

Comparative analyses of extinction risk in vertebrates

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Abstract

Measures of current extinction risk imply that a high proportion of the world's species are threatened with global extinction in the near future, stressing the need for thorough understanding of extinction processes. In this thesis, I investigate three aspects of current global species extinction risk, using novel phylogenetic and spatially-explicit comparative methods. First, I develop a new measure of the phylogenetic-signal strength in extinction risk, and use it to show that the non-randomness in global mammalian extinction risk differs with threatening processes. These results imply that the biological traits which increase species' susceptibility depend on the anthropogenic threat experienced.

Secondly, I investigate the focus of current extinction risk, both spatially and in terms of biological traits increasing risk. I model regional extinction-risk correlates for mammals across the globe, finding strong geographical variation in the influence of biological traits on risk, and in trait interactions with anthropogenic impacts. I also compare biological and anthropogenic correlates of global extinction risk across and within mammals, birds and frogs. Results from this large-scale comparative study further confirm the strong heterogeneity of extinction processes, with taxon-specific traits playing a relatively large role in determining species' fates.

Finally, I estimate possible impacts of current extinction risk using three measures of global mammalian diversity: species richness, phylogenetic diversity and functional diversity. My results show that selective losses of large species will deplete functional variety in mammals, especially in the tropics. Loss of functional diversity is much higher than expected under random species loss, and there is low congruence with losses of species richness and phylogenetic diversity. The selectivity of current extinction risk means that we stand to lose a very biased sample of global diversity, with potentially severe consequences for ecosystem functioning.

Declaration

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

The new version of the mammal supertree used throughout, updated with methods described in chapter 3, was modified from the published original version by Olaf Bininda-Emonds, using a table of topology changes that I had generated myself. He also dated the new topology as described in chapter 3.

Most datasets used in this thesis were compiled by others, and I cite published datasets throughout and acknowledge sources of unpublished data. My own major contributions to data collection were expanding the amphibian dataset used in chapter 4 together with Kennet Mattsson, and contributing the synonym table for the final taxonomy used in the PanTHERIA dataset, which draws together multiple records for species (Jones *et al.* 2009).

I also used some programming code kindly provided by others (see also Acknowledgements): code to compute MPD in chapter 2, the ArcInfo macro used to calculate spatial variable means for chapters 3 and 4, code for fitting PGLMs in chapters 3 and 4, code to optimise AIC values for spatial models in chapter 3, and code to correct for terminal polytomies in chapter 5. Published software and programming code I used is cited throughout.

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“It is most difficult always to remember that the increase of every living being is constantly being checked by unperceived injurious agencies; and that these same unperceived agencies are amply sufficient to cause rarity, and finally extinction. We see in many cases in the more recent tertiary formations, that rarity precedes extinction; and we know that this has been the progress of events with those animals which have been exterminated, either locally or wholly, through man’s agency.”

(Darwin 1859, p. 323)

“Pour qui ont-ils donc travaillé, ces admirables hommes? Hélas!
pour le vent qui souffle, pour l’herbe qui pousse,
pour le lierre qui vient comparer ses feuillages aux leurs,
pour l’hirondelle qui passe, pour la pluie qui tombe,
pour la nuit qui descend.”

Victor Hugo, from “Le Rhin” (on the ruins of Heidelberg Castle)

„Man muss in keiner Pfanne gelegen haben,
um über Schnitzel schreiben zu können.“

Kurt Tucholsky

Table of Contents

ABSTRACT.....	2
DECLARATION	3
ACKNOWLEDGEMENTS	4
TABLE OF CONTENTS	7
LIST OF FIGURES	11
LIST OF TABLES	12
 CHAPTER 1: INTRODUCTION.....	 13
The current extinction crisis	13
Phylogenetic and spatial patterns of extinction risk	15
Correlates of extinction risk.....	17
Future impacts of current extinction risk.....	20
Measuring and analysing extinction risk.....	21
Thesis aims	24
 CHAPTER 2: SELECTIVITY IN MAMMALIAN EXTINCTION RISK AND THREAT TYPES – A NEW MEASURE FOR PHYLOGENETIC SIGNAL STRENGTH IN BINARY TRAITS.....	 25
Abstract	25

Introduction.....	26
Methods	28
Derivation of D	28
Testing the behaviour of D with simulated and real datasets	32
Results.....	34
Discussion	41
Statistical performance of D and comparison with previous methods	41
Global extinction risk and threat patterns in mammals	43

CHAPTER 3: GEOGRAPHICAL VARIATION IN PREDICTORS OF MAMMALIAN EXTINCTION RISK – BIG IS BAD, BUT ONLY IN THE TROPICS.....46

Abstract	46
Introduction.....	47
Methods	49
Dataset and phylogeny	49
Phylogenetic analyses	51
Spatial analyses	52
Results.....	57
Discussion	64
Body mass	67
Geographic range size	69
Abundance and life-history traits	71
Conclusions.....	71

CHAPTER 4: COMPARATIVE ANALYSIS OF EXTINCTION-RISK CORRELATES IN MAMMALS, BIRDS AND FROGS.....73

Abstract	73
-----------------------	-----------

Introduction.....	74
Methods	76
Dataset and phylogeny	76
Phylogenetic analyses	85
Results.....	87
Discussion	99
Anthropogenic impacts	101
Biological traits	103
Conclusions.....	105

CHAPTER 5: GLOBAL MAMMALIAN FUNCTIONAL AND PHYLOGENETIC DIVERSITY AT RISK OF EXTINCTION.....107

Abstract	107
Introduction.....	108
Methods	110
Results.....	114
Discussion	119
Selective losses of large mammals.....	120
Losses of evolutionary history	121
Possible impacts of FD losses	122
Conservation implications.....	123

CHAPTER 6: CONCLUDING REMARKS 125

Summary of results and implications.....	125
Possible sources of bias.....	127
Body size and geographic range size as risk correlates in other taxa.....	130
Conclusion	131



Representation of this thesis generated at www.wordle.net. The size of the words plotted is proportional to their frequency in the text.

List of Figures

Fig. 2-1. Relationship of D for a binary trait and λ for an underlying continuous trait	35
Fig. 2-2. Performance of D for simulated traits	36
Fig. 3-1. Species numbers per ecoregion and results of within-ecoregion models for mammalian species extinction risk	58
Fig. 3-2. Moran's I correlograms of non-spatial and spatial model residuals.....	65
Fig. 3-3. Results of likelihood ratio tests for non-spatial and spatial models across ecoregions	66
Fig. 4-1. Histograms of the within-family proportions of threatened species under different extinction-risk measures within and across taxa.....	88
Fig. 4-2. Scatterplots of extinction risk vs. anthropogenic threats and biological traits across mammalian, avian and anuran families.....	90
Fig. 5-1. Histograms of body mass values for the dataset excluding and including interpolated values	112
Fig. 5-2. The number and proportion of interpolated species body-mass values within ecoregions	113
Fig. 5-3. Projected changes of mammalian diversity and mean body mass within ecoregions	115
Fig. 5-4. Projected changes of mammalian diversity and mean body mass within ecoregions including Near Threatened species	116
Fig. 5-5. Projected and simulated proportional losses of mammalian diversity within ecoregions	118
Fig. 5-6. Areas of significantly non-random PD and FD losses	120
Fig. C-1. Overview of the composite phylogeny showing mammalian, avian and anuran families	165
Fig. C-2. Phylogeny of anuran families	166
Fig. C-3. Phylogeny of mammalian families (part 1)	167
Fig. C-4. Phylogeny of mammalian families (part 2)	168
Fig. C-5. Phylogeny of avian families (part 1)	169
Fig. C-6. Phylogeny of avian families (part 2)	170

List of Tables

Table 2-1. The calculation of D for different types of phylogenetic pattern in binary traits	29
Table 2-2. Simulation results demonstrating significance testing with D	37
Table 2-3. Phylogenetic signal in different categories of conservation concern for 181 British birds, using mean phylogenetic distance from Thomas (2008) and D	38
Table 2-4. Phylogenetic patterns of extinction risk and threat in mammals as indicated by D	40
Table 3-1. Data availability and phylogenetic signal for species traits in the mammal dataset	50
Table 3-2. Description and sources for variables used in the non-spatial and spatial models across ecoregions	54
Table 3-3. Human influence measures and their loadings in the principal components analysis for the first three principal components	55
Table 3-4. Results of global extinction risk models for the complete mammal dataset using PGLM	61
Table 3-5. Results of within-ecoregion models of extinction risk for each biogeographic realm	62
Table 3-6. Results of non-spatial ordinary least-squares and spatially-explicit simultaneous autoregressive models across ecoregions	63
Table 4-1. Data availability for all variables in the dataset	80
Table 4-2. Results of PGLMs for overall extinction risk within and across taxa	89
Table 4-3. Results of PGLMs for extinction risk from habitat loss within and across taxa	94
Table 4-4. Results of PGLMs for extinction risk from harvesting within and across taxa	95
Table 4-5. Results of PGLMs for extinction risk from invasive species within and across taxa	96
Table 4-6. Results of mammal-specific PGLMs for different extinction risk measures	97
Table 4-7. Results of bird-specific PGLMs for different extinction risk measures	98
Table 4-8. Results of frog-specific PGLMs for different extinction risk measures	99
Table 5-1. Losses of species richness, phylogenetic diversity and functional diversity globally and within biogeographical realms	117

Chapter 1: Introduction

The current extinction crisis

There is now little doubt that many populations worldwide are declining or going extinct, causing many species to be threatened with global extinction (Loh *et al.* 2005, Collen *et al.* 2009). Most of the recent and ongoing population declines and species extinctions have anthropogenic causes (Baillie *et al.* 2004, Mace *et al.* 2005). Although direct comparisons are hard to make and quite crude, vertebrate extinction rates over the last hundred years have been 20 to 200 times higher than the background extinction rates estimated from the fossil record (May *et al.* 1995, Pimm *et al.* 1995). Projected impacts of current extinction drivers indicate future extinction rates 1,000 to 10,000 times higher than the fossil background rate (Pimm *et al.* 1995, Mace *et al.* 2005). Due to the global demands of a growing human population, the current extinction crisis looks set to extinguish large numbers of species and dramatically change current ecosystems (Millennium Ecosystem Assessment 2005).

According to the IUCN Red List of Threatened Species, 22% of evaluated vertebrates and 41% of evaluated invertebrates are currently threatened by extinction (IUCN 2008). These numbers may overestimate risk prevalence, because in most taxonomic groups extinction risk has only been assessed for a small proportion of the species known to exist. However, the risk-status of some well-known vertebrate groups has been evaluated completely: 21% of mammal, 12% of bird and 31% of amphibian species are currently listed as threatened with extinction, a total of 4268 threatened species just in these three taxa. Even for these well-known groups, the true extinction risk may be higher: 15% of mammals, 1% of birds and 25% of amphibians are classified as Data Deficient, because insufficient data are available to evaluate their risk status.

The aim of conservation science is to counter this threat of an imminent mass extinction as cost-effectively as possible. To do this, we need to understand what drives species to extinction and why different taxa are not equally susceptible to different threats. The scale of the current extinction crisis is such that global approaches are needed both to understand the complex patterns of extinction risk and to counter them. While species extinction risk is based on population dynamics, the study of population extinctions is necessarily often local and species-specific; also, local population extinctions may be reversible, but a species' global extinction is not. I therefore concentrate on investigating global species extinction risk, rather than population dynamics, in this thesis.

Studying current extinction risk differs from the study of past extinctions. Current extinction processes are probably different from those recorded in the fossil record, as the ultimate causes differ (Purvis 2008); also, timescales today may be shorter and estimated extinction rates higher (Pimm *et al.* 1995, Mace *et al.* 2005). On geological timescales, humans pose a truly new threat, and even their involvement in Pleistocene extinctions (approximately 50,000 to 12,000 years ago) is much debated (Burney and Flannery 2005, Wroe *et al.* 2006). Records of historical extinctions are biased both taxonomically and spatially, and are hard to compare to present-day extinction-risk patterns (May *et al.* 1995). Available data show that the current threats differ, with widespread habitat loss across whole continents replacing introduced species on oceanic islands as the main threat, at least for birds and mammals (Mace and Balmford 2000, Bennett and Owens 2002, Blackburn *et al.* 2004).

All these reasons imply that, to understand current extinction processes, we need to study current global extinction risk rather than past extinction patterns or population extinctions. Comparative analyses across species are a powerful approach for investigating global large-scale patterns, and disentangling extrinsic and intrinsic contributions to species extinction risk (Harvey and Pagel 1991, Fisher and Owens 2004). In this thesis, I investigate the complex patterns of current, global species extinction risk for some well-known vertebrate taxa with

phylogenetic and spatially-explicit comparative methods, to improve understanding of the extinction process at the species scale.

Phylogenetic and spatial patterns of extinction risk

Comprehensive global maps of threatened species richness only exist for a few taxa, with patterns for mammals, birds and amphibians being the most well-known (Baillie *et al.* 2004). High numbers of threatened mammal, bird and amphibian species are found in East Africa, Madagascar, the Indian Western Ghats and Borneo, but the overall congruence of the spatial threat pattern is quite low in these three groups (Grenyer *et al.* 2006). Threatened mammals are most concentrated in the African Eastern Arc and South-East Asia, and occur throughout much of sub-Saharan Africa (Schipper *et al.* 2008, see also Fig. 3-1a), while threatened birds occur mostly in the Andes, the Brazilian Atlantic Rainforest, and the Eastern Himalayas, as well as on tropical islands (Orme *et al.* 2005, Ceballos and Ehrlich 2006). Threatened amphibians are concentrated in Central America, the Andes, Caribbean, Brazilian Atlantic Rainforest, Cameroon, southern India and Sri Lanka (Stuart *et al.* 2004).

As some areas clearly contain more threatened species than others, extinction risk is non-randomly distributed across the globe. This could be caused by regional variation in threat types and intensity, but also by species-richness patterns and species traits. Threats or extrinsic factors driving species to extinction today are overwhelmingly anthropogenic, the main global ones being habitat loss, overexploitation, invasive species, infectious diseases, pollution and climate change (Baillie *et al.* 2004, Mace *et al.* 2005). The low congruence of spatial risk patterns between taxa implies that spatial threat patterns alone cannot account for the regional variation seen in extinction risk (Grenyer *et al.* 2006). Differences in the spatial distribution of species richness between taxa play a role, but there is low global congruence between threatened and total species richness within taxa,

implying that differences in susceptibility exist (Orme *et al.* 2005, Ceballos and Ehrlich 2006, Grenyer *et al.* 2006).

Another way of estimating susceptibility to anthropogenic threats is to investigate phylogenetic patterns in extinction risk. Globally or within regions, threatened taxa are often more closely related than expected if extinction was phylogenetically random (Bennett and Owens 1997, Russell *et al.* 1998, Purvis *et al.* 2000a, Lockwood *et al.* 2002, Stuart *et al.* 2004, Bielby *et al.* 2006). This phylogenetic or taxonomic non-randomness in extinction risk means that some taxa are disproportionately threatened: for example, of the species-rich mammalian orders, artiodactyls, perissodactyls and primates have significantly higher proportions of threatened species than expected under a phylogenetically random extinction scenario, whereas rodents have a much lower proportion of threatened species than expected (Mace and Balmford 2000).

Taxonomic extinction selectivity has long been known from the fossil record (McKinney 1997), and palaeontologists have phrased the possible reasons as “bad genes or bad luck” (Raup 1993): are at-risk species intrinsically more susceptible due to evolved traits shared by close relatives (“bad genes”), or do they just live in highly threatened environments (“bad luck”)? For current extinction risk, some evidence against the bad-luck hypothesis or field-of-bullets scenario, where species go extinct independently of their biology, is provided by the contrasting spatial patterns of extinction risk in different clades described above. Stronger evidence is provided by the phylogenetic or taxonomic selectivity of extinction risk, especially if found at small spatial scales (Davies *et al.* 2008, see Appendix A).

Many previous studies have focused on testing for significant selectivity in extinction risk, but the strength of its phylogenetic signal has not been investigated much, probably because measures of signal strength such as the amount of threatened evolutionary history are not comparable across different phylogenies (Purvis *et al.* 2000a). However, phylogenetic-signal strength of

overall extinction risk and different threat types can give a good indication of the kind of species' traits that increase susceptibility, and so provide valuable information about the extinction process. In chapter 2, I propose a new measure for phylogenetic-signal strength in binary traits such as threatened vs. non-threatened, and apply it to global patterns of extinction risk in mammals. I investigate the magnitude of phylogenetic selectivity in extinction risk for all known mammals on a global scale, and my study is the first to tease apart phylogenetic signal in different threats such as habitat loss and harvesting.

Correlates of extinction risk

The spatial and phylogenetic patterns of extinction risk strongly imply that both anthropogenic threats and biological susceptibility play a role in determining species' fates. This has led to many studies investigating which biological traits (intrinsic factors) and measures of anthropogenic impact (extrinsic factors) influence extinction risk (see Fisher and Owens 2004, Purvis 2008 for recent reviews). The species trait which most consistently predicts extinction risk is geographic range size, because small-ranged species have decreased chances of evading local threats (e.g. Purvis *et al.* 2000b, Cooper *et al.* 2008). Similarly, low population density serves to make species more susceptible to demographic stochasticity (Pimm *et al.* 1988). In birds, population sizes of threatened species correlate positively with geographic range size, indicating that it may be difficult to separate their effects on extinction risk (Blackburn and Gaston 2002).

Another commonly-cited intrinsic correlate of extinction risk is body size, because larger species are preferentially hunted by humans (Bodmer *et al.* 1997, Fa *et al.* 2005). Also, larger species often have larger home ranges, so are more likely to encounter threats (Harcourt 1998, Woodroffe and Ginsberg 1998, Brashares 2003). Evidence for body size as a correlate of extinction risk is mixed; global bird and regional mammalian studies suggest that large body size may have

an impact if species are at risk due to direct persecution or introduced species, but not if they are threatened by habitat loss (Owens and Bennett 2000, Cardillo and Bromham 2001, Norris and Harper 2004, Collen *et al.* 2006).

However, the strong relationships between body size and life-history traits complicate the interpretation of these results (Gaston and Blackburn 1995, Cardillo 2003). Generally, larger species tend to reproduce more slowly (Western 1979), making them more susceptible because their recruitment cannot keep up with high mortality rates imposed by anthropogenic threats (Pimm *et al.* 1988). For example, body size does not directly correlate with extinction risk in artiodactyls threatened by hunting, but weaning age does (Price and Gittleman 2007). Globally, mammalian body size interacts with many other extinction risk correlates; the impacts of intrinsic and extrinsic threat correlates are higher for large-bodied mammals, with species vulnerability arising from life-history traits not scaling simply with body size (Cardillo *et al.* 2005). Correlations of extinction risk with fecundity measures also vary in carnivores with different levels of human population density in their range, and differ with threat type in birds (Owens and Bennett 2000, Cardillo *et al.* 2004). Generally, the impact of fecundity seems to be dependent on other biological traits, as well as on the nature and extent of external threats.

From most studies, small geographic range size, large body size and slow life history or low fecundity emerge as the main biological correlates of high extinction risk. There are many additional hypotheses, most with mixed support in different taxa: high habitat specialisation (Owens and Bennett 2000, Johnson *et al.* 2002, Fisher *et al.* 2003, Jones *et al.* 2003, Gage *et al.* 2004, Safi and Kerth 2004, Cooper *et al.* 2008); high trophic level (Purvis *et al.* 2000b, Carbone and Gittleman 2002, Fisher *et al.* 2003, Cardillo *et al.* 2004, Collen *et al.* 2006); island endemism (Gaston and Blackburn 1995, Manne *et al.* 1999, Jones *et al.* 2003); large home-range size or dispersal distance in mammals, and migratory status in birds (Brashares 2003, Collen *et al.* 2006, Thomas *et al.* 2006); and social

structure, e.g. social group size, mating system or sexual selection (Purvis *et al.* 2000b, Brashares 2003, Jones *et al.* 2003, Morrow and Pitcher 2003).

Many of these biological correlates of extinction risk seem to be scale-dependent, so that results of local or regional studies differ from the global scale (Fisher and Owens 2004, Purvis *et al.* 2005, Cardillo *et al.* 2008). This scale-dependence is also important for extrinsic threats correlating with extinction risk, e.g. human population density (Davies *et al.* 2006, Luck 2007). Additionally, anthropogenic threats and biological traits interact to determine species' extinction risk:

biological correlates of extinction risk differ with the prevalent threat type and the magnitude of threat (Owens and Bennett 2000, Isaac and Cowlshaw 2004, Price and Gittleman 2007). In order to disentangle trait-threat interactions at different scales, I use a global mammalian dataset and a newly-updated species-level phylogeny in chapter 3 to model the influence of the main biological traits on extinction risk with phylogenetic comparative methods, globally and at a regional scale across the world. Additionally, I then analyse how current and anthropogenic impacts throughout the past 300 years relate to the influence of biological traits on risk using global, spatially-explicit models.

The analyses in chapter 3 provide a detailed picture of how anthropogenic threats and biological traits have shaped current mammalian extinction risk, focusing on that single taxon. Similarly, previous studies of extinction-risk correlates have concentrated on one clade or region and, due to the different methods employed, most studies are not directly comparable. For example, global studies on birds have used families as taxonomic units (Owens and Bennett 2000, Norris and Harper 2004), but mammal and amphibian studies have almost exclusively been at the species level (e.g. Purvis *et al.* 2000b, Cardillo *et al.* 2008, Cooper *et al.* 2008, Sodhi *et al.* 2008). While many extinction processes may be taxon-specific, global declines across virtually all taxa imply that the anthropogenic impacts acting globally produce some common patterns (Thomas *et al.* 2004, Collen *et al.* 2009).

Therefore, chapter 4 contains a global, phylogenetic comparative analysis of intrinsic and extrinsic correlates of extinction risk within and across three major vertebrate taxa: mammals, birds and frogs. I compile a family-level composite phylogeny and a dataset on geography, ecology and life-history for these three groups, and then use the same models for each taxon to make direct comparisons possible, but also model the influence of some taxon-specific variables. The analyses in chapters 3 and 4 therefore provide novel information about the focus of the current extinction crisis: which biological traits increase risk of extinction for a (terrestrial vertebrate) species, where in the world species exhibit those traits, and how trait effects are themselves determined by different anthropogenic threats.

Future impacts of current extinction risk

Knowledge about which biological traits affect extinction risk and how these are influenced by different anthropogenic threats is valuable for predicting the impacts the current extinction crisis might have if currently threatened species do indeed vanish or decline. The identification of species attributes which are associated with high extinction risk could enable us to predict future human impacts (Sala *et al.* 2000), as well as highlight susceptible species that are currently not experiencing high threat levels (Cardillo *et al.* 2006, Bielby *et al.* 2008, Corey and Waite 2008). A different way of predicting future patterns of diversity is to look at which biological traits we stand to lose if threatened species went extinct: the phylogenetic non-randomness of extinction risk indicates that a greater variety of traits may be lost with currently threatened species than expected if species extinctions were random (McKinney 1997, Purvis *et al.* 2000a). Since species fulfil different functions in ecosystems depending on their traits, the loss of large amounts of functional-trait diversity may have catastrophic consequences for ecosystem functioning, depending on species irreplaceability (Millennium Ecosystem Assessment 2005). In order to predict future ecosystem

stability, we need to know more about the ecosystem roles of threatened species, and which functions may be lost if currently-threatened species went extinct.

Previous studies have used the amount of evolutionary history that an area or a clade stands to lose as a measure of the trait variation that will be lost, which in turn is thought to reflect functional diversity and may allow conclusions about future ecosystem functioning to be drawn (Vane-Wright *et al.* 1991, Faith 1992, Forest *et al.* 2007). A large body of literature exists on biodiversity effects on ecosystem functioning, and the emerging consensus is that losses of species richness do not directly and linearly predict loss of functional diversity because of widespread species redundancy (Gross and Cardinale 2005, Hooper *et al.* 2005). Additionally, there is some evidence that the amount of shared evolutionary history among threatened species may not correlate well with their functional diversity (Jernvall and Wright 1998).

For these reasons, I investigate in chapter 5 how much functional diversity is at risk with currently threatened mammalian species, using the body mass variance within WWF ecoregions as a simple measure of functional variety in large-scale ecosystems. I then compare expected species-richness losses with the threatened amounts of evolutionary history and functional diversity, and also assess the non-randomness of diversity reductions using within-ecoregion simulations of phylogenetically random species loss. This last analytical chapter of my thesis therefore uses mammals as a model system to assess possible impacts of the current extinction crisis, both in terms of absolute loss of species numbers and possible deterioration of ecosystem functioning.

Measuring and analysing extinction risk

Throughout my thesis, I use classifications from the global IUCN Red List of Threatened Species (IUCN 2007/2008) as estimates of species extinction risk. The

taxa analysed in this thesis, i.e. mammals, birds and frogs, have been completely assessed, so that bias in knowledge of risk status is much reduced (Rodrigues *et al.* 2006). Assessments for the Red List are made using five quantitative criteria that constitute a set of alternative symptoms of extinction risk (Mace and Lande 1991, IUCN 2001). Species with insufficient data to assign to a risk category are designated as Data Deficient. Each species with sufficient data is evaluated for population reduction (criterion A), small geographic range size and decline (criterion B), small population size and decline (criterion C) and very small or restricted population (criterion D); predictions from a quantitative analysis regarding the time to extinction in the wild can be taken into account with criterion E. Species are evaluated under all criteria for which data are available, and are assigned the highest threatened category they qualify for under any of the criteria (Vulnerable, Endangered or Critically Endangered, IUCN 2001).

Criteria were devised from population dynamic principles (Mace and Lande 1991), so that listing species under any criterion for one of the threatened categories would be a probabilistic assessment of the time to extinction as follows: Vulnerable, over 50% chance of extinction within 10 years or three generations (maximum of 100 years); Endangered, over 20% chance of extinction within 20 years or five generations (maximum of 100 years); Critically Endangered, over 10% chance of extinction within 100 years (IUCN 2001). However, these estimates are crude generalisations, as any detailed prediction should involve species-specific parameters such as generation length (Mace 1995). In reality, timescales to extinction are likely to be longer than the estimates above (Mace 1995, Redding and Mooers 2006). If species nearly fulfil any of the quantitative criteria, they can be classified as Near Threatened, whereas species not qualifying under any criterion are ranked as Least Concern. Finally, the IUCN Red List distinguishes between species that are Extinct in the Wild and species that are Extinct.

Because it consistently applies quantitative criteria to assess global species extinction risk, the IUCN Red List is the best available dataset of extinction-risk

estimates (Rodrigues *et al.* 2006, Mace *et al.* 2008). The criteria used are clear, easily comprehensible and flexible, so they can handle uncertainty and give consistent results across taxa (Akçakaya *et al.* 2000). A problem is posed by the many species still ranked as Data Deficient even in well-known groups, because they are probably a non-random sample of species that are excluded from analyses of extinction risk (see also chapter 2). There are also known problems with the Red List classification system, e.g. the uncertainty of the Near Threatened category, and individual differences among assessors in listing ambivalent species as Least Concern or Data Deficient. However, the consistency of the assessment process is improved via a review system, and the classifications seem to be applicable across as widely different organisms as vertebrates, invertebrates and plants (Mace *et al.* 2008).

The IUCN categories going from Least Concern via Near Threatened, Vulnerable, Endangered and Critically Endangered to Extinct in the Wild and Extinct can be seen as a “ladder of extinction”. If a continuous rate of progress along this ladder is assumed, extinction risk can be analysed as a continuous variable ranging from zero (Least Concern) through to five (the two extinct categories combined, Purvis *et al.* 2000b). The continuous concept preserves more information about species risk status than using the binary variable non-threatened vs. threatened, and is often used in analyses modelling correlates of extinction risk across species (reviewed in Fisher and Owens 2004, Purvis 2008). I follow these studies for the analyses in chapter 3.

There are, however, some problems with using the Red List categories in this way. The assumption of linearity is, strictly speaking, statistically unfounded, because there is hardly any reason to believe that the categories should be of equal width, and species estimates can never fall between categories. However, the Red List provides the most comprehensive and reliable extinction-risk dataset currently available, and non-linearity is only rarely detected (Cardillo *et al.* 2005, Redding and Mooers 2006). Also, the most powerful statistical approaches for comparative analyses require continuous response variables. Nevertheless,

because a binary distinction (non-threatened vs. threatened) does not assume continuous progress along the IUCN categories, I use this measure instead in chapters 2, 4, and 5.

Thesis aims

The overall aim of this thesis is to investigate large-scale phylogenetic and spatial patterns in global species extinction risk, using well-known vertebrate taxa as study groups to increase understanding of current extinction processes.

Throughout, I use novel, phylogenetic and spatially-explicit approaches to study three aspects of the current extinction crisis: its magnitude in terms of phylogenetic signal (chapter 2), its focus both spatially and in terms of species susceptibility (chapters 3 and 4), and its possible impacts on diversity (chapter 5).

Chapter 2 uses a new measure to investigate the strength of phylogenetic selectivity in current, global mammalian extinction risk, with the aim of separating the different signatures that biological selectivity of the main threat types produces on a phylogeny. In chapter 3, I aim to show which biological traits increase extinction risk in mammals within ecoregions, and how these interact with different anthropogenic threats across the globe. Chapter 4 further investigates the focus of current extinction risk by comparing biological traits and anthropogenic threats that correlate with different aspects of extinction risk across and within three major vertebrate taxa. Finally, in chapter 5 I aim to estimate possible impacts of the current extinction crisis by investigating spatial patterns of estimated losses of species richness and phylogenetic and functional diversity.

Chapter 2: Selectivity in mammalian extinction risk and threat types – a new measure for phylogenetic signal strength in binary traits

Abstract

The strength of phylogenetic signal in extinction risk can give insight into the mechanisms behind species' decline. However, there is currently no measure for phylogenetic pattern in a binary trait such as extinction-risk status that is also comparable among datasets. I develop such a measure, and use simulations to demonstrate that robust results can be achieved with datasets of more than 50 species, even when the proportion of threatened species is low. I then apply the new measure, D , to the Red-List status of British birds and mammals worldwide. My results indicate that at-risk status for both groups shows moderately strong phylogenetic clumping. I also test the hypothesis that the phylogenetic pattern of species threatened by harvesting should be stronger than for those threatened by either habitat loss or invasive species, because the life-history traits mediating the effects of harvesting themselves show strong evolutionary pattern. The results for mammals support this hypothesis, but also show moderate to strong phylogenetic signal in the pattern of risk caused by the other two drivers as well. I conclude that D is a useful measure of the strength of phylogenetic pattern in many binary traits.

A version of this chapter has been submitted to Conservation Biology as “Selectivity in mammalian extinction risk and threat types: A new measure for phylogenetic signal strength in binary traits”, authors: Susanne A. Fritz and Andy Purvis.

Introduction

Analyses of comprehensive assessments of species extinction risk reveal that risk is often not spread randomly across taxonomy or phylogeny. Rather, there is usually a significant tendency for risk to be concentrated within some major branches of a phylogeny, and for close relatives to share the same risk status. This non-random phylogenetic pattern in extinction risk holds true for many taxa, globally or within regions (Bennett and Owens 1997, Russell *et al.* 1998, Mace and Balmford 2000, Purvis *et al.* 2000a, Schwartz and Simberloff 2001, von Euler 2001, Johnson *et al.* 2002, Lockwood *et al.* 2002, Stuart *et al.* 2004, Sjöström and Gross 2006, Schipper *et al.* 2008). Extinctions in the fossil record are also often non-random with respect to phylogeny (McKinney 1997, Purvis 2008).

Phylogenetic pattern in extinction risk can give insight into the mechanisms of extinction or decline. In a phylogenetically random risk pattern, threatened species occur at random throughout the phylogeny, implying that evolved traits which show strong phylogenetic pattern, e.g. body size, are not important in deciding species' fates. In that case, geographical variation in threat types, or idiosyncratic factors, determine extinction risk mostly independently of biology; threatened species are not intrinsically more susceptible but live in threatened environments. Conversely, a very strong phylogenetic pattern, where threatened species are prevalent in some clades but not others, implies evolutionarily-patterned susceptibility. Biological traits then play a direct or indirect role in determining species extinction risk. Strong evidence for this scenario is phylogenetic selectivity found at smaller spatial scales, where geographical variation in threat intensity tends to be reduced (Bielby *et al.* 2006, Davies *et al.* 2008).

While the *significance* of phylogenetic pattern can reveal whether biological traits are likely to play a role or not, the *strength* of the pattern can indicate what types of biological traits may be involved in determining risk. Considering different threat types and their phylogenetic-signal strength may help to separate the

processes behind extinction risk. For example, hunting pressure and species' ability to compensate for extra mortality are likely to reflect body size and reproductive rates, respectively (Bodmer *et al.* 1997); both these traits show strong evolutionary pattern (Freckleton *et al.* 2002). On the other hand, a general threat such as habitat loss may not depend strongly on life-history traits, but on ecological traits such as habitat specialisation (Owens and Bennett 2000); it is therefore expected to show less phylogenetic signal, or even none at all if all species are equally susceptible to habitat loss. Therefore, the strength of phylogenetic pattern suggests which biological traits might be useful in predicting extinction risk for poorly-known species or clades (Kotiaho *et al.* 2005, Corey and Waite 2008), or for future scenarios of anthropogenic drivers (Cardillo *et al.* 2006, Bielby *et al.* 2008, Willis *et al.* 2008).

For these reasons, a statistically reliable measure of phylogenetic signal strength in variables such as extinction-risk status would be valuable. Most previous studies of phylogenetic pattern in extinction risk have concentrated on significance-testing rather than estimating the strength of phylogenetic signal (Bennett and Owens 1997, Russell *et al.* 1998, Mace and Balmford 2000, Purvis *et al.* 2000a, Schwartz and Simberloff 2001, von Euler 2001, Stuart *et al.* 2004, Bielby *et al.* 2006, Sjöström and Gross 2006, Schipper *et al.* 2008). Good measures of phylogenetic pattern in continuous traits are available (Freckleton *et al.* 2002, Blomberg *et al.* 2003), but these cannot readily be applied to binary traits such as threatened vs. non-threatened. None of the existing methods applicable to binary traits provide a measure of signal strength that can be compared across datasets. Moran's I , which measures taxonomic or phylogenetic autocorrelation of binary traits, is sensitive to the prevalence of threat (Lockwood *et al.* 2002). Another measure for phylogenetic signal in binary traits, MPD or mean phylogenetic distance, is dependent on phylogeny shape and the number of species in the dataset (Webb *et al.* 2002). Methods intended to test phylogenetic pattern in cladistic character matrices used in phylogeny estimation, such as tree-length distribution skewness (Huelsenbeck 1991) or Relative Apparent Synapomorphy Analysis (RASA, Lyons-Weiler *et al.* 1996), focus on

distinguishing between perfect and strong clumping: they do not discriminate well among levels of clumping more likely to be observed in extinction risk, where clades often do not exclusively contain threatened species.

Since it is of interest to compare the strength of phylogenetic selectivity among datasets, as well as test for significance, my first aim is to introduce and test a new measure for phylogenetic-signal strength in a binary trait such as risk status.

Below, I use simulations to assess performance of my new measure for phylogenetic signal in a binary trait, *D*. Significance-testing for *D* is compared with previously published results describing phylogenetic patterns in British birds of conservation concern (Thomas 2008). The second aim of this chapter is to employ *D* to investigate the different processes leading to high extinction risk. I explore global extinction-risk status in mammals as recorded by the Global Mammal Assessment (IUCN 2008), using a comprehensive, newly-updated phylogeny of 5020 mammalian species (Bininda-Emonds *et al.* 2007, chapter 3). Since composite measures of extinction risk such as the Red List risk rankings capture multiple kinds of threat, I also use the IUCN threat classifications to separate phylogenetic patterns in the main types of threat.

Methods

Derivation of D

The measure I propose for phylogenetic-signal strength in a binary trait is based on the sum of sister-clade differences in a given phylogeny. While a maximally clumped trait will be in the same character state in related species, a highly overdispersed trait may never be. Consequently, sister-clade differences will be lowest for strongly clumped traits and highest for strongly overdispersed ones (Table 2-1). The actual amounts will depend on the prevalence of the binary trait (the proportion of species in character state 1) and the size and shape of the

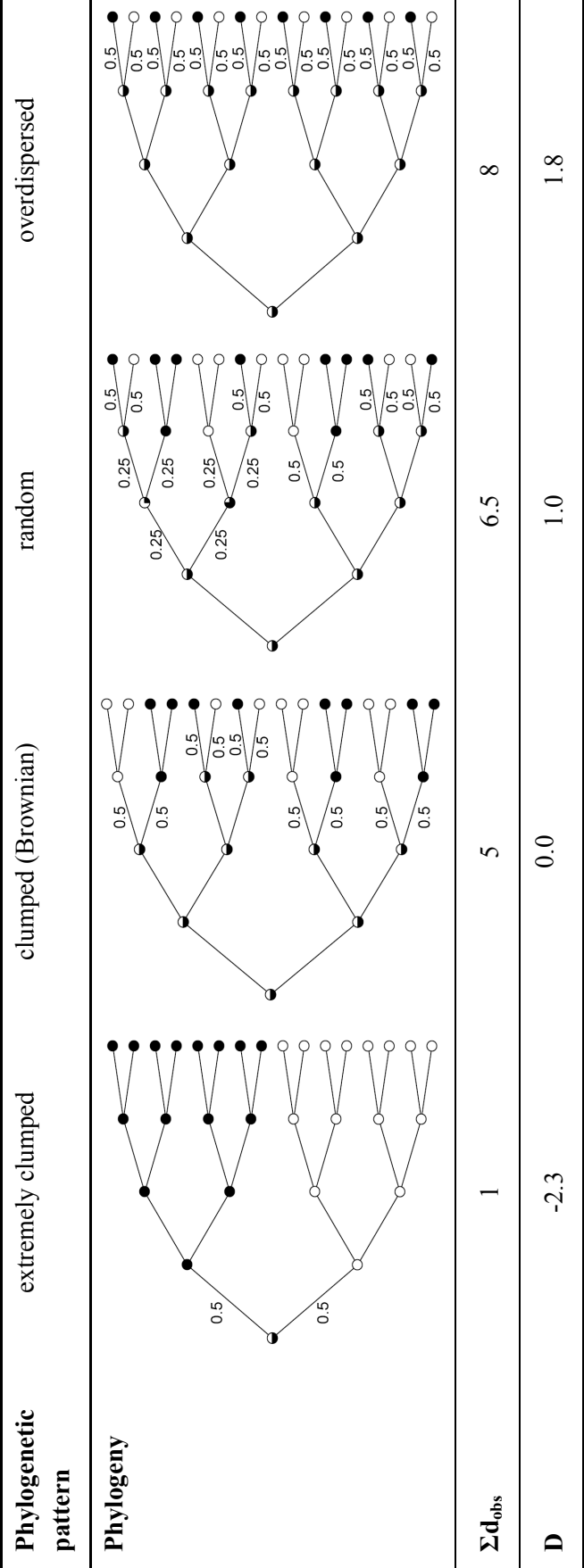


Table 2-1. The calculation of D for different types of phylogenetic pattern in binary traits.

The phylogenetic patterns shown are two extremes (phylogenetically extremely clumped and phylogenetically overdispersed) and two examples of the scaling expectations used to compute D (Brownian and random phylogenetic pattern). The Brownian phylogenetic pattern is generated under a threshold model: I simulate a continuous trait along the phylogeny under Brownian motion and then assign a binary trait based on this, ranking the highest values as ones until the observed trait prevalence is reached. Phylogenetically random patterns are generated by shuffling the tip values along the phylogeny. In this example phylogeny, all branch lengths are set to unity, and trait prevalence is 0.5. Pie

Table 2-1. *Caption continued from previous page.*

diagrams at the tips and nodes indicate tip data and nodal values for the binary character in question, representing values between 0 (completely empty) and 1 (completely filled). I estimate nodal values as the weighted mean of descendant node or tip values (all weights are one in this example due to the chosen branch lengths). The sister-clade differences are then the differences between nodal values at each end of the branch. Branches are labelled with these values, unless their value is 0. Σd_{obs} is the observed sum of sister-clade differences across the whole phylogeny, and D is computed as the observed sum of sister-clade differences minus the Brownian expectation, divided by the difference between the random expectation and the Brownian expectation.

phylogeny, so their effects need to be removed to make the measure of phylogenetic-signal strength comparable among datasets. I address these steps in turn.

At each node in the tree, nodal values for the binary trait are estimated, and the sum of the differences between each pair of sister clades is computed across the whole tree (Table 2-1). Each nodal value is estimated as the mean of the values at its descendant nodes weighted by the lengths of the branches leading to them (Felsenstein 1985). The sum of absolute differences between nodal and tip values for each branch in the phylogeny is the observed sum of sister-clade differences, Σd_{obs} . I then place Σd_{obs} on a common scale with two fixed points (Table 2-1): a value of unity corresponds to the expectation of a phylogenetically random trait distribution, and a value of zero is the expectation for a phylogenetic pattern under Brownian-motion evolution.

Both expectations used to scale Σd_{obs} are generated using permutations based on the trait prevalence and the phylogeny of interest, which makes the scaled Σd_{obs} comparable between datasets. Shuffling the species trait values along the tips of the tree generates a distribution of sums of sister-clade differences expected for a random phylogenetic pattern, Σd_r (see Table 2-1 for an example). The

evolutionary model I use to generate a distribution of sums expected under Brownian evolution, Σd_b , is equivalent to a threshold model: I simulate continuous traits evolving under Brownian motion (i.e. in a random walk with constant trait variance over time, Felsenstein 1985), and generate their corresponding binary traits by ranking species whose values exceed the threshold as character state 1, while other species are in state 0 (see Felsenstein 2005 for discussion of a similar threshold model). The threshold is defined to give the required prevalence, i.e. the proportion of species in state 1 for the original observed binary trait. Clearly, extinction risk is not an evolved trait, but it is correlated with species traits which are, and the threshold model provides a way to scale the measure of phylogenetic-signal strength using a meaningful evolutionary hypothesis.

My final measure of character dispersion on a phylogeny, D , is computed by scaling the observed sum of sister-clade differences with the mean values of the two expected distributions as follows:

$$D = [\Sigma d_{\text{obs}} - \text{mean}(\Sigma d_b)] / [\text{mean}(\Sigma d_r) - \text{mean}(\Sigma d_b)]$$

D is equal to unity if the observed binary trait has a phylogenetically random distribution across the tips of the phylogeny, and to zero if the observed trait is as clumped as if it had evolved by Brownian motion under the threshold model (Table 2-1). Values of D can fall outside this range; an analogy for D is the degrees-centigrade scale, which is also defined using two meaningful points (the freezing and boiling point of water, 0°C and 100°C) that are not at each end of the possible range of values. Increasing phylogenetic clumping in the binary trait is indicated by values of D decreasing from unity. This new method also tests D for significant departure from zero (Brownian expectation) and unity (random expectation) by comparing Σd_{obs} to either of the two expected distributions (Σd_b and Σd_r).

Although D as described here is an entirely new measure for phylogenetic-signal strength in a binary trait, a precursor of D was devised by myself and published in Davies *et al.* (2008, see Appendix A). Similarly to the observed sum of sister-clade differences here, I there used the sum of absolute phylogenetically

independent contrasts, and tested for significant departure from random phylogenetic pattern using simulations. However, the Davies *et al.* (2008) measure is not comparable between datasets, because it is dependent on phylogeny size and prevalence. Similarly, the sum of sister-clade differences itself was used by Sjöström and Gross (2006) to test for phylogenetic non-randomness in risk status, but their study does not include a measure of phylogenetic-signal strength that is independent of dataset size, prevalence and phylogeny structure.

I have implemented D using the R software (R Development Core Team 2008) and the contributed packages *geiger* (Harmon *et al.* 2008) and *CAIC* (Orme *et al.* 2008). The functions to compute D (Appendix B) will be made publicly available as part of the CAIC package (<http://r-forge.r-project.org/projects/caic>). I recommend 1000 permutations for computing both underlying D parameters, because a low number of permutations affect the resolution of p-values and the estimates for the Brownian expectation (data not shown).

Testing the behaviour of D with simulated and real datasets

To test the behaviour of D, I ran two sets of simulations, using 1000 permutations throughout. The first set of simulations evaluated the behaviour of D with a range of known underlying phylogenetic signals by investigating the relationship of D with Pagel's λ (1999) for the underlying continuous trait in the threshold model. Pagel's λ is an indicator of phylogenetic signal in a continuous trait, which varies between zero if the trait is random with respect to phylogeny, and unity if the trait shows clumped phylogenetic signal indicating it evolved according to the Brownian evolutionary model (Freckleton *et al.* 2002). I generated 100 random tree topologies of 100 tips each, using the "rcoal" function in the R package *ape* (Paradis 2006), and simulated continuous characters with a given range of phylogenetic signals along those, using the R package *geiger* (Harmon *et al.* 2008). Values of λ were varied from 0.0 to 1.0 in steps of 0.1. I set the prevalence to 0.3 to reflect the proportion of species at risk commonly found in many real

datasets, and converted the continuous traits to binary ones following the threshold model.

The second set of simulations investigated performance of D with tree topologies reflecting those that might be typically available. I randomly sampled defined numbers (10, 25, 50, 75, 100 and 150) of mammalian species from a global list and obtained their phylogenetic relationships (topology and branch lengths) from a supertree of 5020 extant species (Bininda-Emonds *et al.* 2007, chapter 3). Continuous traits with random ($\lambda = 0$) and very strong ($\lambda = 1$) phylogenetic signal were simulated along these trees and converted to binary traits using different levels of prevalence (from 0.1 to 0.9 in steps of 0.1). For each tree size, prevalence and λ , I ran 100 replicates.

I then applied the new measure to two real data sets. First, I compared it to a published study that used a different test for phylogenetic signal in binary traits. Thomas (2008) recently estimated a species-level phylogeny of British birds, and tested whether birds in different categories of conservation concern (from Gregory *et al.* 2002) showed phylogenetic signal according to their mean phylogenetic distance (MPD, see Webb *et al.* 2002). MPD is the mean of the phylogenetic distances between each pair of species in the phylogeny that are ranked as character state 1, and its significance can be assessed using randomisations. I estimated D for the maximum-credibility tree and the data on 181 bird species supplied by Thomas (2008), and compared significance results with recomputed MPD P -values for the same maximum-credibility tree because Thomas (2008) used the median MPD from a posterior distribution of phylogenies estimated with Bayesian phylogenetic methods.

Finally, I applied D to phylogenetic patterns of extinction risk, threat, and risk-status knowledge across the entire mammalian phylogeny, using data from the recently published Global Mammal Assessment (GMA, IUCN 2008). To investigate global phylogenetic patterns in overall extinction risk, I excluded species ranked as Data Deficient and used two definitions of at-risk species:

species in the three threatened categories only (Vulnerable, Endangered and Critically Endangered) and all species ranked above Least Concern (Near Threatened and threatened categories, IUCN 2001). Phylogenetic pattern in knowledge of extinction-risk status was also assessed (species ranked as Data Deficient in the GMA vs. any other category). Additionally, I investigated phylogenetic signal in the following mammalian threats as classified by the GMA: Human-caused habitat loss or degradation, harvesting (hunting/gathering), invasive alien species, unknown threats, and no threats. I tested each of these across all species (excluding only species with unknown threats where applicable), because the GMA lists threats for non-threatened species as well. Since the threat types affecting threatened species might be better known or more faithfully recorded, each threat-type pattern was also tested within species ranked in one of the three threatened categories for overall extinction risk.

Results

D for a binary trait and λ for its underlying continuous trait were strongly negatively correlated (Fig. 2-1a), as expected from the construction of D . The relationship was non-linear, with D staying around unity for a range of low λ values. Increasing amounts of phylogenetic signal in the underlying continuous trait, as indicated by higher λ values, corresponded to an increasing proportion of D values significantly different from unity for the simulated binary traits (Fig. 2-1b). Only at very high values of λ , i.e. with strong phylogenetic signal, were D values not significantly different from zero (Fig. 2-1b).

The simulations showed that the D estimate was independent of tree size and prevalence (Fig. 2-2). D generally varied around unity for a phylogenetically random trait, and around zero for a phylogenetically clumped one, although small tree sizes led to high variability in D . D values significantly different from unity, i.e. indicating significant phylogenetic signal, were generally rare for binary traits

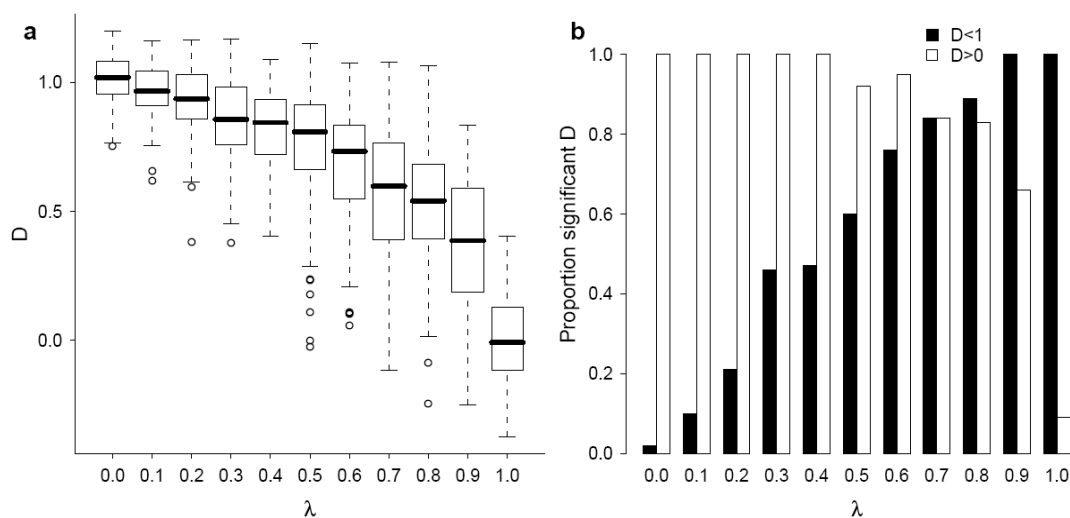


Figure 2-1. Relationship of D for a binary trait and λ for an underlying continuous trait.

Data were simulated with random tree topologies of 100 tips, evolving continuous characters with set λ values along these, and ranking the top 30% of their values as state 1 for the binary character of interest. D should be one for a phylogenetically random trait ($\lambda = 0$), and zero for a trait evolved under the Brownian model ($\lambda = 1$, see Methods). a) Box-and-whisker-plot of D for different values of λ . Solid lines indicate medians, and the bottom and top of the boxes show the 1st and 3rd quartiles. The whiskers extend to either the maximum value or 1.5 times the interquartile range, whichever is smaller, and the circles outside those ranges are outliers. b) Proportion of significant D values for different values of λ . Black bars show proportion of D values significantly smaller than one, indicating significant phylogenetic signal, and white bars show proportion of D values significantly larger than zero, indicating significant departure from the Brownian threshold model.

based on phylogenetically random continuous traits (Table 2-2). The power of detecting significant phylogenetic signal using D was affected by a low number of tips and extreme prevalence: at small tree sizes and very low or very high prevalence, many binary traits showed no significant signal according to D despite their underlying continuous trait being strongly phylogenetically patterned.

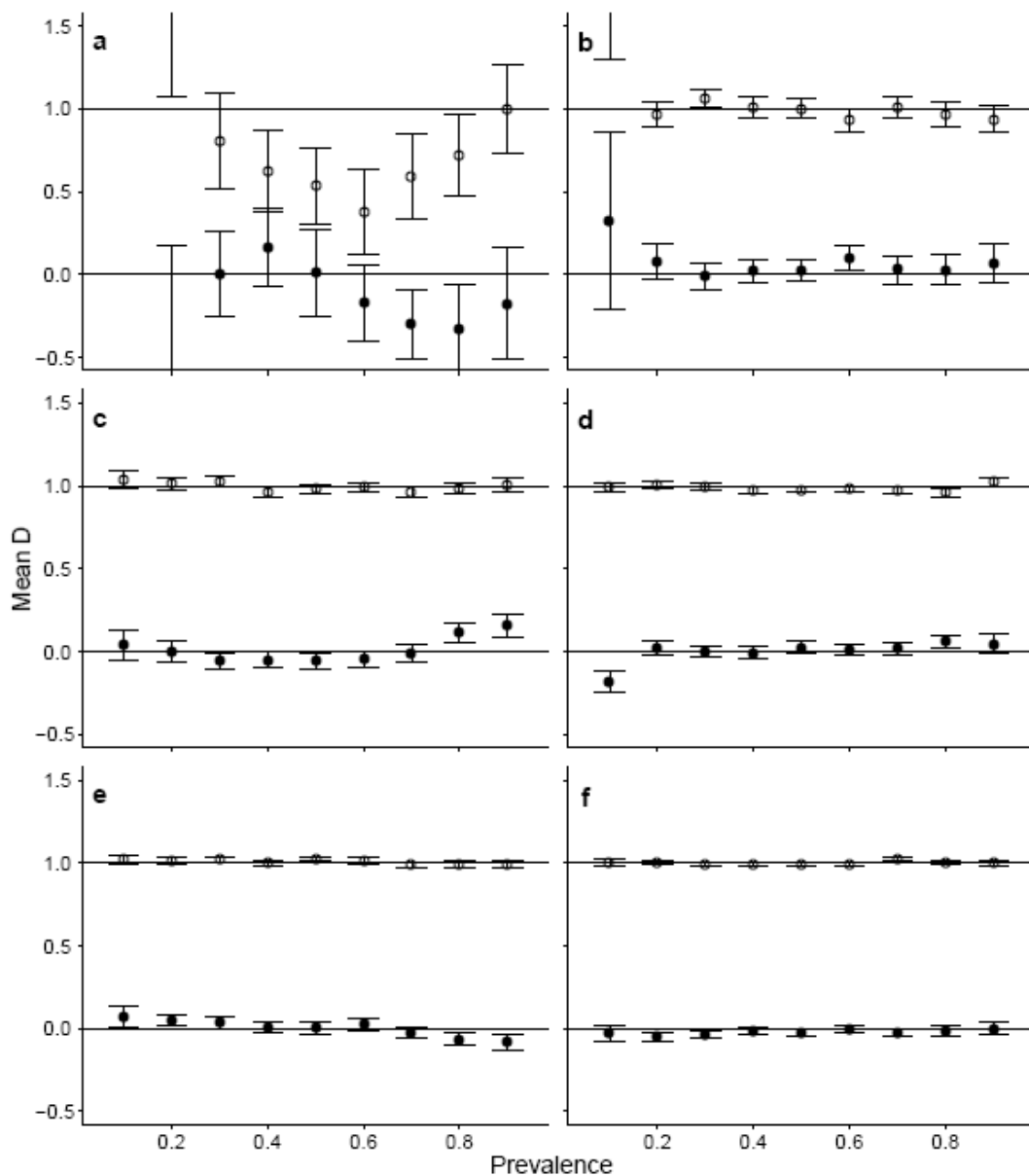


Figure 2-2. Performance of D for simulated traits.

Means and standard errors of 100 replicates each are shown for simulated binary traits with no ($\lambda = 0$, empty symbols) and very strong phylogenetic signal ($\lambda = 1$, filled symbols) in the underlying continuous trait, and for different tree sizes and levels of prevalence in the binary trait. All plots are scaled to the same y-axis extent for ease of comparison, so extreme means may lie outside the plot area. Tree sizes were: a) 10, b) 25, c) 50, d) 75, e) 100, f) 150 tips. Simulations were run by picking the specified number of tips at random from a species-level phylogeny of most extant mammals, simulating continuous traits with set λ values along this tree,

and computing D for binary traits scored on the basis of these continuous traits using the given prevalence.

	$\lambda = 0$						$\lambda = 1$					
	10	25	50	75	100	150	10	25	50	75	100	150
0.1		5	4	2	4	6		14	47	78	80	98
0.2	12	3	6	4	8	6	12	29	74	93	97	100
0.3	8	4	3	4	2	2	14	42	85	98	100	100
0.4	9	9	6	5	3	1	12	46	90	99	99	100
0.5	11	7	9	5	4	5	22	48	90	97	100	100
0.6	8	9	1	6	4	6	24	39	86	98	100	100
0.7	11	8	2	6	6	3	15	46	83	96	100	100
0.8	7	6	6	6	9	5	19	40	68	92	98	100
0.9	6	8	6	2	4	1	19	26	52	76	94	99
0.1		14	38	58	82	96		11	7	1	5	4
0.2	13	21	69	89	96	100	17	5	7	1	4	1
0.3	6	40	82	97	100	100	4	4	2	2	5	2
0.4	12	46	82	100	100	100	9	4	5	4	5	5
0.5	13	52	84	98	100	100	4	2	6	6	4	2
0.6	18	40	88	99	100	100	4	6	5	5	8	6
0.7	13	44	76	96	99	100	4	5	8	5	2	3
0.8	14	29	67	89	96	100	5	6	8	6	3	4
0.9	12	17	50	73	88	100	4	7	6	6	2	4

Table 2-2. Simulation results demonstrating significance testing with D.

Proportions of D values that were significantly different from unity (upper table half) and zero (lower table half) for binary traits simulated under the threshold model with no ($\lambda = 0$) and very strong phylogenetic signal ($\lambda = 1$), for different tree sizes and different levels of prevalence of the binary trait. Column headings give the number of tips in the tree, row headings indicate prevalence of the binary trait. I simulated 100 replicates per tree size, trait prevalence and set λ value as explained for Fig. 2-2, and tested whether computed values of D were significantly smaller than unity ($D=1$ for a randomly distributed binary trait) and significantly larger than zero ($D=0$ for a binary trait under the Brownian threshold model).

Corresponding patterns were seen when testing D for departure from zero (Table 2-2).

Results of significance tests using D for 14 categories of conservation concern in British birds were very similar to those using MPD (Table 2-3). Under a significance level of 0.05, MPD but not D indicated significant phylogenetic

	N	D	<i>P</i> -value (D>0)	<i>P</i> -value (D<1)	<i>P</i> -value (MPD)
All red-listed species	32	0.56	< 0.05	< 0.01	< 0.05
All amber-listed species	121	0.86	< 0.001	n.s.	n.s.
All green-listed species	60	0.86	< 0.001	< 0.1	< 0.05
Historical population decline	8	0.95	< 0.05	n.s.	n.s.
Historical pop. decline, incl. recovering	13	0.70	< 0.05	< 0.1	n.s.
Rapid decline in UK breeding population	22	0.58	< 0.05	< 0.01	< 0.01
Moderate decline in UK breeding pop.	49	0.88	< 0.001	n.s.	< 0.05
Rapid contraction in UK breeding range	6	1.26	< 0.01	n.s.	n.s.
Moderate contraction in UK breeding range	16	1.12	< 0.001	n.s.	n.s.
Population size of 1-300 breeding pairs	21	0.95	< 0.001	n.s.	n.s.
≥ 50% of UK breeding pop. in ≤ 10 sites	28	0.25	n.s.	< 0.001	< 0.05
≥ 20% of European breeding pop. in UK	14	0.76	< 0.05	< 0.1	n.s.
Lowest decile of population size	18	1.01	< 0.001	n.s.	n.s.
Lowest decile of geographic range size	18	0.75	< 0.05	< 0.1	n.s.

Table 2-3. Phylogenetic signal in different categories of conservation concern for 181 British birds, using mean phylogenetic distance (MPD) from Thomas (2008) and D.

MPD *P*-values are from a re-analysis using the maximum credibility tree from Thomas (2008). Categories of conservation concern follow Gregory *et al.* (2002), with N being the number of species in the category in question (coded as state 1 for the binary trait). Historical population declines were measured during 1800-1995. Rapid declines or contractions were ≥ 50%, moderate ones ≥ 25%; all were measured over the last 25 years. The population size was based on a 5-year mean, and the category “≥ 50% of UK breeding population in ≤ 10 sites” excluded rare breeders.

signal for green-listed species and species with a moderate decline in the UK breeding population. Both of these showed no significant signal using MPD when taking an average value from the posterior distribution of trees, as was the case for red-listed species as well ($P < 0.1$ for all three, Thomas 2008). D values showed that phylogenetic signal was strongest in species where most of the UK breeding population can be found in few sites, followed by red-listed species and species showing rapid population decline (Table 2-3). The phylogenetic signal for species breeding at few sites was so strong that it was indistinguishable from the Brownian threshold model (D was not significantly different from zero).

All tested extinction-risk categories and threat types in mammals were significantly phylogenetically clumped (Table 2-4). Strength of phylogenetic signal in extinction risk as indicated by D was similar for species ranked above Least Concern and species ranked in any of the three threatened categories. Species classified as Data Deficient showed less phylogenetic signal. Among known threat classifications, species threatened by harvesting had the highest degree of phylogenetic clumping, and species threatened by habitat loss had the least, with threat by invasives showing intermediate signal. Harvested species were as closely related across the phylogeny as expected under Brownian evolution (D was not significantly different from zero). Species categorised as not affected by any threat and species threatened by unknown threats also showed significant phylogenetic signal. All patterns in these different threat types were similar whether assessed across all evaluated species or within species ranked as threatened.

	N	Prevalence	D	P-value (D>0)	P-value (D<1)
Risk rankings					
Above Least Concern	1311 / 4275	0.31	0.637	< 0.001	< 0.001
Threatened	999 / 4275	0.23	0.653	< 0.001	< 0.001
Data Deficient	744 / 5019	0.15	0.831	< 0.001	< 0.001
Threat classifications					
Habitat loss					
all species	2239 / 4315	0.52	0.600	< 0.001	< 0.001
within threatened spp.	886 / 978	0.91	0.606	< 0.001	< 0.001
Harvesting					
all species	941 / 4208	0.22	0.076	n.s.	< 0.001
within threatened spp.	438 / 950	0.46	-0.006	n.s.	< 0.001
Invasive alien species					
all species	315 / 4204	0.07	0.464	< 0.001	< 0.001
within threatened spp.	166 / 952	0.17	0.527	< 0.001	< 0.001
Unknown					
all species	721 / 4911	0.15	0.775	< 0.001	< 0.001
within threatened spp.	54 / 999	0.05	0.637	0.001	< 0.001
No threats	1956 / 4268	0.46	0.538	< 0.001	< 0.001

Table 2-4. Phylogenetic patterns of extinction risk and threat in mammals as indicated by D.

N indicates sample sizes (the number of species ranked as 1 / total number of species with data and in the phylogeny), and prevalence is the proportion of species ranked as 1 for the binary trait. Risk rankings and threat classifications were from the GMA (IUCN 2008).

Discussion

Statistical performance of D and comparison with previous methods

My results show that my new measure for phylogenetic-signal strength in a binary trait, D , performs well under the assumptions of the threshold model. The curved relationship of D for a binary trait with λ , the measure of phylogenetic signal for the underlying continuous trait (Pagel 1999), may indicate that D is more conservative than λ in detecting phylogenetic pattern. Since D is based on much coarser information than λ , and λ itself is not a strictly linear measure (Freckleton *et al.* 2002), this non-linearity between D and λ is no weakness of the measure.

According to the simulations, significance testing with D works well, and false positive results are rare. D is not powerful for small tree sizes, i.e. below 50 tips for low and high trait prevalence (proportions of species in character state 1), and below 25 tips for all tested levels of prevalence. This is comparable to the recommendations for λ in Freckleton *et al.* (2002), and expected given the coarseness of the binary signal and the low number of tips involved. Above these thresholds, the value of D itself is independent of tree size and trait prevalence, making it comparable across different datasets. My new measure is therefore superior to the conceptually similar one of Davies *et al.* (2008).

Comparison with the results of Thomas (2008) for British birds in different conservation categories further confirmed good performance of significance-testing for D . Generally, D is more useful than MPD as previously used because it is independent of phylogeny size (although MPD could probably be standardised using randomisations in a similar way as I do for Σd_{obs}). The median MPD from a distribution of trees (estimated using a Bayesian phylogenetic approach) for red-listed bird species was non-significant, leading Thomas (2008) to conclude that different threat types showed conflicting phylogenetic patterns, making the overall pattern of extinction risk phylogenetically random. Conversely, my reanalysis of

his data using just the maximum-credibility tree picked up significant phylogenetic signal in red-listed species according to both D and MPD. For the red-listed category and the two other categories that were significant on the maximum-credibility tree according to MPD but not confirmed by D, the MPD P -value for the posterior tree distribution given by Thomas (2008) bordered on significance ($P < 0.1$). These differences serve as a reminder that slight changes in tree topology may change phylogenetic patterns for binary traits quite dramatically.

My D value for red-listed species indicates that clumping was in fact moderately strong ($D = 0.56$), which fits well with global bird studies (Bennett and Owens 1997, Russell *et al.* 1998), but may be based on an unrepresentative tree topology. Since comparison of D and MPD for the maximum-credibility tree demonstrated good performance of D, I did not resolve the issue of whether taking uncertainty in phylogeny estimation into account would broaden the confidence interval enough to make the pattern non-significant for D as well as for MPD. Using the maximum-credibility tree, significance-testing for D seemed to be stricter than for MPD in two cases. I conclude that my new measure, D, is superior to MPD in that it estimates the strength of phylogenetic signal, and that significance-testing for D seems to perform at least as well as for MPD.

The only similar measure of phylogenetic-signal strength in a binary trait I am aware of, Moran's I , is dependent on trait prevalence. Lockwood *et al.* (2002) suggest rarefaction methods as a solution, but these discard threatened species from the dataset until the trait prevalence of all considered datasets is equal. D considers all available information for each dataset, and is independent of trait prevalence and phylogeny size and shape, because the permutations generating the fixed points used to scale Σd_{obs} are based on the trait prevalence and phylogeny of interest. Moran's I might be useful to investigate taxonomic patterns of extinction risk, but D is clearly a more comprehensive measure for phylogenetic-signal strength in a binary trait if a phylogeny is available.

Cladistic approaches rely on parsimony to reconstruct nodal values and therefore test for clear-cut patterns where whole clades have the same trait values (Huelsenbeck 1991, Lyons-Weiler *et al.* 1996). Accordingly, they are expected to perform badly when applied to patterns of extinction risk or threat, which usually show more equivocal patterns; for example, D was nearly always significantly different from the Brownian expectation in both my bird and mammal results. Cladistic approaches are useful for many other applications, but D is probably more appropriate for detecting phylogenetic signal in extinction risk. Generally, D can be used as a measure for phylogenetic-signal strength in any binary trait of interest, but users should be aware of the assumptions of the particular underlying threshold model, i.e. that the binary trait of interest did not evolve itself but its tip pattern is based on one or more evolved, continuous traits.

Global extinction risk and threat patterns in mammals

My results confirm the presence of strong phylogenetic selectivity in global mammalian extinction risk found in previous studies (Russell *et al.* 1998, Mace and Balmford 2000, Purvis *et al.* 2000a). More importantly, this study is the first to demonstrate large differences in phylogenetic-signal strength for the different threat types in mammals. These differences indicate that different threats lead to high extinction risk via different processes, and emphasise the importance of taking different threat types into account to explain extinction-risk processes (Owens and Bennett 2000). They also support claims that analyses of extinction-risk correlates should correct for phylogenetic effects using methods that can take variable amounts of phylogenetic signal into account (Freckleton *et al.* 2002, Purvis 2008).

Species threatened by harvesting showed the strongest phylogenetic signal; in fact, their phylogenetic signal was indistinguishable from the phylogenetic clumping shown by a trait that has evolved under Brownian motion according to my threshold model. This extreme phylogenetic signal is unlikely to be caused purely by spatial pattern in harvesting intensity; instead, it strengthens the

hypothesis that hunting causes declines in large, slowly-reproducing species (Bodmer *et al.* 1997, Isaac and Cowlshaw 2004, Fa *et al.* 2005), given that body mass and life-history traits often fit the Brownian model of evolution (Freckleton *et al.* 2002). My results also imply that susceptibility to harvesting for species in currently pristine habitats should be well predicted by strongly phylogenetically patterned traits such as body mass or fecundity, which could help to select conservation areas in wilderness regions where infrastructure is growing rapidly (e.g. Soares-Filho *et al.* 2006).

Contrary to expectations from previous studies in birds (Owens and Bennett 2000, Thomas 2008), all other types of threat tested also had consistently significant phylogenetic pattern in mammals. Of the known threats I examined, habitat loss was least phylogenetically clumped, but its clumping was still as strong as for overall at-risk species. These results may imply that even a general threat such as habitat loss targets certain biological traits, leading to disproportionate extinction risk for some clades. Previous studies of biological extinction-risk correlates in mammals that have separated different types of threat have been of narrow taxonomic or spatial focus, or concentrated on the effects of hunting (Isaac and Cowlshaw 2004, Price and Gittleman 2007). Given that habitat loss is the greatest threat to biodiversity today and will probably continue to have high impact (Mace *et al.* 2005), gaining an understanding of the biological traits that make mammals susceptible to habitat loss is vital to enable conservation efforts to be effective.

The phylogenetic clumping of species threatened by habitat loss, invasive species, and unknown threats is likely to be partly due to geographical differences in the degree of habitat loss, because of spatial clustering of related species and clades (Bielby *et al.* 2006, Davies *et al.* 2008). Similarly, species impacted by no known threat could be intrinsically less susceptible to ongoing threats or live in “safe” places: either could cause the observed phylogenetic pattern. Studies on smaller geographic scales could resolve the respective roles of biological traits and geography, but are often impeded by small sample size. A different approach is to estimate the strength of phylogenetic and spatial signal in extinction risk in a

single analysis, in order to separate the relative contributions of both; a recently published study (Freckleton and Jetz 2009) introduced a new method to perform this kind of analysis, but this is currently only applicable to continuous traits.

In conclusion, this chapter has shown that my new measure for phylogenetic-signal strength in a binary trait, D , performs well with reasonable sample sizes, takes the whole phylogeny into account, and is comparable across different sizes of phylogeny and levels of trait prevalence. Strong phylogenetic signal in both British birds of conservation concern and global mammalian extinction risk and threat types indicate that biological traits directly or indirectly determine species' fates. The traits increasing susceptibility differ with threat types in mammals, with risk from habitat loss being much less dependent on traits with strong phylogenetic signal such as body size than is risk from hunting. My results highlight a need for studies investigating the phylogenetic signal in different threat types at smaller spatial scales, to disentangle the respective roles of biology and geography. Also, future studies trying to predict species, clades, or areas of conservation concern from biological traits and anthropogenic threats should take different threat types into account where possible, and use phylogenetic methods that account for varying amounts of phylogenetic signal. I conclude that D will be a useful tool for studying the significance and strength of phylogenetic signal in many kinds of binary traits, but especially those that are unlikely to show clear-cut phylogenetic patterns, such as extinction-risk status and threat types.

Chapter 3: Geographical variation in predictors of mammalian extinction risk – big is bad, but only in the tropics

Abstract

Whereas previous studies have investigated correlates of extinction risk either at global or regional scales, this chapter explicitly models regional effects of anthropogenic threats and biological traits across the globe. Using phylogenetic comparative methods with a newly-updated supertree of 5020 extant mammals, I investigate the impact of species traits on extinction risk within each WWF ecoregion. My analyses reveal strong geographical variation in the influence of traits on risk: notably, larger species are at higher risk only in tropical regions. I then relate these patterns to current and recent-historical human impacts across ecoregions using spatial modelling. The body-mass results apparently reflect historical declines of large species outside the tropics due to large-scale land conversion. Narrow-ranged and rare species tend to be at high risk in areas of high current human impacts. The interactions I describe between biological traits and anthropogenic threats increase understanding of the processes determining extinction risk.

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Introduction

The most comprehensive global assessment of species extinction risk, the IUCN Red List, currently lists 12% of bird species, 21% of mammals and 30% of amphibians as threatened by extinction (IUCN 2008). To counter the impending mass extinction with sparse conservation funds, it is necessary to understand the nature of threat factors to which species are exposed, and why species differ in their susceptibility to a given threat. Mammals are an appropriate study group for analyses of extinction risk because a fifth of their species are threatened, risk status for all mammalian species has been evaluated by the Red List (IUCN 2008), and their populations are declining rapidly (Collen *et al.* 2009). They are also of particular conservation concern because they are charismatic and fulfil important ecosystem functions. Additionally, mammals are currently the only species-rich taxon for which a species-level phylogeny, global distribution maps and extensive biological trait data are available (Bininda-Emonds *et al.* 2007, Jones *et al.* 2009).

Previous studies have shown that extinction risk is phylogenetically non-random even at small spatial scales, which implies that some biological traits shared by close relatives shape species' fates in the face of human impacts (Russell *et al.* 1998, Davies *et al.* 2008). The distribution of threatened species varies in space, as do anthropogenic threats such as habitat loss, overexploitation and invasive species (Baillie *et al.* 2004). Successful prediction of future risk will rely on knowledge of threats in a particular place, of traits that make species susceptible to those threats, and of the phylogenetic relationships of the clade in question. This chapter therefore aims to disentangle some of the complex interactions between threats and traits that shape extinction risk patterns both phylogenetically and spatially.

Due to the complexity of extinction risk processes, the global focus of many previous studies may obscure regional variation in both threats and species traits

(Fisher and Owens 2004). Correlates of mammalian risk differ substantially among taxonomic groups and biogeographical regions, indicating that clade- or region-specific processes may drive the divergent patterns (Cardillo *et al.* 2008). The influence of certain traits on population decline or extinction risk in mammals and birds is specific to particular threat processes (Owens and Bennett 2000, Isaac and Cowlshaw 2004, Price and Gittleman 2007). Taxonomically focused analyses can describe taxon-specific threat processes more accurately (Fisher and Owens 2004), but global analyses of wider taxonomic focus can show more general patterns and are less affected by low sample sizes (Purvis 2008). Here, I try to combine advantages of both approaches in this regionally focused study by building separate models for each WWF terrestrial ecoregion (Olson *et al.* 2001). My aim is to map effects of species traits on mammalian extinction risk across taxonomic groups while accounting for both phylogenetic relationships and regional differences in threat processes.

I focus on the main biological traits that global studies have found to be related to high extinction risk: small geographic range size, low abundance or species population density, low fecundity or slow life history, and large body size (see Fisher and Owens 2004, Purvis 2008 for recent reviews). Narrow distributions and/or low abundances make species susceptible, an effect believed to be intensified by habitat loss (Scharlemann *et al.* 2005). Low fecundities and slow life histories reduce the ability of populations to compensate for increased mortality and have been connected to overexploitation in particular (Owens and Bennett 2000, Isaac and Cowlshaw 2004, Price and Gittleman 2007). According to a recent global study, body size interacts with ecological and life-history variables: low reproductive rates and low abundance were associated with high risk, but only among larger mammals (Cardillo *et al.* 2005). Some taxonomically and regionally focused studies also find direct body size effects (Isaac and Cowlshaw 2004, Collen *et al.* 2006, but see Price and Gittleman 2007). Additionally, human impacts often interact with species traits to shape risk patterns. For example, large species are thought to be threatened disproportionately by overexploitation but not by habitat loss, as shown in birds

(Owens and Bennett 2000) and primates (Isaac and Cowlshaw 2004) but not in artiodactyls (Price and Gittleman 2007).

Here, I use a novel two-stage combination of phylogenetic and spatial analyses to describe how anthropogenic threats interact with species traits to shape extinction risk. In contrast to other studies that have tended to focus on current human population density, I additionally use measures for human appropriation of ecosystem services, economic development, and current and historical habitat loss via land conversion, all of which have been connected to extinction risk (Scharlemann *et al.* 2005, Luck 2007). In the first stage, I map regional patterns of the influence that selected species traits have on extinction risk when controlling appropriately for phylogenetic effects. Using spatially explicit analyses, the second stage then models these trait effects as functions of historical and current human impacts across the globe.

Methods

Dataset and phylogeny

Geographic range and life-history data for mammals excluding marine and strictly freshwater species were obtained from the PanTHERIA dataset (Jones *et al.* 2009). Following global studies (Cardillo *et al.* 2005, Cardillo *et al.* 2008), I chose geographic range size, body mass, species population density, and two life-history traits as explanatory variables in our models. To describe life-history variation independently of body size, gestation length and weaning age were chosen to represent reproductive output and timing (Bielby *et al.* 2007). Following Purvis *et al.* (2000b), I converted the IUCN Red List 2007 ratings (IUCN 2007) into a numerical index from 0 to 5 as a measure of extinction risk, and excluded species classified as Data Deficient and threatened species not listed under criterion A (recent or ongoing population decline) to avoid the circularity of including species

listed due to small population sizes or geographic ranges. Risk status for species in both the phylogeny and distribution dataset was: 2447 species in Least Concern, 563 Near Threatened, 444 threatened under criterion A, and one Extinct in the Wild. Data availability for each predictor variable ranged between all 3455 species (geographic range size) and 801 species (23%; species population density) (Table 3-1).

To investigate regional impacts of different biological traits on global mammalian extinction risk, I modelled the relationship of traits with risk for each WWF terrestrial ecoregion in a phylogenetic framework. I chose ecoregions rather than grid cells as spatial units because they are at a relatively small scale for a study of global extent, but yield sufficiently large sample sizes for modelling. Ecoregions also represent more natural units than a grid since they delimit biogeographical units with distinct natural communities (Olson *et al.* 2001). Finally, the coarser scale of ecoregions may avoid some of the errors arising from converting imprecise species ranges to e.g. grid cell occurrence (Jetz *et al.* 2008). I overlaid ecoregion shapefiles (<http://worldwildlife.org/science/data/terreco.cfm>, accessed

Variable	N	λ	χ^2
IUCN extinction risk	3455	0.70	822.7
Geographic range size	3455	0.63	785.6
Body mass	2944	0.99	7610.7
Population density	801	0.88	943.1
Weaning age	957	0.92	1409.4
Gestation length	1112	0.99	2910.1

Table 3-1. Data availability and phylogenetic signal for species traits in the mammal dataset.

Number of species with data per trait (N) and Pagel's λ with results of testing for the departure of λ from zero are shown. All χ^2 values were significant with $P < 0.001$.

August 2006) with mammal species ranges from Jones *et al.* (2009) and extracted the occurrence of species per ecoregion. Of the 825 terrestrial ecoregions, 791 contained mammals.

For the phylogenetic analyses, I updated the species-level supertree of Bininda-Emonds *et al.* (2007) to account for the more recent mammalian taxonomy of Wilson & Reeder (2005). Species identities were associated between the respective taxonomies (Wilson and Reeder 1993/2005) using information on taxonomic synonymy therein. Of the 4510 species in the original phylogeny, 3609 were unchanged between the taxonomies and 368 were simply renamed. Taxonomic lumping resulted in the loss of 111 species, whereas 422 species were split to 1043 tips to incorporate 675 new species names (retaining the original species name when applicable). All of these taxonomic changes to the original topology were performed using the Perl script *synonoTree* v2.2b (Bininda-Emonds *et al.* 2004). The new topology of 5020 species was then redated using exactly the procedures and data sets detailed in Bininda-Emonds *et al.* (2007, corrigendum 2008). The sequence data were also updated for this procedure to account for the new taxonomy using the Perl script *seqCleaner* v1.0.3. To avoid potential ambiguity, only one-to-one renamings were applied here; sequence data affected by taxonomic lumping or splitting were deleted from the dataset.

Phylogenetic analyses

I used Pagel's λ (1999) to test for phylogenetic signal in our variables. If there is no phylogenetic signal in the variable in question, λ is zero, and it approaches one with increasing phylogenetic pattern. Estimates for λ were significantly non-zero for all the traits tested, including IUCN extinction risk rating (Table 3-1).

Therefore, I accounted for phylogenetic effects by using phylogenetic generalised linear models (PGLMs) for within-ecoregion models of extinction risk (Freckleton *et al.* 2002). In a PGLM, Pagel's λ is used to account appropriately for the phylogenetic covariance between response and explanatory variables. This method avoids the errors associated with assuming complete phylogenetic

independence ($\lambda=0$, equivalent to non-phylogenetic analyses) or the over-correcting caused by assuming complete phylogenetic covariance ($\lambda=1$, equivalent to phylogenetically independent contrasts, Purvis 2008). I ran all models in R version 2.6.0 (R Development Core Team 2007), using code provided by R. Freckleton for the PGLM (version 3.2; updated version available as part of the CAIC package from <http://r-forge.r-project.org/projects/caic>).

All explanatory variables were log-transformed for the analyses. To avoid overfitting, I discarded models where the number of fitted parameters was higher than one-third of the number of nodes in the ecoregion phylogeny, a strict measure of sample size (Crawley 2007) for phylogenetic models. As models including all five explanatory variables could be fitted in only 379 ecoregions, I instead built separate models focusing on each of the selected traits in turn, while controlling for independent effects of the most confounding covariates. The only single-predictor model fitted geographic range size as the focal variable; all other models controlled for range size because it was the single most important predictor of species risk. Models for species population density, weaning age and gestation length as focal traits additionally controlled for body mass, which correlates strongly with all three. I did not fit interaction terms because of sample size restrictions within the ecoregions. Each of the five models was fitted to each ecoregion and also to the whole mammalian dataset to compare global and regional results. To facilitate subsequent comparisons of coefficient estimates across the globe, I did not simplify models.

Spatial analyses

In comparative studies, not only phylogenetic but also spatial non-independence can inflate degrees of freedom in statistical testing and violate the assumption of independently distributed errors in ordinary least squares (OLS) regression (Dormann *et al.* 2007). Since each of my phylogenetic models was on the comparatively small scale of a single ecoregion, spatial autocorrelation of species values within these models should be negligible. I therefore only account for the

spatial non-independence in my models across ecoregions, effectively using a two-step process to incorporate both phylogenetic and spatial effects. Approaches that combine phylogeny and space in a single-step analysis are being developed (Freckleton and Jetz 2009) but do not yet support multiple regression models.

I used non-spatial and spatially explicit multiple regression to relate the differences in susceptibility caused by intrinsic traits (i.e. the coefficients from the phylogenetic models) to environmental variables across ecoregions. Using an ArcInfo macro, I calculated ecoregion values for several variables describing available environmental energy, topology, anthropogenic and biological factors. Definitions of variables and data sources are listed in Table 3-2. Prior to analysis, I transformed environmental variables based on best approximation of a normal distribution: ecoregion area and the number of threatened species were log-transformed, and proportional variables were square-rooted (proportions of small-ranged and large species).

To avoid collinearity and reduce the dataset dimensions, I ran a principal components analysis on seven proxy measures of anthropogenic impact (Table 3-3). The first three principal components (PCs) were used as explanatory variables, because they cumulatively explained over 90% of the total variance. PC1 mostly represented measures of current human impact (human population density, human appropriation of net primary productivity, human influence index and gross domestic product; Table 3-3). PC2 had a high negative loading of historical agriculture, reflecting land-use intensity throughout the past 300 years, and PC3 represented current urban land cover (Table 3-3).

I initially fitted all environmental variables in Table 3-2 to each of my five response variables (the coefficient estimates from the phylogenetic models). These starting models were then simplified to minimum adequate models (MAMs) by sequentially removing the most non-significant variable until only significant ones remained in the MAM (Crawley 2007). Between two and six data points were removed from the MAMs because they were overly influential

Variable group	Acronym	Variable description	Source
Energy	AET	Mean annual actual evapotranspiration (mm)	UNEP (1994)
Topology	ELEV	Mean elevation (m)	USGS EROS (1996)
	HABH	Habitat heterogeneity	Olson (1994)
	AREA	Ecoregion area (km ²)	Olson <i>et al.</i> (2001, downloaded from http://worldwildlife.org/science/data/terreco.cfm in August 2006)
Human influence	PC1	Principal component 1, reflecting current human pressures	See Table 3-3
	PC2	Principal component 2, reflecting historical agriculture	See Table 3-3
	PC3	Principal component 3, reflecting current urban land cover	See Table 3-3
Biology	THRSP	Number of threatened species	Jones <i>et al.</i> (2009), IUCN (2007)
	SMALLGR	Proportion of small-ranged species	Jones <i>et al.</i> (2009)
	LARGEGBM	Proportion of large species	Jones <i>et al.</i> (2009)

Table 3-2. Description and sources for variables used in the non-spatial and spatial models across ecoregions.

Habitat heterogeneity was measured as the number of ecosystems. The number of threatened species was the number of species listed above Least Concern (excluding Data Deficient species and species in the three threat categories not listed under criterion A, IUCN 2007). I defined species as small-ranged if their range was in the lowest quartile of all ranges in the dataset, i.e. <33,180 km² (Jetz and Rahbek 2002). Large species were those with a body mass >3 kg (Cardillo *et al.* 2005).

Variable description and source	PC1	PC2	PC3
Mean human population density (individuals/km ²) CIESIN & CIAT (2005)	0.42	0.27	-0.09
Mean human appropriation of net primary productivity (t carbon) Imhoff <i>et al.</i> (2004, downloaded from http://sedac.ciesin.columbia.edu/es/hanpp.html in May 2008)	0.42	0.31	-0.08
Mean human influence index Sanderson <i>et al.</i> (2002, downloaded as Last of the Wild Data Version 2 from http://sedac.ciesin.columbia.edu/wildareas in May 2008)	0.43	0.05	-0.05
Mean gross domestic product (US\$) CIESIN (2004)	0.42	0.20	0.09
Historic agriculture index Klein Goldewijk (2001, downloaded from http://islscp2.sesda.com in May 2008)	0.27	-0.84	-0.18
Proportion of urban land cover in 2000 European Commission and Joint Research Centre (2003)	0.28	-0.21	0.88
Proportion of cropland in 2000 European Commission and Joint Research Centre (2003)	0.36	-0.18	-0.40

Table 3-3. Human influence measures and their loadings in the principal components analysis for the first three principal components.

The historical agriculture index was defined as the sum of the proportions of cropland and pasture in an ecoregion across the years 1700, 1750, 1800, 1850, 1900, 1950 and 1990. To calculate proportions of urban land cover and of cropland in 2000, grid cells in category 22 (artificial surfaces and associated areas) were defined as 100% urban; cells in category 16 (cultivated and managed areas) as 100% cropland; and cells in categories 17 or 18 (mosaic of cropland with other land cover) as 50% cropland.

(absolute studentised residuals > 4). I report results without these, but indicate where results including them differed qualitatively.

Following Lichstein *et al.* (2002), I tested for the presence of spatial non-independence in the regression residuals of the MAMs using Moran's *I* correlograms, and accounted for it using spatial autoregression (SAR, simultaneous autoregressive model). This method assumes that the response is a function of both the explanatory variables and the values of the response at neighbouring locations (Kissling and Carl 2008). The SAR_{error} approach I used models the autoregressive process in the error term, and has been recommended as the most reliable spatial autoregressive method (Kissling and Carl 2008). I report results of both OLS and SAR models for three reasons. First, SAR models have only recently been adopted in spatial ecology and there is no standard approach to model selection yet (Dormann *et al.* 2007). Second, it is unclear whether OLS coefficient estimation is biased by residual spatial autocorrelation (Hawkins *et al.* 2007). Third, OLS models potentially show broad-scale trends, whereas SAR models preferentially select for variables influencing the response at finer spatial scales (Diniz-Filho *et al.* 2003); both are of interest here.

I generated Moran's *I* correlograms and spatial models using the R packages *spdep* (Bivand 2007) and *ncf* (Bjørnstad 2006). Standardised *I* values were tested for significance using a one-tailed randomisation test for positive autocorrelation (999 permutations, Lichstein *et al.* 2002). In the SAR models, I defined neighbours as data points closer than a model-specific maximum distance and used a row-standardised coding scheme for the spatial weights matrix (Kissling and Carl 2008). The maximum neighbour distance chosen for each model optimised its AIC value (Akaike's Information Criterion, Crawley 2007). Following Lichstein *et al.* (2002), I calculated R^2 values for the SAR models using Nagelkerke's formula, and assessed the contribution of each variable to OLS and SAR model fits using likelihood ratio tests for nested models.

Results

Fig. 3-1a shows the total species number and number of threatened species within each ecoregion, illustrating the spatial coverage of the dataset. Globally, each species trait was significantly associated with risk when analysed separately, although gestation length and body mass were non-significant in the global model that included all species traits (Table 3-4). Models for each focal trait were fitted in 602 to 729 ecoregions (Table 3-5). No models could be fitted in Antarctica or Oceania because of low species numbers there, but every other biogeographical realm was represented. We found high regional heterogeneity in influences of some biological traits on extinction risk (Table 3-5, Fig. 3-1b to 3-1f).

Mammalian species extinction risk was negatively correlated with geographic range size in 62% of ecoregions throughout the world (Table 3-5, Fig. 3-1b). Controlling for range size, large body mass was correlated with high extinction risk in approximately half of the ecoregions (Table 3-5); significant correlations were mostly restricted to the Neotropical, Afrotropical and Indo-Malayan realms (Fig. 3-1c). Species population density and life-history variables displayed more heterogeneous spatial patterns of influence on extinction risk after controlling for range size and body mass, and were independently significant in only 19-29% of ecoregions (Table 3-5, Fig. 3-1d-f).

Spatial (SAR) models always had lower AIC values and explained a higher amount of variance than non-spatial (OLS) models (Table 3-6). They also successfully removed nearly all significant residual spatial autocorrelation (Fig. 3-2). At least one anthropogenic variable was significant in each non-spatial model (Table 3-6). In both spatial and non-spatial models, current human impacts were strongly correlated with impacts of geographic range size on risk (Fig. 3-3a), whereas the effects of large body mass were greatest where there had been least historical land conversion (Table 3-6, Fig. 3-3b). Effects of species population density and life-history traits on risk correlated with different anthropogenic

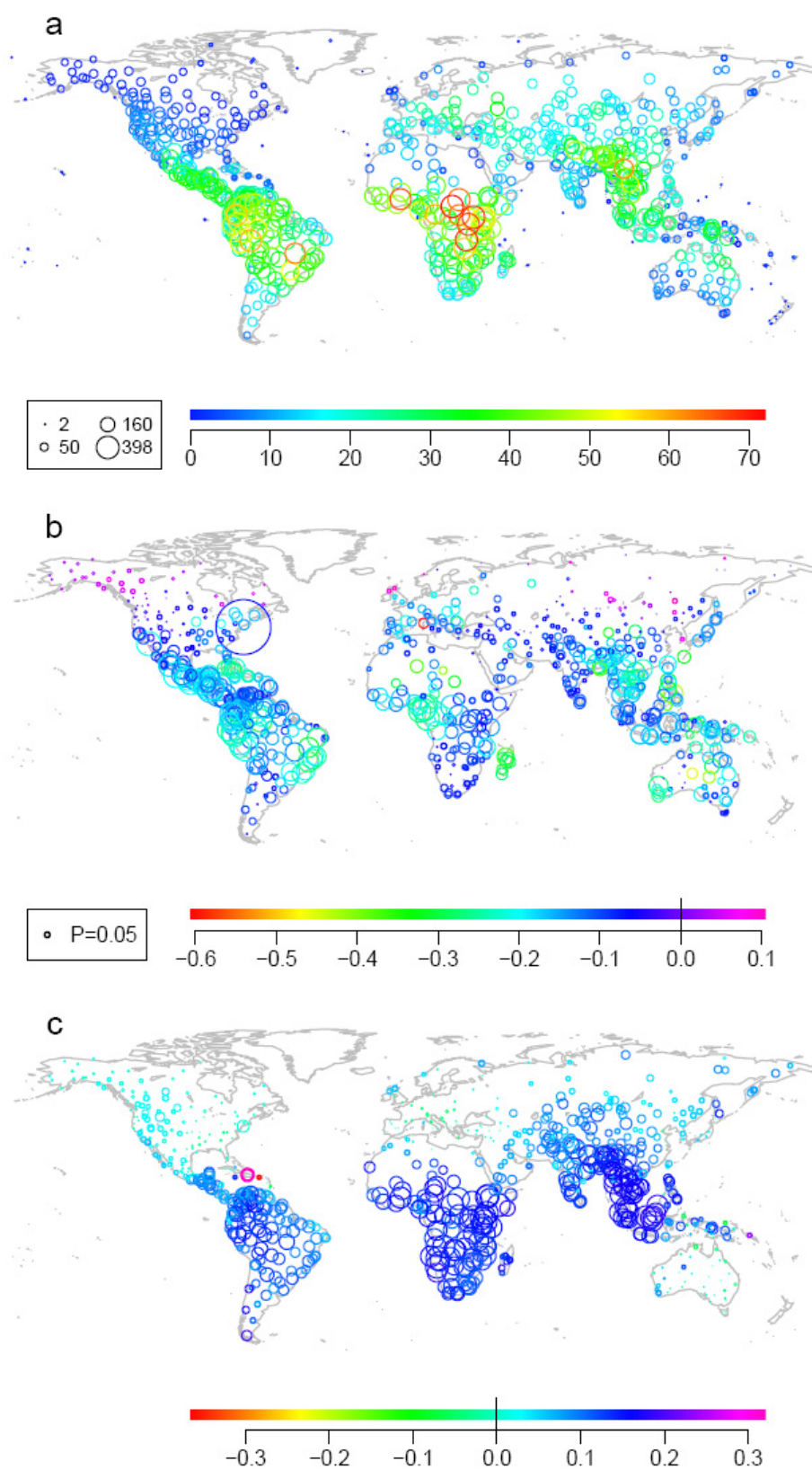


Figure 3-1. *Continued on following pages.*

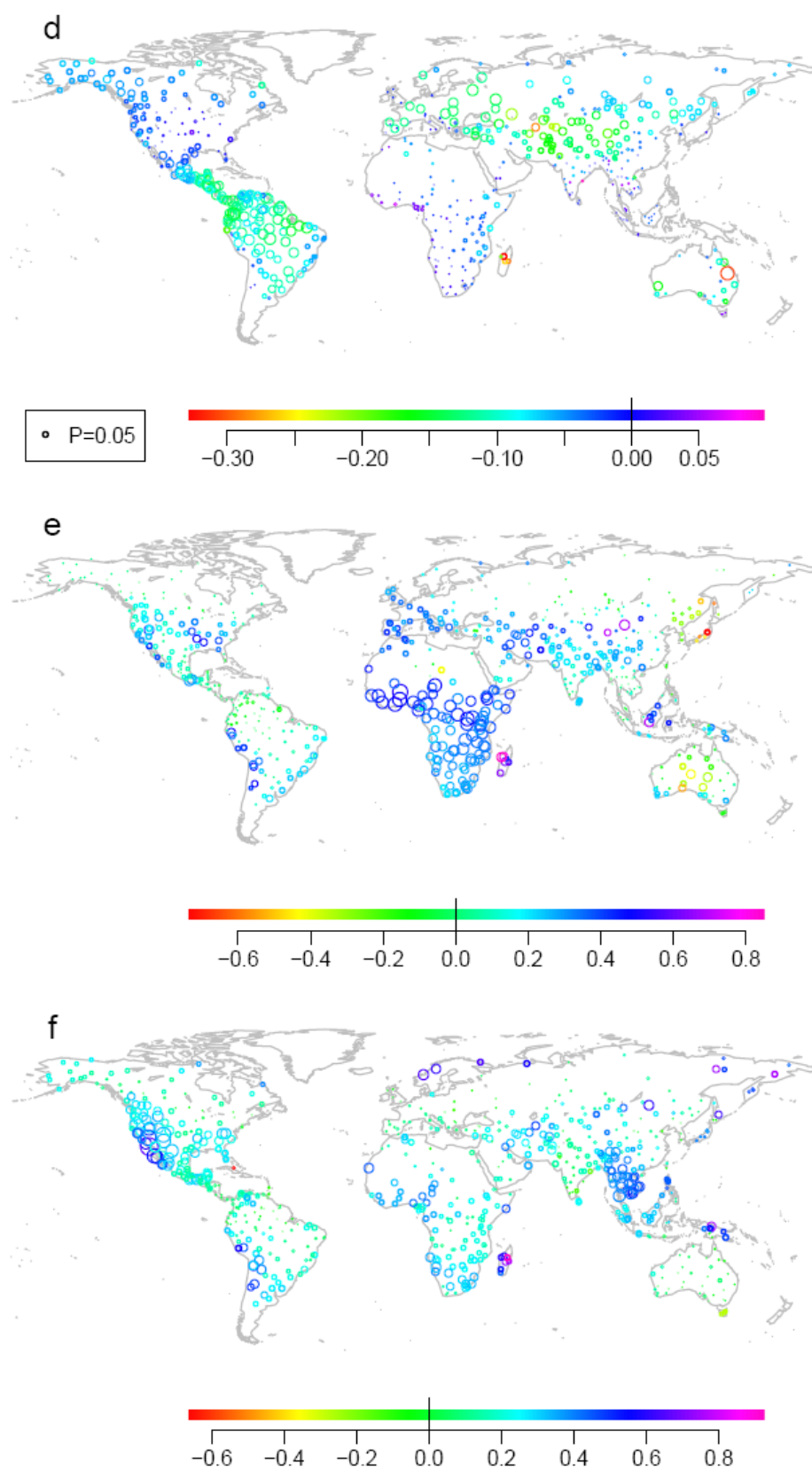


Figure 3-1. Caption on following page.

Figure 3-1. (*Previous pages*). Species numbers per ecoregion (a) and results of within-ecoregion models for mammalian species extinction risk (b-f).

In a), a circle is plotted on the centroid of each ecoregion with >1 mammal species. Circle size is proportional to total species number, and the size legend indicates the minimum, 1st and 3rd quartile and maximum circle size (species numbers were square-root transformed for plotting). Circles are coloured to indicate the number of species ranked above Least Concern, as shown in the colour key (excluding Data Deficient species and species in the three threat categories not listed under criterion A, IUCN 2007). In b) to f), a circle is plotted on the centroid of each ecoregion where a model could be fitted. Circle colour indicates the coefficient estimate for the focal explanatory variable in a PGLM against extinction risk, as given by the colour key, where a coefficient of zero is highlighted by a horizontal line. Circle size shows the significance of this coefficient, illustrated by the size legend in b) and d) for plots b) to f). The size legend indicates the size of a circle if the coefficient estimate is just not significantly different from zero (t -test, $P=0.05$), i.e. smaller circles designate non-significant coefficients. Focal explanatory variables were: b) geographic range size, c) body mass, d) species population density, e) weaning age and f) gestation length. All models controlled for geographic range size, and models d), e) and f) also controlled for body mass.

measures, although associations were non-significant in spatial models for gestation length and species population density (Table 3-6, Fig. 3-3c to 3-3e).

At least one biological variable was significant in each model across ecoregions, and biology explained most of the variance especially in the spatially explicit models (Table 3-6, Fig. 3-3). Available energy predicted the effects of body mass and life-history traits only (Fig. 3-3b, 3-3d, 3-3e). Topological variables (especially habitat heterogeneity) were significant in each of the non-spatial models, although they were nearly all non-significant in spatial models for population density and life-history traits (Table 3-6, Fig. 3-3).

	N	R ²	λ	Slope	Error	d.f.	<i>t</i>
Geogr. range size	3455	0.17	0.72	-0.149	0.006	3453	26.80***
Body mass	2944	0.20	0.64	0.116	0.014	2941	8.56***
Population density	797	0.24	0.59	-0.051	0.016	793	3.11**
Weaning age	943	0.21	0.50	0.171	0.054	939	3.15**
Gestation length	1097	0.23	0.48	0.170	0.074	1093	2.30*
Full model	468	0.24	0.64				
Geogr. range size				-0.213	0.022	462	9.80***
Body mass				0.060	0.034	462	1.77 ^(*)
Population density				-0.070	0.022	462	3.25**
Weaning age				0.203	0.082	462	2.49*
Gestation length				0.036	0.116	462	0.32

Table 3-4. Results of global extinction risk models for the complete mammal dataset using PGLM.

All models for focal traits controlled for geographic range size, and the models for species population density, weaning age and gestation length also controlled for body mass. The number of species for the model (N), adjusted R², optimised λ , and the coefficient estimate (slope) with its standard error, degrees of freedom (d.f.) and absolute *t* value are given. All λ values were significantly different both from zero and one (χ^2 tests, all $P < 0.001$). Significance levels for *t*: ^(*) $P = 0.077$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

There were no qualitative differences in non-spatial models when excluding overly influential points, but three spatial models changed. In the geographic range model, proportion of large species was significant when including all data points ($z = 2.98$, d.f. = 702, $P < 0.01$). When including all data points in the body mass model, the proportion of large species was non-significant ($z = 1.45$, d.f. = 698, $P > 0.05$). In the gestation length model with all data points, proportion of small-ranged species was non-significant ($z = 1.71$, d.f. = 665, $P > 0.05$) and contributed much less to model fit than proportion of large species (likelihood ratio (LR) = 2.9 for small-ranged, LR = 20.3 for large species).

	T	Geographic range		Body mass		Population density		Weaning age		Gestation length	
		M	S	M	S	M	S	M	S	M	S
Australasia	83	65	43	64	8	22	4	48	4	49	1
Antarctic	4	0	0	0	0	0	0	0	0	0	0
Afrotropic	114	102	74	102	96	96	0	101	87	102	25
Indo-Malaysia	106	101	91	100	91	80	0	97	5	98	25
Neartic	118	107	27	107	8	96	13	107	9	106	47
Neotropic	179	166	153	166	125	142	105	145	12	146	26
Oceania	24	0	0	0	0	0	0	0	0	0	0
Paleartic	197	188	62	188	79	166	51	181	11	185	26
Total	825	729	450	727	407	602	173	679	128	686	150

Table 3-5. Results of within-ecoregion models of extinction risk for each biogeographic realm.

T, total number of ecoregions; M, number of ecoregions with fitted models; S, number of ecoregions for which the slope of the focal trait was significantly different from zero in a PGLM ($P<0.05$). All models for focal traits controlled for geographic range size, and the models for species population density, weaning age and gestation length also controlled for body mass.

	Geographic range		Body mass		Population density		Weaning age		Gestation length	
	OLS	SAR	OLS	SAR	OLS	SAR	OLS	SAR	OLS	SAR
AIC	-1835.5	-2090.3	-2556.7	-2996.8	-1780.6	-2261.8	-464.1	-916.2	-682.3	-1043.1
Res. d.f.	698	696	694	692	589	587	657	655	665	663
R ²	40.2	58.5	56.6	76.9	14.1	61.8	18.2	58.7	12.3	48.8
Distance		870.8		1068.2		929.6		1120.7		939.7
Autot. error		0.711		0.871		0.859		0.862		0.789
AET	n.s.		< 0.001***	< 0.001	n.s.		> -0.001***	> -0.001*	> -0.001**	< -0.001***
ELEV	n.s.		n.s.		n.s.		< 0.001***	< 0.001	n.s.	
HABH	0.002***	0.002***	-0.002***	-0.001***	-0.002***	> -0.001	-0.004***	-0.001	n.s.	
AREA	n.s.		n.s.		n.s.		n.s.	-0.010*	-0.012***	
PC1	-0.007***	-0.005***	n.s.		0.008***	0.001	0.022***	0.010**	-0.008**	-0.005
PC2	n.s.		0.012***	0.005***	0.006*	-0.001	n.s.		0.027***	-0.007
PC3	n.s.		n.s.		0.012***	> -0.001	0.018*	-0.010	0.017*	0.005
THRSP	-0.039***	-0.040***	0.035***	0.023***	-0.007*	-0.018***	0.056***	0.043***	0.029***	0.057***
SMALLGR	n.s.		n.s.		n.s.		0.172*	0.075	0.341***	0.190***
LARGE BM	0.221***	0.059	0.228***	0.105***	0.103***	-0.177***	0.465***	0.109	0.260***	0.227*

Table 3-6. Results of non-spatial ordinary least-squares (OLS) and spatially-explicit simultaneous autoregressive (SAR) models across ecoregions.

The response variables were the coefficient estimates for focal traits derived from phylogenetic extinction-risk models within ecoregions. Coefficient estimates and their significance are given for each environmental variable used as an explanatory term (see Table 3-2 for acronyms).

Table 3-6. Caption continued from previous page.

Variable groups were: energy – AET; topology – ELEV, HABH, AREA; anthropogenic – PC1, PC2, PC3 (see Table 3-3); biology – THRSP, SMALLGR, LARGE-BM. For OLS models, variables fitted but not retained in the minimum adequate model are listed as non-significant (n.s.); these variables were not fitted in the corresponding SAR models. Additionally, AIC, residual degrees of freedom and R^2 (or pseudo- R^2) are given for all models, and the maximum neighbourhood distance and estimated autoregressive error coefficient for SAR models. Significance levels for the coefficient estimates: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Discussion

Globally, small geographic range, large body mass, low population density, high weaning age, and high gestation length were associated with high extinction risk, but ecoregion models showed that the influence of each of these species traits varied substantially across the world. The strong spatial variation at the ecoregion scale demonstrates that to understand extinction-risk processes, small-scale analyses are needed. My results also successfully relate current and recent-past human impacts to the influence of biological traits on species extinction risk, emphasising the role of species traits in increasing susceptibility to different anthropogenic threats.

Similarly to previous studies, geographic range size was the single most important predictor of mammalian extinction risk both in my global and ecoregion models (Fisher and Owens 2004, Cardillo *et al.* 2008). Large size mattered in the global model when controlling for range size, but became non-significant when life-history traits and population density were added. Also, global models focusing on life-history traits and species population density did not explain much additional variance compared to the global model for body mass. These findings could be attributed to body-mass interactions with life-history traits (Cardillo *et al.* 2005),

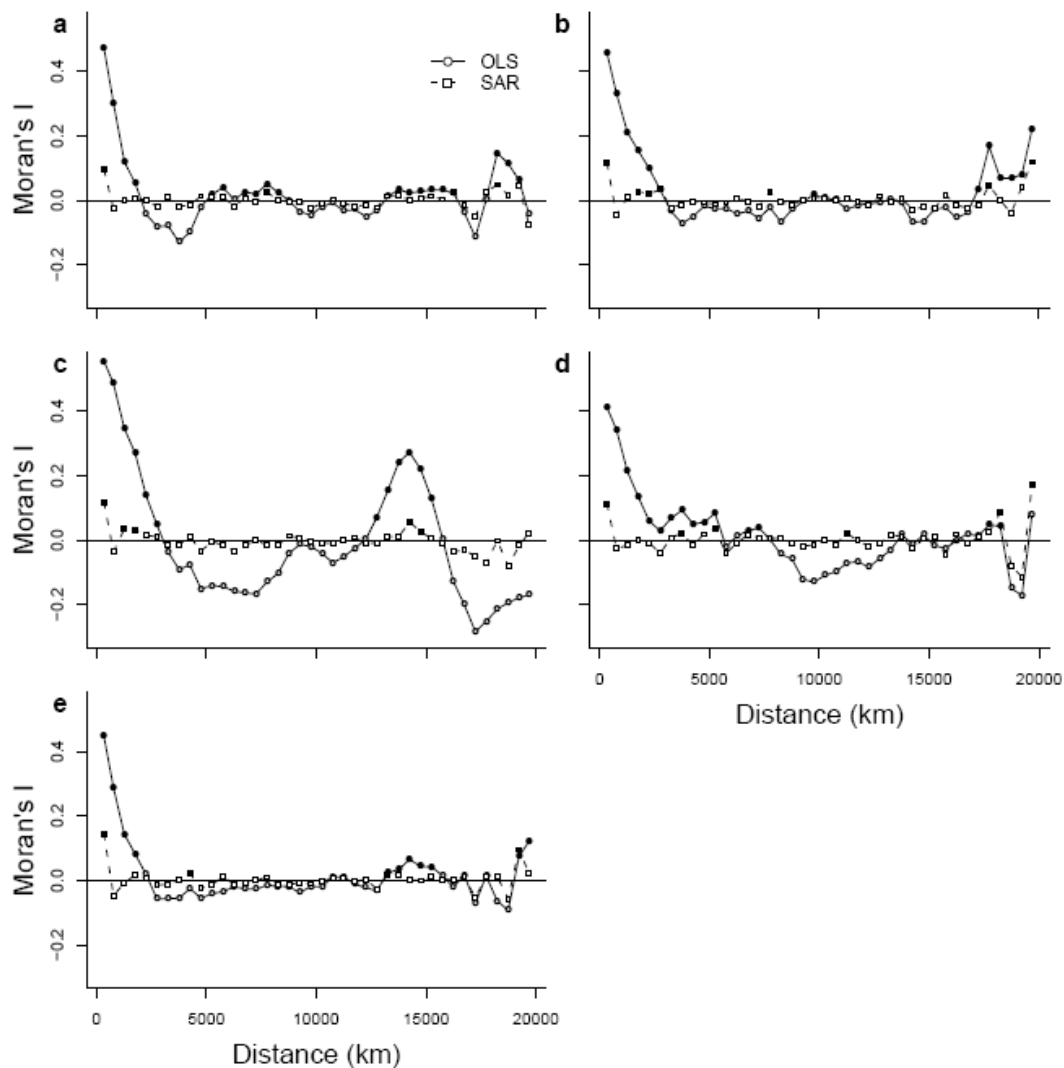


Fig. 3-2. Moran's I correlograms of non-spatial (OLS; circles) and spatial (SAR; squares) model residuals.

Filled symbols indicate significant Moran's I values (999 permutations, one-tailed test). All correlograms are plotted using the same y-axis extent. The models fitted different environmental variables across ecoregions (Table 3-6). Responses were coefficient estimates from phylogenetic models of extinction risk within ecoregions for the following explanatory variables: a) geographic range size, b) body mass, c) species population density, d) weaning age, e) gestation length.

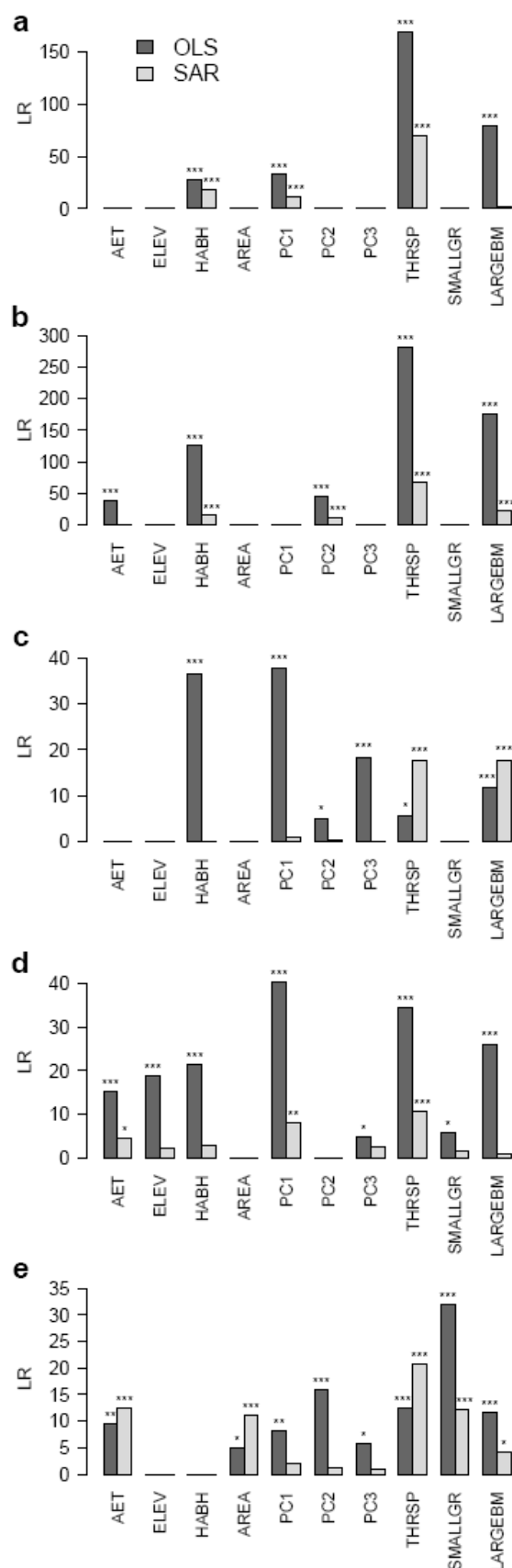


Figure 3-3. Results of likelihood ratio (LR) tests for non-spatial (OLS) and spatial (SAR) models across ecoregions.

LR illustrates the contribution to model fit for explanatory variables that were significant in the non-spatial minimum adequate model (see Table 3-2 for variable acronyms). Stars above the bars indicate significance levels for the variables as in Table 3-6. Responses were the coefficient estimates from phylogenetic models of extinction risk within ecoregions for the following explanatory variables: a) geographic range size, b) body mass, c) species population density, d) weaning age, e) gestation length.

but the ecoregion results reveal that the signal of body mass itself varies in space. Global models mask these regional differences, whereas my combination of phylogenetic and spatial analyses adds further understanding of the processes underlying extinction risk.

Body mass

The striking spatial pattern for body mass impacts, with large species at higher risk only in the tropics, does not stem from a latitudinal gradient in body mass because mammals do not show such a simple pattern (Rodríguez *et al.* 2008, chapter 5). Statistical power of my methods may play a role, because the observed relationship between large body mass and high extinction risk is stronger in ecoregions with more threatened species and a higher proportion of large species. However, when controlling for these variables, body mass additionally influences risk more strongly in areas with lower overall impact of historical agriculture. This suggests the presence of an extinction filter (Balmford 1996), whereby regions with a high agricultural impact throughout the past 300 years have lost their large species already. The implication is that proportion of species threatened due to large body mass should be highest at intermediate levels of land conversion (Davies *et al.* 2008). Accordingly, current human impacts did not correlate with body mass effects on risk here; presumably, most species susceptible due to large size have already been removed in many areas with highest current anthropogenic threat.

Data on historical extinctions and geographic distributions are patchy before the 19th century, but since then medium- and large-sized species in Europe, North America and Australia have definitely suffered range contractions and local extinctions (Ceballos and Ehrlich 2002). Many large species still exist in these areas, but have experienced declines in recent history that are not reflected by current Red List status, as these take only the last 10 years or three generations into account (IUCN 2001). For example, the brown bear (*Ursus arctos*) and the wolf (*Canis lupus*) are rated Least Concern (IUCN 2008). According to the

threshold model of Barnosky (2008), both human and livestock biomass levels have skyrocketed above normally supportable levels since the industrial revolution, sustained by the mining of fossil fuels. If these increases throughout the past 300 years and the related large-scale land conversion have caused declines and local extinctions of large mammals in developed countries, they would have left large species only in the tropics. There, agricultural land conversion and human population have sharply increased only during the last few decades, so the recent and ongoing declines of tropical large species are reflected in the current Red List.

Current body mass patterns have also been shaped by extinction filters much further in the past. Most obviously, the end-Pleistocene megafaunal extinctions removed many large mammals everywhere except Africa. However, these extinctions may have been selective on life-history speed rather than body size itself (Johnson 2002), and were probably caused by a combination of human influence and climate change that may itself have varied among regions (Burney and Flannery 2005, Wroe *et al.* 2006): more recent large-scale anthropogenic impacts are not directly comparable. Survivorship of large mammals in temperate vs. tropical regions through the end-Pleistocene crisis needs to be investigated more closely to assess whether these extinctions could have generated a present pattern where large, slow-reproducing mammals are only extant in the tropics.

Nevertheless, my results provide evidence for a post-industrial extinction filter that has already affected large mammals in temperate regions and is now affecting those in the tropics. These body-mass effects might derive from underlying life-history variation, with large size increasing extinction risk only in areas where species have predominantly slow life histories and low reproductive output (Cardillo *et al.* 2005). On the other hand, body mass remained a significant variable in nearly all tropical ecoregions in my models fitting weaning age or gestation length, which may suggest a life-history-independent effect of body mass in the tropics. As I was not able to control for trait interactions on risk, our results cannot distinguish whether the high tropical impact of body mass on risk is

truly independent of life-history traits or whether it reflects an interaction between body mass and life-history traits in the tropics.

Leaving life-history aside, there are two mechanisms by which large body mass could directly affect risk, which I could not account for due to a shortage of globally consistent data. Firstly, large mammals tend to have large home ranges, so they are more likely to encounter threats (Woodroffe and Ginsberg 1998). Home range size is positively correlated with extinction risk in global models, but not in taxonomically or regionally restricted ones (Cardillo *et al.* 2008). Secondly, human exploitation preferentially targets large mammals, and hunting has been shown previously to cause body mass selectivity in extinction risk (Owens and Bennett 2000, Isaac and Cowlshaw 2004, Collen *et al.* 2006). Subsistence hunting is largely confined to tropical regions and extracts more biomass in the Afrotropics than in the Neotropics (Fa *et al.* 2002), which coincides well with areas of strong body-mass effects on risk identified in this chapter. My results are therefore consistent with the speculation that, in addition to habitat loss via land conversion, subsistence hunting in the tropics contributes to the higher risk faced by large species in the tropics than elsewhere.

Geographic range size

In accordance with global studies (e.g. Cardillo *et al.* 2008), I found a close relationship of high extinction risk and small geographic range size. My ecoregion results additionally show that small range sizes are consistently linked to high risk across most of the world. This relationship appears not to be driven by narrow-ranged endemics, because the proportion of narrow-ranged species within ecoregions was not a significant predictor in my spatial analyses. At high northern latitudes, low species richness and predominantly large range sizes may explain the non-significant relationships (Davies *et al.* 2008).

Additionally, the composite measure of current human impact (PC1) was significantly correlated with the influence of range size on risk, indicating that

high human population densities, high appropriation of net primary productivity and/or high economic development increase the effect of small geographic range size on extinction risk. The overwhelming impact of range size on risk is thought to stem from habitat loss, which affects species globally and narrow-ranged species in particular (Baillie *et al.* 2004, Scharlemann *et al.* 2005). Given that my human impact measure incorporated land transformation as part of the human influence index, my results may provide evidence for this link of habitat loss and high threat in narrow-ranged species. However, my results may also emphasise the role of more subtle habitat changes through extraction of ecosystem services, especially since historical agriculture (another indicator for habitat loss in my models) was non-significant here. I show that current human activities clearly play a role in increasing risk for narrow-ranged mammals virtually everywhere, but future studies should endeavour to separate the effects of different aspects of human influence on the relation between geographic range size and extinction risk (Luck 2007).

I am aware of two possible biases which could lead to consistently more threatened Red List status for narrow-ranged species. First, if the distributions of small-ranged species are mapped at a smaller grid resolution than larger-ranged ones, estimates of range size for risk assessments are exaggerated for all but the smallest ranges (Cowley *et al.* 1999), which could overestimate proportions of threatened narrow-ranged species. This bias is unlikely to affect these analyses because distribution maps usually overestimate range sizes for narrow-ranged species (Jetz *et al.* 2008), and because I excluded species ranked as threatened due to small range size only.

The second possible bias arises if most threatened mammals have already had their ranges reduced, because then small current geographic ranges would reflect susceptibility to human impacts. I found comparatively strong phylogenetic pattern in the geographic range size data ($\lambda = 0.63$, see Table 3-1). This may indicate that either geographic range size can be more phylogenetically conserved than previously thought (Webb and Gaston 2003) or that present range sizes

include effects of phylogenetically selective susceptibility to human threats. This result stresses a need to understand more about the factors that shape geographic range size, both spatially and phylogenetically (e.g. Cooper *et al.* 2008).

Abundance and life-history traits

Species population density, gestation length and weaning age showed much more spatially varied effects on extinction risk than body mass or geographic range size. Clearly, data availability plays a larger role in these three models, with data available for only about a quarter as many species as for body mass and range size. However, over 75% of the ecoregion models were still based on more than 40 species.

My results show that low species population density is more strongly linked with high extinction risk where current human impacts are high, indicating that anthropogenic threats preferentially affect rare species, at least in some regions of the globe. I also provide some evidence that human activities influence the effects of reproductive timing and output on risk when controlling for body mass. High spatial heterogeneity of trait effects may indicate that the spatial scale of this study could be too large to separate mixed signals if extinction drivers vary within ecoregions, given that impacts of life-history variables on risk are likely to be linked to particular threats (Isaac and Cowlshaw 2004, Price and Gittleman 2007). The great importance of threatened species richness and proportion of large species in the species population density and life-history models may be due to the power of my method, but may also signify that low abundances and slow life histories affect the extinction risk of large species more strongly (Cardillo *et al.* 2005).

Conclusions

My regional models of extinction risk revealed strong global heterogeneity in both the impact of biological traits and their interactions with the environment. Clearly,

species extinction risk is determined by anthropogenic threats, environmental factors, species traits and interactions between these, but my analyses have highlighted some of the most important ones. I found that large size correlated strongly with high extinction risk only in tropical regions which are characterised by overall low historical agricultural impact, probably reflecting the effects of an extinction filter acting over the past 300 years, and possibly of current subsistence hunting. My results also indicated that small geographic range sizes predispose species to extinction across much of the world, and that high current human impact increases the effects of low species population density and slow life history on risk.

Although these analyses are still on a larger scale than most protected areas, their spatial resolution makes them more useful for practical conservation science than global models. My results also emphasise the importance of including several measures of both historical and current facets of anthropogenic threats, rather than oversimplifying human impact to just current human population density. The novel regional approach I used here illustrates and explains spatial heterogeneity in risk processes across the globe. Yet, to improve our knowledge of extinction risk further and to make predictions useful for conservation biologists on the ground, we need to better separate the effects of different aspects of human exploitation, and to better understand the reasons behind phylogenetic and spatial patterns of biological traits that shape susceptibility.

Chapter 4: Comparative analysis of extinction-risk correlates in mammals, birds and frogs

Abstract

A large proportion of species are currently threatened by global extinction, prompting a search for biological and anthropogenic predictors of species extinction risk. Previous studies have generally focused on a single taxon or region; here, I compare global effects of biological traits and anthropogenic-impact measures across and within three taxa of vertebrates: mammals, birds and frogs. Using phylogenetic comparative methods, I investigate correlates of the within-family prevalence of extinction risk, both overall and broken down by threat process (habitat loss, harvesting and invasive species).

Controlling for geographic range size, large body size emerges as a consistent predictor of extinction risk from all types of threat, across and within taxa. The influence of other variables tested is very heterogeneous: correlates differ with both threat type and taxon. For example, mammalian risk from all threat types is higher for families with lower levels of recent-historical agriculture in their species ranges, indicating a previous extinction filter, while in frogs anthropogenic variables exclusively predict risk from pollution and invasive species. Across taxa and within mammals and birds, low human population densities in species ranges correlate with overall high risk and risk from habitat loss, further advocating historical extinction filter effects; conversely, risk from harvesting is higher for species experiencing high human population densities in their ranges.

Reproductive output and timing of reproductive bouts are surprisingly weakly associated with risk measures in general, although at least one of these two factors

predicts mammalian and avian risk from harvesting. The heterogeneity found for risk from different threat types implies that extinction processes differ strongly even within vertebrates, due to spatial variation in anthropogenic impacts and threat process, and to the differences in biological susceptibility between taxa.

Introduction

Anthropogenic pressures such as habitat loss, overexploitation, and spread of invasive species currently endanger between 12% and 30% of all known mammal, bird and frog species (IUCN 2008). Studies of phylogenetic patterns in extinction risk have found that threatened species constitute a non-random part of today's biota, caused by selectivity of anthropogenic threats on different biological traits (Bennett and Owens 1997, Russell *et al.* 1998, Stuart *et al.* 2004). Previous studies have investigated both biological and environmental correlates of extinction risk, but these analyses have been focused within taxa or on certain regions (see Fisher and Owens 2004, Purvis 2008 for recent reviews, and chapter 3). The aim of this chapter is to directly compare the global influence of human impacts and ecological and life-history traits on extinction risk among and within three major vertebrate taxa: mammals, birds and frogs.

The abundant evidence for phylogenetic selectivity both in present-day extinction risk and in the fossil record does not directly imply that biological traits determine extinction risk (McKinney 1997, Russell *et al.* 1998, Purvis 2008, chapter 2).

Phylogenetic pattern can also be generated by selective knowledge about risk (Bielby *et al.* 2006); I concentrate on three completely-assessed groups to reduce this uncertainty (IUCN 2008). Further, the geographic variation in threat intensity, together with the tendency for closely related species and clades to live in the same regions, can cause phylogenetic non-randomness in extinction risk. Studies on smaller spatial scales, where variation in threats is less probable, have shown consistent phylogenetic pattern in extinction risk, strongly suggesting that biology

plays a role in determining species' fates (Bielby *et al.* 2006, Davies *et al.* 2008). The analyses in this chapter focus on the global scale to investigate large-scale patterns, but I investigate the influence of different measures of anthropogenic impact in species' ranges in addition to that of biological traits.

Global studies of extinction-risk correlates in mammals and amphibians have exclusively made comparisons across species (e.g. Purvis *et al.* 2000b, Cardillo *et al.* 2005, Cooper *et al.* 2008, Sodhi *et al.* 2008, chapter 3). On the other hand, studies of global avian extinction-risk correlates include family-level analyses (Bennett and Owens 1997, Owens and Bennett 2000, Norris and Harper 2004) as well as species-level ones (Gaston and Blackburn 1995, Morrow and Pitcher 2003). There are also some apparent differences in correlates between taxa that may have been caused by different methods: for example, geographic range size is one of the most important predictors of extinction risk in mammals and amphibians (e.g. Purvis *et al.* 2000b, Cooper *et al.* 2008), but global bird studies have not controlled for its effects when looking at biological risk correlates (Gaston and Blackburn 1995, Owens and Bennett 2000). To achieve comparability between the three taxa and with previous studies, I analyse extinction risk using the same modelling approaches for all taxa on a family level, which also constitutes the first global family-level study of mammalian and amphibian extinction risk.

Species-level analyses often suffer from low data availability: especially when many biological correlates are investigated, models often have comparatively low sample sizes (e.g. Bennett and Owens 1997, 2332 of 9702 bird spp., Cardillo *et al.* 2005, 404 phylogenetically independent contrasts for 4629 mammal spp.). Also, many previous studies control for phylogenetic non-independence on the species level using taxonomic rather than phylogenetic information (e.g. Gaston and Blackburn 1995, Cooper *et al.* 2008, Sodhi *et al.* 2008), but analyses at higher taxonomic levels can employ phylogenies and alleviate bias caused by patchy knowledge. Here, I compile a comprehensive global family-level dataset from species geographic range maps and large species-level databases of mammals,

birds and frogs, and use phylogenetically explicit comparative analyses with a composite, family-level phylogeny to investigate both biological and anthropogenic correlates of current extinction risk.

I concentrate on the following variables because they have been named as main correlates of extinction risk for some or all of the three taxa of interest: species geographic range size, body mass, reproductive output and timing, habitat specificity, and current and historical human pressures throughout a species' range (reviewed by Fisher and Owens 2004, Purvis 2008, chapter 3). My analyses include both biological and anthropogenic variables, because human threats and biological traits interact to shape extinction risk (Fisher *et al.* 2003, Cardillo *et al.* 2004, Davies *et al.* 2006, Sodhi *et al.* 2008, chapter 3). Local and global studies have revealed that correlates of extinction risk differ between taxa, among regions and between different threat types, because biological traits as well as threat types and their intensity show spatial variation (Owens and Bennett 2000, Isaac and Cowlshaw 2004, Price and Gittleman 2007, Cardillo *et al.* 2008, chapter 3). Here, I endeavour to separate some of the different processes by building phylogenetic comparative models for each main threat type, i.e., I investigate correlates of overall extinction risk as well as of risk attributed to habitat loss, overexploitation and invasive species.

Methods

Dataset and phylogeny

Datasets were matched to the taxonomies of Wilson & Reeder (2005) for mammals, Sibley & Monroe (1990) with updates following Monroe and Sibley (1993) for birds, and Frost (2008) for frogs. I focus on anurans rather than include all amphibians because life-history data on caudates and caecilians are scarce and very patchy geographically. The taxonomies I used list 153 families for mammals,

146 families for birds, and 48 families for frogs. Since anthropogenic variables and habitat specificity were obtained from terrestrial data sets, I completely excluded 16 marine mammalian families from the data set (both sirenian families, the dugongs and manatees; three families of carnivores, the pinnipeds; and all 11 cetacean families). Marine birds were excluded from all data obtained from the species geographic ranges, with the definition of the 121 marine species following Orme *et al.* (2005). Additionally, two mammalian families did not have Red List rankings for any of their species: Notoryctidae (marsupial moles, 2 spp.) and Heptaxodontidae (giant hutias, 4 spp.).

Because I used phylogenetic comparative methods (see below), I additionally had to exclude families not in the phylogenies. For the mammals, a supertree of 5020 species (Bininda-Emonds *et al.* 2007, chapter 3) was collapsed to family level, encompassing 148 families. I resolved 18 non-monophyletic families by placing them where their nominal genus was, and three further ones with non-monophyletic nominal genera by placing them at the location of their nominal species. Families not included in this phylogeny were extinct: Chaeropodidae (Pig-Footed Bandicoot), Nesophontidae (nesophontid shrews, 9 spp.), Prolagidae (Mediterranean Giant Pika), and Thylacinidae (Thylacene). The final mammalian phylogeny (excluding marine families and families not qualifying for the response variable) contained 131 families (see Appendix C, Figs. C-3 and C-4), with the root node for all living mammal families dated as 166.2 million years ago (Mya).

The bird phylogeny used was from Sibley & Ahlquist (1990), which excludes Aramidae (Limpkin), Brachypteraciidae (ground-rollers, 5 spp.), Callaeatidae (wattlebirds, 3 spp.), Hypocoliidae (Hypocolius), Mesitornithidae (mesites, 3 spp.), Philepittidae (asities, 4 spp.), Picathartidae (bald crows, 4 spp.), Pluvianellidae (Magellanic Plover), and Raphidae (dodos and solitaires, 3 spp.). Although more recent bird phylogenies are available, these suggest that some passerine families as defined by Sibley and Monroe (1990) may not be monophyletic (Barker *et al.* 2004), and they dispute many of their higher-level taxonomic groups (Ericson *et al.* 2006, Baker *et al.* 2007, Hackett *et al.* 2008). As

the geographic ranges and life-history data followed the taxonomy of Sibley and Monroe (1990) with updates from Monroe and Sibley (1993), I was constrained to use the matching phylogeny.

Sibley and Ahlquist (1990) recommend multiplying non-passerine branches by a factor of 4.7 and passerine ones by 2.3 to obtain branch lengths in million years (their phylogeny has branch lengths estimated from DNA-DNA hybridisation rates). This dates the non-passerine–passerine split at 101.5 Mya, and the first split within passerines at 45.3 Mya. More recent studies give widely differing dates for initial passerine diversification, especially because of the lack of fossils from that time (Brown *et al.* 2008), but most concur that the divergence of living passerine families was much earlier, between 82 and 107 Mya (Barker *et al.* 2004, Pereira and Baker 2006, Brown *et al.* 2008). Multiplying all branches by the factor of 4.7 positions the first divergence within passerines at 92.59 Mya, which seems more reasonable than the original recommendation. I therefore decided to apply this transformation to all branches of the phylogeny, which also means the dating of other passerine nodes better approximates dating from a more recent molecular phylogeny (Barker *et al.* 2004). The final bird phylogeny had 137 families, with the first divergence of living bird families dated as 131.6 Mya (see Appendix C, Figs. C-5 and C-6).

For the frog phylogeny, I collapsed the species phylogeny estimated by Roelants *et al.* (2007), constrained to the backbone topology of Frost *et al.* (2006), to family level. Five missing families were grafted in at the positions they are in Frost *et al.* (2006), with each new node halfway between its neighbouring nodes: Amphignathodontidae (Brazilian treefrogs and marsupial frogs, 61 spp.), Aromobatidae (cryptic forest frogs, 94 spp.), Cryptobatrachidae (backpack frogs and Stefania treefrogs, 21 spp.), Hemiphractidae (horned treefrogs, 6 spp.), and Hylodidae (torrent frogs, spinythumb frogs and big-tooth frogs, 40 spp.). The taxonomy used, Frost (2008), contains three very recently defined families of rain frogs, i.e. Craugastoridae (114 spp.), Eleutherodactylidae (199 spp.) and Strabomantidae (539 spp.), which were previously all contained in

Brachycephalidae (Frost *et al.* 2006). Taxon sampling and resolution for these families is insufficient in both Frost *et al.* (2006) and Roelants *et al.* (2007), so I created a polytomy of the four families descending from the node that is the last common ancestor for all their species in the Roelants *et al.* (2007) phylogeny. The final anuran family phylogeny contained all 48 families recognised by Frost *et al.* (2008); the root node for all living frog families was dated as 237.4 Mya (Appendix C, Fig. C-2).

Finally, to obtain a composite phylogeny for all the groups used, I combined the phylogenies, with mammals and birds as sister clades (comprising the Amniota) to the exclusion of anurans (Amphibia; Appendix C, Fig. C-1). The Amphibia-Amniota split was placed at 355 Mya and the Mammalia-Aves split at 323 Mya (Pereira and Baker 2006, Marjanović and Laurin 2007). The final phylogeny contained 316 families in total (Appendix C, Figs. C-1 to C-6). After all exclusions, the total species and family numbers in the datasets were as follows: 5273 mammalian species in 131 families, 9677 bird species (9556 non-marine) in 137 families, and 5602 frog species in 48 families. Proportional data availability for all variables was computed using these numbers (Table 4-1).

I collated data on extinction risk and threat type classifications from several versions of the IUCN Red List of Threatened Species. All mammal data were extracted from the Global Mammal Assessment (GMA, IUCN 2008). Extinction-risk rankings for birds and frogs were from the previous edition of the Red List (IUCN 2007) because I generated the dataset before the latest version was published, and there have been very few species changing risk category for these two groups. Threat classifications for birds were from BirdLife (<http://www.birdlife.org>, accessed December 2008) and the Global Amphibian Assessment (GAA, IUCN *et al.* 2004, updated in 2008 using information on the website).

The measure of overall extinction risk was the proportion of threatened species within families. Species were defined as threatened if they were ranked in one of

	Species number			Species coverage			Family number			Mean Coverage		
	M	B	F	M	B	F	M	B	F	M	B	F
IUCN Red List Status	4438	9466	3931	84.2	97.8	70.2	131	137	48	89.8	98.4	76.5
Geographic range size	5148	9484	5068	97.6	99.2	90.5	131	137	48	97.2	99.5	93.5
Human population density	5142	9442	5067	97.5	98.8	90.4	131	136	48	97.2	98.8	93.5
Cropland	5125	9340	5055	97.2	97.7	90.2	131	137	48	96.9	98.0	92.2
Historic agriculture index	4997	9104	4954	94.8	95.3	88.4	131	136	48	95.2	96.2	90.7
Habitat specificity index	5148	9484	5067	97.6	99.2	90.4	131	137	48	97.2	99.5	93.5
Body size	3814	7644	1712	72.3	79.0	30.6	130	137	48	84.3	87.7	40.6
Reproductive output	2405	5766	531	45.6	59.6	9.5	128	137	43	67.9	76.3	20.3
Reproductive timing	1224	2397	410	23.3	24.8	7.3	123	122	37	49.6	45.9	30.5
Gestation length	1095			20.8			114			48.9		
Weaning age	1282			24.3			116			52.8		
Diet breadth	2070	3505		39.3	36.2		128	109		70.4	57.2	
Trophic level	2070			39.3			128			70.4		
Development type			5090			90.9			48			93.4

Table 4-1. Data availability for all variables in the dataset.

For each variable in mammals (M), birds (B) and frogs (F), the total number and percentage of species for which data were available are shown, as well as the number of families and means of within-family percentages of species for which data were available (see Methods for total species and family numbers of each taxon). Species geographic range size was measured in km². Mean human popula-

Table 4-1. *Caption continued from previous page.*

tion density (HPD, in individuals/km²), proportion of cropland in 2000 and the historic agriculture index were computed within species ranges. Habitat specificity was defined on the basis of Simpson's index, adapted to biomes within species ranges. Body size was measured as species body mass (g) for mammals and birds and as snout-vent-length (mm) for frogs. Reproductive output was litter or clutch size; reproductive timing was the number of litters or broods per year for mammals and birds, and the length of the breeding season (months) for frogs. Species gestation length and weaning age were measured in days. A species' diet breadth was the number of diet categories, which were defined as follows: vertebrates, invertebrates, fruit, flowers/nectar/pollen, leaves/branches/bark, seeds, grass and roots/tubers for mammals; vertebrates, invertebrates, nectar/sap, fruit/berries, foliage, seeds/nuts and other plant parts for birds. Possible trophic levels were herbivore, carnivore, and omnivore. Development types for frogs were larval, direct or viviparous. See Methods for details on computation of family estimates for each variable.

the three threatened categories on the Red List (Vulnerable, Endangered or Critically Endangered), or if they were ranked as Extinct or Extinct in the Wild (IUCN 2008). Species ranked as Data Deficient or species not included in the Red List (domesticated species or taxonomic mismatches) were excluded from the analyses. Total numbers of threatened species were: 1087 threatened and 67 extinct mammalian species (25.5% of species with known extinction risk), 1086 threatened and 82 extinct bird species (12.3%), and 1539 threatened and 33 extinct frog species (40.0%).

Previous studies have also excluded threatened species not ranked under criterion A (extinction risk due to population declines) because the other criteria are directly or implicitly based on geographic range or population size (IUCN 2001); using geographic range size as an explanatory variable is circular if threatened species include those ranked under other criteria than A (Purvis *et al.* 2000b). On the other hand, correlates of extinction risk if only species ranked under criterion A are used are effectively correlates of decline, which may well be different from

correlates of overall extinction risk. Also, the IUCN Red List only specifies the criteria under which a species qualified for the final risk classification, so it is unclear whether species qualified for lesser categories under different criteria, and how many criteria species could be assessed for given the data. Additional bias is added because population decline data are usually available for well-known species only, which tend to be the larger ones; including body size in models of extinction risk when excluding species not ranked under criterion A may therefore be circular as well. Finally, proportions of threatened species ranked under criterion A only are very small (between 4% and 9% of species with known extinction risk for mammals, birds and frogs, IUCN 2008). I therefore did not exclude these species; as a consequence, all results for geographic range size have to be interpreted with due caution.

I also investigated extinction risk caused by the most important types of current threat in the three taxa: Habitat loss, harvesting, and invasive species for all taxa, and pollution for frogs (non-marine mammal and bird species numbers affected by pollution are negligible). Data Deficient species and threatened species that were affected by unknown threats were excluded. I call these further response variables “risk from habitat loss”, “risk from harvesting” etc., to shorten the accurate description (e.g. for habitat loss: the within-family proportion of species classified as threatened, Extinct or Extinct in the Wild that were affected by habitat loss). Of threatened species, the following species numbers were affected by the main threat types: habitat loss, 984 mammalian (90%), 1042 bird (90%) and 1407 anuran species (93%); harvesting, 471 mammalian (44%), 408 bird (35%), and 81 anuran species (5%); invasive species, 192 mammalian (18%), 353 bird (31%), and 122 anuran species (8%); and pollution, 508 anuran species (34%).

Species range maps were digitised polygons representing extent of occurrence (breeding ranges for birds) and were obtained from the GMA (IUCN 2008), Orme *et al.* (2005) and the GAA (IUCN *et al.* 2006). From these, historical ranges and range parts labelled as “presence uncertain”, “introduced origin” and “extinct”

were excluded. I also excluded frog species from the GAA that were listed as ‘incertae sedis’ in the taxonomy of Frost (2008). While the bird ranges have been compiled using the taxonomy I follow, both the GMA and the GAA used other, unpublished taxonomies, derived from those I follow. Matching anuran GAA range maps to this taxonomy involved some renaming and merging: 5133 species range maps corresponded to 5068 ones in Frost’s (2008) taxonomy. From the GMA, 130 species ranges were excluded from the dataset because they were not included in the taxonomy I followed (Wilson and Reeder 2005). Also, 56 species ranges were added to the mammal set by splitting existing GMA ranges, and 40 species ranges missing from the GMA set were added from Jones *et al.* (2009).

Geographic range size was extracted from the polygon range maps in Behrmann projection (see Table 4-1 for species coverage). Measures of anthropogenic impact and habitat specificity were also extracted from the species ranges. I used mean human population density (CIESIN and CIAT 2005) and the proportion of cropland (European Commission and Joint Research Centre 2003) within species ranges, both measured in 2000, as variables representing current human pressures. To calculate proportion of cropland, cells in category 16 (cultivated and managed areas) were defined as 100% cropland, and cells in categories 17 or 18 (mosaic of cropland with other land cover) as 50% cropland. As an index of historical agriculture within species ranges, proportions of a species’ range that were cropland or pasture were summed across the years 1700, 1750, 1800, 1850, 1900, 1950, and 1990 (Klein Goldewijk 2001). Habitat specificity was computed from the species ranges using an adaptation of Simpson’s diversity index, i.e., the sum of the squared proportions of a species’ range within each of the 14 global biomes defined by Olson *et al.* (2001). Overall data availability for measures extracted from the range maps was good (Table 4-1), although most of the data sets exclude oceanic islands.

For each of the three taxa, variables describing body size, reproductive output and reproductive timing were represented in the dataset, but I also used additional variables in taxon-specific models (see Table 4-1 for a comprehensive list). Body-

mass and life-history data were taken from published datasets for mammals (Jones *et al.* 2009) and birds (Olson *et al.* 2009). For frogs, I extended the global dataset from Cooper *et al.* (2008), incorporating published datasets for Australia (Williams and Hero 1998, Hero *et al.* 2005) and data collected from published literature, field guides, and AmphibiaWeb (2008, see Appendix D for the full list of references). My final frog dataset included 1769 species, nearly tripling the dataset used by Cooper *et al.* (2008). Within species, mean snout-vent length (SVL), clutch size and length of breeding season were calculated from multiple records, weighting male and female estimates for SVL equally. Before calculating species means, an error-checking script was run in R, and extreme outliers were excluded. I used greedy algorithms to calculate species estimates, i.e. if only a minimum or maximum estimate of any variable was available, this was used as the mean (this was the case for only 144 SVL values and 19 clutch size values, which were checked for consistency with their congeners). I supplemented these data with development type, scored by the GAA for virtually all species (IUCN *et al.* 2004, updated in 2008 using information on the website).

For mammals, weaning age and gestation length are alternative measures of reproductive output and timing (see chapter 3), and for birds, incubation length was an additional fecundity measure with better species coverage. I chose litter / clutch size and litters / broods per year as variables for the dataset containing all taxa because high values for these additional variables indicate fast life-history speed or high output, which matches the only available measure for frogs (length of breeding season). Age at sexual maturity, population density and home-range size, which are also contained in the mammal database, were not used. The first is another life-history variable but has worse species coverage than the four other measures (983 species or 18.7% of mammals); the latter two are available for even fewer species (936 and 704 species, 17.8% and 13.4%) and are strongly correlated with body size, so they severely overinflated model variances in combination with the fecundity measures. Similarly, freshwater dependence for frogs is also provided by the GAA for most species (IUCN *et al.* 2004), and I had classified oviposition site, development habitat and adult life style in my dataset.

However, all of these were strongly collinear with development type, so only development type was used in the modelling.

All strictly continuous variables (non-categorical variables that were also neither a proportion nor an index) were log-transformed prior to computing family estimates. Family estimates for each variable were generally computed as the median of all available species values within each family, with the exception of variables representing indices and categorical variables. For the historic agriculture index, the habitat specificity index and diet breadth, family means of species values were used. For categorical variables, I calculated proportions of species for selected categories within families, excluding species with unknown category: trophic level was represented by the proportions of herbivores and carnivores within families, and development type by the proportion of larval developers.

Phylogenetic analyses

Given the strong phylogenetic structure usually found in extinction risk and its correlates (Purvis 2008, chapter 2), it was important to control for variable amounts of phylogenetic non-independence when modelling extinction risk correlates. I used phylogenetic generalised linear models (PGLMs, Freckleton *et al.* 2002, see chapter 3), run in R version 2.8.0 (R Development Core Team 2008) using the contributed package CAIC (Orme *et al.* 2008). Prior to fitting PGLMs, I investigated variance inflation factors for corresponding non-phylogenetic models (VIFs, Fox 2007) and only fit models where all VIFs were below four. The current implementation of PGLMs in CAIC does not fit a link function (Orme *et al.* 2008), so transformation of the response variables was necessary, because these were proportions. I applied the classic arcsine-square root transformation to the response variables, because the more modern logit transformation is infinite for values of zero, which were quite common in the dataset (Crawley 2007).

For each response variable, i.e. overall extinction risk and risk from habitat loss, harvesting and invasive species, a model was fit across the three taxa of interest containing geographic range size, the anthropogenic variables, habitat specificity, body size, reproductive output, reproductive timing and number of species. For comparison, I fitted the same models within each taxon as well. All models controlled for species richness (log-transformed), but I do not describe results for this variable in detail because a regression of a ratio on its denominator is often significant (Crawley 2007). Therefore, no inference should be made about the association of extinction risk and species richness from my models.

Additional taxon-specific models in mammals included gestation length and weaning age as alternative measures for reproductive output and timing, as well as diet breadth and proportion of herbivores, to make them comparable to previously published studies (e.g. Purvis *et al.* 2000b, Jones *et al.* 2003, Cardillo *et al.* 2005). Because incubation length as an alternative measure for reproductive timing was strongly collinear with body mass and caused severe variance inflation, I did not include it in the bird-specific models; also, previous studies have incorporated broods per year, so using this variable again increases comparability (Bennett and Owens 1997, Owens and Bennett 2000). The predictors in the bird-specific models were the same as in the cross-taxon model but additionally included diet breadth. Taxon-specific models for frogs included proportion of larval developers as an additional variable, and extinction risk from pollution was a response variable only available for frogs.

While common practice in ecology and evolution, the use of stepwise modelling and minimum adequate models (MAMs, e.g. Crawley 2007) is increasingly criticised, because this approach is known to be biased in parameter estimation, inconsistent in model selection algorithms, to have inflated type I error rates, and to inherently test multiple hypotheses (Whittingham *et al.* 2006, Mundry and Nunn 2009). Therefore, I report only results of the full models, which also increases comparability between the different explanatory variables and taxa.

Results

Mammalian, avian and anuran families showed very different frequency distributions for the different proportions of threatened species (Fig. 4-1). Patterns for risk from habitat loss were generally very similar to patterns for overall extinction risk, with slight differences only within birds; far fewer families had a substantial proportion of threatened species affected by harvesting or invasive species than by habitat loss. Harvesting affected mammals more than it did birds and frogs, and was a greater threat than invasive species for mammals; for birds, invasive species seem to have affected some families much more than harvesting. Hardly any anuran families were largely threatened by harvesting or invasive species, but overall extinction risk and risk from habitat loss was relatively higher than for mammals and birds.

Fig. 4-2 shows the general relationships between overall extinction risk and the variables that were available for all taxa. PGLMs showed that narrow geographic range size and large body size were the most consistent predictors of extinction risk, but correlates of extinction risk differed between taxa and threat types (Tables 4-2 to 4-5). Across all taxa, families with narrower species geographic range sizes, larger body size, smaller human population density (HPD) and higher proportion of cropland in the species ranges had significantly higher overall extinction risk (Table 4-2). Fitting exactly the same models within taxa led to some differences; notably, high extinction risk in mammals was more associated with low historic agricultural impacts than with low HPD and high proportions of cropland. Also, high extinction risk in frogs was exclusively associated with narrow species ranges and large body size, while bird models broadly reflected results across all taxa. Habitat specificity and reproductive parameters were not associated with overall extinction risk in these models.

Results for extinction risk from habitat loss were very similar, with narrow species range size and large body size as the main correlates of high risk (Table 4-3). High risk from habitat loss in mammals was correlated with low HPD, high

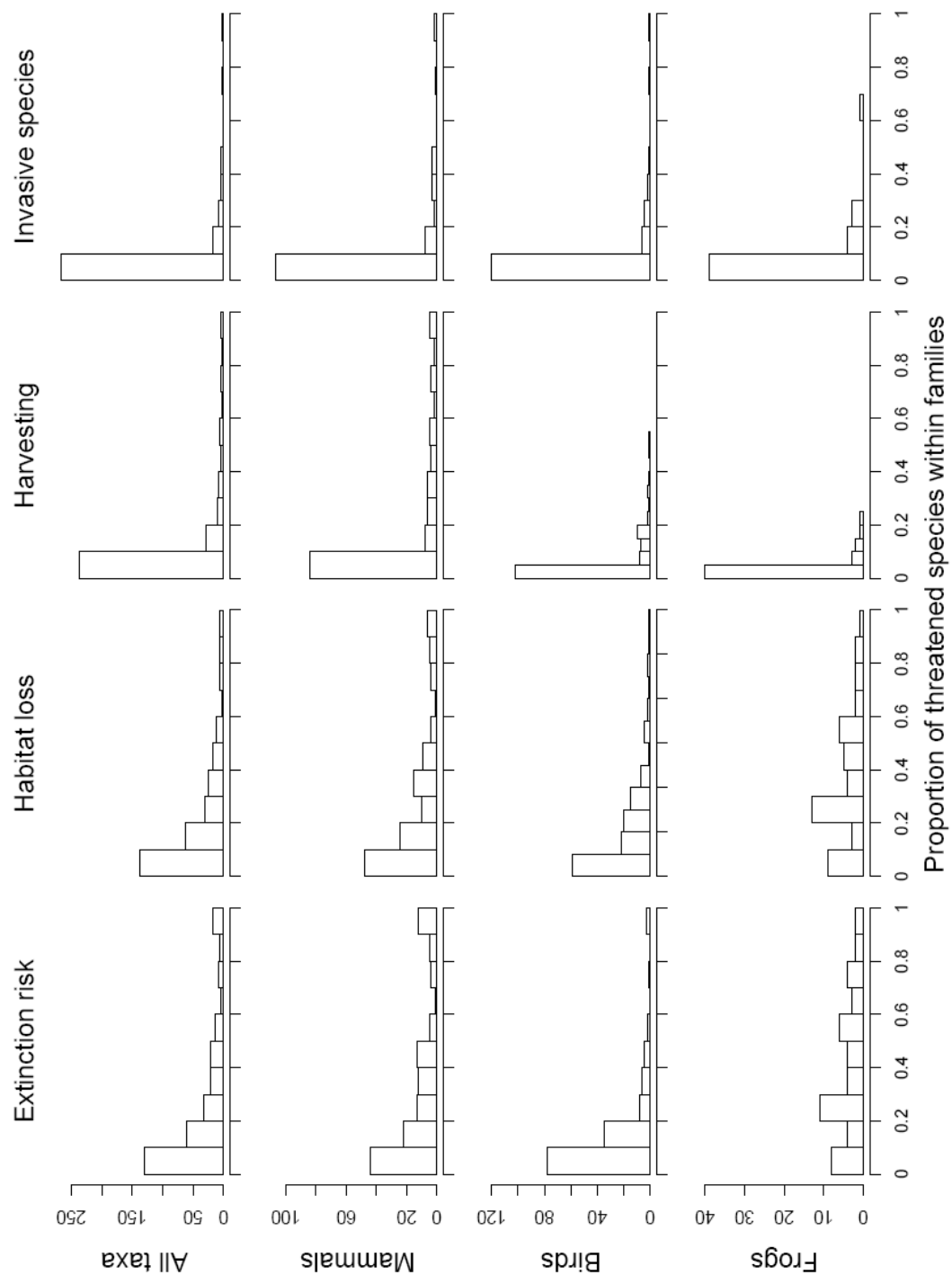


Fig. 4-1. Histograms of the within-family proportions of threatened species under different extinction-risk measures within and across taxa.

Definitions of extinction-risk measures were: extinction risk, proportion of species classified as threatened, Extinct or Extinct in the Wild; habitat loss, proportion of species classified as threatened, Extinct or Extinct in the Wild that were affected by

Fig. 4-1. Caption continued from previous page.

habitat loss; harvesting, proportion of species classified as threatened, Extinct or Extinct in the Wild that were affected by harvesting (hunting/gathering); invasive species, proportion of species classified as threatened, Extinct or Extinct in the Wild that were affected by invasive species.

	All taxa	Mammals	Birds	Frogs
N	281	123	121	37
AIC	125.4	101.3	-8.6	18.8
R ²	43.0	50.5	48.5	57.2
λ	0.25	0.13	< 0.01	< 0.01
P _{$\lambda=0$}	0.048	n.s.	n.s.	n.s.
Geographic range size	-0.117***	-0.146***	-0.087***	-0.115***
Human popltn. density	-0.078***	-0.076*	-0.106***	n.s.
Cropland	0.951***	1.230**	1.001**	n.s.
Historical agriculture	-0.052(*)	-0.139**	n.s.	n.s.
Habitat specificity	n.s.	n.s.	n.s.	n.s.
Body size	0.051***	0.046***	0.063***	0.478*
Reproductive output	n.s.	n.s.	n.s.	n.s.
Reproductive timing	n.s.	n.s.	n.s.	n.s.
Species number	0.036**	0.041(*)	0.050***	n.s.

Table 4-2. Results of PGLMs for overall extinction risk within and across taxa.

The response variable was the within-family proportion of species classified as threatened or extinct. For each model, the sample size N (number of families in the model), AIC value, R² in percent, estimated λ and the *P*-value of a χ^2 -test for $\lambda=0$ are given. Slope estimates and their significance are given for significant variables; n.s. designates non-significant variables in the full model. For variable explanations, see Table 4-1 and Methods. Levels of significance: (*) 0.05 < *P* < 0.10; * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001.

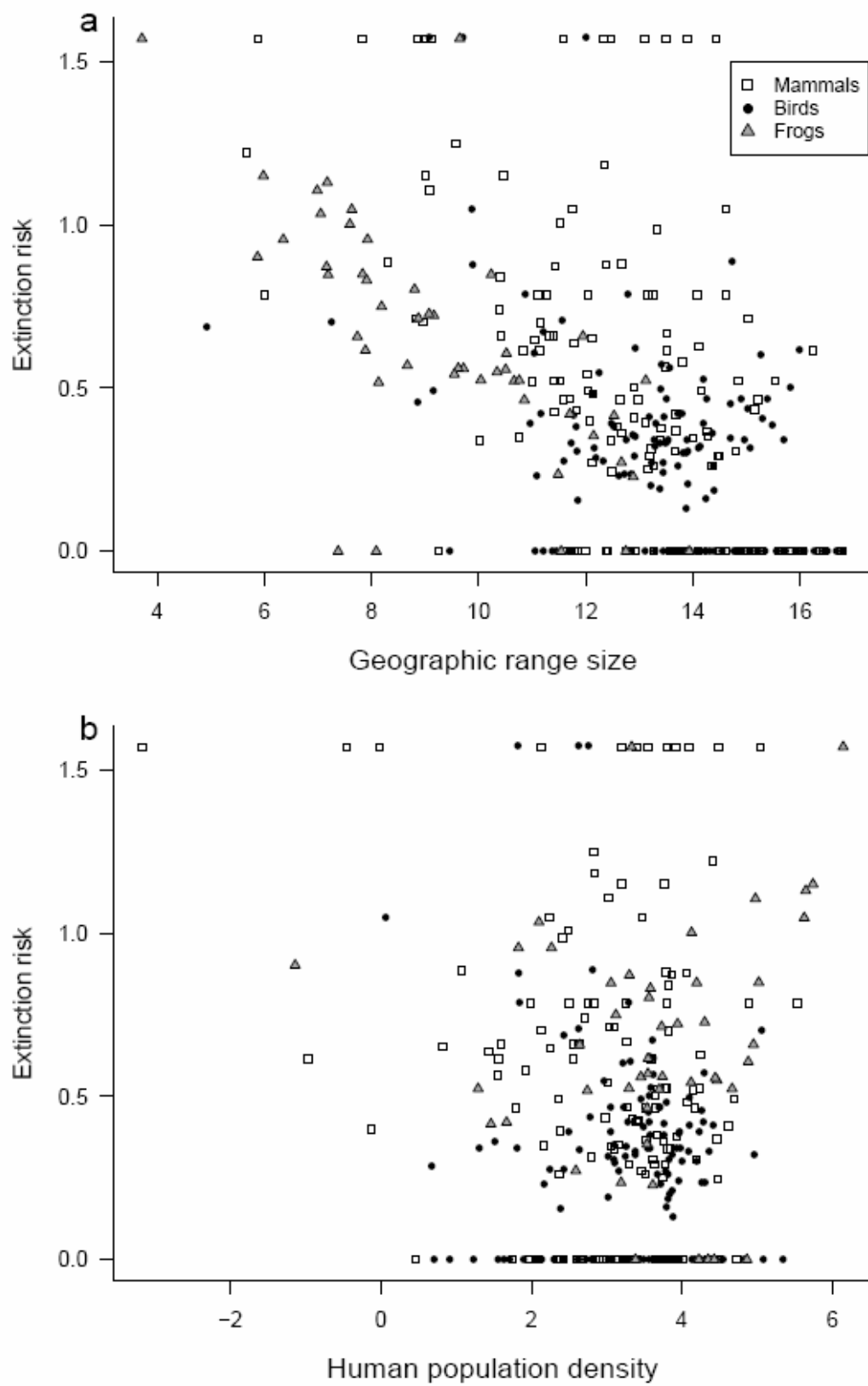


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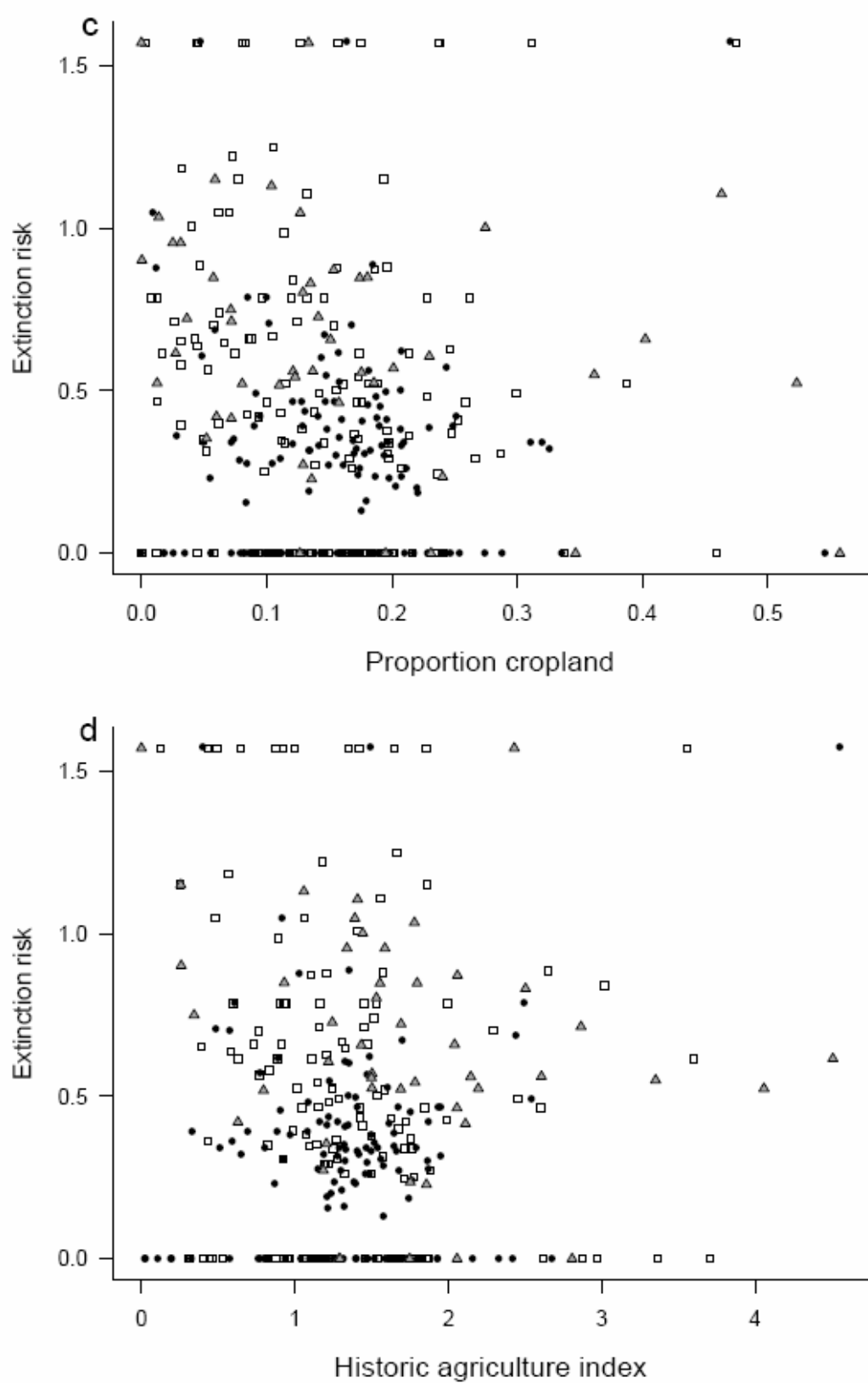


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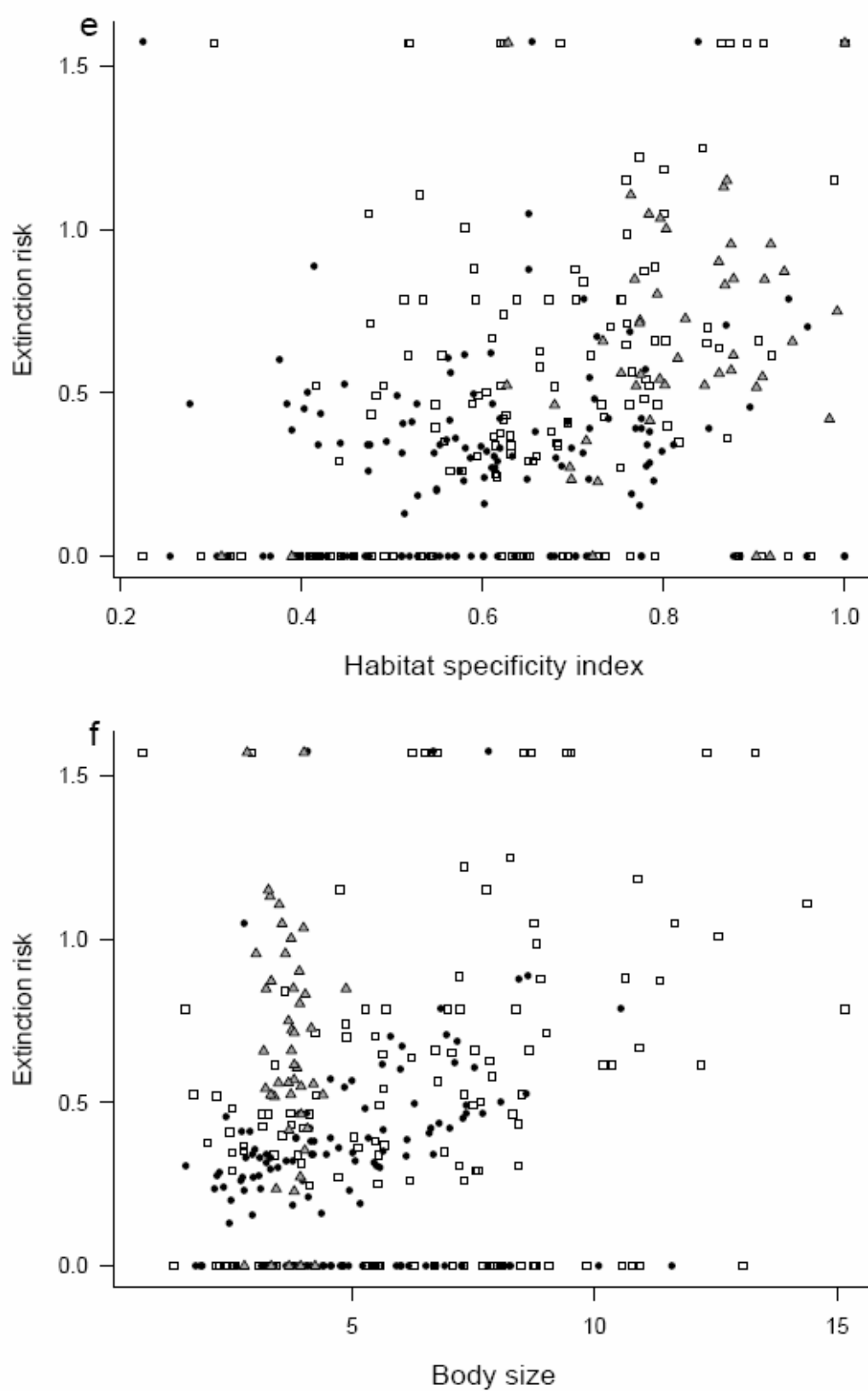


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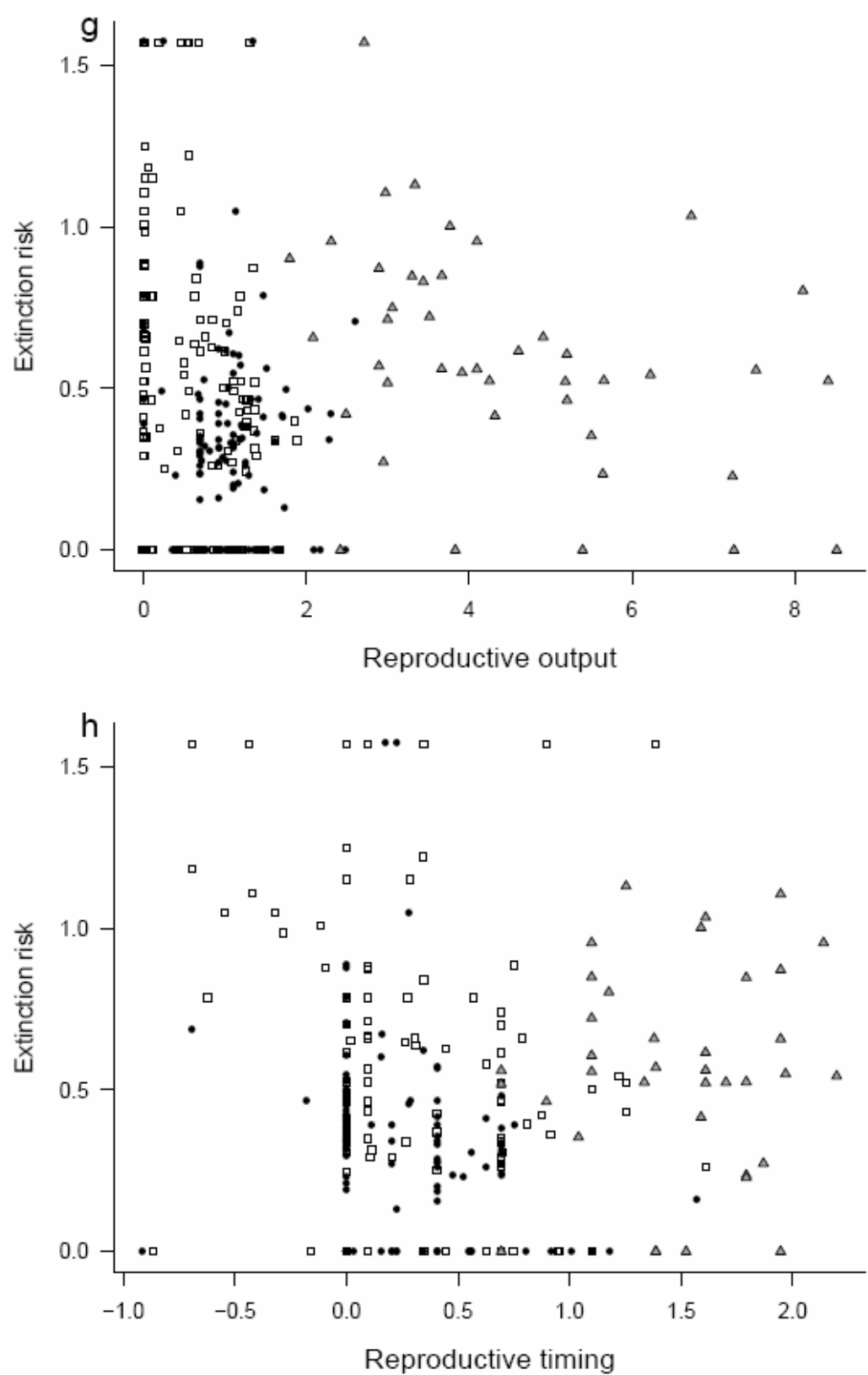


Fig. 4-2. *Caption on following page.*

Fig. 4-2. (Previous pages). Scatterplots of extinction risk vs. anthropogenic threats and biological traits across mammalian, avian and anuran families.

The measure for extinction risk was the within-family proportion of species classified as threatened, Extinct or Extinct in the Wild (arcsine-square root transformed). The species values for variables shown on x-axes were log-transformed before computing family estimates, apart from proportion of cropland and the habitat specificity and historic agriculture indices (see Methods and Table 4-1).

	All taxa	Mammals	Birds	Frogs
N	275	118	120	37
AIC	43.7	72.2	-71.1	18.2
R ²	42.4	49.9	49.2	52.7
λ	0.21	< 0.01	< 0.01	< 0.01
P _{$\lambda=0$}	n.s.	n.s.	n.s.	n.s.
Geographic range size	-0.078***	-0.106***	-0.052***	-0.099**
Human popltn. density	-0.041*	-0.069*	n.s.	n.s.
Cropland	0.535*	1.154*	n.s.	n.s.
Historical agriculture	n.s.	-0.123*	n.s.	n.s.
Habitat specificity	n.s.	n.s.	n.s.	n.s.
Body size	0.060***	0.055***	0.059***	0.426*
Reproductive output	n.s.	n.s.	n.s.	n.s.
Reproductive timing	n.s.	n.s.	n.s.	n.s.
Species number	0.058***	0.078***	0.062***	n.s.

Table 4-3. Results of PGLMs for extinction risk from habitat loss within and across taxa.

For explanations see Table 4-2. The response variable was the within-family proportion of species classified as threatened or extinct that were affected by habitat loss.

proportions of cropland and low historic agricultural impact, while high risk in birds and frogs was not associated with any anthropogenic variable.

Although small geographic range, large body size and high species richness were still the most consistent predictors of high risk, models for extinction risk from harvesting differed in many other aspects (Table 4-4). Most notably, there was a (weak) positive association of HPD and risk across all taxa and within mammals, while cropland was non-significant in all models. Additionally, different life-history variables were associated with risk from harvesting, although associations were in different directions within taxa. In frogs, no variable was significant.

	All taxa	Mammals	Birds	Frogs
N	275	118	120	37
AIC	-17.0	46.4	-117.8	-37.9
R ²	49.8	59.9	55.0	31.4
λ	< 0.01	< 0.01	< 0.01	< 0.01
P _{$\lambda=0$}	n.s.	n.s.	n.s.	n.s.
Geographic range size	-0.029**	-0.060***	-0.030**	n.s.
Human popltn. density	0.030(*)	0.058(*)	n.s.	n.s.
Cropland	n.s.	n.s.	n.s.	n.s.
Historical agriculture	-0.077**	-0.117*	-0.010**	n.s.
Habitat specificity	n.s.	n.s.	-0.287*	n.s.
Body size	0.082***	0.079***	0.075***	n.s.
Reproductive output	n.s.	-0.120*	0.064*	n.s.
Reproductive timing	-0.081*	-0.112(*)	n.s.	n.s.
Species number	0.043***	0.040*	0.056***	n.s.

Table 4-4. Results of PGLMs for extinction risk from harvesting within and across taxa.

For explanations see Table 4-2. The response variable was the within-family proportion of species classified as threatened or extinct that were affected by harvesting (hunting/gathering).

Models for risk from invasive species were quite different from the other models (Table 4-5). Narrow geographic ranges and low HPD consistently predicted high risk from invasives across and within all taxa; large body size was also significant apart from the within-birds models. Across all taxa and within mammals, high proportions of cropland and low historic agricultural impacts were also correlated with increased extinction risk from invasive species. In frogs, high habitat specificity was significantly associated with high risk. Some reproductive parameters were significant in all models apart from the within-frogs one, but associations were generally positive (i.e., high reproductive output and high output per unit time were associated with increased risk).

	All taxa	Mammals	Birds	Frogs
N	275	118	120	37
AIC	-51.3	13.9	-45.4	-14.5
R ²	30.3	33.3	38.1	59.7
λ	0.66	0.20	0.56	< 0.01
$P_{\lambda=0}$	< 0.001	n.s.	n.s.	n.s.
Geographic range size	-0.071***	-0.074***	-0.080***	-0.052*
Human popltn. density	-0.088***	-0.099***	-0.047(*)	-0.122**
Cropland	0.442*	0.840*	n.s.	n.s.
Historical agriculture	-0.045(*)	-0.086*	n.s.	n.s.
Habitat specificity	n.s.	-0.370(*)	n.s.	0.816*
Body size	0.018*	0.017(*)	n.s.	0.309*
Reproductive output	0.035*	n.s.	0.076(*)	n.s.
Reproductive timing	0.111**	0.189**	n.s.	n.s.
Species number	n.s.	n.s.	n.s.	-0.072**

Table 4-5. Results of PGLMs for extinction risk from invasive species within and across taxa.

For explanations see Table 4-2. The response variable was the within-family proportion of species classified as threatened or extinct that were affected by invasive species.

Mammal-specific models confirmed previously-described results, with geographic range size, body size and historic agricultural impact as the main correlates of all measures of extinction risk (Table 4-6). However, HPD and proportion of cropland were not significant in the models for overall and risk from habitat loss. High weaning ages were significantly associated with high overall risk and high risk from habitat loss and harvesting; the association was negative for risk from invasive species. Additionally, trophic level mattered in all models (only weakly for risk from harvesting), with a low proportion of herbivores within families

	Extinction risk	Habitat loss	Harvesting	Invasive species
N	110	107	107	107
AIC	79.2	57.5	52.9	19.4
R ²	54.6	56.0	61.0	38.2
λ	< 0.01	< 0.01	< 0.01	0.19
P _{$\lambda=0$}	n.s.	n.s.	n.s.	n.s.
Geographic range size	-0.157***	-0.129***	-0.078***	-0.084***
Human popltn. density	n.s.	-0.057(*)	0.063*	-0.122***
Cropland	n.s.	n.s.	n.s.	1.014**
Historical agriculture	-0.147**	-0.133*	-0.109*	-0.109*
Habitat specificity	n.s.	n.s.	n.s.	n.s.
Body size	0.041*	0.042**	0.080***	0.035*
Gestation length	n.s.	n.s.	0.071(*)	n.s.
Weaning age	0.104*	0.124**	0.099*	-0.087*
Diet breadth	n.s.	n.s.	n.s.	n.s.
Proportion of herbivores	-0.221**	-0.250**	-0.138(*)	-0.136*
Species number	n.s.	0.052*	0.041(*)	n.s.

Table 4-6. Results of mammal-specific PGLMs for different extinction risk measures.

The response variables were overall extinction risk, extinction risk from habitat loss, extinction risk from harvesting, and extinction risk from invasive species (see Methods for details). For further explanations see Table 4-2.

consistently associated with high risk. Diet breadth was never significant, and gestation length was only very weakly associated with risk from harvesting.

The bird-specific models also gave broadly similar results to results from models containing fewer variables (Table 4-7); as in mammals, diet breadth was never significant. Frog-specific models also reflected the models discussed before, and proportion of larval developers did not correlate with any of the extinction-risk measures (Table 4-8). High extinction risk from pollution in frogs was significantly associated with narrow species ranges, low HPD and large body size.

	Extinction risk	Habitat loss	Harvesting	Invasive species
N	104	104	104	104
AIC	-31.3	-66.7	-89.7	-29.6
R ²	53.5	49.8	55.8	41.1
λ	< 0.01	< 0.01	< 0.01	< 0.01
P _{$\lambda=0$}	n.s.	n.s.	n.s.	n.s.
Geographic range size	-0.117***	-0.080***	-0.041**	-0.100***
Human popltn. density	-0.116**	-0.084**	n.s.	n.s.
Cropland	1.045*	1.005*	n.s.	n.s.
Historical agriculture	n.s.	n.s.	-0.112*	n.s.
Habitat specificity	-0.457*	-0.332(*)	-0.417*	-0.515*
Body size	0.061***	0.061***	0.078***	0.026(*)
Reproductive output	n.s.	0.074(*)	0.063(*)	n.s.
Reproductive timing	n.s.	n.s.	n.s.	n.s.
Diet breadth	n.s.	n.s.	n.s.	n.s.
Species number	0.042**	0.054***	0.054***	n.s.

Table 4-7. Results of bird-specific PGLMs for different extinction risk measures.

For explanations see Table 4-6.

	Extinction risk	Habitat loss	Invasive species	Pollution
N	37	37	37	37
AIC	21.9	21.2	-13.1	1.4
R ²	57.6	53.2	61.8	60.5
λ	< 0.01	< 0.01	< 0.01	> 0.99
P _{$\lambda=0$}	n.s.	n.s.	n.s.	0.078
Geographic range size	-0.109**	-0.092***	-0.043*	-0.091***
Human popltn. density	n.s.	n.s.	-0.120**	-0.118*
Cropland	n.s.	n.s.	n.s.	n.s.
Historical agriculture	n.s.	n.s.	n.s.	n.s.
Habitat specificity	n.s.	n.s.	0.928*	n.s.
Body size	0.485*	0.434*	0.320**	0.348**
Reproductive output	n.s.	n.s.	0.047(*)	n.s.
Reproductive timing	n.s.	n.s.	n.s.	n.s.
Larval development	n.s.	n.s.	n.s.	n.s.
Species number	n.s.	n.s.	-0.078**	n.s.

Table 4-8. Results of frog-specific PGLMs for different extinction risk measures.

For explanations see Table 4-6.

Discussion

Apart from consistent associations of extinction risk with geographic range size and body size, there was strong heterogeneity in correlates of extinction risk across taxa and between different threats. This high variation when applying the same models to different taxa indicates that extinction processes are complex, and that impacts of many biological traits are taxon-specific even within terrestrial vertebrates. My results also confirm that susceptibility and the traits increasing it depend on the anthropogenic threats experienced (e.g. Owens and Bennett 2000,

Isaac and Cowlshaw 2004): overall extinction risk tended to reflect the overwhelming effects of habitat loss, but correlates for risk from harvesting and invasive species differed substantially.

Given that I included species listed as threatened under all criteria by the IUCN Red List, the consistent association of high risk with small species range sizes is far from surprising, and these results should be interpreted with caution. Many other studies, especially those excluding species listed due to small range sizes, have convincingly shown that geographic range size is one of the most important predictors of extinction risk or decline in mammals (e.g. Purvis *et al.* 2000b, Cardillo *et al.* 2008), birds (Blackburn and Gaston 2002, Gage *et al.* 2004), and amphibians (Hero *et al.* 2005, Cooper *et al.* 2008, Sodhi *et al.* 2008). Equally, species richness was controlled for in the models, but no inference about the relationship between extinction risk and species richness can be made because I was regressing a ratio on its denominator.

Large body size is thought to increase susceptibility due to the larger home ranges of large species: species with large home ranges require more intact habitat, and are more likely to encounter hunters (Harcourt 1998, Woodroffe and Ginsberg 1998). Controlling for range size effects, I find consistent evidence for a global correlation of large body size with high extinction risk, both across and within taxa and under different threats, with the only exception of risk from invasive species in birds. This association is much stronger than expected from previous studies claiming that the influence of body size on risk depends on interactions with life-history traits (Cardillo *et al.* 2005, Price and Gittleman 2007), on the region under study (Cardillo *et al.* 2008, chapter 3), and on the threat experienced (Owens and Bennett 2000, Isaac and Cowlshaw 2004, Price and Gittleman 2007). The use of family-level estimates of extinction risk in my study is likely to obscure such variation at the species level, and my global analyses cannot capture regional heterogeneity. At high taxonomic levels and large spatial scales, however, my results convincingly show that large body size consistently predicts high risk status in vertebrates.

Anthropogenic impacts

Human population density (HPD) was generally negatively correlated with extinction risk across taxa and within mammals and birds, but its association with extinction risk from harvesting was significantly positive across taxa and within mammals. The positive correlation is easily explained: within areas where harvesting occurs, places with higher HPD have increased hunting pressure through their better infrastructure and sheer number of people (Fa *et al.* 2002, Laurance *et al.* 2006). This would put species that are susceptible to harvesting at higher risk in these places (e.g. Bodmer *et al.* 1997, Fa *et al.* 2005).

For other threat processes, families with low HPD throughout most species ranges had higher proportions of threatened species, which seems less intuitive than results for risk from harvesting. Together with the negative associations of extinction risk with historic agriculture, the negative associations with HPD could imply that human extinction filters have already shaped today's vertebrate diversity (Balmford 1996, chapter 3). Families whose species' ranges were subject to lower agricultural impact over the past 300 years were at higher risk; this association was strong in mammals for all threat types, and occurred in birds threatened by harvesting. On large spatial scales, species still occurring in places with high HPD and high levels of recent-historical agriculture may be adapted to coexistence with humans and tend not to be threatened, while many threatened species seem to occur in places with comparatively low historic impacts. As the Red List only takes recent, ongoing or projected declines into account (IUCN 2001), species that have already declined in historical times but now exist in stable populations are not flagged as currently threatened, unless they are very restricted in numbers or distribution (see also chapter 3); this could add to the apparent extinction-filter signal in my results, where mostly families whose members have previously experienced agricultural land conversion are at high risk.

The negative association with HPD could also arise from the family-level scale I use, together with spatial scale effects in the impacts of HPD (Luck 2007). HPD is a rough measure of overall anthropogenic impact, and correlates with threatened species richness in global spatial analyses but not within biogeographical realms, where there is less spatial variation in HPD (Davies *et al.* 2006). Thus, a large-scale, positive spatial correlation may not be detectable when comparing family-level estimates phylogenetically, as families usually have compact rather than global ranges.

For frogs, no anthropogenic threats significantly predicted family-level overall extinction risk and risk from habitat loss, which may reflect the fact that many anuran species are red-listed due to their narrow distributions (IUCN 2008). However, HPD was negatively correlated with risk from pollution and invasive species in frogs, partly refuting that line of argument. In fact, low HPD was a consistent predictor of high risk from invasive species within all taxa and across them, and species extirpated from islands by invasive species in prehistoric times were indeed living in relatively untouched places (Blackburn *et al.* 2004). My models for invasive species were based on a response variable with very poor spread in some taxa (see Fig. 4-1), however, so results should be interpreted with caution.

High current proportions of cropland were also significantly associated with high overall extinction risk and risk from habitat loss across taxa and within mammals and birds. These results show that families whose species predominantly live in areas of high land-use are at high risk, confirming a previous species-level study on birds (Scharlemann *et al.* 2005). Surprisingly, this variable did not predict any measure of extinction risk in frogs; it seems that, despite their dependence on freshwater resources, frogs living in predominantly agricultural areas do not cope worse than those in pristine places, which may be a signal of the many “enigmatic declines” (Stuart *et al.* 2004).

Biological traits

Generally, species' reproductive traits mattered much less for family extinction risk than body size itself and anthropogenic predictors did (e.g. Fisher *et al.* 2003, Cardillo *et al.* 2004). However, reproductive traits were important predictors of risk from harvesting, which underlines the importance of recruitment rates: species with slow life histories are thought to be incapable of compensating for high mortality caused by harvesting (Bodmer *et al.* 1997, Fa *et al.* 2005, Price and Gittleman 2007). This hypothesis is supported by my results from models across taxa and within mammals.

In direct contrast to previous studies (Bennett and Owens 1997, Owens and Bennett 2000), my results suggest that bird families with larger clutch sizes are at higher threat from harvesting. It seems that human hunting targets species with high recruitment rates so overwhelmingly that their recruitment cannot keep up. The dramatic extinction of the passenger pigeon has shown that it is possible for human hunting to drive a widespread and abundant species to extinction within a short time, and there are some indications in the literature that formerly widespread and abundant species that are artificially reduced to rarity may be more susceptible to demographic and environmental stochasticity (Lawton 1995, Gaston and Fuller 2008). Additional evidence for such effects of overexploitation may be the negative association of high risk from harvesting with habitat specificity I found, as it seems that bird families where species are mostly not highly specialised in habitat requirements are experiencing higher risk levels from harvesting. This association could also arise due to easier access for hunters to habitat generalists, and a higher likelihood of encounters.

The only other significant association between risk and habitat specificity occurred for risk from invasives in frogs, where my models showed that habitat specialists are at higher risk. From previous studies, a general positive association between habitat specificity and extinction risk from habitat loss would be expected (Owens and Bennett 2000). The lack of this signal in my results implies

either that habitat loss is so widespread now that it affects generalist species as well, or that the index I used performs better at the spatial scale of frogs rather than of birds and mammals.

The taxon-specific models in mammals emphasised the large roles that taxon-specific biological traits can have in determining extinction risk. For example, high weaning ages were significantly associated with high overall risk and with risk from habitat loss and harvesting in mammals, while the reproductive measures used across taxa, i.e. litter size and litters per year, were not significant for overall risk and risk from habitat loss. It may be that weaning age reflects the reproductive timing axis of mammalian life-history speed better than litters per year (Bielby *et al.* 2007); alternatively, the reproductive measure was significant in the mammal-specific models due to interactions with other specific variables, such as the also-significant trophic level.

Trophic level was strongly associated with risk, indicating that families with low proportions of herbivores were at higher risk. This is surprising given that previous studies have emphasised that herbivorous taxa such as ungulates and primates are highly threatened (e.g. Mace and Balmford 2000, Price and Gittleman 2007). Herbivory was only very weakly associated with risk from harvesting, indicating that carnivores and omnivores are not unusually threatened by harvesting, but that they are by all other threats tested. The negative associations I found concur with the hypothesis of chains of extinctions, whereby predators are more threatened because of additive effects of disturbance along food chains (Purvis *et al.* 2000b).

Large body size was the only correlate of overall extinction risk and risk from habitat loss in frogs if narrow range size is controlled for. Contrary to previous studies, I did not find significant associations with clutch size (Cooper *et al.* 2008) or development mode (Lips *et al.* 2003, Hero *et al.* 2005, Sodhi *et al.* 2008). Again, this may be due to differences in taxonomic and spatial scale. Also, many previous studies have concentrated on frogs declining due to chytridiomycosis, an

infectious disease, and/or climate change, neither of which I consider here (Lips *et al.* 2003, Hero *et al.* 2005, Pounds *et al.* 2006, Bielby *et al.* 2008). Given the aquatic spreading mode of the fungus causing chytridiomycosis, reproductive traits would be expected to correlate with these declines (reviewed in Lips *et al.* 2008), but may indeed play no role for frogs threatened by habitat loss.

Conclusions

My results emphasise general heterogeneity in extinction risk across taxa and threats. Taxon-specific variables can play a large role in determining extinction risk, such as weaning age and trophic level in mammals. The three vertebrate taxa I studied here also show different patterns of susceptibility for traits measured across taxa, and differ in anthropogenic correlates of extinction risk. For example, anthropogenic variables mattered only for risk from pollution and invasive species in frogs, and birds showed less evidence of historical agriculture affecting current extinction risk than mammals. Also, there were large differences in significance of anthropogenic impacts between the different measures of extinction risk: Most notably, human population density was generally negatively correlated with most risk measures, but showed a positive association with risk from harvesting.

Large body size emerged as a consistent predictor of overall extinction risk and risk from each main threat process, at least on the global scale and taxonomic level I used. Results for geographic range size are hard to interpret because of the circularity arising from the inclusion of species listed as threatened due to small range sizes. However, from mine and other studies it seems that current and recent-past human actions selectively endanger large vertebrate species and those with small geographic range sizes, but other correlates of extinction risk vary according to the threat process and the taxon in question. This strongly implies that future extinction risk may be hard to predict using global, across-taxon models, and it also means that results from one taxon are not easily applicable to other taxa (Cardillo *et al.* 2008). The implication for conservation is that there may be no easy shortcut to identify susceptible species in as-yet unaffected

habitats, but that models will need to be taxon- and region-specific (Fisher and Owens 2004).

Chapter 5: Global mammalian functional and phylogenetic diversity at risk of extinction

Abstract

Functional diversity (FD) is important for the maintenance of ecosystem health, and estimates of globally threatened FD are needed to inform predictions of future ecosystem stability. Here, I use mammalian body-mass variance within ecoregions as a simple indicator of FD. I produce global maps comparing the losses of mammalian species richness, phylogenetic diversity (PD) and FD that would be incurred if all currently threatened species went extinct. FD losses were much more severe than losses of PD and species richness, and congruence between FD losses and the other two measures was low. Disproportionate loss of large mammals caused most of the reduction in FD. If all species currently classified as threatened or Near Threatened were to go extinct, 65% of the world's ecoregions would lose significantly higher amounts of FD than under random extinction, while only 11% of ecoregions would lose significantly more PD. Ecosystem consequences of large mammal loss are likely to be severe, with possible impacts on ecosystem services via changes in plant biodiversity, habitat heterogeneity, primary productivity and nutrient cycling. The low surrogacy I found stresses a need for conservation prioritisation based explicitly on threatened FD, and for conservation efforts to take an ecosystem perspective.

Introduction

The recently published Global Mammal Assessment emphasised the danger of high imminent losses of many mammalian species as a consequence of human actions (Schipper *et al.* 2008). Globally, 1141 species or 21% of all mammals are currently threatened with extinction, and the proportions are similarly high for other completely assessed groups (IUCN 2008). These assessments count each species loss equally, but species differ in many aspects, such as biological traits, ecosystem roles and evolutionary age. While it is clear that some species are more ecologically important because their biological traits are necessary for the functioning of their ecosystem, the magnitude of functional trait loss may not be easily predicted from species-richness losses (Gross and Cardinale 2005). To infer the future stability of ecosystems, knowledge of which species' traits and their functions will vanish with the loss of currently threatened species is a necessary first step (Hooper *et al.* 2005). This chapter aims to map and compare how much functional diversity (FD) will be lost globally if all currently threatened mammalian species were to go extinct.

Their comparatively large range size and body mass mean that mammals have impacts on ecosystems over large spatial scales. Mammalian seed dispersers, predators and herbivores have been shown to directly or indirectly influence invertebrate and plant community structure, primary productivity and nutrient cycling, implying that extinctions or declines of some species will impact ecosystem properties and functioning (McNaughton *et al.* 1988, Asquith *et al.* 1997, Terborgh *et al.* 2001, Pringle *et al.* 2007). Mammals are of special conservation concern because they are charismatic, they provide recreational value, and their populations are declining rapidly (Collen *et al.* 2009). They are also of direct economic importance in most areas of the world as a source of food and income from meat, fur, and tourism (Milner-Gulland *et al.* 2003), so it is crucial to investigate the impending loss of different aspects of mammalian diversity.

Previous studies have shown that threatened species are non-randomly distributed across phylogenies and taxonomies, with some clades disproportionately threatened even at small spatial scales (Russell *et al.* 1998, Davies *et al.* 2008). This phylogenetic clumping of threat means that the Tree of Life stands to lose a much higher amount of evolutionary history than if threatened species were phylogenetically randomly distributed (Purvis *et al.* 2000a). Highly unbalanced losses from the Tree of Life, and the high loss of evolutionary history or phylogenetic diversity that goes with it, also has implications for the magnitude of biological trait loss, because most traits show strong evolutionary signal (Freckleton *et al.* 2002). The protection of phylogenetic diversity (PD) is therefore claimed to help conserve not only evolutionary heritage but also a wide variety of species traits and possibly high evolutionary potential for the future (Faith 1992, Forest *et al.* 2007). On the other hand, phylogenetic and functional diversity can be independent aspects of communities (Jernvall and Wright 1998, Hooper *et al.* 2005), which would diminish the predictive power of evolutionary-history loss for future ecosystem functioning. The aim of this study is to compare expected losses of species richness and PD with impending loss of global FD in mammals. I also produce global maps showing areas of significantly non-random PD and FD loss for a complete high-level taxon, i.e. areas where disproportionately high amounts of mammalian evolutionary history and FD will be lost as a consequence of biological selectivity of anthropogenic threats.

Measuring FD within an area is notoriously difficult, especially across different ecosystems, because functional group definitions or complex ecological distance measures are problematic at the global scale (Petchey and Gaston 2006). I therefore use the interspecific variance in a key functional character, body mass, as a simple measure of mammalian FD (see Mason *et al.* 2003 for a similar index). Size or body mass is an important predictor of many ecological traits in mammals and an indicator of the ecological niche of a species (Western 1979, Eisenberg 1981). Generally, species of different sizes fulfil different ecosystem functions: for example, the largest mammals are wide-ranging herbivores or carnivores while small mammals are often insectivores or seed-dispersers.

Additionally, large mammals are disproportionately threatened (Cardillo *et al.* 2005), and preferential extirpation of large species can lead to unusually fast loss of functional diversity (Petchey and Gaston 2002). I therefore use the variance in body mass at large spatial scales to describe richness-independent functional variety of mammals in ecosystems.

Body-mass variance is measured within WWF ecoregions, which constitute globally coherent, large-scale ecosystem units (Olson *et al.* 2001). Using a large dataset of 4230 mammalian species body mass values (Jones *et al.* 2009), geographic range maps (IUCN 2008) and a species-level phylogeny (Bininda-Emonds *et al.* 2007, chapter 3), I map global losses for three measures of diversity within ecoregions: species richness, PD as measured by the total sum of branch lengths for the ecoregion phylogeny, and FD as indicated by the variance in body mass. Current values of diversity are compared with values projected if either all species currently classified as threatened on the IUCN Red List, or all of these plus species classified as Near Threatened, went extinct (IUCN 2008). I investigate how well PD and species-richness losses reflect those of FD by comparing congruence of proportional losses for the three diversity measures. Simulations are used to assess the significance of within-ecoregion PD and FD losses compared to random species loss.

Methods

I used the WWF terrestrial ecoregions as spatial units because their scale is more appropriate for investigations of ecosystem functioning than, for example, a global grid: ecoregions are biogeographically coherent units defined on the basis of natural assemblages (Olson *et al.* 2001). They are also widely used in conservation planning, and their large spatial scale ameliorates errors in species distribution maps (Jetz *et al.* 2008). I overlaid the ecoregion shapefiles (<http://worldwildlife.org/science/data/terreco.cfm>, accessed August 2006) with

mammal range maps from the Global Mammal Assessment (GMA, IUCN 2008) (www.iucnredlist.org/mammals, accessed October 2008) and extracted ecoregion occurrences for each species.

Historical ranges and range parts labelled as “presence uncertain”, “introduced origin” and “extinct” were excluded. GMA maps and risk status data were matched to the taxonomy of the body mass data and phylogeny (Wilson and Reeder 2005). I excluded 130 species from the dataset because they were not included in this taxonomy (more recently described or extinct species). A total of 56 species ranges was added to the set by splitting existing GMA maps, and 40 species ranges missing from the GMA set were added from Jones *et al.* (2009). Excluding species classified as Data Deficient, Extinct or Extinct in the Wild, my final range dataset contained 4230 species: 2939 of these were ranked as Least Concern, 306 as Near Threatened, and 985 species were in one of the three threatened categories (Vulnerable, Endangered and Critically Endangered, IUCN 2001).

Body mass values for 3382 of the 4230 species (80%) came from the PanTHERIA dataset (Jones *et al.* 2009). To give maximum coverage for analyses and reduce bias towards large species, I interpolated additional body mass values for the remaining species accounting for phylogenetic relationships (Garland and Ives 2000). Species values were imputed as the value of their closest relative (or the mean of several equally close relatives), on the basis of a supertree of 5020 extant mammalian species (Bininda-Emonds *et al.* 2007, chapter 3). The software R version 2.7.2 was used for all analyses (R Development Core Team 2007). The mean of the resulting frequency distribution of $\log_{10}$ -transformed body mass values including the interpolated species was lower than the mean without interpolated species, indicating the need to interpolate the missing data to avoid bias (Fig. 5-1; mean with imputed values=141.2 g, mean without imputed values = 166.0 g; t-test: $t = -2.64$, d.f. = 7155, $P < 0.01$).

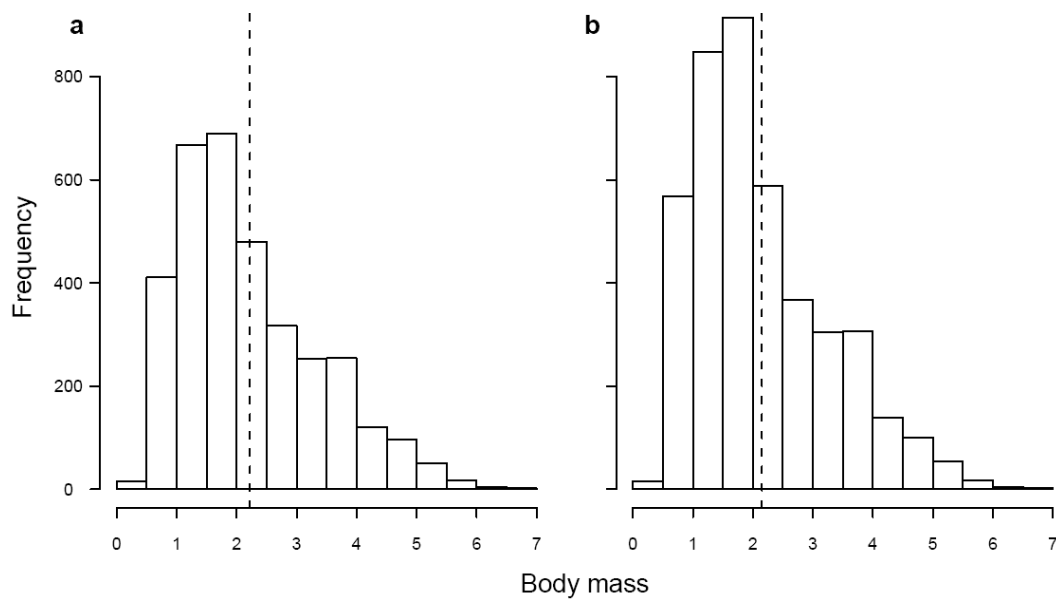


Figure 5-1. Histograms of body mass values for the dataset excluding and including interpolated values.

Histograms are of log₁₀-transformed body mass values (in g) for a) 3382 species values taken from the PanTHERIA dataset and b) the same PanTHERIA species values plus 848 interpolated values. The dashed lines indicate body mass means.

I excluded three ecoregions from all analyses because 50% or more of their body mass values were interpolated (Cape Verde Islands dry forests, 1 of 2 species; Christmas and Cocos Islands tropical forests, 1 of 2; Galapagos Islands scrubland mosaic, 4 of 6). Only 58 ecoregions did not contain any interpolated species values; the mean proportion of interpolated values within ecoregions was 0.10 (maximum 0.48). There was strong spatial pattern in the number and proportion of species for which body mass data were interpolated, highlighting lack of knowledge in South-East and East Asia (Fig. 5-2).

I mapped total species richness, richness of Least Concern and Near Threatened species, and richness of just Least Concern species within ecoregions to illustrate future biodiversity patterns for mammals if all currently threatened or all currently threatened and Near Threatened species were lost. Similarly, I mapped the within-

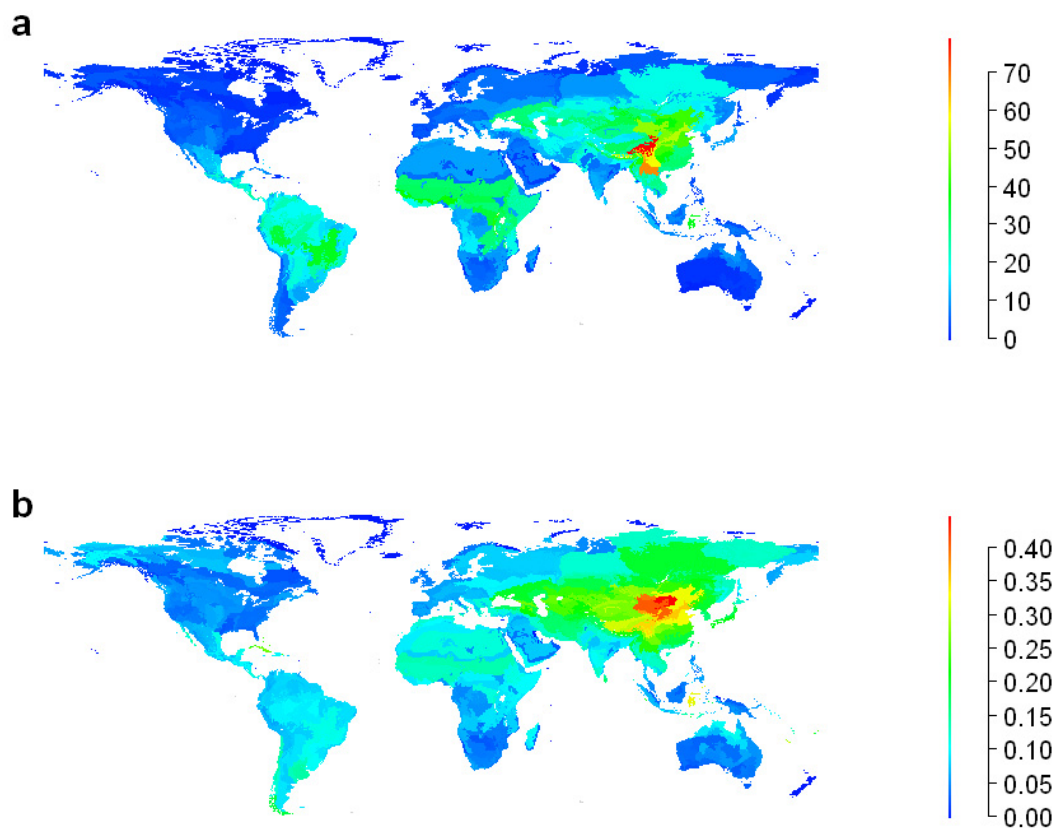


Figure 5-2. The number and proportion of interpolated species body-mass values within ecoregions.

Maps of a) number and b) proportion of interpolated species body-mass values. Three ecoregions where >50% of species values were imputed are excluded (see Methods).

ecoregion variance and mean of body mass of these species sets (after applying $\log_{10}$ transformation). PD was mapped using the total sum of branch lengths in an ecoregion phylogeny derived from the species-level supertree. This measure of PD is severely overinflated because of polytomies in the original supertree that mostly reflect lack of resolution rather than real speciation pattern. I corrected for the influence of terminal polytomies by assuming they had arisen under a pure birth process, because then the terminal branch lengths can be calculated following the appendix by S. Nee in Mooers and Atkins (2003). Total branch length for the whole mammalian phylogeny was 66.1 billion years without, and

59.2 billion years with the correction. The phylogeny contained 4183 of the 4230 species in the dataset.

I assessed congruence of estimated proportional losses for the three diversity measures (species richness, PD, and FD) with Pearson correlation coefficients. Because of spatial autocorrelation in the ecoregion dataset, I did not test these for significance, since spatial non-independence overinflates degrees of freedom in statistical testing. Nevertheless, the coefficients themselves are thought to be unbiased measures of the correlation strength (Legendre 1993). To simulate PD and FD losses expected if threatened species were phylogenetically randomly distributed, I used 1000 shuffles of threat status data in each ecoregion. Significance tests were one-tailed (proportion of random values that were smaller than the observed value).

Results

Extinction of all but currently Least Concern species reduced body mass variance or FD much more dramatically than either species richness or PD (Fig. 5-3). Some current hotspots of FD completely vanished, while areas of high species richness or PD retained comparatively high values. Patterns of mean body mass within ecoregions indicated that most of the large reduction in variance was due to selective losses of large species (Fig. 5-3, bottom row). Geographical patterns of losses for all diversity measures were similar whether species classified as Near Threatened were also lost or not (Fig. 5-4), so I concentrated on the more severe scenario which just left currently Least Concern species. Absolute losses for all three diversity measures were highest in the Indo-Malayan realm, with the Afrotropics and Neotropics also strongly affected (Fig. 5-3; Table 5-1). If all currently threatened and Near Threatened species went extinct, each ecoregion would lose a global average of 14 species, 283 million years of evolutionary history, and 14% of its current functional variety (Table 5-1).

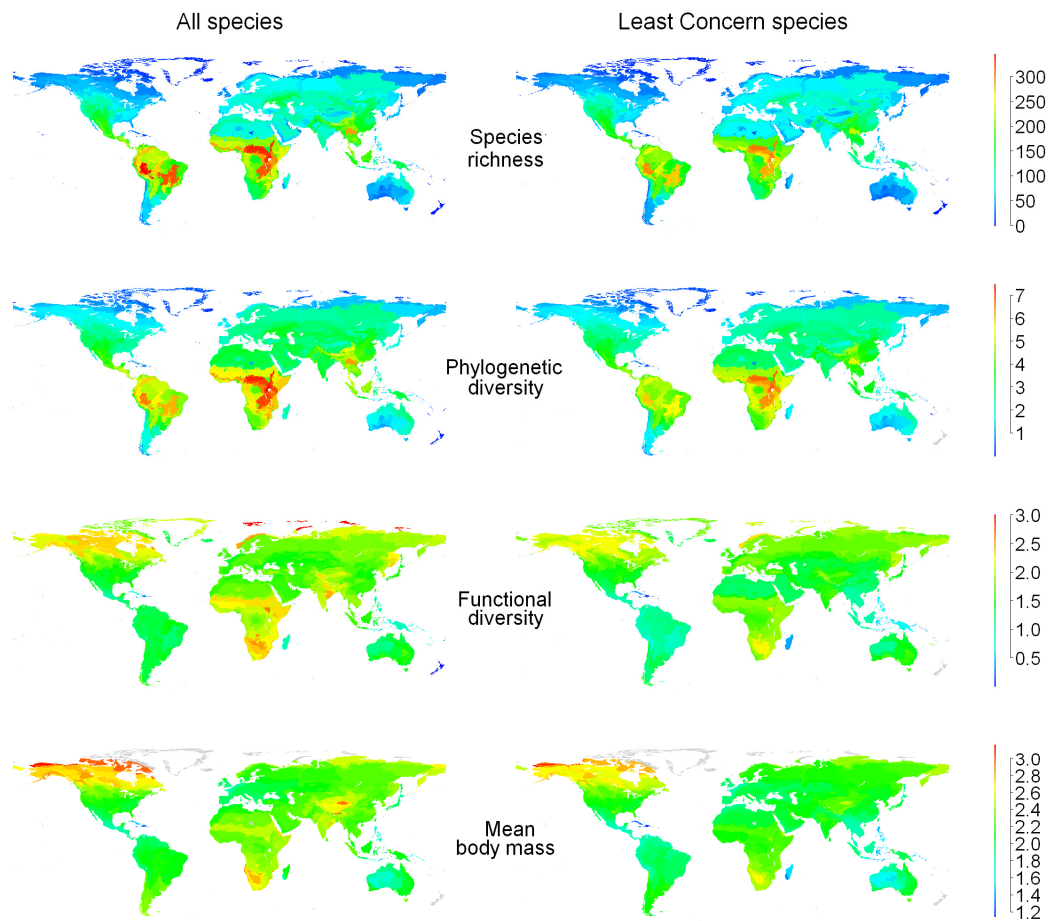


Figure 5-3. Projected changes of mammalian diversity and mean body mass within ecoregions.

Maps show mammalian species richness, phylogenetic diversity (PD), functional diversity (FD), and mean body mass for all species (left column) and species currently rated as Least Concern (right column). Species richness is the number of species, PD (in billion years) is the total sum of branch lengths for the ecoregion phylogeny modified to account for terminal polytomies (see Methods), and the variance in body mass is used as an indicator for FD. The colour scales each apply to a row of maps. Mean body mass within ecoregions is shown for ecoregions with ≥ 20 species only. Both body mass variance and mean were computed from $\log_{10}$ -transformed species values.

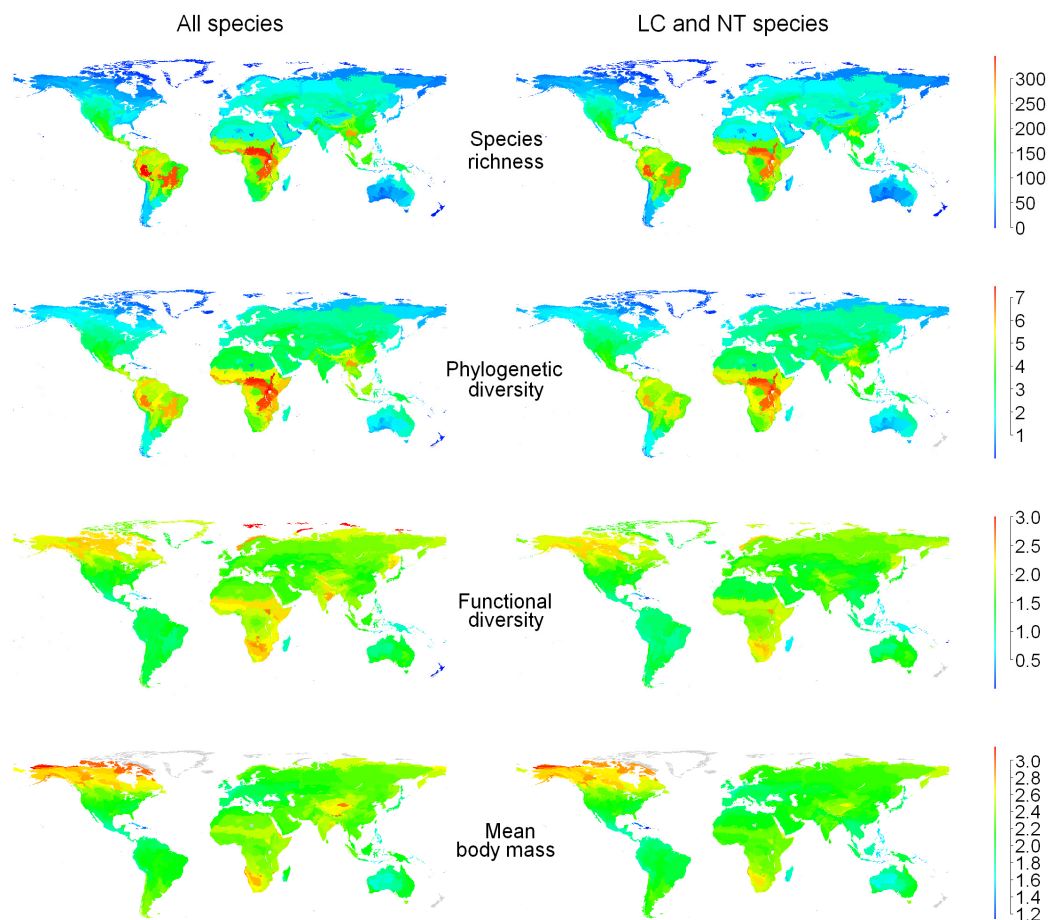


Figure 5-4. Projected changes of mammalian diversity and mean body mass within ecoregions including Near Threatened species.

Maps show mammalian species richness, phylogenetic diversity (PD), functional diversity (FD), and mean body mass for all species (left column) and species currently rated as Least Concern or Near Threatened (right column). The left column of maps is identical with the left column of Fig. 5-3 and is shown again here to facilitate comparison. For explanations see Fig. 5-3.

Proportional losses differed strongly between the three diversity measures (Fig. 5-5 a-c, Table 5-1). Proportional losses were high for all three measures in the tropical realms apart from Australasia, but FD losses were much greater than losses in richness or PD. The Indo-Malayan realm stood out especially, as each

	Species richness		Phylogenetic diversity			Functional diversity		
	Absolute	Proportion	Absolute	Proportion	% sig.	Absolute	Proportion	% sig.
Global	-14.4 ± 0.47	-0.15 ± 0.01	-282.7 ± 9.1	-0.09 ± 0.00	11	-0.23 ± 0.01	-0.14 ± 0.01	65
Australasia	-7.6 ± 0.76	-0.27 ± 0.03	-154.2 ± 16.4	-0.09 ± 0.01	4	-0.01 ± 0.03	0.00 ± 0.05	26
Antarctic	-18.0 ± 1.08	-0.13 ± 0.01	-373.4 ± 16.9	-0.10 ± 0.01	24	-0.28 ± 0.02	-0.15 ± 0.01	94
Afrotropic	-30.8 ± 1.78	-0.23 ± 0.01	-659.8 ± 32.4	-0.18 ± 0.01	20	-0.60 ± 0.03	-0.33 ± 0.02	96
Indo-Malaysia	-2.9 ± 0.32	-0.04 ± 0.00	-37.9 ± 3.7	-0.02 ± 0.00	1	-0.05 ± 0.01	-0.02 ± 0.00	24
Nearctic	-17.9 ± 0.75	-0.13 ± 0.01	-314.5 ± 10.4	-0.09 ± 0.01	20	-0.22 ± 0.01	-0.20 ± 0.01	80
Neotropic	-1.3 ± 0.40	-0.45 ± 0.12						
Oceania	-11.4 ± 0.58	-0.14 ± 0.01	-196.3 ± 8.9	-0.07 ± 0.00	1	-0.21 ± 0.02	-0.11 ± 0.01	56

Table 5-1. Losses of species richness, phylogenetic diversity (PD), and functional diversity (FD) globally and within biogeographical realms.

The means and standard errors for absolute and proportional losses within ecoregions are shown; for PD and FD, percentages of ecoregions with significant losses are given. All diversity changes are assuming that species currently ranked as threatened or Near Threatened will go extinct; negative numbers indicate diversity losses. Species richness is the number of species, PD (in million years) is the total sum of branch lengths for the ecoregion phylogeny modified to account for terminal polytomies, and FD is indicated by the variance in body mass ($\log_{10}$ -transformed). Significance of loss within each ecoregion was assessed using a one-tailed test based on 1000 permutations for random species loss of the same magnitude as the actual loss.

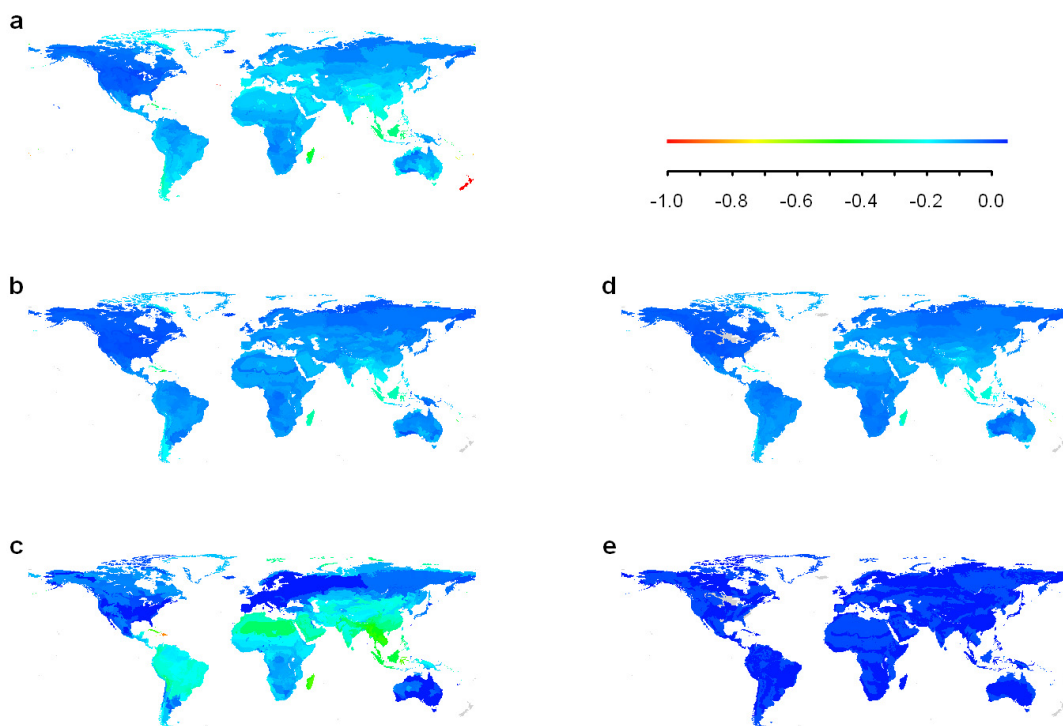


Figure 5-5. Projected and simulated proportional losses of mammalian diversity within ecoregions.

Maps of projected losses show proportional losses if all mammalian species currently ranked as threatened or Near Threatened were lost, for a) species richness, b) phylogenetic diversity (PD) and c) functional diversity (FD) within ecoregions. Maps of simulated proportional losses are shown for d) PD and e) FD within ecoregions. Simulated losses are the mean values of 1000 randomisations for random species loss of the same number of species as in a) to c) within each ecoregion. Negative proportions indicate losses; in c) and e), all positive proportions (gains in body mass variance) were set to dark blue and do not reflect the magnitude of proportional gains. Species richness is the number of species, PD is the total sum of branch lengths for the ecoregion phylogeny modified to account for terminal polytomies, and FD is indicated by the variance in body mass ($\log_{10}$ -transformed).

ecoregion would lose an average of 23% of its species and 18% of evolutionary history, but 33% of its current FD (Table 5-1). Conversely, Australasian ecoregions stand to lose a higher proportion of species (27%) but much less PD

and FD (9 and 0%, respectively; Table 5-1). Congruence across a sample size of 757 ecoregions as assessed by Pearson correlation coefficients was high between proportional losses of species richness and PD (coefficient=0.893), but low between PD and FD (coefficient=0.388) and very low between richness and FD (coefficient=0.192).

Random species-loss simulations for FD within ecoregions differed hugely from proportional losses as predicted from Red List risk status, especially in the tropical realms (Fig. 5-5 c, e). Conversely, simulated PD losses showed a pattern highly similar to actual predictions (Fig. 5-5 b, d). Globally, 65% of ecoregions would lose significantly more FD than in a random species loss scenario, whereas only 11% of ecoregions would lose a significantly higher amount of evolutionary history (Table 5-1). Large areas in the northern Holarctic and most tropical areas apart from Australia are expected to lose significantly higher amounts of current FD than expected under random species loss, and only some of these areas also experienced significantly higher PD losses in my simulations (Fig. 5-6).

Discussion

My results demonstrate low congruence between prospective losses of species richness and PD on the one hand and of FD on the other (as measured by the variance in body mass). The amount of mammalian FD that might be lost with currently threatened and Near Threatened species is high, with more than half of the world's ecoregions losing significantly more of their current functional variety than expected under random species loss. Consequences for these ecosystems could be severe and may impinge on ecosystem services and goods (Millennium Ecosystem Assessment 2005). The low surrogacy implies conservation efforts based on species richness or PD will fail to preserve many areas that stand to lose high proportions of their current FD.

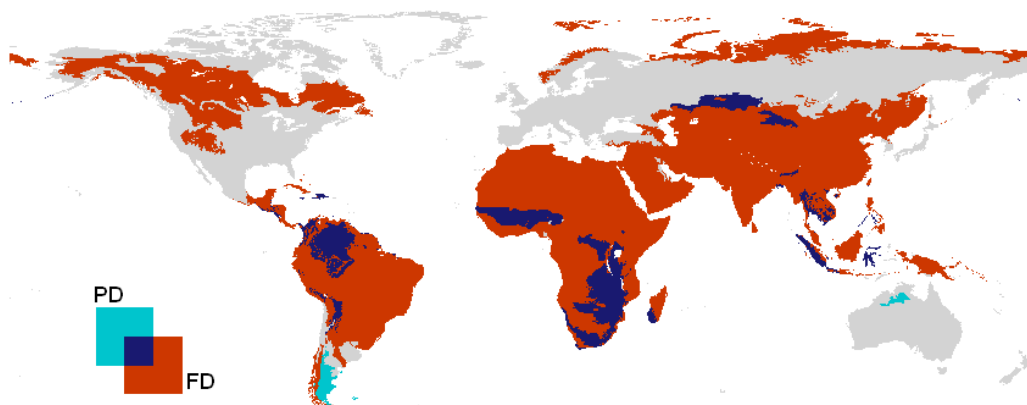


Figure 5-6. Areas of significantly non-random PD and FD losses.

Coloured ecoregions lose significantly more phylogenetic diversity (PD, light blue) or functional diversity (FD, red) or both (dark blue) than expected under random species loss, assuming all species currently ranked as threatened or Near Threatened were lost. PD is the total sum of branch lengths for the ecoregion phylogeny modified to account for terminal polytomies, and FD is indicated by the variance in body mass ($\log_{10}$ -transformed). Significance of losses within each ecoregion was assessed using a one-tailed test based on 1000 permutations for random species loss of the same magnitude as the actual loss.

Selective losses of large mammals

Reductions in FD as measured in this study were mostly due to the selective loss of large mammals. Large mammals face disproportionate threats, because they are often exploited by humans for meat and fur (Bodmer *et al.* 1997, Fa *et al.* 2002), and because their larger home ranges lead to increased exposure to habitat loss and other threats (Harcourt 1998, Woodroffe and Ginsberg 1998). Additionally, life-history traits increasing extinction risk scale with body size, and impacts of both biological and environmental extinction-risk correlates are higher for large mammals (Cardillo *et al.* 2005). My results also agree with previous results showing that selective loss of large mammalian species from assemblages leads to faster declines in FD than random species losses (Petchey and Gaston 2002).

If all but Least Concern species were to disappear, nearly all ecoregions in the large tropical realms (Afrotropic, Neotropic, and Indo-Malay) would experience significantly non-random reductions in FD. These are places where larger species are particularly likely to be declining or at risk of extinction (Collen *et al.* 2009, chapter 3), apparently because of high recent and ongoing rates of land conversion for agricultural use (Millennium Ecosystem Assessment 2005, chapter 3). In temperate regions and Australia, historic agricultural impacts have already caused local declines and extinctions during the last few centuries, so that non-tropical large mammals tend either to be locally extinct or not perceived as currently under threat (chapter 3). My results here also imply that boreal forests in North America and most of the Siberian tundra stand to experience significant reductions of mammalian functional diversity, which highlights the high intrinsic susceptibility of these species-poor but currently relatively pristine areas (Cardillo *et al.* 2006). It seems that at least since the industrial revolution, human actions have disproportionately affected large mammals, and Fig. 6-3 vividly illustrates what the world might look like if these actions continue unchanged.

Losses of evolutionary history

Only 11% of ecoregions worldwide stand to lose a significantly higher amount of their current mammalian PD than expected under random species loss. The high redundancy of phylogenetic trees means that while a global average of 15% of the species in an ecoregion are at risk, representing 14% of regional FD on average, only 9% of PD would be lost on average within ecoregions. Congruence with proportional losses in FD was higher for PD than for species richness, but still only 39% of ecoregions stand to experience similar losses in FD and PD. Clearly, my measure of FD captures a very different aspect of diversity compared to evolutionary history, which casts doubt over claims that preserving PD would also conserve feature diversity and with it FD (Faith 1992, Forest *et al.* 2007). Whenever extinction risk correlates with features and functions, FD loss will be worse than richness or PD loss (Petchey and Gaston 2002, Gross and Cardinale 2005).

Conservation efforts should still take PD into account, because we should care about irretrievably losing evolutionary heritage, and because it does act as a surrogate of diversity for features not correlated with extinction risk (Vane-Wright *et al.* 1991). Surrogacy between predicted species-richness and PD losses was high in this study, so classic global conservation schemes trying to capture high numbers of threatened species could perform well for the preservation of mammalian evolutionary history. However, the low surrogacy between losses of PD and FD indicates an urgent need for conservation priorities specifically based on threatened FD. The magnitude and geographical scale of FD loss shown by my results means it should be considered more important than PD, especially given the global human dependence on ecosystem services (Millennium Ecosystem Assessment 2005).

Possible impacts of FD losses

Ecosystem consequences of losing the ecological functions of all 1291 currently threatened and Near Threatened mammalian species would probably be severe. Impacts can be expected to be high particularly in the areas that stand to lose significantly higher amounts of FD than under random species loss, i.e. nearly throughout the tropics and in 65% of terrestrial ecoregions in total. The loss of large herbivores would lead to changes in plant community structure, with knock-on effects for invertebrate and vertebrate community structure and, consequently, the whole ecosystem (McNaughton *et al.* 1988, Augustine and McNaughton 2004, Pringle *et al.* 2007). The difficulty of maintaining biodiversity in the few remnants of North American tallgrass prairie without the original balance of bison grazing and wildfires illustrates how ecosystem functioning may be impacted by loss of large herbivores, and that livestock populations only compensate partly (Knapp *et al.* 1999). In forest ecosystems, seed dispersal is directly affected by selective losses of large frugivores and indirectly by losses of large predators via mammalian community interactions, with potentially large effects on plant species composition and abundance patterns (Asquith *et al.* 1997, Muller-Landau 2007). Losses of large predators are also claimed to trigger extinction cascades, because

they lead to short-term hyperabundance of herbivores and smaller predators, causing plant species impoverishment and local extinctions of prey species (Crooks and Soulé 1999, Terborgh *et al.* 2001).

Given the reliance of the growing human population on ecosystem services especially provided by tropical systems, the economic consequences of ecosystem changes caused by loss of FD could be severe. Thousands to millions of tons of meat from subsistence hunting help to feed the poorest people in the tropical realms most affected by the losses predicted in this study (Fa *et al.* 2002, Milner-Gulland *et al.* 2003). Additionally, tourism is an important source of income in many tropical countries, and largely relies on the aesthetics of large mammals.

Of course, this study does not provide exact predictions for any of these impacts. Shortcomings include that my measure of FD is necessarily rough: I only consider native wild species, and not all species currently red-listed will vanish completely or simultaneously. Importantly, species irreplaceability and ecosystem resilience are likely to differ between species and regions (Hooper *et al.* 2005). However, even though not all species currently threatened by extinction may actually die out globally, local extinctions or declines are sufficient to impact local ecosystem services. My results provide the first global sketch of how the mammalian functional variety currently present in ecosystems may be reduced in the future, and the emerging picture is not encouraging.

Conservation implications

While ‘hotspot’ approaches to global conservation priorities offer a seemingly simple and cost-efficient strategy by protecting a high proportion of globally threatened species in comparatively few areas (Myers *et al.* 2000), the low congruence between losses of FD and the other measures of diversity in this study implies that any set of hotspots selected under one criterion will be different from sets selected under others. Other studies have reported low congruence between distributions of total, restricted-range and threatened species within and across

taxa, as well as low surrogacy between prioritisation of species richness, evolutionary history and current and projected threat (Orme *et al.* 2005, Grenyer *et al.* 2006, Forest *et al.* 2007, Davies *et al.* 2008). My study has shown that losses of mammalian FD alone could affect nearly the whole of the tropics, which further argues against easy global solutions. I conclude that there seems to be no shortcut, but conservation planning will have to consider a range of taxa using a range of biological criteria, such as different measures of richness and its impending losses.

Current conservation efforts mainly rely on protected areas as a tool to stop species declines and extinctions. Yet how useful can preserved FD and ecosystem functioning be if they are restricted to protected areas? It is unclear whether protected areas alone could offer a large enough natural ecosystem to ensure continued supply of ecosystem goods and services (Millennium Ecosystem Assessment 2005), so future strategies should include conservation measures outside protected areas (Ceballos *et al.* 2005). This study highlights the need for systematic conservation planning to move the focus from species and area protection to an ecosystem perspective.

Chapter 6: Concluding Remarks

Summary of results and implications

In this thesis, I have investigated phylogenetic and spatial patterns in the magnitude, focus and impact of current extinction risk, in order to increase understanding of the underlying extinction processes. Consistent phylogenetic selectivity in extinction risk (chapter 2) confirms that the current extinction crisis is targeting species with certain characteristics. More importantly, differences in the strength of phylogenetic signal indicate that biological selectivity differs with threat types such as habitat loss, harvesting and invasive species, even within mammals. Further analyses of phylogenetic-signal strength using my newly devised measure, D , would be useful if performed at multiple spatial scales for different taxa and risk from different threat processes, as the results would indicate whether and how the impact of strongly-patterned biological traits differs from global to assemblage scales.

I found high regional heterogeneity in the influence of mammalian biological traits on extinction risk, which further argues that the biological traits increasing susceptibility are specific to the threat processes experienced (chapter 3). Accordingly, different measures of anthropogenic impacts predicted the strength of influence that separate biological traits had on extinction risk. Global comparisons of extinction-risk correlates across mammals, birds and frogs further highlighted the heterogeneity of extinction processes (chapter 4). Different biological traits and anthropogenic impacts predicted overall risk in each taxon, and patterns varied with main threat process as well.

These results improve current understanding of global relationships between risk and its anthropogenic and biological causes for terrestrial vertebrates; for these

groups, more local and clade-specific models are needed now to better understand why some species are at risk and some are not (Fisher and Owens 2004, Cardillo *et al.* 2008). Future studies identifying correlates of vertebrate extinction risk should be tightly focused spatially, and concentrate on one threat process and one major taxon at a time, if they are not to be affected by regional and biological heterogeneity and variation in threat type and level. However, the global approaches I have taken in this thesis have proven powerful in showing general trends and relationships across taxa and regions, so their application is promising for other taxa as new risk data on hitherto less well-known groups become available (Fisher and Owens 2004).

Two variables emerged as consistent predictors of extinction risk across taxa and threat types: small geographic range size, which at least in mammals increases species' extinction risk worldwide, and large body size, the effect of which was high in the tropics but not in temperate regions for mammals. As discussed in chapter 3, there are ways in which the extinction-risk measures I used could be overinflated for small-ranged species; for the analyses in chapter 4 I know that they are, because I (in common with some previous workers, e.g. Owens and Bennett 2000) do not exclude threatened species listed on the basis of small range size. Nevertheless, it is tempting to conclude that habitat loss and degradation are now so widespread that small-ranged species are threatened nearly everywhere. I found some evidence for large effects of current land-use on risk in mammals and birds, and previous studies have reported similar correlations (Scharlemann *et al.* 2005, Davies *et al.* 2006).

I have explored possible impacts of the striking regional differences in selectivity for large body size on a global scale for mammals (chapter 5). My analyses highlight that we stand to lose large amounts of functional diversity with currently threatened mammal species, as functional variety in mammals is likely to be reflected by the body-mass variance within large-scale ecosystems. The loss of functional diversity I estimated was higher than expected from species richness and phylogenetic diversity in more than half of the world's ecoregions, indicating

a need for conservation measures to be based on functional diversity, or variance in body mass, rather than on species richness or phylogenetic diversity.

There are several mechanisms by which large body size can increase species extinction risk. The most direct is human hunter preferences (Bodmer *et al.* 1997, Fa *et al.* 2005), which are known to cause higher risk for at least some large species (Owens and Bennett 2000, Isaac *et al.* 2005, Collen *et al.* 2006). My analyses indicate that even risk from habitat loss and invasive species affect large species disproportionately, so other mechanisms are likely to play a role. Correlations of body size with life-history traits such as reproductive output are often claimed to underlie or strengthen body size impacts (Cardillo *et al.* 2005). I controlled for separate effects of these traits in my analyses, as far as was possible, and large species were still generally at higher risk, although in mammals there was striking spatial variation. Finally, the larger home-range sizes of many large species mean they are more likely to encounter threats (Harcourt 1998, Woodroffe and Ginsberg 1998). All of these factors probably play some role in generating the strong global-scale signal I found, but there are also several ways in which data bias could have increased the signal.

Possible sources of bias

The most serious shortcoming, intrinsic to all analyses of extinction risk as recorded by the IUCN Red List, is likely to be the proportions of species ranked as Data Deficient (DD): these are 15% for mammals, <1% for birds, and 25% for amphibians (IUCN 2008). I had to exclude all these species from my analyses, which potentially removed a biased set of diversity, as it is highly probable that most of the DD species are small, rare and have relatively small ranges. If DD species turn out to be mostly threatened, the strong correlations of risk and geographic range size may even underestimate the true importance of range size in determining extinction risk. On the other hand, if those DD species occur in

remote areas, they might not currently be threatened, in which case the correlation of risk and range size is overestimated with the currently available data.

Within DD species, I found significant, moderately strong phylogenetic signal, indicating that there is a systematic bias to knowledge about extinction risk (chapter 2). The imputation of missing body-mass values in chapter 5 showed that most species for which body mass was unknown were small (Fig. 5-1), an indication that less well-known species might often have low body mass. The exclusion of the probably mostly small DD species could artificially increase the correlation of large body mass with high extinction risk. There may also be a spatial dimension to the bias caused by removing DD species: most of these are probably tropical (Baillie *et al.* 2004, Schipper *et al.* 2008). This means that the strong influence of mammalian body mass on risk in the tropics I found may be an overestimation (chapters 3, 5).

A possible solution to the problem of DD species for future studies could be multiple imputation of the missing values for extinction risk (e.g. Fisher *et al.* 2003). In practice, this is likely to be difficult as the imputation for risk needs to be both phylogenetically and spatially explicit, considering the strong phylogenetic and spatial signal in extinction risk and threat types (see also chapter 2). Given the moderately strong phylogenetic clumping of DD species, there may be a danger of extrapolating from very few known species to whole clades (Smith and Jungers 1997). Additionally, many DD species may be so poorly known that their biological trait values will be missing as well.

As previously mentioned, the correlations of geographic range size and extinction risk in chapter 4 (but not in chapter 3) are biased due to the inclusion of species listed as threatened under Red List criteria based on geographic range size. On the other hand, the correlates of extinction risk in chapter 3 are essentially correlates of population declines, because only species listed as threatened under criterion A were included in that analysis; this may have biased results simply due to the exclusion of so many species. Also, risk rankings recorded on the Red List for

species threatened under criteria other than A do not provide any information on whether the species was evaluated under criterion A or not, and whether if evaluated it would have qualified as threatened under criterion A but for a lower risk category than under other criteria (IUCN 2008). Recording the risk categories qualified for under every criterion in the Red List could ameliorate this particular source of error.

Other sources of bias for Red list risk rankings include differences in the perception of declines for large and small species and scale issues in estimating geographic range size, as discussed in chapter 3. Despite all possible kinds of systematic bias, the Red List remains the single most comprehensive global dataset of extinction risk for many taxa (Mace *et al.* 2008). It is also continuously updated and growing, which decreases most sources of error discussed here for future studies.

Two of the chapters presented here use ecoregions as biologically-defined spatial sampling units (chapters 3, 5). While the WWF ecoregions are now widely used for conservation and other purposes, they have also been criticised, especially in a conservation planning context (Jepson and Whittaker 2002, but see Wikramanayake *et al.* 2002). As the only spatial regression analysis here (chapter 3) accounts for overinflation of the degrees of freedom due to spatial autocorrelation, overestimations of similarity between some ecoregions due to inexact border definition are unlikely to bias the results seriously (Magnusson 2004). However, if there are systematic differences in ecoregion definition between realms or biomes (as claimed by Jepson and Whittaker 2002), some of my findings could be affected: for example, if tropical ecoregions are always (artificially) smaller than temperate ones, the spatial pattern in the influence of body mass on risk may be less pronounced in reality than my ecoregion results imply.

As is typical for complex, global analyses, there are many other possible sources of error; the more important ones have been discussed in the relevant chapters.

However, only large-scale, complex analyses as presented here can give insight into general patterns and processes. My main result, i.e. the complexity and heterogeneity of extinction risk processes, somewhat speaks against any truly overwhelming data bias. Also, the consistent influence of small geographic range size and large body size on extinction risk of terrestrial vertebrates has been found in many different datasets using widely disparate methods (reviewed in Fisher and Owens 2004, Purvis 2008).

Body size and geographic range size as risk correlates in other taxa

Some studies of extinction-risk correlates for taxa other than the three I investigated also came to the conclusion that body size is an important predictor of risk; for example, large marine fish are at higher risk, probably due to their later maturity (reviewed by Reynolds *et al.* 2005). The most comprehensive study for fish published so far concluded that body-size selectivity differed with threat types, with large marine and freshwater fish at high risk due to overexploitation, and small marine fish due to habitat loss (Olden *et al.* 2007). In reptiles, however, geographic range size and habitat specialisation seem to be more important than body size for determining extinction risk (Foufopoulos and Ives 1999, Reed and Shine 2002, Collen *et al.* 2006); even though Meiri (2008) found a positive association between lizard extinction risk and body size, he concluded that selective knowledge caused this pattern.

Similarly, poor dispersal ability and a small geographical distribution appear to be linked to high extinction risk in insects, but evidence for body-size effects is mixed (Sullivan *et al.* 2000, Koh *et al.* 2004, Kotiaho *et al.* 2005, Mattila *et al.* 2006). In butterflies, habitat specificity seems to play a larger role in determining extinction risk than my results suggest for vertebrates, and body size does not predict risk (Koh *et al.* 2004, Kotiaho *et al.* 2005, Mattila *et al.* 2006). On the other hand, hoverflies with longer wingspans are at higher risk in two European regions, indicating that body size may play a role (Sullivan *et al.* 2000).

Given these results in other groups, the strong body-size signal I found for terrestrial vertebrates may not hold true across the whole of biodiversity; there may be a threshold size above which body size matters (Cardillo *et al.* 2005). Data from Britain and the Netherlands suggest that pollinators specialised in their habitat and dietary requirements have experienced more severe declines than less specialised species, in parallel with declines in plants that are dependent on insect pollination (Biesmeijer *et al.* 2006). If geographic range sizes and habitat specialisation are indeed the most important predictors of extinction risk in insects, widespread habitat loss will have large impacts on them; indeed, declines in invertebrates may be larger than in vertebrates (Thomas *et al.* 2004). This implication should urgently be investigated more closely, especially considering the paucity of data for invertebrates (McKinney 1999).

Conclusion

Conservation implications from this thesis are twofold: firstly, studies trying to predict future risk levels for terrestrial vertebrates should ideally be threat-specific, confined to regions or realms, and take variable amounts of phylogenetic signal into account. More locally-focused comparative models of extinction-risk correlates may identify highly susceptible species from their biological traits and the prevailing threats (Cardillo *et al.* 2006, Bielby *et al.* 2008). Secondly, conservation efforts need to focus on preserving ecosystem functioning: the scale of threatened mammalian functional diversity, together with the lack of surrogacy between different measures of diversity, suggests that conserving areas with high numbers of threatened species is no effective shortcut for global biodiversity conservation.

Admittedly, the focus of my and similar studies on vertebrates is likely to distort the global situation, since terrestrial vertebrates constitute a very small and atypical part of global biodiversity. Given that most species are small, and that unicellular organisms constitute by far the largest part of global biomass and the

Tree of Life, it could be argued that even the extinction of all currently-threatened vertebrate species will make little difference to life on Earth (Nee 2005). There is, however, some indication that invertebrates may be declining at least as fast as the large vertebrates (McKinney 1999, Thomas *et al.* 2004, Biesmeijer *et al.* 2006). As discussed in chapter 5, vertebrates do provide many important ecosystem services, not the least as food for humans; clearly, *Homo sapiens* should care about vertebrate conservation. The data-hungry approaches I used here required the focus to be on well-studied groups, but there is a need to investigate more taxa, and functional-diversity investigations for groups such as pollinators or plants would certainly add important knowledge useful for conservation prioritisation.

My results strongly suggest that, at least since the industrial revolution, human actions have selectively caused declines in large mammals and birds. Anthropogenic land-use seems to have acted as a filter, driving susceptible species to global extinction or into refugia. Global extinctions have been comparatively rare given recent rates of habitat loss, probably because the most species-rich places on land, the tropical rainforests, still survive in some large blocks of “the Last of the Wild” (Sanderson *et al.* 2002), while the places long cultivated by humans were relatively species-poor to start with. There is still hope that it may not be too late to save at least some parts of global biodiversity, now that humankind has come to appreciate its dependence on it, and global efforts exist to understand extinction processes and protect species, habitats and ecosystems.

References

- Akçakaya H. R., Ferson S., Burgman M. A., Keith D. A., Mace G. M., and Todd C. R. (2000) Making consistent IUCN classifications under uncertainty. *Conservation Biology* 14: 1001-1013
- AmphibiaWeb (2008) *Information on amphibian biology and conservation* [Online Database]. URL www.amphibiaweb.org, accessed Aug.-Dec. 2008
- Asquith N. M., Wright S. J., and Clauss M. J. (1997) Does mammal community composition control recruitment in Neotropical forests? Evidence from Panama. *Ecology* 78: 941-946
- Augustine D. J. and McNaughton S. J. (2004) Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology* 41: 45-58
- Baillie J. E. M., Hilton-Taylor C., and Stuart S. N. (eds.) (2004) *2004 IUCN Red List of Threatened Species. A global species assessment*. IUCN, Gland, Switzerland and Cambridge, UK
- Baker A. J., Pereira S. L., and Paton T. A. (2007) Phylogenetic relationships and divergence times of Charadriiformes genera: multigene evidence for the Cretaceous origin of at least 14 clades of shorebirds. *Biology Letters* 3: 205-210
- Balmford A. (1996) Extinction filters and current resilience: the significance of past selection pressures for conservation biology. *Trends in Ecology and Evolution* 11: 193-196
- Barker F. K., Cibois A., Schikler P., Feinstein J., and Cracraft J. (2004) Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences of the United States of America* 101: 11040-11045

- Barnosky A. D. (2008) Megafauna biomass tradeoff as a driver of Quaternary and future extinctions. *Proceedings of the National Academy of Sciences of the United States of America* 105: 11543-11548
- Bennett P. M. and Owens I. P. F. (1997) Variation in extinction risk among birds: chance or evolutionary predisposition? *Proceedings of the Royal Society B: Biological Sciences* 264: 401-408
- Bennett P. M. and Owens I. P. F. (2002) *Evolutionary ecology of birds*. Oxford University Press, Oxford, UK
- Bielby J., Cunningham A. A., and Purvis A. (2006) Taxonomic selectivity in amphibians: ignorance, geography or biology? *Animal Conservation* 9: 135-143
- Bielby J., Mace G. M., Bininda-Emonds O. R. P., Cardillo M., Gittleman J. L., Jones K. E., Orme C. D. L., and Purvis A. (2007) The fast-slow continuum in mammalian life history: an empirical reevaluation. *American Naturalist* 169: 748-757
- Bielby J., Cooper N., Cunningham A. A., Garner T. W. J., and Purvis A. (2008) Predicting susceptibility to future declines in the world's frogs. *Conservation Letters* 1: 82-90
- Biesmeijer J. C., Roberts S. P. M., Reemer M., Ohlemüller R., Edwards M., Peeters T., Schaffers A. P., Potts S. G., Kleukers R., Thomas C. D., Settele J., and Kunin W. E. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313: 351-354
- Bininda-Emonds O. R. P., Jones K. E., Price S. A., Cardillo M., Grenyer R., and Purvis A. (2004) Garbage in, garbage out: data issues in supertree reconstruction. In: *Phylogenetic supertrees: combining information to reveal the tree of life* (ed. Bininda-Emonds O. R. P.), pp. 267-280. Kluwer Academic Publishers, Dordrecht, Netherlands
- Bininda-Emonds O. R. P., Cardillo M., Jones K. E., MacPhee R. D. E., Beck R. M. D., Grenyer R., Price S. A., Vos R. A., Gittleman J. L., and Purvis A. (2007) The delayed rise of present-day mammals. *Nature* 446: 507-512. Corrigendum (2008) *Nature* 456: 274

- Bivand R. (2007) *spdep. Spatial dependence: weighting schemes, statistics and models. R package version 0.4-7.*
- Bjørnstad O. N. (2006) *ncf. Spatial nonparametric covariance functions. R package version 1.0-9.* URL <http://onb.ent.psu.edu/onb1/>
- Blackburn T. M. and Gaston K. J. (2002) Extrinsic factors and the population sizes of threatened birds. *Ecology Letters* 5: 568-576
- Blackburn T. M., Cassey P., Duncan R. P., Evans K. L., and Gaston K. J. (2004) Avian extinction and mammalian introductions on oceanic islands. *Science* 305: 1955-1958
- Blomberg S. P., Garland T. J., and Ives A. R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57: 717-745
- Bodmer R. E., Eisenberg J. F., and Redford K. H. (1997) Hunting and the likelihood of extinction of Amazonian mammals. *Conservation Biology* 11: 460-466
- Brashares J. S. (2003) Ecological, behavioral, and life-history correlates of mammal extinctions in West Africa. *Conservation Biology* 17: 733-743
- Brown J. W., Rest J. S., García-Moreno J., Sorenson M. D., and Mindell D. P. (2008) Strong mitochondrial DNA support for a Cretaceous origin of modern avian lineages. *BMC Biology* 6: 6
- Burney D. A. and Flannery T. F. (2005) Fifty millennia of catastrophic extinctions after human contact. *Trends in Ecology and Evolution* 20: 395-401
- Carbone C. and Gittleman J. L. (2002) A common rule for the scaling of carnivore density. *Science* 295: 2273-2276
- Cardillo M. and Bromham L. (2001) Body size and risk of extinction in Australian mammals. *Conservation Biology* 15: 1435-1440
- Cardillo M. (2003) Biological determinants of extinction risk: why are smaller species less vulnerable? *Animal Conservation* 6: 63-69
- Cardillo M., Purvis A., Sechrest W., Gittleman J. L., Bielby J., and Mace G. M. (2004) Human population density and extinction risk in the world's carnivores. *PLoS Biology* 2: 0909-0914

- Cardillo M., Mace G. M., Jones K. E., Bielby J., Bininda-Emonds O. R. P., Sechrest W., Orme C. D. L., and Purvis A. (2005) Multiple causes of high extinction risk in large mammal species. *Science* 309: 1239-1241
- Cardillo M., Mace G. M., Gittleman J. L., and Purvis A. (2006) Latent extinction risk and the future battlegrounds of mammal conservation. *Proceedings of the National Academy of Sciences of the United States of America* 103: 4157-4161
- Cardillo M., Mace G. M., Gittleman J. L., Jones K. E., Bielby J., and Purvis A. (2008) The predictability of extinction: biological and external correlates of decline in mammals. *Proceedings of the Royal Society B: Biological Sciences* 275: 1441-1448
- Ceballos G. and Ehrlich P. R. (2002) Mammal population losses and the extinction crisis. *Science* 296: 904-907
- Ceballos G., Ehrlich P. R., Soberón J., Salazar I., and Fay J. P. (2005) Global mammal conservation: what must we manage? *Science* 309: 603-607
- Ceballos G. and Ehrlich P. R. (2006) Global mammal distributions, biodiversity hotspots, and conservation. *Proceedings of the National Academy of Sciences of the United States of America* 103: 19374-19379
- CIESIN (2004) *Global Grids of Gross Domestic Product (GDP) Density* [Online Database]. Center for International Earth Science Information Network (CIESIN), Socioeconomic Data and Applications Center (SEDAC), Columbia University, Palisades, USA. URL <http://islsdp2.sesda.com>, accessed Oct. 2007
- CIESIN and CIAT (2005) *Gridded population of the world version 3 (GPWv3)* [Online Database]. Center for International Earth Science Information Network (CIESIN), Centro Internacional de Agricultura Tropical (CIAT), Socioeconomic Data and Applications Center (SEDAC), Columbia University, Palisades, USA. URL <http://sedac.ciesin.columbia.edu/gpw>, accessed Feb. 2007
- Collen B., Bykova E., Ling S., Milner-Gulland E. J., and Purvis A. (2006) Extinction risk: a comparative analysis of Central Asian vertebrates. *Biodiversity and Conservation* 15: 1859-1871

- Collen B., Loh J., Whitmee S., McRae L., Amin R., and Baillie J. E. M. (2009) Monitoring change in vertebrate abundance: the Living Planet Index. *Conservation Biology* 23: 317-327
- Cooper N., Bielby J., Thomas G. H., and Purvis A. (2008) Macroecology and extinction risk correlates of frogs. *Global Ecology and Biogeography* 17: 211-221
- Corey S. J. and Waite T. A. (2008) Phylogenetic autocorrelation of extinction threat in globally imperilled amphibians. *Diversity and Distributions* 14: 614-629
- Cowley M. J. R., Thomas C. D., Thomas J. A., and Warren M. S. (1999) Flight areas of British butterflies: assessing species status and decline. *Proceedings of the Royal Society B: Biological Sciences* 266: 1587-1592
- Crawley M. J. (2007) *The R book*. John Wiley & Sons, Chichester, UK
- Crooks K. R. and Soulé M. E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400: 563-566
- Darwin C. (1859) *The origin of species by means of natural selection*. Edition (1968) by Penguin Books, London, UK
- Davies R. G., Orme C. D. L., Olson V. A., Thomas G. H., Ross S. G., Ding T.-S., Rasmussen P. C., Stattersfield A. J., Bennett P. M., Blackburn T. M., Owens I. P. F., and Gaston K. J. (2006) Human impacts and the global distribution of extinction risk. *Proceedings of the Royal Society B: Biological Sciences* 273: 2127-2133
- Davies T. J., Fritz S. A., Grenyer R., Orme C. D. L., Bielby J., Bininda-Emonds O. R. P., Cardillo M., Jones K. E., Gittleman J. L., Mace G. M., and Purvis A. (2008) Phylogenetic trees and the future of mammalian biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* 105: 11556-11563
- Diniz-Filho J. A. F., Bini L. M., and Hawkins B. A. (2003) Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography* 12: 53-64
- Dormann C. F., McPherson J. M., Araújo M. B., Bivand R., Bolliger J., Carl G., Davies R. G., Hirzel A., Jetz W., Kissling W. D., Kühn I., Ohlemüller R.,

- Peres-Neto P. R., Reineking B., Schröder B. *et al.* (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30: 609-628
- Eisenberg J. F. (1981) *The mammalian radiations. An analysis of trends in evolution, adaptation, and behaviour*. Athlone Press, London, UK
- Ericson P. G. P., Anderson C. L., Britton T., Elzanowski A., Johansson U. S., Källersjö M., Ohlson J. I., Parsons T. J., Zuccon D., and Mayr G. (2006) Diversification of Neoaves: integration of molecular sequence data and fossils. *Biology Letters* 2: 543-547
- European Commission and Joint Research Centre (2003) *Global Land Cover 2000 database* [Online Database]. European Commission, Joint Research Centre, Institute for Environment and Sustainability, Ispra, Italy. URL <http://www-gem.jrc.it/glc2000>, accessed Oct. 2007
- Fa J. E., Peres C. A., and Meeuwig J. (2002) Bushmeat exploitation in tropical forests: an intercontinental comparison. *Conservation Biology* 16: 232-237
- Fa J. E., Ryan S. F., and Bell D. J. (2005) Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in afro-tropical forests. *Biological Conservation* 121: 167-176
- Faith D. P. (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation* 61: 1-10
- Felsenstein J. (1985) Phylogenies and the comparative method. *American Naturalist* 125: 1-15
- Felsenstein J. (2005) Using the quantitative genetic threshold model for inferences between and within species. *Philosophical Transactions of the Royal Society London Series B* 360: 1427-1434
- Fisher D. O., Blomberg S. P., and Owens I. P. F. (2003) Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. *Proceedings of the Royal Society B: Biological Sciences* 270: 1801-1808
- Fisher D. O. and Owens I. P. F. (2004) The comparative method in conservation biology. *Trends in Ecology and Evolution* 19: 391-398
- Forest F., Grenyer R., Rouget M., Davies T. J., Cowling R. M., Faith D. P., Balmford A., Manning J. C., Procheş Ş., van der Bank M., Reeves G.,

- Hedderson T. A. J., and Savolainen V. (2007) Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* 445: 757-760
- Foufopoulos J. and Ives A. R. (1999) Reptile extinctions on land-bridge islands: life-history attributes and vulnerability to extinction. *American Naturalist* 153: 1-25
- Fox J. (2007) *car. Companion to Applied Regression. R package version 1.2-7.*
- Freckleton R. P., Harvey P. H., and Pagel M. (2002) Phylogenetic analysis and comparative data: A test and review of evidence. *American Naturalist* 160: 712-726
- Freckleton R. P. and Jetz W. (2009) Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. *Proceedings of the Royal Society B: Biological Sciences* 276: 21-30
- Frost D. R., Grant T., Faivovich J., Bain R. H., Haas A., Haddad C. F. B., De Sá R. O., Channing A., Wilkinson M., Donnellan S. C., Raxworthy C. J., Campbell J. A., Blotto B. L., Moler P., Drewes R. C. *et al.* (2006) The amphibian tree of life. *Bulletin of the American Museum of Natural History* 297: 1-370
- Frost D. R. (2008) *Amphibian Species of the World: an Online Reference. Version 5.2* [Online Database]. American Museum of Natural History, New York, USA. URL <http://research.amnh.org/herpetology/amphibia/index.php>, accessed Dec. 2008
- Gage G. S., Brooke M. d. L., Symonds M. R. E., and Wege D. (2004) Ecological correlates of the threat of extinction in Neotropical bird species. *Animal Conservation* 7: 161-168
- Garland T. J. and Ives A. R. (2000) Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *American Naturalist* 155: 346-364
- Gaston K. J. and Blackburn T. M. (1995) Birds, body size and the threat of extinction. *Philosophical Transactions of the Royal Society London Series B* 347: 205-212
- Gaston K. J. and Fuller R. A. (2008) Commonness, population depletion and conservation biology. *Trends in Ecology and Evolution* 23: 14-19

- Gregory R. D., Wilkinson N. I., Noble D. G., Robinson J. A., Brown A. F., Hughes J., Proctor D., Gibbons D. W., and Galbraith C. A. (2002) The population status of birds in the United Kingdom, Channel Islands and Isle of Man: an analysis of conservation concern 2002-2007. *British Birds* 95: 410-448
- Grenyer R., Orme C. D. L., Jackson S. F., Thomas G. H., Davies R. G., Davies T. J., Jones K. E., Olson V. A., Ridgely R. S., Rasmussen P. C., Ding T.-S., Bennett P. M., Blackburn T. M., Gaston K. J., Gittleman J. L. *et al.* (2006) Global distribution and conservation of rare and threatened vertebrates. *Nature* 444: 93-96
- Gross K. and Cardinale B. J. (2005) The functional consequences of random vs. ordered species extinctions. *Ecology Letters* 8: 409-418
- Hackett S. J., Kimball R. T., Reddy S., Bowie R. C. K., Braun E. L., Braun M. J., Chojnowski J. L., Cox W. A., Han K.-L., Harshman J., Huddleston C. J., Marks B. D., Miglia K. J., Moore W. S., Sheldon F. H. *et al.* (2008) A phylogenomic study of birds reveals their evolutionary history. *Science* 320: 1763-1768
- Harcourt A. (1998) Ecological indicators of risk for primates, as judged by species' susceptibility to logging. In: *Behavioural Ecology and Conservation Biology* (ed. Caro T.), pp. 56-79. Oxford University Press, Oxford, UK
- Harmon L. J., Weir J. T., Brock C. D., Glor R. E., and Challenger W. (2008) GEIGER: investigating evolutionary radiations. *Bioinformatics* 24: 129-131
- Harvey P. H. and Pagel M. D. (1991) *The comparative method in evolutionary biology*. Oxford University Press, Oxford, UK
- Hawkins B. A., Diniz-Filho J. A. F., Bini L. M., De Marco P., and Blackburn T. M. (2007) Red herrings revisited: spatial autocorrelation and parameter estimation in geographical ecology. *Ecography* 30: 375-384
- Hero J.-M., Williams S. E., and Magnusson W. E. (2005) Ecological traits of declining amphibians in upland areas of eastern Australia. *Journal of Zoology* 267: 221-232

- Hooper D. U., Chapin III F. S., Ewel J. J., Hector A., Inchausti P., Lavorel S., Lawton J. H., Lodge D. M., Loreau M., Naeem S., Schmid B., Setälä H., Symstad A. J., Vandermeer J., and Wardle D. A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75: 3-35
- Huelsenbeck J. P. (1991) Tree-length distribution skewness: an indicator of phylogenetic information. *Systematic Zoology* 40: 257-270
- Imhoff M. L., Bounoua L., Ricketts T. H., Loucks C. J., Harriss R., and Lawrence W. T. (2004) Global patterns in human consumption of net primary production. *Nature* 429: 870-873
- Isaac N. J. B. and Cowlishaw G. (2004) How species respond to multiple extinction threats. *Proceedings of the Royal Society B: Biological Sciences* 271: 1135-1141
- Isaac N. J. B., Jones K. E., Gittleman J. L., and Purvis A. (2005) Correlates of species richness in mammals: body size, life history, and ecology. *American Naturalist* 165: 600-607
- IUCN (2001) *IUCN Red List categories and criteria: version 3.1*. IUCN Species Survival Commission, Gland, Switzerland and Cambridge, UK
- IUCN, Conservation International, and NatureServe (2004/2006) *Global Amphibian Assessment* [Online Database]. URL <http://www.globalamphibians.org>, accessed July 2008
- IUCN (2007/2008) *2007/2008 IUCN Red List of Threatened Species* [Online Database]. International Union for Conservation of Nature (IUCN), SSC Red List Programme, Cambridge, UK. URL www.iucnredlist.org, accessed Apr./Oct. 2008
- Jepson P. and Whittaker R. J. (2002) Ecoregions in context: a critique with special reference to Indonesia. *Conservation Biology* 16: 42-57
- Jernvall J. and Wright P. C. (1998) Diversity components of impending primate extinctions. *Proceedings of the National Academy of Sciences of the United States of America* 95: 11279-11283
- Jetz W. and Rahbek C. (2002) Geographic range size and determinants of avian species richness. *Science* 297: 1548-1551

- Jetz W., Sekercioglu C. H., and Watson J. E. M. (2008) Ecological correlates and conservation implications of overestimating species geographic ranges. *Conservation Biology* 22: 110-119
- Johnson C. N. (2002) Determinants of loss of mammalian species during the Late Quaternary 'megafauna' extinction: life history and ecology, but not body size. *Proceedings of the Royal Society B: Biological Sciences* 269: 2221-2227
- Johnson C. N., Delean S., and Balmford A. (2002) Phylogeny and the selectivity of extinction in Australian marsupials. *Animal Conservation* 5: 135-142
- Jones K. E., Purvis A., and Gittleman J. L. (2003) Biological correlates of extinction risk in bats. *American Naturalist* 161: 601-614
- Jones K. E., Bielby J., Cardillo M., Fritz S. A., O'Dell J., Orme C. D. L., Safi K., Sechrest W., Boakes E. H., Carbone C., Connolly C., Cutts M. J., Foster J. K., Grenyer R., Habib M. *et al.* (2009) PanTHERIA: A species-level database of life-history, ecology and geography of extant and recently extinct mammals. *Ecology*. In press
- Kissling W. D. and Carl G. (2008) Spatial autocorrelation and the selection of simultaneous autoregressive models. *Global Ecology and Biogeography* 17: 59-71
- Klein Goldewijk K. (2001) Estimating global land use change over the past 300 years: the HYDE database. *Global Biogeochemical Cycles* 15: 417-433
- Knapp A. K., Blair J. M., Briggs J. M., Collins S. L., Hartnett D. C., Johnson L. C., and Towne E. G. (1999) The keystone role of bison in North American tallgrass prairie. *BioScience* 49: 39-50
- Koh L. P., Sodhi N. S., and Brook B. W. (2004) Ecological correlates of extinction proneness in tropical butterflies. *Conservation Biology* 18: 1571-1578
- Kotiaho J. S., Kaitala V., Komonen A., and Päävinen J. (2005) Predicting the risk of extinction from shared ecological characteristics. *Proceedings of the National Academy of Sciences of the United States of America* 102: 1963-1967

- Laurance W. F., Croes B. M., Tchignoumba L., Lahm S. A., Alonso A., Lee M. E., Campbell P., and Ondzeano C. (2006) Impacts of roads and hunting on Central African rainforest mammals. *Conservation Biology* 20: 1251-1261
- Lawton J. H. (1995) Population dynamic principles. In: *Extinction rates* (eds. Lawton J. H. and May R. M.), pp. 197-213. Oxford University Press, Oxford, UK
- Legendre P. (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology* 74: 1659-1673
- Lichstein J. W., Simons T. R., Shriner S. A., and Franzreb K. E. (2002) Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs* 72: 445-463
- Lips K. R., Reeve J. D., and Witters L. R. (2003) Ecological traits predicting amphibian population declines in Central America. *Conservation Biology* 17: 1078-1088
- Lips K. R., Diffendorfer J., Mendelsohn III J. R., and Sears M. W. (2008) Riding the wave: reconciling the roles of disease and climate change in amphibian declines. *PLoS Biology* 6: e72
- Lockwood J. L., Russell G. J., Gittleman J. L., Daehler C. C., McKinney M. L., and Purvis A. (2002) A metric for analyzing taxonomic patterns of extinction risk. *Conservation Biology* 16: 1137-1142
- Loh J., Green R. E., Ricketts T. H., Lamoreux J., Jenkins M., Kapos V., and Randers J. (2005) The Living Planet Index: using species population time series to track trends in biodiversity. *Philosophical Transactions of the Royal Society London Series B* 360: 289-295
- Luck G. W. (2007) A review of the relationships between human population density and biodiversity. *Biological Reviews* 82: 607-645
- Lyons-Weiler J., Hoelzer G. A., and Tausch R. J. (1996) Relative Apparent Synapomorphy Analysis (RASA) I: the statistical measurement of phylogenetic signal. *Molecular Biology and Evolution* 13: 749-757
- Mace G., Masundire H., and Baillie J. (2005) Biodiversity. In: *The Millennium Ecosystem Assessment. Current Status and Trends: Ecosystems and*

- Human Well-being* (ed. World Resources Institute), pp. 77-122. Island Press, Washington, D.C.
- Mace G. M. and Lande R. (1991) Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. *Conservation Biology* 5: 148-157
- Mace G. M. (1995) Classification of threatened species and its role in conservation planning. In: *Extinction rates* (eds. Lawton J. H. and May R. M.), pp. 197-213. Oxford University Press, Oxford, UK
- Mace G. M. and Balmford A. (2000) Patterns and processes in contemporary mammalian extinction. In: *Priorities for the conservation of mammalian diversity. Has the panda had its day?* (eds. Entwistle A. and Dunstone N.), pp. 27-52. Cambridge University Press, Cambridge, UK
- Mace G. M., Collar N. J., Gaston K. J., Hilton-Taylor C., Akçakaya H. R., Leader-Williams N., Milner-Gulland E. J., and Stuart S. N. (2008) Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology* 22: 1424-1442
- Magnusson W. E. (2004) Ecoregion as a pragmatic tool. *Conservation Biology* 18: 4-5
- Manne L. L., Brooks T. M., and Pimm S. L. (1999) Relative risk of extinction of passerine birds on continents and islands. *Nature* 399: 258-261
- Marjanović D. and Laurin M. (2007) Fossils, molecules, divergence times, and the origin of Lissamphibians. *Systematic Biology* 56: 369-388
- Mason N. W. H., MacGillivray K., Steel J. B., and Wilson J. B. (2003) An index of functional diversity. *Journal of Vegetation Science* 14: 571-578
- Mattila N., Kaitala V., Komonen A., Kotiaho J. S., and Päävinen J. (2006) Ecological determinants of distribution decline and risk of extinction in moths. *Conservation Biology* 20: 1161-1168
- May R. M., Lawton J. H., and Stork N. E. (1995) Assessing extinction rates. In: *Extinction rates* (eds. Lawton J. H. and May R. M.), pp. 1-24. Oxford University Press, Oxford, UK

- McKinney M. L. (1997) Extinction vulnerability and selectivity: Combining ecological and paleontological views. *Annual Review of Ecology and Systematics* 28: 495-516
- McKinney M. L. (1999) High rates of extinction and threat in poorly studied taxa. *Conservation Biology* 13: 1273-1281
- McNaughton S. J., Ruess R. W., and Seagle S. W. (1988) Large mammals and process dynamics in African ecosystems. *BioScience* 38: 794-800
- Meiri S. (2008) Evolution and ecology of lizard body sizes. *Global Ecology and Biogeography* 17: 724-734
- Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Biodiversity Synthesis*. World Resources Institute, Washington, DC
- Milner-Gulland E. J., Bennett E. L., and SCB 2002 Annual Meeting Wild Meat Group (2003) Wild meat: the bigger picture. *Trends in Ecology and Evolution* 18: 351-357
- Monroe B. L. and Sibley C. G. (1993) *A world checklist of birds*. Yale University Press, New Haven, CT, USA
- Mooers A. Ø. and Atkins R. A. (2003) Indonesia's threatened birds: over 500 million years of evolutionary heritage at risk. *Animal Conservation* 6: 183-188
- Morrow E. H. and Pitcher T. E. (2003) Sexual selection and the risk of extinction in birds. *Proceedings of the Royal Society B: Biological Sciences* 270: 1793-1799
- Muller-Landau H. C. (2007) Predicting the long-term effects of hunting on plant species composition and diversity in tropical forests. *Biotropica* 39: 372-384
- Mundry R. and Nunn C. L. (2009) Stepwise model fitting and statistical inference: turning noise into signal pollution. *American Naturalist* 173: 119-123
- Myers N., Mittermeier R. A., Mittermeier C. G., da Fonseca G. A. B., and Kent J. (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858

- Nee S. (2005) Phylogenetic futures after the latest mass extinction. In: *Phylogeny and conservation* (eds. Purvis A., Gittleman J. L. and Brooks T. M.), pp. 387-399. Cambridge University Press, Cambridge, UK
- Norris K. and Harper N. (2004) Extinction processes in hot spots of avian biodiversity and the targeting of pre-emptive conservation action. *Proceedings of the Royal Society B: Biological Sciences* 271: 123-130
- Olden J. D., Hogan Z. S., and Vander Zanden M. J. (2007) Small fish, big fish, red fish, blue fish: size-biased extinction risk of the world's freshwater and marine fishes. *Global Ecology and Biogeography* 16: 694-701
- Olson D. M., Dinerstein E., Wikramanayake E. D., Burgess N. D., Powell G. V. N., Underwood E. C., d'Amico J. A., Itoua I., Strand H. E., Morrison J. C., Loucks C. J., Allnutt T. F., Ricketts T. H., Kura Y., Lamoreux J. F. *et al.* (2001) Terrestrial ecoregions of the world: a new map of life on earth. *BioScience* 51: 933-938
- Olson J. S. (1994) *Global Ecosystems V. 1* [Online Database]. U.S. Geological Survey Center for Earth Resources Observation and Science (USGS EROS). URL <http://edcns17.cr.usgs.gov/glcc>, accessed May 2008
- Olson V. A., Davies R. G., Orme C. D. L., Thomas G. H., Meiri S., Blackburn T. M., Gaston K. J., Owens I. P. F., and Bennett P. M. (2009) Global biogeography and ecology of body size in birds. *Ecology Letters* 12: 249-259
- Orme C. D. L., Davies R. G., Burgess M., Eigenbrod F., Pickup N., Olson V. A., Webster A. J., Ding T.-S., Rasmussen P. C., Ridgely R. S., Stattersfield A. J., Bennett P. M., Blackburn T. M., Gaston K. J., and Owens I. P. F. (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436: 1016-1019
- Orme C. D. L., Freckleton R. P., and Thomas G. H. (2008) *CAIC. Comparative analyses using independent contrasts. R package version 1.0.4-81*. URL <http://r-forge.r-project.org/projects/caic>
- Owens I. P. F. and Bennett P. M. (2000) Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators.

- Proceedings of the National Academy of Sciences of the United States of America* 97: 12144-12148
- Pagel M. (1999) Inferring the historical patterns of biological evolution. *Nature* 401: 877-884
- Paradis E. (2006) *Analysis of phylogenetics and evolution with R*. Springer, New York, USA
- Pereira S. L. and Baker A. J. (2006) A mitogenomic timescale for birds detects variable phylogenetic rates of molecular evolution and refutes the standard molecular clock. *Molecular Biology and Evolution* 23: 1731-1740
- Petchey O. L. and Gaston K. J. (2002) Extinction and the loss of functional diversity. *Proceedings of the Royal Society B: Biological Sciences* 269: 1721-1727
- Petchey O. L. and Gaston K. J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters* 9: 741-758
- Pimm S. L., Jones H. L., and Diamond J. (1988) On the risk of extinction. *American Naturalist* 132: 757-785
- Pimm S. L., Russell G. J., Gittleman J. L., and Brooks T. M. (1995) The future of biodiversity. *Science* 269: 347-350
- Pounds J. A., Bustamante M. R., Coloma L. A., Consuegra J. A., Fogden M. P. L., Foster P. N., La Marca E., Masters K. L., Merino-Viteri A., Puschendorf R., Ron S. R., Sánchez-Azofeifa G. A., Still C. J., and Young B. E. (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439: 161-167
- Price S. A. and Gittleman J. L. (2007) Hunting to extinction: biology and regional economy influence extinction risk and the impact of hunting in artiodactyls. *Proceedings of the Royal Society B: Biological Sciences* 274: 1845-1851
- Pringle R. M., Young T. P., Rubenstein D. I., and McCauley D. J. (2007) Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. *Proceedings of the National Academy of Sciences of the United States of America* 104: 193-197

- Purvis A., Agapow P.-M., Gittleman J. L., and Mace G. M. (2000a) Nonrandom extinction and the loss of evolutionary history. *Science* 288: 328-330
- Purvis A., Gittleman J. L., Cowlishaw G., and Mace G. M. (2000b) Predicting extinction risk in declining species. *Proceedings of the Royal Society B: Biological Sciences* 267: 1947-1952
- Purvis A., Cardillo M., Grenyer R., and Collen B. (2005) Correlates of extinction risk: phylogeny, biology, threat and scale. In: *Phylogeny and conservation* (eds. Purvis A., Gittleman J. L. and Brooks T. M.), pp. 295-316. Cambridge University Press, Cambridge, UK
- Purvis A. (2008) Phylogenetic approaches to the study of extinction. *Annual Review of Ecology, Evolution, and Systematics* 39: 301-319
- R Development Core Team (2007/2008) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL: <http://www.R-project.org>
- Raup D. M. (1993) *Extinction. Bad genes or bad luck?* Oxford University Press, Oxford, UK
- Redding D. W. and Mooers A. Ø. (2006) Incorporating evolutionary measures into conservation prioritization. *Conservation Biology* 20: 1670-1678
- Reed R. N. and Shine R. (2002) Lying in wait for extinction: ecological correlates of conservation status among Australian elapid snakes. *Conservation Biology* 16: 451-461
- Reynolds J. D., Dulvy N. K., Goodwin N. B., and Hutchings J. A. (2005) Biology of extinction risk in marine fishes. *Proceedings of the Royal Society B: Biological Sciences* 272: 2337-2344
- Rodrigues A. S. L., Pilgrim J. D., Lamoreux J. F., Hoffmann M., and Brooks T. M. (2006) The value of the IUCN Red List for conservation. *Trends in Ecology and Evolution* 21: 71-76
- Rodríguez M. Á., Olalla-Tárraga M. Á., and Hawkins B. A. (2008) Bergmann's rule and the geography of mammal body size in the Western Hemisphere. *Global Ecology and Biogeography* 17: 274-283
- Roelants K., Gower D. J., Wilkinson M., Loader S. P., Biju S. D., Guillaume K., Moriau L., and Bossuyt F. (2007) Global patterns of diversification in the

- history of modern amphibians. *Proceedings of the National Academy of Sciences of the United States of America* 104: 887-892
- Russell G. J., Brooks T. M., McKinney M. M., and Anderson C. G. (1998) Present and future taxonomic selectivity in bird and mammal extinctions. *Conservation Biology* 12: 1365-1376
- Safi K. and Kerth G. (2004) A comparative analysis of specialisation and extinction risk in temperate-zone bats. *Conservation Biology* 18: 1293-1303
- Sala O. E., Chapin III F. S., Armesto J. J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke L. F., Jackson R. B., Kinzig A., Leemans R., Lodge D. M., Mooney H. A., Oesterheld M., Poff N. L. *et al.* (2000) Global biodiversity scenarios for the year 2100. *Science* 287: 1770-1774
- Sanderson E. W., Jaiteh M., Levy M. A., Redford K. H., Wannebo A. V., and Woolmer G. (2002) The Human Footprint and the Last of the Wild. *BioScience* 52: 891-904
- Scharlemann J. P. W., Balmford A., and Green R. E. (2005) The level of threat to restricted-range species can be predicted from mapped data on land use and human population. *Biological Conservation* 123: 317-326
- Schipper J., Chanson J. S., Chiozza F., Cox N. A., Hoffmann M., Katariya V., Lamoreux J., Rodrigues A. S. L., Stuart S. N., Temple H. J., Baillie J., Boitani L., Lacher T. E. J., Mittermeier R. A., Smith A. T. *et al.* (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* 322: 225-230
- Schwartz M. W. and Simberloff D. (2001) Taxon size predicts rates of rarity in vascular plants. *Ecology Letters* 4: 464-469
- Sibley C. G. and Ahlquist J. E. (1990) *Phylogeny and classification of birds*. Yale University Press, New Haven, CT, USA
- Sibley C. G. and Monroe B. L. (1990) *Distribution and taxonomy of birds of the world*. Yale University Press, New Haven, CT, USA
- Sjöström A. and Gross C. L. (2006) Life history characters and phylogeny are correlated with extinction risk in the Australian angiosperms. *Journal of Biogeography* 33: 271-290

- Smith R. J. and Jungers W. L. (1997) Body mass in comparative primatology. *Journal of Human Evolution* 32: 523-559
- Soares-Filho B. S., Nepstad D. C., Curran L. M., Cerqueira G. C., Garcia R. A., Ramos C. A., Voll E., McDonald A., Lefebvre P., and Schlesinger P. (2006) Modelling conservation in the Amazon basin. *Nature* 440: 520-523
- Sodhi N. S., Bickford D., Diesmos A. C., Lee T. M., Koh L. P., Brook B. W., Sekercioglu C. H., and Bradshaw C. J. A. (2008) Measuring the meltdown: drivers of global amphibian extinction and decline. *PLoS ONE* 3: e1636
- Stuart S. N., Chanson J. S., Cox N. A., Young B. E., Rodrigues A. S. L., Fischman D. L., and Waller R. W. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science* 306: 1783-1786
- Sullivan M. S., Gilbert F., Rotheray G., Croasdale S., and Jones M. J. (2000) Comparative analyses of correlates of Red data book status: a case study using European hoverflies (Diptera: Syrphidae). *Animal Conservation* 3: 91-95
- Terborgh J., Lopez L., Nuñez V. P., Rao M., Shahabuddin G., Orihuela G., Riveros M., Ascanio R., Adler G. H., Lambert T. D., and Balbas L. (2001) Ecological meltdown in predator-free forest fragments. *Science* 294: 1923-1926
- Thomas G. H., Lanctot R. B., and Székely T. (2006) Can intrinsic factors explain population declines in North American breeding shorebirds? A comparative analysis. *Animal Conservation* 9: 252-258
- Thomas G. H. (2008) Phylogenetic distributions of British birds of conservation concern. *Proceedings of the Royal Society B: Biological Sciences* 275: 2077-2083
- Thomas J. A., Telfer M. G., Roy D. B., Preston C. D., Greenwood J. J. D., Asher J., Fox R., Clarke R. T., and Lawton J. H. (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* 303: 1879-1881

- UNEP (1994) *GRID-Europe dataset GNV183* [Online Database]. United Nations Environment Programme, Nairobi, Kenya. URL <http://www.grid.unep.ch>, accessed Feb. 2007
- USGS EROS (1996) *GTOPO30 global digital elevation model* [Online Database]. U.S. Geological Survey (USGS), Center for Earth Resources Observation and Science (EROS), Sioux Falls, USA. URL <http://edc.usgs.gov>, accessed Mar. 2007
- Vane-Wright R. I., Humphries C. J., and Williams P. H. (1991) What to protect? Systematics and the agony of choice. *Biological Conservation* 55: 235-254
- von Euler F. (2001) Selective extinction and rapid loss of evolutionary history in the bird fauna. *Proceedings of the Royal Society B: Biological Sciences* 268: 127-130
- Webb C. O., Ackerly D. D., McPeck M. A., and Donoghue M. J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33: 475-505
- Webb T. J. and Gaston K. J. (2003) On the heritability of geographic range sizes. *American Naturalist* 161: 553-566
- Western D. (1979) Size, life-history and ecology in mammals. *African Journal of Ecology* 17: 185-204
- Whittingham M. J., Stephens P. A., Bradbury R. B., and Freckleton R. P. (2006) Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology* 75: 1182-1189
- Wikramanayake E. D., Dinerstein E., Loucks C. J., Olson D. M., Morrison J. C., Lamoreux J., McKnight M. W., and Hedao P. (2002) Ecoregions in ascendance: reply to Jepson and Whittaker. *Conservation Biology* 16: 238-243
- Williams S. E. and Hero J.-M. (1998) Rainforest frogs of the Australian Wet Tropics: guild classification and the ecological similarity of declining species. *Proceedings of the Royal Society B: Biological Sciences* 265: 597-602
- Willis C. G., Ruhfel B., Primack R. B., Miller-Rushing A. J., and Davis C. C. (2008) Phylogenetic patterns of species loss in Thoreau's woods are driven

- by climate change. *Proceedings of the National Academy of Sciences of the United States of America* 105: 17029-17033
- Wilson D. E. and Reeder D. M. (eds.) (1993/2005) *Mammal species of the world: a taxonomic and geographic reference*. Smithsonian Institution Press/John Hopkins University Press, Washington D.C./Baltimore, USA
- Woodroffe R. and Ginsberg J. R. (1998) Edge effects and the extinction of populations inside protected areas. *Science* 280: 2126-2128
- Wroe S., Field J., and Grayson D. K. (2006) Megafaunal extinction: climate, humans and assumptions. *Trends in Ecology and Evolution* 21: 61-62

Appendix A: Davies *et al.* (2008) - Phylogenetic trees and the future of mammalian biodiversity

Phylogenetic trees and the future of mammalian biodiversity

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Phylogenies describe the origins and history of species. However, they can also help to predict species' fates and so can be useful tools for managing the future of biodiversity. This article starts by sketching how phylogenetic, geographic, and trait information can be combined to elucidate present mammalian diversity patterns and how they arose. Recent diversification rates and standing diversity show different geographic patterns, indicating that cradles of diversity have moved over time. Patterns in extinction risk reflect both biological differences among mammalian lineages and differences in threat intensity among regions. Phylogenetic comparative analyses indicate that for small-bodied mammals, extinction risk is governed mostly by where the species live and the intensity of the threats, whereas for large-bodied mammals, ecological differences also play an important role. This modeling approach identifies species whose intrinsic biology renders them particularly vulnerable to increased human pressure. We outline how the approach might be extended to consider future trends in anthropogenic drivers, to identify likely future battlegrounds of mammalian conservation, and the likely casualties. This framework could help to highlight consequences of choosing among different future climatic and socioeconomic scenarios. We end by discussing priority-setting, showing how alternative currencies for diversity can suggest very different priorities. We argue that aiming to maximize long-term evolutionary responses is inappropriate, that conservation planning needs to consider costs as well as benefits, and that proactive conservation of largely intact systems should be part of a balanced strategy.

extinction risk | latent risk | mammals

The Tree of Life—phylogeny—is a powerful metaphor for life's diversity, showing all species, including our own, as part of an interrelated whole. But phylogeny is more than a metaphor. It is also a research tool—the result of evolutionary processes integrated over the history of life, it can be analyzed for insights into how those processes have shaped today's biota (1). This approach is becoming increasingly powerful as the trees become ever more inclusive, built from rapidly accumulating databases using methods that continue to be improved (2, 3).

Species' histories are of interest, but their futures are of more pressing concern. The Tree of Life is currently under sustained attack, as people increasingly dominate landscapes (4). Comparisons of extinction rates between today and geological history are difficult for many reasons (5), but the Tree of Life is already being pruned more quickly than it is growing (6), and extinction rates are projected to rise by at least another order of magnitude over the next centuries (7). This article describes how phylogeny has a role to play in understanding the pattern of survivors and casualties and how it can help us both to predict species' futures and to estimate some of the biodiversity value that would be lost if they went extinct.

We focus on mammals as a model system. They are much better known than almost any other group, with a mature

species-level taxonomy (8), a largely complete evaluation of species' extinction risk (9), a large database of ecological, life history, and geographical information (K.E.J., J.B., A.P., C.D.L.O., S.A.F., Christina Connolly, Amber Teacher, J.L.G., R.G., Elizabeth Boakes, Michael Habib, Janna Rist, Chris Carbone, Christopher A. Plaster, O.R.P.B.-E., Janine K. Foster, Elisabeth A. Rigby, Michael J. Cutts, Samantha A. Price, Wes Sechrest, Justin O'Dell, Kamran Safi, M.C., and G.M.M., unpublished data), and a comprehensive species-level estimate of phylogeny (11). [Many node ages in ref. 11 were slightly affected by a software bug; all our analyses use corrected dates (O.R.P.B.-E., M.C., K.E.J., Ross D. E. MacPhee, Robin M. D. Beck, R.G., Samantha A. Price, Rutger A. Vos, J.L.G., and A.P., unpublished data).] As always with a model system, advantages come at a price. Mammals are atypical (e.g., they are much larger than most other species), so results from them cannot necessarily be extrapolated more broadly. However, mammals are a charismatic group of special interest to many people, so results have value even if they cannot be generalized. We start with a snapshot of present mammalian diversity and the (overwhelmingly anthropogenic) pressures that species face, before going on to describe recent and ongoing attempts to understand the present and possible future consequences of those pressures.

A Snapshot of Mammalian Biodiversity

Mammalian species are distributed very unevenly among genera, families, and orders (6, 8). Differences in age among taxa of a given rank (13) confound evolutionary interpretation of the pattern, but the phylogeny permits a test of whether the chances of diversification have indeed varied among lineages. Under the equal-rates Markov model (ERM), in which chances are equal, phylogenies should have a weighted mean I [the degree to which species are partitioned unequally between sister clades (14)], not significantly >0.5 . The estimate of phylogeny (11) has a weighted mean I of 0.657 (SE = ± 0.0131), well above 0.5 (weighted t test vs. 0.5: $t_{848} = 11.98, p \ll 0.001$), indicating that lineages have had different propensities to diversify. Such inequality is common throughout the Tree of Life (15, 16) and prompts the search for traits that might be responsible. Phylogenetic analyses reveal that large litter size and high abundance are both linked with high richness in sister-clade comparisons pooled across four orders

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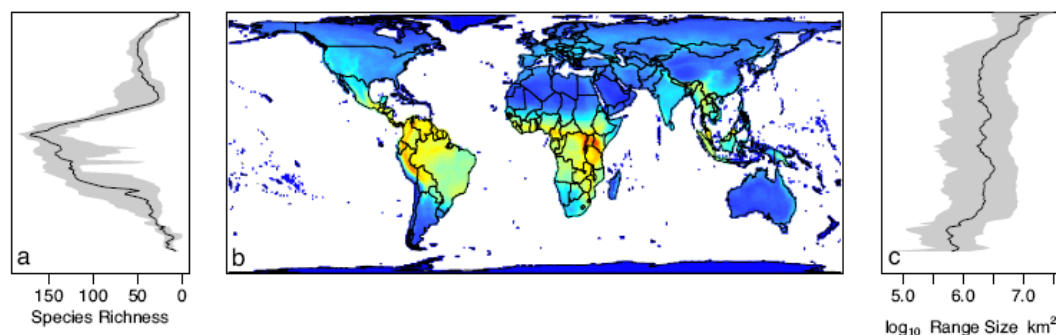


Fig. 1. Geographic patterns in mammalian biodiversity. (a) The latitudinal gradient in species-richness. The solid line shows the median; gray bands demarcate the interquartile range; species are counted in every latitudinal band (100 km north to south) in which they occur. (b) A map of species richness within 100 × 100-km grid cells, ranging from deep blue (minimum = 0 species) to deep red (maximum = 258 species). (c) The latitudinal pattern of mean geographic range size; details as for a.

(primates, carnivores, marsupials, and bats), whereas small body size and short gestation period also predict high richness within carnivores (17). In common with most comparable studies on other taxa (18), however, the biological traits leave most of the variance in richness unexplained, suggesting a possible role for the environment.

The geographic distribution of mammalian species is also very uneven (Fig. 1). Mammals follow global trends for higher tropical diversity, with a strong latitudinal diversity gradient (Fig. 1a). Within the tropics, richness seems to correlate with productivity and water-energy dynamics, peaking in Amazonia at the base of the Andes, in the Great Rift Valley in Africa (where richness exceeds 250 species per 10,000 km²), and in an arc running from the Himalayas into southeastern Asia (Fig. 1b). These peaks suggest that topographical heterogeneity has also shaped species-richness patterns (19). At higher latitudes, the relationship between richness and productivity is much weaker, and ambient energy is a better predictor of richness (19). The geographic pattern of mammalian richness is highly congruent with those of birds and amphibians (20), which are also well predicted by the same environmental variables (21, 22). All these groups have many narrow-range species on the Neotropical mainland, but other “hotspots of endemism” differ—continental shelf island systems for mammals, oceanic archipelagoes for birds, and mainland locations for amphibians (20). The latitudinal gradient in median geographic range size in mammals (Fig. 1c) correlates strongly with the land area available within the same latitudinal bands ($r = 0.68$, although spatial autocorrelation complicates significance testing). However, median range size remains high in the northernmost bands despite the rapid decline in land area toward the Pole. Bird range sizes show similar patterns (23).

The tropics have been described as an evolutionary powerhouse, acting as a “cradle” for diversity (24). Might Fig. 1, therefore, reflect long-standing geographic differences in diversification rates? Cradles of diversity could be of particular interest if conservation actions are to be targeted toward conserving the processes that generate diversity, a point to which we return below. The geographic pattern of recent diversification can be examined in terms of taxonomy or phylogeny, although both have their problems. Boundaries to higher taxa can be arbitrary (13), whereas both the relative and absolute divergence times in molecular phylogenies can be controversial (25). Because of these reservations, we use both approaches.

Taxonomically, the ratio of species to genera should indicate the regional diversification rate over the past several million years, if genera are approximately equal in age. This ratio correlates strongly with log(species richness) among equal-area grid cells (Pearson's $r = 0.61$; Fig. 2a). This correlation remains highly significant (corrected $F = 78.49$, corrected $P < 0.001$, $n = 4,152$; based on a subsample of cells and excluding single species occurrences) when degrees of freedom are reduced to account for spatial autocorrelation (26). Moving to phylogeny, places where a high proportion of species are on short terminal branches in the tree are likely to have rapid diversification, turnover, or immigration in their recent history (27). However, analyses are complicated by the low resolution (uncertain relationships) at the tips of the phylogeny, which introduces overestimates of the respective branch lengths. We ameliorated this problem by reducing ages of terminal polytomies using the correction suggested by Nee in ref. 28 and by assuming that the descendants from each polytomy diversified under a Yule process (29). Fig. 2b highlights the Andean and Himalayan diversity peaks, but not the African great lakes, as recent evolutionary crucibles. Much of the temperate north stands out more than much of the tropics in this map, and there is a negative overall correlation between the proportion of short branches and log(species richness) ($r = -0.38$, corrected $F = 21.01$, corrected $P < 0.001$, $n = 4,210$, analyses as above), although this depended on how we corrected for terminal polytomies. This result partially echoes recent findings of higher recent speciation and extinction rates in temperate than in tropical mammals (30). These maps also imply that some regions have seen marked shifts in net diversification rate, whereas others may have remained steady.

Areas of “old” and “young” diversity can be identified from the residuals of a loess regression across cells of total evolutionary history (i.e., total branch length in the phylogeny of a cell's species) on species number. The African diversity peak emerges as old, whereas much of Andean diversity is young (Fig. 2c). Character disparity—among-species variation in morphology—also shows geographic pattern: Fig. 2d maps one index of disparity, the variance in log(body mass). Disparity tends to be high where diversity is old ($r = 0.29$, corrected $F = 5.10$, corrected $P < 0.05$, $n = 4,210$, analyses as above), although tropical regions drive this relationship.

Mammalian biodiversity, then, shows complex geographic and phylogenetic patterns of richness, recent diversification, and character variation. The African diversity peak is old and

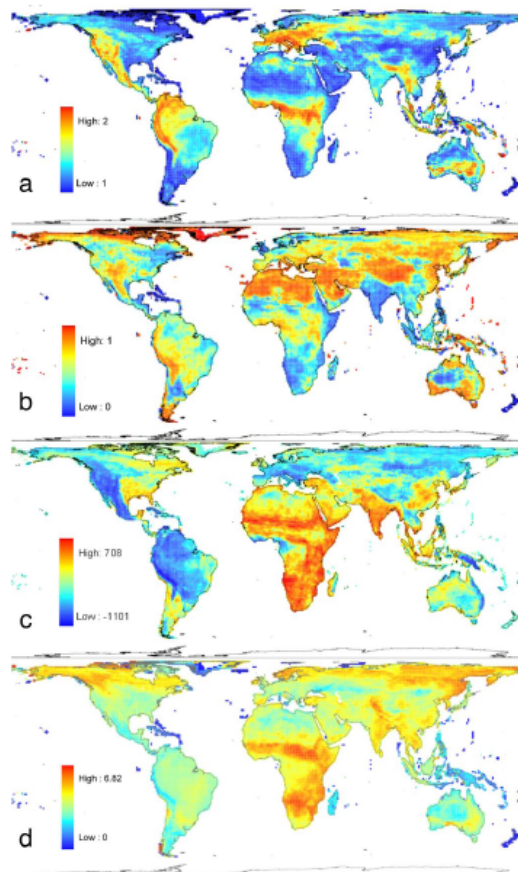


Fig. 2. Maps showing four aspects of mammalian diversification and diversity. (a) Mean numbers of species per genus within cells. (b) Proportion of species with shorter terminal branch lengths than the overall median (phylogeny from ref. 11, with branch lengths corrected and modified as explained in the previous page). (c) Residuals from a loess regression of cell total evolutionary history against cell species number (phylogeny as above). (d) Variance in log(body mass) (unpublished data), with missing data inferred as the mean of all closest relatives with data.

disparate, that in Asia is young and disparate, and the Andean peak is young with low disparity. These patterns reflect a complex history of speciation, extinction, anagenesis, and dispersal, with each factor probably shaped by biological traits and both biotic and abiotic environmental features in ways that have changed through time. Environmental features could provide much of the missing explanation for phylogenetic asymmetry (31), whereas traits may help to complete the explanation of geographic patterns. Other, less well known taxa doubtless have different patterns, but there is no particular reason to expect the patterns to be any simpler.

Natural diversity patterns increasingly bear the stamp of widespread anthropogenic system change. The biota we see today is already affected by anthropogenic extinction. Large, slowly reproducing mammals went extinct almost everywhere (with the notable exception of Africa, perhaps linking to the

patterns in Fig. 2 c and d) $\approx 7,000$ to 50,000 years ago (32). In the past few centuries, mammalian extinctions have mostly been on islands, notably the West Indies, with continental extinctions largely confined to Australia (9). Our analyses are therefore of an already reduced fauna. The next section considers the main ways in which human actions continue to reduce and reshape mammalian biodiversity.

Threats Facing Mammalian Biodiversity

The terrestrial environment is now dominated by people—1/4 to 1/3 of the land area has been transformed for human use (33). Additionally, human population density tends to be higher in species-rich areas, probably because productivity shapes both (34). Only a few mammal species fare well in human-dominated environments; the vast majority are vulnerable to the widespread and rapid anthropogenic changes. The main direct human-induced drivers that impact biodiversity now are habitat loss and fragmentation (the most important present threat), alien invasive species, overutilization, disease, pollution, and climate change (9). The International Union for Conservation of Nature (IUCN) assessed how these drivers are affecting mammals. Nearly all mammal species have been evaluated and, provided enough information was available, placed in one of the following extinction risk categories: least concern (LC), near-threatened (NT), vulnerable (VU), endangered (EN), critically endangered (CR), extinct in the wild (EW), and extinct (EX). The resulting IUCN Red List (35) lists 74 mammal species as having gone extinct in their native range since 1500 A.D., 1,094 (22.5% of those evaluated) as being threatened (i.e., VU, EN, or CR), and only 2,652 (54.5%) as giving no cause for concern (i.e., as being LC).

Does extinction risk show any patterns that might help us to understand the processes affecting biodiversity loss? The “field of bullets” scenario, in which extinction strikes completely at random, is a widely used null model for extinction (36, 37). The metaphor comes from trench warfare, where soldiers’ survival may have depended more on luck than skill. This scenario predicts that threatened species should constitute a stochastically constant fraction of any sample. Mammalian extinction risk is not a simple field of bullets but shows both geographic and phylogenetic patterns (9, 38, 39). The prevalence of risk is higher in the Old World than in the New World and higher on islands than on continents (9, 38). It varies among clades too, being higher than average in primates and perissodactyls and lower than average in rodents (9). Species with few close relatives are also more likely to be at risk (39, 40).

These patterns reject the original field of bullets model, but the model lacks a geographic dimension because there may have been fields that were near to the battle but that nevertheless had no bullets. Likewise, human pressures have changed some places beyond recognition but left others almost untouched. Because closely related species often live in the same region, geographic heterogeneity in threat intensity could, by itself, cause taxonomic selectivity in extinction risk (39). Alternatively, the selectivity could arise because biological differences among clades affect species’ abilities to withstand threats (41). How important for species’ survival is staying out of the firing line, and how important is being bullet proof?

Human population density predicts proportions of threatened mammal species among continental countries (42), supporting the “firing-line” model. However, an analysis of extinction risk within terrestrial World Wildlife Fund (WWF) ecoregions shows that phylogenetic nonrandomness is common within single ecoregions, where pressures may be more even than across the globe. Within each ecoregion, we generated phylogenetically independent contrasts (essentially, differences between sister clades) (43) in extinction risk (0 for LC species, 1 for species having a higher status; data-deficient and unevaluated species were excluded) on the phylogeny (with polytomies resolved

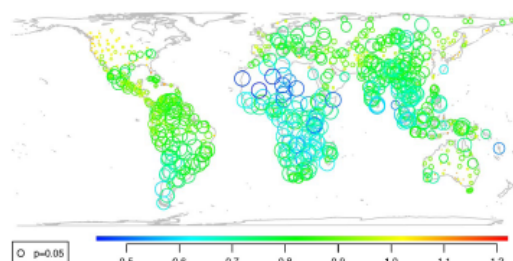


Fig. 3. Strength and significance of clumping in extinction risk within WWF ecoregions. Scale bar below the map indicates clumping strength. A value of 1 indicates randomness, and clumping is stronger for lower values. Circle size indicates the p value (radius is proportional to $-\ln(p)$); circle size for $P = 0.05$ is shown at the lower left.

arbitrarily and branch lengths set to unity) and compared the sum of the absolute values of standardized contrasts with the sums obtained from 1,000 randomizations of the risk data among the ecoregion's species. If high-risk species are strongly clumped in the phylogeny, the observed sum will be lower than in 95% of the simulations. Of 691 ecoregions with at least three higher-risk species and some variance in extinction risk, 386 (54%) showed significant clumping. Interestingly, the strength (rather than the significance) of the clumping is high in most realms apart from the Nearctic (Fig. 3). It also appears to be stronger in ecoregions with high disparity (Spearman's $\rho = 0.316$) and with relatively old diversity (Spearman's $\rho = 0.195$). These correlations should not be taken as evidence of a functional syndrome unless confirmed at more local scales: Some of the signal probably derives from differences among, rather than within, major biogeographic realms. The prevalence of clumping of risk implies that, faced with approximately equal pressures, species differ in their ability to persist because of lineage-specific characteristics. This finding invites a search for biological correlates of extinction risk.

Comparative Analyses of Mammalian Extinction Risk

Perhaps the most obvious proposed risk factor for extinction is large body size. The end-Pleistocene mass extinction of mammals removed mostly large species (32), and declining mammals are an order of magnitude heavier, on average, than are non-threatened species (44). There are several possible reasons: Large-bodied species are more tempting targets than small ones for hunters; they are, on average, less abundant; and they take longer to reach sexual maturity, have smaller litters of larger offspring, and have larger individual home ranges. Narrow ecological tolerances are also a plausible risk factor—habitat specialists may be more at risk than generalists from habitat loss (45). A small geographic range size may reflect narrow tolerances and increase the risk that the whole of the species' range is in the firing line. Which of these features matter most for extinction risk, and are any associations consistent across all mammals?

Cardillo *et al.* (44) carried out the most comprehensive investigation to date. Threatened species were included only if they were on the IUCN Red List because of observed decline, to avoid autocorrelation with predictor variables. Red List status, on a 0–5 scale, was used as the response variable. Many facets of geography (including human population density), ecology, and life history were tested as predictors of extinction risk, by using phylogenetically independent contrasts. A phylogenetic approach is needed because, although extinction risk and some of the possible predictors listed above (e.g., geographic range

size) do not evolve along the phylogeny's branches like, say, body size does, they nonetheless tend to show phylogenetic signal [i.e., they tend to take more similar values in close relatives than in species chosen at random; (41, 45, 46)]. Minimum adequate models were derived from a large initial set of predictors. This approach helps exclude variables that correlate only indirectly with extinction risk, for example, because another variable shapes both them and risk.

The predictors of risk were significantly different for smaller and larger species, with the importance of many predictors changing markedly at a body size of ≈ 3 kg. Species smaller than this fit the firing-line model: They are more likely to be threatened if they have small geographic ranges, live in temperate areas, face high human population densities, and live where a high proportion of the other mammal species are also threatened. Larger species, however, face multiple jeopardy: Biology matters as well as geography, with high abundance, small neonates, and many litters per year all independently helping to bullet-proof species. High abundance is predicted to bullet-proof species if the field of bullets model operates at the level of individuals rather than species (47), but such a model also predicts that no other biological traits would independently predict risk.

For both large and small mammals, the most important single risk factor is small geographic range size. The firing-line model predicts that small-ranged species will be most at risk because a single localized threat can impact their entire distribution. However, range size itself varies systematically among clades [although it shows weaker phylogenetic signal than, e.g., body size (48, 49)], suggesting that it is shaped, at least in part, by organismal traits such as dispersal ability (50) or niche breadth as well as by circumstances of geography. For example, small-ranged species are more common at low latitudes and within climatically stable regions. Any traits, including geographic location, that confer large species ranges also help make species bullet-proof (although geographical variation in species' range sizes again complicates separation of geographical variability in threat intensity from intrinsic biological vulnerability).

Large-scale analyses can find general predictors of extinction risk but can miss interesting variation among regions or clades, which more narrowly focused models might pick up (45). Order-specific models typically have higher explanatory power than the large-scale models. These models have some common features, such as the importance of geographic range size, but also differ considerably (51). For example, body size is a predictor in bats but not in rodents, whereas different life history traits predict risk in carnivores (gestation length) and ungulates (weaning age, interlitter interval). Likewise, different environmental factors and measures of human impact are implicated in different taxa. The models also vary regionally, with life history mattering less in North temperate regions than elsewhere (51).

One likely source of variation in models is that different drivers may select against different characteristics and show spatial variation in intensity. Broad-scale analyses may therefore lump competing signals together (52). Within artiodactyls, predictors of extinction risk differ between hunted and nonhunted species: Late weaning age was the sole risk factor among the former, whereas low income levels among local people and small range size predicted risk among the latter (53). More generally, low reproductive rates and large size are likely risk factors for overexploitation, but a specialized habitat may matter more under habitat loss (52). Analyses focused more tightly on driver-specific responses often tend to consider far fewer species, in which case far fewer predictor variables can be considered simultaneously without overfitting, and statistical power may be lower. On the plus side, the tighter focus can reduce the chance of mixed signals [although interaction terms can also do this (51)], and more precise measures of driver intensity and extinc-

tion risk might be available than can be had globally (54, 55). Broad- and narrow-scale analyses each give part of an obviously very complex picture. Furthermore, we have focused on phylogenetic nonindependence, but to fully consider the interaction between biology and geography, the development of methods that also deal with spatial nonindependence in comparative data will be critical.

Analyses modeling risk as a function of intrinsic biology (i.e., not including driver information) can highlight species at lower risk than expected from their geography, ecology, and life history (56). Such species may be particularly likely to decline rapidly if drivers intensify, because their attributes are repeatedly found in rapidly declining taxa. Cardillo *et al.* (56) termed this “latent risk” and proposed 20 regions with largely intact, but intrinsically susceptible, mammalian faunas. These include the Nearctic boreal forests and the island arc of Southeast Asia, and are mostly not exceptionally high in numbers of total, endemic, or threatened species. Many have much less than 10% of their land within reserves, and some (especially in southeast Asia) face very rapid human population growth. As such, latent-risk hotspots might represent cost-effective options for long-term conservation. However, these analyses do not yet consider realistic scenarios of future driver patterns; rather, they implicitly assume that places with low intensity will experience an increase to more typical levels (56). The next section discusses how more policy-relevant predictions could be obtained by projecting future driver patterns based on explicit scenarios.

Modeling Future Declines

Predicting future declines is more complex than explaining present declines, because the future is not just a linear extrapolation from the past and present. Past extinctions were largely caused by invasive species and overexploitation; habitat alteration is now a more important driver (9). Changes in land use have been mapped historically (www.mnp.nl/hyde) and are tracked in the present day (<http://glcf.umd.edu/data>), but analogous spatial data for other main drivers are more problematic. Wild species might be most vulnerable to overexploitation where people live at high density and have few other protein sources, suggesting that predictive models can be developed at regional scales (57, 58). The patterns and driving processes behind invasive species have varied over time (59), and, although there are clear associations with global movements from human migration and trade, identifying clear predictive methods for the intensity of invasives is a work in progress (60). The same is true for disease (61).

Given the difficulties in obtaining spatial data on the present intensity of direct drivers, let alone future projections, an alternative is to work with information on indirect drivers—in particular, human population density and growth and patterns of land conversion. Projections of these drivers are available under a range of socioeconomic scenarios (62). Intensity data alone are not enough, however; the response curves linking intensity to decline are also needed, and responses will depend on how bullet-proof the biota is. Thus, declines need to be modeled as a function of both driver intensity and relevant biological attributes. A first step (63) considered a single driver (human population density) under a single growth scenario, coupling explanatory models of carnivore extinction risk from comparative analyses with human population projections to identify species whose conservation status was likely to worsen.

Here, we enlarge this approach in a preliminary analysis of two drivers and all mammals. Across ecoregions, the proportion of species with risk status higher than LC was modeled (as a binomial denominator) as a function of two drivers and two summaries of biological vulnerability by using generalized additive models (64) to avoid forcing any particular form on the relationship. A smooth relationship was fitted to link risk level

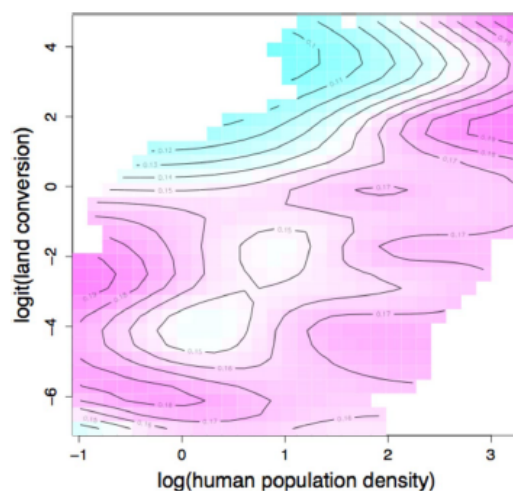


Fig. 4. The surface relating extinction-risk prevalence to urban and agricultural land use and human population density (HPD), controlling for two indices of biological susceptibility, among ecoregions. White regions in the upper left and lower right corners contain no ecoregions. Blue, low risk; purple, high risk.

to mean human population density (65) and the proportion of land converted to urban or cropland (66, 67). A second smooth relationship was fitted to control for two biotic variables [proportion of species weighing >3 kg, the size at which ecology and life history begin to influence risk strongly (44), and the proportion of species in the lowest quartile of global range size (K.E.J., J.B., A.P., C.D.L.O., Susanne A. Fritz, Christina Connolly, Amber Teacher, J.L.G., R.G., Elizabeth Boakes, Michael Habib, Janna Rist, Chris Carbone, Christopher A. Plaster, O.R.P.B.-E., Janine K. Foster, Elisabeth A. Rigby, Michael J. Cutts, Samantha A. Price, Wes Sechrest, Justin O'Dell, Kamran Safi, M.C., and G.M.M., unpublished data)]. Fig. 4 shows the marginal effect of the drivers on extinction risk. The two drivers are strongly correlated across ecoregions and interact strongly. As expected, risk is low when both drivers are at the very lowest levels. However, risk rises rapidly as either driver increases. Medium levels of land conversion and low density are associated with high levels of risk, but risk falls as land conversion rises further. This suggests that land conversion is an extinction filter (68), removing one set of species sufficiently thoroughly that highly converted regions can again have low levels of risk, with only the more bullet-proof taxa remaining. Scenario analysis will obviously need to count projected extinctions as well as declines and may need to consider historical as well as present driver patterns. As human density reaches high levels, risk levels become uniformly higher.

A more refined model, perhaps incorporating other drivers, could be combined with projected future driver intensity to predict where a high proportion of species will decline. Such an approach uses the spatial heterogeneity in present driver intensity as a surrogate time series, with high-intensity ecoregions suggesting what will happen elsewhere as conditions deteriorate. However, incorporating climate change into this modeling approach presents major challenges. Because it has not been a major driver of present risk patterns, we have not yet seen how intensity will relate to impact and cannot use spatial heterogeneity as a guide. Bioclimatic envelope models suggest that

Table 1. Numbers of ecoregions jointly ranked in the top 50 (of a total of 791) by each pair of currencies, according to greedy complementarity searches

	Richness	EDGE	ELEH	Extinctions	Diversification	Latent risk	Evolutionary history
Richness	50	41	22	21	34	15	36
EDGE		50	26	22	33	17	39
ELEH			50	34	18	10	26
Extinctions				50	20	9	21
Diversification					50	16	30
Latent risk						50	16
Evolutionary history							50

climate change is already affecting many species including mammals (69) and may soon be the dominant driver, possibly exacerbated by interactions with invasive species and other threats (70). Climate change is likely to particularly impact species that face geographical or biological barriers to dispersal or that depend on environmental cues that may break down as climate changes (71).

Setting Priorities Among Areas

Conservation spending is not nearly enough to maintain even the current inadequate network of reserves and protected areas (72). The identification and prioritization of global conservation networks are a major focus of conservation dollars (73). However, rankings inherently depend on the currency used to evaluate regions. A simple demonstration can be provided by ranking ecoregions, in this case by applying a greedy complementarity algorithm, to maximize the capture of seven possible currencies for mammalian conservation: species richness; total numbers of species extinctions predicted in the next 100 years from current Red List status (using the probabilities of extinction in ref. 74); two measures combining evolutionary uniqueness and present extinction risk [EDGE (75) and ELEH (74), both summed across species in the ecoregion]; evolutionary dynamism (indexed as the sum of the reciprocal of the terminal branch lengths of species in the ecoregion); evolutionary history (estimated as the total branch length in the phylogeny of the ecoregion's species, adjusted for polytomies as described above); and total latent risk (56). Species-rich areas are likely to sum to higher values and, hence, rank highly across all currencies. Nonetheless, Table 1 shows that rank order differs considerably even for similar measures designed to optimize the same currency (e.g., EDGE and ELEH). The biggest difference is between latent risk and numbers of extinctions. This is perhaps unsurprising, because latent risk gives high weights to species that are less threatened (although not all species were weighted for latent risk, weakening the comparison). A greedy algorithm makes choices based on maximizing the immediate gain in currency at each step and so may give globally suboptimal complementarity networks (76). In addition, ecoregions are, in any case, larger than most current conservation-management units (20). Our aim here is simply to show that surrogacy among currencies may be low. Furthermore, other more subjective or hard-to-quantify criteria might also be considered important—for example, the ecological function of a species or lineage, its cultural significance, or its charismatic appeal to humans (77)—further impeding comparisons between areas with similar numbers of species.

Even if a currency can be agreed upon, a reserve network optimized for one clade is likely to be suboptimal for another (20). It is often tempting to use a single group as a surrogate for biodiversity as a whole, but other clades are likely to have very different—and equally complex—patterns of diversity and extinction risk. The lack of strong surrogacy among groups intro-

duces extra uncertainty into the measured biodiversity value of the regions being considered. In addition, we have focused on conservation benefits rather than costs, but costs vary spatially by several orders of magnitude (72, 78). Cost-benefit models can suggest very different priorities from allocations based solely on perceived biodiversity value (79). So, if we assume that rational decision making must consider both benefits and costs, perhaps the most sensible investment would be in intact but susceptible regions (56, 78). Public health-care systems may provide a useful analogy: A balanced health-care strategy includes money for preventative medicine as well as for hospital wards and life support.

Beyond the Declines: The Evolutionary Future?

The primary goal for most conservation management has been to maximize preservation of current diversity. However, by altering the environment, humans also influence future evolution (80). A previous National Academy of Sciences Colloquium (81, 82) raised an important question: Should conservation goals be extended to consider the evolutionary future? A range of time scales might be considered. In the short term, species-recovery plans can address the requirements needed for continued adaptive evolution within populations (83). But what of the longer term? We can identify clades that have recently diversified and the regions in which they are found (Fig. 2*b*). These lineages or areas might represent engines of speciation: Are they therefore conservation priorities? The distinction between maximizing evolutionary history versus centers of diversification is non-trivial. A network of reserves designed to capture maximal evolutionary history would look very different from one designed to capture rapidly speciating lineages (Table 1), because rapid diversification results in low phylogenetic diversity per species (27, 84). However, past “success” may be a poor indicator of future performance because of the contingent nature of evolution (84, 85). The geographic pattern of mammalian diversification rates has changed markedly through time (Fig. 2*a–c*), and different lineages have also radiated at different times (11, 86).

One secure prediction is that future environmental conditions will almost certainly differ from those in the past. Nonetheless, extrapolating current trends, key environmental changes are likely to include increasing habitat loss and fragmentation, drastic shifts in species abundances and distributions, and climate change (see above) (81, 87). Changes in the biotic and abiotic composition of the environment (including extinctions) may restructure niche space and moderate constraints on diversification imposed by niche saturation. Major turnovers in species composition may therefore be expected (88). Unfortunately, we lack detailed information on the past states of these attributes in geological history and so cannot easily construct quantitative empirical models that can be projected forward. Predicting the evolutionary future is hampered by large uncertainty about the magnitude and form of environmental change

and by lineage-specific responses. If we wished to safeguard the evolutionary future, a sensible strategy would be to maintain a set of species that is overdispersed with respect to their ecological adaptations and (as a simple proxy) their phylogeny, maximizing the possibility of having the right set of features in an uncertain future (89).

Returning to our original question, should conservation goals consider the long-term evolutionary future? We sound two notes of caution. First, although we have restricted our focus to mammals, they are only a tiny branch on the Tree of Life, and many of the major limbs, from ciliates to *Chlamydia*, may be better insulated from anthropogenic disturbances (10). The evolutionary future of life on Earth is therefore unlikely to be in serious jeopardy. Second, anthropogenic environmental change and extinctions are occurring on the order of tens to hundreds

of years, but times to speciation are frequently estimated in thousands to millions of years (87), and recovery times after previous mass extinction events were perhaps 5–10 million years (12). These time scales are too great for practical management. Diversity will almost certainly rebound after the current extinction event; however, it may be composed of species descended from a different, as yet unknown, subset of lineages from those that dominate now, and humans will likely not be included among them. Practical conservation should retain its focus on minimizing declines and extinctions in the present day.

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- Harvey PH, Leigh Brown AJ, Maynard Smith J, Nee S (1996) *New Uses For New Phylogenies* (Oxford Univ Press, Oxford).
- Bininda-Emonds ORP (2004) The evolution of supertrees. *Trends Ecol Evol* 19:316–322.
- Cracraft J, Donoghue MJ (2004) *Assembling the Tree of Life* (Oxford Univ Press, Oxford).
- Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Biodiversity Synthesis* (World Resources Institute, Washington DC).
- Jablonski D (1994) Extinctions in the fossil record. *Phil Trans R Soc London Ser B* 344:11–16.
- Purvis A, Hector A (2000) Getting the measure of biodiversity. *Nature* 405:212–219.
- Mace GM, et al. (2005) In *The Millennium Ecosystem Assessment: Current Status and Trends: Findings of the Conditions and Trends Working Group*. Ecosystems and Human Well-Being (Island, Washington DC), pp 53–96.
- Wilson DE, Reeder DM (2005) *Mammal Species of the World: A Taxonomic and Geographic Reference* (The Johns Hopkins Univ Press, Baltimore), Third Ed.
- Baillie JEM, Hilton-Taylor C, Stuart SN (2004) *A Global Species Assessment* (International Union for Conservation of Nature, Gland, Switzerland).
- Nee S (2005) In *Phylogeny and Conservation*, eds Purvis A, Gittleman JL, Brooks T (Cambridge Univ Press, Cambridge), pp 387–399.
- Bininda-Emonds ORP, et al. (2007) The delayed rise of present-day mammals. *Nature* 446:507–512.
- Erwin DH (2001) Lessons from the past: Biotic recoveries from mass extinctions. *Proc Natl Acad Sci USA* 98:5399–5403.
- Avise JC (2008) Three ambitious (and rather unorthodox) assignments for the field of biodiversity genetics. *Proc Natl Acad Sci USA* 105(Suppl):11564–11570.
- Purvis A, Katourakis A, Agapow P-M (2002) Evaluating phylogenetic tree shape: Two modifications to Fusco and Cronk's method. *J Theor Biol* 214:99–103.
- Moore AD, Heard SB (1997) Inferring evolutionary process from phylogenetic tree shape. *Q Rev Biol* 72:31–54.
- Purvis A (1996) In *New Uses for New Phylogenies*, eds Harvey PH, Leigh Brown AJ, Maynard Smith J, Nee S (Oxford Univ Press, Oxford), pp 153–168.
- Isaac NJB, Jones KE, Gittleman JL, Purvis A (2005) Correlates of species richness in mammals: Body size, life-history and ecology. *Am Nat* 165:600–607.
- Coyne JA, Orr HA (2004) *Speciation* (Sinauer, Sunderland MA).
- Kerr JT, Packer L (1997) Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature* 385:252–254.
- Grenyer R, et al. (2006) Global distribution and conservation of rare and threatened vertebrates. *Nature* 444:93–96.
- Hawkins BA, et al. (2003) Energy, water and broad-scale geographic patterns of species richness. *Ecology* 84:3105–3117.
- Buckley LB, Jetz W (2007) Environmental and historical constraints on global patterns of amphibian richness. *Proc R Soc London Ser B* 274:1167–1173.
- Orme CDL, et al. (2006) Global patterns of geographic range size in birds. *PLoS Biol* 4:1276–1283.
- Stebbins GL (1974) *Flowering Plants: Evolution Above the Species Level* (A Edwards Arnold, London).
- Pulquerio MJF, Nichols RA (2007) Dates from the molecular clock: How wrong can we be? *Trends Ecol Evol* 22:180–184.
- Clifford P, Richardson S, Hémon D (1989) Assessing the significance of the correlation between two spatial processes. *Biometrics* 45:123–134.
- Roy K, Goldberg EE (2007) Origin, extinction, and dispersal: Integrative models for understanding present-day diversity gradients. *Am Nat* 170:571–585.
- Moore AD, Atkins RA (2003) Indonesia's threatened birds: Over 500 million years of evolutionary heritage at risk. *Anim Cons* 7:183–188.
- Nee S (2006) Birth–death models in macroevolution. *Ann Rev Ecol Syst* 37:1–17.
- Weir JT, Schluter D (2007) The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* 315:1574–1576.
- Ricklefs RE (2003) Global diversification rates of passerine birds. *Proc R Soc London Ser B* 270:2285–2292.
- Barnosky AD (2008) Megafauna biomass tradeoff as a driver of Quaternary and future extinctions. *Proc Natl Acad Sci USA* 105(Suppl):11543–11548.
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. *Science* 277:494–499.
- Luck GW (2007) A review of the relationships between human population density and biodiversity. *Biol Rev* 82:607–645.
- Union for Conservation of Nature (2007) *2007 IUCN Red List of Threatened Species*. (Union for Conservation of Nature, Gland, Switzerland).
- Van Valen L (1976) The Red Queen lives. *Nature* 260:575.
- Raup DM, Gould SJ, Schopf TJM, Simberloff DS (1973) Stochastic models of phylogeny and the evolution of diversity. *J Geol* 81:525–542.
- Mace GM, Balmford A (2000) In *Future Priorities for the Conservation of Mammalian Diversity*, eds Entwistle A, Dunstone N (Cambridge Univ Press, Cambridge), pp 27–52.
- Russell GJ, Brooks TM, McKinney MM, Anderson CG (1998) Present and future taxonomic selectivity in bird and mammal extinctions. *Cons Biol* 12:1365–1376.
- Purvis A, Agapow P-M, Gittleman JL, Mace GM (2000) Nonrandom extinction risk and the loss of evolutionary history. *Science* 288:328–330.
- McKinney ML (1997) Extinction vulnerability and selectivity: Combining ecological and paleontological views. *Ann Rev Ecol Syst* 28:495–516.
- McKinney ML (2001) Role of human population size in raising bird and mammal threat among nations. *Anim Cons* 4:45–57.
- Harvey PH, Pagel MD (1991) *The Comparative Method in Evolutionary Biology* (Oxford Univ Press, Oxford).
- Cardillo M, et al. (2005) Multiple causes of high extinction risk in large mammal species. *Science* 309:1239–1241.
- Fisher DO, Owens IPF (2004) The comparative method in conservation biology. *Trends Ecol Evol* 19:391–398.
- Purvis A, Jones KE, Mace GM (2000) Extinction. *BioEssays* 22:1123–1133.
- Erwin DH (2006) *Extinction: How Life Nearly Died 250 Million Years Ago* (Princeton Univ Press, Princeton).
- Jones KE, Sechrist W, Gittleman JL (2005) In *Phylogeny and Conservation*, eds Purvis A, Gittleman JL, Brooks TM (Cambridge Univ Press, Cambridge), pp 141–165.
- Gaston KJ (2003) *The Structure and Dynamics of Geographic Ranges* (Oxford Univ Press, Oxford).
- Böhning-Gaese K, Caprano T, van Ewijk K, Velth M (2006) Range size: Disentangling current traits and phylogenetic and biogeographic factors. *Am Nat* 167:555–567.
- Cardillo M, et al. (2008) The predictability of extinction: Biological and external correlates of decline in mammals. *Proc R Soc London Ser B* 275:1441–1448.
- Owens IPF, Bennett PM (2000) Ecological basis of extinction risk in birds: Habitat loss versus human persecution and introduced predators. *Proc Natl Acad Sci USA* 97:12144–12148.
- Price SA, Gittleman JL (2007) Hunting to extinction: Biology and regional economy influence extinction risk and the impact of hunting in artiodactyls. *Proc R Soc London Ser B* 274:1045–1051.
- Isaac NJB, Cowlishaw G (2004) How species respond to multiple extinction threats. *Proc R Soc London Ser B* 271:1135–1141.
- Fisher DO, Blomberg SP, Owens IPF (2003) Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. *Proc R Soc London Ser B* 270:1801–1808.
- Cardillo M, Mace GM, Gittleman JL, Purvis A (2006) Latent risk and the future battle-grounds of mammal conservation. *Proc Natl Acad Sci USA* 103:4157–4161.
- Fa JE, Currie D, Meeuwij J (2003) Bushmeat and food security in the Congo Basin: Linkages between wildlife and people's future. *Env Cons* 30:71–78.
- Ling S, Milner-Gulland EJ (2006) Assessment of the sustainability of bushmeat hunting based on dynamic bioeconomic models. *Cons Biol* 20:1294–1299.
- Mack RN, Lonsdale WM (2001) Humans as global plant dispersers: Getting more than we bargained for. *BioScience* 51:95–102.
- Hastings A, et al. (2005) The spatial spread of invasions: New developments in theory and evidence. *Ecol Lett* 8:91–101.
- Pedersen AB, Jones KE, Nunn CL, Altizer S (2007) Infectious diseases and extinction risk in wild mammals. *Cons Biol* 21:1269–1279.
- Millennium Ecosystem Assessment (2005) *Synthesis* (World Resources Institute, Washington DC).
- Cardillo M, et al. (2004) Human population density and extinction risk in the world's carnivores. *PLoS Biol* 2:909–914.
- Wood SN (2006) *Generalized Additive Models: An Introduction with R* (Chapman & Hall/CRC, Boca Raton, FL).

65. Center for International Earth Science Information Network (CIESIN), Centro Internacional de Agricultura Tropical (CIAT) (2005) *Gridded Population of the World Version 3 (GPWv3)* [Socioeconomic Data and Applications Center (SEDAC), (Columbia Univ, Palisades, NY)].
66. Center for International Earth Science Information Network (CIESIN), International Food Policy Research Institute (IFPRI), The World Bank, Centro Internacional de Agricultura Tropical (CIAT) (2004) *Global Rural-Urban Mapping Project (GRUMP), Alpha Version: Urban Extents* [Socioeconomic Data and Applications Center (SEDAC) (Columbia Univ, Palisades, NY)].
67. European Commission, Joint Research Centre (2003) *Global Land Cover 2000 Database* (European Commission, Joint Research Centre).
68. Balmford A (1996) Extinction filters and current resilience: the significance of past selection pressures for conservation biology. *Trends Ecol Evol* 11:193–196.
69. Parmesan C, Yoha G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
70. Thuiller W (2007) Biodiversity—Climate change and the ecologist. *Nature* 448:550–552.
71. Bradshaw WE, Holzapfel CM (2006) Evolutionary response to rapid climate change. *Science* 312:1477–1478.
72. James A, Gaston KJ, Balmford A (2001) Can we afford to conserve biodiversity? *BioScience* 51:43–52.
73. Halpern BS, et al. (2006) Gaps and mismatches between global conservation priorities and spending. *Cons Biol* 20:56–64.
74. Redding DW, Mooers AO (2006) Incorporating evolutionary measures into conservation prioritization. *Cons Biol* 20:1670–1678.
75. Isaac NJB, Turvey ST, Collen B, Waterman C, Baillie JEM (2007) Mammals on the EDGE: Conservation priorities based on threat and phylogeny. *PLoS One* 2:e296.
76. Pressey RL, Possingham HP, Margules CR (1996) Optimality in reserve selection algorithms: When does it matter and how much? *Biol Cons* 76:259–267.
77. Avise JC (2005) In *Phylogeny and Conservation*, eds Purvis A, Gittleman JL, Brooks TM (Cambridge Univ Press, Cambridge), pp 76–100.
78. Balmford A, Gaston KJ, Blyth S, James A, Kapos V (2003) Global variation in terrestrial conservation costs, conservation benefits, and unmet conservation needs. *Proc Natl Acad Sci USA* 100:1046–1050.
79. Possingham HP, et al. (2002) Limits to the use of threatened species lists. *Trends Ecol Evol* 17:503–507.
80. Smith TB, Bernatchez L (2008) Evolutionary change in human-altered environments. *Mol Ecol* 17:1–8.
81. Myers N, Knoll AH (2001) The biotic crisis and the future of evolution. *Proc Natl Acad Sci USA* 98:5389–5392.
82. Cowling RM, Pressey RL (2001) Rapid plant diversification: Planning for an evolutionary future. *Proc Natl Acad Sci USA* 98:5452–5457.
83. Mace GM, Purvis A (2008) Evolutionary biology and practical conservation: Bridging a widening gap. *Mol Ecol* 17:9–17.
84. Mace GM, Gittleman JL, Purvis A (2003) Preserving the Tree of Life. *Science* 300:1707–1709.
85. de Queiroz A (2002) Contingent predictability in evolution: Key traits and diversification. *Syst Biol* 56:917–929.
86. Alroy J (2000) New methods for quantifying macroevolutionary patterns and processes. *Paleobiology* 26:707–733.
87. Barraclough TG, Davies TJ (2005) In *Phylogeny and Conservation*, eds Purvis A, Gittleman JL, Brooks TM (Cambridge Univ Press, Cambridge), pp 400–418.
88. Tilman D, Lehman C (2001) Human-caused environmental change: Impacts on plant diversity and evolution. *Proc Natl Acad Sci USA* 98:5433–5440.
89. Crozier RH (1997) Preserving the information content of species: Genetic diversity, phylogeny and conservation worth. *Annu Rev Ecol Syst* 28:243–268.

Appendix B: R code to compute D

```
d.data <- function (ds, phy, bininds, tipsinds, permut=1000,
  verbose=FALSE) {

  if (verbose) (print("Computing phylogenetically random
    permutations..."))
  kseq <- seq(length(ds)+1, by=1, length.out=permut)
  for (k in kseq) {
    ds[,k] <- sample(ds[,bininds])
    names(ds)[k] <- paste("Var", k, sep="")
  }
  names(ds)[tipsinds] <- "tipnames"
  explvarsrn <- paste(paste("Var", kseq, sep=""),
    collapse="+")

  if (verbose) (print("Computing phylogenetically
    clumped permutations..."))
  lamtree <- lambdaTree(phy, 1)
  simmat <- matrix(rep(0,permut^2), nrow=permut,
    ncol=permut)
  for (i in 1:permut) (simmat[i,i] <- 1)
  simchar <- sim.char(lamtree, simmat)
  simds <- as.data.frame(simchar[1:length(ds[,1]),
    1:permut,1])
  simds$tipnames <- rownames(simds)
  simds$resp <- sample(simds[,1])
  propone <- length(which(ds[,bininds]==1)) /
    length(ds[,bininds])
  for (k in 1:permut) {
    tipvals <- simds[,k]
    names(tipvals) <- rownames(simds)
    tipvals <- sort(tipvals)
    ones <- names(tipvals)[(length(tipvals)-
      round(length(tipvals)*propone,
        0)+1):length(tipvals)]
    simds[which(is.element(rownames(simds), ones)),k]
      <- round(1,0)
    simds[which(!is.element(rownames(simds),
      ones)),k] <- round(0,0)
  }
  explvarssim <- paste(paste("V", c(1:permut), sep=""),
    collapse="+")

  return(list(ds.random=ds, formula.random=
    paste(names(ds)[bininds], "~", explvarsrn,
      sep=""), ds.brownian=simds,
    formula.brownian=paste("resp~", explvarssim,
      sep="")))
}
```

```

d.fit <- function(d.ds, phy, verbose=FALSE) {

  if (verbose) (print("Getting nodal value
    estimates..."))
  ran <- crunch(as.formula(d.ds[[2]]), d.ds[[1]], phy,
    names.col=tipnames, polytomy.brlen=0)
  brw <- crunch(as.formula(d.ds[[4]]), d.ds[[3]], phy,
    names.col=tipnames, polytomy.brlen=0)
  return(list(contr.random=ran, contr.brownian=brw,
    ds.random=d.ds$ds.random,
    ds.brownian=d.ds$ds.brownian))

}

sumofdifs <- function (caicobj, ds, tipnames) {

  tipnames <- deparse(substitute(tipnames))
  tipsinds <- match(tipnames, names(ds))
  if (is.na(tipsinds)) (stop("'", tipnames, "' is not a
    column name in ds."))

  edges <- as.data.frame(caicobj$phy$edge)
  edges$bl <- caicobj$phy$edge.length
  responsev <-
    attr(caicobj$contrast.data$contr$response,
      "dimnames")[[2]]
  variables <-
    attr(caicobj$contrast.data$contr$explanatory,
      "dimnames")[[2]]

  nvs <- caicobj$contrast.data$nodalVals$response[,1]
  edges$startnv <- nvs[match(edges[,1], names(nvs))]
  tips <- ds[match(caicobj$phy$tip.label,
    ds[,tipsinds]),which(names(ds)==responsev)]
  names(tips) <- c(1:length(tips))
  allnvs <- c(nvs, tips)
  allnvs <- allnvs[order(as.numeric(names(allnvs)))]
  edges$endnv <- allnvs[match(edges[,2], names(allnvs))]
  edges$change <- abs(edges$startnv-edges$endnv)
  rtvr <- sum(edges$change)
  names(rtvr) <- responsev

  rtv <- numeric(0)
  for (i in seq(along=variables)) {
    nvs <-
      caicobj$contrast.data$nodalVals$explanatory
      [,which(attr(caicobj$contrast.data$nodalVal
        s$explanatory, "dimnames")[[2]]
        ==variables[i])]
    edges$startnv <- nvs[match(edges[,1],
      names(nvs))]
  }
}

```

```

        tips <- ds[,which(names(ds)==variables[i])]
        [match(caicobj$phy$tip.label,
              ds[,tipsinds])]
      names(tips) <- c(1:length(tips))
      allnvs <- c(nvs, tips)
      allnvs <-
        allnvs[order(as.numeric(names(allnvs)))]
      edges$endnv <- allnvs[match(edges[,2],
                                names(allnvs))]
      edges$change <- abs(edges$startnv-edges$endnv)
      rtv <- append(rtv, sum(edges$change))
      names(rtv)[i] <- variables[i]
    }

    return(list(sumod.resp=rtvr, sumod.expl=rtv))
  }

d.compute <- function(d.fit.obj, verbose=FALSE) {

  if (verbose) (print("Computing output..."))
  ran <- sumofdiffs(d.fit.obj$contr.random,
                  d.fit.obj$ds.random, tipnames)
  brw <- sumofdiffs(d.fit.obj$contr.brownian,
                  d.fit.obj$ds.brownian, tipnames)
  d.est <- (as.numeric(ran$sumod.resp)-
            mean(brw$sumod.expl)) / (mean(ran$sumod.expl)-
            mean(brw$sumod.expl))
  d.pval.1 <- length(which(ran$sumod.expl
                          <as.numeric(ran$sumod.resp))) /
            length(ran$sumod.expl)
  d.pval.0 <- length(which(brw$sumod.expl
                          >as.numeric(ran$sumod.resp))) /
            length(brw$sumod.expl)
  ret <- list(DEstimate=d.est, Pval1=d.pval.1,
            Pval0=d.pval.0, Parameters=list(Observed=
            as.numeric(ran$sumod.resp),
            MeanRandom=mean(ran$sumod.expl),
            MeanBrownian=mean(brw$sumod.expl)),
            Permutations=list(random=ran$sumod.expl,
            brownian=brw$sumod.expl))
  if (verbose) (print(str(ret)))
  return(ret)
}

```

```
phylo.d <- function(ds, phy, binvar, tipnames, permut=1000,
  verbose=TRUE) {

  if (!is.data.frame(ds)) (stop("'",
    deparse(substitute(ds)), "' must be an object of
    class 'data.frame'.")
  if (!inherits(phy, "phylo")) (stop("'",
    deparse(substitute(phy)), "' is not of class
    'phylo'.")
  binvar <- deparse(substitute(binvar))
  bininds <- match(binvar, names(ds))
  if (is.na(bininds)) (stop("'", binvar, "' is not a
    column name in ds.")
  tipnames <- deparse(substitute(tipnames))
  tipsinds <- match(tipnames, names(ds))
  if (is.na(tipsinds)) (stop("'", tipnames, "' is not a
    column name in ds.")
  if (!is.numeric(permut)) (stop("'", permut, "' is not
    numeric.")

  myds <- d.data(ds=ds, phy=phy, bininds=bininds,
    tipsinds=tipsinds, permut=permut,
    verbose=verbose)
  myfit <- d.fit(d.ds=myds, phy=phy, verbose=verbose)
  myd <- d.compute(myfit, verbose=verbose)
  return(myd)
}
```

Appendix C: The composite phylogeny of mammalian, avian and anuran families



Fig. C-1. Overview of the composite phylogeny showing mammalian, avian and anuran families.

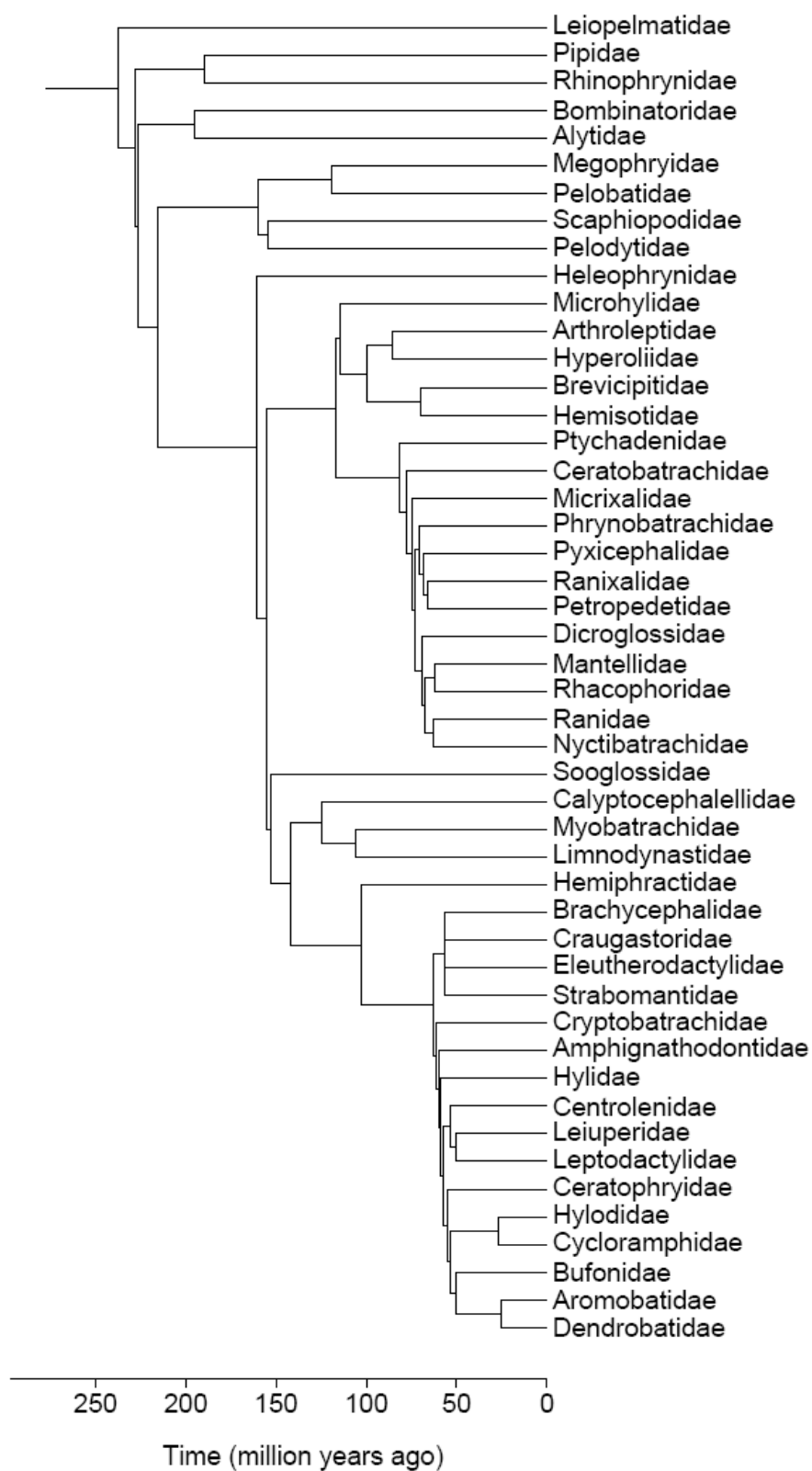


Fig. C-2. Phylogeny of anuran families.

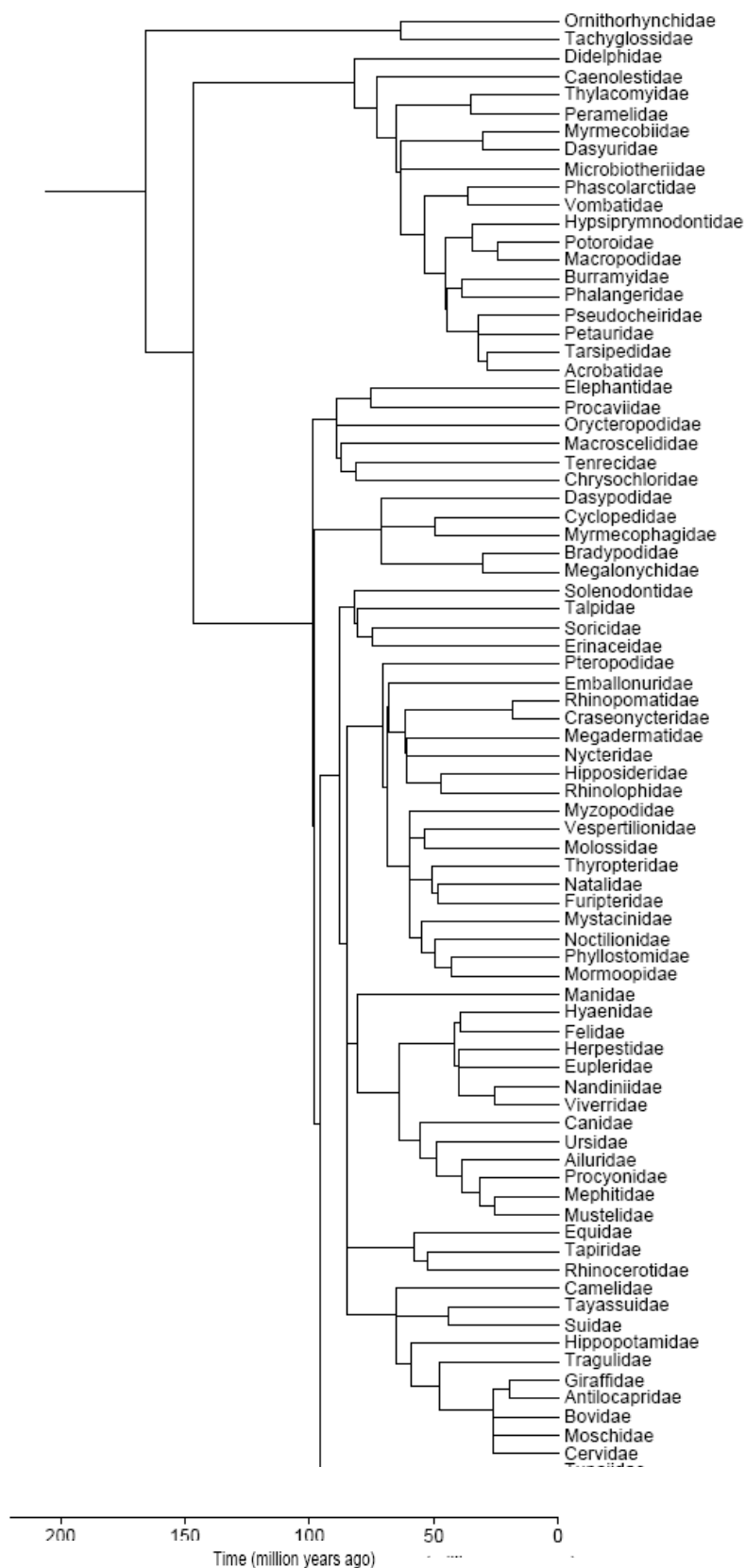


Figure C-3. Phylogeny of mammalian families (part 1 of 2).

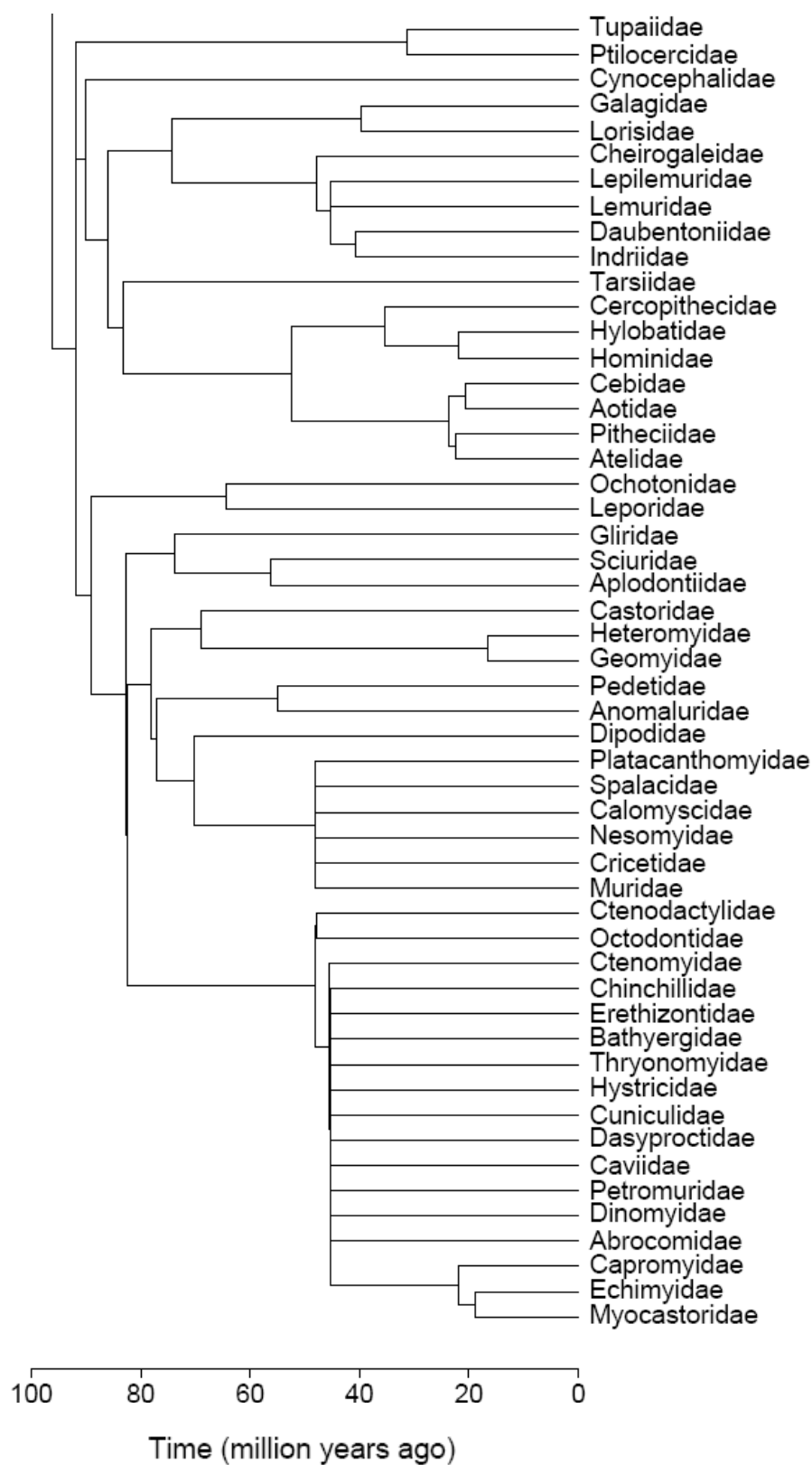


Figure C-4. Phylogeny of mammalian families (part 2 of 2).

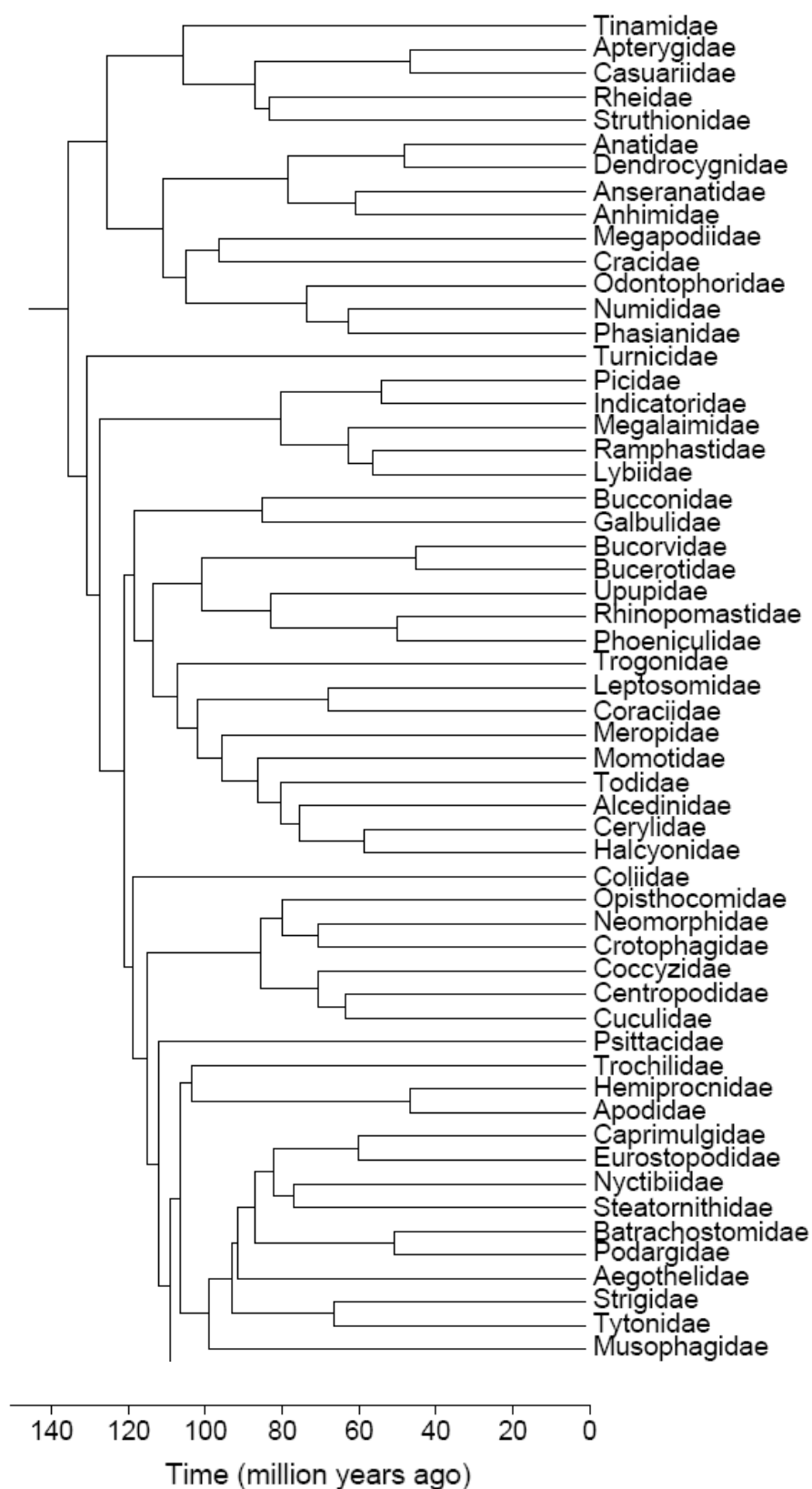


Figure C-5. Phylogeny of avian families (part 1 of 2).

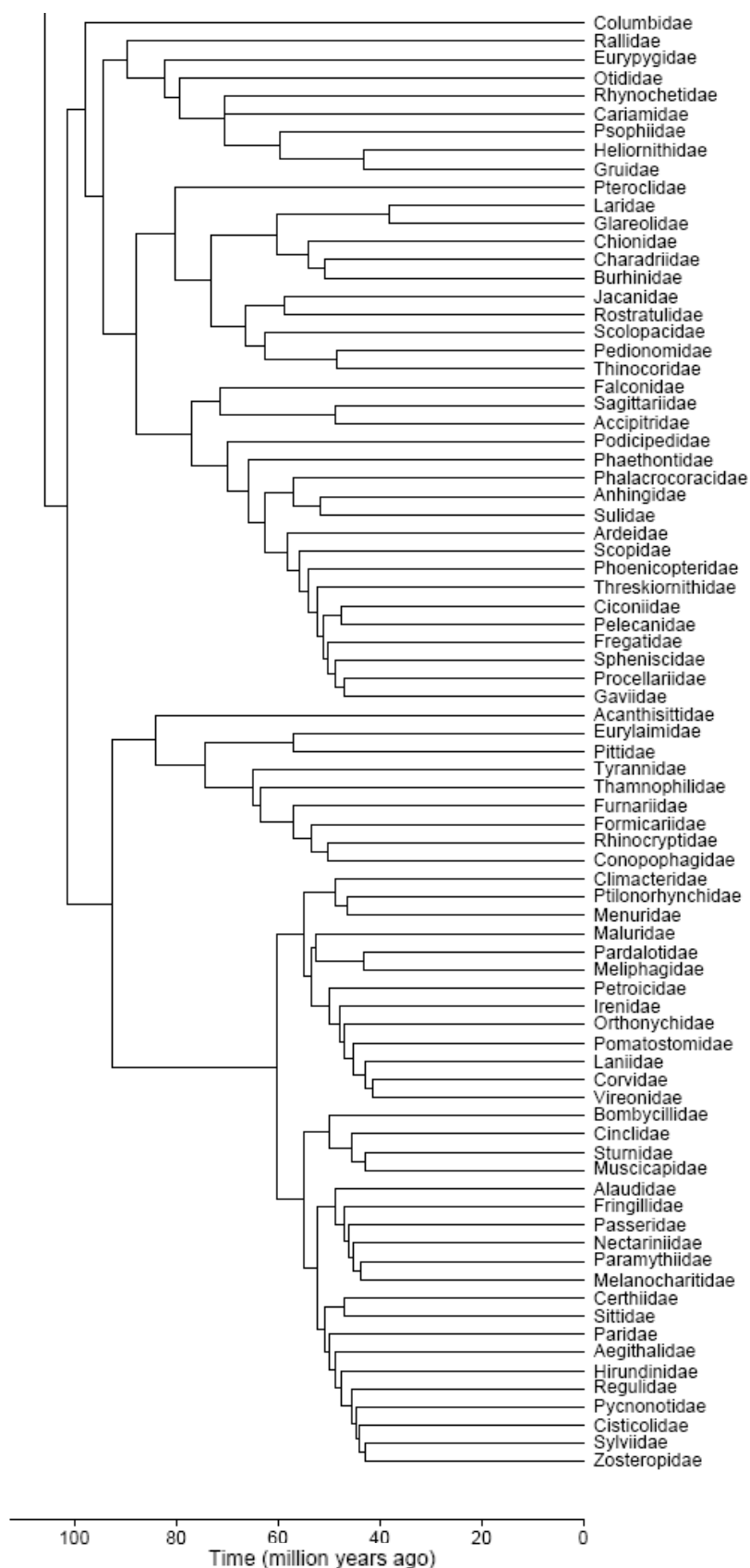


Figure C-6. Phylogeny of avian families (part 2 of 2).

Appendix D: References for the anuran dataset

- Amiet J.-L. (1991) Images d' Amphibiens camerounais. III. Le comportement de garde des oeufs. *Alytes* 9: 15-22
- AmphibiaWeb (2008) *Information on amphibian biology and conservation* [Online Database]. URL www.amphibiaweb.org, accessed Aug.-Dec. 2008
- Bagnara J. T., Iela L., Morrisett F., and Rastogi R. K. (1986) Reproduction in the Mexican leaf frog (*Pachymedusa dacnicolor*). I. Behavioral and morphological aspects. *The University of Kansas, Natural History Museum, Occasional Papers* 121: 1-31
- Block J. E., Unser S. L., Mooney J. K., and Wild E. R. (2003) *Agalychnis craspedopus*. Reproduction. *Herpetological Review* 34: 134-135
- Campbell J. A. and Duellman W. E. (2000) New species of stream-breeding hyliid frogs from the northern versant of the highlands of Oaxaca, Mexico. *The University of Kansas, Natural History Museum, Scientific Papers* 16: 1-28
- Cannatella D. C. (1984) Two new species of the leptodactylid frog genus *Phrynopis*, with comments on the phylogeny of the genus. *The University of Kansas, Natural History Museum, Occasional Papers* 113: 1-16
- Carruthers V. (2001) *Frogs and frogging in Southern Africa*. Struik Publishers, Cape Town, South Africa
- Channing A. (2001) *Amphibians of Central and Southern Africa*. Cornell University Press, Ithaca, USA
- Channing A. and Howell K. M. (2006) *Amphibians of East Africa*. Edition Chimaira, Frankfurt am Main, Germany
- Clarke B. T., and Lanza B. (1990) Notes on the morphology and distribution of the Corsican painted frogs: *Discoglossus sardus* and *D. montalentii*. *Museo Regionale di Scienze Naturali Bolletino* 8: 531-544
- Coloma L. A. (1995) Ecuadorian frogs of the genus *Colostethus* (Anura: Dendrobatidae). *The University of Kansas, Natural History Museum,*

Miscellaneous Publications 87: 1-72

- Cooper N., Bielby J., Thomas G. H., and Purvis A. (2008) Macroecology and extinction risk correlates of frogs. *Global Ecology and Biogeography* 17: 211-221
- Daniels R. J. R. (2005) *Amphibians of peninsular India*. Universities Press (India) Private Limited, Hyderabad, India
- De la Riva I. (1999) A new *Phyllomedusa* from southwestern Amazonia (Amphibia: Anura: Hylidae). *Revista Espanola Herpetologia* 13: 123-131
- Diaz N., Sallaberry M., and Nunez H. (1983) The tadpole of *Telmatobufo venustus* (Anura: Leptodactylidae) with a consideration of generic relationships. *Herpetologica* 39: 111-113
- Duellman W. E. (1970) *Hylid frogs of Middle America. Volumes I & II*. Monograph of the Museum of Natural History, the University of Kansas, Kansas City, USA
- Duellman W. E. and Maness S. J. (1980) The reproductive behaviour of some hylid marsupial frogs. *Journal of Herpetology* 14: 213-222
- Duellman W. E. and Burrowes P. A. (1986) A new species of marsupial frog (Hylidae: *Gastrotheca*) from the Andes of Southern Colombia. *The University of Kansas, Natural History Museum, Occasional Papers* 120: 1-11
- Duellman W. E. and Pramuk J. B. (1999) Frogs of the genus *Colostethus* (Anura: Leptodactylidae) in the Andes of Northern Peru. *The University of Kansas, Natural History Museum, Scientific Papers* 13: 1-78
- Duellman W. E., Lehr E., and Aguilar C. (2001) A new species of marsupial frog (Anura: Hylidae: *Gastrotheca*) from the Cordillera Azul in Peru. *The University of Kansas, Natural History Museum, Scientific Papers* 22: 1-10
- Duellman W. E. and Senaris J. C. (2003) A new species of glass frog (Anura: Centrolenidae) from the Venezuelan Guyana. *Herpetologica* 59: 247-252
- Duellman W. E. (2004) Frogs of the genus *Colostethus* (Anura: Dendrobatidae) in the Andes of Northern Peru. *The University of Kansas, Natural History Museum, Scientific Papers* 35: 1-49
- Duellman W. E., Lehr E., Rodriguez D., and von May R. (2004) Two new species

- of marsupial frogs (Anura: Hylidae: *Gastrotheca*) from the Cordillera Oriental in Central Peru. *The University of Kansas, Natural History Museum, Scientific Papers* 32: 1-10
- Dutta S. K. and Manamendra-Arachchi K. (1996) *The amphibian fauna of Sri Lanka*. Wildlife Heritage Trust of Sri Lanka, Columbo, Sri Lanka
- Ford L. S. and Savage J. M. (1984) A new frog of the genus *Eleutherodactylus* (Leptodactylidae) from Guatemala. *The University of Kansas, Natural History Museum, Occasional Papers* 110: 1-9
- Formas J. R. (1979) New observations of *Telmatobufo australis* (Anura: Leptodactylidae) in Southern Chile. *Journal of Herpetology* 13: 359-361
- Formas J. R. (1988) The tadpole of *Telmatobufo bullocki* (Anura: Leptodactylidae). *Herpetologica* 44: 458-460
- Gallardo J. M. (1987) *Anfibios Argentinas: guía para su identificación*. Librería Agropecuaria, Buenos Aires, Argentina
- Garcia P. C. A., Vinciprova G., and Haddad C. F. B. (2003) The taxonomic status of *Hyla pulchella joaquina* (Anura: Hylidae) with description of its tadpole and vocalization. *Herpetologica* 59: 350-363
- Giaretta A. A. and Facure K. G. (2003) *Cycloramphus boraceiensis*. Clutch attendance. *Herpetological Review* 34: 50
- Glaw F. and Vences M. (1994) *A field guide to the amphibians and reptiles of Madagascar*. Moos Druck and FARBO, Leverkusen and Köln, Germany
- Glos J. and Linsenmair K. E. (2004) Descriptions of the tadpoles of *Aglyptodactylus laticeps* and *Aglyptodactylus securifer* from Western Madagascar, with notes on life history and ecology. *Journal of Herpetology* 38: 131-136
- Guayasamin J. M. and Trueb L. (2007) A new species of glass frog (Anura: Centrolenidae) from the lowlands of northwestern Ecuador, with comments on centrolenid osteology. *Zootaxa* 1447: 27-45
- Haddad C. F. B. and Pombal J. P. (1995) A new species of *Hylodes* from Southeastern Brazil (Amphibia: Leptodactylidae). *Herpetologica* 51: 279-286
- Hero J.-M., Williams S. E., and Magnusson W. E. (2005) Ecological traits of

- declining amphibians in upland areas of eastern Australia. *Journal of Zoology* 267: 221-232
- Hillis D. M. and Frost J. S. (1985) Three new species of leopard frogs (*Rana pipiens* complex) from the Mexican plateau. *The University of Kansas, Natural History Museum, Occasional Papers* 117: 1-14
- IUCN, Conservation International, and NatureServe (2006) *Global Amphibian Assessment* [Online Database]. URL www.globalamphibians.org, accessed Feb.-July 2008
- Junca F. A. and Rodriguez M. T. (2006) The reproductive success of *Colostethus stepheni* (Anura: Dendrobatidae). *Studies on Neotropical Fauna and Environment* 41: 9-17
- Kanamadi R. D., Kadadevaru G. G., and Schneider H. (2002) Advertisement call and breeding period of the frog *Kaloula pulchra* (Microhylidae). *Herpetological Review* 33: 19-21
- Köhler J., Bwong B. A., Schick S., Veith M., and Lötters S. (2006) A new species of arboreal *Leptopelis* (Anura: Arthroleptidae) from the forests of Western Kenya. *Herpetological Journal* 16: 183-189
- Kok P. J. R., Sambhu H., Roopsind I., Lenglet G. L., and Bourne G. L. (2006) A new species of *Colostethus* (Anura: Dendrobatidae) with maternal care from Kaieteur National Park, Guyana. *Zootaxa* 1238: 35-61
- Kokubum M. N. d. C. and Giaretta A. A. (2005) Reproductive ecology and behaviour of a species of *Adenomera* (Anura, Leptodactylinae) with endotrophic tadpoles: Systematic implications. *Journal of Natural History* 39: 1745-1758
- Kolenc F., Borteiro C., and Tedros M. (2003) La larva de *Hyla uruguayana* Schmidt, 1944 (Anura: Hylidae), con comentarios sobre su biología en Uruguay y su status taxonómico. *Cuad. herpetol.* 17: 87-100
- Kunte K. (2004) Natural history and reproductive behaviour of *Nyctibatrachus* cf. *humayuni* (Anura: Ranidae). *Herpetological Review* 35: 137-140
- Kwet A. and Di-Bernardo M. (1999) *Pró-Mata: Anfíbios-Amphibien-Amphibians*. EDIPUCRS, Porto Alegre, Brazil
- Kwet A. (2000) The genus *Pseudis* (Anura: Pseudidae) in Rio Grande do Sul,

- southern Brazil, with description of a new species. *Amphibia-Reptilia* 21: 39-55
- Kwet A. (2005) *Reptilien und Amphibien Europas*. Franckh-Kosmos Verlag, Stuttgart, Germany
- Lannoo M. (2005) *Amphibian declines: the conservation status of United States species*. University of California Press, Berkeley, CA, USA. Accessed online at www.amphibiaweb.org
- Lea J., Halliday T. R., and Dyson M. (2003) The mating strategy of *Alytes muletensis*: some males are less ready to mate than females. *Amphibia-Reptilia* 24: 169-180
- Lescure J. and Marty C. (2000) *Atlas des amphibiens de Guyane*. Museum National d'Histoire Naturelle, Paris, France
- Lima A. P., Magnusson W. E., Menin M., Erdtmann L. K., Rodriguez D. J., Keller C., and Hödl W. (2005) *Guia de sapos da Reserva Adolpho Ducke, Amazônia Central*. Áttema Design Editorial, Manaus, Brazil. Accessed online at www.amphibiaweb.org
- Lima A. P., Sanchez D. E. A., Souza J. R. D., and Lannoo M. J. (2007) A new Amazonian species of the frog genus *Colostethus* (Dendrobatidae) that lays its eggs on the undersides of leaves. *Copeia* 2007: 114-122
- MacCulloch R. D. and Lathrop A. (2002) Exceptional diversity of *Stefania* (Anura: Hylidae) on Mount Ayanganna, Guyana: three new species and new distribution records. *Herpetologica* 58: 327-346
- Malkmus R., Manthey U., Vogel G., Hoffmann P., and Kosuch J. (2002) *Amphibians and Reptiles of Mount Kinabalu*. A. R. G. Gantner Verlag, Ruggell, Liechtenstein
- McCraine J. R., Wilson L. D., and Williams K. (1989) A new genus and species of toad (Anura: Bufonidae) with an extraordinary stream-adapted tadpole from Northern Honduras. *The University of Kansas, Natural History Museum, Occasional Papers* 129: 1-18
- McCraine J. R. and Wilson L. D. (2002) *The amphibians of Honduras*. Society for the Study of Amphibians and Reptiles, Ithaca, USA
- Menzies J. (2006) *The frogs of New Guinea and the Solomon Islands*. Pensoft

Publishers, Sofia, Bulgaria

- Mijares-Urrutia A. and Arends A. (1999) A new *Mannophryne* (Anura: Dendrobatidae) from western Venezuela, with comments on the generic allocation of *Colostethus larandinus*. *Herpetologica* 55: 106-114
- Myers C. W., Paolillo A., and Daly J. W. (1991) Discovery of a defensively malodorous and nocturnal frog in the family Dendrobatidae: Phylogenetic significance of a new genus and species from the Venezuelan Andes. *American Museum of Natural History* 3002: 1-33
- Myers C. W. and Donnely M. A. (1997) A Tepui herpetofauna on a granitic mountain (Tamacuari) in the borderland between Venezuela and Brazil: report from the Phipps Tapirapeco expedition. *American Museum of Natural History* 3213: 1-71
- Nascimento L. B., Carvalho R. R. J., Wogel H., Fernandes D. S., and Feiro R. N. (2001) Reprodução e descrição do girino de *Physalaemus rupestris* Caramaschi, Carcerelli & Feio, 1991 (Amphibia, Anura, Leptodactylidae). *Boletim do Museu Nacional, Nova Série, Rio de Janeiro, Brasil* 450: 1-10
- Ovaska K. and Estrada A. R. (2003) *Eleutherodactylus antillensis*. Reproduction. *Herpetological Review* 34: 229
- Papp M. G. and Papp C. O. G. (2000) Decline in a population of the treefrog *Phyllodytes luteolus* after fire. *Herpetological Review* 31: 93-95
- Passmore N. I. and Carruthers V. (1995) *South African frogs: a complete guide*. Witwatersrand University Press, Johannesburg, South Africa
- Paton P. W., Egan R. S., Osenkowski J. E., Raithel C. J., and Brooks R. T. (2003) *Rana sylvatica*. Breeding behaviour during drought. *Herpetological Review* 34: 236
- Pombal J. P., Feio R. N., and Haddad C. F. B. (2002) A new species of torrent frog genus *Hylodes* (Anura: Leptodactylidae) from Southeastern Brazil. *Herpetologica* 58: 462-471
- Poynton J. C. and Broadley D. G. (1985) Amphibia Zambesica 1. Scolecomorphidae, Pipidae, Microhylidae, Hemisidae, Arthroleptidae. *Annals of the Natal Museum* 26: 50-553
- Ribeira Matos R. H., Andrade G. V., and Hass A. (2000) Reproductive biology

- and territoriality of *Phyllomedusa hypocondrialis* in Northeastern Brazil. *Herpetological Review* 31: 84-86
- Rödel M. O. (2000) *Herpetofauna of West Africa. Vol. I Amphibians of the West African savanna*. Edition Chimaira, Frankfurt am Main, Germany
- Schiøtz A. (1999) *Treefrogs of Africa*. Edition Chimaira, Frankfurt am Main, Germany. Accessed online at www.amphibiaweb.org
- Sheil C. A. and Mendelson J. R. (2001) A new species of *Hemiphractus* (Anura: Hylidae: Hemiphractinae), and a redescription of *H. johnsoni*. *Herpetologica* 57: 189-202
- Sindaco R., Doria G., Razzetti E., and Bernini F. (2006) *Atlante degli anfibi e dei rettili d'Italia*. Polistampa, Florence, Italy
- Smith J. M., Buchanan J., Downie J. R., and Riehle M. O. (2006) Larval transport does not affect locomotor performance in the stream frog *Mannophryne trinitatis*. *Herpetological Journal* 16: 333-336
- Spawls S., Howell K. M., and Drewes R. C. (2006) *Pocket guide to the reptiles and amphibians of East Africa*. A&C Black Publishers Ltd., London, UK
- Vences M., Andreone F., Glaw F., Kosuch J., Meyer A., Schaefer H. C., and Veith M. (2002) Exploring the potential of life-history key innovation: brook breeding in the radiation of the Malagasy treefrog genus *Boophis*. *Molecular Ecology* 11: 1453-1463
- Wheeler C., Welsh H. H., and Heise L. L. (2003) *Rana boylii*. Oviposition behaviour. *Herpetological Review* 34: 234
- Whitfield S. M. and Pierce M. S. F. (2003) *Eleutherodactylus noblei*. Reproduction and parental care. *Herpetological Review* 34: 357-358
- Wild E. R. (1994) Two new species of centrolenid frogs from the Amazonian slope of the Cordillera Oriental, Ecuador. *Journal of Herpetology* 28: 299-310
- Wogel H. and Abrunhosa P. A. (2003) *Hyla berthallutzae*. Oviposition behavior. *Herpetological Review* 34: 51