny. A smaller number of cells ($n = 587$) show non-random phylogenetic patterning consistent with a Brownian threshold model and the remaining cells ($n = 1356$) have intermediate D values that do not reject either model. An ANOVA comparing cells in each of these three groups indicated that all groups had significantly different ω to each other ($F_{2,6648} = 31.9$, $p < 0.0001$). In particular, the cells where the Brownian model could not be rejected had significantly lower ω (mean = 0.510) than cells with intermediate D values (mean = 0.561) although caution must be used in interpreting these results due to spatial autocorrelation in D estimates: Moran's I coefficients were significantly different to 0 at the shortest distance class across all realms. Note that there are many cells where D cannot be calculated, either because they contain too few species for the measure to be reliable ($n = 5038$) or because all species in the cell have range edges there (i.e., coastal cells; $n = 2025$).

Both ω_i and ω_e show a strong decrease in variance with increasing range size (figure 5.3), as estimates for the largest ranged species inevitably converge on the global mean value.

Observed ω_e is significantly higher ($t = 20.6$, $df = 1690.2$, $p < 0.0001$) for species with no interior cells (mean $\omega_e = 0.675$) than for the remaining species (mean $\omega_e = 0.595$), although the decrease in variance of ω_e (F test comparing the variance in ω_e for species with interior cells versus those without: $F_{1041, 2724} = 1.295$, $p < 0.0001$) with increasing range size affects statistical testing. In addition, ω_e is significantly lower ($t = 6.16$, $df = 1619.1$, $p < 0.0001$) and range size significantly larger ($t = -20.47$, $df = 1902.1$, $p < 0.0001$) for species whose

ranges include omitted coastline cells ($n = 2705$, mean $\omega_e = 0.610$) than for the remaining species ($n = 1062$, mean $\omega_e = 0.636$).

Figures 5.4 and 5.5 show the results of models of ω_i and ω_e (see Appendix 5.1 for these results in tabulated form). For ω_e , relationships were similar whether or not only species with interior cells were included in the models. Significant relationships were qualitatively identical in the global and multiple predictor models; in the realm-specific models significance of life history variables sometimes varied. I report here only the models including species with both interior and exterior cells (but see table A5.1.3 in Appendix 5.1 for the results including all species). In general, niche breadth is positively associated with ω_i and ω_e both globally and within realms. However all of these models had low explanatory power. A negative correlation with range size was also recovered in most tests. Although the adjusted R^2 was higher for this variable, these results should be interpreted with caution given the decrease in variance in both measures as range size increases. Life history variables did not show consistent relationships among realms.

There is a significant positive correlation between ω_i and ω_e (figures 5.5 (top-left panel) & 5.6, table A5.1.2). This is mostly a reflection of the right skew of species' distributions: most species have small ranges and reside wholly within low or high ω areas, such that modelling ω_e as a function of ω_i approximates fitting a spatial term. Note that the outlying species in the bottom right and top left of the plot are species with fragmented ranges and relatively few interior cells. Fitting ω_i as a co-variate in the trait models for ω_e substantially increased the models' explanatory powers (figure 5.7, table A5.1.4). Nevertheless, niche breadth remained significantly positively correlated with ω_e globally and in four realms. Range size lost significance in most realms and switched sign to a significantly positive correlation globally

and in the Neotropics and Indomalaya. Again, life history variables did not show consistent relationships among realms.

A positive association with niche breadth and a negative association with geographic range were found for both ω_i and ω_e in the multiple predictor models (table 5.3) although geographic range became marginally non-significant in the model for ω_e including ω_i as a covariate, where the most important variable was ω_i .

Partitioning species into those with subspecies and those without revealed no significant differences in ω_i (average score: 0.543 and 0.544 respectively; $t = -0.1499$, $df = 2349.6$, $p = 0.8808$). Similarly, partitioning species into members of monotypic or polytypic genera also revealed no significant differences in ω_e (average score: 0.618 and 0.617 respectively; $t = 0.0817$, $df = 2563.4$, $p = 0.935$).

Table 5.4 shows the partitioning of spatial and phylogenetic effects on relative landscape occupancy measures. ω_e showed a slight tendency to have a stronger pure phylogenetic signal (λ) than ω_i , but in all realms the phylogenetic signal accounting for spatial structure (λ') is largely subsumed into variation explained by space (φ). For both measures, the spatial effect was strongest in Indomalaya, the Nearctic and the Neotropics. For ω_i , neither space nor phylogeny explained any variation in the Palearctic.

The lowest ranking species for ω_e are concentrated away from high ω areas, in the centres of large biomes such as the tropical and subtropical moist broadleaf forests in central Africa and Brazil (figure 5.8a). As expected, the highest scoring species for ω_i are concentrated in montane areas and at biome edges, where ω is highest (figure 5.8b).

Discussion

Many factors must influence the ability of a species to occupy a landscape. These include intrinsic traits, the local community, external factors such as the nature and stability of the environment, and the biogeographic history of the species and region (Gaston, 2003).

Previous work has identified significant correlates of species richness (e.g., Ruggiero & Kitzberger, 2004), of high densities of range margins (e.g., McInnes *et al.*, 2009; chapters 3 & 4) and of range size (e.g., Davies *et al.*, 2009). Taken together, this research captures the influence of environmental variables that most commonly correlate with species' range extents. Here, I am interested in assessing the use of simple measures to identify those species that are most likely to be misrepresented by such approaches, either by overcoming, or failing to reach, the constraints that act on other species.

Species' relative occupancies are influenced by both phylogeny and space. Whether a species had a range edge in a cell did not consistently show phylogenetic structure according to D . Indeed, in high ω areas, landscape features are expected to impede species irrespective of their phylogenetic position. Phylogenetic structure was mostly found in low ω areas such as the Amazon basin. This is perhaps a signal of the abutting edges of congeners or phylogenetic selectivity in the impact of river barriers on the area's biota (figure 5.2; and see Ayres & Clutton-Brock, 1992). In contrast, when assessing the phylogenetic and spatial signal in the measures of relative occupancy, both ω_i and ω_e showed relatively strong phylogenetic signal globally, but the spatial effect was much more important at the realm level (table 5.4). This result does not indicate that related species do not occupy the landscape similarly: rather, it suggests that within realms, related species co-occur and exhibit similar abilities to occupy the landscape (although the direction of causality cannot be confirmed with this analysis). That the phylogenetic component was far greater than the spatial component globally

underlines this: related species in different realms are occupying spatially-distinct but similarly structured landscapes. Cooper *et al.*'s (2011) analysis of thermal niche conservatism also found that phylogenetic signal in the thermal niche transferred to a spatial effect when the spatial relationships among related mammalian species were included.

Correlates of relative occupancy

The strong spatial variation and environmental correlates identified for ω suggests that many species occupy homogeneous tracts of habitat with range boundaries in impermeable areas at the edges of biomes and in montane regions (McInnes *et al.*, 2009, chapters 3 & 4). They are expected to have low ω_i and high ω_e . For example, the forest giant pouched rat, *Cricetomys emini* ($\omega_i = 0.502$; $\omega_e = 0.601$), inhabits the tropical forest biome in central Africa with its range edges along the biome boundary. There is, in fact, a strong positive association between ω_i and ω_e , globally and in all realms, driven by small-range species that have restricted ranges exclusively within high or low ω areas (figure 5.6). While table 5.1 outlines hypotheses on the traits that might be associated with high and low ω_e and ω_i , few species possess certain combinations (figure 5.6). In particular, there are few species with high ω_i and low ω_e , which would require a species to exclusively occupy high ω areas, except at its range margin. More surprisingly, few species have low ω_i and high ω_e because the species with highest ω_e are small-range species found exclusively within high ω areas (= high ω_i). There is, however, a final striking feature of figure 5.6: a group of species with much higher ω_e than the overall relationship predicts, matching the expectation of low ω_i and high ω_e more convincingly. Such species are all Neotropical with one range edge in the Andes and include the capybara, *Hydrochaerus hydrochaeris*, the tayra, *Eira barbara* and the Argentinean brown bat, *Eptesicus furinalis*.

Weak support for broad climatic tolerance (niche breadth) and high abundance (population density) as predictors of high ω_i was found in four and two realms, respectively, suggesting that strong occupancy is influenced by the physiological capacity to occupy a variety of habitats (see also Swihart *et al.*, 2006) and sometimes from the ability to compete successfully with co-occurring species (if high abundance is considered a valid proxy for competitive ability). Better occupiers also tend to reproduce rapidly: fast life histories will facilitate wide landscape occupancy if they enable a species to colonise additional habitats and outcompete other species there. The lack of a consistent relationship across all realms may reflect that species with low occupancy may also have fast life-histories. Fagan *et al.* (2009), using a spatially explicit theoretical framework, have shown that species with identical life histories could have very different landscape occupancies dependent on landscape structure.

For ω_e , few consistently significant trait correlates were identified. This may be due to there being multiple potential determinants of ω_e , although there was consistent, albeit weak, support for a positive association with niche breadth. Many of the low ω_e species are members of speciose genera, each species occupying restricted ranges within homogeneous areas: the red-handed howler monkey (*Alouatta belzebul*), the red-bellied titi (*Callicebus moloch*) and the white-lipped tamarin (*Saguinus labiatus*) all have some of the lowest ω_e scores and occupy restricted sections of the Amazon basin with congeners nearby.

Nevertheless, overall, there was not a significant relationship between number of congeners and ω_e . That species whose ranges reach the coast have significantly lower ω_e and larger range sizes than those that do not also merits attention. It indicates that, barring the absolute barrier of the coastline, such species' are able to span large areas, reaching idiosyncratic limits at least in parts of the rest of their range margin.

Relative occupancy and climate change responses

Schurr *et al.* (2007) found that colonisation and persistence ability was positively correlated with range filling, using ratios of realised to potential range size for 37 species of Proteaceae in the Fynbos. They concluded that species most vulnerable to increasing rates of environmental change will be those that currently compensate for low colonisation ability with high persistence. Similarly, many species with high ω_i are expected to be safe in the face of climate change. Found throughout the Andes or the Central Asian mountains, respectively, the Culpeo or Andean wolf (*Lycalopex culpaeus*) and the silver mountain vole (*Alticola argentatus*) both have high ω_i and are good examples of wide-ranging species occupying a landscape impermeable to many co-occurring species. Heterogeneous areas are often highlighted as meriting conservation attention due to their rich biota of restricted-range endemics (e.g., Kark *et al.*, 2007), I show here that there exist species capable of spanning such areas. My result, that broad niches are sometimes associated with high relative occupancy, is also consistent with predictions from the contemporary climate change literature (e.g., Engler *et al.*, in press; La Sorte & Jetz, 2010) and from prehistoric climate change (Blois *et al.*, 2010) that suggest that altered habitats will probably be dominated by weedy species. Species with very restricted ranges, but high ω_i , are expected to manage less well and we can expect to lose, for example, some high-elevation specialists (Engler *et al.*, in press; Şekercioğlu *et al.*, 2008). Some species may still be able to cope, however, as the velocity of climate change in montane areas is expected to be low (Loarie *et al.*, 2009).

The fate of low ω_e species appears more precipitous. They predominately occur within homogeneous habitats and are not currently limited by landscape features. On the face of things, range tracking might be easier for them if there are no major landscape barriers between their old and new ranges. Cooper *et al.* (2011) suggested that the strong spatial

component to conservatism of the mammalian thermal niche indicates that recent evolution and available niche space underline current mammalian distributions. They proposed that this demonstrates a lack of deep conservatism that will facilitate species' tracking of current change until they hit impermeable barriers. However, for low ω_e species, if their idiosyncratic limits stem from traits such as poor dispersal capacity or habitat specialism, range tracking even across homogeneous areas may not be easy. Tropical lowland species may be at particular risk if the climate warms beyond their physiological limits (Colwell *et al.*, 2008). If these low ω_e species are biotically-limited through competitive interactions, their responses will depend critically on the rest of the biota (Davis & Shaw, 2001). I observed a weak, but fairly consistent association between small body size (often used as a proxy for fast life history, e.g., Roy *et al.*, 2002; Lyons *et al.*, 2010) and low ω_e . Fast life histories could favour *in situ* adaptive responses and alleviate the need to track a changing climate (Reed *et al.*, 2010). Investigating Pleistocene range shifts in Nearctic mammals, Lyons *et al.* (2010) found that the species whose range centroids shifted the most were those with slow life histories; species with faster life histories presumably adapted *in situ*. Whatever the factors underlying species' low ω_e , simple range projection modelling is unlikely to provide reliable predictions on their expected response to climate change. Furthermore, the expected high velocities of climate change in homogeneous areas (Loarie *et al.*, 2009) will compound their difficulties.

Caveats – the data

As with all macroecological studies, these results must be interpreted with a consideration of scale. Using a grid size of 96.5 km² (~ 1° at the equator) is generally accepted to strike the best balance between the expected accuracy of the available range data and the finer scale at which species' ranges actually end (Hurlbert & Jetz, 2007). It is well-documented that in mountainous areas, 1° cells span steep elevational gradients with substantial microclimatic

variation (Hawkins & Diniz-Filho, 2006). Species with range edges assigned to cells in such areas are thus not all expected to come into contact with one another. However, for ω_i , I am most interested in species able to span high ω areas such as mountains. Even species whose ranges are incorrectly assigned to grid cells at the edge of high ω areas (for example in the foothills of a mountain that they span) will still be correctly identified as a high ω_i species if they occur widely along the elevational gradient. Similarly, scaling issues do not affect ω_e . An additional explanation for relatively low ω_e would be if a species' range spanned high ω areas with its range edge (either actually, through errors in range map construction, or through scaling issues) in abutting low ω areas. This is unlikely to have systematically biased the results: the map of low ω_e species shows highest richness in homogeneous areas (figure 5.8a) and there are few species with high ω_i and low ω_e (figure 5.6). Finally, our ability to identify trait correlates may have been hampered by data availability: niche breadth, body mass and range size were the only variables available for all species.

Caveats - the approach

There are a number of outstanding difficulties with this approach that must be acknowledged. First, as with models derived from realised niches (e.g., Cooper *et al.*, 2011), species that happen to occur within areas of low ω may have higher ability to cross boundaries than their correspondingly low ω_i would suggest. Similarly, in this first analysis of relative occupancy, intraspecific responses (beyond our division into range exterior and range interior) have not been considered, although there may be substantial variability in the occupancy profile of populations within the range (Brown *et al.*, 1995; Pearman *et al.*, 2010). Second, like realised to potential (R/P) range size ratios arising from species distribution modelling (Svenning & Skov, 2004), my measures make the assumption that current ranges are at equilibrium. ω_e may still be a useful measure of likely responses to rapid environmental change: I am

interested in species' current relative landscape occupancy and not their occupancy when given unlimited time to fill their range. Lastly, the inevitable decrease in variation in both ω_e and ω_i with increasing species' range size makes it difficult to interpret results for the largest ranged species. A simulation approach may be needed to establish expectations for such species.

My aim was to use an assemblage-based measure of landscape impermeability to create species-specific relative measures of landscape occupancy and then to identify traits associated with species with strong, or weak, relative abilities to occupy the landscape. Few significant trait correlates were identified and the measures are strongly influenced by the spatial location of species (underlined by the significant positive relationship between the two measures, figure 5.6). My results underscore that species' distributions are determined by a complex interplay of intrinsic traits, extrinsic conditions and biotic interactions which combine to make predicting species' responses to climate change difficult (Lavergne *et al.*, 2011; Thuiller *et al.*, 2008). They also suggest that predicting responses may be most difficult in permeable (low ω) habitat where it is least clear what factors are limiting species. Labour-intensive mechanistic models have had the greatest success so far in predicting species' responses (e.g., Kearney & Porter, 2009). My results suggest that species inhabiting low ω areas may benefit most from such models.

Tables

Table 5.1. Possible interpretations of ω_i and ω_e

<i>Measure</i>	<i>Score</i>	<i>Definition</i>	<i>Interpretation</i>
ω_i	High	Range interior contains the range edges of co-occurring species	Species possesses traits that conveys high relative occupancy, for example broad climatic tolerances, strong dispersal ability, habitat generalism
	Low	Few ranges end within focal species' interior	Species occupies homogeneous, permeable landscape
ω_e	High	Range ends alongside other species	Species ends in heterogeneous habitat: biome boundary, mountain range, climatic threshold
	Low	Range ends idiosyncratically	Species is biotically or dispersal limited

Table 5.2. Correlations among traits calculated using only those species with data available for all variables. Values above the diagonal refer to the 303 species with data available for ω_i ; below the diagonal the 301 species with data available for ω_e . Range size refers to the number of cells making up the interior and exterior measures respectively. All values log10-transformed except niche breadth which was square-root transformed. Weaning age (days), gestation length (days), population density (average number of individuals per km²), generalism (product of number of dietary items eaten and number of habitat types occupied), body mass (grams), niche breadth (standard deviation of mean annual temperature recorded for each cell in the range exterior or interior), range size (number of cells in range exterior or interior).

	Weaning age	Gestation length	Population density	Generalism	Body mass	Niche breadth	Range size
Weaning age		0.607	-0.443	-0.180	0.681	-0.293	-0.152
Gestation length	0.605		-0.513	-0.221	0.775	-0.294	-0.015
Population density	-0.442	-0.513		0.334	-0.721	-0.116	-0.263
Generalism	-0.180	-0.221	0.332		-0.313	0.005	0.011
Body mass	0.682	0.777	-0.720	-0.311		-0.088	0.047
Niche breadth	-0.278	-0.266	-0.101	0.057	-0.099		0.579
Range size	-0.012	0.145	-0.411	-0.090	0.251	0.506	

Table 5.3. Results of multi predictor models using phylogenetic GLS

Variable	ω_i			ω_e			ω_e with ω_i as covariate					
	Slope	Error	T	Slope	Error	T	Slope	Error	T			
Body mass	-0.100	0.122	-0.821	-0.019	0.147	-0.126	-0.012	0.103	-0.112			
Gestation length	0.113	0.129	0.876	0.140	0.150	0.934	0.148	0.097	1.526			
Population density	0.132	0.084	1.576	0.075	0.102	0.727	-0.036	0.074	-0.495			
Weaning age	0.110	0.094	1.171	0.227	0.112	2.032	*	0.094	0.076	1.243		
Niche breadth	0.544	0.059	9.248	***	0.335	0.068	4.918	***	0.151	0.053	2.842	**
Generalism	-0.017	0.048	-0.349		-0.015	0.059	-0.255		0.048	0.044	1.077	
Range size	-0.540	0.056	-9.626	***	-0.295	0.067	-4.367	***	-0.102	0.053	-1.903	(*)
ω_i								0.698	0.046	15.106	***	
Adjusted R ²	0.287			0.111			0.489					
λ	0.556			0.448			0.192					
n	303			301			301					

Variables as described in table 5.2. Significance levels for T: (*) p = 0.058, * p < 0.05, ** p < 0.01, *** p < 0.001. λ was significantly different from 0 and 1 (χ^2 tests, p < 0.001) apart from the model for ω_e with ω_i as a covariate where λ was not significantly different from 0 (p = 0.301).

Table 5.4. Phylogenetic and spatial signal in the measures of relative occupancy. To the left of the grey bar is the maximum likelihood (ML) estimate of λ without considering space. To the right of the grey bar are the ML estimates of φ , λ' and γ which sum to 1.

Realm	n	λ	ML	φ	λ'	γ	ML
<i>Interior</i>							
Global	2761	0.591	2389.4	0.047	0.534	0.419	2390.3
Afrotropics	767	0.202	947.5	0.373	0.007	0.621	954.4
Australasia	160	0.095	164.8	0.517	0.005	0.479	169.5
Indomalaya	431	0.052	395.4	0.884	0.004	0.112	426.5
Nearctic	329	0.471	298.1	0.917	0.001	0.082	316.4
Neotropics	832	0.647	459.4	0.885	0.001	0.114	532.2
Paleoartic	663	0.000	640.7	0.056	0.009	0.934	640.9
<i>Exterior</i>							
Global	2725	0.633	2725.0	0.061	0.577	0.361	2726.4
Afrotropics	766	0.041	1298.0	0.250	0.020	0.731	1301.3
Australasia	159	0.316	214.9	0.546	0.005	0.449	220.8
Indomalaya	396	0.010	408.6	0.694	0.003	0.303	423.3
Nearctic	329	0.468	335.7	0.916	0.025	0.060	356.3
Neotropics	830	0.703	577.2	0.904	0.047	0.049	639.1
Paleoartic	662	0.139	707.0	0.330	0.007	0.664	717.1

Figures

Figure 5.1. The different combinations of ω_e and ω_i possible. The thick grey rectangle represents high ω habitat while the remaining habitat (white) is low ω . The black lines are the range edges of four species found in the area, each demonstrating an alternative combination of high or low ω_e and ω_i .

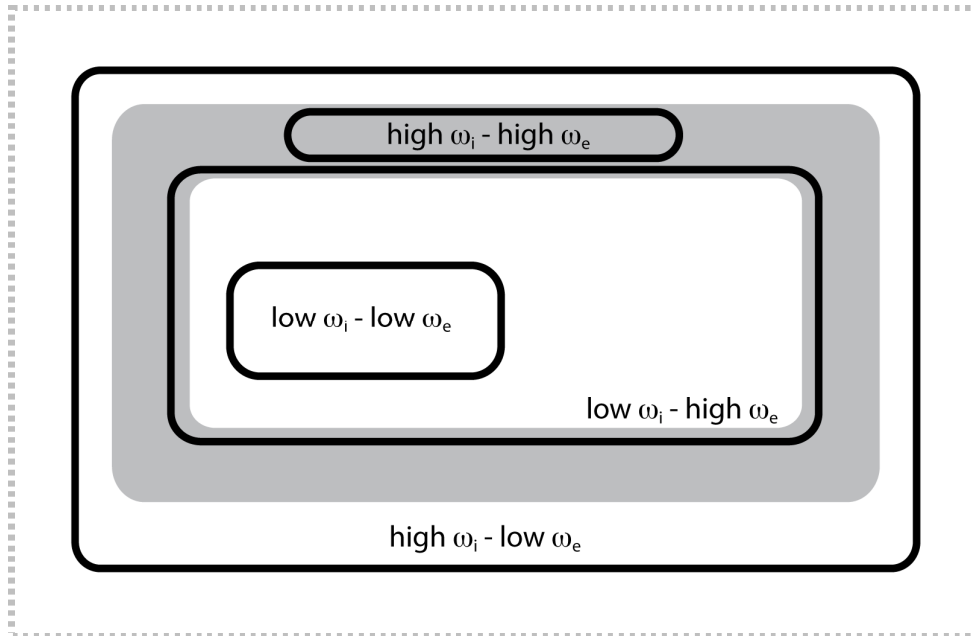


Figure 5.2. Assessing phylogenetic selectivity in range determinants. Measuring the phylogenetic dispersion of species with a range edge in the focal cell according to D . Phylogenetic clustering indistinguishable from random ($D \sim 1$, yellow) or from Brownian motion ($D \sim 0$, blue). Green cells are those with D non-significantly different from both 0 and 1. Cells with too few species to compute D (pale grey) or with no variation (i.e., all resident species have a range edge; dark grey).

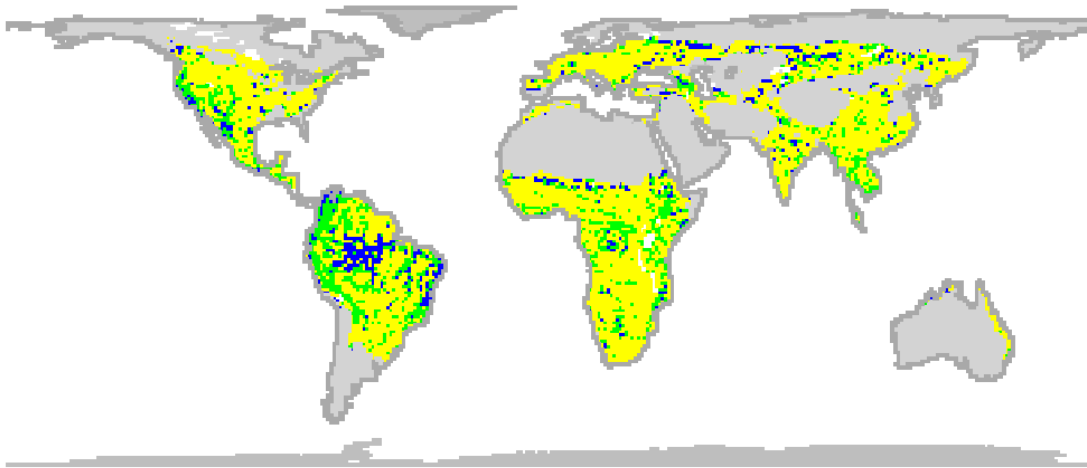


Figure 5.3. Relationship between measures of relative occupancy and range size. Top plot: ω_i ; bottom plot: ω_e . Solid lines: global mean ω (0.527). Dashed lines: mean ω_i (0.543) and ω_e (0.617), respectively. Grey points are ω_e for those species without interior cells. Dotted lines mean ω_e of species without interior cells (grey, 0.675) and with interior cells (black, 0.595).

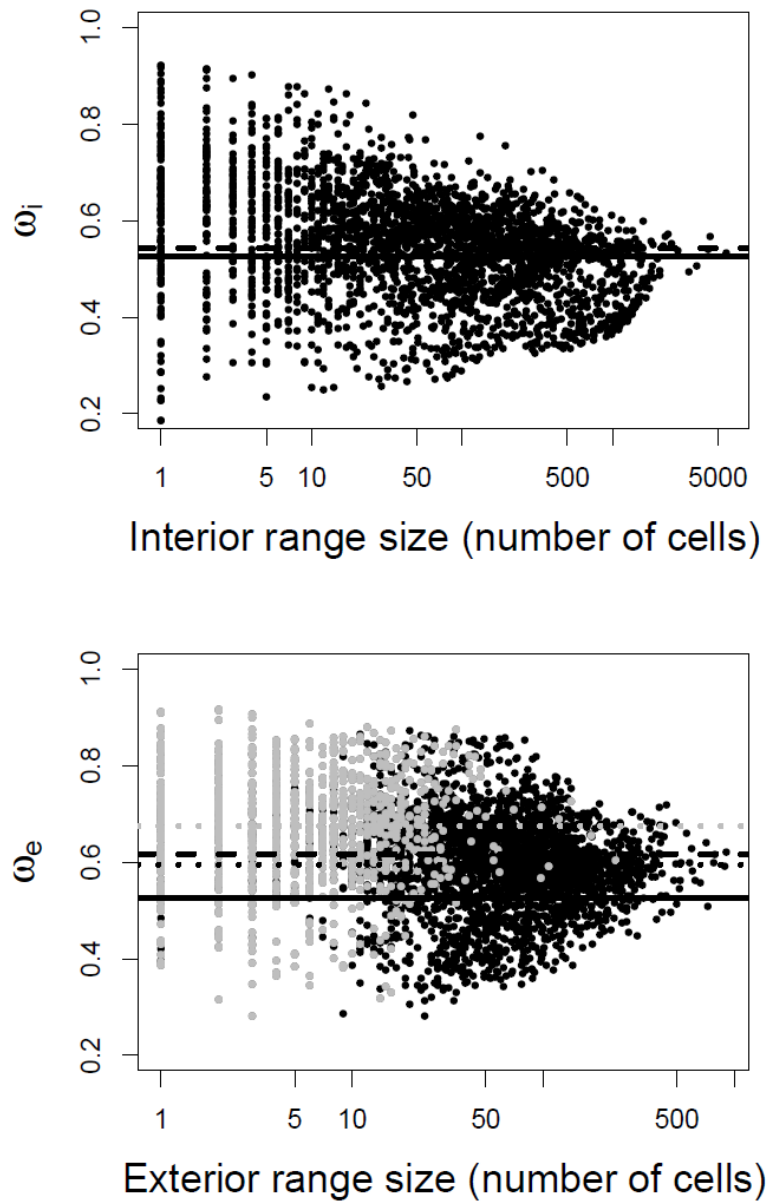


Figure 5.4. Results of models predicting ω_i . Variables as described in table 5.2. Each panel depicts that variables' slope estimate in each realm and globally. The error bars are the 95% confidence limits on the slope estimate. The shape of the point corresponds to the λ estimate (up triangle: not significantly different from 0, down triangle: not significantly different from 1, diamond: intermediate). The shading corresponds to the adjusted R^2 (higher values are darker). Note that the lower panel contains the results from bivariate models where body mass was fitted as a covariate. These results are available in tabulated form in Appendix 5.1, table A5.1.1.

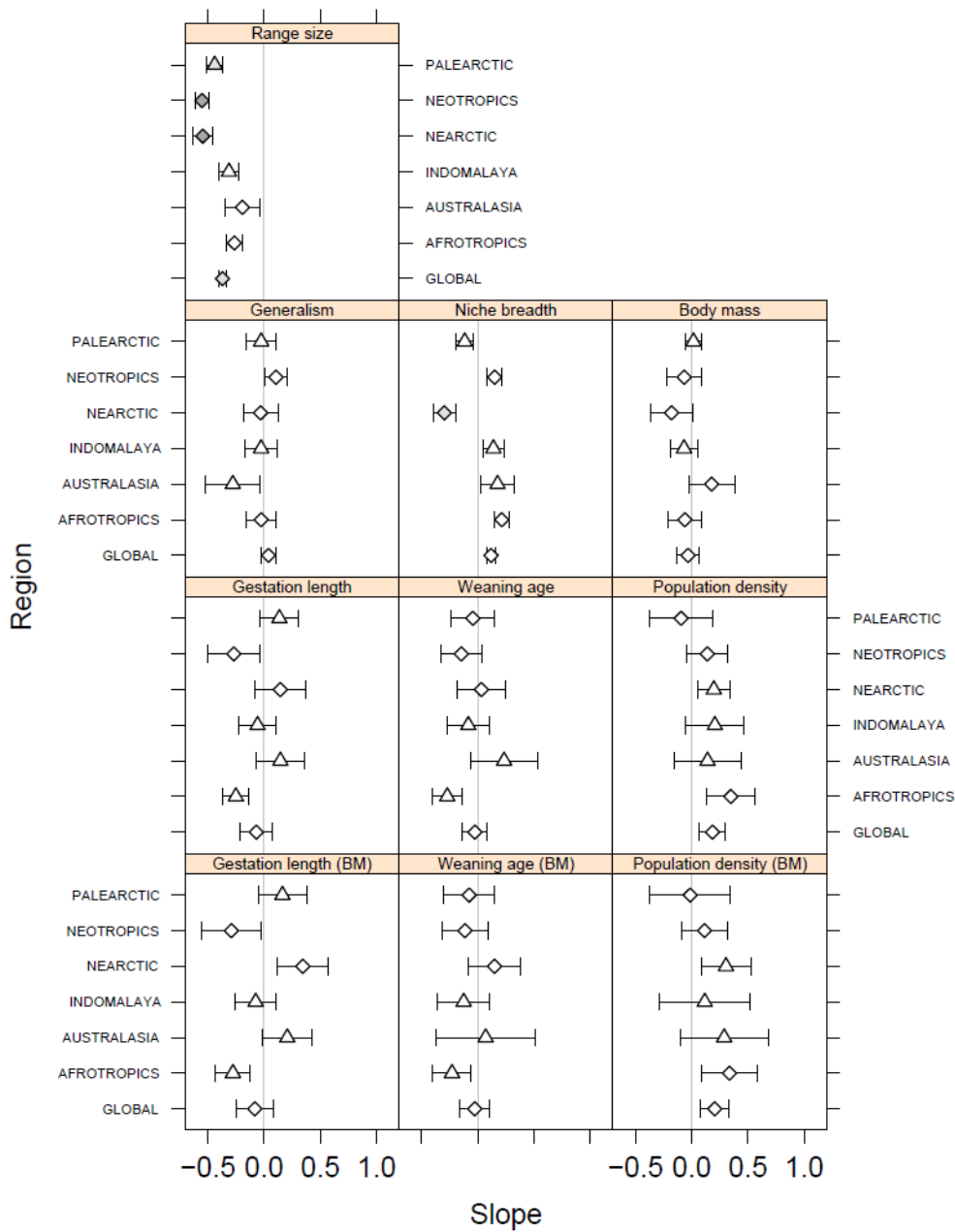


Figure 5.6. Relationship between ω_i and ω_e . Bubbles are scaled by range size (total number of cells in range). Range size has not been log10-transformed.

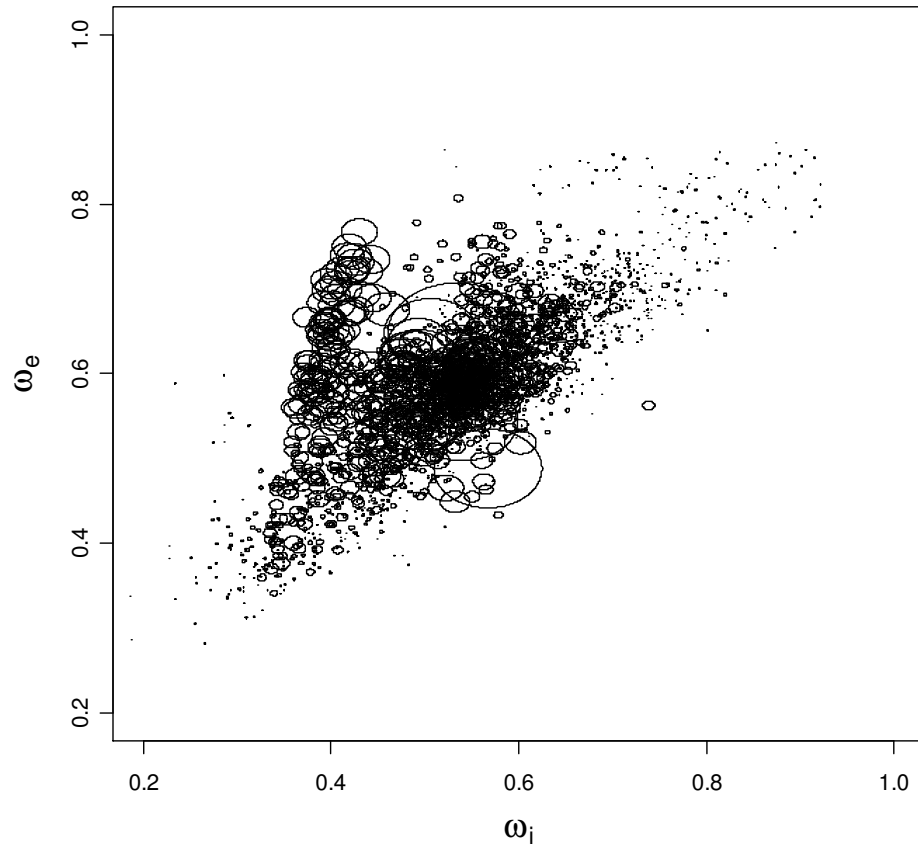


Figure 5.7. Results of models predicting ω_e with ω_i fitted as a covariate in all models. Figure arrangement as explained in figure 5.4. These results are available in tabulated form in Appendix 5.1, table A5.1.4.

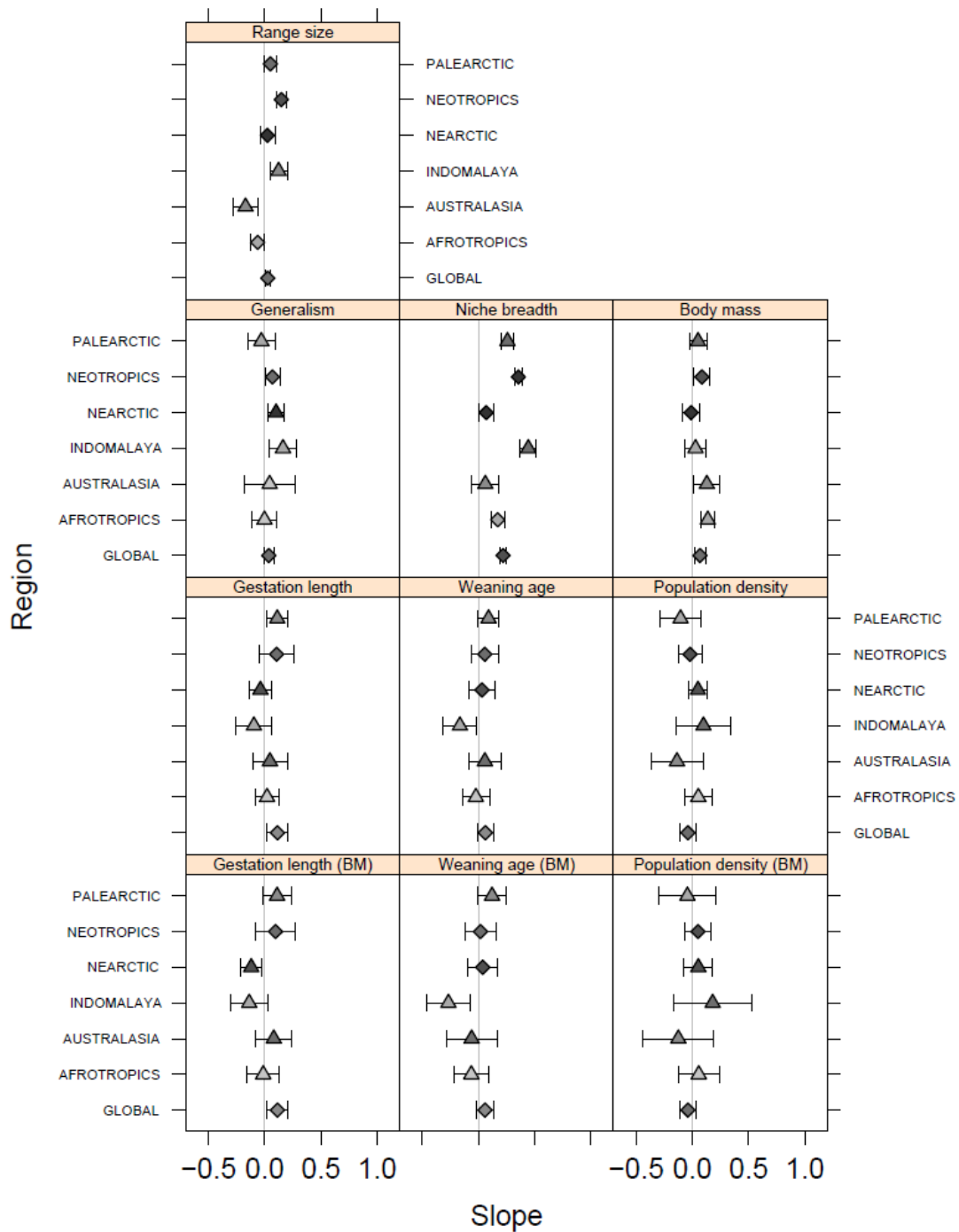
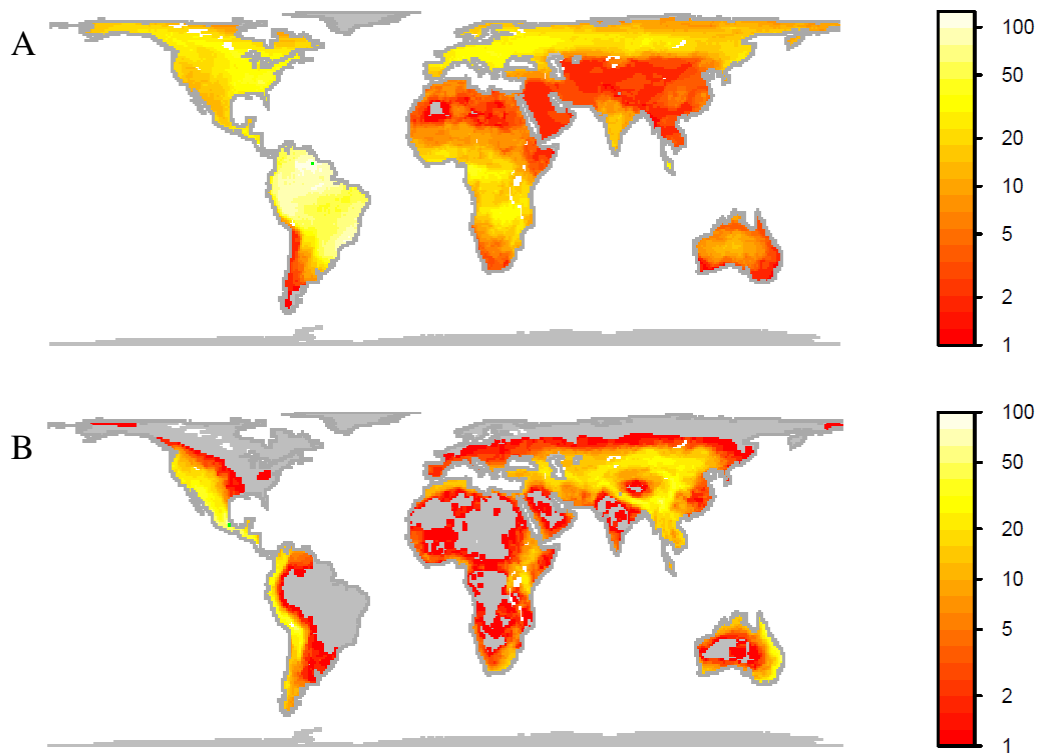


Figure 5.8. Richness of good and poor occupiers. (A) Richness (\log_{10}) of lowest-ranked quartile of ω_e species. Richness ranged from 0 to 113. The green cell in the northeastern Neotropics corresponds to the richest cell. (B) Richness (\log_{10}) of top-ranked quartile of ω_i species. Richness ranged from 0 to 71. The green cell in Mexico corresponds to the richest cell. Light grey cells no species. Dark grey cells coastline. Greenland and Antarctica omitted from all analyses.



Chapter 6. Detecting shifts in diversity limits from molecular phylogenies: what can we know?³

Abstract

Large complete species-level molecular phylogenies can provide the most direct information about the macroevolutionary history of clades having poor fossil records. However, extinction will ultimately erode evidence of pulses of rapid speciation in the deep past. Assessment of how well, and for how long, phylogenies retain the signature of such pulses has hitherto been based on a – probably untenable – model of ongoing diversity-independent diversification. Here I develop two new tests for changes in diversification ‘rules’ and evaluate their power to detect sudden increases in equilibrium diversity in clades simulated with diversity-dependent speciation and extinction rates. Pulses of diversification are only detected easily if they occurred recently and if the rate of species turnover at equilibrium is low; rates reported for fossil mammals suggest that the power to detect a doubling of species diversity falls to 50% after less than 50 million years even with a perfect phylogeny of extant species. Extinction does eventually draw a veil over past dynamics, suggesting that some questions are beyond the limits of inference, but sudden clade-wide pulses of speciation can be detected after many millions of years, even when overall diversity is constrained. Applying my methods to existing phylogenies of mammals and angiosperms identifies intervals of elevated diversification in each.

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Introduction

Clades are unlikely to have diversified at a constant per-lineage rate over deep time (Ricklefs, 2009). The fossil record has long been used to study tempo of evolution (Simpson, 1953; Stanley, 1979), but its incompleteness and temporal biases have often limited the strength of inference about macroevolutionary dynamics (Alroy *et al.*, 2001; Smith *et al.*, 2001). Time-calibrated phylogenies of extant taxa provide another window on diversification (reviewed in Nee, 2006). Analyses of such phylogenies have recently been used to identify pulses of speciation wherein clade richness rapidly increases (Bininda-Emonds *et al.*, 2007), and to test whether such pulses coincide with the times of climatic shifts (e.g., Alfaro *et al.*, 2009), tectonic movement (Williams & Duda, 2008) or mountain uplift (Hughes & Eastwood, 2006). Because these phylogenies do not contain extinct lineages, the signal of pulses will tend to be eroded by subsequent extinction (Liow *et al.*, 2010; Rabosky & Lovette, 2008b).

Under what circumstances might we expect a diversification pulse to still be detectable? There has been some investigation of the power of phylogenies to reveal temporal changes in diversification (Nee *et al.*, 1994; Pybus & Harvey, 2000; Rabosky, 2006), but many studies have relied on two simplifying assumptions. First, they have assumed that extinction played a negligible role in producing current patterns of diversity (reviewed in Nee, 2006), despite evidence from the fossil record that extinction is important (e.g., Alroy, 2008; Sepkoski, 1978). The lack of a record of extinction therefore results in a biased account of diversification (Kubo & Iwasa, 1995; Liow *et al.*, 2010). Secondly, many studies have implicitly assumed that per-lineage rates of speciation and extinction have been constant, implying that there is no upper limit to clade diversity (e.g., Alfaro *et al.*, 2009; Magallon & Sanderson, 2001).

More recent studies have shown that patterns of clade accumulation through time are often consistent with models incorporating diversity limits (Morlon *et al.*, 2010; Phillimore & Price, 2008; Rabosky, 2009a, b). Diversification slows as available geographic or niche space becomes saturated. Beyond this point, turnover continues but clade size stabilizes or increases more slowly (e.g., Alroy, 2009; Kisel *et al.*, in press; Morlon *et al.*, 2010; Phillimore & Price, 2008; Rabosky, 2009a, b; Ricklefs, 2009). Controversy persists as to whether declining diversification rates are driven by decreasing speciation, increasing extinction rates or a combination (Alroy, 1998; Levinton, 1979; Quental & Marshall, 2009; Rabosky & Lovette, 2008b; Walker & Valentine, 1984), although declines driven by increasing extinction rates may not be detectable (Quental & Marshall, 2009; Rabosky & Lovette, 2008b). Additionally, the ability to detect declines depends on a high ratio of initial speciation rate to equilibrium extinction rate and is greatest when clades first reach equilibrium diversity (Liow *et al.*, 2010; Quental & Marshall, 2009). As yet, however, there has been little exploration of how improved models using equilibrium diversity affect our ability to detect changes in diversification (but see Rabosky, 2009c).

Equilibrium diversity emerges from the attributes of a clade and extrinsic factors including climate and the nature and size of the area available for diversification (Alroy, 2010; Kisel *et al.*, in press; Rabosky, 2009a; Ricklefs, 2009). Extrinsic changes that add or remove suitable habitat, such as major climatic change, can therefore affect diversity limits (Alroy, 2009; Barnosky, 2005; Blois & Hadly, 2009), even without intrinsic changes such as key innovations. The fossil record indicates many biotic turnovers induced by climate change (e.g., mammalian responses reviewed in Blois & Hadly, 2009). In particular, the Paleocene-Eocene Thermal Maximum (PETM; 55 – 55.5 Mya) is associated with the dispersal of the modern mammalian orders

Primates, Artiodactyla and Perissodactyla into new continents with subsequent rapid diversification (Gingerich, 2006). A time-calibrated phylogeny of extant mammals shows an increase in diversification rate around the same time (Bininda-Emonds *et al.*, 2007), but for how long should phylogenies retain a signal of past events?

Here, I simulate diversity-dependent cladogenesis to assess when a major change in maximum equilibrium diversity can be detected from a perfect molecular phylogeny of extant taxa. In the light of recent evidence for the importance of diversity limits to clade diversification (Rabosky, 2009a, b) and the impact of discrete events on clade diversification (Alfaro *et al.*, 2009; Hughes & Eastwood, 2006; Williams & Duda, 2008), I focus on detecting transient pulses of diversification associated with changing equilibria rather than declines in diversification (e.g., Liow *et al.*, 2010; Phillimore & Price, 2008; Quental & Marshall, 2009) or shifts from one constant rate to another (e.g., Alfaro *et al.*, 2009; Rabosky, 2006). I propose and use two new statistical tests to explore how the timing and size of changes in diversity, and the background turnover rate, affect my ability to recover rate changes from a time-calibrated phylogeny of extant species. Finally, I apply these tests to a species-level supertree of mammals (Fritz *et al.*, 2009) and a family-level supertree of angiosperms (Davies *et al.*, 2004).

Methods

Evidence for diversity-dependent cladogenesis is mounting (e.g., Alroy, 2009, 2010; Rabosky, 2009a, b), but uncertainty remains over the form of diversity-dependence (Nee *et al.*, 1992; Rabosky, 2006) and whether it acts through speciation rates, extinction rates or both (Alroy, 1998; Levinton, 1979; McPeck, 2008; Rabosky & Lovette, 2008a; Walker & Valentine, 1984).

Here, I use an equal-rates logistic model of diversity-dependent cladogenesis (Nee *et al.*, 1992) and vary instantaneous per-lineage rates of both speciation (λ) and extinction (μ) as a function of initial speciation rate (b) and extinction rate at equilibrium (d), as the number of extant lineages (N) approaches the maximum possible diversity of the clade (M) (Ricklefs, 2009):

$$\lambda = b * (1-(N/M))$$

$$\mu = d * (N/M)$$

As N rises, extinction increases and speciation decreases until N fluctuates stochastically around an equilibrium diversity, K , defined by $bM/(b+d)$, with a turnover rate of $d/(b + d)$. Thus, when $d > 0$, M will not be reached (Walker & Valentine, 1984). This model differs from the critical birth-death model (where $\lambda = \mu$), which has no diversity limit, and from a Moran process, where N is deterministically held constant with every extinction met with by immediate speciation (both reviewed in Nee, 2006). I use stochastic simulation, drawing each species' waiting time to the next speciation or extinction using the current N , and re-drawing waiting times after each event.

To this basic model, I introduce an increase in maximum diversity – a rule change – from M_1 to M_2 after a set time (T_1) from the start of the simulation (T_0), resulting in an immediate increase in speciation and decrease in extinction. The simulation continues under this higher M for a further time period (T_2). In my first set of simulations, I examine how variation in the size of the shift in M and the rate of turnover affect detection of the change in diversification. Simulations start with a single species at T_0 and I fix $M_1 = 500$, $b = 1$, and vary M_2 from 600 to 1000 in steps of 100 and d from 0.1 to 0.5 in steps of 0.1. These values of d correspond to turnover rates at equilibrium between 0.091 and 0.333, bracketing estimates from the mammalian fossil record of ~ 0.24

species per lineage per million years (Alroy, 2009). I run the simulation over 110 My with the shift from M_1 to M_2 occurring at the PETM (55 Mya); both T_1 and T_2 are therefore 55 My in length. Equilibrium diversity levels are reached within 10 My of T_0 and T_1 (figure 6.1). I also investigate decreases in maximum diversity, using $b = 1$, $T_1 = 55$ My, $T_2 = 55$ My, $M_1 = 1000$, $M_2 = 500$ and varying d from 0.1 to 0.5 in steps of 0.1. These ‘downshift’ simulations represent a permanent reduction in diversity limits.

I consider two further scenarios, looking at how the signal deteriorates over time since the shift and at the signal left by non-selective mass extinctions. Both these simulations use $b = 1$ with d varying between 0.1 and 0.5. The first scenario additionally varies T_2 between 10 and 100 My with $T_1 = 55$ My, $M_1 = 500$ and $M_2 = 1000$. For mass extinction, I randomly remove 50% of extant species from equilibrium diversity ($M_1 = 1000$) at $T_1 = 55$ My, and then allow diversity to recover from around 500 to then remain at the original equilibrium ($M_1 = M_2$) for a further 55 My (T_2). I compare this scenario to previous simulations where, after an initial 55 My (T_1), equilibrium diversity simply increases from 500 (M_1) to 1000 (M_2) until the end of the simulation 55 My later (T_2). I consider only random extinction for simplicity. Harvey *et al.* (1994) and Rabosky (2009c) discuss the signal left by non-random mass extinction. Finally, I investigate how detectability changes when only a subset of lineages is affected by the rule change with the remaining lineages continuing to diversify under M_1 (details in Appendix 6.1).

To assess the type I error rates and power of my detection methods, I also simulate a set of null trees with no diversification shift. All trees have $b = 1$, $M = 500$ and I vary d between 0.1 and 0.5 and tree age between 65 My and 155 My, as above. In all scenarios, I simulate 100 replicate trees under each set of parameters; in total 14000 trees are analysed.

Detecting changes in diversification

My simulated phylogenies contain all extant and extinct lineages, and plots of the number of then-extant lineages against time clearly show the effects of diversification shifts (figure 6.1, solid line). To represent the best data that molecular phylogenies could provide, I only analyse phylogenies from which all extinct lineages have been removed (figure 6.1, dashed line). The resulting complete, perfectly time-calibrated molecular trees are, of course, far better than data currently available (Felsenstein, 2004). However, my primary interest is in identifying situations in which there is no prospect of *ever* confidently making inferences, rather than those where potentially-recoverable signal is erased by incomplete sampling or imperfect dates (see e.g., Moore & Donoghue, 2009; Pybus & Harvey, 2000).

I developed two methods to detect the signal of shifts in diversification within phylogenies, both of which use temporal windows sliding across evolutionary history to identify anomalous 1 My intervals. In both cases, I discard estimates for the first and last 20 My because they are biased: estimates in the first period are biased upwards because clades that happened to diversify slowly initially are likely to have gone extinct before the present, while the second period gives rise to new lineages that will go extinct but have not yet done so (Nee, 2006). Analyses are therefore based on a 70 My sequence centred on the change in diversification at 55 My. When analysing simulations where T_2 varies, I include the final 35 My of T_1 and only truncate T_2 where it is longer than 35My; some sequences are therefore shorter than 70 My.

The first method extends Pybus & Harvey's (2000) γ statistic. Given a sequence of internode distances, γ measures whether those nodes are clustered towards the start ($\gamma < 0$) or end ($\gamma > 0$) of the sequence, compared to the expectations of a pure-birth process. Although it is more typically

used to measure changes in diversification across a whole tree, it also applies to a sequence of nodes drawn from a time window. A diversification pulse within a 1 My slice will lead to a positive γ for a longer window that ends with that 1 My, and to a negative γ for a longer window that starts with the pulse (figure 6.2). The difference ($\Delta\gamma$) in γ between the earlier and later window therefore reflects changes in the per-lineage rates, with a negative $\Delta\gamma$ indicating a diversification pulse in the 1 My where the windows overlap (figure 6.2). I simulated the distribution of $\Delta\gamma$ and found it follows a normal distribution under both (a) a constant-rates pure-birth process ($\lambda = 0.06$, $T = 110$ My, 100 replicates: mean = -0.0425, sd = 1.65) and (b) single logistic decline ($b = 1$, $d = 0.1$, $T = 110$ My, $M = 500$ lineages, 100 replicates: mean = 0.0183, sd = 1.69). The $\Delta\gamma$ statistic seems to avoid some of the biases exhibited by γ , for instance correlations with clade size (Phillimore & Price, 2008) and number of branching times in the overlap window (results not shown), presumably because I sample only in narrow intervals and discard the intervals at the beginning and end of each tree. From my simulations, I calculate the significance of $\Delta\gamma$ at 1 My intervals, using local windows of 5 My.

My second method uses the maximum likelihood (ML) diversification rate estimate for each 1 My time slice, $(n-m)/s$, where n and m equal the number of lineages at the end and beginning of the slice, respectively, and s equals the total branch length within the slice (Nee *et al.*, 1994). Because I use phylogenies of currently extant species, lineage number can only increase with time ($n \geq m$) and the ML estimates are therefore bounded at zero. When $M_2 > M_1$, the expectation is that the slice including the rule change will have a higher rate than its neighbours. To detect elevated rates statistically, I fit generalised additive models (GAMs: Wood, 2006) to the rate estimates through time, weighting by the number of lineages present at the end of each interval. The smoothed term from the GAM allows local rate heterogeneity in the tree to be modelled

(rather than assuming rate constancy apart from the rule change) and hence the significance of outliers can be assessed using Studentised residuals relative to neighbouring time intervals within the tree, rather than relative to the predictions of null models parameterised from the tree. This method removes both the need to estimate background turnover rate and the assumption that there even *is* a background turnover rate: I am trying to recover major perturbations against a background of rate constancy or rate heterogeneity. However, the smoothing parameter (k) in GAMs always needs to be chosen with care (Wood, 2006): too high and the model will trace all fluctuations, including large outliers; too low and the background rate will not be adequately characterised and, following preliminary tests, I have used $k = 5$. For those simulations where $T_2 < 35$ My (i.e., where the rule change occurs close to the present), I retain all time intervals up to the present (see above); this may impede my ability to detect a shift, as any increase in M will be conflated with the signal from lineages present that are committed to extinction in the future.

I assessed each method's Type I error rate as the proportion of null simulations in which a significant shift in diversification rate was detected at the end of T_I . The power of each method for each scenario was calculated as the number of simulations showing a significant change at the end of T_I , minus the corresponding Type I error rate from null simulations. I also recorded the number of other intervals identified as significant for each parameter combination and used a binomial test to compare this proportion to 0.05. Finally, I applied my methods to a suite of models of exponential diversification to determine whether the type I error rates are still reasonable under these scenarios (and thus that my results were not contingent on there being zero net-diversification apart from at the rule change; see Appendix 6.1).

Testing my methods with empirical data

I applied both methods to a species-level supertree of mammals (Fritz *et al.*, 2009) and a family-level supertree of angiosperms (Davies *et al.*, 2004). It is unlikely that either clade evolved under a single or even two-phase homogeneous diversification process (Davies *et al.*, 2004; Purvis *et al.*, in press); however, I was interested in whether my methods detect anomalous time intervals despite the heterogeneity of process expected within trees of this size. Similarly, it is not problematic that the angiosperm tree has families as tips, as I am testing for diversification pulses deeper in the tree where sampling is effectively complete. I also use one of the most parsimonious supertrees rather than the strict consensus (as in Davies *et al.*, 2004) in order to exploit its completeness and full resolution. Diversification within older families is not reflected in the branching pattern of the supertree, so my methods will not detect diversification bursts exclusively occurring within these families. In mammals, I also applied the method to four subclades (marsupials and the three placental groups: Atlantogenata (Afrotheria + Xenathra), Laurasiatheria, and Euarchontoglires) to identify shared or unique pulses of diversification in these groups. The mammal tree has a number of extrapolated dates for taxa lacking sequence data; these tend to be distributed uniformly through time and will bias against detecting diversification pulses. Because of this and other imprecisions in dating phylogenies, I also assessed wider focal intervals than in my simulations, testing both 2 and 5 My intervals (for the $\Delta\gamma$ method I also adjusted the time windows to 10 My and 25 My, respectively). The results of the three interval sizes are quantitatively similar and I present results only from the 2 My window analyses.

I initially tested whether diversification bursts are associated with the Cretaceous-Tertiary boundary (65.5 My ago), the PETM (55 – 55.5 My ago) and the Eocene-Oligocene boundary

(33.9 My ago), given their association with responses in the mammalian and angiosperm fossil record (Alroy, 2009; Blois & Hadly, 2009; Jaramillo *et al.*, 2006). In addition to testing these specific hypotheses, I also assessed the use of both methods for data exploration by identifying all significant time slices. This requires conducting multiple tests simultaneously. Numerous corrections for multiple testing have been proposed, most adjusting the level at which a result is considered significant to make it more stringent (reviewed in Moran, 2003); however, some methods have been criticised as being too conservative (Moran, 2003). In particular, there is debate on whether it is necessary to control the probability of erroneously rejecting even one of the true null hypotheses (the family-wise error rate, FWE) or whether controlling the expected proportion of falsely rejected hypotheses (false discovery rate, FDR) is adequate (Benjamini & Yekutieli, 2001). An additional problem with my data is the expected autocorrelation among consecutive time intervals. To address these issues I report significant intervals (a) unadjusted for multiple testing, (b) using the sequential Bonferroni correction (an FWE method), (c) using the Benjamini and Yekutieli method (2001) that controls the FDR when tests are not independent, and (d) the sequential Bonferroni correction using the effective sample size after autocorrelation is accounted for (see Appendix 6.2).

Results

The power analyses shown in figure 6.3 demonstrate that statistical tests are more likely to detect a diversification pulse when it is large, when it occurs against a background of low turnover and when it is recent. The two methods also do not differ substantially in the regions in which they demonstrate reasonable power (> 0.8). For instance, when turnover rates correspond to those

estimated for the mammalian fossil record ($d \sim 0.24$; Alroy, 2009), both methods' power to detect a diversification pulse falls to 50% after 50 My (figure 6.3). Validity testing reveals a similar picture (table A6.3): the proportion of false positives is lowest where the diversification pulse is most pronounced. Validity of the GAM method decreases as T_2 and turnover rate increase, whereas validity of the $\Delta\gamma$ method is less variable through parameter space.

The rebound from a 50% random mass extinction is detected with similar power to a doubling in equilibrium diversity, although significant signal is maintained with higher turnover under the mass extinction scenario (table 6.1). Conversely, decreases in equilibrium diversity are much less likely to be detected than increases: plots of the ML rate estimates per My interval (figure A6.4) indicated that there is no unambiguous signal of a rate change across the five values of d tested. Rate estimates for the specified interval are zero but this zero rate also occurs in adjacent intervals and – for trees with high d - is the modal rate until near the present.

Applying $\Delta\gamma$ to the mammal and angiosperm phylogenies revealed significant increases in diversification for intervals close or coincident with the Eocene-Oligocene boundary (~ 33.9 My ago) in the Laurasiatherian, Marsupial and complete mammal tree. A signal was also found for the first two groups using the GAM method, but these results were not retained in marsupials once I had adjusted for multiple testing. Neither the Cretaceous-Tertiary boundary (65.5 My ago) nor the PETM (55 – 55.5 My ago) were associated with significant changes in diversification once I had adjusted for multiple testing. Looking throughout the phylogenies, significant diversification bursts were recovered (figure 6.4) in the angiosperm tree and the mammal tree both when analysed as a whole and by superorder, although adjusting for multiple tests removed some intervals. This correction was notably severe for two groups, Atlantogenata and

marsupials, where significant intervals were identified only using the $\Delta\gamma$ method (see also table A6.5).

Finally, my methods are robust in the face of alternative models of diversification. I tested a variety of null and non-null diversity-independent models of cladogenesis and found the type I error rate was reasonable in all cases (see Appendix 6.1).

Discussion

My results indicate that some large rule changes long ago may still, in principle, be detectable from information gleaned exclusively from extant diversity. It should therefore be possible to combine information on known past events with phylogenies of extant species to ask whether the event had an impact on diversification (see also Alfaro *et al.*, 2009; Moore & Donoghue, 2009). My analyses of mammalian and angiosperm supertrees (figure 6.4, Table A6.5) also demonstrate that my methods are useful for data exploration. However, my results indicate unambiguously that, under diversity-dependent cladogenesis with rapid turnover, even large increases in M will often not be apparent from reconstructed phylogenies (figure 6.3, see also Quental & Marshall, 2009; Rabosky & Lovette, 2008b). In these cases, strong inferences will require fossil evidence (Liow *et al.*, 2010; Quental & Marshall, 2010), though this remains a difficult endeavour because of the paucity of both suitable data and tractable methodologies (but see Etienne & Apol, 2009).

Signals of alternative rule changes

Mass extinctions followed by rebounds produced equivalent signals to increases in M (table 6.1). Diversification pulses not associated with a change in M (e.g., Rabosky, 2009c) are also expected

to produce similar signals. Additional methods may therefore be required to distinguish between these events, for example by investigating the time intervals preceding the identified rule change (Crisp & Cook, 2009; Harvey *et al.*, 1994). For example, random extinction culls a higher proportion of young lineages and so clades rebounding from extinction events retain a surplus of early lineages in comparison to increases in equilibrium diversity (figure A6.6). Once an event has been recognised using a time-slice method, differences in the LTT plots may distinguish different scenarios, perhaps in conjunction with simulations (see also Crisp & Cook, 2009). Any such approach, of course, assumes that, other than at the proposed event, the clade has been diversifying according to some diagnosable model of cladogenesis.

Some events, such as extensive habitat loss or the disappearance of suitable climatic regimes, may lead to permanently reduced equilibrium diversity. Such decreases (“downshifts”) are difficult to detect using time-slice methods alone (figure A6.4), with intervals at and around the shift characterised by zero net diversification. This is unsurprising: until extinction forces clade size to the new equilibrium, diversity dependence will constrain further speciation. Higher d facilitates a more rapid approach to the new equilibrium, but is also associated with larger fluctuations (and more zero-rate intervals) across the rest of tree, eroding any signal of the downshift. Downshifts may be more easily detected when specific traits or conditions have led to a diversity loss in one part of a tree and stasis or gain in another part (Moore & Chan, 2004; Purvis *et al.*, in press). While periods of low diversification across the tree can be inferred, unambiguously pinpointing clade-wide reductions in M on a reconstructed phylogeny will be difficult.

Empirical results

Application of my methods to the angiosperm family (Davies *et al.*, 2004) and mammal (Fritz *et al.*, 2009) supertrees highlighted a number of time intervals associated with diversification bursts (figure 6.4, Table A6.5), each also associated with fossil evidence for diversification shifts (Bell *et al.*, 2010; Meredith *et al.*, 2008; Poux *et al.*, 2006; Price *et al.*, 2005). The Eocene-Oligocene boundary was significant in two groups (figure 6.4): in Laurasiatheria, as artiodactyl radiations replace the previously dominant perissodactyls (Price *et al.*, 2005); and in marsupials corresponding to the origin of crown-group Macropodiformes (Meredith *et al.*, 2008). The Oligocene (34 – 23 My ago) is commonly considered the epoch linking the archaic faunas of the hothouse Eocene to the modern faunas that had become well-established by the mid-Miocene. My data exploration approach identified additional diversification bursts during this epoch for Laurasiatheria and Euarchontoglires, coincident with major clades of rodents and primates dispersing and diversifying into South America (figure 6.4; Poux *et al.*, 2006). In angiosperms, significant intervals are clustered in the Cretaceous, associated with the origin of the major orders (Bell *et al.*, 2010). The GAM method also highlights two Cretaceous intervals (100 My and 90 My ago) associated with the origin of the mammalian superorders (Bininda-Emonds *et al.*, 2007); however, these results must be interpreted conservatively, as deep polytomies will also be recovered as diversification bursts. The $\Delta\gamma$ method identified bursts at 48 My and 34 My ago, intervals also associated with low resolution in the tree. Although these polytomies might be hard and indicative of true diversification bursts, further tests are required to identify the underlying process. At the least, my methods underline these unusual intervals in the tree.

My empirical results attest to the heterogeneity of processes occurring within large trees: while I identify pulses coincident with intervals identified by Bininda-Emonds *et al.* (2007) and Davies

et al. (2004) using different methods, there are also discrepancies. For instance, the pulse at the PETM for mammals was not recovered, nor were the more recent diversification shifts found by Davies *et al.* Recent analyses highlight that diversification in both mammals and angiosperms is heavily influenced by available area (in agreement with my model of cladogenesis), but also trait variation, innovations and abiotic conditions (Kisel *et al.*, in press; Purvis *et al.*, in press; Vamosi & Vamosi, 2010). Although the intervals I identify do correspond to events in the fossil record, a robust understanding of the diversification of large clades will entail incorporating fossil evidence and the effects of intrinsic traits and the extrinsic environment.

Limitations

I have modelled diversity-dependent cladogenesis using a single M . Although an improvement on density-independent alternatives, my model is a caricature of the complex interplay between clades and their environments (Kisel *et al.*, in press; Purvis *et al.*, in press; Vamosi & Vamosi, 2010). A more realistic model may comprise distinct adaptive zones (Simpson, 1953), each able to sustain some equilibrium species diversity, and sub-clades diversifying in a diversity-dependent manner within them. While each adaptive zone persists, sub-clades will maintain deep nodes in the reconstructed phylogeny, retaining a signal of their initial diversification into their zones. Even if only certain sub-clades respond to regime change, my methods should then detect the diversification pulses within these sub-clades. My supplementary analyses showed that, when only a subset of lineages responds to the change in M , the pulse is still detectable (Appendix 6.1). Indeed, some of the pulses detected in my empirical trees are probably caused by only a subset of lineages (Purvis *et al.*, in press; Vamosi & Vamosi, 2010). Pinpointing the lineages responsible for diversification pulses requires additional tests incorporating tree

topology (Moore & Chan, 2004; Purvis *et al.*, in press). My methods are, however, unlikely to perform well if changes are weak or affect different sub-clades in opposite ways.

The above scenario suggests a route by which downshifts could be retained indefinitely in a phylogeny (Purvis *et al.*, in press): if incumbency effects (Jablonski, 2008) make it difficult to remove all members of an established group, extinction will be over-dispersed at the deepest levels of phylogeny and relict taxa will survive to be detected. This speculation does not contradict the evidence that extinction risk is phylogenetically clumped (e.g., Davies *et al.*, 2008): it may be difficult to fully extirpate a group occupying extensive geographic or niche space, whether extinction is random or clumped at low taxonomic levels (Jablonski, 2008).

Other valuable extensions will be to systematically investigate the effect of incomplete taxon sampling (e.g., Pybus & Harvey, 2000) and to develop methods that are robust to dating mismatches between hypothesised impact events and the responding nodes. Moore & Donoghue (2009) recently outlined a Bayesian method that accommodates uncertainty stemming from dating, rate and event-timing estimates. Although employing pure birth (Nee, 2006) as their null model of diversification, the explicit incorporation of uncertainty is an important step. Finally, adaptation of existing likelihood (e.g., Alfaro *et al.*, 2009; Rabosky, 2006) or approximate Bayesian (e.g., Rabosky, 2009c) techniques may provide more robust tools for the detection of rate changes, and may even be able to estimate parameters like turnover rates and the absolute magnitude of the pulse.

Conclusions

My analysis is timely given the recent rapid proliferation of large phylogenies (Bininda-Emonds *et al.*, 2007; Smith *et al.*, 2009) and the recognition that diversity dynamics are probably often at

least approximately equilibrial (Alroy, 2009; Morlon *et al.*, 2010; Rabosky, 2009b). As phylogenies become more complete and more accurate, it will be possible to mine them for information about the impact of deep-time events on diversification. My simulations of simple models of diversity-dependent cladogenesis show that low turnover and large shifts are required if rule changes in the deep past are to be recovered robustly: there is much that we cannot know.

Tables

Table 6.1. Comparing power to detect rule changes – doubling-in- M versus mass extinction and rebound to initial M . d is the extinction rate (see text for details).

d	0.1	0.2	0.3	0.4	0.5
Doubling-in- M					
GAM	0.97	0.71	0.33	0.21	0.12
$\Delta\gamma$	0.95	0.62	0.35	0.18	0.16
Mass extinction					
GAM	0.97	0.79	0.47	0.42	0.28
$\Delta\gamma$	0.96	0.65	0.44	0.27	0.22

Figures

Figure 6.1. Example lineage-through-time plots showing the loss of information when going from a complete phylogeny with all extinct and extant taxa included (solid line) to the best reconstructed phylogeny possible (all extinct taxa pruned from the tree, dashed line). The tree was grown under the following parameters: $b = 1$, $d = 0.1$, $M_1 = 500$, $M_2 = 1000$, $T_1 = T_2 = 55$ My.

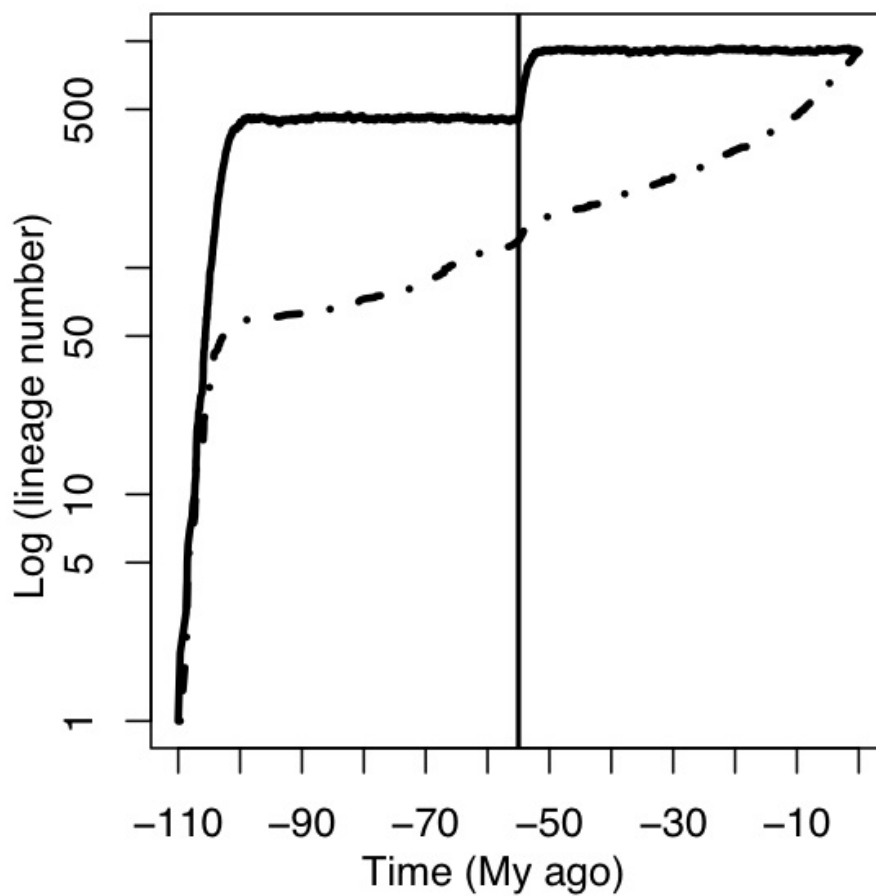


Figure 6.2. Schematic explaining $\Delta\gamma$. The top panel displays a complete reconstructed phylogeny where $b = 1$, $d = 0.1$, $M_1 = 50$, $M_2 = 100$, $T_1 = T_2 = 15$ My. The middle panel displays the set of overlapping time intervals involved in the calculation of $\Delta\gamma$ with vertical bars to represent each node. The calculation for $\Delta\gamma$ is displayed for two representative windows. The bottom panel displays $\Delta\gamma$ for all time intervals.

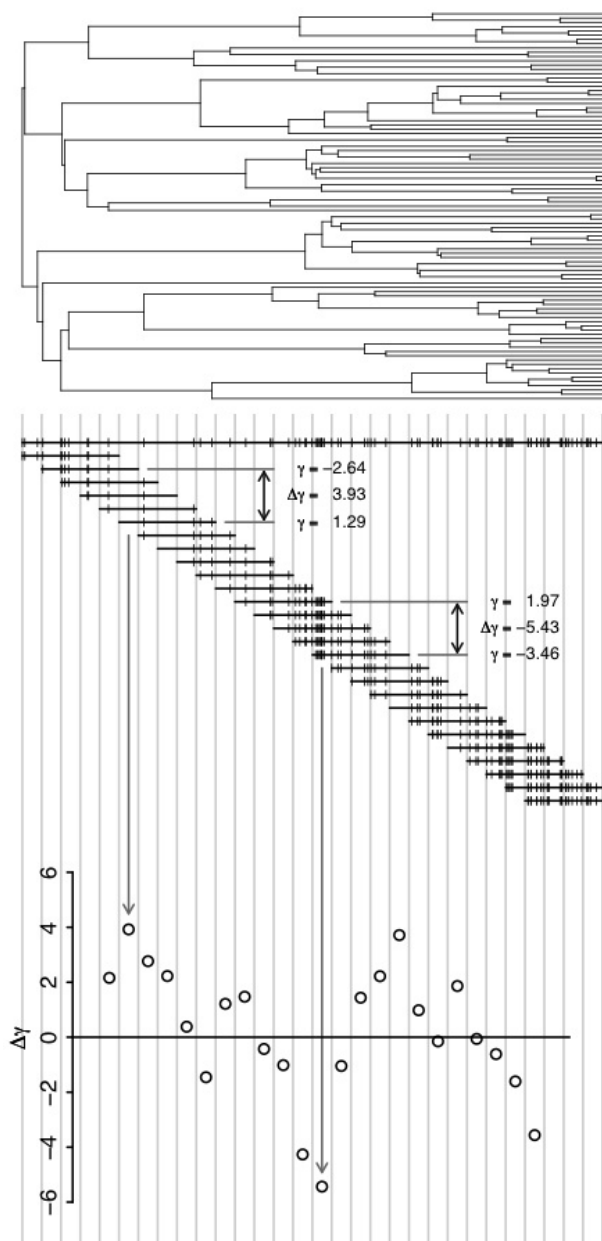


Figure 6.3. Contour plots of power to detect the rule change in the specified interval. (A, B) effect of shift timing versus extinction rate (C, D) effect of shift magnitude versus extinction rate. (A, C) GAM method (B, D) $\Delta\gamma$ method. That area of parameter space where power > 0.8 is indicated by a white contour line.

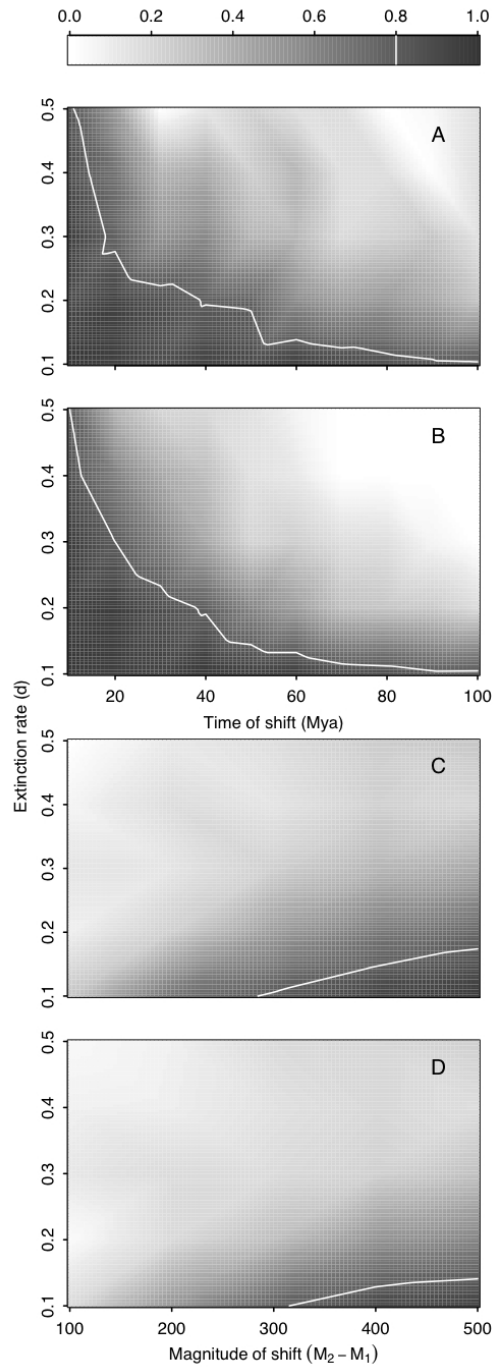
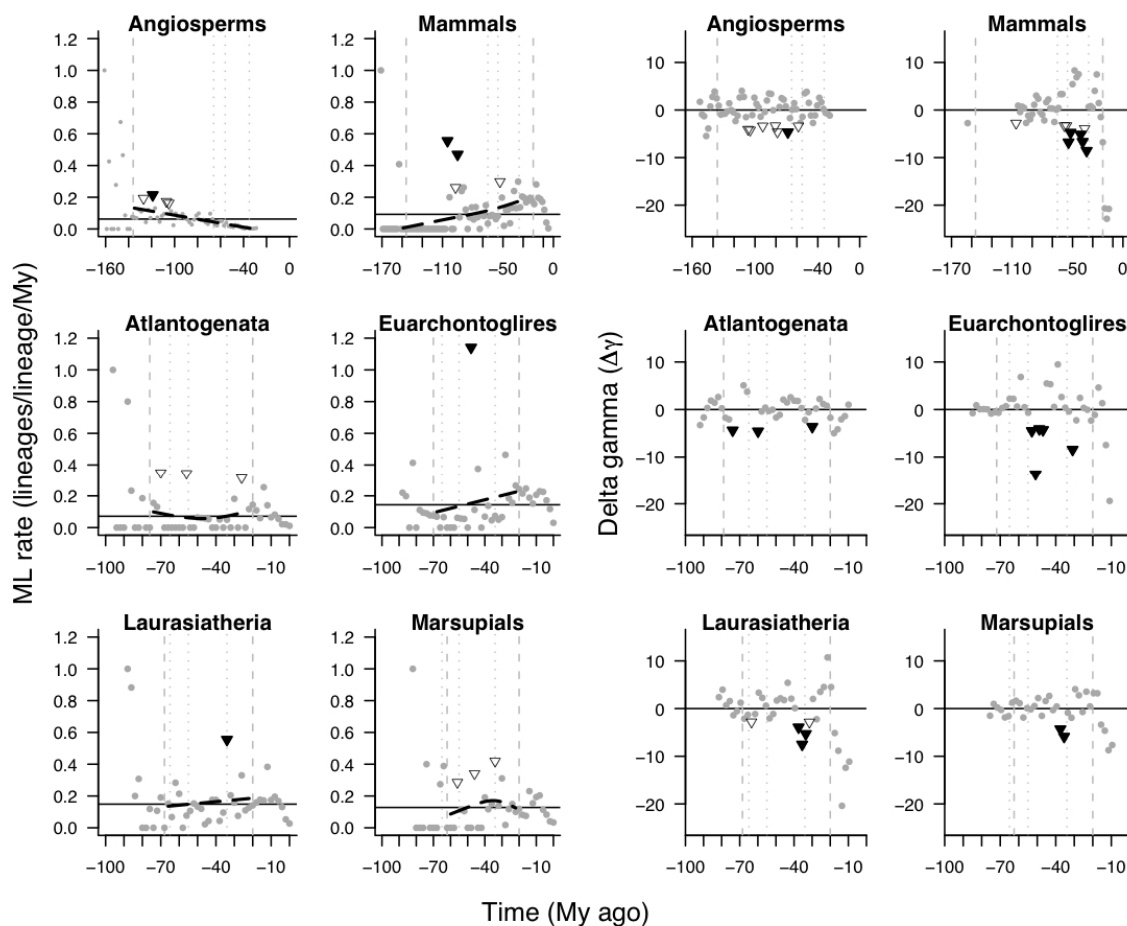


Figure 6.4. Diversification bursts in the angiosperm family, mammal and mammalian superorder trees analysed using 2 My intervals. Solid triangles denote significant intervals after correcting for multiple tests according to my modified sequential Bonferroni method. Open triangles are the additional intervals, significant only before correction. (left two panels) GAM method: the blue dashed line is the fitted curve. (right two panels) $\Delta\gamma$ method. Dotted lines on both plots delimit the boundaries of the Cenozoic epochs tested (Cretaceous-Tertiary boundary, 65 My; Paleocene-Eocene Thermal Maximum, 55 My; Eocene-Oligocene boundary, 34 My). Dashed lines mark the cut-offs for unanalysed intervals due to biases (see text). Results for 1 My and 5 My intervals in supplementary material (Table A6.5).



Chapter 7. Conclusion

In this thesis, I have explored spatial and temporal signatures of constraints on diversity across three major vertebrate groups and through simulations. Using a combination of phylogenetic and biogeographical approaches, I have investigated the macroecology and macroevolution of range limits and quantified our ability to detect the signal of temporal changes to diversity limits.

Summary of results

A full understanding of broad-scale diversity gradients requires an integrated understanding both of the traits of species that allow them to persist in a region and the capacity of that region to harbour a certain set of species, both now and in the past. While it was previously popular to try and distinguish ecological and evolutionary processes contributing to biodiversity gradients, it has since become clear that processes acting along a continuum of timescales probably contribute to the generation and maintenance of biodiversity (Mittelbach *et al.*, 2007; Ricklefs, 2004). In this thesis, I have assessed whether, using data on extant species alone, it is possible to untangle the influences of historical and contemporary factors driving diversity patterns and speculate on the possibility of accurately inferring likely future patterns of biodiversity.

Many taxa have more species in the tropics than at temperate latitudes (Hillebrand, 2004). Such diversity gradients require turnover of species in space without replacement. My approach to understanding broad-scale variation in diversity has been to investigate the constraints acting on species and explore the factors limiting species' ranges. I approached this study of range limits in a variety of ways. In chapter 2, I investigated conservatism in climatic tolerances in two major vertebrate taxa and found that cold tolerance - or the lack of it - was similarly conserved in both

mammals and amphibians despite major differences in the ecologies of the two taxa. The strength of this conservatism in both groups suggests that the (in)ability to evolve cold tolerance is a common feature limiting the distributions of many species to tropical latitudes (Wiens & Donoghue, 2004).

In chapters 3 & 4, I investigated range limits directly by mapping the overlap of range limits in space – landscape impermeability (ω) - in Afrotropical birds (chapter 3) and mammals and amphibians globally (chapter 4). Despite the strong signal of limiting climatic factors found in chapter 2, the most consistently important correlates found for ω were measures of habitat heterogeneity. This indicates that while climatic thresholds limit individual species, when the range limits of all species within a taxon are considered together, the areas of greatest overlap are in heterogeneous areas such as along steep altitudinal gradients or at biome transitions. Taken together these results emphasise that species distributions are determined not only by climatic or resource requirements, but also by landscape structure, with range limits collecting in hard-to-pass areas. Such areas are also known as hotspots of diversification, the complex landscape facilitating proliferation of endemic species (Rahbek & Graves, 2001). Thus, a failure to consider landscape structure in analyses of diversity patterns may lead to poorly-fitting models (as shown by e.g., Davies *et al.*, 2007). More importantly, perhaps, a failure to consider the nature of the habitat in which species are found and through which they are expected to move, will render erroneous predictions of the redistribution of diversity under climate change (e.g., Luoto & Heikkinen, 2008).

In chapter 5, I explored the possibility of converting my assemblage-based measure of mammalian landscape impermeability into a species-based measure of relative landscape occupancy by summarising the impermeability within each species' range. The aims were to

rank species on their relative ability to overcome constraints operating on the co-occurring biota and then to identify traits associated with this ability. However, few strong trait correlates could be identified for my relative measures: relative occupancy was more strongly related to where species were found. One possible reason for a failure to find strong relationships is that the key explanatory variables were missing from my analyses. Another possible explanation is that the relationships are complex and apparently idiosyncratic and that searching for common correlates is, as it turns out, a fruitless endeavour. In some respects, this in itself is an interesting result: while I identified areas of high and low ω and strong environmental/landscape correlates of these areas, the particular reasons why certain species do not adhere to these patterns can vary. They are likely to include dispersal and biotic limitations, historical accidents and real variation in occupancy abilities, perhaps precluding the use of a single summary measure relevant to all species.

Chapters 2-5 explained current distribution patterns by exploring the constraints acting on species and the traits and locations associated with overcoming these constraints. Two conclusions emerged: species are limited by both resource availability and landscape structure; and a failure to consider historical processes leads to an incomplete understanding of how current diversity patterns came to be. Chapter 6 assumed diversity to be constrained and explored our ability to detect the signal of changes to diversity limits through time.

The idea that ecological constraints operate to control clade diversity limits stems from fossil evidence for equilibrium diversity dynamics (e.g., Alroy, 2009) alongside mounting evidence in reconstructed phylogenies of diversification slowdowns (Morlon *et al.*, 2010; Phillimore & Price, 2008), a disconnect between clade age and richness (Rabosky, 2009b; Ricklefs *et al.*, 2007) and an association between clade richness and area occupied (Rabosky, 2009b; Vamosi & Vamosi,

2010). In short, diversification cannot be understood without considering the landscape upon which it plays out. Furthermore, it is unreasonable to assume that diversity limits do not change through time, as a result of extrinsic perturbations or intrinsic innovations (Alfaro *et al.*, 2009; Ezard *et al.*, 2011). In chapter 6, I explored the conditions under which we can expect to detect a signal of a shift in diversity limits using data only from extant taxa. I found that, for a signal of an increase in diversity limits to be detected, the change has to have been large and recent with low background rates of turnover. As phylogenetic data proliferate, it is useful to know what information we can hope to glean from it and what signals are likely to be lost without additional evidence. My study indicates that there are reasons to be hopeful, particularly when testing for the effect of extrinsic events identified *a priori* and expected to impact a clade as a whole.

Directions for future work

Climate change predictions

My analyses of impermeability and its species-centred derivatives were motivated, in part, by a desire to generate straightforward predictions on the expected redistribution of biodiversity under climate change using only the distribution data of a taxon. I find range edges are clustered in heterogeneous areas; this result complementing others that suggest that range movement will be extensive in such areas (La Sorte & Jetz, 2010; Williams *et al.*, 2007). An additional way in which ω maps could be used is in creating least-cost paths of range movement (Chetkiewicz *et al.*, 2006). If distribution modelling indicates that a species' new range is located beyond an impermeable region, it is unreasonable to assume that the species will be able to reach it unaided. Conversely, a species whose new range is more geographically distant may have little difficulty reaching it if the area through which the species must pass is permeable. Therefore, ω of

intervening regions could be used to identify the most likely route a species might take to reach suitable habitat and could also be used to anticipate the most likely sources of seed populations of the new range. Of course, these responses rest on there also being no further biotic or intrinsic constraints on species movement.

Understanding clade diversity dynamics

My thesis emphasises that diversity patterns are the result of clades diversifying on a landscape whose nature and size determine the level of diversity each clade can achieve as well as patterning the range limits of its component species. As the idea of ecological constraints limiting clade diversity takes root, it is becoming clear that a single carrying capacity will not apply for globally-distributed taxa, but rather that distinct carrying capacities might exist for different subclades occupying separate realms (e.g., Purvis *et al.*, in press). It would be of interest to see if impermeability calculated for higher taxa, for example mammalian families, would be useful in delimiting biotic regions and whether within each region there was also evidence for distinct carrying capacities. Rabosky (2010b) reported evidence that a model incorporating diversity limits fitted the distribution of diversities of ant genera much better than a model dependent on differential diversification rates. He suggests that, if models incorporating ecological limits fit higher taxa more generally, this would support Simpson's (1953) idea of higher taxa radiating within adaptive zones, with entry into a new zone (geographic, ecological) constituting origin of a new higher taxon. Mammals represent an ideal taxon with which to pursue these ideas: there is a relatively robust phylogeny available alongside distributional and trait data available for all species (see also Kisel *et al.*, in press; Purvis *et al.*, in press).

This thesis made use exclusively of data from extant taxa both because this data is more readily available and generally more comprehensive and in order to test how much we can infer without recourse to additional data. An important future direction will be to incorporate fossil data into analyses of diversity dynamics through time (e.g., Quental & Marshall 2010), particularly given the accumulating evidence that omitting extinct lineages from diversification analyses limits or even biases inferences possible (chapter 6; Rabosky, 2010a; Liow *et al.*, 2010).

Integrating niche evolution and diversification

Chapter 2 documented the clustering of climatic ‘escapees’ in the North Temperate Zone, the species having colonised the region during or after evolving the cold tolerance necessary to succeed there. Data limitations precluded formal analysis of whether colonisation of temperate latitudes led to increased diversification and higher diversities. When a dated amphibian phylogeny becomes available, and both the mammal and amphibian trees become better resolved, more nuanced questions can be asked of the impact of niche evolution on diversification. Similarly, a dated amphibian phylogeny will permit a better comparison of rates of niche evolution across the two groups.

I inferred recent evolution of cold tolerance by using the residuals from a nested ANOVA to quantify species-level change from their genus means. Consistency with parallel phylogenetic analyses in mammals suggested that this crude proxy for recent evolution is likely to be reflecting true events. Both analyses, however, are silent on the tempo and mode of niche evolution deeper in the phylogeny. If niche conservatism is prevalent – as our results and others suggest – it is unreasonable to use an unbounded model of trait evolution such as Brownian motion to model niche evolution. Our results, and intuition, suggest that entry into new ecospace,

for example into temperate latitudes, requires a major change in the underlying physiological trait(s) that determine the conditions under which a lineage can persist. A better null model for the evolution of niche traits may be one that accommodates periods of stasis with bursts of change (Estes & Arnold, 2007; Hunt, 2008). Further interesting avenues would be to investigate how generally jumps in climatic tolerances are associated with shifts in diversification rates/diversity limits and whether finding evidence for one can be used to target searches for the other. Reciprocal illumination may come from methods designed to partition phylogenies into subclades apparently diversifying along independent trajectories (e.g., Barraclough, 2010) combined with methods designed to detect discontinuities in trait evolution (e.g., Butler & King, 2004). However, without incorporating additional data, for example from the fossil record, we may really be reaching the limits of inferences possible using the branching pattern of phylogenies alone.

Incorporating intraspecific variation

Throughout this thesis, I have used species as units while frequently eluding to the expectation that intraspecific variation will modify species' responses. My measures of relative occupancy distinguished a species' range core from its range margin, but occupancy ability varies at a much finer scale than this, as seen, for example, from the spatial variation in abundance typically found across a species' range (Brown *et al.*, 1995). We investigated conservatism in climatic means and extremes, but it is likely that there is substantial local adaptation in climatic tolerances across the range. An understanding of how such variation impacts evolution of niche traits will help us to see for example, how niche requirements shape the diversification of entire clades.

Macroevolution does not exist without microevolution; thus, an understanding of the forces acting below the species level will help our understanding of patterns emergent above the species

level. It is noted that assimilating intraspecific variation into broad-scale analyses is generally hampered by data availability (but see Jetz *et al.* (2009) for a successful recent example). As data accumulates, the additional inferences possible are expected to be substantial.

Concluding remarks

Concise explanations of spatial diversity gradients and diversity differences among clades remain elusive despite centuries of research. It is becoming apparent that no single explanation is likely to be found; rather, a combination of contemporary environmental factors together with historical contingencies and species' traits have combined to produce the diversity patterns we see today. A full understanding of biodiversity at the macro-scale can only come through an integration of geography, phylogeny and history: every pattern I have studied bears the fingerprints of all three.

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Appendix 1. How diversification rates and diversity limits combine to create large-scale species-area relationships⁴

Abstract

Species-area relationships have mostly been treated from an ecological perspective, focusing on immigration, local extinction, and resource-based limits to species coexistence. However, a full understanding across large regions is impossible without also considering speciation and global extinction. Rates of both speciation and extinction are known to be strongly affected by area and thus should contribute to spatial patterns of diversity. Here, we explore how variation in diversification rates and ecologically-mediated diversity limits among regions of different sizes can result in the formation of species-area relationships. We explain how this area-related variation in diversification can be caused by either the direct effects of area or the effects of factors that are highly correlated with area, such as habitat diversity and population size. We also review environmental, clade-specific, and historical factors that affect diversification and diversity limits but are not highly correlated with region area, and thus are likely to cause scatter in observed species-area relationships. We present new analyses using data on the distributions, ages and traits of mammalian species to illustrate these mechanisms; in doing so we provide an integrated perspective on the evolutionary processes shaping species-area relationships.

⁴ A version of this appendix is in press as: Kisel, Y.*, McInnes, L.*, Toomey, N.H. & Orme, C.D.L. (in press) How diversification rates and diversity limits combine to create large-scale species-area relationships. *Philosophical Transactions of the Royal Society B-Biological Sciences*. *Joint first authors.

Introduction

The species-area relationship (SAR), which describes an increase in the number of species as region size increases, is a nearly ubiquitous pattern of biodiversity. SARs exist at a wide range of spatial scales, from local to global, and in a wide range of taxa, including mammals (Pagel *et al.*, 1991). In the ecological literature, SARs have been explained by considering the factors that limit species from immigrating into, establishing, and persisting in a region (Arrhenius, 1921; MacArthur & Wilson, 1967; Preston, 1960). However, at large geographic scales, *in situ* diversification contributes significantly to generating diversity, and so a full understanding of the generation of species-area relationships at such scales is impossible without also considering the macroevolutionary processes of speciation and extinction (Losos & Schluter, 2000; Rosenzweig, 1995; 1998).

Here, we explore the evolutionary underpinnings of large-scale SARs, outlining the roles of area itself, environmental variation, clade traits and historical contingency. We adopt a model of clade diversity in which clade diversification within regions is diversity-dependent and SARs are created by the scaling of both diversity limits and diversification rates with area. We support this discussion with new analyses using mammals as they are a well-known, diverse, and globally-distributed group with a wide variety of life histories, occupying a wide range of habitats and with robust data for many key traits (Jones *et al.*, 2009).

SARs have traditionally been treated as the outcome of differences between regions in the balance between immigration and local extinction (MacArthur & Wilson, 1967) and in the number of species that can coexist (Arrhenius, 1921; Preston, 1960). However, it was later recognized that SARs may not be controlled by the same processes at all spatial scales (Palmer &

White, 1994; Rosenzweig, 1995). At the smallest scales, SARs result from more complete sampling of the local biota as the area sampled increases, and as such they are sampling rather than biological phenomena. At larger scales (sampling all of the local biota), classical ecological explanations apply, with SARs emerging as a result of more species being able to immigrate into and persist in larger areas. Finally, at the largest scales, differences between regions in rates of speciation and extinction should be the main factor generating SARs (Losos & Schluter, 2000; Rosenzweig, 1995; 1998). Here, we focus on SARs at the largest geographic scale. For mammals, this large-scale phase is likely to occur only when considering quite large regions: in Kisel & Barraclough's (2010) study of the spatial scale of speciation, the two mammal groups represented (bats and carnivores) both required a region larger than 400,000 - 500,000 km² for any *in situ* speciation to occur.

We use a framework of diversity-dependent cladogenesis (Section 1) to explore how the area (Section 2) and environment (Section 3) of regions affect diversification and diversity limits in the generation of SARs. We also examine the role of clade traits (Section 4) and temporal patterns of diversification (Section 5) in modulating the shape of SARs. See table A1.1 for a summary of the factors addressed.

Methods

We used the geographic distributions of 4650 terrestrial mammal species within PanTHERIA (Jones *et al.*, 2009) to explore the scaling of species richness with area. The choice of appropriate regions at a global scale is not obvious, so we have taken two approaches to identifying provinces. First, we used botanical sampling regions based on geopolitical units (Taxonomic Database Working Group (TDWG), Brummit, 2001) to subdivide continental landmasses,

although we further separated disjunct sub-regions, such as islands. Second, we identified species presence in equal-area grid cells at a resolution (96.5 km) comparable to a 1° grid. We then used complete linkage hierarchical clustering on the Jaccard distance (Linder *et al.*, 2005; but see Kreft & Jetz, 2010) between grid cells to identify approximate mammalian biotic regions. Both methods are hierarchically nested between levels but regions within the same level are not nested. The fineness of subdivision can also be varied: the TDWG standard defines four levels, ranging roughly from different biomes at the coarsest scale (level 1) to subdivisions within countries at the finest scale (level 4); the hierarchical clustering can be cut at different “heights” to give different numbers of regions and we have used 50, 100, 150 and 200 regions (mapped in figure S1.1). The two region types differ in ways that are likely to affect the outcome: for example, political boundaries are likely to more finely partition large biotically homogenous regions in the temperate zone and agglomerate smaller biotically heterogeneous tropical regions. We used both methods and the variety of scales to assess the robustness of our conclusions to the details of sampling. Separating discontinuous parts of detailed polygons of TDWG regions, in combination with the imprecision in global species distribution maps, led to a large number of tiny islands and boundary regions with implausible biotas. We therefore removed all regions at the coarsest TDWG scale that did not contain at least one species endemic to that region, reducing 3974 candidate regions to 117. All nested subdivisions of these 117 regions at the finer TDWG scales were retained.

The areas of both geopolitical and clustered regions were calculated using an equal-area projection of the land within each region (figure S1.2). We recorded both the total and endemic mammalian species richness for each region and fitted SARs at each scale of subdivision using linear models on log-log axes to estimate the slope. We modelled species richness (S) as a power

of area (A) as $S = cA^z$ (Arrhenius, 1921; Rosenzweig, 1995): although there has been considerable debate about the shape of SARs (Lomolino, 2000; Scheiner, 2003), our results should be general to alternative functions. For all further analyses, we used the most finely divided regions and compared results using TDWG Level 4 and 200 biotic regions. We also explored the differences between slopes of SARs arising from species endemic to a region versus those occurring in more than one region, and the variation among mammalian orders in slopes of SARs.

To investigate the additional explanatory power of habitat diversity and environmental variables, we used two variables to capture different elements of habitat diversity: the diversity of land cover classes (GLCC v2.0, <http://edc2.usgs.gov/glcc/glcc.php>), calculated as the inverse of Simpson's diversity index ($1 - D$) on the relative areas of the classes within each region; and the log range in elevation (GTOPO30, <http://eros.usgs.gov/>) within each region. We considered two environmental variables within regions: the mean annual temperature (www.worldclim.org) and the mean normalized difference vegetation index (NDVI, Los, pers. comm., updated versions of Los *et al.*, 2000). We fitted multiple regressions with log area and each of these four variables in turn as predictors of log species richness. For each variable, we tested whether it showed a significant interaction with area as well as its significance as a main effect. All covariates were mean centred and standardized to facilitate the interpretation and comparison of these models (Schielzeth, 2010).

An approximate measure of habitat breadth for mammalian species was found by counting the number of GLCC habitat cover classes across all the 96.5km cells intersecting each species' range. This number correlates strongly with the species' geographic range (Kendall's tau = 0.61) and we therefore also estimated a number of major habitats by counting only those habitats with

a proportional contribution of at least 0.142. This cutoff was selected because it minimises the observed correlation between the resulting number of major habitats and the species' range size (Kendall's tau = -0.0002). We then calculated the Kendall's correlation between family species richness and both the number of habitats and number of major habitats.

In order to explore the effects of area on the temporal patterns of recent diversification within mammals, we identified two sets of monophyletic clades from the mammal supertree (Bininda-Emonds *et al.*, 2007, 2008), excluding monotypic clades. One set had crown ages younger than 20 My (421 clades), the other had crown ages younger than 10 My (616 clades) and was nested inside the older set. We recorded each clade's species richness, stem-group age and present-day area (either the total area of all TDWG level 4 provinces or of all biotic regions (finest scale) in which the component species occurred). We then fitted a suite of six models of diversification rate across each set (Phillimore, 2010; Rabosky, 2009b). The most complex model is an extension of those outlined in Rabosky (2009b) and Phillimore (2010) and fits an exponential decline in diversification with rate z over clade age (t) from an initial diversification rate (λ), but where log present-day area (A) contributes to both initial λ (scaling by c) and the rate of decline (scaling by p); the overall diversification rate is always scaled by the relative extinction rate (ε):

$$r_i = (\lambda + c \log A_i) e^{-(z + p \log A_i)t_i} (1 - \varepsilon)$$

We also fitted five simplifications of this model by fixing sets of parameters at zero: a constant diversification rate across clades (c , z and p fixed), a constant diversification rate scaled by individual clade area (z and p fixed), an exponential decline in rate within clades (c and p fixed), an exponential decline from an initial λ scaled by area (p fixed) and an exponential decline at a rate z scaled by area (c fixed). We optimized parameter estimates for the free variables in each

model by maximizing the sum of log likelihoods of the observed species richness (n) across clades given clade age and the model estimates (following Bokma, 2003; Phillimore, 2010; Ricklefs, 2009). The models were not nested and we therefore used AIC to assess relative model support. As the two methods to define regions gave qualitatively similar results, we report only the TDWG analysis here.

Section 1: A verbal model for clade diversification in space

Diversity-dependent models of diversification have two main features: a growth phase, where the clade in question diversifies until it reaches an external limit; and an equilibrium phase, where species identity turns over but clade size fluctuates about that limit (Alroy, 1998; Sepkoski, 1978). The precise shape of diversity-dependent diversification has been debated (Nee *et al.*, 1992; Rabosky, 2009a), but the exact shape of the diversification trajectory should not change the broad-scale implications of the existence of diversity-dependent diversification. There is taxonomic, phylogenetic, and paleontological evidence to support the existence of diversity-dependent diversification in many cases, described variously as “ecological limits on diversity,” “diversification slowdowns,” and “diversity equilibria” (Alroy, 1998; Cardillo, in press; Nee *et al.*, 1992; Purvis *et al.*, in press; Rabosky, 2009a; Rabosky & Lovette, 2008; Sepkoski, 1976; Vamosi & Vamosi, 2010).

A variety of processes could generate diversity-dependent diversification. Perhaps the most commonly referenced is a model of ecological limits wherein, as available niches are filled, speciation declines and new species are only added to a region following extinctions and release of sufficient niche space (McKinney, 1998; Rabosky, 2009a). Such a mechanism would provide a link between the ecological processes typically associated with SARs and the evolutionary

processes being proposed here. Alternatively, reduction of both population and range sizes as diversity increases could lead to decreased rates of speciation and increased rates of extinction and thus a diversification slowdown conceivably divorced from any niche-based mechanism (Pigot *et al.*, 2010; Rosenzweig, 1975).

Within our diversity-dependent framework, there are only three features of a clade's diversification curve that can vary: the speed at which a region initially accumulates species (figure A1.1a), the diversity limit (or equilibrium species richness, figure A1.1b), and the age at which diversification begins (figure A1.1c) (see also Rabosky, 2009a). Before equilibrium is reached, the richness of clades depends only on their age and their rate of diversification. In contrast, clade sizes at equilibrium depend on their diversity limits, which are controlled by the interaction of external factors with clade traits (Mallet, submitted and see below). SARs will emerge from this model whenever diversification rates and/or diversity limits are higher in larger regions (figure A1.2). When a clade inhabits multiple separate regions of different areas, the species richness of that clade will be higher in the larger regions, creating a SAR.

Globally, mammalian species richness shows strong scaling with area between non-nested provinces for both TDWG and clustered regions at all four scales (figure A1.3). These are well described by power laws but there are differences between the two region types (figure A1.3a): clustered regions show consistent slopes across changing scales (0.41 - 0.43), whereas TDWG regions show a decline in slope from 0.47 to 0.24 with increasing subdivision. These slopes lie within the range of 65 previously reported slopes from mammal power law SARs (figure A1.3b; Drakare *et al.*, 2006), but the higher values fall toward the top of the reported range (92% quantile). The changes in slope between TDWG scales is accompanied by higher intercepts (table S1.1, figures S1.3-4) and is primarily driven by small political units, such as the Vatican

City and Likoma, within species-rich areas (figure A1.3c); these outliers are not found in small regions based on mammalian biotas (figure A1.3d). In all cases, endemic species also show significant scaling with area but with reduced slopes compared to total and non-endemic species richness (figure A1.3b-c, table S1.1, figures S1.3-4).

We also tested how well area explains variation in diversification rate across sets of mammalian clades. For both sets of clades (crown group age < 20 My and < 10 My, table A1.2), an exponential decline in diversification rate is best supported, demonstrating apparent limits to diversity. For clades younger than 20 My, the most complex model was best supported, with clades occupying larger areas having increased initial diversification rates and decreased rate of decline. For clades < 10 My, a simpler model, with area affecting only the rate of decline, could not be rejected. These results suggest that for mammals the decline in diversification rate as a region fills is more strongly affected by available area than the initial rate. Nevertheless, support for an effect of available area on initial rate was still found for both clade sets and the similar likelihoods for the younger clades may simply reflect individual clade differences within the set tested (see also Cardillo *et al.*, 2005; Linder, 2008).

Section 2: Generating SARs in an evolutionary framework

In explanations of SARs, area is frequently viewed as a proxy or summary variable (Hubbell, 2001) acting only indirectly via other variables, such as population size and habitat diversity that are highly correlated with area (MacArthur & Wilson, 1967). The individual effects of area and such correlated factors are difficult to separate in practice (Kallimanis *et al.*, 2008; Triantis *et al.*, 2003), and their relative importance is likely to vary depending on the taxon concerned (Ricklefs

& Lovette, 1999; Rosenzweig, 1995). However, we believe that area could conceivably have some direct effects, and we discuss these first.

Direct effects of area

We can see only two ways that area could control diversity directly (i.e., without invoking increased population sizes or habitat variety). Firstly, extinction rates should be lower in larger regions, in which refuge populations are more likely to survive after any catastrophic disturbance affecting only part of the region (Wiley & Wunderle, 1994). Secondly, if populations are patchily distributed, speciation rates should be higher in larger areas (Losos & Schluter, 2000), where distances between populations can be larger and barriers that can cause vicariant speciation are likely to be larger and more numerous (Rosenzweig, 1995). It could be argued that the effect of barriers is really an indirect effect of area via fragmentation, and we discuss this point further below. Greater geographic isolation between populations will lead to higher speciation rates if: 1) there is sufficient selection pressure and/or genetic drift to drive population divergence through to reproductive isolation (although there is no evidence for speciation via genetic drift on its own: Coyne & Orr, 2004); 2) gene flow is the main force preventing population divergence and speciation (Slatkin, 1987); and 3) the regions considered are large enough for populations to be sufficiently isolated to permit speciation. The definition of 'large enough' will depend on the dispersal ability of the organism and the strength of selection relative to gene flow, as poorer dispersers will attain sufficient isolation in smaller regions (Kisel & Barraclough, 2010), as will species whose populations experience stronger divergent selection (Slatkin, 1973, 1985).

Effects of area via population size

Because larger regions are able to support greater total numbers of individuals (Brown, 1995), and thus are also likely to have species with larger population sizes, the effects of population size on diversification can contribute to the generation of SARs. In fact, many of the effects of population size that we describe below have previously been described as direct effects of area itself (MacArthur & Wilson, 1967; Ricklefs & Lovette, 1999). It is well established that larger populations are less likely to go extinct, as they are more buffered from the effects of demographic stochasticity, environmental disasters, and habitat loss (Lande, 1993; Rosenzweig, 1995). Additionally, there are three ways that larger population size may drive higher speciation rates. First, new beneficial mutations will arise faster in larger populations (Willi *et al.*, 2006), allowing faster divergence between separated populations if mutation limits speciation (Schluter, 2009). Second, larger populations hold more standing genetic variation (Frankham, 1996; Leimu *et al.*, 2006) for selection to work on (Schluter & Conte, 2009; Weber, 1990). Third, newly isolated populations resulting from the break-up of larger populations will also be larger, and therefore more likely to survive long enough to diverge into new species (Chown & Gaston, 2000). In addition to effects on rates of diversification, the total abundance of individuals supported by a region places a hard limit on the number of species that the region can hold. If we assume that all species are ecologically identical and so have the same minimum viable population size (Gilpin & Soule, 1986; Hubbell, 2001), then larger regions will be able to support more species at sustainable equilibrium population sizes.

Effects of area via habitat diversity and fragmentation

Some authors have suggested that SARs are only a proxy for the scaling of species richness with habitat diversity (Baldi, 2008; Losos & Parent, 2010; MacArthur & Wilson, 1967; Triantis *et al.*, 2003), and indeed habitat diversity and area are typically very highly correlated. Along steep environmental gradients, and in heterogeneous habitats, populations can more easily become specialised to different habitats, making ecological speciation more likely and perhaps more rapid (Schluter, 2009). Regions with high habitat diversity also have a higher number of possible distinct niches or niche combinations (Hutchinson & MacArthur, 1959), thus increasing the number of species that can coexist at equilibrium.

High levels of regional fragmentation can also elevate diversification rate and diversity limits, by providing a textured landscape with subunits that are physically isolated from one another but environmentally equivalent. Barrier formation can occur through many processes, including river formation, mountain building, sea-level fluctuation, volcanic uplift, and habitat fragmentation, and is more likely in larger regions. Barriers elevate diversification rate by separating previously interacting populations, which are then more likely to evolve reproductive isolation (Rosenzweig, 1995). In addition, fragmentation can boost equilibrium diversity, as ecologically equivalent species can be maintained in separated sub-regions (Shmida & Wilson, 1985; Orme *et al.* in prep). For example, Esselstyn *et al.* (2009) suggest that tree shrew diversity in the Philippines has arisen predominantly via speciation in allopatry on newly formed islands, with limited apparent morphological or ecological differentiation. One particularly important measure of regional fragmentation is topographic complexity, as environmental turnover along altitude gradients is a barrier to many species' ranges (McInnes *et al.*, 2009). The richness of uniquely adapted, restricted-range endemics found along altitudinal transects in tropical mountains is

perhaps the classic example of such fine-scale spatial partitioning (Janzen, 1967; Rahbek & Graves, 2001).

The effects of fragmentation on species richness will show a complex relationship to the total summed area of the subunits. While greater fragmentation of a region may permit more species to exist within the same total area, it may also push the area of the component fragments below a size which can maintain viable populations (Gilpin & Soule, 1986; Maurer & Nott, 1998) or generate endemics (Kisel & Barraclough, 2010; Losos & Schluter, 2000). Thus, plots of species richness against total area occupied may not yield significant relationships unless the degree of fragmentation is also considered and total area is scaled appropriately (see Orme *et al.* in prep). In addition, the dispersal ability of a clade in combination with the geographic structure of the fragments will influence the number of fragments that can be occupied. Finally, the effect of barriers will depend on the average range sizes of species in a region: if the average range size is small, barriers need not be large or bisect an entire region to cause speciation (Rosenzweig, 1975).

Attesting to the importance of environmental features in the generation of SARs, increased elevational range is associated with higher diversity in both geopolitical and biotic regions; habitat diversity also drives higher diversity, but only in geopolitical regions (table A1.3, figure S1.5). This arises from differences between the clustering methods: areas with similar habitat are likely to be biotically homogenous and therefore form a single biotic region, whereas political boundaries are more likely to cut across such regions. As a result, Simpson's index ($1 - D$) of habitat diversity is low in biotic clusters and scales extremely weakly with region area (intercept: 0.227, se = 0.042, $t=3.83$; slope: 0.018, se = 0.014, $t = 1.27$; $df = 148$) whereas in TDWG regions it is higher and scales strongly with area (intercept: 0.356, se = 0.025, $t=14.39$; slope: 0.055, se =

0.005, $t = 10.27$; $df = 578$). In all these models, the high relative magnitude of the standardized parameter estimate for area also implies it is not simply acting as a proxy for either variable.

Section 3: Abiotic factors modulating the species-area relationship

Some abiotic factors, such as energy availability, do not correlate closely with area but may still affect diversification rates or diversity limits of different regions, leading to departures from SARs that depend on a region's prevailing environmental conditions.

Energy availability is one of the key variables thought to contribute to large-scale spatial patterns of diversity, and has mainly been discussed for its part in generating latitudinal differences in diversity (reviewed in Mittelbach *et al.*, 2007; Willig *et al.*, 2003 and see Davies *et al.*, in press). On average, energy availability (either ambient, e.g., temperature, or productive, e.g., plant biomass) explains 60% of the variation in broad-scale richness across a range of plant and animal groups (Hawkins *et al.*, 2003 and see Davies *et al.*, in press). This variation should lead to consistent differences between SARs of high- and low-energy regions.

As expected, increases in both mean annual temperature and mean NDVI act to significantly elevate both overall mammal diversity and slopes of mammalian SARs (table A1.3, figure S1.5). Again though, as in analyses including habitat and topographical diversity, the relative magnitudes of standardized regression coefficients show that area is the main driver of diversity within regions.

We expect energy to affect SARs through both diversification rates and diversity limits. First, it could affect speciation rates through faster rates of molecular evolution, with increased metabolic rates in higher-energy regions leading to both shorter generation times and higher

mutation rates (Bromham, in press; Rohde, 1992). There has been mixed evidence for this molecular rate hypothesis, with particularly weak support in endotherms (Cardillo *et al.*, 2005) and no support in angiosperms (although a direct effect of energy on species richness is supported: Davies *et al.*, 2004). However, Gillman *et al.* (2009) recently presented evidence for higher rates of microevolution in tropical mammals and explained this as an indirect consequence of more rapid co-evolution with other tropical ectotherms (see also Fischer, 1960; Schemske, 2002). Energy is also expected to increase diversification rates through effects on population dynamics, as aseasonal and elevated productive energy can support larger populations, resulting in increased speciation and reduced extinction, as described above (and see Davies *et al.*, in press). Such an aseasonal and high-energy environment will also increase the equilibrium diversity limit by increasing resource availability, facilitating specialisation to very narrow niches, and thus increasing the number of distinct niches available (Janzen, 1967). Conversely, seasonal habitats in temperate regions may select for more motile, generalist species. These traits should decrease both speciation rate and the number of species that can be supported in a region (Dynesius & Jansson, 2000; Sheldon, 1996). Although not attempted here, incorporating ecological covariates into our diversification models could lend insight into the effects of, for example, energy availability on the diversification trajectory of clades in different regions (Vamosi & Vamosi, 2010).

Section 4: Clade traits modulating the species-area relationship

So far our framework has considered species richness within a region as an outcome of solely environmental and geographic influences, taking a neutral view of the organisms themselves (MacArthur & Wilson, 1967). However, there is abundant research (reviewed in Coyne & Orr, 2004) indicating that species traits affect clade diversity. Any clade traits that affect diversity

will give rise to clade-specific SARs, and create scatter around SARs that aggregate species richness across multiple clades. The effects of clade traits on SARs are reflected in the clear differences between mammalian orders in the scaling of species richness with area: order-specific slopes vary between -1.71 to 0.59 with medians of 0.16 for clustered regions and 0.11 for geopolitical regions (table S1.2; because regions are not nested, negative slopes arise simply where orders have high diversity in small regions).

According to our general model, clade traits can modulate SARs by modifying the net rate of diversification (figure A1.1a) and/or the diversity limit (figure A1.1b). It is not straightforward to assign traits to one of these mechanisms. Firstly, data are lacking: studies analysing differences between clades in diversification (reviewed in: Jablonski, 2008b; Rabosky & McCune, 2010) have not discriminated between effects on diversification rate and effects on diversity limits (but see Vamosi & Vamosi, 2010), and studies of diversification slowdowns in phylogenies (e.g., Phillimore & Price, 2008) have not investigated the influence of species' traits. Secondly, individual traits are unlikely to act solely through modification of either diversification rates or diversity limits (Mallet, submitted). Finally, many clade traits are strongly correlated (e.g., geographic range size, dispersal distance and body size: Jablonski, 2008b; Jones *et al.*, 2009) and so any traits acting through one mechanism are likely to be associated with traits acting through the other. Below, we discuss traits expected to influence SARs, with particular emphasis on those that affect species' use of space.

While most traits are likely to influence both diversification rates and diversity limits, life history traits are perhaps the only class of traits expected to influence only diversification rate.

Typically, *r* selected species exhibit higher net rates of diversification than *K* selected species, and several mechanisms have been proposed to explain this (Bromham, in press; Marzluff &

Dial, 1991; Mayhew, 2007). Short generation times are associated with high rates of population increase and the ability to rapidly exploit favourable conditions (Mayhew, 2007), conferring resilience to disturbance and leading to lower rates of extinction. They are also associated with increased rates of evolution due to shorter nucleotide generation times (Bromham, in press; Martin & Palumbi, 1993; Mittelbach *et al.*, 2007), higher metabolic rates (Bromham, in press; Martin & Palumbi, 1993), larger population sizes and increased fecundity (Bromham, in press), in all cases leading to higher rates of speciation. In addition, the larger population sizes associated with *r* selection should directly increase speciation rates and decrease extinction rates, as discussed in Section 2.

Clade traits that determine how space is occupied within a region also affect both the generation and maintenance of SARs. Larger species' ranges are associated with lower clade diversity limits as well as reduced rates of extinction (e.g., Jablonski, 2008a; Payne & Finnegan, 2007), and increased rates of speciation (Phillimore *et al.*, 2006, but see Jablonski & Roy, 2003). Regarding diversity limits, there is evidence from both mammals (Orme *et al.* in prep) and birds (Phillimore *et al.*, 2008) that increasing species' range overlap is a stronger predictor of increased species richness than decreased median range size.

Similarly to species' range size, several aspects of narrow niche breadth, such as ecological specialisation, high host specificity and narrow environmental tolerances, have been associated with increased diversity limits as well as increased rates of extinction and speciation (Davies *et al.*, in press; Jablonski, 2008b). Increased clade diversity is also associated with greater niche overlap rather than decreased niche breadth (see also Safi *et al.*, in press). Ricklefs (2009) has shown that South American bird families of varying species richness do not differ in the average number of habitats occupied by species, suggesting that niche overlap between species increases

as family size increases. We find the same in mammals, using simple measures of the number of habitats used by species. There is no significant correlation between the richness of mammalian families and either the average total number of habitats occupied ($\tau = -0.076$, $p=0.21$) or the average number of major habitats occupied ($\tau = -0.043$, $p=0.49$) nor is there a decrease in mean species range size with increasing family richness ($\tau=-0.001$, $p=0.99$).

Finally, increased dispersal ability has been found to reduce speciation and extinction rates in some cases (Xiang *et al.*, 2004), while in others it has been shown to increase diversification rate (Phillimore *et al.*, 2006; Phillimore & Price, 2009). With respect to diversity limits, high dispersal ability may lead to low equilibrium diversity within a region if it leads to clades consisting of few species with large ranges (Davies *et al.*, in press). At the other extreme, strong philopatry, where individuals retain or return to natal locations, might both increase rates of diversification by accelerating rates of genetic differentiation (Peterson, 1992) and increase equilibrium diversity by impeding range expansion and boosting the number of equivalent species that can persist in a region (Seehausen, 2006; Shmida & Wilson, 1985). Alternatively, high dispersal ability can increase the rate at which new regions are occupied, increasing clade richness through occupation of multiple regions. Such long-distance dispersal may significantly distort SARs if newly colonised regions harbour clades with higher diversity due to competitive release (Purvis *et al.*, in press).

Section 5: Historical and temporal effects on the species area relationship

In general, diversification in any region is influenced by the climatic, geological, and biogeographical history of the region (Esselstyn *et al.*, 2009; Purvis *et al.*, in press; Springer *et al.*, in press), and as a result, SARs should be affected by history as well. SARs will be clearest

when clades have reached equilibrium throughout their ranges, but this requires that they have had enough time to diversify to their limit in each region that they occupy. Thus, in parts of the world where the current habitat has only recently become available, current diversity is likely to be lower than expected (e.g., a recently-formed island, Esselstyn *et al.*, 2009, or a recently deglaciated region, Davies *et al.*, in press; Pielou, 1979) and may be biased toward large-ranged generalists (Davies *et al.*, in press; Dynesius & Jansson, 2000; Safi *et al.*, in press). In contrast, a comparison of mammalian sister taxon pairs with disjunct distributions across two realms indicated that sisters remaining in the realm unambiguously reconstructed as ancestral (DIVA: Ronquist, 1997) are significantly less species rich (12 out of 41, binomial $p = 0.004$ table S1.3) than sisters that dispersed. This suggests a diversification burst in newly colonized regions, driven by competitive release (more in Purvis *et al.*, in press). Finally, if a region is subject to frequent extrinsic perturbations (such as an archipelago subject to repeated sea-level changes), fluctuating extinction rates make it unlikely that equilibrium diversity will ever be reached or maintained (Esselstyn *et al.*, 2009; Whittaker *et al.*, 2008). Indeed, explanations for high tropical diversity, such as the time-for-speciation effect (Stephens & Wiens, 2003) and reduced extinction due to long-term climatic stability (Fischer, 1960), are compatible with tropical regions being able to more closely approach diversity limits (more in Davies *et al.*, in press).

Diversity may also transiently over- or under-shoot the diversity limit of a region if speciation or extinction occurs very rapidly, or if perturbations occur that suddenly alter clade diversity limits (Gavrilets & Vose, 2005). Alternatively, non-ecological modes of speciation (e.g., via sexual selection or polyploidy), may produce transient species that are unable to persist in the long-term given the niche space available, and thus are committed to eventual extinction (Chesson, 2000; McPeck, 2008; Rosenzweig, 1995). This may also apply to ecologically equivalent species

formed in allopatry, if the barriers separating them are themselves transient. Transient dynamics are now thought to be crucial in predicting biodiversity responses to current global change (recently reviewed in Jackson & Sax, 2010); though the changes will likely not be as immediately apparent as for ecological processes such as community assembly, evolutionary clade dynamics will certainly be affected as well (Rosenzweig, 2001).

Conclusions

We have presented a framework, based on a diversity-dependent model of clade diversification, for understanding how evolutionary processes contribute to the creation of large-scale SARs. This framework is supported by analyses on mammals using data from the PanTHERIA database (Jones *et al.*, 2009). SARs themselves result from direct and positive effects of area on diversification rates and diversity limits, as well as indirect effects of area through population size, habitat diversity, and habitat fragmentation. We found that these effects are apparent in the histories of mammal diversification – clades occupying larger areas had higher initial diversification rates and lower rates of decline in diversification. We also confirmed that habitat and topographical diversity are significant predictors of regional diversity in mammals, but found that neither is a proxy for area - the most predictive models of diversity always include area as well. Environmental factors and clade traits that are not tightly correlated with area also cause systematic differences in SARs between clades or regions, and cause scatter around any general SAR generated without accounting for them. We tested the influence of energy availability on mammal diversity and showed that high energy availability significantly increases the slopes and intercepts of SARs. In addition, mammal orders vary greatly in the slopes of their SARs. Finally, we provide evidence that historical contingencies impact SARs, demonstrating

that mammal clades able to colonize new, competitor-free regions are more diverse than their stay-at-home sisters.

Schoener (1976) referred to the species-area relationship as the phenomenon closest to attaining rule status in ecology, and SARs are indeed one of the most general diversity patterns, existing for a wide range of organisms across a range of spatial scales. However, we argue here that in addition to the processes most discussed in the ecological literature – immigration, local extinction and species coexistence - SARs are also influenced by macroevolutionary processes, in particular speciation and global extinction. None of these processes operates in isolation, and every SAR is the result of interplay between both ecological and evolutionary processes.

Diversity limits, for instance, must ultimately result from ecological limits on the number of species that can coexist in a region, though the speed at which they are reached may depend on evolutionary processes. We suggest that a full understanding of species-area relationships will require integrating both ecological and evolutionary perspectives on the processes that generate and constrain diversity.

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Tables

Table A1.1. Summary of factors affecting diversification rates and diversity limits.

Type of factor	Factor	Effects on speciation rate	Effects on extinction rate	Effects on diversity limits
	<i>Area</i>	↑ potential for geographic isolation of separated populations	↓ by ↑ survival of refuge populations	
Environmental factors strongly correlated with area	<i>Population Size</i>	↑ rate of appearance of beneficial mutations, standing genetic variation, persistence of incipient species	↓ by buffering populations from demographic stochasticity, environmental disasters, habitat loss	↑ number of species with viable populations supported
	<i>Habitat Diversity</i>	↑ population divergence through local adaptation		↑ niche space available
	<i>Fragmentation / Topographic Diversity</i>	↑ isolation of populations; however past a certain point, will ↓ speciation by ↓ population size	if fragmentation results in too small patches of area or habitat, will ↑ extinction rate	↑ by allowing more ecologically equivalent species to be supported
Environmental factors <i>not</i> strongly correlated with area	<i>Energy availability</i>	↑ rate of molecular evolution, rate of co-evolutionary dynamics, size of populations supported		↑ by facilitating specialization to narrow niches
Clade traits	<i>Life history traits</i>	faster life cycle ↑ speciation by increasing mutation rate	faster life cycle ↓ extinction by ↑ resilience to disturbance	
	<i>Range size</i>	larger range sizes ↑ speciation by ↑ potential for isolation of populations	larger range sizes ↓ extinction by ↑ survival of refuge populations	smaller range sizes ↑ diversity limit by allowing more species to pack into same area
	<i>Niche breadth</i>	narrower niche breadths associated with ↑ speciation	narrower niche breadths associated with ↑ extinction	narrower niche breadths ↑ diversity limit by allowing finer subdivision of niche space
	<i>Dispersal</i>	↓ by reducing potential isolation of populations, but can also ↑ speciation rate by ↑ rate at which species colonize new regions	↓ by ↑ resilience to disturbance	↓ if high dispersal ability is associated with large, non-overlapping species ranges

Table A1.2. Summary of diversification models fitted to mammalian clades. Models were fit using TDWG Level 4 data to calculate present clade distribution area, for clades with crown ages younger than (a) 20 or (b) 10 million years before present. Six models of diversification were fitted representing: (1) constant rate, (2) constant rate scaled by region area, (3) exponential decline, and exponential decline with region area scaling (4) initial rate, (5) rate of decline or (6) both. In each case, the maximum likelihood estimate of the model is reported for each free parameter within the bounds shown. Dashed parameter estimates were fixed at zero. The overall best-fit model for each set of clades is shown in bold.

	lambda [-1,1]	c [-0.2,0.2]	z [-0.2,0.2]	p [-0.2,0.2]	epsilon [0.5,0.999]	Δ AICc	likelihood
a) 20 MY							
1	0.340	---	---	---	0.990	222.4	-1410.0
2	-0.300	0.040	---	---	0.990	136.8	-1366.2
3	0.790	---	-0.030	---	0.990	187.2	-1391.4
4	-0.300	0.040	-0.030	---	0.610	53.1	-1323.3
5	0.474	---	-0.138	0.007	0.814	19.1	-1306.3
6	-0.260	0.040	-0.100	0.004	0.610	0.0	-1295.8
b) 10 MY							
1	0.265	---	---	---	0.999	164.2	-1578.3
2	-0.223	0.030	---	---	0.990	93.4	-1541.9
3	0.530	---	-0.043	---	0.999	110.6	-1550.5
4	-0.193	0.031	-0.043	---	0.520	30.0	-1509.1
5	0.377	---	-0.232	0.012	0.711	0.0	-1494.1
6	-0.064	0.023	-0.120	0.005	0.500	1.16	-1493.7

Table A1.3. Multivariate SARs, with mammal species richness regressed against area and other environmental variables.

	a) geopolitical regions			b) biotic regions		
	estimate	SE		estimate	SE	
a) n	580			150		
intercept	1.7419	0.0186	***	1.2670	0.0342	***
habitat diversity	0.0234	0.0194		-0.0649	0.0340	
log area	0.3407	0.0203	***	0.7608	0.0352	***
interaction	0.0410	0.0152	**	-0.0340	0.0325	
b) n	578			200		
intercept	1.6810	0.0202	***	1.0211	0.0391	***
log elevation range	0.0533	0.0297		0.2383	0.0573	***
log area	0.3956	0.0237	***	0.5869	0.0478	***
Interaction	0.1114	0.0162	***	0.1923	0.0343	***
c) n	477			130		
intercept	1.8201	0.0160	***	1.0802	0.0496	***
NDVI	0.0142	0.0174		0.1947	0.0521	***
log area	0.3075	0.0218	***	0.8997	0.0536	***
interaction	0.1007	0.0218	***	-0.0442	0.0550	
d) n	525			196		
intercept	1.7463	0.0158	***	1.1339	0.0343	***
temperature	0.0577	0.0168	***	0.2750	0.0407	***
log area	0.4110	0.0201	***	0.8411	0.0341	***
interaction	0.0979	0.0179	***	-0.0545	0.0432	

In addition to area, models included (a) habitat diversity, (b) log range in elevation, (c) mean annual temperature and (d) mean NDVI. The models were fitted to log 10 species richness within both geopolitical and biotic regions and the explanatory covariates in all models were centred and standardized to facilitate model comparison. The statistical significance of each parameter is given (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$), as well as the number of regions with available data (n) for each model.

Figures

Figure A1.1. Variation in patterns of clade diversification from a) initial rate of diversification, b) equilibrium diversity, c) clade age and d) reinforcing (solid grey) and opposing (dashed grey) combinations of rate and equilibrium diversity. Sampling clade diversity at the time specified by the vertical line demonstrates the variation possible.

Figure A1.2. Development of the species area relationship. a) The development of a species area relationship (SAR) across three regions (X, Y, Z), in which both initial rate of diversification and equilibrium diversity increase with area. b) The resulting SAR across regions exhibits power law scaling both before (dashed line) and after (solid line) the regions have reached equilibrium diversity. It is important to discriminate between the clade diversification curves (a) and SARs (b); each region will follow a particular diversification trajectory but contributes a single point to the SAR.

Figure A1.3. Species area relationships in mammals across scales. a) Slopes and their standard errors of species area relationships (SARs) for 4560 terrestrial mammals at four different scales across geopolitical regions (T 1-4) and biotic regions (C 1-4). b) Distribution of power law exponents from mammalian SARs showing the range of non-nested region sizes considered (grey lines – data from Drakare *et al.* (2006); black lines – values from panel above). Scatterplots show the distribution and least squares fit of SARs for T4 (c) and C4 (d) for total (black) and endemic species richness (grey). See also table S1.1 and figures S1.3-4.

Figure A1.1

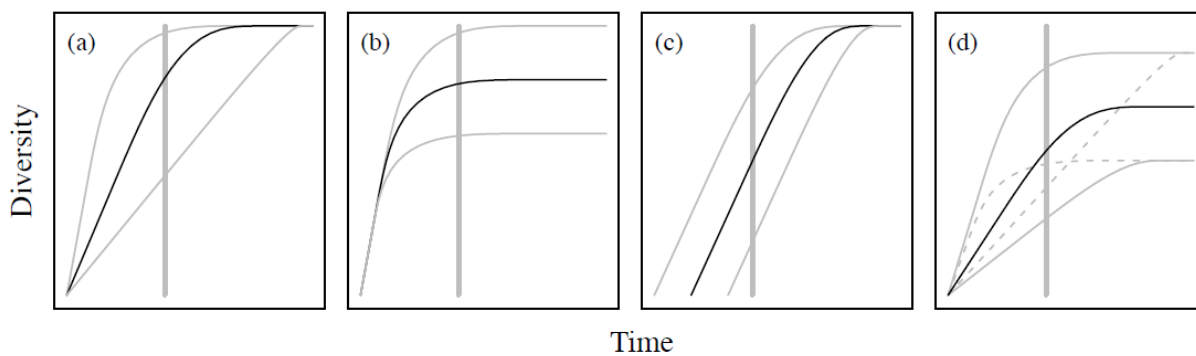


Figure A1.2.

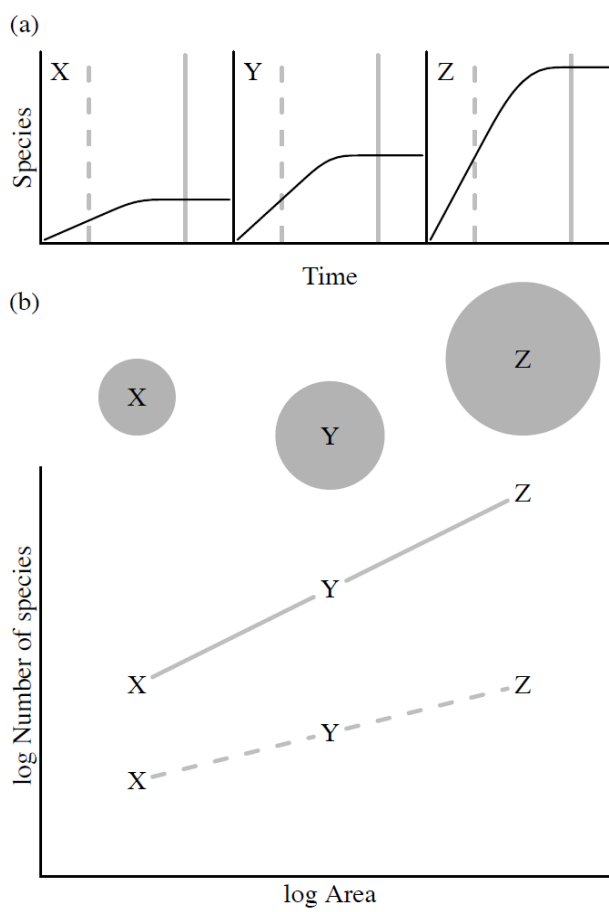


Figure A1.3

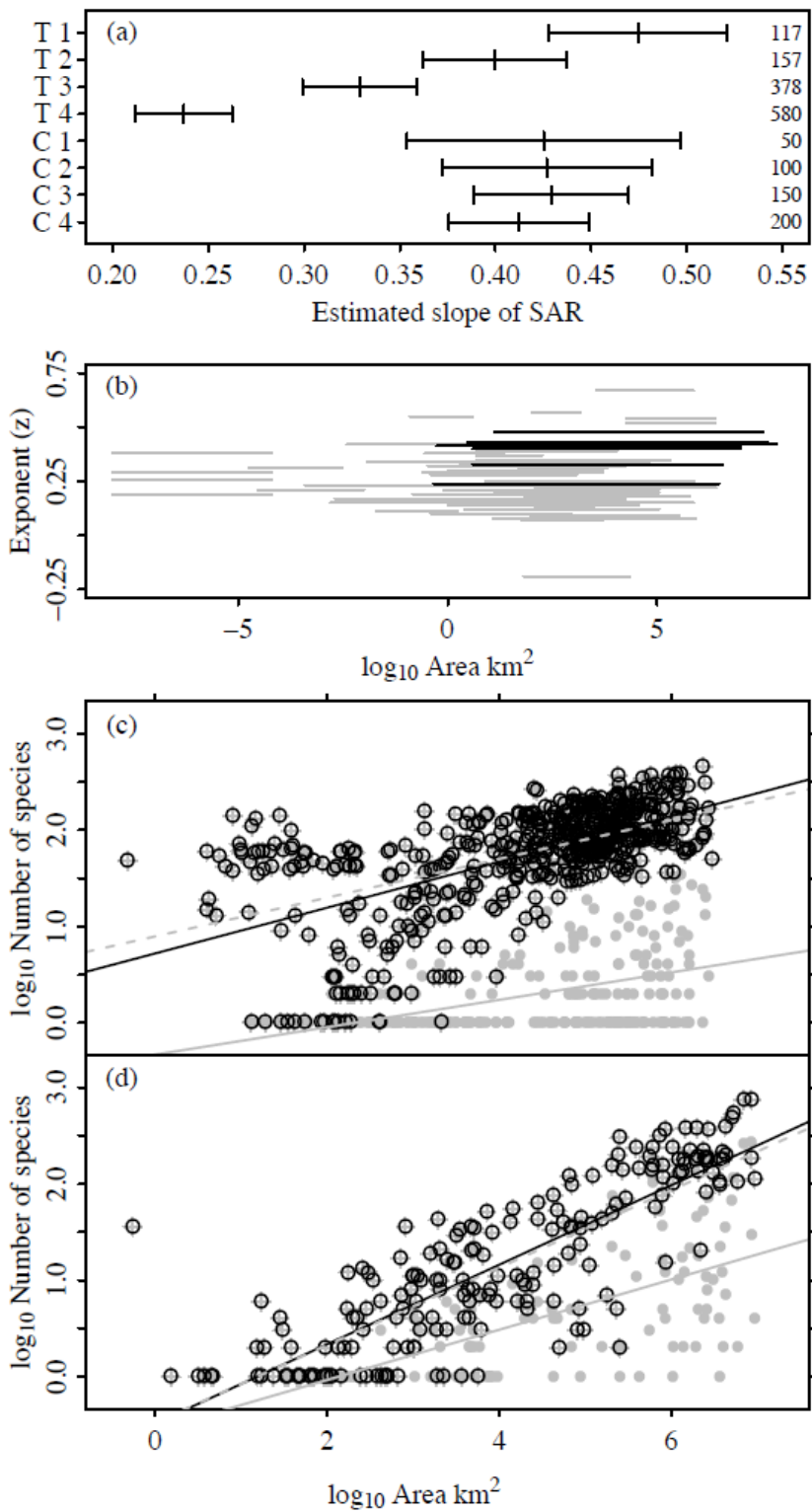


Table S1.2. Slopes of SARs for mammalian orders for both (a) geopolitical and (b) biotic regions.

	a) TDWG		N	b) Clustering		
	Slope	SE		Slope	SE	N
Afrosoricida	-0.015	0.077	37	-0.733	0.382	5
Artiodactyla	0.112	0.013	482	0.304	0.033	79
Carnivora	0.106	0.009	498	0.304	0.027	92
Chiroptera	0.131	0.014	557	0.285	0.021	167
Cingulata	0.183	0.040	129	0.111	0.068	18
Dasyuromorphia	0.311	0.047	11	0.372	0.057	15
Dermoptera	0.000	0.000	16	0.000	0.000	7
Didelphimorphia	0.127	0.031	160	0.091	0.066	19
Diprotodontia	0.302	0.058	26	0.334	0.046	31
Erinaceomorpha	0.035	0.010	199	0.115	0.071	30
Hyracoidea	-0.006	0.021	72	0.130	0.067	9
Lagomorpha	0.079	0.010	416	0.175	0.042	57
Macroscelidea	0.053	0.028	39	-0.685	0.681	5
Microbiotheria	0.000	0.000	5	0.000	0.000	3
Monotremata	0.001	0.049	12	0.096	0.069	12
Notoryctemorphia	0.623	0.546	3	0.396	0.268	4
Paucituberculata	0.099	0.203	5	0.388	0.067	4
Peramelemorphia	0.174	0.035	17	0.127	0.054	18
Perissodactyla	0.022	0.020	142	0.240	0.074	30
Pholidota	0.037	0.011	132	0.079	0.030	23
Pilosa	0.212	0.032	70	0.041	0.042	9
Primates	0.120	0.023	230	0.217	0.043	51
Proboscidea	0.075	0.018	73	0.182	0.079	11
Rodentia	0.209	0.011	547	0.403	0.025	132
Scandentia	0.036	0.023	63	0.038	0.040	24
Soricomorpha	0.111	0.013	406	0.274	0.033	65
Tubulidentata	0.000	0.000	53	0.000	0.000	6

Table S1.3. Dispersal analysis. Sister clade pairs identified using DIVA that show unambiguous reconstructed ancestral ranges and where one sister clade retains that ancestral range and the other occupies a differing new range. Italicized rows show clades with higher species richness in the new range.

Family	Mammal Tree		Species in		
	Node	Ancestral Area	New Area	Ancestral Area	Species in New Area
<i>Bovidae</i>	-1008	<i>IndoMalay</i>	<i>Nearctic, Palearctic</i>	1	2
<i>Bovidae</i>	-940	<i>Afrotropics</i>	<i>Palearctic</i>	12	22
<i>Bovidae</i>	-973	<i>Afrotropics</i>	<i>Palearctic</i>	4	3
<i>Canidae</i>	-1217	<i>Palearctic</i>	<i>Neotropics</i>	1	9
<i>Canidae</i>	-1225	<i>Palearctic</i>	<i>Afrotropics</i>	9	1
<i>Canidae</i>	-1226	<i>Palearctic</i>	<i>Nearctic</i>	9	2
<i>Cercopethicidae</i>	-780	<i>Afrotropics</i>	<i>IndoMalay</i>	8	11
<i>Cercopethicidae</i>	-790	<i>IndoMalay</i>	<i>Australasia</i>	2	4
<i>Cercopethicidae</i>	-801	<i>Afrotropics</i>	<i>IndoMalay</i>	9	23
<i>Cervidae</i>	-1029	<i>Palearctic</i>	<i>Neotropics</i>	1	14
<i>Cervidae</i>	-1023	<i>Palearctic</i>	<i>IndoMalay</i>	5	18
<i>Emballonuridae</i>	-1429	<i>Australasia</i>	<i>Neotropics</i>	7	18
<i>Emballonuridae</i>	-1417	<i>Australasia</i>	<i>Afrotropics</i>	7	2
<i>Equidae</i>	-1116	<i>Palearctic</i>	<i>Afrotropics</i>	2	3
<i>Erinaceidae</i>	-1788	<i>Palearctic</i>	<i>IndoMalay</i>	11	6
<i>Heteromyidae</i>	-891	<i>Nearctic</i>	<i>Neotropics</i>	4	31
<i>Leporidae</i>	-878	<i>Afrotropics</i>	<i>Nearctic</i>	6	15
<i>Loridae</i>	-909	<i>Afrotropics</i>	<i>IndoMalay</i>	3	3
<i>Manidae</i>	-1328	<i>Afrotropics</i>	<i>IndoMalay</i>	3	4
<i>Molossidae</i>	-1513	<i>Afrotropics</i>	<i>Neotropics</i>	2	3
<i>Molossidae</i>	-1524	<i>Neotropics</i>	<i>IndoMalay</i>	15	4
<i>Molossidae</i>	-1538	<i>Neotropics</i>	<i>Afrotropics</i>	15	22
<i>Muridae</i>	-68	<i>IndoMalay</i>	<i>Palearctic</i>	2	20
<i>Muridae</i>	-881	<i>Afrotropics</i>	<i>IndoMalay</i>	11	4
<i>Mustelidae</i>	-1138	<i>Palearctic</i>	<i>Neotropics</i>	3	2
<i>Mustelidae</i>	-1159	<i>IndoMalay</i>	<i>Neotropics</i>	2	3
<i>Mustelidae</i>	-1164	<i>IndoMalay</i>	<i>Afrotropics</i>	1	2
<i>Mustelidae</i>	-1166	<i>IndoMalay</i>	<i>Neotropics</i>	4	8
<i>Myoxidae</i>	-670	<i>Palearctic</i>	<i>Afrotropics</i>	2	14
<i>Ochotonidae</i>	-783	<i>Palearctic</i>	<i>Nearctic</i>	2	2
<i>Pteropodidae</i>	-1342	<i>Australasia</i>	<i>IndoMalay</i>	14	21
<i>Pteropodidae</i>	-1357	<i>Australasia</i>	<i>Afrotropics</i>	60	28
<i>Rhinolophidae</i>	-1474	<i>IndoMalay</i>	<i>Australasia</i>	3	14
<i>Rhinolophidae</i>	-1476	<i>Australasia</i>	<i>Afrotropics</i>	1	2
<i>Rhinolophidae</i>	-1491	<i>Afrotropics</i>	<i>Australasia</i>	2	5
<i>Sciuridae</i>	-503	<i>Nearctic</i>	<i>Palearctic</i>	2	11
<i>Sciuridae</i>	-617	<i>IndoMalay</i>	<i>Nearctic</i>	4	2
<i>Tapiridae</i>	-1111	<i>IndoMalay</i>	<i>Neotropics</i>	1	3
<i>Vespertilionidae</i>	-1631	<i>IndoMalay</i>	<i>Palearctic</i>	5	7
<i>Viverridae</i>	-1310	<i>Afrotropics</i>	<i>IndoMalay</i>	1	2
<i>Viverridae</i>	-1312	<i>Afrotropics</i>	<i>IndoMalay</i>	1	5

Figures

Figure S1.1. Geographic distributions of biotic clusters defined by between-cell Jaccard distances (a – 50, b – 100, c – 150 and d – 200 clusters).

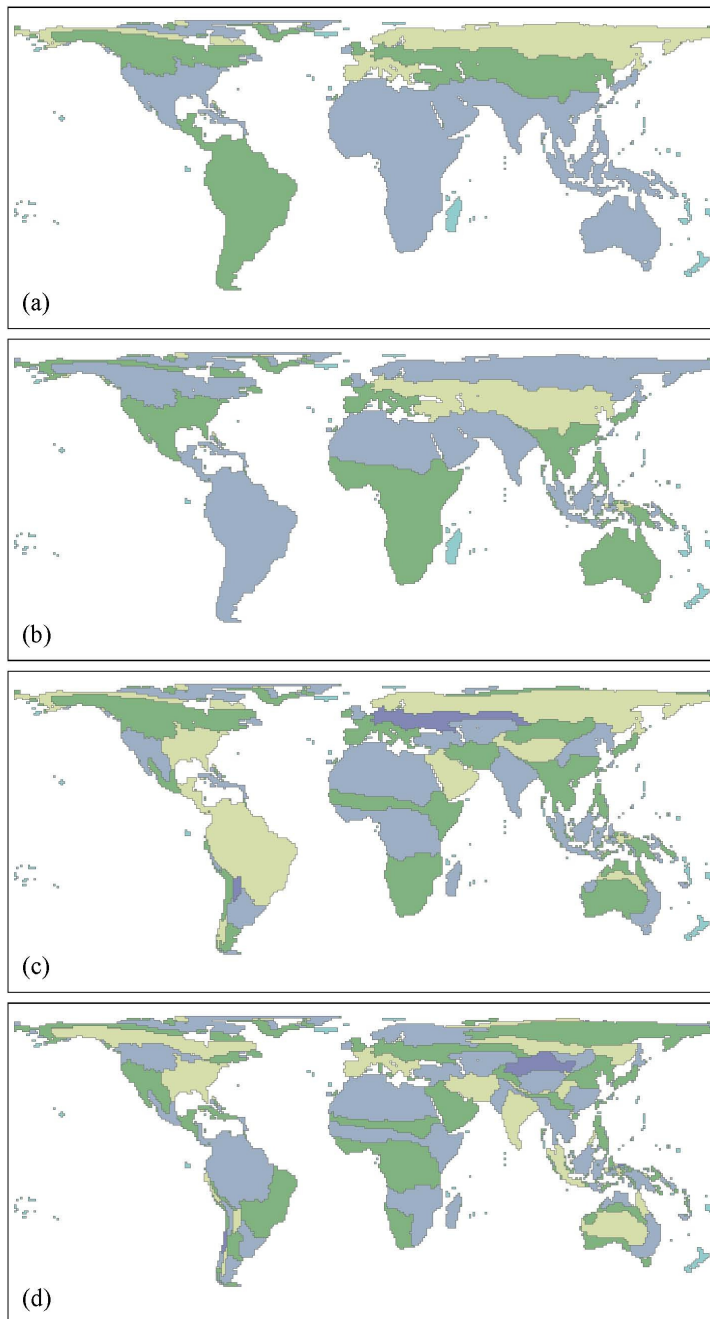


Figure S1.2. Size distributions of geopolitical (TDWG) and clustered biotic regions used to measure species-area relationships.

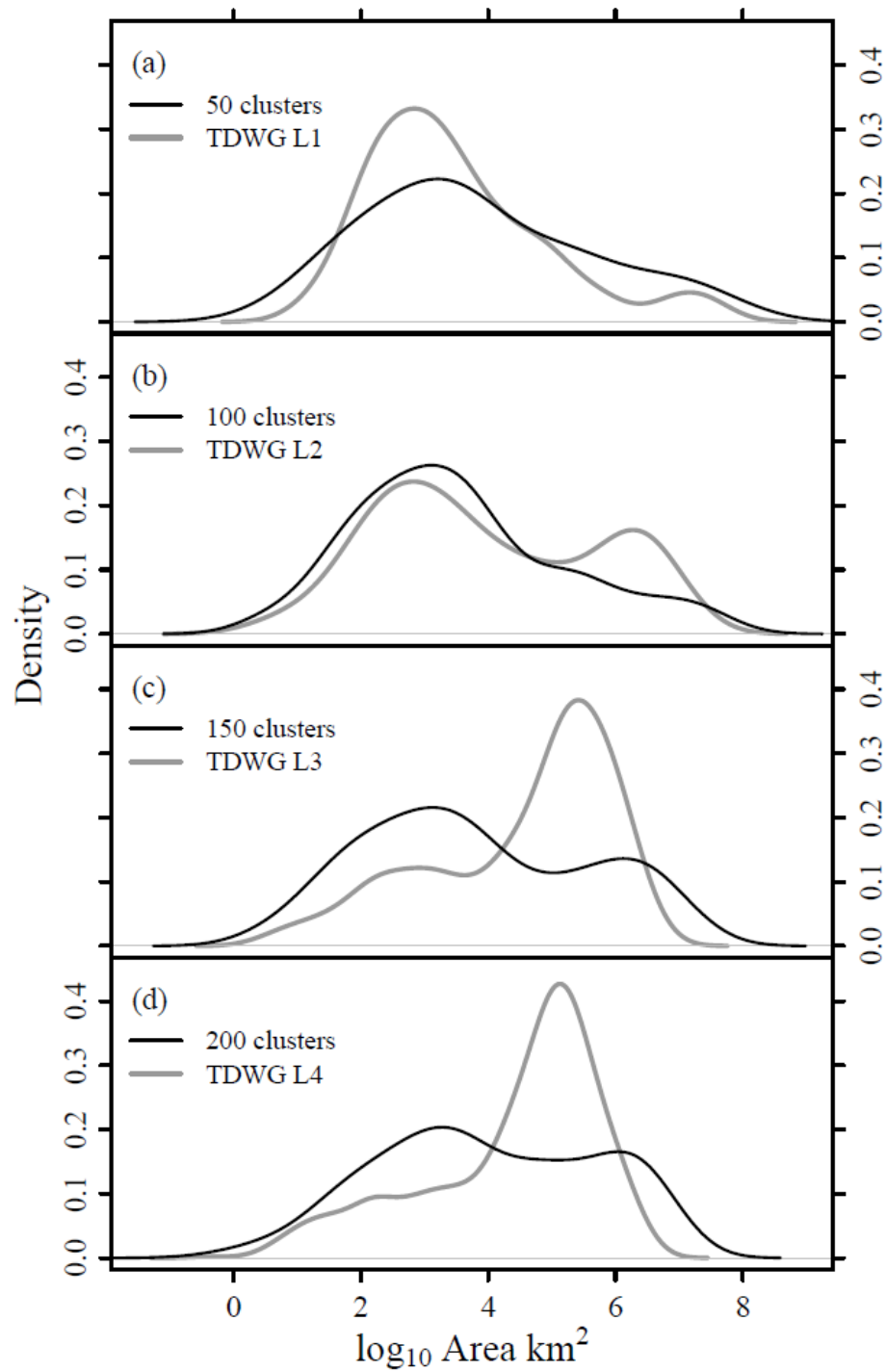


Figure S1.3. Species-area relationships for geopolitical regions at four spatial scales from TDWG

Level 1 (a) to TDWG Level 4 (d) for all (black circles and line, S_A), widespread (grey crosses and dashed grey line, S_W) and endemic (grey dots and grey solid line, S_E) species in each region.

See also table S1.1.

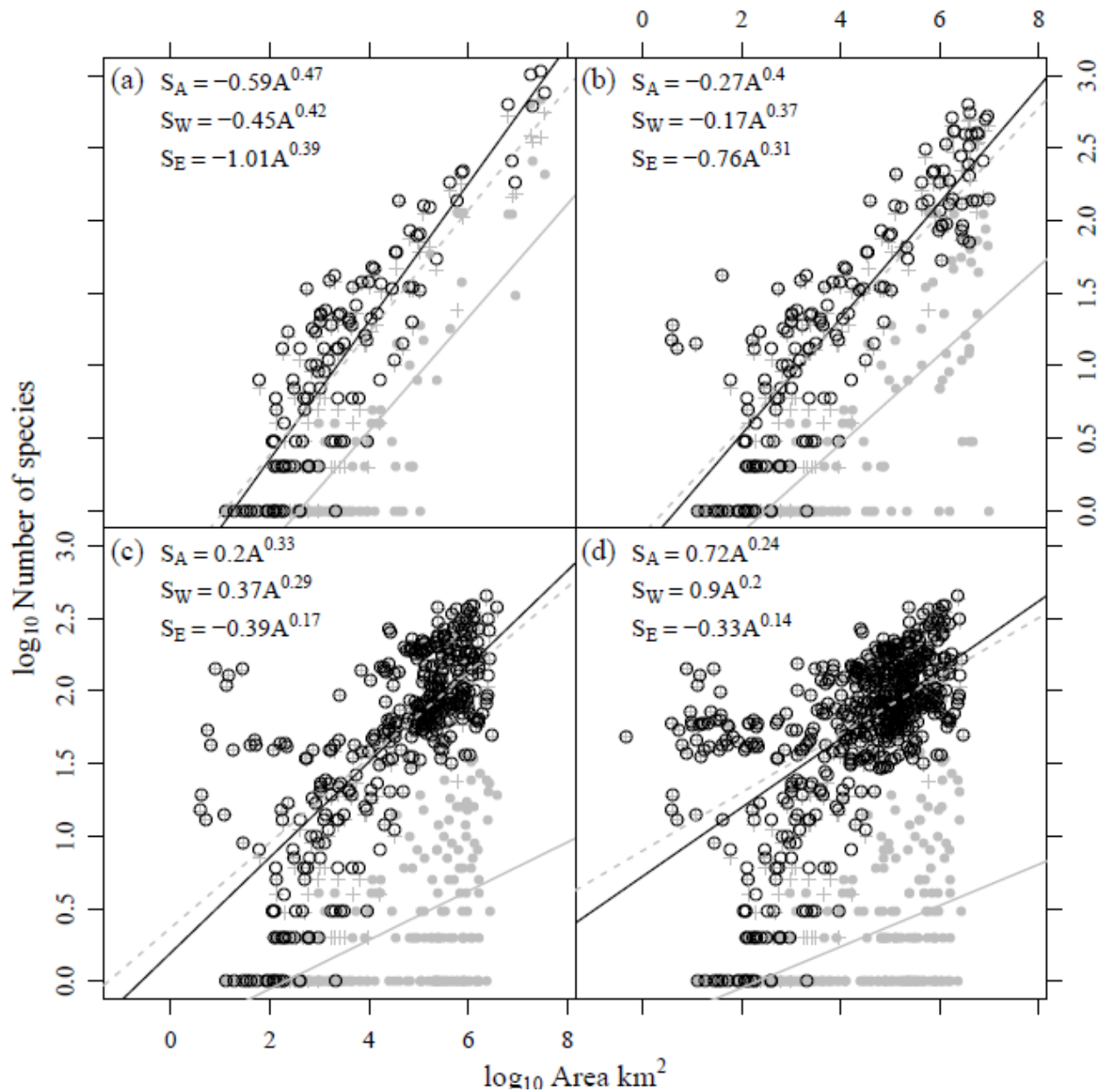


Figure S1.4. Species-area relationships for clustered biotic regions at four spatial scales from 50 (a) to 200 (d) clusters for all (black circles and line, S_A), widespread (grey crosses and dashed grey line, S_W) and endemic (grey dots and grey solid line, S_E) species in each region. See also table S1.1.

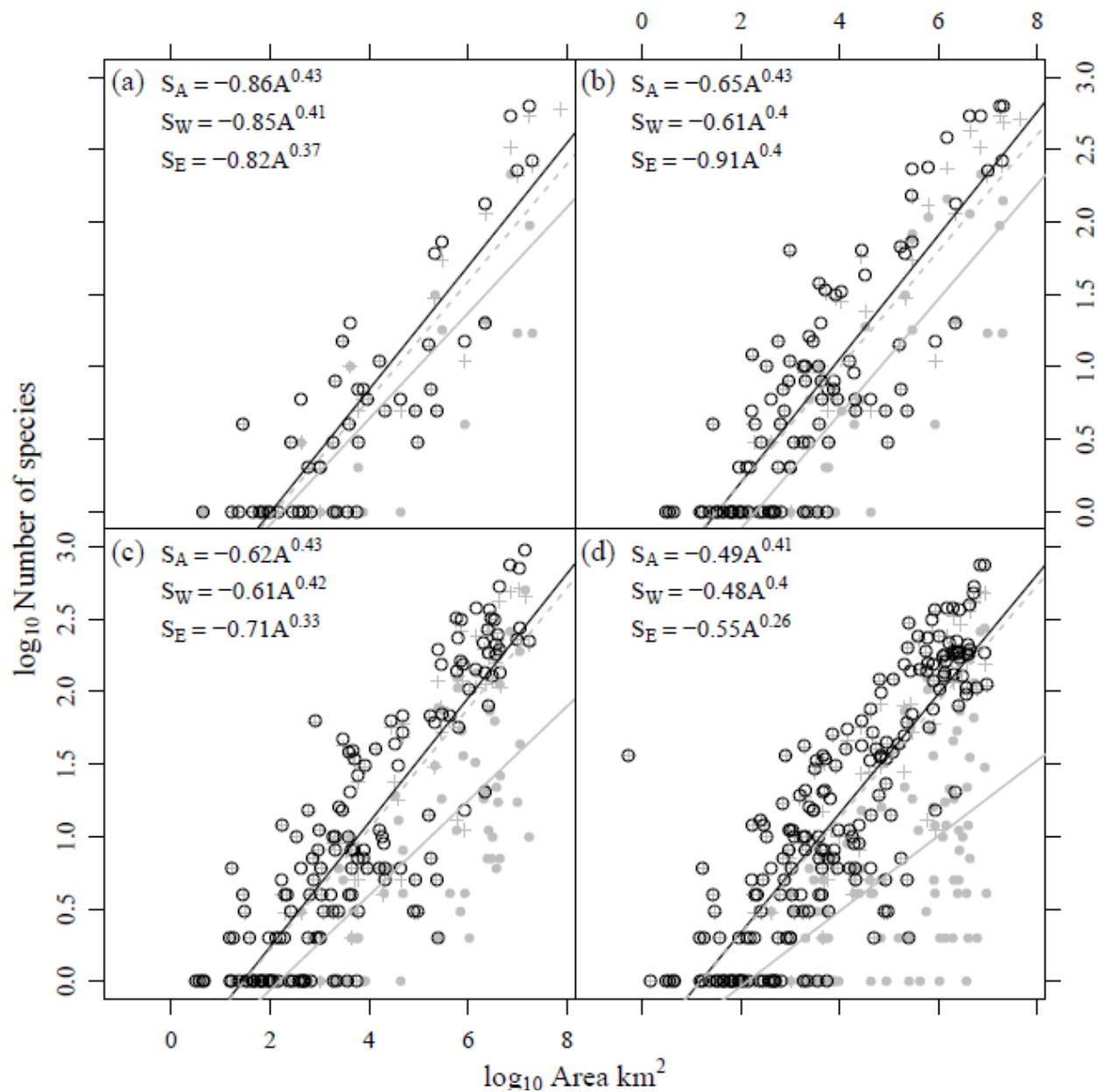
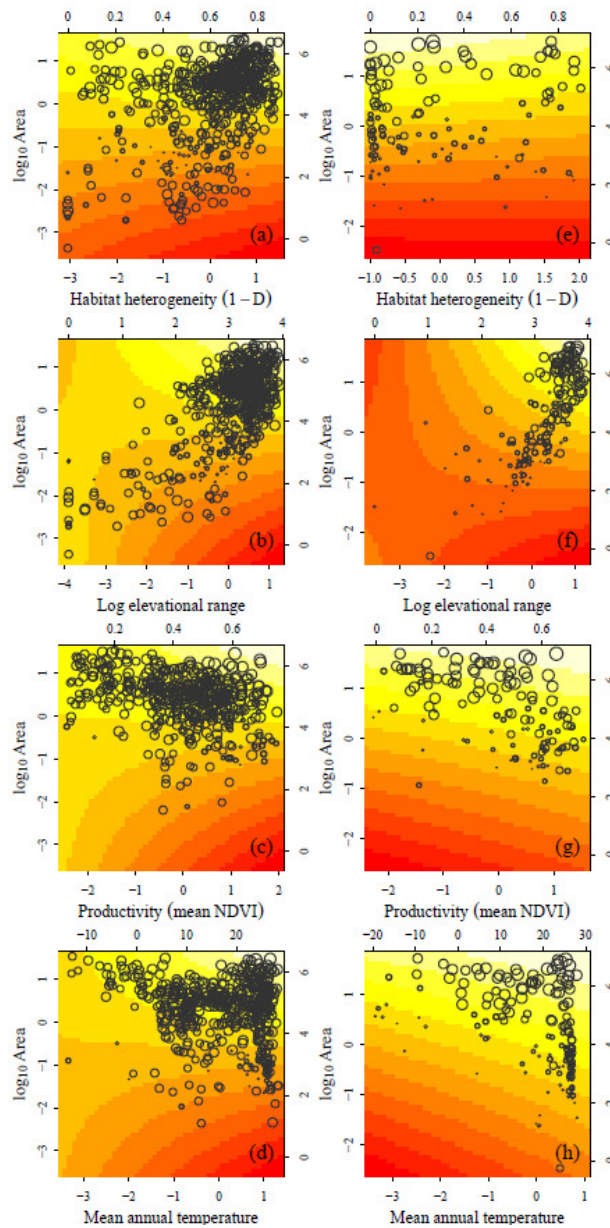


Figure S1.5. Prediction surfaces from models of log species richness. Four variables (Simpson's diversity index in habitat diversity, log elevational range, mean NDVI and mean temperature) with regions were fitted in turn as a covariate with regional area with the model including the interaction between each pair. The coloured surface shows the predicted diversity (white – high, red – low) and the relative size of the points show the observed diversity. Model coefficients were estimated using scaled and centred covariates (bottom and left axes) but these plots also show the variables on their original scale (top and right axes).



Appendix 2. Supporting information for chapter 2

Climatic niche conservatism and the evolutionary dynamics in species' range boundaries: global congruence across mammals and amphibians

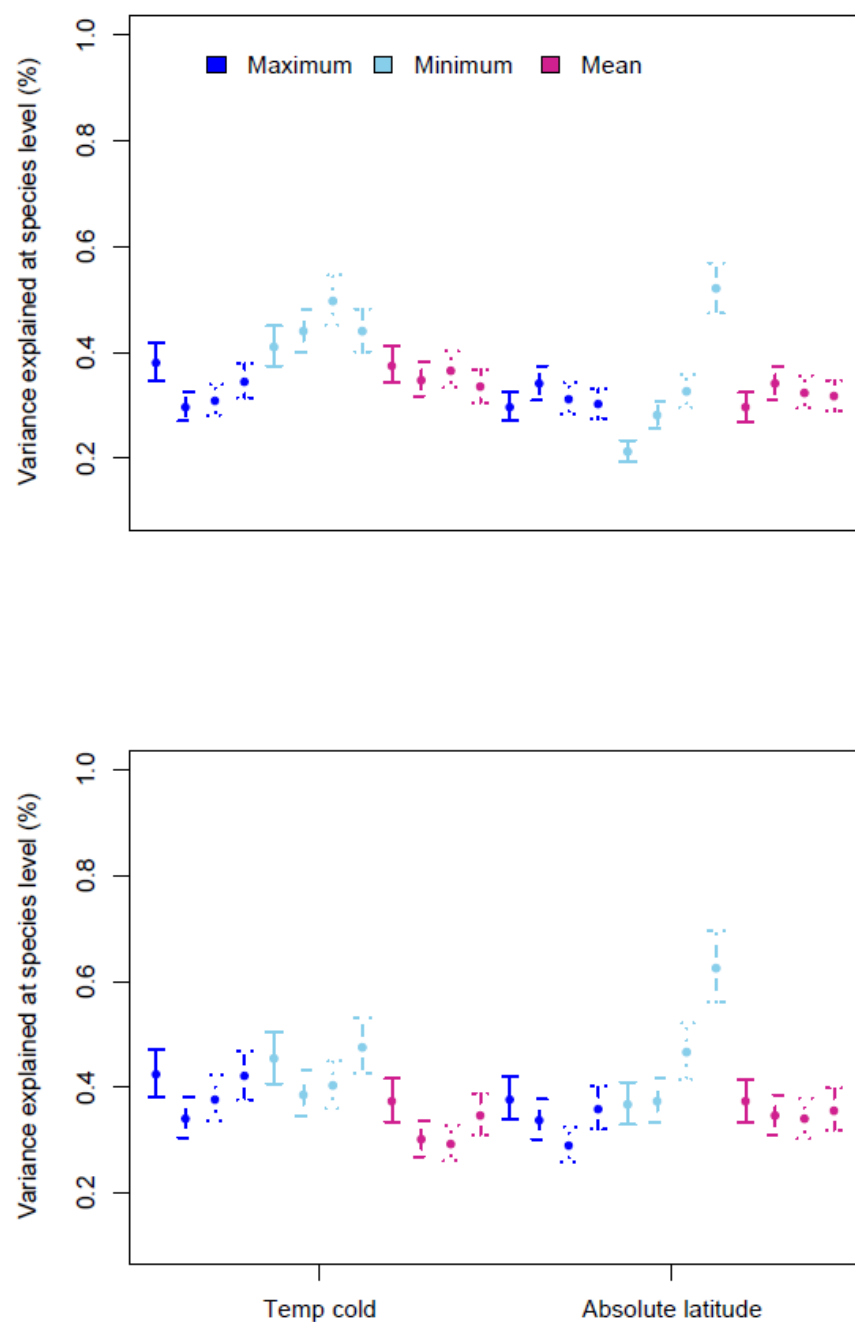
2.1 – Latitude analysis

Mean temperature of the coldest quarter is latitudinally structured ($r = -0.934$, $p < 0.0001$). Thus, we found phylogenetic signal in absolute latitude to be similar in magnitude to the most highly conserved climatic variable in both taxa. We investigated whether latitude and our climatic variables may both be acting as proxies for an as yet unidentified additional variable or suite of variables (Hawkins & Diniz-Filho, 2004). We extracted the first axis of a principal components analysis of the four BioClim variables in our dataset. This component had high loadings for the two temperature components and was highly correlated with latitude. We performed a partial regression to extract the independent contribution of the climatic variables and latitude to PC1. We found that most variation was shared between the two sets of variables but that 22.9% could be independently attributed to climate and 0% to latitude. This reassured us that our results could be interpreted as a real signal of the tolerances in the climatic variables under test. While latitude can be used as a proxy for environmental variation in the absence of the variables themselves (e.g., Roy *et al.*, 2009), we show here that it does not provide any additional information.

2.2 – Range size analysis

The geographic range size for each species was calculated as the number of 0.1° grid cells occupied, and species were divided into range-size quartiles. We extracted approximate 95% confidence intervals for the restricted maximum likelihood variance components estimates and used box plots to assess whether variance explained at each taxonomic level differed among quartiles. We found this was not the case. Thus, our findings on the conservatism of cold tolerance are not driven by differences between narrow- and wide-ranging species, further underlining the robustness of our results. In particular, the confidence intervals on the variance components for mean temperature in the coldest quarter overlapped between the species from the most narrowly distributed and the most widely distributed quartiles in both mammals and amphibians (figure A2.2). This indicates that the strong signals we identify are not driven by a subset of species or by non-physiological dispersal limitations, but rather have a broader basis. Our results also agree with recent studies reporting that even wide-ranging European amphibians are limited by current climate (Araújo *et al.*, 2008) and that, among New World mammals, both widespread and restricted-range species are similarly limited by minimum winter temperatures (Szabo *et al.*, 2009). Our results apparently contradict the expectation that competitive interactions and dispersal lags also contribute to the patterning of range limits in space, as these should differ between narrowly-distributed and wide-ranging species (Jetz & Rahbek, 2002; Szabo *et al.*, 2009).

Figure A2.2. Variance explained at the species level across range-size quartiles (with 95% confidence intervals) for mean temperature of coldest quarter and absolute latitude. Range size increases from left to right for each summary statistic. Top bar: amphibians, bottom bar: mammals.



2.3 – Amphibian phylogeny construction

The amphibian supertree was constructed by hand as a consensus of published molecular phylogenies from many sources. The family backbone followed (Frost *et al.*, 2006) with these updates: their Amphignathodontidae and Cryptobatrachidae were included in Hemiphractidae (Guayasamin *et al.*, 2008; Wiens *et al.*, 2007), so the Nobleobatrachia consist of the newly-defined Hemiphractidae and Meridianura; the Meridianura consist of Athesphatanura and Terrarana (Hedges *et al.*, 2008), which corresponds to Frost *et al.*'s (2006) Brachycephalidae; family relationships within Terrarana follow Hedges *et al.* (2008), those within Leptodactyliformes follow Grant *et al.* (2006). Family relationships within Natatanura follow different sources: Ptychadenidae were placed basally (Bossuyt *et al.*, 2006; Frost *et al.*, 2006; Van Bocxlaer *et al.*, 2006; Wiens *et al.*, 2009); Africanura and Aglaioanura were preserved as valid clades (Bossuyt *et al.*, 2006; Van Bocxlaer *et al.*, 2006); and the Victoranura constituted a polytomy of Africanura, Aglaioanura, Ceratobatrachidae, Micrixalidae, Nyctibatrachidae, and Ranixalidae due to disagreement and low branch support values in the literature (Bossuyt *et al.*, 2006; Van Bocxlaer *et al.*, 2006; Wiens *et al.*, 2009). Within families, we followed a range of published sources for between-genera relationships (Fritz & Rahbek, unpublished manuscript), and species were added on as within-genera polytomies, assuming monophyly of genera.

2.4 – Character-dependent diversification analyses

The best model in character-dependent diversification analyses was one in which the escapee species have a slightly higher speciation rate ($\lambda_1=0.0880$ versus $\lambda_0=0.0759$), but zero extinction rates, identical to non-escapee species (table A2.4). The analysis suggests that escapees have slightly higher speciation rates than non-escapees. However, the analysis also suggested that reversions from escapee to non-escapee are much more rapid (four-fold higher) than initial evolution of escapee status. These differences would be interesting if real, but could arise through either of two artefacts. First, loss of power through the number of terminal polytomies could have led to elevated estimates of reversion rate. Second, escapee status could depend on underlying continuous traits with a threshold; because many escapee species are recent escapees, they will tend to be near the threshold value of the underlying trait and so have high reversion rates, whereas a large proportion of the non-escapee clades would be far from the threshold.

Table A2.4. Comparing character-dependent diversification models. The full model includes six parameters (two speciation rates, two extinction rates, and transition rates between state 0 to 1 and 1 to 0). Escapee species are coded with character state 1. Constrained models are compared to the full model using a likelihood ratio test; p values reported are the results of a χ^2 test. AIC and log likelihoods (LnLik) are also reported. The best model (that with extinction rates constrained to be equal), is highlighted.

Model	n	AIC	LnLik	P
$\lambda_0=0.0759, \lambda_1=0.0879, \mu_0=0.0, \mu_1=0.0, p_{01}=0.00696, p_{10}=0.0297$	6	26074	-13031	
$\lambda_0=0.0759, \lambda_1=0.0880, \mu_0=\mu_1=0.0, p_{01}=0.00696, p_{10}=0.0297$	5	26072	-13031	0.973
$\lambda_0= \lambda_1=0.0802, \mu_0=0.0, \mu_1=0.0, p_{01}=0.00792, p_{10}=0.0270$	5	26081	-13036	0.00235
$\lambda_0= \lambda_1=0.0802, \mu_0=\mu_1=0.0, p_{01}=0.00796, p_{10}=0.0270$	4	26079	-13036	0.00985
$\lambda_0= \lambda_1=0.0802, p_{01}=0.00795, p_{10}=0.0269$	3	26077	-13036	0.0263

2.5 – Variance components obtained from nested ANOVAS

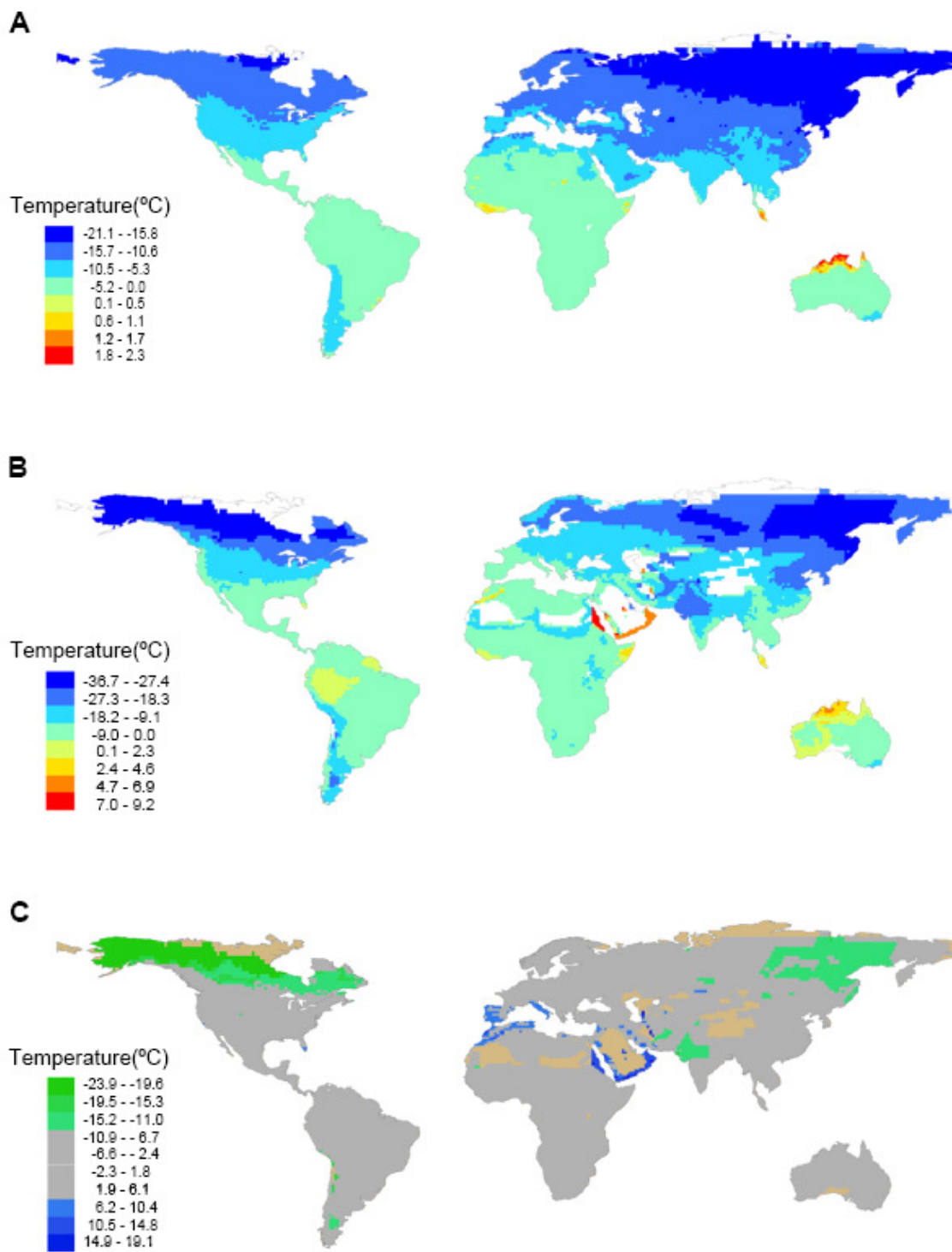
Table A2.5. Variance components obtained from nested ANOVAs. Variance is partitioned among taxonomic levels (family, genus and species) using linear mixed-effects models fitted using a restricted maximum likelihood algorithm. In each case, except \log_{10} (range size), we provide variance estimates for three summary statistics characterizing species' climatic niches: maxima, minima and means. We highlight those estimates where higher-level taxonomy (family + genus) explains >50% of the variance.

Taxon	Level	Climatic variables						Latitude	Range size
			Temp. Warm	Temp. Cold	Annual precipitation	Precipitation seasonality	NDVI		
Amphibians	Max.	Family	0.202	0.438	0.135	0.142	0.108	0.562	0.125
		Genus	0.268	0.237	0.176	0.260	0.219	0.242	0.254
		Species	0.530	0.325	0.689	0.598	0.673	0.196	0.621
	Min.	Family	0.075	0.400	0.120	0.084	0.105	0.508	
		Genus	0.217	0.239	0.225	0.271	0.219	0.240	
		Species	0.707	0.362	0.655	0.645	0.676	0.251	
	Mean	Family	0.176	0.485	0.257	0.136	0.125	0.572	
		Genus	0.299	0.249	0.290	0.301	0.284	0.228	
		Species	0.524	0.266	0.453	0.563	0.591	0.201	
Mammals	Max.	Family	0.193	0.261	0.368	0.243	0.235	0.367	0.205
		Genus	0.187	0.361	0.201	0.128	0.204	0.388	0.160
		Species	0.620	0.378	0.431	0.630	0.561	0.245	0.635
	Min.	Family	0.233	0.210	0.182	0.112	0.225	0.208	
		Genus	0.136	0.293	0.182	0.111	0.153	0.333	
		Species	0.631	0.497	0.636	0.777	0.623	0.458	
	Mean	Family	0.186	0.246	0.294	0.083	0.277	0.258	
		Genus	0.322	0.412	0.340	0.196	0.340	0.394	
		Species	0.493	0.342	0.366	0.721	0.383	0.348	

2.6 – Ancestral state reconstructions using one-parameter maximum likelihood (Brownian motion) models.

Figure A2.6. Mean assemblage (grid cell) values for independent evolution in cold tolerance calculated as the average deviation from reconstructed ancestral values for the species occurring in each cell. (a) Mammals; (b) amphibians and (equal-intervals above and below zero are used in the colour scale). (c) their difference (amphibians minus mammals). Only extreme differences are coloured; brown cells are unoccupied by amphibians; grey cells are those where the difference is small. We used the mammal supertree (Fritz *et al.*, 2009) and a newly-constructed genus-level undated amphibian supertree (see above Appendix 2.3).

Figure A2.6



Appendix 3. Supporting information for chapter 3

Where do species' geographic ranges stop and why? Landscape impermeability and the Afrotropical avifauna

3.1 – References used in the construction of the distribution maps

Brown, L., Urban, E. & Newman, K. (eds.) *The Birds of Africa: Vol 1* (Academic Press, London, 1982).

Fry, C. & Keith, S. (eds.) *The Birds of Africa: Vol 7* (Academic Press, London, 2004).

Fry, C., Keith, S. & Urban, E. (eds.) *The Birds of Africa: Vol 6* (Academic Press, London, 2002).

Keith, S. & Fry, C. (eds.) *The Birds of Africa: Vol 4* (Academic Press, London, 1992).

Keith, S., Urban, E. & Fry, C. (eds.) *The Birds of Africa: Vol 3* (Academic Press, London, 2002).

Urban, E., Fry, C. & Keith, S. (eds.) *The Birds of Africa: Vol 2* (Academic Press, London, 1982).

Urban, E., Keith, S. & Fry, C. (eds.) *The Birds of Africa: Vol 5* (Academic Press, London, 1997).

3.2 – References used to construct the predictor variables

Human population density: Center for International Earth Science Information Network (CIESIN) (2003) Gridded Population of the World (GPW), Version 2. Available at <http://sedac.ciesin.columbia.edu/plue/gpw>.

Mean annual temperature: New M., Lister D., Hulme M., Makin I. 2002 A high-resolution data set of surface climate over global land areas. *Climate Research*, **21**, 1-25.

Mean annual actual evapotranspiration: University of Delaware Global Climate Resource Pages (UD GCRP) Available at http://climate.geog.udel.edu/~climate/html_pages/download.html.

Mean elevation: US Geological Survey (USGS) National Center for Earth Resources Observation & Science (2003) Global 30-arc-second elevation data set (GTOPO30). Available at <http://edcdaac.usgs.gov/gtopo30/gtopo30.asp>.

Landscape heterogeneity: US Geological Survey (USGS) National Center for Earth Resources Observation & Science (2003) global land cover characterisation data base v2.0 (GLCC). Available at http://edc2.usgs.gov/glcc/globe_int.php. There are 96 land cover types in the GLCC v.2 database.

3.3 – Preliminary analyses to determine the minimum adequate model

Single-predictor ordinary least squares (OLS) regression was carried out to assess the consistency and robustness of the multivariate analyses subsequently performed and to compare the significance and directions of slopes obtained from each mode of analysis (table A3.3.1). Human population density is included here although ultimately was not used in the main analyses.

With one categorical and six continuous variables, there are a great many higher-order and interaction terms possible in the maximal model. To restrict analyses to manageable levels, preliminary studies were made to identify which terms were sensible and relevant to include. Single-predictor analyses by biome indicated the significant modulating effect of this factor (tables A3.3.2a,b).

Variables which are repeatedly found nested together in tree models are potential candidates for interaction terms. Following tree modelling, two additional interaction terms were included in the maximal model, AET with temperature and AET with elevational range (figure A3.3.1).

Generalised additive models (GAMs) were also used to determine whether any of the explanatory variables required higher-order terms to describe their relationship with ω . GAMs fit non-parametric smoothers through the data and their graphical representation facilitates decisions on whether a higher-order term or a transformation is necessary. This, plus the increase in degrees of freedom necessary to fit the smoother, indicates whether or not a linear term is sufficient. A multivariate GAM was fitted using all of the continuous variables as well as interaction terms identified through tree modelling. The GAMs indicated that no relationship benefited from description using higher-order terms (figure A3.3.2).

Table A3.3.1. Regression statistics for the single-predictor non-spatial analyses. Elevational range and human population density have been log-transformed. Significance codes: $p < 0.0001$

***, $0.0001 \leq p < 0.001$ **, $0.001 \leq p < 0.01$ *, $0.01 \leq p < 0.05$., $p \geq 0.05$ n.s.

Predictor	Slope	\pm SE	F _{1,2016}	T	P	R ²
Mean elevation	0.00014	0.00003	18.85	4.34	***	0.00927
Mean annual AET	-0.00071	0.00004	329.10	-18.14	***	0.14030
Mean annual temperature	0.00600	0.00413	2.11	1.45	n,s	0.00105
Elevational range	0.16734	0.01412	140.50	11.85	***	0.06516
Landscape heterogeneity	-0.01651	0.00367	20.28	-4.50	***	0.00947
Biome heterogeneity	0.19294	0.01400	190.00	13.79	***	0.08614
Human population density	-0.00117	0.00925	0.02	-0.13	n.s	0.00001

Table A3.3.2. Analyses by biome. (A) Mean values of each predictor by biome. Shaded values are not significantly different from one another under TukeyHSD criteria. For logit (ω), biomes 1 and 7 and biomes 10 and 13 are not significantly different from each other. (B) Regression statistics for single predictor analyses by biome (residual degrees of freedom for each biome: (1) 299, (7) 1446, (10) 70, (13)195). Biomes: 1. Tropical & subtropical moist broadleaf forests; 7. Tropical & subtropical grasslands, savannas & shrublands; 10. Montane grasslands & savannas; 13. Deserts & xeric shrublands.

Abbreviations as follows: ELEV: mean elevation (metres); AET: mean annual actual evapotranspiration (mm); TEMP: mean annual temperature ($^{\circ}$ C); ELEVR: elevational range (log(metres)); LandHet: landscape heterogeneity (number of co-occurring ecosystem types); BiomeHet: biome heterogeneity (number of biome edges); HPD: human population density (log(people per km²)).

(A)

Biome	ELEV	AET	TEMP	ELEVR	LandHet	BiomeHet	HPD	Logit (ω)
1	622	1173.4	24.0	5.961	11.27	0.9203	2.6885	-0.7837
7	666	705.9	25.1	5.988	8.52	0.5753	2.3346	-0.6881
10	1686	702.2	16.8	7.349	12.03	1.6389	1.0274	-0.4003
13	1044	312.9	20.6	6.559	5.55	0.6091	0.6380	-0.2865

(B)

	Slope	±SE	F	P	R²
Biome/Predictor	ELEV				
1	0.00058	0.00009	40.95	***	0.12050
7	-0.00014	0.00004	12.39	***	0.00850
10	0.00004	0.00009	0.21	ns	0.00295
13	0.00030	0.00015	3.98	ns	0.02002
	AET				
1	-0.01408	0.00020	52.02	***	0.14820
7	-0.00082	0.00005	278.00	***	0.16130
10	0.00026	0.00039	0.46	ns	0.00647
13	-0.00032	0.00033	0.91	ns	0.00467
	TEMP				
1	-0.20038	0.01838	29.83	***	0.09072
7	0.03918	0.00518	57.31	***	0.03812
10	0.02759	0.01830	2.27	ns	0.03146
13	0.08930	0.01587	31.66	***	0.13970
	ELEVR				
1	0.34557	0.02796	152.70	***	0.33810
7	0.02039	0.01764	1.34	ns	0.00092
10	0.29120	0.05220	31.12	***	0.30780
13	0.51583	0.04976	107.50	***	0.35530
	LandHet				
1	0.04421	0.01232	12.88	***	0.0381
7	-0.02136	0.00431	24.61	***	0.0085
10	0.04016	0.01011	15.77	***	0.1722
13	-0.00571	0.01537	0.138	ns	0.0007
	BiomeHet				
1	0.30170	0.03256	85.88	***	0.22310
7	0.20986	0.01649	161.90	***	0.10070
10	0.08229	0.03186	6.67	ns	0.08701
13	-0.02473	0.05940	0.17	ns	0.00089
	HPD				
1	0.22519	0.02629	73.35	***	0.19700
7	-0.06729	0.01129	35.53	***	0.02398
10	0.02454	0.04398	0.31	ns	0.06644
13	0.23779	0.02558	86.47	***	0.30720

Figure A3.3.1. Tree diagram of the seven hypothesised predictor variables. Only the first four splits are shown. The tips of the tree show mean $\logit(\omega)$ under the specified splitting criteria.

Abbreviations as table A3.3.2.

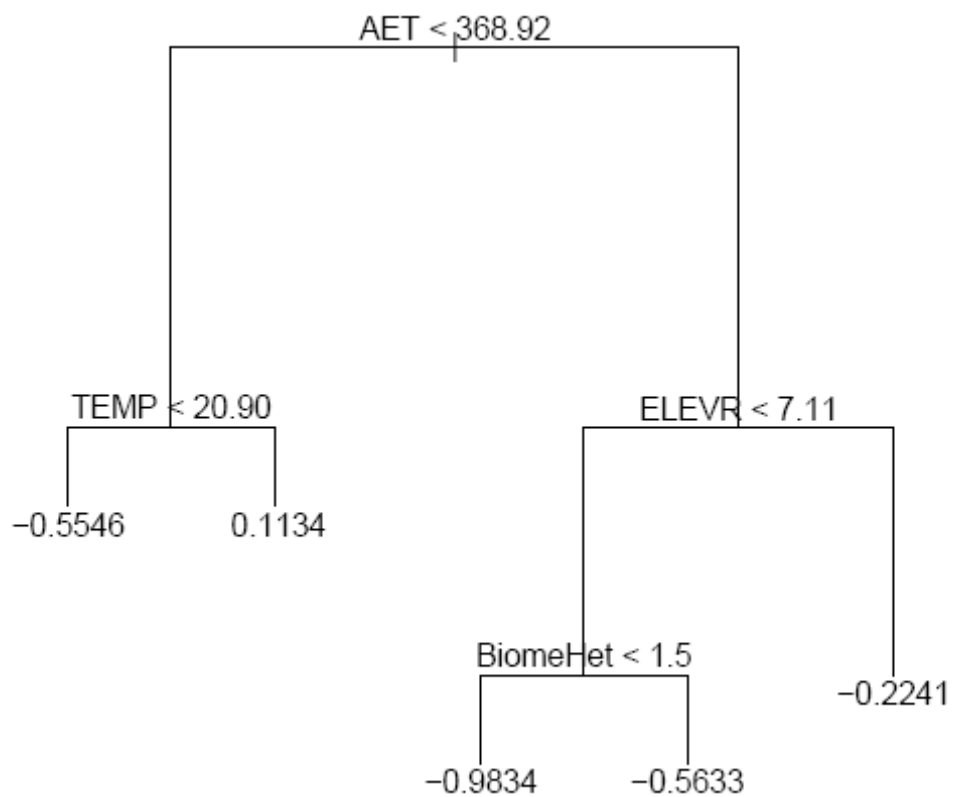
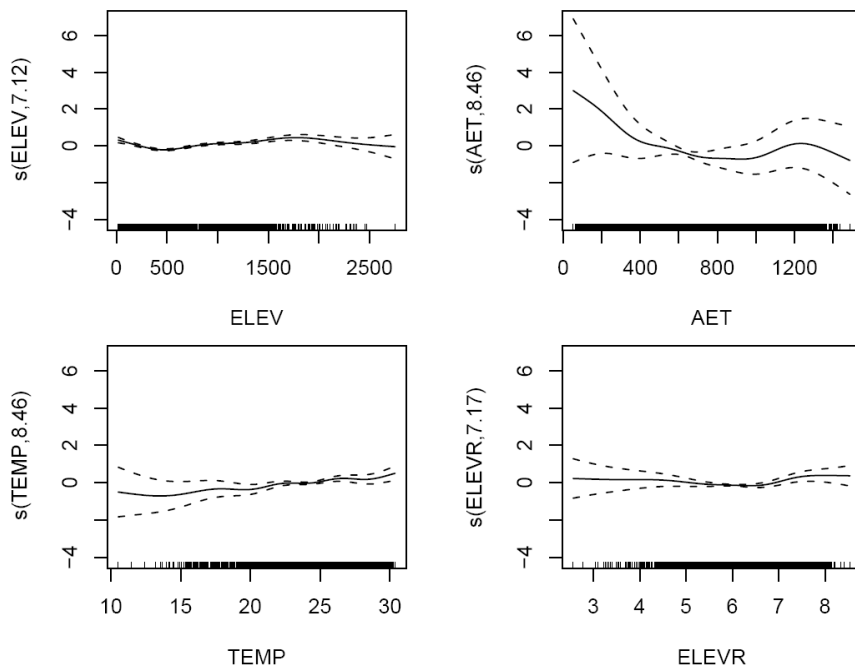
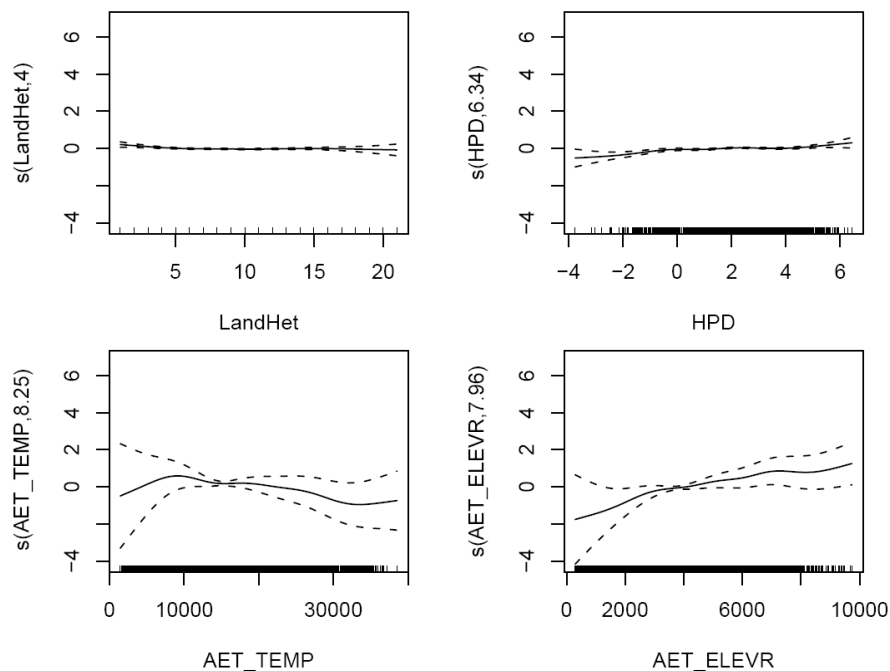


Figure A3.3.2. Generalised additive models. Plots of a generalised additive model including each continuous explanatory variable plus the two interaction terms, AET and temperature and AET and elevational range. Abbreviations as table A3.3.2.

The figures given on the y axis are the degrees of freedom necessary to fit the smoothed term. BiomeHet was not included in the GAM as, although it can be represented as a continuous variable, it has only 5 values (the integers between 0 and 4) and >4 degrees of freedom are necessary to fit a non-parametric smoother. The smoothers indicate that no term is clearly demonstrating an easily parameterized non-linear relationship with ω , suggesting that linear terms will be sufficient in multiple regression analyses. The rugs at the base of the plot represent the distribution of the actual values of the explanatory variable to which the plot applies.





3.4 – Exploring spatial autocorrelation in response and explanatory variables and in the best-fit models

Plotted (figure A3.4.1a) are correlograms for all continuous predictor variables and for the response, logit ω . Climatic variables (AET, TEMP) exhibit high spatial autocorrelation (SA) up to distances of 4000km (TEMP). Conversely, variables capturing habitat heterogeneity display only short-range SA, up to distances of <2000km. SA in the response is also visible up to 2000km.

A comparison of residual SA between models including only AET (the most significant predictor in non-spatial analyses) and the best-fit models indicates that inclusion of all identified

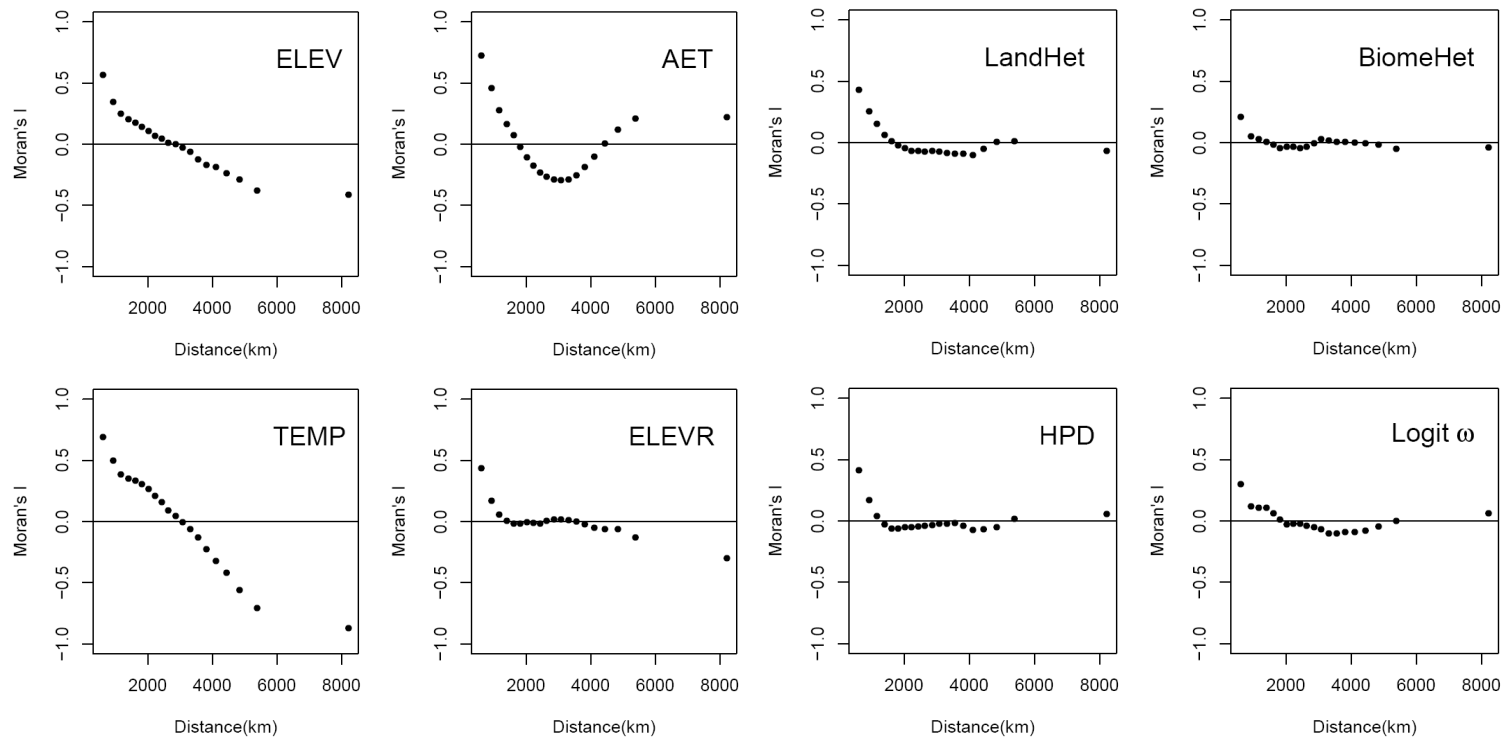
significant predictors substantially reduces SA but that SA remains in the shortest distance class (up to 600km), upholding the decision to fit spatially-explicit models (figure A3.4.1b).

Finally, comparison of residual SA between the top spatial model (Akaike weight = 0.810) and a non-spatial model including the same set of predictors indicates that the remaining spatial structure of the data has been adequately accounted for in the spatial model (figure A3.4.1c).

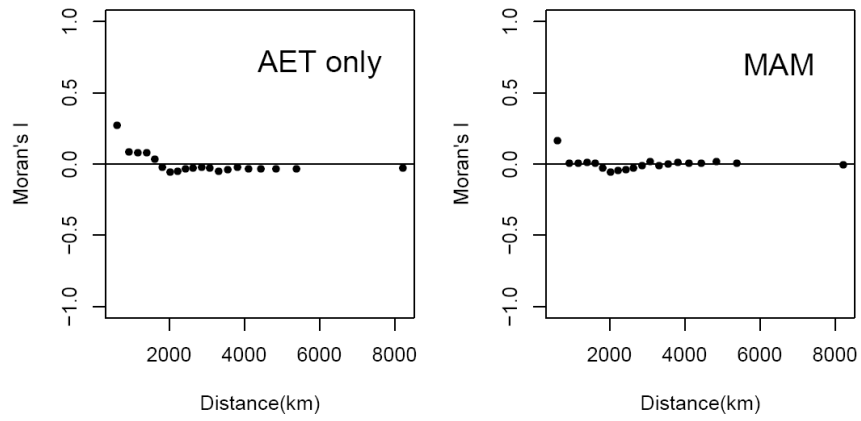
Here, standardised residuals (pre-multiplied by the inverse square-root factor of the estimated error correlation matrix) are used rather than the raw residuals. GLS incorporates spatial structure directly into model residuals in order to estimate the “true” regression coefficients with the raw residuals now containing a strong spatial component.

Figure A3.4.1. Moran's I correlograms of (A) the explanatory and response variables, (B) the residuals from non-spatial models including AET only and from the best-fit non-spatial model ($w_i = 0.184$) and (C) the standardised residuals from the best-fit spatial model ($w_i = 0.810$) and an equivalent model not considering the effect of space. The study area was divided into 20 distance classes. Rather than ensure constant intervals, lags were defined to maximize the similarity of the number of comparisons within each lag, each lag containing ~ 100000 pairwise comparisons. Distance classes (km) were as follows: 616, 922, 1166, 1395, 1612, 1816, 2023, 2226, 2436, 2641, 2858, 3081, 3309, 3557, 3824, 4109, 4440, 4839, 5388, 8211. Abbreviations as table A3.3.2.

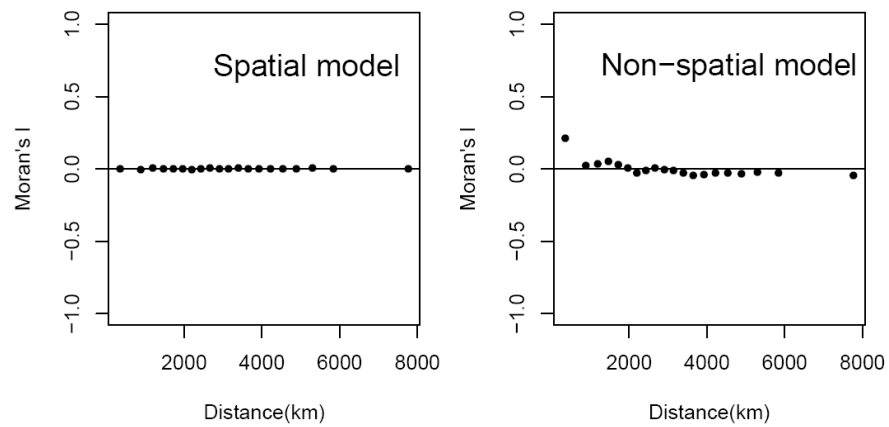
(A)



(B)



(C)



3.5 – F ratios for each term retained in the (A) non-spatial and (B) spatial models

Table A3.5.1. F ratios for each term retained in the (A) non-spatial and (B) spatial models. The significance of each term does not change across the different models of the non-spatial set and is indicated only once. For continuous main effects, significance shows the sign of the slope with ω . Elevational range is log-transformed and the Akaike weights and AICc of all models are also shown ($p < 0.0001$ ***, $0.0001 \leq p < 0.001$ **, $0.001 \leq p < 0.01$ *, $0.01 \leq p < 0.05$ ·, $p \geq 0.05$ n.s.).

	(A) Non-spatial											(B) Spatial			
<i>Main effects</i>															
Biome	***	61.54	61.50	61.38	61.40	61.37	61.40	61.20	61.17	61.32	61.28	-	-		
Mean elevation	n.s.	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	-	-		
Mean annual AET	+++	497.82	497.52	496.48	496.70	496.44	496.69	495.07	494.79	496.03	495.68	-	-		
Mean annual temperature	+++	124.42	124.35	124.09	124.14	124.08	124.14	123.74	123.66	123.97	123.89	-	-		
Elevational range	+++	359.28	359.07	358.32	358.48	358.29	358.47	357.30	357.10	357.99	357.74	33.59	+++	-	
Landscape heterogeneity	n.s.	0.30	0.30	-	-	0.29	0.29	-	-	0.29	0.29	23.86	+++	28.58	+++
Biome heterogeneity	+++	204.74	204.61	204.19	204.28	204.17	204.27	203.61	203.49	204.00	203.86	50.61	+++	61.74	+++
Mean annual AET ²	---	291.32	291.14	284.56	284.69	290.51	290.66	283.75	283.59	290.27	290.07	-	-		
Elevational range ²	+++	40.68	40.66	43.90	43.92	40.57	40.59	43.77	43.75	40.54	40.51	-	19.47	+++	
<i>Biome interactions</i>															
Mean elevation	***	15.48	15.47	15.22	15.23	15.43	15.44	15.18	15.17	15.42	15.41	-	-		
Mean annual AET	***	26.41	26.40	26.07	26.09	26.34	26.35	26.00	25.98	26.32	26.30	-	-		
Mean annual temperature	***	19.12	19.10	19.48	19.49	19.06	19.07	19.43	19.42	19.05	19.03	-	-		
Elevational range	***	41.99	41.96	42.91	42.93	41.87	41.89	42.79	42.76	41.84	41.81	-	-		
Landscape heterogeneity	***	6.37	6.37	-	-	-	-	-	-	6.48	6.48	-	-		
Biome heterogeneity	**	3.87	3.87	3.85	3.86	3.86	3.86	-	-	-	-	-	-		
Mean annual AET ²	***	18.15	18.14	17.73	17.74	17.72	17.73	18.47	18.46	18.81	18.80	-	-		
Elevational range ²	***	8.42	8.41	11.20	11.21	11.20	11.20	11.34	11.34	8.26	8.25	-	-		
Mean annual AET: Mean annual temperature	---	17.47	17.46	21.13	21.14	21.92	21.93	19.96	19.95	16.49	16.48	-	-		
Mean annual AET: Elevational range	+++	2.19	-	-	1.90	-	2.01	2.14	-	2.38	-	-	-		
Akaike weights		0.1842	0.1705	0.1703	0.1594	0.0923	0.0909	0.0278	0.0264	0.0237	0.0199	0.8100	0.1540		
AICc		2578.13	2578.28	2578.29	2578.42	2579.51	2579.54	2581.91	2582.02	2582.23	2582.57	-47.16	-43.84		

3.6 – Analysis of species in the largest range size quartile

Table A3.6.1. F ratios for largest range size quartile, for each term retained in the (A) non-spatial and (B) spatial models constituting the 95% confidence set for analyses including only species in the largest range size quartile. The significance of each term is indicated and, for continuous main effects, significance also shows the sign of the slope with ω . Elevational range is log-transformed and the Akaike weights and AICc of all models are also shown ($p < 0.0001$ ***, $0.0001 \leq p < 0.001$ **, $0.001 \leq p < 0.01$ *, $0.01 \leq p < 0.05$ ·, $p \geq 0.05$ n.s.).

(A) Non-spatial														
<i>Main effects</i>														
Biome	134.84	***	134.64	***	134.55	***	134.51	***	134.42	***	134.73	***	134.37	***
Mean elevation	34.71	***	34.66	***	34.64	***	34.63	***	34.61	***	34.68	***	34.59	***
Mean annual AET	870.41	+++	869.09	+++	868.53	+++	868.30	+++	867.72	+++	869.69	+++	867.37	+++
Mean annual temperature	259.79	+++	259.40	+++	259.23	+++	259.16	+++	258.99	+++	259.57	+++	258.88	+++
Elevational range	205.11	+++	204.79	+++	204.66	+++	204.61	+++	204.47	+++	204.94	+++	204.39	+++
Landscape heterogeneity	1.46	n.s.	-		1.46	n.s.	1.46	n.s.	-		1.46	n.s.	-	
Biome heterogeneity	141.19	+++	140.97	+++	140.88	+++	140.84	+++	140.75	+++	141.07	+++	140.69	+++
Mean annual AET ²	251.50	---	252.19	---	250.96	---	250.89	---	251.79	---	251.29	---	251.69	---
Elevational range ²	10.54	++	10.86	++	10.52	++	10.52	++	10.85	++	10.53	++	10.84	++
<i>Biome interactions</i>														
Mean elevation	24.63	***	24.34	***	24.58	***	24.57	***	24.30	***	24.61	***	24.29	***
Mean annual AET	32.52	***	32.38	***	32.45	***	32.44	***	32.33	***	32.50	***	32.32	***
Mean annual temperature	14.28	***	14.40	***	14.24	***	14.24	***	14.38	***	14.26	***	14.38	***
Elevational range	55.70	***	55.44	***	55.58	***	55.56	***	55.35	***	55.65	***	55.33	***
Landscape heterogeneity	-		-		-		-	***	-		1.91	n.s.	-	
Biome heterogeneity	4.58	**	4.61	**	4.57	**	4.57	**	4.60	**	4.58	**	4.60	**
Mean annual AET ²	16.23	***	16.12	***	16.20	***	16.19	***	16.10	***	16.44	***	16.09	***
Elevational range ²	11.88	***	11.86	***	11.86	***	11.85	***	11.84	***	10.50	***	11.84	***
Mean annual AET: Mean annual temperature	11.17	---	8.81	--	11.14	---	-		-		10.18	--	8.80	--
Mean annual AET: Elevational range	5.30	++	4.95	+	-		10.62	++	9.62	++	5.34	+	-	
Akaike weight	0.4772		0.1750		0.0911		0.0700		0.0606		0.0424		0.0399	
AICc	2683.27		2685.28		2686.58		2687.11		2687.40		2688.12		2688.23	

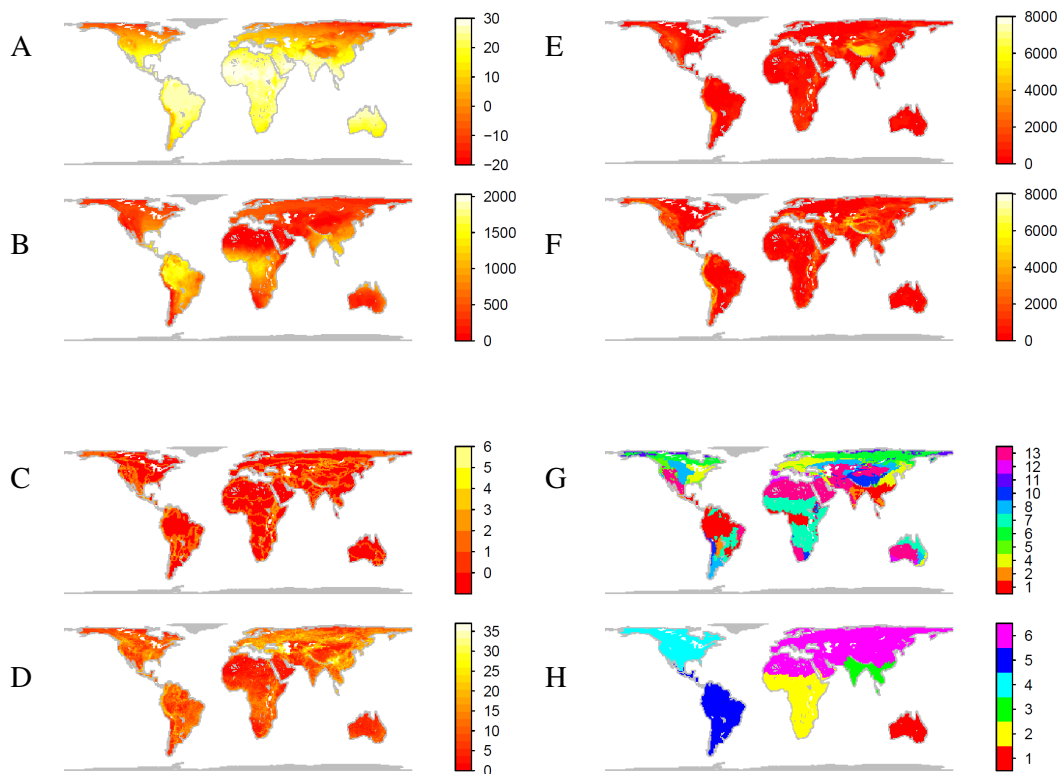
(B) Spatial									
<i>Main effects</i>									
Biome	-	-	-	-	-	-	-	-	-
Mean elevation	-	-	-	-	-	-	-	-	-
Mean annual AET	-	-	-	-	-	-	-	-	-
Mean annual temperature	-	-	-	-	-	-	-	-	-
Elevational range	20.81	+++	20.68	+++	-	-	-	-	-
Landscape heterogeneity	13.27	+++	-	-	16.04	+++	16.13	+++	-
Biome heterogeneity	23.00	+++	22.86	+++	28.86	+++	29.01	+++	28.85
Mean annual AET ²	-	-	-	-	-	-	-	-	-
Elevational range ²	-	-	-	-	-	11.77	+++	15.16	+++
<i>Biome interactions</i>									
Mean elevation	-	-	-	-	-	-	-	-	-
Mean annual AET	-	-	-	-	-	-	-	-	-
Mean annual temperature	-	-	-	-	-	-	-	-	-
Elevational range	-	-	-	-	-	-	-	-	-
Landscape heterogeneity	-	-	-	-	-	-	-	-	-
Biome heterogeneity	-	-	-	-	-	-	-	-	-
Mean annual AET ²	-	-	-	-	-	-	-	-	-
Elevational range ²	-	-	-	-	-	-	-	-	-
Mean annual AET: Mean annual temperature	-	-	-	-	-	-	-	-	-
Mean annual AET: Elevational range	-	-	-	-	-	-	-	-	-
Akaike weight	0.4966	0.2765	0.1038	0.0394	0.0297	0.0146			
AICc	241.16	242.33	244.29	246.23	246.79	248.21			

Appendix 4. Supporting information for chapter 4

Global patterns and inter-realm differences in mammalian landscape impermeability

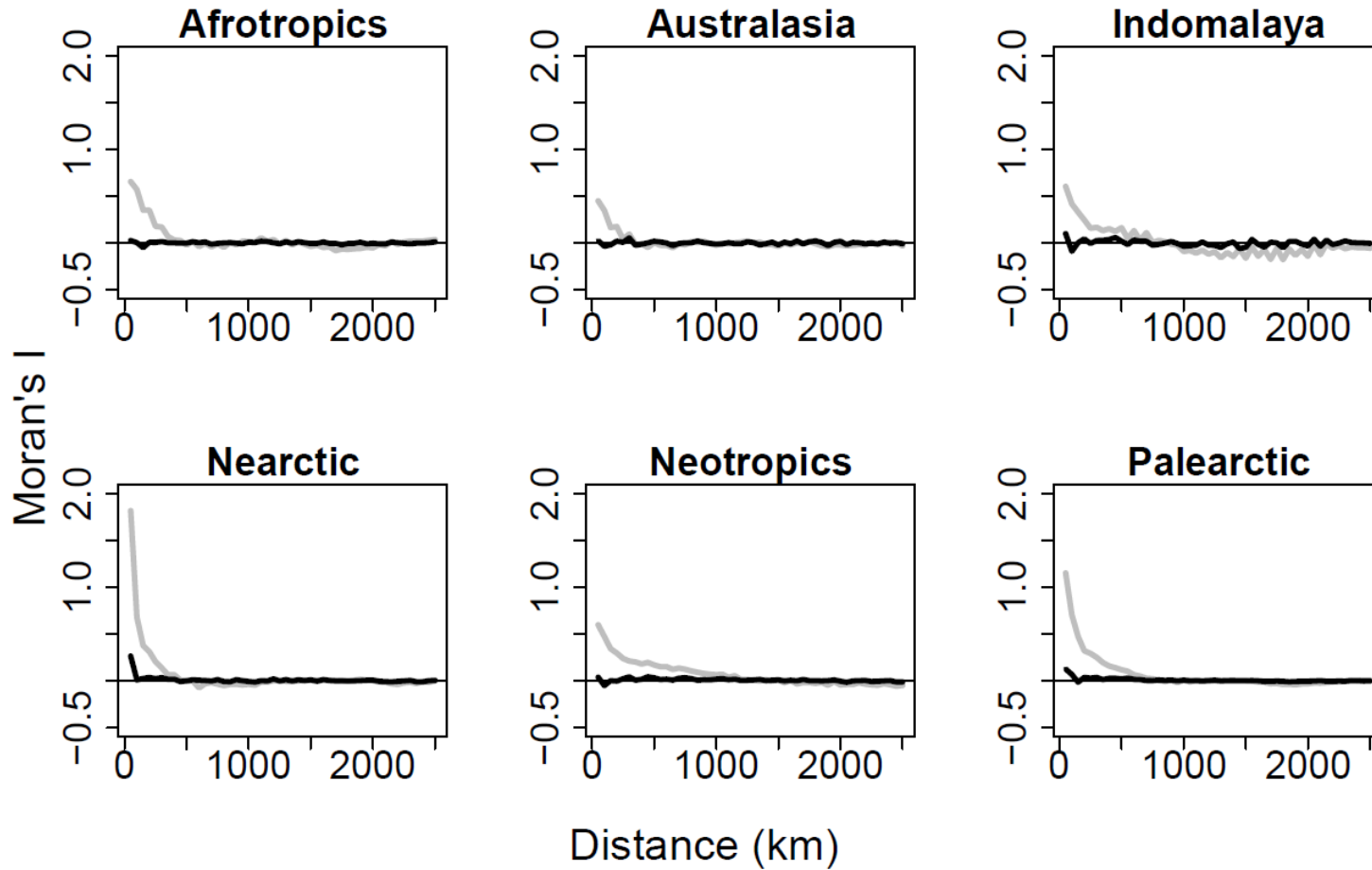
4.1 – Distributions of variables included in the models. For sources see Appendix 3.2.

(A) Mean annual temperature (°C) (B) Mean annual actual evapotranspiration (mm) (C) Biome heterogeneity (count of biome edges) (D) Landscape heterogeneity (count of habitat types) (E) Mean elevation (metres) (F) Mean elevation range (metres) (G) Biomes (for biome codes see table 4.2) (H) Realms (1. Australasia, 2. Afrotropics, 3. Indomalaya, 4. Nearctic, 5. Neotropics, 6. Palearctic)



4.2 – The use of spatially-explicit models to control for spatial autocorrelation

Figure A4.2.1. Moran's I correlograms of the top OLS model versus the top SAR model in each realm. Moran's I was calculated for model residuals in distance classes from 50km to 2500km in increments of 50km. Grey line: OLS model; black line: SAR model.



Appendix 5. Supporting information for chapter 5

Can landscape impermeability be co-opted into a measure of species' relative occupancy?

5.1 – Tables for single predictor models of relative occupancy

Table A5.1.1. Results of models predicting ω_i . The number of species in each model (n), coefficient estimate (*Slope*), standard error (*Error*), t-value (t), p-value (p), degrees of freedom ($d.f.$), adjusted R^2 ($Adj. R^2$) and optimised λ are given. All λ values were significantly different from one (χ^2 test, all $p < 0.001$); this result is not presented to save space. Results comparing λ to zero using χ^2 tests are given ($p\lambda 0$). All variables as described in table 5.2. BM refers to models fitted with body mass as a covariate.

	<i>Variable</i>	n	λ	$p\lambda 0$	<i>Slope</i>	<i>Error</i>	t	p	$d.f.$	$Adj. R^2$
AFROTROPICS										
	Gestation length (BM)	288	0.000	0.997	-0.276	0.078	-3.530	0.000	285	0.056
	Weaning age (BM)	222	0.000	0.987	-0.229	0.086	-2.656	0.008	219	0.021
	Population density (BM)	208	0.348	0.008	0.337	0.124	2.723	0.007	205	0.035
	Gestation length	288	0.000	0.999	-0.250	0.057	-4.357	0.000	286	0.059
	Weaning age	222	0.000	0.985	-0.271	0.065	-4.183	0.000	220	0.018
	Population density	208	0.351	0.006	0.349	0.107	3.264	0.001	206	0.037
	Generalism	266	0.315	0.000	-0.025	0.067	-0.372	0.710	264	-0.003
	Niche breadth	767	0.164	0.000	0.213	0.036	5.940	0.000	765	0.044
	Body mass	767	0.193	0.000	-0.059	0.074	-0.795	0.427	765	0.000
	Range size	767	0.173	0.000	-0.263	0.036	-7.399	0.000	765	0.066
AUSTRALASIA										
	Gestation length (BM)	84	0.000	0.993	0.207	0.110	1.886	0.063	81	0.059
	Weaning age (BM)	92	0.119	0.291	0.070	0.224	0.313	0.755	89	0.014
	Population density (BM)	46	0.000	0.988	0.290	0.195	1.488	0.144	43	0.007
	Gestation length	84	0.000	0.991	0.146	0.109	1.332	0.187	82	0.010
	Weaning age	92	0.136	0.140	0.234	0.151	1.555	0.124	90	0.015
	Population density	46	0.000	0.989	0.142	0.149	0.952	0.346	44	-0.002
	Generalism	64	0.010	0.874	-0.277	0.122	-2.259	0.027	62	0.063
	Niche breadth	160	0.081	0.089	0.176	0.077	2.280	0.024	158	0.024
	Body mass	160	0.093	0.014	0.179	0.103	1.738	0.084	158	0.013
	Range size	160	0.111	0.017	-0.192	0.077	-2.499	0.013	158	0.035
INDOMALAYA										
	Gestation length (BM)	149	0.000	0.989	-0.074	0.093	-0.796	0.428	146	-0.009
	Weaning age (BM)	117	0.000	0.989	-0.125	0.118	-1.058	0.292	114	-0.012
	Population density (BM)	59	0.000	0.993	0.117	0.200	0.585	0.561	56	0.015
	Gestation length	149	0.000	0.989	-0.057	0.082	-0.696	0.487	147	-0.003
	Weaning age	117	0.000	0.990	-0.084	0.093	-0.902	0.369	115	-0.003
	Population density	59	0.000	0.993	0.207	0.130	1.600	0.115	57	0.026
	Generalism	185	0.000	0.988	-0.026	0.074	-0.353	0.725	183	-0.005

Niche breadth	431	0.054	0.076	0.139	0.048	2.926	0.004	429	0.017
Body mass	431	0.033	0.255	-0.067	0.061	-1.104	0.270	429	-0.001
Range size	431	0.028	0.142	-0.311	0.046	-6.760	0.000	429	0.090
<i>NEARCTIC</i>									
Gestation length (BM)	203	0.252	0.036	0.345	0.114	3.023	0.003	200	0.097
Weaning age (BM)	182	0.508	0.009	0.149	0.116	1.292	0.198	179	0.041
Population density (BM)	176	0.000	0.985	0.306	0.111	2.743	0.007	173	0.039
Gestation length	203	0.409	0.000	0.145	0.113	1.280	0.202	201	0.006
Weaning age	182	0.576	0.000	0.032	0.109	0.296	0.768	180	-0.005
Population density	176	0.000	0.986	0.198	0.074	2.661	0.009	174	0.036
Generalism	202	0.560	0.000	-0.030	0.078	-0.389	0.698	200	0.009
Niche breadth	329	0.438	0.000	-0.297	0.051	-5.850	0.000	327	0.105
Body mass	329	0.437	0.000	-0.178	0.094	-1.894	0.059	327	0.019
Range size	329	0.404	0.000	-0.544	0.045	-12.121	0.000	327	0.325
<i>NEOTROPICS</i>									
Gestation length (BM)	202	0.454	0.000	-0.290	0.132	-2.201	0.029	199	0.080
Weaning age (BM)	178	0.472	0.000	-0.114	0.102	-1.113	0.267	175	0.036
Population density (BM)	200	0.541	0.000	0.115	0.104	1.101	0.272	197	0.045
Gestation length	202	0.457	0.000	-0.268	0.116	-2.310	0.022	200	0.084
Weaning age	178	0.484	0.000	-0.146	0.091	-1.612	0.109	176	0.033
Population density	200	0.545	0.000	0.140	0.093	1.510	0.133	198	0.041
Generalism	456	0.494	0.000	0.107	0.049	2.170	0.031	454	0.013
Niche breadth	832	0.635	0.000	0.150	0.034	4.407	0.000	830	0.029
Body mass	832	0.643	0.000	-0.065	0.079	-0.830	0.407	830	0.003
Range size	832	0.650	0.000	-0.551	0.029	-18.977	0.000	830	0.300
<i>PALEARCTIC</i>									
Gestation length (BM)	266	0.085	0.992	0.164	0.110	1.487	0.138	263	0.008
Weaning age (BM)	216	0.380	0.017	-0.076	0.116	-0.651	0.516	213	-0.005
Population density (BM)	119	0.428	0.000	-0.012	0.181	-0.067	0.946	116	0.018
Gestation length	266	0.082	0.715	0.137	0.087	1.565	0.119	264	0.011
Weaning age	216	0.390	0.003	-0.044	0.098	-0.443	0.658	214	-0.005
Population density	119	0.445	0.000	-0.093	0.143	-0.651	0.516	117	-0.008
Generalism	210	0.000	0.994	-0.025	0.069	-0.364	0.716	208	-0.004
Niche breadth	663	0.000	0.979	-0.116	0.039	-2.993	0.003	661	0.011
Body mass	663	0.000	0.980	0.017	0.039	0.436	0.663	661	-0.001
Range size	663	0.014	0.662	-0.438	0.035	-12.384	0.000	661	0.194
<i>GLOBAL</i>									
Gestation length (BM)	980	0.472	0.000	-0.082	0.084	-0.980	0.327	977	-0.001
Weaning age (BM)	826	0.503	0.000	-0.027	0.066	-0.400	0.689	823	-0.002
Population density (BM)	703	0.502	0.000	0.206	0.064	3.227	0.001	700	0.013
Gestation length	980	0.474	0.000	-0.068	0.074	-0.913	0.361	978	0.000
Weaning age	826	0.503	0.000	-0.026	0.057	-0.463	0.644	824	-0.001
Population density	703	0.506	0.000	0.186	0.058	3.227	0.001	701	0.013
Generalism	1166	0.483	0.000	0.040	0.033	1.204	0.229	1164	0.000
Niche breadth	2761	0.567	0.000	0.118	0.019	6.258	0.000	2759	0.013
Body mass	2761	0.590	0.000	-0.031	0.049	-0.632	0.527	2759	0.000
Range size	2761	0.611	0.000	-0.369	0.017	-21.582	0.000	2759	0.144

Table A5.1.2. Results of models predicting ω_e including only those species with interior cells.

Table as described in table A5.1.1.

<i>Variable</i>	<i>n</i>	λ	$p\lambda 0$	<i>Slope</i>	<i>Error</i>	<i>t</i>	<i>p</i>	<i>d.f.</i>	<i>Adj. R²</i>
<i>AFROTROPICS</i>									
Gestation length (BM)	287	0.000	0.981	-0.137	0.081	-1.695	0.091	284	0.004
Weaning age (BM)	221	0.000	0.984	-0.171	0.089	-1.914	0.057	218	0.015
Population density (BM)	207	0.000	0.982	0.158	0.107	1.478	0.141	204	0.021
Gestation length	287	0.000	0.985	-0.094	0.059	-1.594	0.112	285	0.005
Weaning age	221	0.000	0.985	-0.154	0.067	-2.309	0.022	219	0.019
Population density	207	0.000	0.981	0.174	0.069	2.535	0.012	205	0.026
Generalism	265	0.000	0.994	-0.010	0.062	-0.165	0.869	263	-0.004
Niche breadth	766	0.045	0.000	0.338	0.035	9.740	0.000	764	0.109
Body mass	766	0.020	0.051	0.079	0.046	1.710	0.088	764	0.003
Range size	766	0.031	0.031	-0.181	0.037	-4.926	0.000	764	0.030
ω_i	766	0.057	0.001	0.587	0.030	19.735	0.000	764	0.430
<i>AUSTRALASIA</i>									
Gestation length (BM)	83	0.059	0.529	0.149	0.119	1.257	0.213	80	0.086
Weaning age (BM)	91	0.138	0.402	-0.045	0.228	-0.199	0.843	88	0.044
Population density (BM)	46	0.000	0.988	0.071	0.198	0.361	0.720	43	-0.027
Gestation length	83	0.194	0.338	0.016	0.137	0.116	0.908	81	0.011
Weaning age	91	0.163	0.132	0.220	0.157	1.397	0.166	89	0.012
Population density	46	0.000	0.989	-0.041	0.151	-0.269	0.789	44	-0.021
Generalism	63	0.000	0.989	-0.114	0.127	-0.897	0.373	61	-0.003
Niche breadth	159	0.202	0.168	0.197	0.077	2.568	0.011	157	0.040
Body mass	159	0.240	0.061	0.276	0.121	2.289	0.023	157	0.032
Range size	159	0.393	0.031	-0.296	0.072	-4.084	0.000	157	0.082
ω_i	159	0.164	0.784	0.660	0.060	10.983	0.000	157	0.336
<i>INDOMALAYA</i>									
Gestation length (BM)	142	0.125	0.195	-0.208	0.122	-1.707	0.090	139	0.013
Weaning age (BM)	112	0.000	0.991	-0.335	0.117	-2.869	0.005	109	0.053
Population density (BM)	46	0.187	0.329	0.273	0.241	1.135	0.263	43	0.010
Gestation length	142	0.162	0.079	-0.167	0.111	-1.505	0.134	140	0.007
Weaning age	112	0.122	0.306	-0.200	0.111	-1.792	0.076	110	0.036
Population density	46	0.186	0.330	0.293	0.162	1.809	0.077	44	0.032
Generalism	167	0.000	0.987	0.176	0.077	2.293	0.023	165	0.025
Niche breadth	396	0.000	0.992	0.611	0.040	15.307	0.000	394	0.370
Body mass	396	0.024	0.605	-0.025	0.061	-0.410	0.682	394	-0.002
Range size	396	0.028	0.502	0.061	0.051	1.209	0.227	394	0.001
ω_i	396	0.037	0.306	0.636	0.039	16.248	0.000	394	0.399
<i>NEARCTIC</i>									
Gestation length (BM)	203	0.248	0.010	0.279	0.117	2.380	0.018	200	0.030
Weaning age (BM)	182	0.376	0.001	0.203	0.113	1.792	0.075	179	0.014
Population density (BM)	176	0.087	0.577	0.276	0.123	2.254	0.025	173	0.044
Gestation length	203	0.295	0.005	0.125	0.106	1.176	0.241	201	-0.005
Weaning age	182	0.418	0.002	0.089	0.104	0.858	0.392	180	-0.004
Population density	176	0.109	0.306	0.215	0.092	2.326	0.021	174	0.042
Generalism	202	0.497	0.000	0.012	0.082	0.151	0.880	200	-0.005
Niche breadth	329	0.416	0.000	-0.170	0.054	-3.155	0.002	327	0.052
Body mass	329	0.431	0.000	-0.176	0.096	-1.833	0.068	327	0.016
Range size	329	0.329	0.004	-0.337	0.051	-6.601	0.000	327	0.155
ω_i	329	0.112	0.028	0.857	0.031	28.022	0.000	327	0.709

<i>NEOTROPICS</i>									
Gestation length (BM)	201	0.560	0.000	-0.104	0.143	-0.728	0.468	198	0.015
Weaning age (BM)	177	0.540	0.000	-0.062	0.104	-0.594	0.553	174	0.055
Population density (BM)	199	0.554	0.000	0.156	0.106	1.465	0.145	196	-0.001
Gestation length	201	0.564	0.000	-0.078	0.126	-0.615	0.539	199	0.017
Weaning age	177	0.536	0.000	-0.045	0.092	-0.491	0.624	175	0.060
Population density	199	0.559	0.000	0.115	0.095	1.217	0.225	197	0.003
Generalism	455	0.509	0.000	0.138	0.049	2.836	0.005	453	0.007
Niche breadth	830	0.705	0.000	0.565	0.027	21.254	0.000	828	0.354
Body mass	830	0.691	0.000	0.037	0.081	0.456	0.648	828	0.003
Range size	830	0.682	0.000	-0.141	0.032	-4.374	0.000	828	0.035
ω_i	830	0.282	0.000	0.776	0.021	36.116	0.000	828	0.624
<i>PALEARCTIC</i>									
Gestation length (BM)	266	0.441	0.003	0.066	0.145	0.458	0.647	263	0.029
Weaning age (BM)	216	0.503	0.002	-0.003	0.119	-0.022	0.983	213	0.004
Population density (BM)	119	0.172	0.122	-0.019	0.172	-0.109	0.913	116	0.036
Gestation length	266	0.440	0.003	0.116	0.121	0.954	0.341	264	0.032
Weaning age	216	0.503	0.002	0.010	0.102	0.101	0.920	214	0.008
Population density	119	0.217	0.016	-0.134	0.131	-1.022	0.309	117	0.008
Generalism	210	0.230	0.030	-0.040	0.081	-0.497	0.620	208	0.003
Niche breadth	662	0.067	0.033	0.373	0.037	10.128	0.000	660	0.134
Body mass	662	0.159	0.075	0.012	0.071	0.170	0.865	660	0.000
Range size	662	0.183	0.003	-0.152	0.039	-3.900	0.000	660	0.019
ω_i	662	0.076	0.016	0.721	0.027	27.111	0.000	660	0.527
<i>GLOBAL</i>									
Gestation length (BM)	973	0.432	0.000	0.055	0.074	0.738	0.461	970	-0.001
Weaning age (BM)	821	0.454	0.000	0.039	0.058	0.670	0.503	818	0.000
Population density (BM)	691	0.427	0.000	0.126	0.061	2.085	0.037	688	0.006
Gestation length	973	0.432	0.000	0.055	0.074	0.738	0.461	971	0.000
Weaning age	821	0.452	0.000	0.044	0.057	0.770	0.441	819	0.000
Population density	691	0.435	0.000	0.130	0.061	2.149	0.032	689	0.005
Generalism	1148	0.391	0.000	0.068	0.034	2.014	0.044	1146	0.003
Niche breadth	2725	0.568	0.000	0.416	0.018	23.136	0.000	2723	0.164
Body mass	2725	0.632	0.000	0.028	0.051	0.546	0.585	2723	0.000
Range size	2725	0.637	0.000	-0.107	0.018	-5.787	0.000	2723	0.012
ω_i	2725	0.302	0.000	0.764	0.013	59.725	0.000	2723	0.567

Table A5.1.3. Results of models predicting ω_e using all species with available data. Table as described in table A5.1.1.

<i>Variable</i>	<i>n</i>	λ	$p\lambda 0$	<i>Slope</i>	<i>Error</i>	<i>t</i>	<i>p</i>	<i>d.f.</i>	<i>Adj. R²</i>
<i>AFROTROPICS</i>									
Gestation length (BM)	314	0.000	0.391	-0.134	0.079	-1.697	0.091	311	0.003
Weaning age (BM)	237	0.000	0.892	-0.173	0.087	-2.001	0.047	234	0.019
Population density (BM)	232	0.000	0.918	0.261	0.100	2.601	0.010	229	0.064
Gestation length	314	0.000	0.983	-0.087	0.056	-1.539	0.125	312	0.004
Weaning age	237	0.000	0.984	-0.165	0.064	-2.571	0.011	235	0.023
Population density	232	0.000	0.988	0.269	0.064	4.239	0.000	230	0.068
Generalism	300	0.112	0.017	-0.069	0.062	-1.105	0.270	298	0.001
Niche breadth	1024	0.152	0.000	0.074	0.031	2.379	0.018	1022	0.005
Body mass	1024	0.148	0.000	0.001	0.064	0.008	0.993	1022	-0.001
Range size	1024	0.055	0.006	-0.365	0.030	-11.979	0.000	1022	0.122
<i>AUSTRALASIA</i>									
Gestation length (BM)	113	0.054	0.007	0.012	0.104	0.120	0.905	110	0.038
Weaning age (BM)	133	0.105	0.156	0.170	0.188	0.905	0.367	130	0.020
Population density (BM)	82	0.000	0.627	-0.077	0.131	-0.584	0.561	79	-0.020
Gestation length	113	0.204	0.157	-0.088	0.121	-0.728	0.468	111	-0.004
Weaning age	133	0.156	0.193	0.265	0.134	1.975	0.050	131	0.021
Population density	82	0.000	0.988	-0.044	0.112	-0.395	0.694	80	-0.011
Generalism	101	0.000	0.990	0.121	0.100	1.213	0.228	99	0.005
Niche breadth	244	0.361	0.005	-0.101	0.062	-1.623	0.106	242	0.007
Body mass	244	0.343	0.080	0.191	0.111	1.712	0.088	242	0.008
Range size	244	0.311	0.010	-0.450	0.057	-7.953	0.000	242	0.204
<i>INDOMALAYA</i>									
Gestation length (BM)	199	0.101	0.007	-0.284	0.114	-2.499	0.013	196	0.021
Weaning age (BM)	158	0.000	0.011	-0.430	0.098	-4.365	0.000	155	0.098
Population density (BM)	75	0.128	0.132	0.033	0.182	0.184	0.855	72	-0.001
Gestation length	199	0.149	0.014	-0.208	0.098	-2.133	0.034	197	0.018
Weaning age	158	0.128	0.064	-0.282	0.094	-2.991	0.003	156	0.048
Population density	75	0.109	0.218	0.147	0.129	1.145	0.256	73	0.004
Generalism	225	0.107	0.128	0.126	0.078	1.627	0.105	223	0.007
Niche breadth	613	0.359	0.000	0.351	0.036	9.775	0.000	611	0.134
Body mass	613	0.308	0.000	-0.018	0.089	-0.200	0.842	611	-0.002
Range size	613	0.282	0.000	-0.083	0.040	-2.098	0.036	611	0.006
<i>NEARCTIC</i>									
Gestation length (BM)	246	0.381	0.000	0.416	0.120	3.477	0.001	243	0.043
Weaning age (BM)	216	0.457	0.000	0.342	0.102	3.360	0.001	213	0.047
Population density (BM)	212	0.279	0.004	0.192	0.123	1.564	0.119	209	0.003
Gestation length	246	0.400	0.000	0.248	0.104	2.383	0.018	244	0.019
Weaning age	216	0.496	0.000	0.233	0.094	2.487	0.014	214	0.024
Population density	212	0.287	0.005	0.150	0.102	1.472	0.143	210	0.005
Generalism	280	0.503	0.000	-0.078	0.068	-1.156	0.249	278	0.001
Niche breadth	485	0.495	0.000	-0.342	0.041	-8.425	0.000	483	0.126
Body mass	485	0.543	0.000	-0.176	0.090	-1.961	0.051	483	0.006
Range size	485	0.400	0.000	-0.537	0.036	-14.894	0.000	483	0.313
<i>NEOTROPICS</i>									
Gestation length (BM)	246	0.627	0.000	-0.024	0.141	-0.172	0.863	243	-0.008
Weaning age (BM)	214	0.615	0.000	-0.054	0.098	-0.550	0.583	211	-0.008

Population density (BM)	242	0.609	0.000	0.220	0.095	2.317	0.021	239	0.014
Gestation length	246	0.627	0.000	-0.027	0.122	-0.222	0.824	244	-0.004
Weaning age	214	0.614	0.000	-0.048	0.087	-0.553	0.581	212	-0.003
Population density	242	0.617	0.000	0.181	0.086	2.103	0.036	240	0.014
Generalism	573	0.492	0.000	0.130	0.043	3.019	0.003	571	0.014
Niche breadth	1234	0.762	0.000	0.362	0.023	15.444	0.000	1232	0.162
Body mass	1234	0.441	0.000	-0.235	0.035	-6.783	0.000	1232	-0.001
Range size	1234	0.363	0.000	-0.273	0.080	-3.422	0.001	1232	0.092
<i>PALEARCTIC</i>									
Gestation length (BM)	340	0.306	0.001	0.154	0.128	1.207	0.228	337	0.004
Weaning age (BM)	265	0.449	0.000	0.043	0.116	0.369	0.713	262	-0.006
Population density (BM)	148	0.000	0.002	0.159	0.125	1.268	0.207	145	0.068
Gestation length	340	0.298	0.001	0.187	0.106	1.766	0.078	338	0.006
Weaning age	265	0.447	0.000	0.060	0.098	0.618	0.537	263	-0.002
Population density	148	0.110	0.103	-0.142	0.108	-1.309	0.193	146	0.005
Generalism	291	0.249	0.001	-0.050	0.072	-0.693	0.489	289	-0.002
Niche breadth	937	0.209	0.000	0.121	0.032	3.725	0.000	935	0.014
Body mass	937	0.227	0.000	-0.019	0.073	-0.255	0.799	935	-0.001
Range size	937	0.174	0.004	-0.284	0.032	-8.928	0.000	935	0.078
<i>GLOBAL</i>									
Gestation length (BM)	1122	0.467	0.000	0.068	0.074	0.922	0.357	1119	-0.001
Weaning age (BM)	948	0.528	0.000	0.068	0.057	1.197	0.232	945	-0.001
Population density (BM)	822	0.542	0.000	0.144	0.056	2.584	0.010	819	0.006
Gestation length	1122	0.468	0.000	0.067	0.074	0.913	0.361	1120	0.000
Weaning age	948	0.528	0.000	0.068	0.056	1.201	0.230	946	0.000
Population density	822	0.542	0.000	0.142	0.056	2.552	0.011	820	0.007
Generalism	1409	0.431	0.000	0.063	0.030	2.057	0.040	1407	0.002
Niche breadth	3767	0.687	0.000	0.001	0.004	0.303	0.762	3765	0.000
Body mass	3767	0.672	0.000	0.014	0.047	0.293	0.769	3765	0.000
Range size	3767	0.659	0.000	-0.045	0.003	-15.680	0.000	3765	0.061

Table A5.1.4. Results of models predicting ω_e with ω_i as a covariate in all models. Table as described in table A5.1.1.

<i>Variable</i>	<i>n</i>	λ	$p\lambda 0$	<i>Slope</i>	<i>Error</i>	<i>t</i>	<i>p</i>	<i>d.f.</i>	<i>Adj. R²</i>
<i>AFROTROPICS</i>									
Gestation length (BM)	287	0.000	0.984	-0.012	0.073	-0.166	0.869	283	0.206
Weaning age (BM)	221	0.000	0.989	-0.063	0.080	-0.793	0.429	217	0.235
Population density (BM)	207	0.000	0.987	0.058	0.091	0.637	0.525	203	0.295
Gestation length	287	0.000	0.988	0.022	0.054	0.401	0.689	284	0.207
Weaning age	221	0.000	0.990	-0.023	0.061	-0.369	0.713	218	0.237
Population density	207	0.000	0.987	0.054	0.060	0.908	0.365	204	0.299
Generalism	265	0.018	0.636	-0.001	0.055	-0.022	0.982	262	0.233
Niche breadth	766	0.066	0.000	0.171	0.031	5.533	0.000	763	0.362
Body mass	766	0.000	0.976	0.138	0.029	4.734	0.000	763	0.351
Range size	766	0.056	0.001	-0.062	0.031	-1.988	0.047	763	0.339
<i>AUSTRALASIA</i>									
Gestation length (BM)	83	0.000	0.988	0.081	0.081	1.008	0.316	79	0.519
Weaning age (BM)	91	0.000	0.984	-0.060	0.114	-0.528	0.599	87	0.521
Population density (BM)	46	0.000	0.989	-0.123	0.155	-0.796	0.431	42	0.404
Gestation length	83	0.000	0.987	0.047	0.078	0.606	0.546	80	0.510
Weaning age	91	0.000	0.985	0.057	0.074	0.775	0.441	88	0.517
Population density	46	0.000	0.989	-0.136	0.115	-1.179	0.245	43	0.418
Generalism	63	0.000	0.995	0.045	0.114	0.393	0.695	60	0.262
Niche breadth	159	0.000	0.998	0.061	0.061	0.999	0.319	156	0.441
Body mass	159	0.000	0.984	0.130	0.059	2.206	0.029	156	0.455
Range size	159	0.289	0.503	-0.170	0.058	-2.939	0.004	156	0.455
<i>INDOMALAYA</i>									
Gestation length (BM)	142	0.029	0.642	-0.137	0.084	-1.626	0.106	138	0.329
Weaning age (BM)	112	0.000	0.987	-0.266	0.096	-2.789	0.006	108	0.372
Population density (BM)	46	0.215	0.131	0.182	0.171	1.060	0.295	42	0.519
Gestation length	142	0.061	0.345	-0.095	0.080	-1.187	0.237	139	0.324
Weaning age	112	0.000	0.998	-0.165	0.076	-2.161	0.033	109	0.360
Population density	46	0.246	0.097	0.100	0.121	0.827	0.413	43	0.525
Generalism	167	0.000	0.987	0.163	0.061	2.682	0.008	164	0.386
Niche breadth	396	0.041	0.290	0.443	0.036	12.438	0.000	393	0.568
Body mass	396	0.033	0.371	0.029	0.050	0.590	0.555	393	0.399
Range size	396	0.023	0.593	0.124	0.039	3.191	0.002	393	0.413
<i>NEARCTIC</i>									
Gestation length (BM)	203	0.000	0.986	-0.119	0.049	-2.424	0.016	199	0.668
Weaning age (BM)	182	0.185	0.022	0.039	0.068	0.572	0.568	178	0.614
Population density (BM)	176	0.000	0.987	0.054	0.064	0.849	0.397	172	0.695
Gestation length	203	0.084	0.514	-0.037	0.050	-0.743	0.458	200	0.661
Weaning age	182	0.180	0.013	0.032	0.058	0.555	0.580	179	0.617
Population density	176	0.000	0.987	0.051	0.043	1.209	0.228	173	0.696
Generalism	202	0.000	0.985	0.102	0.038	2.683	0.008	199	0.715
Niche breadth	329	0.143	0.008	0.070	0.031	2.226	0.027	326	0.706
Body mass	329	0.117	0.029	-0.010	0.039	-0.250	0.803	326	0.704
Range size	329	0.120	0.023	0.025	0.034	0.743	0.458	326	0.704
<i>NEOTROPICS</i>									
Gestation length (BM)	201	0.374	0.000	0.097	0.089	1.094	0.275	197	0.507
Weaning age (BM)	177	0.405	0.001	0.019	0.070	0.266	0.790	173	0.532

Population density (BM)	199	0.275	0.006	0.052	0.059	0.871	0.385	195	0.675
Gestation length	201	0.367	0.000	0.106	0.078	1.365	0.174	198	0.510
Weaning age	177	0.394	0.002	0.057	0.062	0.920	0.359	174	0.531
Population density	199	0.385	0.001	-0.019	0.053	-0.363	0.717	196	0.660
Generalism	455	0.193	0.000	0.070	0.033	2.093	0.037	452	0.538
Niche breadth	830	0.313	0.000	0.355	0.019	18.822	0.000	827	0.726
Body mass	830	0.267	0.000	0.086	0.037	2.311	0.021	827	0.614
Range size	830	0.246	0.000	0.149	0.022	6.853	0.000	827	0.634
<i>PALEARCTIC</i>									
Gestation length (BM)	266	0.000	0.988	0.111	0.064	1.742	0.083	262	0.435
Weaning age (BM)	216	0.000	0.994	0.121	0.065	1.854	0.065	212	0.493
Population density (BM)	119	0.052	0.769	-0.043	0.128	-0.334	0.739	115	0.345
Gestation length	266	0.000	0.986	0.112	0.046	2.417	0.016	263	0.437
Weaning age	216	0.000	0.995	0.090	0.049	1.858	0.064	213	0.494
Population density	119	0.097	0.338	-0.104	0.094	-1.106	0.271	116	0.339
Generalism	210	0.130	0.100	-0.029	0.061	-0.480	0.632	207	0.377
Niche breadth	662	0.032	0.245	0.258	0.026	10.083	0.000	659	0.589
Body mass	662	0.064	0.086	0.052	0.040	1.298	0.195	659	0.527
Range size	662	0.068	0.035	0.052	0.028	1.844	0.066	659	0.528
<i>GLOBAL</i>									
Gestation length (BM)	973	0.268	0.000	0.114	0.049	2.331	0.020	969	0.441
Weaning age (BM)	821	0.203	0.006	0.059	0.037	1.606	0.109	817	0.490
Population density (BM)	691	0.241	0.003	-0.038	0.037	-1.013	0.311	687	0.577
Gestation length	973	0.269	0.000	0.114	0.049	2.326	0.020	970	0.441
Weaning age	821	0.204	0.003	0.062	0.037	1.693	0.091	818	0.489
Population density	691	0.240	0.003	-0.038	0.037	-1.024	0.306	688	0.577
Generalism	1148	0.141	0.000	0.037	0.023	1.597	0.111	1145	0.509
Niche breadth	2725	0.292	0.000	0.219	0.013	17.233	0.000	2722	0.610
Body mass	2725	0.243	0.000	0.069	0.026	2.651	0.008	2722	0.571
Range size	2725	0.293	0.000	0.028	0.013	2.245	0.025	2722	0.568

Appendix 6. Supporting information for chapter 6

Detecting shifts in diversity limits from molecular phylogenies: what can we know?

6.1 – Assessing alternative diversification scenarios

Methods

To explore the performance of my methods more broadly, I simulated trees under a range of diversity-independent models (figure A6.1). Specifically, I use two null models – the pure birth and the constant-rate birth-death – and a third model where the rate change is an increase in net diversification rate.

For consistency with the rest of my simulations, all trees have a tree age (T) of 110 My and I identity parameters that are expected to produce ~500 or 1000 extant lineages (N) at the present day.

For the pure birth trees, I used $\ln(N)/T$ to identify appropriate speciation rates: $\ln(500)/110 = 0.0565$ and $\ln(1000)/110 = 0.06280$. To test a range of rates I use $\lambda = 0.03, 0.06$ and 0.09 .

This upper bound is similar to that estimated by Magallon & Sanderson (2001) for angiosperms in the absence of extinction.

For the constant-rate birth-death trees, I used the method of moments estimator (cited in Magallon & Sanderson, 2001) to obtain appropriate net diversification rates:

$$r = (1/T) * \log(N(1-\varepsilon) + \varepsilon)$$

Here ε = the extinction fraction (μ/λ). I used three values of ε (0.2, 0.5, 0.8) with the two values of N (500, 1000) to produce six parameter combinations ($\lambda = 0.068, 0.100, 0.210, 0.0760, 0.113, 0.241; \mu = 0.0136, 0.0500, 0.1680, 0.0152, 0.0565, 0.1928$).

Finally, I simulate a set of “rate-increase” trees using $\lambda = 0.1$ and extinction fraction = 0.5, but after $T_1 = 55$ My I introduce a rule change: an increase in net diversification rate (r) such that both speciation and extinction rates increase by some factor between 1.2 and 2 (different runs differing by steps of 0.2). The simulations continue at these new rates for $T_2 = 55$ My. Because diversity is not constrained under this scenario, the rule change is not expected to be associated with a pulse of diversification. I wanted to know if this alternative scenario would nevertheless produce a similar signal of pulsed diversification.

I assess Type I error rates as the proportion of null simulations in which a significant shift in diversification rate was detected at 55 My (i.e., the end of T_1). For the “rate-increase” trees, I assessed the power of my methods by calculating the number of simulations showing a significant change at the end of T_1 , minus the corresponding Type I error rate from the corresponding null simulations. For all parameter combinations, I simulate 100 replicate trees. In total 1400 trees were analysed.

Incorporating lineage-specific rate heterogeneity

As a simple means of assessing the effects of lineage-specific rate heterogeneity on my ability to recover rule changes, I simulated trees where only a fraction of clades extant at the time of the rule change are affected by the change in M . Biologically, such a scenario could occur if only a fraction of lineages enter new ecospace while the remaining lineages persist in the original area.

I retain most features from my original logistic diversity-dependent model of diversification including the parameters: $b = 1$, $T_1 = 55$ My, $T_2 = 55$ My, $M_1 = 500$ (and see text of chapter 6). At the end of T_1 , I randomly select a proportion of lineages and update their diversification rate to incorporate the new M ($M_2 = 1000$). The remaining lineages continue to

diversify under the original M (M_I). I test proportions of 0.2, 0.5 and 0.8 and extinction rates between 0.1 and 0.5 in steps of 0.1 (see figure A6.1).

I am only interested here in determining whether rule changes can still be detected when they affect only a subset of lineages. Therefore, I choose lineages randomly rather than according to some relatedness rule. Because my methods do not depend on tree topology, but only on the temporal clustering of nodes, the power of my methods should be similar whether or not responding lineages are clustered or located randomly on the tree.

Results & discussion

Type I error rates were reasonable for all the diversity-independent null simulations (table A6.1.1). Furthermore, my methods did not consistently recover a diversification pulse in the “rate-increase” trees (table A6.1.2). These results underline that my methods are robust to alternative diversification scenarios and provide assurance that when an interval is identified as significant in empirical data it really is likely to stem from a diversification pulse localised to that interval.

Power was high to detect diversification pulses when only a proportion of lineages are affected by the rule change (table A6.1.2). In fact, as the proportion of lineages affected decreases, my ability to detect the pulse increases. Because most lineages at the present day (and thus present in the reconstructed phylogeny) are derived from that small proportion that responded to the rule change, the pulse appears more pronounced and remains detectable even in the face of high turnover rates.

Figure A6.1. Example lineage-through-time plots for alternative diversification scenarios. A. Yule model, $\lambda = 0.06$. B. Constant-rate birth-death model, $\lambda = 0.113$, $\mu = 0.565$. C. Birth-death model with rate shift at 55 My, $\lambda = 0.1$, $\mu = 0.5$, rate multiplier = 2. D. Diversity-dependent model with a subset of lineages responding, $b = 1$, $d = 0.3$, $M_1 = 500$, $M_2 = 1000$ (for those responding), proportion responding: 0.2 (solid lines), 0.5 (dashed lines), 0.8 (dotted lines). In all plots black lines include all lineages, grey lines include only lineages extant at the present day.

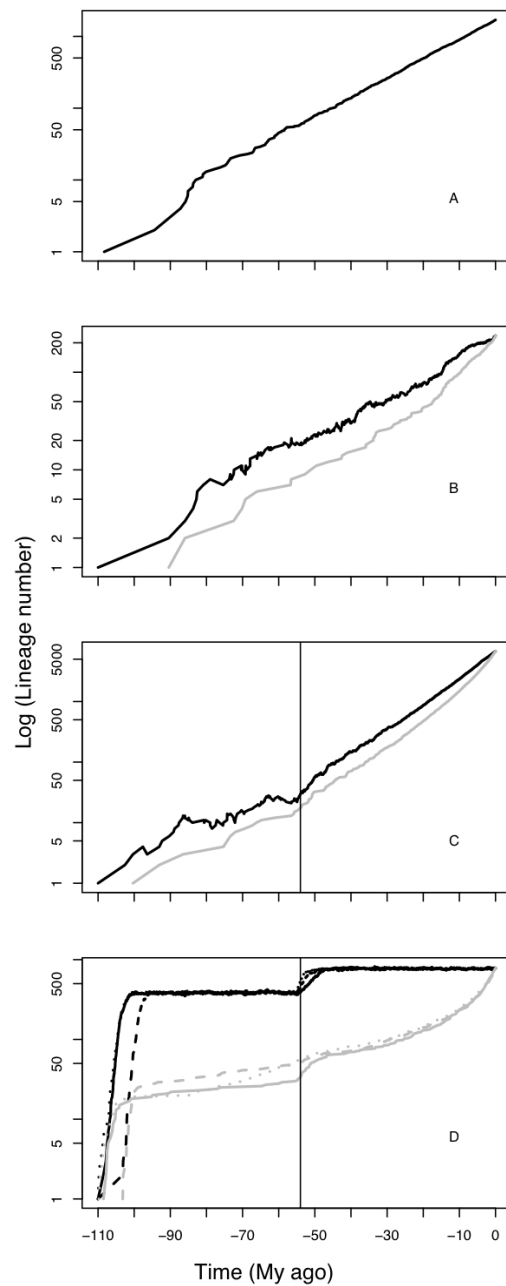


Table A6.1.1. Type I error rates of diversity-independent null simulations. For details of parameters involved in the simulations, see text.

Yule		λ	0.03	0.06	0.09
	GAM		0.06	0.04	0.02
	$\Delta\gamma$		0.13	0.01	0.08
Birth-death		<i>Extinction fraction</i>	0.2	0.5	0.8
Expected $N = 500$	GAM		0.06	0.06	0.07
	$\Delta\gamma$		0.00	0.04	0.16
Expected $N = 1000$	GAM		0.05	0.06	0.12
	$\Delta\gamma$		0.02	0.04	0.04

Table A6.1.2. Power of alternative diversification scenarios to detect rule changes at the end of T1 (55 My ago). For details of parameters involved in the simulations and how power was calculated, see text.

Birth-death with rate shift		<i>Diversification rate multiplier</i>	1.2	1.4	1.6	1.8	2.0
	GAM		0.05	0.00	0.01	0.04	0.03
	$\Delta\gamma$		0.02	0.01	0.01	0.02	0.01
Prop. of clades responding		Prop./ μ	0.1	0.2	0.3	0.4	0.5
GAM		0.2	0.97	0.95	0.86	0.92	0.79
		0.5	0.97	0.89	0.8	0.77	0.56
		0.8	0.97	0.84	0.51	0.5	0.23
		1	0.97	0.71	0.33	0.21	0.12
$\Delta\gamma$		0.2	0.96	0.96	0.88	0.85	0.76
		0.5	0.96	0.84	0.66	0.66	0.44
		0.8	0.95	0.71	0.45	0.35	0.25
		1	0.95	0.36	0.35	0.18	0.16

6.2 – Correcting for multiple tests

When conducting multiple tests (i.e., assessing the significance of each time interval in the absence of any *a priori* hypothesised intervals of interest), it is necessary to adjust the level at which a result is considered significant to avoid inflating type I errors (the more intervals tested, the more likely one will be considered significant by chance). The sequential Bonferroni adjusts the threshold p value (α) to reflect the number of tests (n) being made. Thus the most significant interval must be more significant than α/n , the second most significant by $\alpha/n-1$, and so on (Holm, 1979). However, because such corrections consider each test independent the enforced penalties may be unduly conservative (Moran, 2003). In autocorrelated data such as these, a less conservative method is to determine the effective sample size using the autocorrelation coefficient or, as here, estimating the spectral density at frequency zero after fitting an autoregressive model to the time series (Plummer *et al.*, 2010). Specifically, I removed intervals identified as significant using my unadjusted test (as I found they otherwise removed all apparent autocorrelation) and then calculated the effective sample size (ESS) of the remaining intervals. To this value I added the number of intervals removed, to obtain a conservative ESS. I then used this value in a modified sequential Bonferroni correction.

6.3 – Validity testing

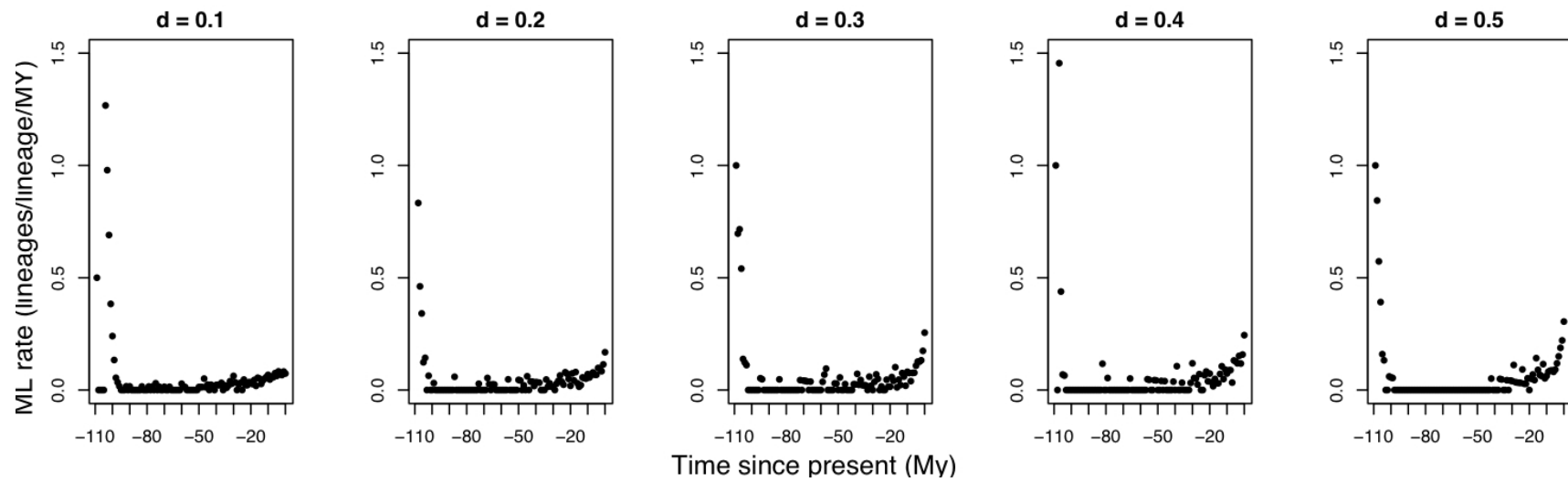
Table A6.3. Validity testing. For each parameter combination, the proportion of false positives was calculated. Validity was assessed using a binomial test where the alternative hypothesis is that the proportion of false positives is greater than 0.05.

		0.1		0.2		0.3		0.4		0.5	
GAM	K_2	<i>Prop.</i>	<i>p</i>	<i>Prop.</i>	<i>p</i>	<i>Prop.</i>	<i>p</i>	<i>Prop.</i>	<i>p</i>	<i>Prop.</i>	<i>p</i>
	600	0.068	0.000	0.069	0.000	0.076	0.000	0.084	0.000	0.090	0.000
	700	0.059	0.001	0.069	0.000	0.065	0.000	0.079	0.000	0.085	0.000
	800	0.050	0.530	0.065	0.000	0.065	0.000	0.074	0.000	0.080	0.000
	900	0.042	1.000	0.061	0.000	0.065	0.000	0.067	0.000	0.075	0.000
	1000	0.032	1.000	0.057	0.004	0.067	0.000	0.067	0.000	0.073	0.000
$\Delta\gamma$	K_2										
	600	0.050	0.551	0.050	0.464	0.058	0.001	0.056	0.012	0.055	0.027
	700	0.049	0.616	0.053	0.155	0.051	0.421	0.054	0.067	0.054	0.067
	800	0.060	0.000	0.049	0.716	0.051	0.400	0.051	0.338	0.052	0.212
	900	0.057	0.004	0.055	0.039	0.053	0.131	0.054	0.074	0.056	0.019
	1000	0.064	0.000	0.049	0.657	0.050	0.442	0.053	0.168	0.055	0.024
		0.1		0.2		0.3		0.4		0.5	
GAM		<i>Prop.</i>	<i>p</i>	<i>Prop.</i>	<i>p</i>	<i>Prop.</i>	<i>p</i>	<i>Prop.</i>	<i>p</i>	<i>Prop.</i>	<i>p</i>
	Doubling-in-M	0.035	1.000	0.057	0.007	0.063	0.000	0.069	0.000	0.076	0.000
	Mass extinction	0.025	1.000	0.057	0.004	0.058	0.002	0.064	0.000	0.069	0.000
$\Delta\gamma$											
	Doubling-in-M	0.055	0.031	0.053	0.131	0.055	0.031	0.061	0.000	0.062	0.000
	Mass extinction	0.061	0.000	0.050	0.530	0.053	0.131	0.053	0.100	0.050	0.573

GAM		0.1		0.2		0.3		0.4		0.5	
	T_2	<i>Prop.</i>	<i>p</i>	<i>Prop.</i>	<i>p</i>	<i>Prop.</i>	<i>p</i>	<i>Prop.</i>	<i>p</i>	<i>Prop.</i>	<i>p</i>
	10	0.017	1.000	0.026	1.000	0.039	1.000	0.056	0.032	0.064	0.000
	20	0.017	1.000	0.039	1.000	0.055	0.046	0.059	0.001	0.064	0.000
	30	0.019	1.000	0.045	0.973	0.063	0.000	0.066	0.000	0.065	0.000
	40	0.023	1.000	0.049	0.716	0.062	0.000	0.064	0.000	0.065	0.000
	50	0.027	1.000	0.056	0.012	0.065	0.000	0.066	0.000	0.071	0.000
	60	0.031	1.000	0.064	0.000	0.066	0.000	0.066	0.000	0.069	0.000
	70	0.042	0.999	0.065	0.000	0.068	0.000	0.067	0.000	0.081	0.000
	80	0.045	0.979	0.065	0.000	0.071	0.000	0.079	0.000	0.083	0.000
	90	0.051	0.379	0.065	0.000	0.075	0.000	0.089	0.000	0.091	0.000
	100	0.053	0.120	0.070	0.000	0.077	0.000	0.090	0.000	0.096	0.000
$\Delta\gamma$	T_2										
	10	0.086	0.000	0.073	0.000	0.064	0.000	0.043	0.988	0.052	0.256
	20	0.067	0.000	0.053	0.127	0.044	0.979	0.045	0.972	0.037	1.000
	30	0.059	0.000	0.050	0.485	0.042	0.999	0.040	1.000	0.041	1.000
	40	0.061	0.000	0.046	0.936	0.047	0.845	0.044	0.992	0.050	0.464
	50	0.062	0.000	0.057	0.005	0.051	0.358	0.049	0.594	0.056	0.014
	60	0.059	0.001	0.055	0.024	0.054	0.091	0.051	0.400	0.055	0.043
	70	0.060	0.000	0.051	0.400	0.052	0.212	0.052	0.182	0.052	0.182
	80	0.053	0.120	0.053	0.100	0.053	0.109	0.057	0.003	0.049	0.657
	90	0.057	0.004	0.050	0.573	0.054	0.054	0.056	0.009	0.056	0.009
	100	0.053	0.120	0.057	0.004	0.058	0.001	0.058	0.001	0.056	0.008

6.4 – Exploring downshifts

Figure A6.4. Exploring downshifts. ML rate estimates are plotted against time for five exemplar trees simulated with $b = 1$, $M_1 = 1000$, $M_2 = 500$, $T_1 = 55$ My, $T_2 = 55$ My and $d = 0.1$ to 0.5 in steps of 0.1 .



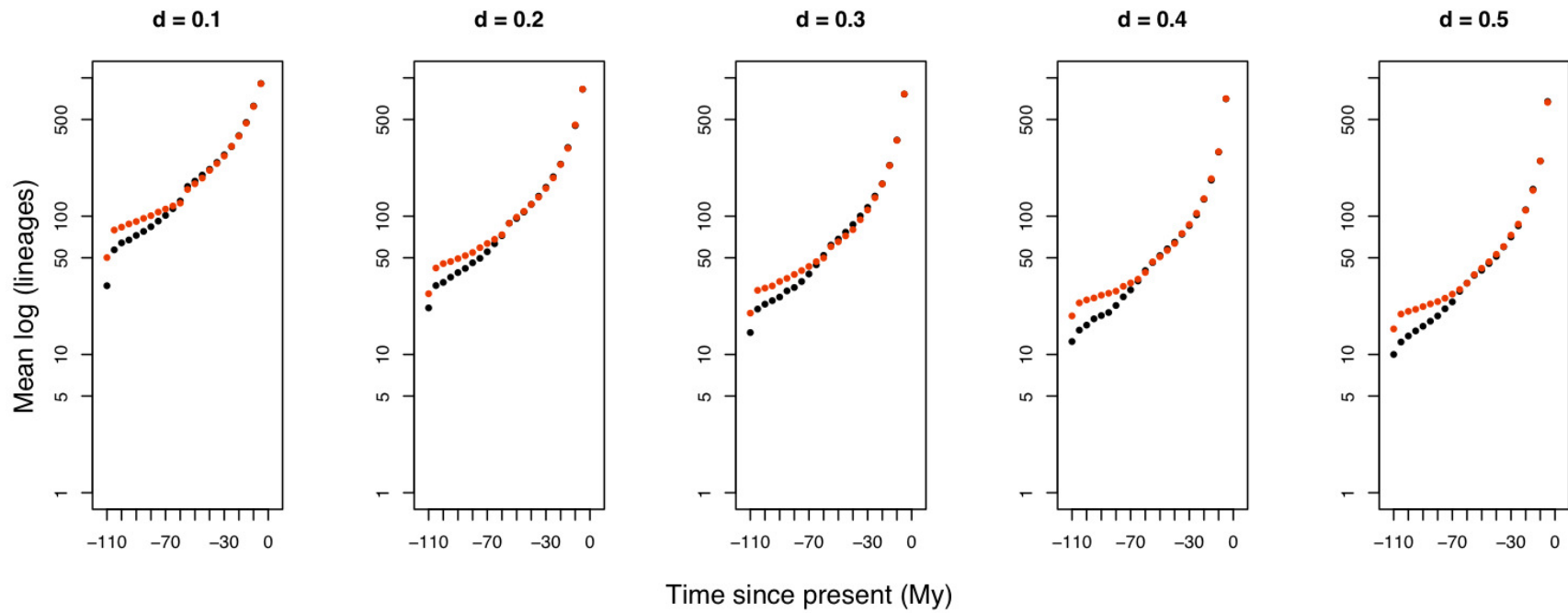
6.5 – Empirical results tables

Table A6.5. Significant intervals identified in the angiosperm and mammal supertrees. Bold values are those that remain significant when p values are adjusted for multiple testing according to all three methods. Italicised values remain significant only under my modified sequential Bonferroni method.

	1My	2My	5My
GAM			
All mammals	99 , 97, 92, 90 , 89, 86, 83, 48, 30	100 , 92, 90 , 48	<i>100</i> , 90, 85
Atlantogenata	70, 56, 26	70, 56, 26	70, 55
Euarchothoglires	48 , 29	48	65, 50
Laurasiatheria	62, 33 , 26	<i>34</i>	---
Marsupials	34, 30	56, 46, 34	---
Angiosperms	130, 125, 121, 118 , <i>105</i> , 103, 78	126, <i>118</i> , 106, 104	<i>105</i>
$\Delta\gamma$			
All mammals	99.2, 83.2, 62.2, 48.2 , 47.2 , 46.2 , 41.2, 40.2, 35.2, 33.2 , 32.2 , 31.2, 30.2, 26.2 , 24.2	100.2, 52.2, 50.2, 48.2 , <i>46.2</i> , 36.2 , 34.2 , 32.2, 30.2	101.2, <i>96.2</i> , 91.2, 26.2 , 21.2
Atlantogenata	71.9, 57.9, 40.9, 27.9, 22.9	72.9, 58.9, 28.9	28.9 , 23.9
Euarchothoglires	64.9, 48.9 , 47.9, 45.9, 38.9, 31.9, 30.9, 29.9 , 23.9	<i>51.9</i> , 49.9 , 47.9, 45.9, 29.9	56.9 , 51.9 , 26.9 , 21.9
Laurasiatheria	62.5, <i>61.5</i> , 60.5, 41.5 , 40.5, 34.5 , 33.5 , 32.5 , 27.5, 26.5	62.5, 36.5, 34.5 , 32.5 , 30.5	43.5, 38.5, 23.5
Marsupials	46.5, 45.5, 30.5, 23.5	36.5, 34.5	37.5
Angiosperms	118.1, 103.1, 80.1, 78.1, 68.1, <i>67.1</i> , 66.1, 58.1, 27.1	106.6, 104.6, 92.6, 80.6, 78.6, 68.6, 58.6	<i>107.1</i> , 72.1

6.6 – Signal from mass extinction

Figure A6.6. Comparing lineage-through-time plots for doubling-in-M (black points) versus mass extinction (red points) trees (see text for details). Mean lineage number (from 100 replicate trees) is plotted every 5 My.



Appendix 7. Additional references from appendices 2-6

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