University of Southampton

Faculty of Environmental and Life Sciences

Biological Sciences

Analyzing the ecological diversity of the world's mammals and birds

by

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Thesis for the degree of Doctor of Philosophy

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Abstract

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Global biodiversity loss threatens the continued provision of ecosystem function and ecosystem services, upon which we all rely. Biodiversity is multidimensional, encompassing taxonomic, phylogenetic and ecological diversity; yet taxonomic diversity has received the majority of research effort. In this thesis, I focus on the ecological diversity of the world’s mammals and birds, based on species traits, as ecological diversity strongly relates to species’ ecological roles and to the functions species perform. I show that mammals and birds are ecologically comparable and provide complementary and comparative macroecological perspectives. I find a global trade-off between the similarity of species roles (functional redundancy) and the breadth of roles across taxa (functional dispersion) (Chapter 2). I also demonstrate different contributions of mammals and birds to functional redundancy and functional dispersion, and unique geographic patterns of redundancy and dispersion by including both taxa. I then show that the ecological diversity of mammals and birds is structured by life-history speed (fast-slow) and body mass (small-large) in one dimension, and diet (invertivore-herbivore) and habitat breadth (generalist-specialist) in the other dimension (Chapter 3). Using a probabilistic extinction framework, I predict a greater decline in ecological diversity than expected at random over the next century, shifting the mammal and bird species pool towards small, fast-lived, highly fecund, insect-eating, generalists. I also quantify ecological distinctiveness for mammals and birds (Chapter 4), identifying conservation priority species with potentially irreplaceable ecological roles. I find that high ecological distinctiveness is associated with both highly threatened species, such as Amsterdam Albatross and Sumatran rhinoceros, and non-threatened hyper-generalists, such as Lesser Black-backed Gull and wild boar. Finally, using structural equation models, I determine a strong role of trophic interactions for global patterns of mammalian species richness, but a surprisingly weak role for functional diversity and phylogenetic diversity (Chapter 5). My thesis demonstrates that ecological diversity can offer novel and complementary insights and can inform the prioritization of conservation actions. Overall, I recommend maintaining the complex ecological diversity of the world’s mammals and birds as a fundamental goal for conservation.

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Research Thesis: Declaration of Authorship

Print name:	Robert Scott Charles Cooke

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I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. Parts of this work have been published as:

Cooke, R. S. C., Bates, A. E. and Eigenbrod, F. (2019) ‘Global trade-offs of functional redundancy and functional dispersion for birds and mammals’, *Global Ecology and Biogeography*, 28(4), pp. 484–495. doi: 10.1111/geb.12869.

R.S.C.C, A.E.B. and F.E. formulated the study, R.S.C.C developed and implemented the analyses and wrote the first draft. All authors contributed to interpreting the results and the editing of manuscript drafts.

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Chapter 1 Introduction

1.1 Background

1.1.1 Changing selection pressures and species extinction

The natural world is changing. The combined effects of habitat transformation and climate change represent major drivers of ongoing biodiversity loss, with potentially serious consequences for the resilience of ecosystem functions, on which humans depend (Cardinale *et al.*, 2012; Eigenbrod *et al.*, 2015; Oliver, Heard, *et al.*, 2015; Oliver, Isaac, *et al.*, 2015). Humanity and nature form a coupled system (Liu *et al.*, 2007). Yet humans are the primary cause of accelerating environmental change, and our dominance of the energetic and material dynamics of the biosphere is increasing (Hannah *et al.*, 1994; Vitousek *et al.*, 1997; Sanderson *et al.*, 2002; Imhoff *et al.*, 2004; Steffen *et al.*, 2015; Venter *et al.*, 2016). The principal forcing mechanisms are human population growth and rising resource use (Vitousek *et al.*, 1997; McDaniel and Borton, 2002; Brown *et al.*, 2011; Steffen *et al.*, 2011). Human population has grown from 2.5 billion in 1950 to 7.6 billion today (UN, 2017), at a rate of approximately 1.7% per annum, while per capita growth in human footprint on the landscape has increased at around 0.52% per year (from 1993 to 2009) (Venter *et al.*, 2016). The product of the two - population size and per capita demand - has thus grown exponentially faster than either on its own (Otto, 2018). Population growth and resource use, in turn, lead to pervasive human impacts (primarily habitat transformation and climate change) affecting an estimated 75% of the land surface of the Earth (Venter *et al.*, 2016). Although the exploitation of terrestrial systems has been vital for human development throughout history (Ellis *et al.*, 2013), the cost to biosphere integrity has been high (Newbold *et al.*, 2016).

Humans have caused widespread extinctions, at an increasing rate (Barnosky *et al.*, 2011; Dirzo *et al.*, 2014; Pimm *et al.*, 2014; Ceballos *et al.*, 2015; Newbold *et al.*, 2015). For example, 379 vertebrate species have been classified as extinct since 1500 (IUCN, 2019), including recent extinctions, such as the Bramble Cay melomys *Melomys rubicola* and the Christmas Island pipistrelle *Pipistrellus murrayi* (both last seen in 2009). In addition, humans have driven global and local compositional changes, such as shifts in community composition, declines in species' populations, local extinctions, local gains, increases in human commensals, novel species interactions and spatial homogenization of Earth's biota (Ceballos and Ehrlich, 2002; Schipper *et al.*, 2008; Butchart *et al.*, 2010; Capinha *et al.*, 2015; Scheffers *et al.*, 2016). These extensive impacts on biodiversity, influenced by humans, are therefore considered a primary driver of global environmental change in their own right (Dirzo *et al.*, 2014), and are fundamentally altering global species composition. Consequently, humans have been described as a hyperkeystone species (Worm and Paine, 2016).

In addition, past and present anthropogenic impacts have led to the accumulation of extinction debts, which means that a large number of species are already committed to extinctions that are yet to occur (Tilman *et al.*, 1994; Kuussaari *et al.*, 2009; Halley *et al.*, 2016; Isbell *et al.*, 2017). The recent Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services report (IPBES, 2019), for example, highlights that 25% of IUCN assessed species are threatened with extinction, and threatened species have a 10-99% of extinction in the next hundred years (Mooers, Faith and Maddison, 2008). These extinction debts could therefore take years to centuries to realize, depending on the extent of habitat loss (Halley *et al.*, 2016).

Furthermore, our impact on biodiversity is expected to increase into the future (Jetz, Wilcove and Dobson, 2007; Newbold *et al.*, 2015; Visconti *et al.*, 2016). Global human population is expected to reach approximately 9.8 billion by 2050 (UN, 2017), coupled with increased wealth and demand for more varied diets, the extent of land-use change is likely to increase rapidly (Newbold *et al.*, 2013), with direct effects on biodiversity. For instance, Powers and Jetz (2019) estimate that approximately 1,700 terrestrial vertebrates are expected to become imperilled due to land-use change alone by 2070. While Visconti *et al.* (2016) predict, for 440 terrestrial mammalian carnivores and ungulates, declines in mean abundance of 18-35% and increases in extinction risk for 8-23% of species by 2050. Thus, human-driven biodiversity change has dominated the natural world for the past century, the present and will continue into the future.

Biodiversity is also restructuring through both ecological and evolutionary processes. Human activities have reshaped selection pressures, favouring individuals that better survive in our built and agricultural landscapes, that avoid our hunting, and that best tolerate the species that we have introduced (Otto, 2018). Hill, DeVault and Belant (2019) estimate that humans are directly responsible for more than one-quarter of terrestrial vertebrate mortality worldwide. Although, the amount of total anthropogenic mortality is likely to be higher than reported when indirect impacts, such as the introduction of invasive species, habitat loss and poisoning, are considered (Hill, DeVault and Belant, 2019). For instance, Feral cats (*Felis catus*) kill 1.3-4.0 billion birds and 6.3-22.3 billion mammals annually in the US alone (Loss, Will and Marra, 2013). Anthropogenic impacts have therefore generated species-level selection pressures against those ecological and evolutionary strategies that elevate extinction risk. Larger body size, for example, is associated with increased extinction risk, especially for mammals and birds (Cardillo *et al.*, 2005; Fritz, Bininda-Emonds and Purvis, 2009; Ripple *et al.*, 2017; Smith *et al.*, 2018), with over half of large terrestrial mammalian species eliminated over the past 50,000 years (Tilman *et al.*, 2017). Plus, human impacts often interact with species' ecology to shape extinction risk patterns (Fritz, Bininda-Emonds and Purvis, 2009). Large-bodied mammals and birds are most threatened by direct harvesting (Owens and Bennett, 2000; Isaac and Cowlishaw, 2004; Collen *et al.*, 2006; Ripple *et al.*, 2017, 2019), whereas small-bodied mammals and birds are primarily threatened by habitat loss and habitat modification (Dirzo *et al.*, 2014; Ripple *et al.*, 2017; Smith *et al.*, 2018). Our world is therefore evolving less under the pressures of natural selection and more under the pressures of anthropogenic selection (Otto, 2018).

There is growing evidence that the loss and restructuring of biodiversity is disrupting processes important to the sustainability of ecosystems, and thus the provision of ecosystem services (Loreau *et al.*, 2001; Hooper *et al.*, 2005, 2012; Tilman, Reich and Knops, 2006; Cadotte, Dinnage and Tilman, 2012; Oliver, Heard, *et al.*, 2015). Biodiversity has been shown to sustain ecosystem productivity and stability under environmental disturbances (Isbell, Craven, *et al.*, 2015; Schneider *et al.*, 2016). For example, the insurance (or redundancy) hypothesis proposes that ecosystem function is more stable over time when multiple species contribute to, and therefore safeguard, each ecosystem process (Walker, 1992; Naeem, 1998; Yachi and Loreau, 1999; Laliberté *et al.*, 2010; Oliver, Isaac, *et al.*, 2015; Nash *et al.*, 2016). Furthermore, non-random species loss can have greater functional consequences (Larsen, Williams and Kremen, 2005) and can generate cascading evolutionary and ecological effects on other species and processes (Estes *et al.*, 2011). Consequently, preventing the loss of biodiversity, and conserving the most evolutionary, ecologically and functionally important species, is a global priority (Rands *et al.*, 2010; Thuiller *et al.*, 2015; Pollock, Thuiller and Jetz, 2017).

1.1.2 Biodiversity is multidimensional

Yet global conservation funding is limited. For example, McCarthy *et al.* (2012) estimated the cost of reducing the extinction risk of all globally threatened bird species (by ≥ 1 International Union for Conservation of Nature Red List category) to be U.S. $0.875 to $1.23 billion annually over the next decade, of which 12% is currently funded. We therefore need to prioritise the allocation of scarce conservation funding.

To date, conservation biology has primarily focused on conserving taxonomic diversity - species richness - to prevent local and global species' extinctions (McGill *et al.*, 2006; Cadotte, 2011; Cadotte, Carscadden and Mirotchnick, 2011; Winter, Devictor and Schweiger, 2013). Although conserving species richness is a fundamental priority, richness considers species to be equally different and therefore ignores species' ecological and evolutionary attributes (Brum *et al.*, 2017). In response, biodiversity is increasingly viewed as a multidimensional concept, comprised of taxonomic diversity, phylogenetic diversity and functional diversity (Brum *et al.*, 2017; Pollock, Thuiller and Jetz, 2017; Rapacciuolo *et al.*, 2019).

Phylogenetic diversity reflects the phylogenetic relationships among taxa and thus emphasizes the accumulated evolutionary history of a community (Webb, 2000; Safi *et al.*, 2011), while functional diversity summarizes the diversity of traits within a community (Petchey and Gaston, 2002; Violle *et al.*, 2007; Laliberté and Legendre, 2010). Thus, two communities with equal species richness can differ greatly in their phylogenetic and functional diversity (Petchey and Gaston, 2006; Safi *et al.*, 2011), due to different evolutionary histories, different selection pressures, different biogeographical histories, and/or different environmental disturbances. In addition, there is increasing evidence that phylogenetic diversity and functional diversity better characterize patterns and processes within ecosystems and may be more sensitive to human pressures than taxonomic diversity (Hooper *et al.*, 2005; Petchey and Gaston, 2006; D'agata *et al.*, 2014). Biodiversity research is therefore moving from counting species to accounting for species.

In this thesis, I primarily focus on functional diversity, also known as ecological diversity, as I am interested in the ecological structure, ecological hypotheses and ecological mechanisms shaping life on this planet. Ecological and evolutionary research is increasingly moving from species- to trait-based approaches because traits can provide a more mechanistic understanding of community dynamics via trait-environment relationships and a stronger link to organism's function and fitness (Lavorel and Garnier, 2002; McGill *et al.*, 2006; Cadotte, 2017; Gross *et al.*, 2017).

1.1.3 Traits

Traits are morphological, physiological, phenological, ecological or behavioural features affecting fitness or performance measurable at the individual level (Lavorel and Garnier, 2002; Violle *et al.*, 2007). Properties measurable at the population/community/ecosystem level, such as geographic range size, population abundance, climatic niche or population density are therefore not considered to be traits (Violle *et al.*, 2007; Mlambo, 2014).

Southwood (1977, 1988) proposed the use of species traits in developing his habitat templet concept, which asserts that in any given community habitat templets select species with suitable traits to coexist (Mlambo, 2014). Traits are therefore selected via effects on fitness of individuals through ecological time (Southwood, 1988), and reflect species' adaptations to their environment and their ability to acquire resources, disperse and persist (Petchey and Gaston, 2002; McGill *et al.*, 2006; Violle *et al.*, 2007). In addition, traits characterize species' average long-term responses to natural selection (Ricklefs, Cochran and Pianka, 1981; Pianka *et al.*, 2017) and therefore reflect the outcome of continuous evolutionary pressures by biotic and abiotic factors (McGill *et al.*, 2006; Petchey and Gaston, 2006). Hence, traits may summarise species-environment relationships better than direct measurements of immediate ecological conditions (Ricklefs, Cochran and Pianka, 1981; Pianka *et al.*, 2017). For example, different species show widely different responses to environmental change, and the extent and form of the response often depends on species' traits, such as diet, body size and reproductive rate (Newbold *et al.*, 2013).

Some authors argue the importance of removing phylogenetic autocorrelation in trait data (Diniz-Filho *et al.*, 2009; Pavoine *et al.*, 2011; Fountain-Jones, Baker and Jordan, 2015), as species are phylogenetically non-independent and species' traits often reflect shared evolutionary history. A comprehensive review showed that 60% of 103 ecological traits exhibited significant phylogenetic signal (Freckleton, Harvey and Pagel, 2002). Yet, there is considerable uncertainty about if, and when, phylogenetic information is needed to answer various trait-based ecological questions (de Bello *et al.*, 2015). Recently, de Bello *et al.* (2015) have argued that correction is not always required and that tests conducted with and without phylogeny focus on different questions. They argue that when assessing evolutionary mechanisms behind present trait-environment patterns, for example the evolution of traits (Garland, Harvey and Ives, 1992), it might be necessary to account for phylogeny (de Bello *et al.*, 2015). However, phylogenetic relatedness between species should not be considered a bias to be corrected, but rather an evolutionary signal that allows results to be interpreted at different temporal scales (de Bello *et al.*, 2015). Hence, phylogenetically 'corrected' and 'uncorrected' results highlight different aspects and evolutionary scales (de Bello *et al.*, 2015). In my analyses, I do not 'correct' for phylogeny, as I am not focussing on the evolutionary mechanisms behind ecological diversity. Instead, I am interested in the contemporary ecological patterns and structure that are resultant from evolutionary and ecological processes. Across my thesis, I therefore compare and contrast functional diversity with phylogenetic diversity, and thus treat these aspects of biodiversity as separate dimensions. Overall, I investigate the diversity of traits across species and relate this to their ecological roles.

In addition, traits can provide a more direct link, than taxonomy, to ecosystem processes and functions (Diaz and Cabido, 2001; Hooper *et al.*, 2005; Sekercioğlu, 2006; Cadotte, 2017; Gross *et al.*, 2017). For instance, body mass is linked to most biological rates and processes (Peters, 1983; Smith and Lyons, 2013; Rapacciuolo *et al.*, 2017), including animal nutrient transport capacity (Sekercioğlu, 2006; Ripple *et al.*, 2015) and seed dispersal (Sekercioğlu, Daily and Ehrlich, 2004; Jordano *et al.*, 2007). By contrast, diet determines impacts on ecosystem functioning through trophic interactions with other food web components (Duffy, 2002; Burin *et al.*, 2016; Barnagaud *et al.*, 2019), as well as relating to functions such as pollination, seed dispersal, predation, herbivory and scavenging (Sekercioğlu, 2006; Wenny *et al.*, 2011; Ghanem and Voigt, 2012; Ripple *et al.*, 2014, 2015). Yet, I avoid the use of the term ‘functional trait’, as defining which traits are functional can be problematic. Instead, I agree with Mlambo (2014) that traits should only be described as functional when a direct relationship between the trait and a function is demonstrable, and when this relationship has been experimentally tested. Direct trait-function links are more evident and have been more fully tested for producers. For example, plant traits have been shown to influence primary production, litter decomposition, soil respiration, nutrient cycling and soil moisture retention (Eviner and Chapin III, 2003). However, across this thesis I focus on mammals and birds, for which traits may or may not directly reflect the ecosystem functions performed by species (Huang, Stephens and Gittleman, 2012). Instead, I hypothesise the relationships between the selected traits and function, while primarily focussing on the importance of the traits for species’ ecological strategies and ecological diversity.

1.1.4 Mammals and birds

Contemporary mammals and birds - comprising over 15,000 species - are extraordinarily diverse, having adapted to a wide variety of ecological roles (Eisenberg, 1981; Wilson and Reeder, 2005; Price *et al.*, 2012; del Hoyo *et al.*, 2013; Pineda-Munoz and Alroy, 2014; Lovette and Fitzpatrick, 2016). From long-lived megaherbivores, to nectarivorous birds, to pack-hunting carnivores, to large flightless birds, to arboreal primates, to forest floor rodents (Figure 1.1).

Figure 1.1 The diversity of mammal and bird life. Top-row (left to right): African elephant *Loxodonta africana*, Rufous-tailed Hummingbird *Amazilia tzacatl*, lion *Panthera leo*. Bottom-row (left to right): Common Ostrich *Struthio camelus*, guereza colobus *Colobus guereza*, Central American agouti *Dasyprocta punctata* (all images Robert Cooke).

The complex ecological diversity of mammals and birds leads to key roles in the dynamics of the ecosystems in which they live (Sinclair, 2003; Jones and Safi, 2011; Sekercioglu, Wenny and Whelan, 2016). For instance, mammals and birds are important ecological components for cycling nutrients across and within ecosystems, distributing propagules such as seeds, and interactively connecting species and habitats (Lundberg and Moberg, 2003; Sekercioğlu, 2006; Ripple *et al.*, 2017; Lacher *et al.*, 2019). Thus, mammals and birds influence an array of ecosystem functions, including nutrient distribution, herbivory, seed dispersal, seed predation, scavenging, herbivore abundance regulation, and pollination (Sekercioğlu, 2006; Karp *et al.*, 2011; Luck *et al.*, 2012; Díaz *et al.*, 2013; Sekercioglu, Wenny and Whelan, 2016; Lacher *et al.*, 2019). Moreover, these functions are often ecologically and economically valued (Sekercioğlu, 2006; Díaz *et al.*, 2013; Sekercioglu, Wenny and Whelan, 2016) - reinforcing the need for efficient and effective conservation management of mammals and birds. There is also a growing awareness that the loss of these ecological functions, which species underpin, could be the most critical impact under accelerating global changes (Naeem, Duffy and Zavaleta, 2012) and could compromise the functionality of ecosystems across the globe (Scheffers *et al.*, 2016).

Mammals and birds are the two tetrapod classes with the highest number of widely distributed species (Rapacciuolo *et al.*, 2017), and are therefore exposed to a similarly broad range of environmental gradients and selection pressures. In addition, the magnitude of human pressure effects is highest (across tetrapods) for mammals and birds (Rapacciuolo *et al.*, 2017). For example, most of the nearly 800 mammal and bird global species-level extinctions documented in the last 12,000 years are likely to have been at least partly driven by human factors (Koch and Barnosky, 2006; Pimm *et al.*, 2006; Sandom *et al.*, 2014; Crees *et al.*, 2016; Rapacciuolo *et al.*, 2017). The most comprehensive global assessment of species extinction risk, the International Union for Conservation of Nature (IUCN) Red List, currently lists 14% of bird species and 25% of mammals as threatened by extinction (IUCN, 2019). Moreover, from 1980 to 2004, 223 bird and 156 mammal species moved one category closer to extinction on the IUCN Red List (Hoffmann *et al.*, 2010). Additionally, more than half of all mammal populations are in decline (Schipper *et al.*, 2008). A synthesis of hundreds of experiments and observational studies (Murphy and Romanuk, 2014) found that local species loss was greater for endothermic animals, such as mammals and birds, than for ectothermic animals, and for terrestrial biomes than for aquatic biomes. Here I focus on global impacts on terrestrial mammals and birds.

I investigate both the combined and independent ecological roles of mammals and birds across the globe - fusing the often-separate ecological research literatures for mammals (Safi *et al.*, 2011; Chillo and Ojeda, 2012; Oliveira *et al.*, 2016; Brum *et al.*, 2017) and birds (Luck, Carter and Smallbone, 2013; Newbold *et al.*, 2013; Monnet *et al.*, 2014; Barbet-Massin and Jetz, 2015;

Schipper *et al.*, 2016). Mammals and birds are highly mobile, often widely distributed, consumers, and can potentially fulfil similar and/or complementary ecological and functional roles (Dehling and Stouffer, 2018), and are thus potentially ecologically comparable. Yet, mammals and birds also have very different evolutionary histories and therefore innate differences. For instance, volancy (flight ability) and oviparity (egg laying) are common attributes for birds, but rare for mammals, whereas most mammals, including strictly diurnal species, exhibit sensory adaptations to nocturnal activity, due to a nocturnal evolutionary history - nocturnal bottleneck hypothesis (Maor *et al.*, 2017). Hence, throughout this thesis, I explore both the similarities and differences between mammals and birds.

1.2 Thesis overview and objectives

Overall, I quantify the ecological diversity, based on traits, of the world's mammals and birds. I then identify novel and fundamental macroecological patterns and help inform conservation management and conservation prioritization.

The primary objectives of this thesis are to:

- **investigate** the ecological diversity of the world's mammals and birds, including their ecological strategies, ecological distinctiveness and trophic interactions;
- **develop** cross-taxa trait analyses for mammals and birds, thus widening the taxonomic focus of current research;
- **inform** conservation prioritization of mammals and birds, both spatially and aspatially (species-focussed)

1.2.1 Chapter 2 - Global trade-offs of functional redundancy and functional dispersion for birds and mammals

Cooke, R. S. C., Bates, A. E. and Eigenbrod, F. (2019) 'Global trade-offs of functional redundancy and functional dispersion for birds and mammals', *Global Ecology and Biogeography*, 28(4), pp. 484–495. doi: 10.1111/geb.12869.

1.2.1.1 Objective

To quantify the global similarity of species roles (functional redundancy) and the breadth of roles across taxa (functional dispersion), using a comparative trait framework for both birds and mammals.

1.2.1.2 Summary

Functional redundancy (the extent that multiple species perform the same function) and functional dispersion (response diversity - differential responses by species to disturbance) are increasingly seen as essential ecosystem properties (Walker, 1992; Elmqvist *et al.*, 2003; Laliberté *et al.*, 2010; Luck, Carter and Smallbone, 2013; Mouillot *et al.*, 2014; Oliver, Isaac, *et al.*, 2015). However, global measures of functional redundancy and functional dispersion remain lacking, while functional metrics are usually only applied to single taxonomic groups at a time in terrestrial systems (e.g., mammals OR birds), despite the fact that different taxa can potentially provide very similar function. In Chapter 2, I address both issues in a new global synthesis and analysis.

The major limiting factor to trait-based analyses is the availability and comparability of trait data. Here, I compile and impute a new database for six cross-taxa traits to provide the first global comparisons of functional dispersion and functional redundancy across and between 15,485 extant mammal and bird species for all 825 terrestrial ecoregions (Olson *et al.*, 2001) of the world (Figure 1.2).

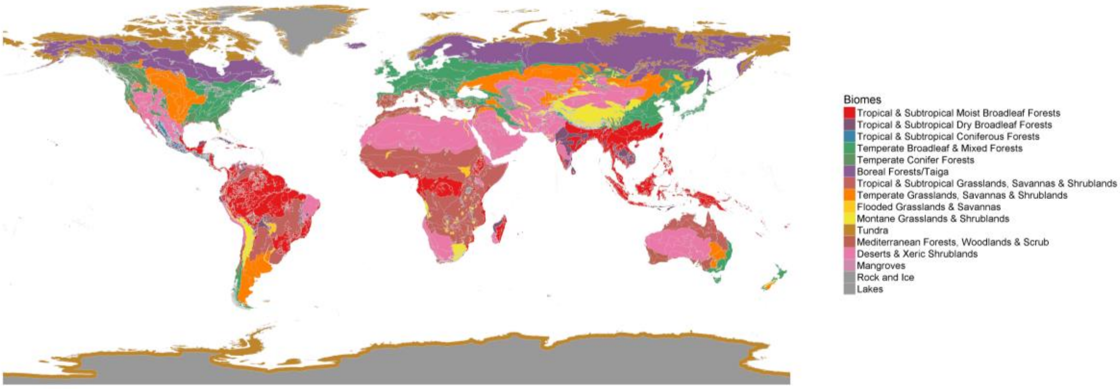

Figure 1.2 The 825 terrestrial ecoregions of the world (Olson *et al.*, 2001), coloured by their respective biome.

I then calculate the standardized effect size (SES) of the observed values of the functional metrics compared with null expectations (i.e., accounting for species richness). Overall, Chapter 2 improves our understanding of potential ecological responses of mammals and birds to species extinctions and environmental change.

1.2.1.3 Main findings

- I find that mammals and birds are ecologically comparable

- I find that functional redundancy is coupled with species richness, resulting in high functional redundancy across the tropics, whereas functional dispersion is largely decoupled from richness.
- I then show that the Neotropics, especially the Andean region, has much higher redundancy than expected at random (i.e., after accounting for species richness). I suggest that the high redundancy SES in the Neotropics could be due to the rapid accumulation of species with little time for ecological divergence. The Neotropics should therefore, theoretically, be less vulnerable to species loss.
- In addition, I find that functional dispersion is generally highest outside of the tropics, such as Eastern Asia, western USA and Madagascar. These regions should therefore be less vulnerable to environmental disturbances.
- I identify a global trade-off between functional redundancy SES and functional dispersion SES, with ecoregions generally demonstrating high functional redundancy SES coupled with low functional dispersion SES, or vice versa.
- Finally, before accounting for species richness, birds have greater functional redundancy than mammals, whereas mammals show greater functional dispersion than birds. However, when accounting for species richness I find the reverse, with greater functional redundancy SES for mammals and greater functional dispersion SES for birds.

1.2.1.4 Outputs

- Research paper published in Global Ecology and Biogeography
- Associated paper: Bates, A. E., **Cooke, R. S. C**, Duncan, M. I., Edgar, G. J., Bruno, J. F., Benedetti-Cecchi, L., Côté, I. M., Lefcheck, J. S., Costello, M. J., Barrett, N. and Bird, T. J. (2019) ‘Climate resilience in marine protected areas and the ‘Protection Paradox’’ *Biological Conservation*, 236, pp. 305-314. doi: 10.1016/j.biocon.2019.05.005Get
- Media coverage (e.g., https://www.sciencedaily.com/releases/2019/02/190207111303.htm)
- A database of six traits for all 15,485 terrestrial extant bird and mammal species: body mass, litter/clutch size, diel activity, diet, volancy and habitat breadth (https://figshare.com/articles/Global_trade-offs_of_functional_redundancy_and_functional_dispersion_for_birds_and_mammals/5616424)
- Empirical and null values for functional dispersion and functional redundancy for all 825 terrestrial ecoregions (https://figshare.com/articles/Global_trade-offs_of_functional_redundancy_and_functional_dispersion_for_birds_and_mammals/5616424)

1.2.2 Chapter 3 - Projected losses of global mammal and bird ecological strategies

Cooke, R. S. C., Eigenbrod, F. and Bates, A. E. (2019) ‘Projected losses of global mammal and bird ecological strategies’, *Nature Communications*, 10, p. 2279. doi: 10.1038/s41467-019-10284-z.

1.2.2.1 Objective

To evaluate the ecological strategies, represented by trait combinations, of extant terrestrial mammals and birds, with the goal of assessing both the current and projected, 100-years into the future, global ecological strategy space (trait space).

1.2.2.2 Summary

Here, I provide the first global quantitative analysis of the diversity of mammal and bird ecological strategies by indexing their positions across multiple ecological gradients, based on a multi-trait approach. Previous research has analyzed ecological strategies for plants (Grime, 1977; Díaz *et al.*, 2016), fish (Winemiller, 1989; Winemiller and Rose, 1992; Mims *et al.*, 2010) and lizards (Mesquita *et al.*, 2016; Pianka *et al.*, 2017), but with only a single study at the global species pool scale - for plants (Díaz *et al.*, 2016). In addition, singular ecological gradients have previously been described, such as the fast-slow continuum - the trade-off between the number of offspring and the timing of reproduction (Bielby *et al.*, 2007). However, comparisons of multiple ecological strategies for large numbers of species, and across taxa, are lacking, especially for mammals and birds.

In contrast to Chapter 2, here I take an aspatial species-level approach to investigate the ecological composition of the global species pool of mammals and birds. I achieve this by building an ecological strategy surface (2-dimensions), via a principal components analysis, and ecological strategy spaces (5-dimensions), via hypervolume estimation, using five traits.

Human impacts have led to the accumulation of extinction debts - numerous species are already committed to extinctions that are yet to occur (Tilman *et al.*, 1994; Kuussaari *et al.*, 2009; Halley *et al.*, 2016). By employing probabilistic extinction frameworks (Mooers, Faith and Maddison, 2008) I investigate the ecological impacts of paying off these extinction debts. Our analyses therefore relate to the increasing body of research examining how traits correlate with threat status and extinction risk (Fisher, Blomberg and Owens, 2003; Cardillo *et al.*, 2004; Davidson *et al.*, 2009; Murray *et al.*, 2014). However, instead of assessing which traits relate to increased extinction risk, I reverse the focus, evaluating the impact of extinction on the trait combinations and trait values of mammals and birds into the future.

1.2.2.3 Main findings

- I reveal an ecological strategy surface, structured by life-history (fast-slow) and body mass (small-large) as one dimension, and diet (invertivore-herbivore) and habitat breadth (generalist-specialist) as the other.
- I show that the ecological strategy space currently occupied by mammals and birds is strongly restricted. Specifically, of all possible trait combinations, only 9% are realized in contemporary mammal and bird ecological strategies and are therefore currently evolutionarily viable on Earth.
- Mammals and birds overlap across 31% of the combined strategy space; however, birds occupy 19% unique space and mammals 51% unique space.
- Future projected extinctions lead to over double the loss of ecological diversity for the next 100 years than expected at random. Thus, human activities have the potential to initiate greater ecological, and potentially functional, loss than would be expected under random species loss.
- I then predict that, without intervention, the global composition of birds and mammals will shift to small, fast-lived, highly fecund, insect-eating, habitat generalists, fundamentally restructuring life on our planet.

1.2.2.4 Outputs

- Research paper published in Nature Communications
- Media coverage (e.g., https://www.theguardian.com/environment/2019/may/23/humans-causing-shrinking-of-nature-as-larger-animals-die-off)
- A Nature Research Ecology & Evolution Community ‘Behind the paper’ blog (https://natureecoevocommunity.nature.com/users/257813-robert-cooke/posts/48688-the-extraordinary-diversity-of-the-world-s-mammals-and-birds)
- Source data for all main and supplementary figures (https://www.nature.com/articles/s41467-019-10284-z#Sec17)
- The principal components from the ecological strategy surface (https://github.com/03rcooke/hyper_pca)
- The code and data (without generation length due to data restrictions) to replicate our analyses is available on Github: https://github.com/03rcooke/hyper_pca

1.2.3 Chapter 4 - Ecological distinctiveness of birds and mammals at the global scale

1.2.3.1 Objective

To quantify the ecological distinctiveness of the world's birds and mammals, and evaluate the relationship between ecological distinctiveness and both extinction risk and evolutionary distinctiveness.

1.2.3.2 Summary

Conservation frameworks have previously been developed that focus on extinction risk, such as the IUCN Red List (IUCN, 2018a), or evolutionary distinctiveness, such as the Evolutionarily Distinct and Globally Endangered (EDGE) index (Isaac *et al.*, 2007; Gumbs *et al.*, 2018). Although these frameworks are crucial to safeguarding the diversity of life, they do not directly account for the ecological differences between species. Thus, we could be losing species with potentially irreplaceable ecological roles (Chapter 3) (Cooke, Eigenbrod and Bates, 2019). Moreover, the loss of species with distinct ecological strategies could have very different consequences from the loss of species with common ecological strategies (Larsen, Williams and Kremen, 2005; Mouillot, Bellwood, *et al.*, 2013; Monnet *et al.*, 2014). Here I quantify ecological distinctiveness, based on six traits, for 10,960 bird and 5,278 mammal species. I then compare and contrast ecological distinctiveness with extinction risk and evolutionary distinctiveness to evaluate how these dimensions of biodiversity interrelate.

1.2.3.3 Main findings

- Greater Rhea, Pink-backed Pelican and White-tailed Sea-eagle are the most ecologically distinct birds.
- Leopard, polar bear and grey wolf are the most ecologically distinct mammals.
- I find that, on average, threatened birds and mammals are the most ecologically distinct. Yet the most ecologically distinct mammals and birds also have larger range sizes on average.
- High ecological distinctiveness is therefore associated with both highly threatened species, such as Amsterdam Albatross and Sumatran rhinoceros, and non-threatened hyper-generalists, such as Lesser Black-backed Gull and wild boar.
- I also show that evolutionary distinctiveness is a poor surrogate for ecological distinctiveness. Thus, consideration of extinction risk, evolutionary distinctiveness and ecological distinctiveness together could better account for species irreplaceability and the multidimensionality of biodiversity.

1.2.3.4 Outputs

- Research paper submitted to Global Ecology and Conservation
- Updated trait data for 10,960 bird and 5,278 mammal species (https://figshare.com/s/e9da4dabb4a6b5a7d4f0; currently private, to be made public when the paper is published)
- Ecological distinctiveness scores for 10,960 bird and 5,278 mammal species (https://figshare.com/s/e9da4dabb4a6b5a7d4f0)

1.2.4 Chapter 5 - The global importance of trophic interactions across multiple dimensions of mammalian diversity

1.2.4.1 Objective

To evaluate the importance of trophic interactions for all three dimensions of biodiversity - species richness, functional diversity and phylogenetic diversity.

1.2.4.2 Summary

Trophic interactions, in particular predator-prey interactions, have been shown to be important drivers of large-scale species richness gradients, in combination with environmental effects (Sandom *et al.*, 2013; Zhang *et al.*, 2018). Thus, species interactions across trophic levels are important for creating and maintaining richness (Sandom *et al.*, 2013). Yet richness does not fully account for the evolutionary or ecological differences between species (Brum *et al.*, 2017). Moreover, the global role of trophic interactions, as drivers or mediators of functional and phylogenetic diversity, remains uncertain (Speed *et al.*, 2019). In Chapter 5, I use Structural Equation Models (SEMs) to quantify the importance of trophic interactions, when accounting for environmental predictors, for species richness, functional diversity and phylogenetic diversity across mammalian predators and prey. I therefore provide novel insights into diversity patterns and predator-prey relationships.

1.2.4.3 Main findings

- I find a strong role for trophic interactions, especially bottom-up interactions, for mammalian predator and prey species richness, supporting previous findings (Sandom *et al.*, 2013).
- However, I demonstrate very weak effects of trophic interactions for predator and prey functional diversity and phylogenetic diversity.

- I also observe strong direct (and indirect via plant productivity) effects of climate, specifically temperature, precipitation and temperature seasonality, on predator and prey functional diversity.

1.2.4.4 Outputs

- Research paper prepared for submission

Chapter 2 Global trade-offs of functional redundancy and functional dispersion for birds and mammals

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2.1 Abstract

Aim

While the diversity of birds and mammals is typically described in separate analyses, species may play similar roles. Here, we develop a comparative trait framework for birds and mammals to provide a global quantification of the similarity of species roles (functional redundancy) and the breadth of roles across taxa (functional dispersion). We predict different contributions of birds and mammals to redundancy and dispersion, and unique geographic patterns of redundancy and dispersion by including both taxa.

Location

Global.

Time period

Contemporary.

Major taxa studied

Birds and mammals.

Methods

We systematically select, compile and impute the same six traits (i.e., a common currency of traits) across 15,485 bird and mammal species from multiple databases. We use these six traits to compute functional redundancy and functional dispersion for birds and mammals across all 825 terrestrial ecoregions. We then calculate the standardized effect size (SES) of these observed values compared to null expectations, based on a randomization of species composition (i.e., independently of differences in species richness).

Results

We find that species rich regions, such as the Neotropics, have high functional redundancy coupled with low functional dispersion, characterizing a global trade-off. Thus, in general, as species richness increases, the similarity in species functional roles also increases. We therefore suggest that different processes generate species richness/functional redundancy and functional dispersion, leading to a novel, and generally non-tropical, distribution of hotspots of high functional dispersion across Madagascar, Eastern Asia and western USA.

Main conclusions

We recommend consideration of both the similarity and breadth of functional roles across species pools, including taxa that may play similar roles. We therefore suggest that functional redundancy, as a means of insurance, and functional dispersion, as an indicator of response diversity, should be further evaluated as conservation objectives.

2.2 Introduction

Regions of the world are exposed to multiple interacting disturbances (e.g., habitat loss, drought, disease) that are increasing in rate and intensity due to human activities (Brook, Sodhi and Bradshaw, 2008; Oliver, Heard, *et al.*, 2015). At the same time, global biodiversity continues to decline, with birds and mammals priority species of concern (Dirzo *et al.*, 2014). These combined pressures threaten entire networks of species and thus their ecological strategies and functional roles (Cardinale *et al.*, 2012; Dirzo *et al.*, 2014; Oliver, Heard, *et al.*, 2015; Oliver, Isaac, *et al.*, 2015). In particular, birds and mammals act as critical connecting nodes among genetic (pollinators and seed dispersers), resource (nutrient depositor) and trophic processes (primary/secondary consumers across habitats), especially across broad scales (Lundberg and

Moberg, 2003; Sekercioğlu, 2006). These taxa also support a variety of ecosystem functions, such as nutrient cycling, predation, herbivory, pollination and seed dispersal, across the globe (Sekercioğlu, 2006; Luck *et al.*, 2012; Newbold *et al.*, 2012; Díaz *et al.*, 2013). Moreover, the size and mobility of birds and mammals results in large contributions to ecological functions and processes through top-down trophic control (Lundberg and Moberg, 2003; Sekercioğlu, 2006).

Birds and mammals, together, thus have the potential to influence components of biodiversity, beyond species richness. First, different species can play similar ecological and functional roles - functional redundancy (Walker, 1992; Naeem, 1998). Second, species can be functionally dissimilar, leading to a diversity of species' responses - functional dispersion (response diversity) (Chapin *et al.*, 1997; Yachi and Loreau, 1999; Elmqvist *et al.*, 2003). Functional redundancy and functional dispersion are determined by the ecological strategies of species via trait-environment interactions; and can be quantified by functional indices (Diaz and Cabido, 2001; Laliberté *et al.*, 2010; Luck, Carter and Smallbone, 2013; Mouillot, Bellwood, *et al.*, 2013; Mouillot *et al.*, 2014). Specifically, functional redundancy quantifies the extent that multiple species share functional roles, thereby providing biological insurance against the loss of function due to species extinctions (Walker, 1992; Yachi and Loreau, 1999; Oliver, Isaac, *et al.*, 2015). By contrast, functional dispersion quantifies the breadth of functional roles across species, and, on average, systems with species pools representing higher dispersion should display greater functional dissimilarity and a broader range of responses to environmental perturbations (Elmqvist *et al.*, 2003; Laliberté *et al.*, 2010; Luck, Carter and Smallbone, 2013) (see AppendixA.1 for further detail on functional redundancy and functional dispersion). Thus functional redundancy and functional dispersion may not relate directly to specific ecological functions or processes, but describe different components of biodiversity (versus species richness) related to the overlap in functional roles (redundancy) and breadth of functions (dispersion) performed by species.

Here, we look beyond species richness and offer three major advances on previous analyses of global terrestrial vertebrate functional diversity (Safi *et al.*, 2011; Barbet-Massin and Jetz, 2015; Oliveira *et al.*, 2016).

To date, functional metrics have generally been applied to single taxonomic groups at a time in terrestrial systems, despite the fact that different taxa can potentially fulfil similar and/or complementary ecological and functional roles (Dehling and Stouffer, 2018). Here, we recognize that birds and mammals, as mobile consumers, are potentially ecologically comparable, especially at broad scales and across generalizable traits. Comparable to how taxonomically and ecologically diverse plants, such as large trees and small grasses have previously been analyzed together (e.g., Díaz *et al.*, 2016). We therefore systematically selected a common currency of traits for both birds and mammals (and an increase in the number of traits previously included for either birds or mammals) with strong links to how species respond to change and their influence on ecological and biogeochemical processes (see Appendix A.2). The selected traits are widely applicable to terrestrial vertebrates, leading to the first direct comparisons of functional redundancy and functional dispersion across and between birds and mammals.

Second, we account for the effects of species richness on functional metrics for multiple taxa at the global scale - key because richness is correlated with ecoregion area (Spearman's rho_{823} = 0.27, $P < 0.001$) and functional redundancy ($rho_{823} = 0.94$, $P < 0.001$). In addition, to compare functional metrics among ecoregions with different species richness, it is most appropriate to consider observed values relative to those expected at random (Villéger, Mason and Mouillot, 2008).

Third, we quantify both functional redundancy and dispersion for species pools across the terrestrial biosphere at the ecoregion scale. Ecoregions are geographic units based on delineations in taxonomic compositions, inferred evolutionary histories, and shared climatic domains (Olson *et al.*, 2001). Ecoregions are a compelling spatial unit in representing the best available global measure of coherent, spatially-bounded, biologically-derived systems (Olson and Dinerstein, 2002), and have close relationships with taxonomic and functional compositions (Belmaker and Jetz, 2013; González-Maya *et al.*, 2017). In addition, ecoregions respect spatial changes in ecosystem attributes, disturbance regimes and species interactions (Olson *et al.*, 2001; González-Maya *et al.*, 2017) and changes in ecoregions can propagate across the entire biosphere (Peters *et al.*, 2009; Barnosky *et al.*, 2012). Furthermore, ecoregions are widely used to guide global conservation investments, assessments and action (Funk and Fa, 2010; Watson, Iwamura and Butt, 2013).

Global quantification of functional redundancy and functional dispersion remains lacking, and thus we develop a framework that allows us to quantify different taxonomic, trait and spatial signals of diversity for both birds and mammals. Our first objective is to identify a common currency of traits that allow comparisons and analyses across and between birds and mammals. Our second objective is to use our novel dataset to test two fundamental predictions: (i) functional redundancy will be coupled with species richness, due to expected greater overlap in species' traits with greater species richness, while functional dispersion will be weakly related to richness, as functional dispersion has previously been shown to increase asymptotically, rather than linearly, with species richness for mammals globally (Oliveira *et al.*, 2016); and (ii) birds, as a more speciose group, will have higher functional redundancy, while mammals will show higher functional dispersion, due to greater expected ecological diversity (inferred from greater range in body size). Our third objective is to determine the degree to which redundancy and dispersion of birds and mammals is different from the null expectation, given their species richness in a particular ecoregion, thereby identifying regions with unique patterns of redundancy and dispersion. Our third objective is exploratory as we do not have sufficient information to make *a priori* predictions of the expected patterns and relationships of redundancy and dispersion for birds and mammals when accounting for species richness.

2.3 Methods

We extracted geographic range distributions, and, following a systematic trait selection process, compiled trait data from multiple databases - imputing missing values - for six traits: body mass, litter/clutch size, diel activity (diurnal/nocturnal), diet, volancy (flight ability) and habitat breadth for 10,253 bird and 5,232 mammal species. These six traits relate to both species' functional influences on and responses to the environment (see Appendix A.2 for the ecological relevance of the selected traits). We then calculated functional redundancy and functional dispersion for each ecoregion, as well as the standardized effect size (SES) of these observed values compared to null expectations, based on a randomization of species composition (i.e., independently of differences in species richness).

An extended version of our methods is also available, with further detail on all methodological processes and justifications (see Appendix A.3). All analyses were performed in R (R Core Team, 2018), version 3.4.3 (see Appendix A.3 for the specific functions and packages used).

2.3.1 Spatial data

We used 825 terrestrial ecoregions (Olson and Dinerstein, 2002), excluding 'Lake' and 'Rock and Ice' ecoregions, because they are not coherent systems, i.e., they occur at multiple locations across the globe. We paired these ecoregions with species range maps for 15,485 species (all extant terrestrial mammals and birds): 5,232 terrestrial mammals (http://www.iucnredlist.org/technical-documents/spatial-data) and 10,253 birds (http://datazone.birdlife.org/species/requestdis). We then cropped a presence-absence matrix (polygon-to-grid procedure at 0.5° resolution; lets.presab() function - letsR package (Vilela and Villalobos, 2015)) based on species distributions to the ecoregion boundaries (lets.pamcrop() function - letsR package (Vilela and Villalobos, 2015)), to generate ecoregional composition data. The range maps used represent the best available data, and although they are susceptible to commission errors, the coarse resolution (ecoregion scale) of our analyses reduces pseudoreplication (Jetz and Fine, 2012; Belmaker and Jetz, 2015; Buschke *et al.*, 2015) (see

Appendix A.3). Range maps also reduce the effects of differences in detectability between species and over- or under-sampling (see Appendix A.3).

2.3.2 Trait data

We followed a systematic three-step trait selection process: (1) compiled an extensive list of potential traits that may relate birds and mammals to their environment (seventeen traits; Table A.1); (2) filtered to those that had >50% species coverage (Laliberté *et al.*, 2010) for our species list (seven traits); and (3) had low multicollinearity (based on variance inflation factors - leading to the exclusion of generation length) (Zuur, Ieno and Elphick, 2010; Luck *et al.*, 2012). Our trait selection process resulted in six traits that summarise both a species' effect on ecological and biogeochemical processes and response to environmental change: body mass, diel activity, diet, habitat breadth, litter/clutch size and volancy (see Appendix A.2; Table A.2). These traits reflect the spatiotemporal distribution of resource capture, utilisation and release by species and are commonly used in assessments of mammal and bird functional diversity (Flynn *et al.*, 2009; Safi *et al.*, 2011; Chillo and Ojeda, 2012; Luck *et al.*, 2012; Newbold *et al.*, 2012, 2013; Luck, Carter and Smallbone, 2013; Leitão *et al.*, 2016).

We extracted trait data from a number of available databases (Jones *et al.*, 2009; Pacifici *et al.*, 2013; Wilman *et al.*, 2014; Myhrvold *et al.*, 2015), taking the median value across estimates when applicable (see Appendix A.3 for details on the data compilation process). To ensure species were matched across the geographic data and the available trait data, which often use different taxonomic frameworks, we sourced species synonyms from the Integrated Taxonomic Information System and the International Union for Conservation of Nature databases via their application programming interfaces (see Appendix A.3).

Trait data were transformed where it improved normality, as recommended by Villéger *et al.*, (2008): log10 for body mass and litter/clutch size, square root for habitat breadth, and all traits were standardized to zero mean and unit variance (z-transformation).

To achieve complete species trait coverage we imputed missing data using Multivariate Imputation with Chained Equations (MICE), based on functional (the transformed traits) and phylogenetic (the first 10 phylogenetic eigenvectors extracted from trees for birds (Prum *et al.*, 2015) and mammals (Fritz, Bininda-Emonds and Purvis, 2009)) relationships between species. MICE has been shown to have improved sample size and smaller error and bias than the data deletion approach and other multiple imputation approaches (Penone *et al.*, 2014; Taugourdeau *et al.*, 2014; Kim, Blomberg and Pandolfi, 2018). The data deletion approach was performed for comparative purposes (Figure A.1; Table A.3). We also evaluated the effect of the imputation procedure by analyzing the 25 imputed datasets separately and found very strong agreement between the datasets (Figure A.2). Thus for all analyses we used a single, randomly selected, imputation dataset, due to the high computational costs associated with running the null models for all the imputed datasets. For completeness we also present the mean results (correlation between single, randomly selected, imputation dataset and mean imputation values: functional redundancy $rho_{823} = 0.99$, $P < 0.001$, functional dispersion $rho_{823} > 0.99$, $P < 0.001$) across the 25 imputed datasets (Figure A.3).

To test the sensitivity of the results to the inclusion of the number and the identity of traits, we reran all analyses with all combinations of five out of six traits. We did not reduce the number of traits lower than five because we might have missed important dimensions of the functional space (Mouillot *et al.*, 2014). The results were robust to this procedure (Figure A.1; Table A.3).

2.3.3 Functional metrics

Functional redundancy was computed using the Unique Trait Combination (UTC) approach (Keyel, Wiegand and Orme, 2016), where the continuous traits (body mass, litter/clutch size and habitat breadth) were binned using Sturges' algorithm (Sturges, 1926). Sturges' algorithm breaks the data into classes based on the sample size and distribution of values across each trait (Sturges, 1926). Our characterization of functional redundancy has a broad resolution and we therefore do not expect species in the same UTC to fully compensate for the loss of group members. Instead, we propose that species with similar traits have similar ecological strategies, and hence can be considered as functionally redundant (Laliberté *et al.*, 2010; Carmona *et al.*, 2016). Our broad resolution also avoids a potential pitfall, where including too many traits or too many fine scale features leads to a metric that simply reflects taxonomy (every species is unique) and thus is equivalent to species richness. We calculated functional dispersion from a Gower dissimilarity matrix produced from the transformed traits.

2.3.4 Null model

To test whether observed functional values differed from the expected distribution of functional values given the observed species richness of an ecoregion, we used a null model based on global randomisation of species composition (Villéger, Mason and Mouillot, 2008; Oliveira *et al.*, 2016). We also implemented a null model based on biome-scale randomisation of species composition, i.e., using biome species pools, to potentially better account for the spatial filtering of trait combinations due to biogeographic and historical processes. Results were qualitatively similar when using a global or biome null model (Figure A.1; Table A.3; Figure A.4); here we present the global null model, to allow functional contributions across biomes to be assessed. To implement the null model, for each ecoregion, we constructed 999 randomised assemblages drawn from a global species pool, while holding species richness constant (the R and bash scripts to run the null models on a High Performance Computer [we used the IRIDIS High Performance Computing Facility, and associated support services at the University of Southampton] are available from the author upon request). To assess the magnitude of the difference for functional redundancy and functional dispersion between the observed (F_{obs}) and null (F_{null}) results we calculated the standardized effect size: SES = $[F_{obs} – \text{mean}(F_{null})]/\text{SD}(F_{null})$. We also carried out one-tailed permutation tests, where the null hypothesis was that the observed and null functional values were equivalent and the alternative hypothesis was that observed functional values were greater (or less) than the expected value under the null model assumptions. If the alternative hypothesis was greater, a p-value was estimated as: (number of $F_{null} \geq F_{obs} + 1)/(999 + 1)$. If the alternative hypothesis was less, a p-value was estimated as: (number of $F_{null} \leq F_{obs} + 1)/(999 + 1)$. Our rarefied analysis therefore maps functional patterns independently of differences in species richness, allowing us to assess the degree to which the observed functional values differ from the null distribution of functional values, revealing regions with higher (positive SES; permutation test [H_1 = greater]) or lower (negative SES; permutation test [H_1 = less]) functional values than expected at random (Villéger, Mason and Mouillot, 2008; Maire *et al.*, 2015). Moreover, the use of SES, which represents the magnitude of the difference between the observed and null results, allows us to compare values across functional dispersion and functional redundancy, and across taxonomic groups with greatly different species richness, such as birds and mammals. Thus, we also performed the functional analyses for birds and mammals independently (Figure A.5; Figure A.6) and assessed the differences in the functional metrics between birds and mammals using two-tailed Kolmogorov-Smirnov tests.

Overall our results and conclusions were similar (i) with and without imputed data (compare Figure 2.1 and Figure A.1; Table A.3; Figure A.2; Figure A.3), (ii) with all combinations of five out of six traits (Figure A.1; Table A.3), and (iii) with a null model based on a global or biome species pool (Figure A.1; Table A.3; Figure A.4).

To facilitate reproducibility and encourage open science, the code (R script), data and results are available in a Figshare repository at: https://figshare.com/articles/Global_trade-offs_of_functional_redundancy_and_functional_dispersion_for_birds_and_mammals/5616424.

2.4 Results

We classify 2,991 ecological strategies, quantified here as Unique Trait Combinations (UTCs), across 15,485 species of birds and mammals. The mean number of species per UTC is 5.2 at the global scale (Figure A.7) and 1.5 within ecoregions. The most speciose UTC contains 327 species and is characterised by ecologically-similar species that are 10-32 g, have 2.0-2.5 offspring per litter/clutch, are diurnal, can fly, exist across 2-4 habitats and are invertivores. By contrast, 43% of UTCs are comprised of only one species, of these ecologically unique species, 55% are mammals (719 mammal species) and 45% are birds (578 bird species) (Figure A.7).

We further identify a common currency of traits (body mass, diel activity, diet, habitat breadth, litter/clutch size and volancy) across birds and mammals. We find cross-taxa redundancy for the traits included here, with 31 cross-taxa UTCs (335 species: 175 bird and 160 mammal species). For example, we identify a UTC composed of four bird species and five mammal species: Spangled Owlet-nightjar *Aegotheles tatei*, Sri Lankan Frogmouth *Batrachostomus moniliger*, cinnamon dog-faced bat *Cynomops abrasus*, Archbold's Nightjar *Eurostopodus archboldi*, cyclops roundleaf bat *Hipposideros cyclops*, Pratt's roundleaf bat *Hipposideros pratti*, Rufous-bellied Nighthawk *Lurocalis rufiventris*, Medje free-tailed bat *Mops congicus* and Pel's pouched bat *Saccolaimus peli*. These nine species thus have similar ecological strategies and play similar roles, such as nocturnal insect predation.

Patterns of functional redundancy and functional dispersion are geographically structured. Tropical ecoregions display the highest functional redundancy, conforming to previously described patterns of taxonomic diversity (Gaston, 2000; Hillebrand, 2004) (Figure 2.1a and Figure 2.1b; correlation between species richness and functional redundancy: $\text{rho}_{823} = 0.94$, $P < 0.001$). Conversely, we observe a weak relationship between species richness and functional dispersion (Figure 2.1a and Figure 2.1c; $\text{rho}_{823} = 0.15$, $P < 0.001$), although the relationship is stronger and contrasting for birds (Figure A.5; $\text{rho}_{823} = -0.51$, $P < 0.001$) and mammals (Figure A.6; $\text{rho}_{823} = 0.56$, $P < 0.001$). Ecoregions with the highest functional dispersion are primarily located outside the tropics: 95% of the top 10% of ecoregions are non-tropical, based on functional dispersion. Specifically, ecoregions with the highest functional dispersion are located across Madagascar, Eastern Asia (especially the Gobi and Taklimakan deserts and the Tibetan and Mongolian plateaus), western USA and the Pontic steppe (Russia, Kazakhstan, Ukraine) (Figure 2.1c). Thus we find, as predicted, that functional redundancy is coupled with species richness, resulting in high functional redundancy across the tropics, while functional dispersion is largely decoupled from richness (Figure 2.1).

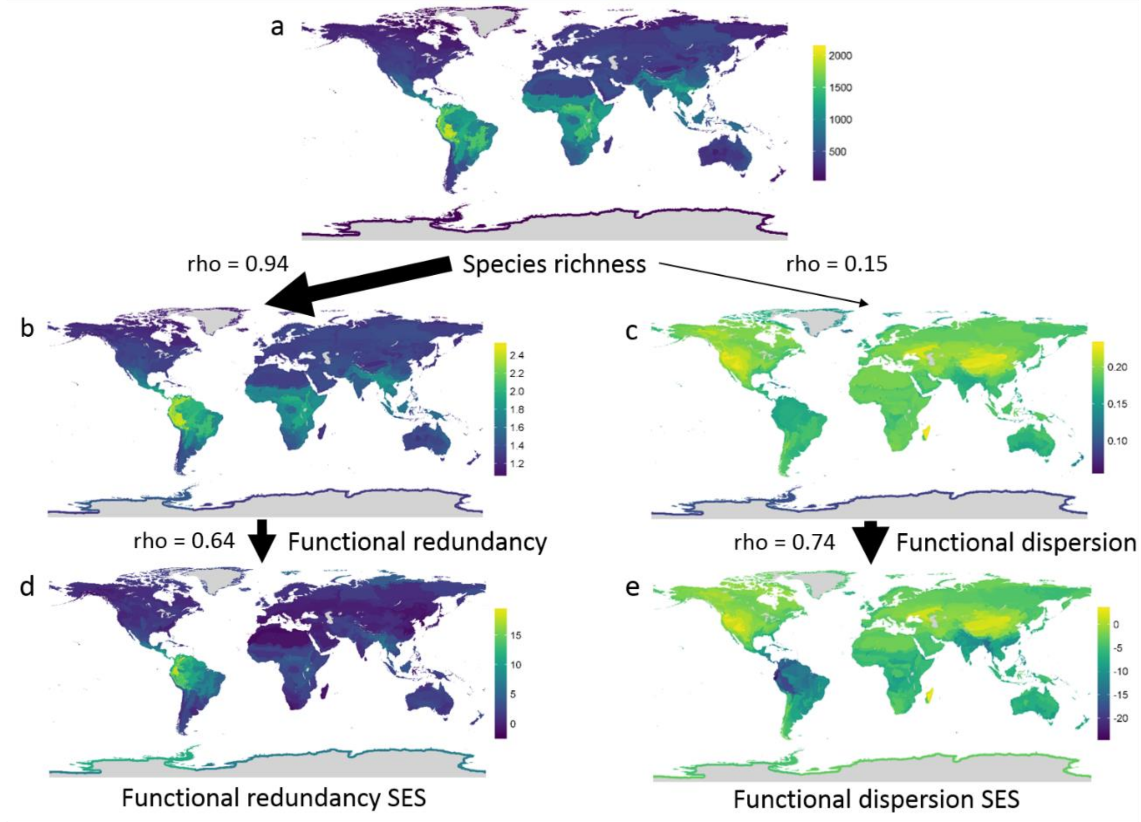

Figure 2.1 Functional dispersion and functional redundancy across 825 terrestrial ecoregions for 15,485 species (all extant terrestrial birds and mammals). (a) Species richness. (b) Functional redundancy. (c) Functional dispersion. (d) Functional redundancy standardized effect size (SES; calibrating against species richness, positive SES values indicate higher functional values than expected at random given their species richness and negative values vice versa). (e) Functional dispersion SES. Arrows are proportional to Spearman’s ρ correlation coefficients (all correlations are significant; rho823, *P* < 0.001). Ecoregions in grey were not considered in the analyses (“lake” and “rock and ice” ecoregions, because they are not coherent systems, i.e., they occur at multiple locations across the globe).

However, we find a different geographic signal after accounting for species richness: standardized effect size (SES), reveals that on average, ecoregions are more redundant (global mean functional redundancy SES = 2.9; 47% of ecoregions have greater functional redundancy than expected at random, *P* ≤ 0.05) and are less dispersed (global mean functional dispersion SES = -6.2; 84% of ecoregions have less functional dispersion than expected at random, *P* ≤ 0.05) than expected under null model assumptions (Figure 2.1d and Figure 2.1e; see https://figshare.com/articles/Global_trade-offs_of_functional_redundancy_and_functional_dispersion_for_birds_and_mammals/5616424 for SES values and permutation test p-values per ecoregion). The Neotropics, especially the

Andean region, present an extreme example of this pattern, with functional redundancy around 10 standard deviations higher and functional dispersion around 15 standard deviations lower than expected at random (Figure 2.1d and Figure 2.1e). Thus, ecoregions in the Neotropics are composed of many species with similar ecological strategies and functional roles.

Ecoregions with the highest functional redundancy SES are concentrated within the Neotropics (Figure 2.1d): 92% of the top 10% of ecoregions were Neotropical, based on functional redundancy SES, which differs from the broader inclusion of tropical ecoregions as hotspots of functional redundancy (Figure 2.1b and Figure 2.1d; $\text{rho}_{823} = 0.64$, $P < 0.001$). Functional dispersion SES shows similar patterns to functional dispersion (Figure 2.1c and Figure 2.1e; $\text{rho}_{823} = 0.74$, $P < 0.001$).

Our functional lens therefore identifies ecoregions, which have equal species richness, such as the Patagonian steppe (Argentina and Chile) and Northern short grasslands (USA and Canada) (419 species each), but very different functional values: Patagonian steppe functional redundancy SES = 2.5, functional dispersion SES = -4.8; Northern short grasslands functional redundancy SES = 0.7, functional dispersion SES = 0.1.

We also identify a spatial disconnect between functional redundancy SES and functional dispersion SES (Figure 2.2; $\text{rho}_{823} = -0.64$, $P < 0.001$). For example, ecoregions generally have either (i) high functional redundancy SES coupled with low functional dispersion SES, characterized by much of the area south of the tropic of cancer (Figure 2.2a; dark red areas) or (ii) high functional dispersion SES and low functional redundancy SES, such as across Madagascar, Eastern and Central Asia and western USA (Figure 2.2a; yellow areas). While some ecoregions, such as across the Sahara and North America, show a more balanced relationship between functional redundancy SES and functional dispersion SES (Figure 2.2a; orange areas), although there are few ecoregions with both high redundancy and dispersion (Figure 2.2b). We thus reveal a global trade-off between functional redundancy SES and functional dispersion SES.

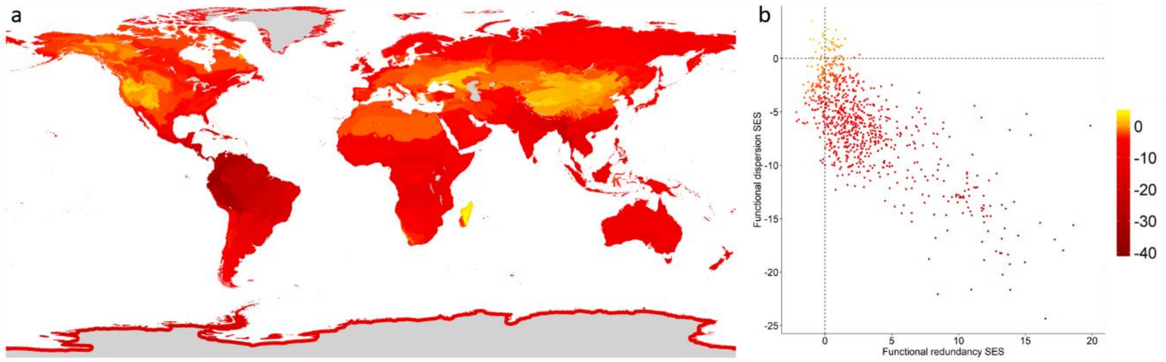

Figure 2.2 The trade-off between functional redundancy and functional dispersion across 825 terrestrial ecoregions for 15,485 species (all extant terrestrial birds and mammals). (a) Mapped spatially. (b) Plotted. The trade-off is calculated as functional dispersion standardized effect size (SES) minus functional redundancy SES. Thus, negative values (dark red) demonstrate greater redundancy than dispersion based on null expectations, positive values (yellow) indicate the dominance of dispersion, and zero values (orange) highlight a balance between the two. The SES represents the magnitude of the difference between the observed and null results and is therefore scaled relative to the null and is directly comparable between the two metrics. The same colour/transparency scheme is applied to the map and scatter plot. Ecoregions in grey were not considered in the analyses ("lake" and "rock and ice" ecoregions, because they are not coherent systems, i.e., they occur at multiple locations across the globe).

Finally, our results highlight that birds and mammals do not equally contribute to redundancy and dispersion (Figure 2.3). Before accounting for species richness, birds have greater functional redundancy than mammals (Figure 2.3a; D = 0.53, $P < 0.001$), while mammals show greater functional dispersion than birds (Figure 2.3b; D = 0.97, $P < 0.001$), confirming our predictions. However, when accounting for species richness, we find the reverse, with greater functional redundancy SES for mammals (Figure 2.3c; D = 0.51, $P < 0.001$) and greater functional dispersion SES for birds (Figure 2.3d; D = 0.25, $P < 0.001$).

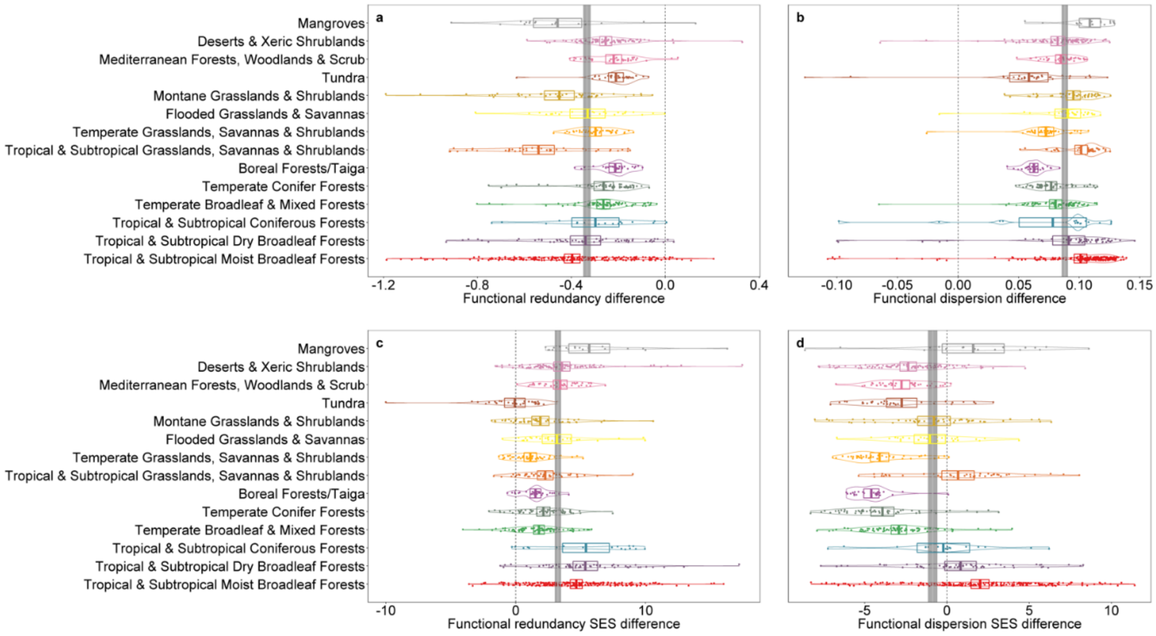

Figure 2.3 Functional differences (functional value for mammals minus functional value for birds) between birds and mammals across the world’s biomes. Differences for: (a) functional redundancy; (b) functional dispersion; (c) functional redundancy standardized effect size (SES; calibrating against species richness); and (d) functional dispersion SES. Negative values indicate greater functional values for birds compared with mammals, whereas positive values represent greater contributions from mammals. Included for each panel is a dashed line with an intercept of zero (i.e., the null hypothesis of no difference between birds and mammals) and a line for the global average across all ecoregions (light grey line) with 95% confidence intervals (dark grey envelope). Also included are the values for each ecoregion per biome as jittered points, violins of data density and boxplots where the central thick line is the mean and the edges of the rectangle are the 95% confidence intervals around the mean.

The greater contribution to functional redundancy SES for mammals is particularly strong across tropical biomes, such as Mangroves; Tropical & Subtropical Coniferous Forests; and Tropical & Subtropical Dry Broadleaf Forests (Figure 2.3c). Conversely, the greater contribution to functional dispersion SES for birds is strongest across temperate and polar biomes, such as Boreal Forests/Taiga; Temperate Grasslands, Savannas & Shrublands; and Temperate Conifer Forests (Figure 2.3d). The difference in functional dispersion SES for birds and mammals is also reflected spatially, where birds have high functional dispersion SES across temperate ecoregions and mammals show high functional dispersion SES across tropical ecoregions (Figure A.5e; Figure A.6e).

Our findings were robust to the imputation of missing trait data, the traits selected and the scale at which the randomised pool was constructed (Figure A.1; Figure A.2; Figure A.4; Table A.3).

2.5 Discussion

Here we quantify functional redundancy and functional dispersion globally for 15,485 bird and mammal species, using a systematic approach. Previous global analyses have focussed on either functional redundancy (Huang, Stephens and Gittleman, 2012) or functional dispersion (Oliveira *et al.*, 2016) for mammals only, but here we summarise both redundancy and dispersion across birds and mammals for the first time. We also establish a common currency of traits that allow comparisons and analyses to be made across and between birds and mammals - broadening current single-taxon approaches (Safi *et al.*, 2011; Barbet-Massin and Jetz, 2015; Oliveira *et al.*, 2016). We find overlap in the roles played by birds and mammals, even when including flight ability and diel activity (two major differentiators between birds and mammals), indicating cases where birds and mammals have converged on similar ecological strategies. Thus single-taxon analyses testing for functional redundancy and functional dispersion offer limited insights, as an unknown number of roles fulfilled by other taxa is ignored (Dehling and Stouffer, 2018). These results therefore demonstrate the importance of considering ecological comparability between birds and mammals in conservation strategies.

Species richness has dominated our view of global biodiversity patterns for centuries (Gaston, 2000; Hillebrand, 2004), however functional redundancy and functional dispersion are increasingly recognized as essential biodiversity components (Elmqvist *et al.*, 2003; Laliberté *et al.*, 2010; Luck, Carter and Smallbone, 2013; Oliver, Isaac, *et al.*, 2015). While high species richness, functional redundancy and functional dispersion are all predicted to increase the capacity of communities to adapt, reassemble, retain biotic interactions and maintain ecosystem functions with disturbance events (Holling, 1973; Hooper *et al.*, 2005; Laliberté *et al.*, 2010; Luck, Carter and Smallbone, 2013; Oliver, Heard, *et al.*, 2015; Oliver, Isaac, *et al.*, 2015) (see Appendix A.1), our results show that all three do not generally coexist in the ecoregional species pools of birds and mammals. Instead, we observe that the overall breadth of functional roles for bird and mammal species combined does not increase proportionally with richness - leading to a global trade-off between functional redundancy and functional dispersion (Figure 2.2). We therefore suggest that different processes generate species richness/functional redundancy and functional dispersion, leading to a novel, and generally non-tropical, distribution of hotspots of high functional breadth for birds and mammals, across Madagascar, Eastern Asia, western USA and the Pontic steppe. A potential explanation is that these predominantly steppe and desert regions are highly dynamic and environmentally variable, resulting in high levels of competition, strong spatiotemporal resource partitioning, and therefore high ecological dissimilarity.

We also find strong spatial differences in the contributions of birds and mammals to functional redundancy and dispersion (Figure 2.3). Before accounting for species richness, birds have greater functional redundancy than mammals, simply because birds are more speciose compared to mammals (almost double the number of species of birds). As species richness increases, the similarity in species functional roles also increases (Safi *et al.*, 2011). However, after accounting for species richness, mammals show greater similarity in their functional roles, whereas birds support greater breadth of functional roles. This is particularly apparent in the tropics where mammals have relatively higher functional redundancy SES. Birds, by comparison, have higher functional dispersion SES, predominantly across temperate and polar biomes. We propose that this latitudinal trade-off between birds and mammals could be underpinned by the pronounced mobility of birds, which could allow them to exploit transient mid/high latitude resources (Kirby *et al.*, 2008). For instance, one of the most common patterns for migratory birds is to breed in northern temperate or polar biomes, before spending the non-breeding season in tropical biomes (Kirby *et al.*, 2008). Birds may therefore provide ecological and functional links (Lundberg and Moberg, 2003) between tropical and temperate biomes. Alternatively, the latitudinal trade-off between birds and mammals could be the consequence of the late Quaternary extinctions and extirpations, which reshaped patterns of mammalian species richness and functional diversity (Faurby and Svenning, 2015). In particular, the late Quaternary extinctions led to reduced functional diversity of mammals outside sub-Saharan Africa (Faurby and Svenning, 2015). We therefore suggest that the late Quaternary extinction filter could have resulted in the higher functional dispersion SES for birds compared to mammals across temperate and polar biomes.

The greater functional dispersion SES of birds at high latitudes has the potential to stabilise ecosystem functions (e.g. process rates), through compensatory dynamics between species (i.e., the portfolio effect), where a diversity of responses should lead to some bird species successfully responding to a specific disturbance (Elmqvist *et al.*, 2003; Luck, Carter and Smallbone, 2013; Mori, Furukawa and Sasaki, 2013) (see Appendix A.1). On the other hand, the higher functional redundancy SES of mammals than birds across the tropics could insure these regions against species loss and declines (Fonseca and Ganade, 2001; Luck, Carter and Smallbone, 2013; Carmona *et al.*, 2016) - the loss of species from ecoregions with high redundancy should not result in a substantial decrease in function, because other species with similar traits are likely to remain (Flynn *et al.*, 2009; Carmona *et al.*, 2016).

Under null model assumptions, on average, ecoregional species pools are functionally more redundant and less dispersed than expected. Therefore species within ecoregions are more clustered (had more similar trait values) than expected at random, which could be due to several different processes. A plausible candidate for this finding of over-redundancy and under-dispersion is environmental filtering. Environmental filtering theory states that abiotic factors, such as climatic stress, increasingly constrain the trait combinations expressed in environments (Lamanna *et al.*, 2014). Thus, environmental filtering at the ecoregion scale may limit the trait space that species can occupy, increasing functional similarity within ecoregions compared to a global- or biome-based null, especially across the Neotropics and for mammals. For instance, the higher functional redundancy SES for mammals compared to birds could be due to stronger environmental filtering, leading to greater ecological similarity for mammals within ecoregions - whereby ecoregional scale selection favours a restricted set of mammalian traits. Consequently, we suggest that weaker environmental filtering for birds may allow a greater breath of functional roles to coexist within the species pool.

The highest functional redundancy SES is across the Neotropics. Neotropical ecoregions are therefore composed of many species with similar functional roles and ecological strategies. There are a number of potential, non-mutually exclusive, mechanisms for the finding of greater redundancy than expected across the Neotropics, such as high environmental stability, relaxed competition, low environmental heterogeneity, strong environmental filtering, high productivity and/or slow trait evolution (Safi *et al.*, 2011; Lamanna *et al.*, 2014; Belmaker and Jetz, 2015; Oliveira *et al.*, 2016). For instance, low seasonality and high resource availability, as observed across the Neotropics, might together facilitate the coexistence of functionally redundant species (Safi *et al.*, 2011; Oliveira *et al.*, 2016) - the ‘more individuals’ hypothesis (Currie *et al.*, 2004). Alternatively, or in addition to resource availability, we suggest that the high species richness observed in the Neotropics could result from a fast accumulation of species, due to higher rates of speciation (via increased opportunities for the evolution of reproductive isolation, or faster molecular evolution, or the increased importance of biotic interactions) and/or low extinction rates (Currie *et al.*, 2004; Mittelbach *et al.*, 2007; Rolland *et al.*, 2014; Belmaker and Jetz, 2015). This high Neotropical richness may then promote stabilizing selection on traits, inhibiting evolutionary responses within species (de Mazancourt, Johnson and Barraclough, 2008) and ultimately lead to strong ecological similarities, highly conserved trait combinations and high functional redundancy SES. The high functional redundancy SES across the Neotropics could therefore simply be the result of rapid accumulation of species with little time for ecological divergence. In addition, our results add further evidence that the high species richness in the Neotropics is associated with a denser occupation of trait space (‘niche packing’), which could arise through finer specialization or greater overlap in resource use, rather than a consequence of more ecological opportunities (‘niche expansion’) (Klopfer and MacArthur, 1961; MacArthur, 1965; Belmaker and Jetz, 2015; Pigot, Trisos and Tobias, 2016).

It is possible that the interrelationship between redundancy and dispersion - such as hotspots of each - could be used to identify the mechanisms by which environmental change may impact ecoregional species pools. For example, a given disturbance may result in greater species loss from an ecoregion with low dispersion, but if functional redundancy is high this perturbation may have little impact on functioning overall (Luck, Carter and Smallbone, 2013). Conversely, if dispersion is high, an assemblage may overall respond successfully to environmental changes, but the loss of even a few species could have major implications if redundancy is low (Luck, Carter and Smallbone, 2013). Ecoregions can therefore be generally divided into those potentially more vulnerable to disturbance events (high redundancy, low dispersion, e.g., the Neotropics) and those potentially more vulnerable to species loss (low redundancy, high dispersion, e.g., Madagascar).

Thus overall our results illustrate that focussing conservation efforts in regions with high species richness, as is traditionally done (Reid, 1998; Olson and Dinerstein, 2002), will simultaneously benefit species richness and functional redundancy, but will not maintain functional dispersion. Although the relationship between species richness and functional dispersion differs for birds and mammals when analyzed separately. For birds, the prioritization of species richness will have undesirable consequences for functional dispersion, due to a negative relationship between richness and dispersion, whereas for mammals the conservation of species richness will provide some support of functional dispersion. In addition, phylogenetic diversity, which is often used to guide conservation management, has been found to capture functional diversity unreliably (Mazel *et al.*, 2018), thus functional indices provide a complementary and distinct dimension of biodiversity, in combination with taxonomic and phylogenetic diversity. Hence we suggest that functional dispersion should be further evaluated as a conservation objective. For instance, ecoregions with high functional dispersion should have greater capacity to successfully respond to multiple disturbances, as greater functional dispersion is predicted to lead to asynchrony between species’ population sizes and enhanced compensatory responses following environmental change, and therefore greater ecological recovery and stability (Mori, Furukawa and Sasaki, 2013; Oliver, Heard, *et al.*, 2015). Furthermore, the importance of functional dispersion is predicted to become increasingly evident in an ever-changing world (Elmqvist *et al.*, 2003; Laliberté *et al.*, 2010; Luck, Carter and Smallbone, 2013), especially in relation to disturbances that span the globe and are difficult to manage directly, such as climate change (Barbet-Massin and Jetz, 2015). We therefore recommend further study of the identified regions of high and low functional dispersion for birds and mammals combined and separately, which could elucidate the mechanisms and temporal impacts of high functional breadth for these taxa.

The traits employed were selected to reflect the spatiotemporal distribution of resource capture, utilisation and release by birds and mammals. However, the ecological importance of any particular trait might vary across and between bird and mammal taxa, and the selection of ecologically relevant traits is always somewhat subjective and dependent on data availability (Mouillot *et al.*, 2014; Belmaker and Jetz, 2015; Oliveira *et al.*, 2016). To tackle this we implemented a transparent and systematic trait selection process (Appendix A.3) (Luck *et al.*, 2012), within the constraints of data availability and data resolution, to construct the most complete and inclusive database of bird and mammal traits to date. The patterns and relationships we outline here reflect a complex history of speciation, extinction, anagenesis, and dispersal, with each factor probably shaped by species' traits (Davies *et al.*, 2008) and dynamically driven by both natural (e.g., environmental filtering, biogeography, competition) and human pressures (e.g., habitat loss, invasive species). Here we analyse only the resultant outcome of these two types of drivers on species composition, as disentangling these processes is beyond the scope of our study. We also only explicitly accounted for two of the major components of species' functional roles: species' distributions and species' ecological strategies (traits). We did not however account for the direct interactions between species and their effects on each other, known as the 'Eltonian shortfall' (Peterson *et al.*, 2011), although information on species interactions is indirectly contained within our analysis through species' diets (Dehling and Stouffer, 2018). Thus, future work that explicitly accounts for the interactions between species within the regional species pool, for instance by employing network analysis (Dehling and Stouffer, 2018), could reveal further insights into how species' roles and functional contributions summate across the regional pools.

In conclusion, we show that the analysis of functional redundancy and functional dispersion at the global scale can provide new insights into taxonomic, trait and spatial signals of bird and mammal diversity. We recommend consideration of both the similarity and breadth of functional roles across multi-taxa species pools, to accommodate the global trade-off between functional redundancy and functional dispersion and to support the maintenance of insurance and response diversity between and within ecoregions.

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Chapter 3 Projected losses of global mammal and bird ecological strategies

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3.1 Abstract

Species, and their ecological strategies, are disappearing. Here we use species traits to quantify the current and projected future ecological strategy diversity for 15,484 land mammals and birds. We reveal an ecological strategy surface, structured by life-history (fast-slow) and body mass (small-large) as one major axis, and diet (invertivore-herbivore) and habitat breadth (generalist-specialist) as the other. We also find that of all possible trait combinations, only 9% are currently realized. Based on species' extinction probabilities we predict this limited set of viable strategies will shrink further over the next 100 years, shifting the mammal and bird species pool towards small, fast-lived, highly fecund, insect-eating, generalists. In fact, our results show that this projected decline in ecological strategy diversity is much greater than if species were simply lost at random. Thus, halting the disproportionate loss of ecological strategies associated with highly threatened animals represents a key challenge for conservation.

3.2 Introduction

Maintaining biodiversity is crucial to the functioning of ecosystems and the delivery of ecosystem services (Mace, Norris and Fitter, 2012), yet biodiversity is disappearing (Dirzo *et al.*, 2014). Mammals and birds, in particular, are diverse - comprising more than 15,000 living species - and are important ecological components in nutrient distribution, propagule (e.g., seed) dispersal, and as interactive connectors between species and habitats (Sekercioğlu, 2006; Ripple *et al.*, 2017). However, mammals and birds are subject to strong human pressure, leading to high extinction rates (Rapacciuolo *et al.*, 2017). The diversity and extinction of mammals and birds has, to date, predominantly been studied according to taxonomy (Schipper *et al.*, 2008; Thomas *et al.*, 2008; Jenkins, Pimm and Joppa, 2013) and phylogenies (Schipper *et al.*, 2008; Jetz *et al.*, 2012; Davis, Faurby and Svenning, 2018). However, species are also characterized by their traits - morphological, physiological, phenological or behavioural features measurable at the individual level (Violle *et al.*, 2007), which can provide a more direct link than taxonomy or phylogeny to ecosystem processes and functions (Diaz and Cabido, 2001; Hooper *et al.*, 2005; Sekercioğlu, 2006). Traits jointly determine a species' ecological role (Violle *et al.*, 2007; Wilman *et al.*, 2014) and thus combinations of traits are increasingly being used to summarise species' ecological strategies (Brum *et al.*, 2017).

Mammals and birds exhibit strong ecological variation - from large hypercarnivores, to long-lived arboreal frugivores, to wide-ranging scavengers. Even so, many species share fundamentally similar strategies, such as flying insectivores (bats and birds), and many traits co-vary across species (Bielby *et al.*, 2007). Many mammal and bird species compete for resources and thus face a broadly similar range of selection pressures (e.g., climatic events, predation, habitat change). Although similar selection pressures should lead to the adoption of comparable strategies (i.e., convergent evolution), evolutionary history (Johnson, McKinney and Sorenson, 1999) has applied constraints that will likely lead to divergence between mammals and birds. The contrast between the high ecological diversity but convergent strategies across mammal and bird species raises a fundamental question: how are ecological strategies presently organized across these two groups? We predict that mammals will show greater ecological diversity, given the rapid morphological, ecological, and phylogenetic diversification in terrestrial mammals during the Cenozoic that led to an expansion in mass by four orders of magnitude (Alroy, 1998; Smith *et al.*, 2010).

In addition, past and present human impacts have led to the accumulation of extinction debts - numerous species are already committed to extinctions that are yet to occur (Tilman *et al.*, 1994; Isbell *et al.*, 2017). Extinction is a selective process because both extrinsic and intrinsic factors result in the non-random loss of species (Cardillo *et al.*, 2005). Thus, although exposure to threatening processes (extrinsic) is the ultimate cause of extinction, a species' ecological strategy (intrinsic) determines how well it is able to withstand the threats to which it is exposed (Cardillo *et al.*, 2004). Ecological strategies, and the individual traits that comprise them, can therefore be seen as adaptations to extrinsic rates of mortality (Charnov, 1993; Bielby *et al.*, 2007). For example, traits that confer ecological flexibility (e.g., generalist species) and allow populations to recover rapidly from depletion may offer a degree of protection from external threats (Cardillo *et al.*, 2004), while large-bodied species generally have higher extinction risk than small-bodied species (Ripple *et al.*, 2017). Employing probabilistic extinction frameworks allows us to evaluate the impact of paying off these extinction debts and forewarn us of potential ecological consequences, enabling us to act - before it is too late. For instance, when species become extinct locally and globally, their ecological strategies are lost (Estes *et al.*, 2011; Ripple *et al.*, 2017), with potentially strong implications for ecosystem functions (Sekercioğlu, Daily and Ehrlich, 2004; Estes *et al.*, 2011; Dirzo *et al.*, 2014; Brum *et al.*, 2017; Smith *et al.*, 2018).

Here we focus on three primary research questions: (i) what are the major gradients across the diversity of mammal and bird ecological strategies? (ii) how do mammals and birds share ecological strategy space? (iii) how do projected extinctions affect ecological diversity when compared with random species loss?

To explore species' ecological strategies, we ordinated (principal components analysis; PCA) all 15,484 living land mammals and birds based on five traits: body mass, litter/clutch size, habitat breadth, diet, and generation length (Chapter 2) (Cooke, Bates and Eigenbrod, 2019). The ordination of species across this surface represents a 2-dimensional continuum, integrating ecological strategies within each of the five trait dimensions to form an ecological strategy surface, through which gradients can be identified (Winemiller *et al.*, 2015; Díaz *et al.*, 2016). We then constructed 5-dimensional ecological strategy spaces, via hypervolume estimation(Blonder, 2017, 2018), for mammals and birds combined and separately. These ecological strategy spaces were compared to four alternative null models of multivariate trait variation, previously applied to plants (Díaz *et al.*, 2016), to understand strategy convergence across and between mammals and birds. Finally, we modelled the impact of future projected extinctions (i.e., evaluating the cost of the current extinction debt) on the global ecological strategy space. We forecasted the volume of ecological strategy space 100 years into the future, given extinction probabilities assigned to the IUCN Red List categories (Mooers, Faith and Maddison, 2008). To put the loss of species with high extinction risk in perspective we compared the projected scenario to a randomized scenario, controlling for species richness. Overall, we summarize the ecological consequences of biodiversity loss.

Here, we find that the ecological diversity of mammals and birds is structured by life-history speed (fast-slow) and body mass (small-large) in one dimension, and diet (invertivore-herbivore) and habitat breadth (generalist-specialist) in the other dimension. We also show that the ecological strategy space currently occupied by mammals and birds is strongly restricted compared to null expectations. Moreover, we demonstrate that future projected extinctions result in a larger reduction of ecological strategy space than expected at random. Consequently, we find that paying off current extinction debts leads to a shift in the global composition of mammals and birds to smaller, faster-lived, more fecund, more generalist and preferentially insect-eating species, fundamentally restructuring life on our planet.

3.3 Results

3.3.1 Ecological strategy surface

Despite high diversity in form and function of mammals and birds across the world, there are distinct patterns among trait combinations that define species' ecological strategies (Figure 3.1). The first two principal components (PC1 and PC2) explained more than half (60%) of the total trait variation (Figure 3.1), but there was some variation in all five principal components (Figure B.1).

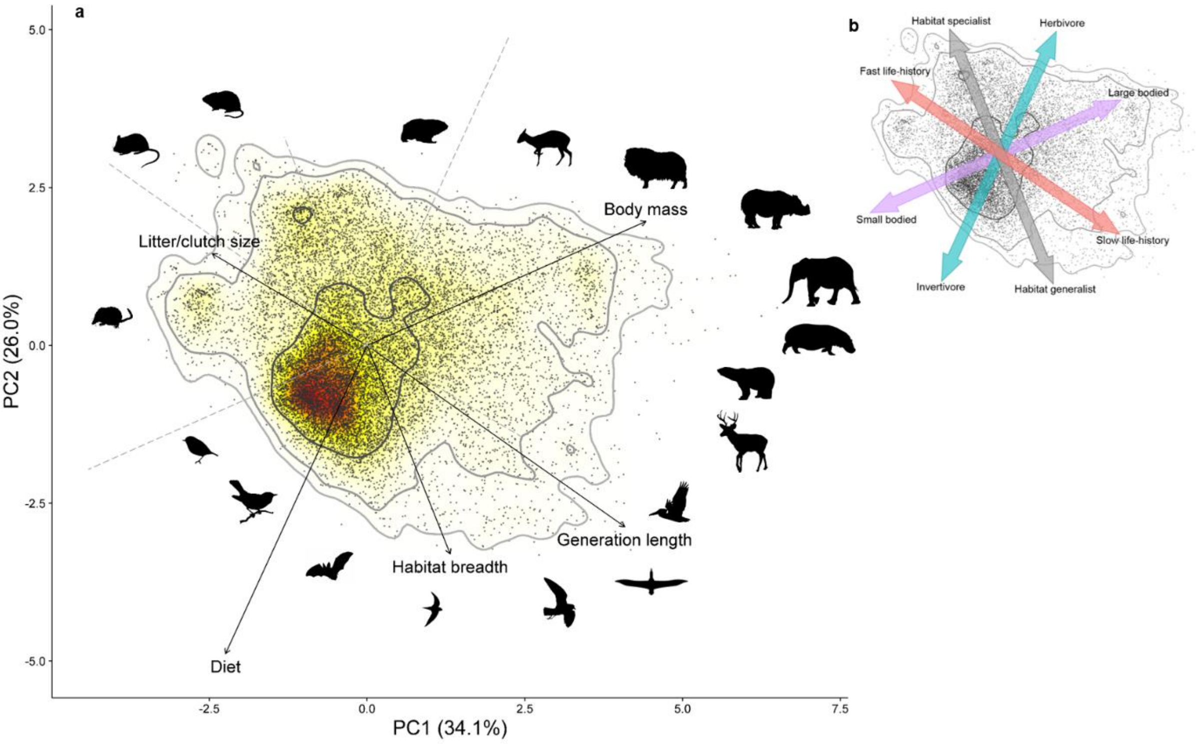

Figure 3.1 The ecological strategy surface for mammals and birds. (a) Projection of 15,484 living land mammal and bird species (dots) on the surface defined by principal component

axes (PC) 1 and 2 (mean values across 25 imputed datasets; Appendix B.1; Figure B.2). Solid arrows indicate direction and weighting of vectors representing the five continuous traits analyzed (Table B.1 for loadings). Silhouettes show a selection of species characterizing the edges of strategy space (eight silhouettes were freely downloaded from PhyloPic www.phylopic.org, under CC0 1.0 Public Domain Dedication, while the rest were created in Inkscape by the authors; Figure B.3 for species locations, scientific names and image sources). The colour gradient indicates regions of highest (red) to lowest (white) occurrence probability of species across the ecological strategy surface, with contour lines indicating 0.5, 0.95 and 0.99 quantiles. Percentage values represent proportion of the total variation explained by each PC. To quantify diet, we extracted the dominant diet gradient across ten diet categories for all species, using a principal coordinates analysis (PCoA; Figure B.4). (b) The ecological strategy surface is also illustrated with simplified gradients.

The primary axis of differentiation, PC1, integrates both a body mass gradient (body mass loading = 0.63) and the fast-slow continuum (Purvis, Gittleman, *et al.*, 2000; Cardillo *et al.*, 2004; Bielby *et al.*, 2007) - here, the trade-off between litter/clutch size (loading = -0.35) and generation length (loading = 0.58) (Figure 3.1). Species with low PC1 values are therefore generally characterized by small body mass and fast life-history (short generation length, high litter/clutch size), e.g., shrews, rodents, passerines; whereas species with high PC1 values are distinguished by large body mass and slow life-history, e.g., elephants, rhinos, deer, pelicans (Figure 3.1). PC1 therefore also reflects how quickly populations can recover from low levels, as slow life histories reduce the ability of populations to compensate for increased mortality (Owens and Bennett, 2000). Moreover, body mass relates to the contributions of species to multiple ecological functions, such as pollination (Sekercioğlu, Daily and Ehrlich, 2004; Luck *et al.*, 2012), predation (Ripple *et al.*, 2014), herbivory (Ripple *et al.*, 2015), food-web structure (Williams and Purves, 2011) and seed-dispersal (Sekercioğlu, Daily and Ehrlich, 2004; Jordano *et al.*, 2007). PC2 characterises a gradient between invertivorous, habitat generalists (diet loading = -0.70, habitat breadth loading = -0.47) at low PC2 values, e.g., echolocating bats, swifts, seabirds; to herbivorous, habitat specialists at high PC2 values, e.g., marmots, duikers, rodents (Figure 3.1). PC2 therefore reflects the trophic interactions of species with other food web components and, consequently, their effect on nutrient cycling (Sekercioğlu, 2006; Ripple *et al.*, 2017). PC2 also characterizes species responses to changes in resource availability and their capacity to adapt to environmental change, especially habitat modifications (Luck, Carter and Smallbone, 2013). For instance, a broad habitat breadth confers greater ecological flexibility and thus the opportunity to shift resource use or distribution in response to environmental change. PC2 also generally distinguishes volant species from non-volant species (Figure B.5c), not directly through their aerial mode (which was not used as a trait within our PCA), but via ecomorphological differences (reflecting previous results for mammals only (Holt *et al.*, 2018)). The strongest correlations across the traits were between body mass and diet (Pearson's r = -0.45), body mass and generation length (r = 0.41), and generation length and litter/clutch size (r = -0.34) (Figure B.6). The weakest correlations were between diet and litter/clutch size (r = -0.02), diet and generation length (r = 0.06), and body mass and habitat breadth (r = 0.08).

3.3.2 Ecological strategy space

We further find that the ecological strategy space currently occupied by mammals and birds is strongly restricted (9-62% occupation of null strategy spaces, all permutation tests $P \leq 0.001$; Table B.2) when compared to four alternative null models (Díaz *et al.*, 2016): 1 - traits uniformly distributed and independent from each other, approximately a hypercube (9% occupation); 2 - traits normally distributed and independent from each other, approximately a hypersphere (37%); 3 - traits distributed as observed and independent from each other (62%); 4 - traits normally distributed and correlated as observed, approximately a hyperellipsoid (51%). Specifically, of all possible trait combinations - null model 1 assumes any combination of trait values can arise and escape natural selection with equal probability (Leimar, 2002; Díaz *et al.*, 2016) - only 9% are realized in contemporary mammal and bird ecological strategies and are therefore currently evolutionarily viable on Earth.

Our comparative analysis of mammals and birds reveals that the avian strategy space is more than a third smaller than that for mammals, despite birds being represented by around double the number of species (10,252 birds occupy a volume of 534 SD^5, while 5,232 mammals occupy 881 SD^5 in volume) (Figure 3.2). This contrast means that birds (19.2 species SD^{-5}) are more than three times more concentrated within their ecological strategy space than mammals (5.9 species SD^{-5}), indicating high strategy convergence and suggesting that ecological diversity and taxonomic diversity could be generated by different processes. We also observe low overlap between mammals and birds in strategy space (Figure B.5a), with mammals and birds overlapping across 31% (intersection volume = 332 SD^5) of the total combined strategy space (combined volume = 1084 SD^5). Birds occupy 19% of space unoccupied by mammals (unique volume = 202 SD^5) and mammals 51% of the space unoccupied by birds (unique volume = 549 SD^5) (Figure 3.2). Mammals therefore show a greater range of ecological modes, which we hypothesize indicates both greater net evolutionary change - the dissimilarity between species regardless of the evolutionary pathways - and possibly greater ecological adaptive potential, which should enhance the probability that at least some species will survive into the future (Foote, 1997). Although, the adaptive potential of mammals and birds will depend on the specific nature and types of selection pressures. Thus, in an adaptation context, we suggest that mammals show a greater range of specialization and adaptation, enabling them to persist and compete in dynamic environments, whereas birds have converged on a more generalized strategy (i.e., a diurnal, volant, invertivorous strategy; Figure 3.1). We suggest that the high convergence and generalized strategy of birds could be facilitated by their ability to fly (reflected by the high convergence shown by bats; Table B.3), allowing volant species to escape from disturbances (Berg *et al.*, 2010) and competition.

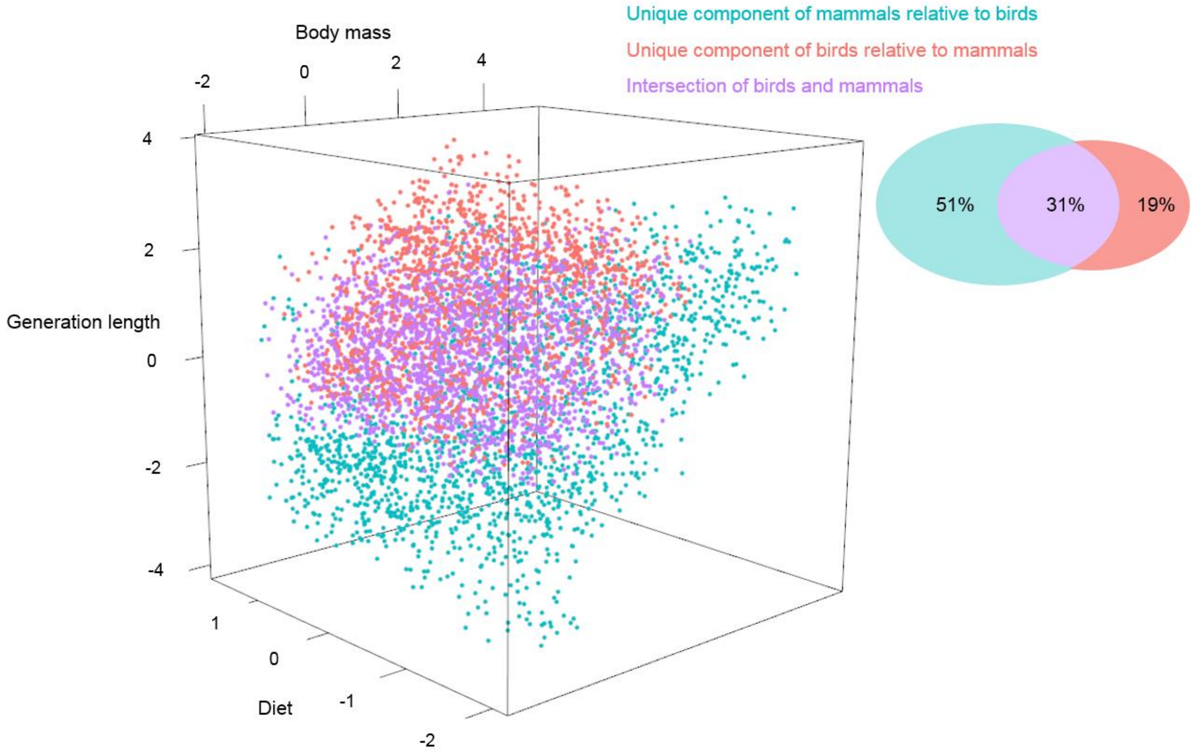

Figure 3.2 Overlap between mammal and bird ecological strategy spaces. The separation (unique components) and overlap (intersection) of 15,484 living land mammal and bird species across ecological strategy spaces (hypervolumes). The two ecological strategy spaces (one for mammals, one for birds) are constructed on the basis of the five z-transformed traits, although only the three traits with the highest loadings across the ecological strategy surface are used for visualization: $\log_{10}$(body mass), $\log_{10}$(generation length) and diet (Figure 3.1a; Table B.1). The Venn diagram shows the percentage of the total combined volume occupied by each component (the percentages sum to 100 before rounding).

3.3.3 Projected extinctions

We contrast projected and randomized extinction scenarios. For the projected extinction scenario, we assigned extinction probabilities to IUCN Red List categories, for example 66.7% of

Endangered species and 10% of Vulnerable species went extinct for each simulation (Mooers, Faith and Maddison, 2008). The randomized extinction scenario selected an equivalent number of species for extinction over the next 100 years, but randomly with respect to species identity/traits. We replicated the projected and randomized scenarios 999 times each. We find that the global ecological strategy space contracts more than expected at random under the projected extinction scenario (Kolmogorov-Smirnov test: randomized extinction mean = 1058 SD^5, projected extinction mean = 1021 SD^5; $D = 0.77$, $P < 0.001$) (Figure 3.3). We also forecast over double the loss of ecological diversity over the next 100 years than expected at random (randomized compared to observed, effect size = -25.2 [95% CI: +6.0, -57.7] SD^5; projected compared to observed, effect size = -62.5 [-34.3, -91.5] SD^5; Figure 3.3). Thus, the ecological, and potentially functional, consequences of the projected extinctions are greater than would be expected under random species loss.

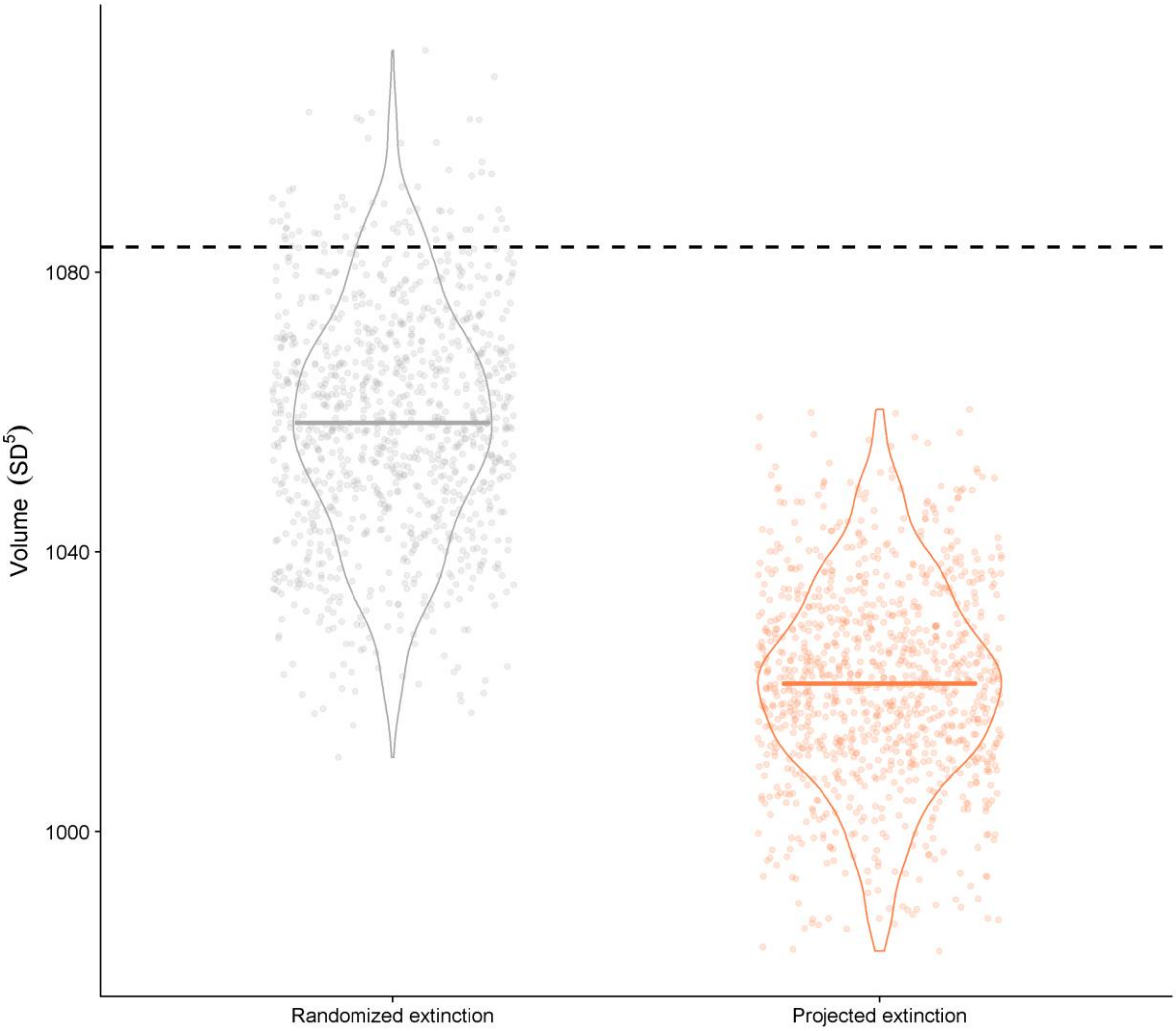

Figure 3.3 The ecological strategy space for mammals and birds under 100-year extinction scenarios. The dashed horizontal line indicates the observed ecological strategy space (hypervolume). For both scenarios we include jittered points for each of the

999 replicates, violins of data density and a central thick line of the mean. Due to the stochastic nature of the hypervolume algorithm (Blonder, 2017), the ecological strategy space may increase as species are removed. 1,095 mammal and bird species are lost under both the projected and randomized extinction scenarios, reflecting the probabilistic extinctions based on the IUCN threat categories (3.5 Methods).

After 100 years of projected extinctions, the global composition of mammals and birds is predicted to shift to smaller (permutation test: body mass observed mean = 70.3 g, body mass projected mean across runs [minimum – maximum across replicates] = 64.1 g [63.4 – 64.7 g]; $P \leq 0.001$), faster-lived (generation length observed mean = 4.27 years, projected mean = 4.22 years [4.21 – 4.23 years]; $P \leq 0.001$), more fecund (litter/clutch size observed mean = 2.51, projected mean = 2.55 [2.54 – 2.56]; $P \leq 0.001$), more generalist (habitat breadth observed mean = 3.23, projected mean = 3.32 [3.31 – 3.33]; $P \leq 0.001$) and more invertivorous species (diet observed mean = -0.00032, projected mean = 0.0012 [0.00087 – 0.0014]; $P \leq 0.001$) (Figure B.5f; Figure B.7). These shifts are relatively large for the species pool and temporal scale investigated, for example, Davis, Faurby and Svenning (2018) showed that current median mammal body mass is 14% lower than during the Last Interglacial (~130,000 years ago), while we predict an extra 25.2% (23.9 – 25.8%) reduction in median mammal body mass over the next 100 years from the current level. These declines in body mass equate to a reduction rate of -0.00011% per year between the Last Interglacial and now, compared to a predicted reduction rate of -0.25% (-0.24 – -0.26%) per year between now and the next 100 years.

3.4 Discussion

Despite high diversity across mammals and birds, we find a limited set of strategies that allow mammals and birds to survive natural selection, physiological challenges, and competitive exclusion currently on Earth. In particular, birds occupy a third less strategy space than mammals, despite around double the number of species. This supports our suggestion that rapid mammalian diversification during the Cenozoic led to high mammal ecological diversity (Alroy, 1998; Smith *et al.*, 2010), but limited taxonomic diversity. More generally, some trait combinations may be unobserved because they are non-viable (physically impossible, e.g., large-bodied and short generation length**,** or maladaptive), whereas others may be viable but not present within living species (Winemiller *et al.*, 2015). Strategies that are viable but are not currently realized could be due to a number of reasons, including: evolutionary factors (e.g., never evolved), ecological factors (e.g., competitively inferior strategies, strategies incapable of persisting within the current environment (Winemiller *et al.*, 2015), such as extinct species), or they could occur in taxa not included in our analyses. Hence, as more trait data becomes available, comparative analyses among more distantly related taxa (e.g., all tetrapods - all vertebrates) will become possible, ultimately leading to a wider understanding of ecological strategy differentiation across species (Pianka *et al.*, 2017).

We forecast a substantial ecological downsizing for mammals and birds, supporting recent findings (Rapacciuolo *et al.*, 2017; Ripple *et al.*, 2017; Smith *et al.*, 2018). Ecological downsizing can entail the loss of unique ecological functions (Estes *et al.*, 2011; Boyer and Jetz, 2014; Dirzo *et al.*, 2014) and can impact ecosystem structure, function, and biogeochemical cycles (Rule *et al.*, 2012; Berzaghi *et al.*, 2018). Hence, downsizing could be a driver, as well as a consequence, of global change with implications for the long-term sustainability of ecological and evolutionary processes (Smith *et al.*, 2010; Dirzo *et al.*, 2014; Berzaghi *et al.*, 2018; Davis, Faurby and Svenning, 2018). Here we reveal that this extinction-driven shift in body mass extends to additional traits: generation length, litter/clutch size, habitat breadth and diet, with further potential ecological consequences. For example, the predicted shortening of generation length could impact the timing and stability of ecological processes, such as scavenging. Among living vertebrates, only vultures are obligate scavengers (Ruxton and Houston, 2004). Vultures are slow-lived (long generation length, low clutch size), highly threatened and are fundamentally involved in the scavenging of carrion in large packages (Ruxton and Houston, 2004). Thus the predicted loss of many vulture species (e.g., 8 are Critically Endangered) could have significant implications for scavenging and the spread of disease, as the initial loss of the most important species can cause rapid declines in ecosystem processes (Larsen, Williams and Kremen, 2005). Additionally, the predicted shift towards insect-eating species could potentially increase the susceptibility of the global species pool to specific threats, such as land use intensification or insect declines. For instance, insectivorous birds are less resilient to high-intensity than low-intensity land use (Karp *et al.*, 2011), thus future land intensification could lead to further extinctions. Overall, species' ecological strategies are intrinsically linked to extinction, and extinction to species' ecological strategies.

We demonstrate that the projected loss of mammals and birds will not be ecologically random, but a selective process across strategy space, where specific ecological strategies (e.g., slow-lived scavengers, herbivores, habitat specialists) will be filtered out; although, these directional changes could be directly or indirectly related to body mass, as many traits co-vary across species (Bielby *et al.*, 2007). For example, diet and generation length were moderately correlated with body mass. Selection on body mass could therefore act as an extinction filter (Rapacciuolo *et al.*, 2017; Ripple *et al.*, 2017), driving shifts in the associated traits. Still, body mass-associated extinction is likely to have further ecological consequences, as outlined above, due to the combinatory nature of traits (selection occurs on species' ecological strategies). In addition, we predict strong shifts in traits that are generally unrelated to body mass, such as habitat breadth and litter/clutch size. We therefore suggest that the ecological implications of the extinction debt go beyond body mass and emphasize that additional traits could have important roles in the process of extinction and selection.

There could also be additional impacts on species' ecological strategies not captured by our analyses. For instance, although we have summarized the breadth of a species' habitat use, which should confer its capacity to adapt to environmental change (Luck, Carter and Smallbone, 2013), habitat identity could also play an important role in a species' ecological strategy and function. We therefore suggest that further studies are needed to evaluate the fine-scale and spatial changes associated with paying off the extinction debt, as well as to establish the mechanisms leading to the compositional shifts in the ecological strategies of species quantified here.

The future defaunation explored here also shows parallels to historic extinction events, such as the late Quaternary extinctions, which likely disrupted species interactions, reduced long-distance seed dispersal, and fundamentally restructured energy flow and nutrient cycling through communities (Hansen and Galetti, 2009; Doughty *et al.*, 2016; Pires *et al.*, 2018; Smith *et al.*, 2018). Moreover, a growing number of studies support the hypothesis that the late Quaternary extinctions had cascading effects on small vertebrates and plant community biodiversity and function, resulting in ecosystem shifts comparable in magnitude to those generated by climatic fluctuations (Rule *et al.*, 2012; Doughty, 2013; Berzaghi *et al.*, 2018). Thus, the implications of the projected ecological impacts outlined here are extensive and complex.

While millennial-scale human pressures could have already filtered out the vast majority of sensitive species (Sandom *et al.*, 2014; Faurby and Araújo, 2017; Rapacciuolo *et al.*, 2017), we show that recent human activities might have generated an extinction debt with the capacity to non-randomly restructure mammals and birds on Earth, with potentially severe ecological consequences. Extinction debts were previously viewed as tragic, deterministic inevitabilities (Tilman *et al.*, 1994), but they can also be seen as opportunities for targeted conservation actions. As long as a species that is projected to become extinct persists, there is time for conservation action, such as habitat restoration or population management. For example, in the Amazon, recolonization due to forest regrowth slowed extinction rates and reduced the extinction debt for birds in rain forest fragments (Stouffer, Strong and Naka, 2009).

Here we highlight that continuing to protect the most at risk species could help to preserve a diversity of ecological strategies, which could be important for coping with environmental change (Larsen, Williams and Kremen, 2005), and maintaining ecosystem functionality. Moreover, we suggest that greater consideration of the ecological importance and diversity of mammals and birds could benefit conservation planning. Our work therefore underlines the multidimensionality of biodiversity and suggests that analyses of conservation prioritization across dimensions could be increasingly important into the future (Brum *et al.*, 2017; Pollock, Thuiller and Jetz, 2017; Rapacciuolo *et al.*, 2019). Finally, forecasting the loss of ecological diversity and the associated functional consequences should improve our ability to predict and mitigate future responses that sustain ecosystems in the long-term.

3.5 Methods

In brief, using five traits, we built an ecological strategy surface (2-D), via a PCA, and ecological strategy spaces (5-D), via hypervolume estimation.

All analyses were carried out using R version 3.5.1 (R Core Team, 2018).

3.5.1 Traits

We used five traits: body mass, litter/clutch size, habitat breadth (number of IUCN habitats listed as suitable), generation length and diet (the dominant diet gradient across ten diet categories for all species; Figure B.4) for 5,232 mammal and 10,252 bird species. These traits reflect the resource acquisition, utilization and release by species and thus summarise a species' ecological strategy (Chapter 2) (Flynn *et al.*, 2009; Newbold *et al.*, 2013; Cooke, Bates and Eigenbrod, 2019). We extracted trait data for body mass, litter/clutch size and habitat breadth from our recently compiled - from four main sources (Jones *et al.*, 2009; Pacifici *et al.*, 2013; Wilman *et al.*, 2014; Myhrvold *et al.*, 2015) - database for mammals and birds (Chapter 2) (Cooke, Bates and Eigenbrod, 2019). For full details on the compilation of these three traits see Cooke, Bates and Eigenbrod (2019) (Chapter 2). Generation length for birds was supplied by BirdLife. For mammals we obtained generation length values for mammals from a published dataset (Pacifici *et al.*, 2013), although we corrected three mammal generation length observations that have since been found to be anomalous (Cooke *et al.*, 2018): *Cephalophus adersi*, *Cephalophus leucogaster* and *Cephalophus spadix*.

We removed four species from the trait dataset that have been confirmed as globally extinct since the trait data were compiled in 2016: Guam Reed-warbler *Acrocephalus luscinius* (last seen 1969), Bramble Cay melomys *Melomys rubicola* (last seen 2009), Christmas Island pipistrelle *Pipistrellus murrayi* (last seen 2009) and Bridled White-eye *Zosterops conspicillatus* (last seen 1983).

For diet, we calculated a continuous measure of a species' diet. Raw diet information was available as semi-quantitative records (percentage use of ten different dietary categories)

(Wilman *et al.*, 2014). To convert this information into a continuous measure, we first calculated Gower distances between species based on the diet data, gowdis() function in the FD package (Laliberté, Legendre and Shipley, 2014). We then performed a principal coordinates analysis (PCoA) on the Gower distances, dudi.pco() function (ade4 package (Dray and Dufour, 2007)). PCoA rotates the matrix of Gower distances to summarise inter-species (dis)similarity in a low-dimensional, Euclidean space (Legendre and Legendre, 1998). Thus, PCoA does not change the positions of the species relative to each other but changes the coordinate system. Trait space and hypervolume analyses assume that all axes contribute equally to distances and volumes (Blonder, 2018). Thus, only the first principal component from the diet PCoA was used in the trait space and hypervolume analyses, so that each trait dimension had equal weight (although see Appendix 3.5 and Figure B.11, where both the first and second principal components were used). The values yielded by the first principal component of the PCoA serve as synthetic trait values (i.e., new trait values based on the relative importance of diet categories in the initial dataset) and are referred to as 'diet'. Diet explained 36.2% of the variation across the diet categories and was predominantly loaded positively on invertebrates (PCoA loading = 3.69) and negatively on plant material (-1.66), fruit (-1.18) and seed (-0.80) (Figure B.4); thus representing a gradient from invertivore to herbivore, reflecting previous diet ordination for mammals only (Pineda-Munoz and Alroy, 2014).

Trait data were transformed where it improved normality: $\log_{10}$ for body mass, generation length and litter/clutch size; square root for habitat breadth; and all traits were standardized to zero mean and unit variance (z-transformation). Transformation and standardization to unitless coordinates is recommended for trait analyses (Villéger, Mason and Mouillot, 2008; Pianka *et al.*, 2017) and hypervolume calculations (Blonder *et al.*, 2014).

3.5.2 Trait imputation

Trait data were not available for all species. Overall 12% of trait values were missing. The common practice of using only species with complete data (data-deletion approach) not only reduces sample size and consequently the statistical power of any analysis, but may also introduce bias (Penone *et al.*, 2014; Taugourdeau *et al.*, 2014). Moreover, missing data would restrict the dimensionality of our analysis, as any species with at least one missing trait value cannot be used for hypervolume estimation, because an n-dimensional object is not well defined in fewer than n dimensions (Blonder *et al.*, 2014). Instead, to achieve complete species-trait coverage we imputed missing data for litter/clutch size (42% imputed), habitat breadth (10%), diet (8%) and generation length (0.2%). Body mass data had complete species coverage. We used Multivariate Imputation with Chained Equations (MICE), based on the ecological (the transformed traits) and phylogenetic (the first ten phylogenetic eigenvectors extracted from trees for birds (Prum *et al.*, 2015) and mammals (Fritz, Bininda-Emonds and Purvis, 2009)) relationships between species (Chapter 2) (Cooke, Bates and Eigenbrod, 2019). MICE has been shown to have greater accuracy, improved sample size and smaller error and bias than single imputation methods and the data deletion approach (Penone *et al.*, 2014; Taugourdeau *et al.*, 2014). The data deletion approach was performed for comparative purposes (8,294 species; Figure B.8). To generate imputed values, we used the mice() function from the mice package (Van Buuren and Groothuis-Oudshoorn, 2011).

To capture the uncertainty in the imputation process we imputed 25 trait datasets (Figure B.2). These imputed datasets are based on the same input trait data, but differ in their estimations for the missing-data. Where possible we performed our analyses across the 25 imputed datasets (Figure 3.1). However, utilizing the multiple datasets was not possible for the hypervolume analyses, due to the computational cost of the analyses (each hypervolume analysis took up to a day to run on a computer with an Intel Xeon CPU E5-2407 0 @ 2.2 GHz processor and 96GB of RAM, thus running multiple analyses 25 times each was unfeasible). Instead, for the hypervolume analyses, we used a single, randomly selected, imputation dataset.

3.5.3 Ecological strategy surface

We built an ecological strategy surface (2-D) from the transformed and standardized traits via a PCA, using the princomp() function in the vegan package (Oksanen *et al.*, 2017) (Figure 3.1). The ordination of species across this surface represents a two-dimensional continuum, integrating ecological strategies within each of the five trait dimensions (i.e., creating an ecological strategy surface).

We used multivariate kernel density estimation to calculate the occurrence probability of given combinations of trait values (probability contours) across the ecological strategy surface (Díaz *et al.*, 2016), via the kde() function (ks package (Duong, 2017)). We extracted contours at the 0.5, 0.95 and 0.99 quantiles of the probability distribution (Figure 3.1). Because results depend on the choice of the bandwidth used for the smoothing kernel, we used unconstrained bandwidth selectors (Duong, 2007). Specifically, we used the sum of asymptotic mean squared error pilot bandwidth selector (Duong and Hazelton, 2003), through the Hpi() function in the ks package (Duong, 2017).

3.5.4 Ecological strategy space

To evaluate the ecological strategy spaces of mammals and bird combined, and separately, we constructed trait hypervolumes. One of the major advantages of the hypervolume approach is that it can accurately measure the volume of a high-dimensional shape that may include holes, disjunctions or other complex geometrical features (Blonder *et al.*, 2014; Blonder, 2018), and thus hypervolumes model multidimensional spaces better than linear and continuous dimensions, such as convex hulls (Cornwell, Schwilk and Ackerly, 2006). Moreover, hypervolumes are not as sensitive to outliers as convex hulls (Cornwell, Schwilk and Ackerly, 2006; Blonder *et al.*, 2014) and do not assume any parametric probability distribution (Blonder *et al.*, 2014; Blonder, 2018). To build our hypervolumes we used the one-class support vector machine (SVM) estimation method (Blonder, 2018). SVM provides a smooth fit around data that is insensitive to outliers, yields a binary boundary classification ('in' or 'out'), is invariant to rotational transformation (i.e., correlations between axes), and is computationally viable in large datasets and high-dimensional hyperspaces (Blonder, 2018). SVM is the most appropriate hypervolume method when extreme values in the observed data are thought to represent the true boundaries of the data (Blonder, 2018), as is the case here. However, the principal disadvantage is that the boundaries of the hyperspace (and therefore volume) can change non-monotonically when species are removed (see Extinction scenarios), due to the stochastic nature of the SVM algorithm (Blonder, 2017). In other words, the volume can increase when species are removed, due to the stochastic re-drawing of the hyperspace boundaries. We calculated the observed hypervolume based on the transformed and standardised traits using the hypervolume_svm() function in the hypervolume package (Blonder, 2017). Conversion to unitless coordinates (here z-transformation) is required so that volumes or overlaps can be defined (Blonder *et al.*, 2014; Blonder, 2018). The units of the hypervolumes are reported as the standard deviations of centred and scaled transformed trait values, raised to the power of the number of dimensions ($SD^{\text{number of dimensions}}$).

The observed hypervolumes were compared to four alternative null models of multivariate variation of the transformed traits (see Díaz *et al.* (2016) for full null model specifications). To compare the hypervolumes, we calculated the occupation by the observed ecological strategy space of the mean of 999 strategy spaces generated from the assumptions of each null model (Monte-Carlo permutations), with the as.randtest() function (ade4 package (Dray and Dufour, 2007)).

Null model 1: Species traits vary independently and each of them comes from a uniform distribution (Díaz *et al.*, 2016). This null model assumes that each of the traits represents an independent axis of specialization and that the occurrence of extreme and central values is equally probable (Díaz *et al.*, 2016).

Null model 2: Species traits vary independently and each of them comes from a normal distribution (Díaz *et al.*, 2016). This null model assumes that all traits evolve independently, as in null model 1, but extreme trait values are selected against during evolution (Díaz *et al.*, 2016).

Null model 3: Species traits vary independently but - unlike in the previous null models - there is no assumption about the distribution of trait variation; each trait varies according to the observed univariate distributions (Díaz *et al.*, 2016).

Null model 4: Species traits are normally distributed and follow the estimated correlation structure of the observed dataset (Díaz *et al.*, 2016). This null model assumes that there are less than six independent axes of specialization and that extreme values are selected against (Díaz *et al.*, 2016).

3.5.5 Extinction scenarios

To test the impact of future projected extinctions over the next 100 years, we assigned extinction probabilities to the IUCN Red List categories (Mooers, Faith and Maddison, 2008): 0.999 for Critically Endangered (CR), 0.667 for Endangered (EN), 0.1 for Vulnerable (VU), 0.01 for Near Threatened (NT) and 0.0001 for Least Concern (LC) species. In addition, 13% of mammals (665 species) and 1% of birds (59 species) are categorized as Data Deficient (DD). DD species were, for simplicity, treated as LC (i.e., assigned them an extinction probability of 0.0001) (Purvis, Gittleman, *et al.*, 2000; Veron *et al.*, 2016). For our dataset this results in the loss of 380 CR species (99.9%), 576 EN (66.7%), 125 VU (10%), 13 NT (1%) and 1 LC/DD species (0.01%) (total = 1,095 species). Although we also provide alternative analyses where we (i) removed DD species and (ii) assigned DD species an average predicted extinction probability of 0.277 (Appendix B.1). We also show the distribution of the IUCN Red List categories across the ecological strategy surface (Figure B.5f).

We compared these projected extinctions to a null model based on randomized species extinctions, where an equivalent number of species go extinct over the next 100 years (1,095 species) but randomly with respect to species identity/traits. We replicated both the projected and randomized scenarios 999 times. To evaluate the difference between the projected and randomized extinction scenarios we used a Kolmorgorov-Smirnov test with the ks.test() function (stats package (R Core Team, 2018)). We also calculated absolute effect sizes as observed volume – randomized volume and observed volume – projected volume, with 95% confidence intervals of the differences. To assess shifts in the trait distributions we used permutation tests, via the as.randtest() function (ade4 package (Dray and Dufour, 2007)) (Figure B.7).

3.5.6 Sensitivity

Overall our results and conclusions were qualitatively similar (i) with and without imputed trait data (Figure B.2; Figure B.8; Figure B.9; Figure B.10), (ii) when including the first or the first and second principal components from the diet PCoA (Figure B.4; Figure B.11), (iii) with and without DD species (Figure B.12; Figure B.13), and (iv) when assigning DD species an extinction probability of 0.0001 or 0.277 (Figure B.14; Figure B.15). Further information on these analyses is provided in Appendix B.1.

3.6 Acknowledgements

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Chapter 4 Ecological distinctiveness of birds and mammals at the global scale

4.1 Abstract

Ecologically distinct species - species with distinct trait combinations - are not directly prioritized in current conservation frameworks. The consequence of this blindspot means that we could be losing species with the most unique ecological strategies. Here, we quantify ecological distinctiveness, based on six traits, for 10,960 bird and 5,278 mammal species, summarizing species-level ecological irreplaceability. We find that threatened birds and mammals are, on average, more ecologically distinct, including highly ecologically distinct species, such as Great Indian Bustard (Endangered), Amsterdam Albatross (Critically Endangered), Asian elephant (Endangered) and Sumatran rhinoceros (Critically Endangered). These species have potentially irreplaceable ecological roles and their loss could undermine the integrity of ecological processes and functions. Yet, we also identify ecologically distinct widespread, generalists, such as Lesser Black-backed Gull and wild boar. These generalist species have distinct strategies that allow them to thrive across multiple environments. Thus, we suggest that high ecological distinctiveness is associated with either high extinction risk or successful hyper-generalism. We also find that ecologically distinct species are generally charismatic. We thus highlight a conservation opportunity: capitalizing on public preferences for charismatic species could provide support for the conservation of the most ecologically distinct birds and mammals. Overall, we encourage greater consideration of ecological distinctiveness, in combination with extinction risk and evolutionary distinctiveness, when prioritizing species-focussed conservation.

4.2 Introduction

A fundamental goal of conservation biology is to safeguard the diversity of life. Yet, global conservation funding falls short of what is required to prevent the loss of the world's biodiversity (McCarthy *et al.*, 2012). Conservation expenditure must therefore be prioritized to effectively and efficiently minimise extinction and maintain nature’s variability. Indices of priority species are an important tool for the allocation of scarce conservation resources (Isaac *et al.*, 2012). Traditionally, species prioritization frameworks have focussed on vulnerability (i.e., extinction risk), endemism, and ‘flagship’ status (Brooks *et al.*, 2006; Veríssimo, MacMillan and Smith, 2011; Jenkins, Pimm and Joppa, 2013; IUCN, 2018b). Although these aspects are important in identifying priority species, they focus on a single dimension of biodiversity - taxonomic diversity. Yet biodiversity in all its dimensions (i.e., taxonomic, phylogenetic and functional diversity) is required for the persistence of ecosystems (Hooper *et al.*, 2005; Gamfeldt, Hillebrand and Jonsson, 2008).

The application of phylogenetic diversity to set conservation priorities is gaining momentum (Isaac *et al.*, 2007; Thuiller *et al.*, 2015; Brum *et al.*, 2017; Pollock, Thuiller and Jetz, 2017; Gumbs *et al.*, 2018). Phylogenetic diversity captures the uniqueness of linages through deep time, and has been applied to species prioritization through the Evolutionarily Distinct and Globally Endangered index (EDGE), to highlight the role of species-level evolutionary irreplaceability (Isaac *et al.*, 2007, 2012; Gumbs *et al.*, 2018). Researchers have advocated that maximizing phylogenetic diversity will also conserve evolutionary feature diversity (Faith, 1992), and potentially capture trait diversity (Monnet *et al.*, 2014), as species traits often reflect shared evolutionary history (Mazel *et al.*, 2018). However, traits are not necessarily concordant with phylogeny, as phylogenetically divergent species can converge on analogous ecological strategies, due to similar adaptive responses to similar selection pressures and convergent evolution (Thuiller *et al.*, 2015; Winemiller *et al.*, 2015; Pianka *et al.*, 2017). For example, pangolins and armadillos, which belong to separate Orders, both have armoured bodies and consume termites and ants. Thus, while maximizing phylogenetic diversity can sometimes help to support trait diversity (Redding and Mooers, 2015), phylogenetic diversity captures trait diversity unreliably (Mazel *et al.*, 2018).

Here, we recognise species' traits as a complementary dimension of biodiversity, as has been previously acknowledged spatially (Thuiller *et al.*, 2015; Brum *et al.*, 2017; Pollock, Thuiller and Jetz, 2017). Traits reflect species' adaptations to their environment, where species live and how they interact (Violle *et al.*, 2007). Traits also jointly determine a species ecological role and function (Wilman *et al.*, 2014). Thus trait combinations are increasingly being used to summarise species' ecological strategies (Chapter 3) (Brum *et al.*, 2017; Cooke, Eigenbrod and Bates, 2019). Moreover, a diversity of ecological strategies is required to support and maintain ecosystem processes and functions (Hector and Bagchi, 2007). However, species, and their ecological strategies, are disappearing, with strong implications for the environment (Chapter 3) (Cooke, Eigenbrod and Bates, 2019). For instance, the loss of species with distinct ecological strategies may have very different consequences from the loss of species with common ecological strategies (Larsen, Williams and Kremen, 2005; Mouillot, Graham, *et al.*, 2013; Monnet *et al.*, 2014). Yet, the relationship between the distinctiveness of species' ecological strategies and extinction risk remains little explored. Here, we quantify ecological distinctiveness of birds and terrestrial mammals and ask how rare are the traits of a given species compared to all other species globally (Violle *et al.*, 2017; Grenié *et al.*, 2018). Our goal is to identify the most distinct ecological strategies for birds and mammals, and potentially irreplaceable ecological roles, building upon the taxonomic (IUCN, 2018b) and phylogenetic (Isaac *et al.*, 2007; Gumbs *et al.*, 2018) dimensions of biodiversity evaluated previously.

We quantify: (1) whether ecologically distinct species are at greater risk of extinction, (2) the relationship between ecological distinctiveness and evolutionary distinctiveness, and (3) which trait extremes dominate the most ecologically distinct species. We make three predictions. First, we predict that threatened species will be more ecologically distinct. Our prediction is based on multiple lines of evidence. For instance, extinction risk is evolutionary and ecologically non-random (Chapter 3) (Purvis, Agapow, *et al.*, 2000; Cooke, Eigenbrod and Bates, 2019), specific traits can therefore lead to higher extinction rate, e.g., large body size (Smith *et al.*, 2018), essentially filtering out similar taxa so that survivors of extinction processes are more distinct. In addition, we previously found a disproportionate reduction in ecological diversity associated with the loss of threatened species (Chapter 3) (Cooke, Eigenbrod and Bates, 2019), suggesting that threatened species have relatively high ecological distinctiveness. Moreover, specialist species are associated with elevated extinction risk (Clavel, Julliard and Devictor, 2011; Sekercioglu, 2011; Otto, 2018), and we therefore expect these taxa to have specialized trait adaptations for specific environmental conditions, which would be dissimilar to the traits of species occupying other habitats (Gaston, 1994; Chapman, Tunnicliffe and Bates, 2018). Second, we predict that evolutionarily distinct species will also be more ecologically distinct, based on the theory that unique ancestry leads to unique evolutionary features (Faith, 1992), which is then reflected in unique trait combinations for species (Monnet *et al.*, 2014). Third, we predict that body mass will have the greatest influence on ecological distinctiveness, as there is a strong body mass gradient across mammals in particular, and birds. Plus, body mass is arguably the most important trait of birds and mammals, underlying many of their physiological, ecological and evolutionary processes (Smith *et al.*, 2011; Smith and Lyons, 2013; Rapacciuolo *et al.*, 2017).

4.3 Materials and methods

We performed our analyses separately for 10,960 extant bird and 5,278 extant terrestrial mammal species, to ensure comparability to previous prioritization frameworks, such as the EDGE framework (Isaac *et al.*, 2007; Gumbs *et al.*, 2018). We excluded marine mammals due to the energetic, thermal and metabolic differences that shape ecological strategies in the marine realm (Tucker and Rogers, 2014; Gearty, McClain and Payne, 2018).

All analyses were carried out using R version 3.5.1 (R Core Team, 2018).

4.3.1 Taxonomy

Taxonomies often vary, due to name revisions at the generic or specific levels, lumping or splitting lower taxa (genera, species) among higher taxa (families), and nomenclature changes (Chamberlain, Szoecs and Boettiger, 2012). We used a taxonomy of 10,960 bird and 5,278 mammal species (IUCN, 2018b) derived from the IUCN (International Union for Conservation of Nature and Natural Resources) taxonomic framework. All other datasets were then matched to this reference taxonomy.

4.3.2 Trait data

We selected six traits - body mass, litter/clutch size, habitat breadth, diet type, diet diversity and generation length - that together summarize a species' form, function and ecological strategy. Body mass reflects the type and amount of resources that species consume and release (Chapter 2) (Chillo and Ojeda, 2012; Cooke, Bates and Eigenbrod, 2019). Litter/clutch size relates to a species' reproductive strategy and output (Newbold *et al.*, 2013). Habitat breadth indicates a species' habitat specialism and the extent of resource use (Chapter 2) (Cooke, Bates and Eigenbrod, 2019). Diet type defines the major trophic interactions of species (Duffy, 2002; Chillo and Ojeda, 2012; Burin *et al.*, 2016). Diet diversity dictates how species respond to changes in resource availability and summarizes the diversity of food web interactions (Duffy, 2002; Newbold *et al.*, 2013; Burin *et al.*, 2016). Generation length signifies reproductive rate (Newbold *et al.*, 2013).

We extracted raw trait data (i.e., excluding imputed values) for body mass, litter/clutch size, habitat breadth and diet type from a database for 10,252 birds and 5,232 mammals - compiled by Cooke, Bates and Eigenbrod (2019) (Chapter 2) from four main sources (Jones *et al.*, 2009; Pacifici *et al.*, 2013; Wilman *et al.*, 2014; Myhrvold *et al.*, 2015). Habitat breadth was coded using the IUCN Habitats Classification Scheme and was quantified as the number of suitable habitats listed for each species (Chapter 2) (Cooke, Bates and Eigenbrod, 2019). Diet type categorizes species into five groups according to their primary diet: plant/seed, fruit/nectar, invertebrates, vertebrates (including carrion), and omnivore (score of ≤ 50 in the four other diet categories) (Chapter 2) (Wilman *et al.*, 2014; Cooke, Bates and Eigenbrod, 2019). For diet diversity, we calculated a Shannon Index on the proportions of 10 diet categories (Santini *et al.*, 2019) extracted from the EltonTraits database (Wilman *et al.*, 2014). BirdLife supplied generation length for birds but restrictions apply to these data, which we used under license for the current study. However, these data can be manually downloaded from the BirdLife website (http://datazone.birdlife.org/species/search). For mammals we obtained generation length values from Pacifici *et al.* (2013), although we corrected three mammal generation length observations that have since been found to be anomalous (Cooke *et al.*, 2018): *Cephalophus adersi*, *Cephalophus leucogaster* and *Cephalophus spadix*.

We supplemented the trait data with additional data from multiple sources (Dunning, 2008; Jones *et al.*, 2009; Pacifici *et al.*, 2013; Wilman *et al.*, 2014; Myhrvold *et al.*, 2015), so that every species had at least one trait value. We therefore updated the trait data to reflect the changes to the IUCN taxonomy since the trait data was first compiled. The updated trait data (excluding generation length for birds, due to data restrictions) are provided online (https://figshare.com/s/e9da4dabb4a6b5a7d4f0).

Trait data were transformed where it improved normality: $\log_{10}$ for body mass, generation length and litter/clutch size; square root for habitat breadth; and all numeric traits were standardized to zero mean and unit variance (z-transformation). Transformation and standardization is recommended, so that each trait has the same weight in the analyses and the units used to measure the traits have no influence (Villéger, Mason and Mouillot, 2008).

4.3.3 Trait imputation

Complete trait data were not available for all species. To avoid excluding species, which can lead to reduced statistical power and introduce bias (Penone *et al.*, 2014; Taugourdeau *et al.*, 2014; Kim, Blomberg and Pandolfi, 2018), we estimated missing data using Multivariate Imputation with Chained Equations (MICE). MICE has been shown to have greater accuracy, improved sample size and smaller error and bias than single imputation methods and the data deletion approach (Penone *et al.*, 2014; Taugourdeau *et al.*, 2014). We implemented MICE based on the functional, the transformed traits, and phylogenetic, the first 10 phylogenetic eigenvectors extracted from trees for birds (Prum *et al.*, 2015) and mammals (Fritz, Bininda-Emonds and Purvis, 2009), relationships between species (Chapter 2) (Cooke, Bates and Eigenbrod, 2019). We imputed missing data for birds and mammals for body mass (0.4% imputed for birds; 0% imputed for mammals), litter/clutch size (44% for birds; 37% for mammals), habitat breadth (18% for birds; 6% for mammals), diet type (26% for birds; 4% for mammals), diet diversity (26% for birds; 4% for mammals) and generation length (0.2% for birds; 0.4% for mammals). To generate imputed values, we used the mice() function (mice package (Van Buuren and Groothuis-Oudshoorn, 2011)). We imputed 25 trait datasets to capture the uncertainty in the imputation process. We then performed subsequent analyses across the 25 trait datasets and calculated the associated total variance according to Rubin’s rules - accounting for within imputation variance, between imputation variance and the number of imputations (Vink and van Buuren, 2014).

4.3.4 Ecological distinctiveness

To summarize species' ecological distinctiveness, based on their traits, we employed the framework of 'functional distinctiveness' (Violle *et al.*, 2017). Here we use the term 'ecological distinctiveness' in preference to 'functional distinctiveness', as the selected traits may or may not directly reflect the ecosystem functions performed by species (Huang, Stephens and Gittleman, 2012), but do directly relate to their ecological strategies (Chapter 3) (Cooke, Eigenbrod and Bates, 2019). We calculated ecological distinctiveness via the distinctiveness_com() function in the funrar package (Grenié *et al.*, 2017), which uses trait dissimilarities to represent how rare the traits of a given species are compared to all other species globally (Violle *et al.*, 2017; Grenié *et al.*, 2018). To generate trait dissimilarities we computed Gower pairwise distances between species, which allows mixed trait types (e.g., continuous, categorical, ordinal data) while giving them equal weight (Villéger, Mason and Mouillot, 2008), using the compute_dist_matrix() function in the funrar package (Grenié *et al.*, 2017). Because ecological distinctiveness is computed using multiple traits, it can be difficult to disentangle the influence of individual traits on the metric. We therefore recalculated ecological distinctiveness excluding each trait one by one and then compared the values to ecological distinctiveness when measured across all six traits. We did not reduce the number of traits lower than five because we might have missed important dimensions of the possible trait space (Mouillot *et al.*, 2014).

4.3.5 Extinction risk

We used the rl_history() function in the rredlist package (Chamberlain, 2016) to download up-to-date (as of 8th Jan 2019) IUCN categories for birds and mammals (IUCN, 2018b). We then performed a multiple comparison Kruskal-Wallis rank-sum test to compare ecological distinctiveness across IUCN categories, using the kruskal() function in the agricolae package (de Mendiburu, 2017). We also performed post-hoc tests using Fisher's least significant difference to differentiate between groups (de Mendiburu, 2017).

4.3.6 Evolutionary distinctiveness

Evolutionary distinctiveness measures the relative contribution of a species to the total evolutionary history of their taxonomic group (Gumbs *et al.*, 2018). The evolutionary distinctiveness of a species is high when the species has a long unshared branch length with all the other species (Grenié *et al.*, 2018). We obtained evolutionary distinctiveness scores for 10,960 bird species and 5,454 mammal species from the EDGE website (https://www.edgeofexistence.org/edge-lists/, accessed October 2018), but excluded marine mammals and species that were not classified by the IUCN (e.g., taxonomic mismatches or domesticated species, such as *Equus caballus*). We used Spearman's rank correlation coefficients to analyse the relationship between ecological and evolutionary distinctiveness in birds and mammals.

4.3.7 Geographic range

We also calculated geographic range size for birds and mammals, using spatial polygons from the IUCN (2018b) and BirdLife (BirdLife International and Handbook of the Birds of the World, 2018). Although we expect range size to be associated with habitat breadth, they are derived independently (range size is derived from distributional data and habitat breadth is derived from IUCN habitats listed as suitable by species' experts). We filtered the polygons to include only those coded as presence: 'Extant' (i.e., we removed polygons coded as presence: 'Probably Extant', 'Possibly Extant', 'Possibly Extinct', 'Extinct' or 'Presence Uncertain'). We reprojected the polygons to cylindrical equal area and then calculated their area in square kilometres, using the area() function in the raster package (Hijmans, 2019), and summed the area across all extant polygons per species. We could not calculate range size for 1,928 birds and 294 mammals, due to lack of spatial data, changes to taxonomy and/or no 'Extant' polygons, resulting in data for 9,032 birds and 4,984 mammals.

4.4 Results

4.4.1 Ecological distinctiveness

Bird ecological distinctiveness (mean across 25 imputed trait datasets) ranges from 0.28 (Chestnut-winged Cinclodes *Cinclodes albidiventris*) to 0.69 (Greater Rhea *Rhea americana*) (Figure 4.1). Mammal ecological distinctiveness (mean across 25 imputed trait datasets) ranges from 0.33 (Stephen's woodrat *Neotoma stephensi*) to 0.62 (leopard *Panthera pardus*) (Figure 4.1). Mean bird ecological distinctiveness is 0.37 (median = 0.36) and mean mammal ecological distinctiveness is 0.41 (median = 0.41). Of the twenty most distinctive birds, only five are threatened (Critically Endangered, Endangered or Vulnerable), while seven of the twenty most distinctive mammals are threatened.

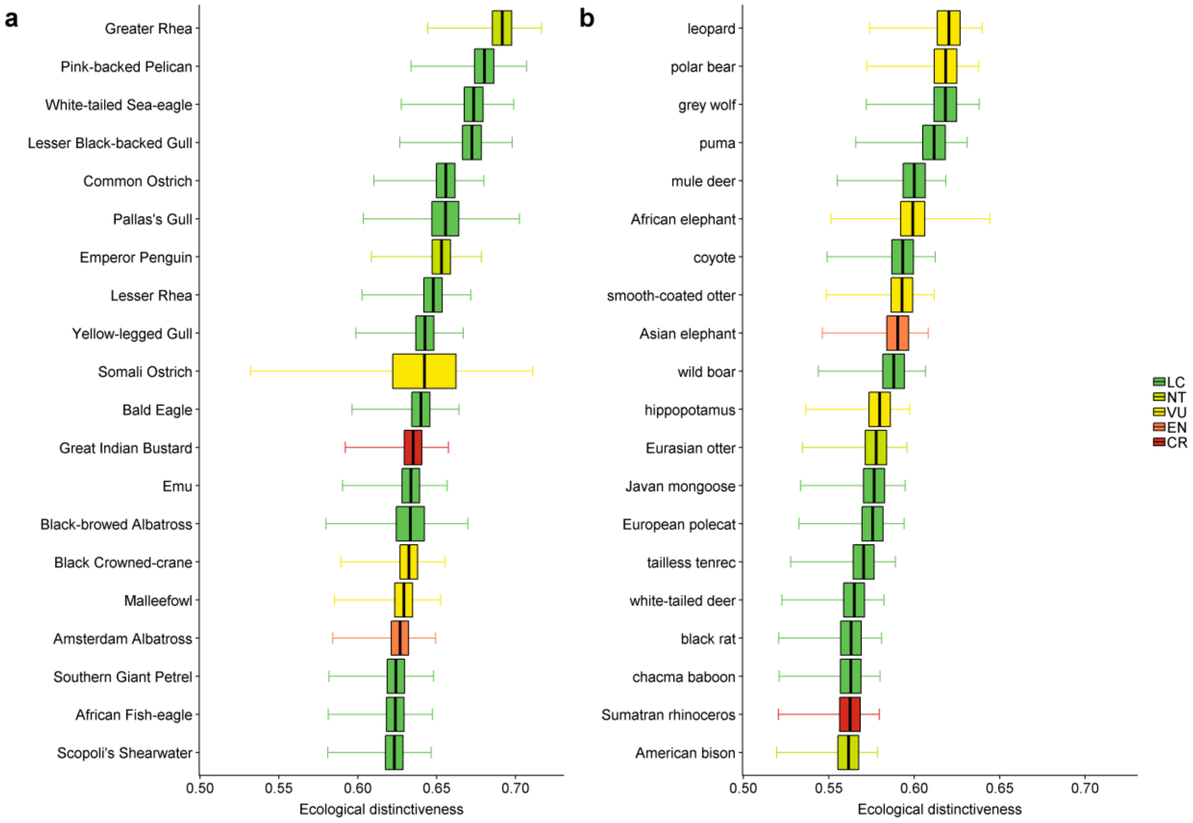

Figure 4.1 The twenty most ecologically distinct species globally for (a) birds and (b) mammals. Mean (thick line), 95% confidence intervals around the mean (box) and minimum and maximum (whiskers) for ecological distinctiveness across 25 imputed trait datasets according to Rubin’s rules, based on 10,960 bird species and 5,278 mammal species. Colours depict IUCN Red List status. We follow the convention of capitalizing common names for birds but using lower case for mammals, except for pronouns. For ecological distinctiveness scores for all bird and mammal species see https://figshare.com/s/e9da4dabb4a6b5a7d4f0.

4.4.2 Ecological distinctiveness and threat status

Ecological distinctiveness differs between IUCN categories for both birds (Figure 4.2a; Kruskal-Wallis χ2 = 137, df = 5, *P* < 0.001) and mammals (Figure 4.2b; χ2 = 110, df = 5, *P* < 0.001). For birds ecological distinctiveness is highest for Critically Endangered (CR; mean ecological distinctiveness = 0.40, statistical sub-group = a), Endangered (EN; 0.39, a) and Vulnerable species (VU; 0.39, a), followed by Near Threatened species (NT; 0.38, b), then Data Deficient species (DD; 0.37, bc), and then Least Concern species (LC; 0.37, c) (Figure 4.2a). Ecological distinctiveness for mammals is highest for CR species (0.42, a), followed by EN (0.42, ab) and VU species (0.42, ab), then NT (0.42, b), then LC (0.41, c), and then DD species (0.40, d) (Figure 4.2b). Thus, in general, threatened (CR, EN, VU) bird and mammal species are more ecologically distinct than non-threatened (NT, LC) species.

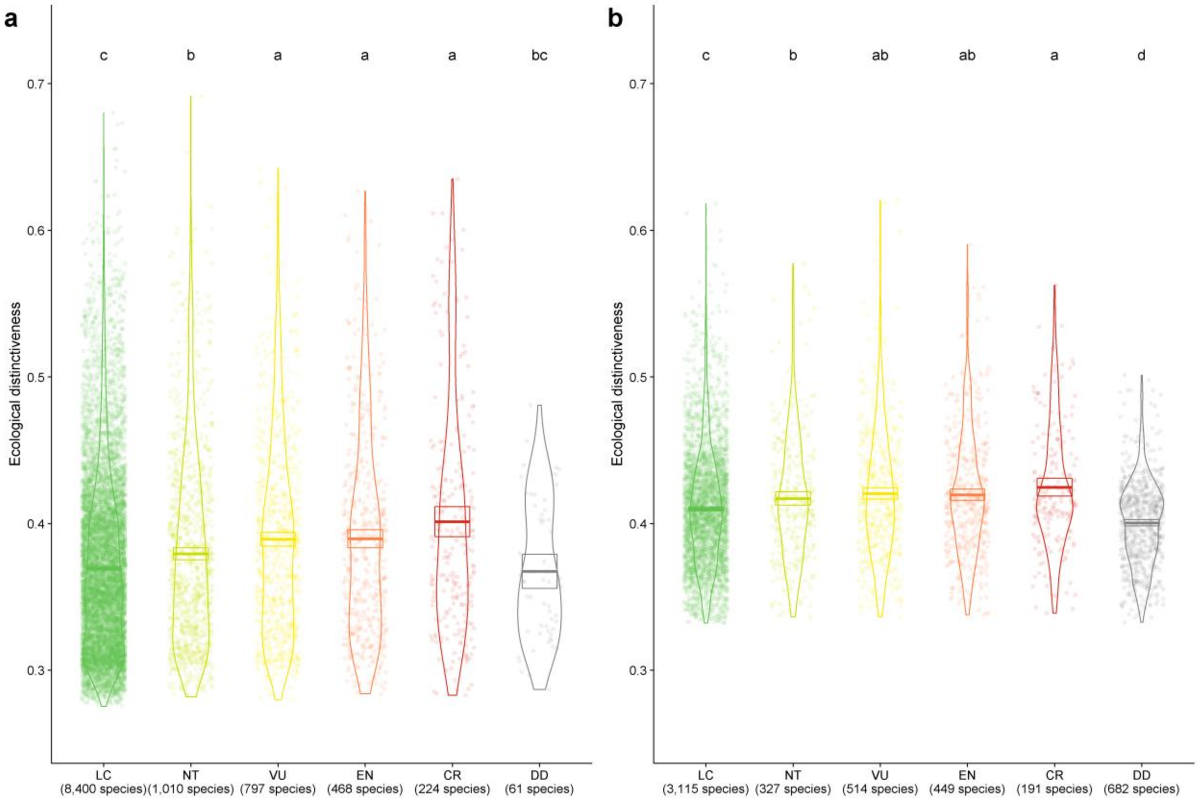

Figure 4.2 Ecological distinctiveness within each IUCN category for (a) birds (b) mammals. The jittered points represent mean ecological distinctiveness across 25 imputed trait datasets for each species for 10,960 bird species and 5,278 mammal species. Also included are violins of data density and boxplots where the central thick line is the IUCN category mean distinctiveness and the edges of the rectangle are the 95% confidence intervals around the mean. Letters show statistical sub-groups from a Kruskal-Wallis rank-sum test (group ‘a’ has the highest distinctiveness).

4.4.3 Ecological distinctiveness and evolutionary distinctiveness

Ecological distinctiveness is weakly positively correlated with log evolutionary distinctiveness for birds (Spearman’s $\rho_{10958} = 0.024$, $P = 0.014$), and there is a weak negative correlation for mammals ($\rho_{5276} = -0.018$, $P = 0.18$) (Figure C.1).

4.4.4 Ecological distinctiveness and range size

Although threatened species are, on average, more ecologically distinct than non-threatened species (Figure 4.2), we find a weak positive correlation between range size and ecological distinctiveness for both birds (Spearman's $\rho_{9030} = 0.11$, $P < 0.001$; Figure 4.3a) and mammals ($\rho_{4982} = 0.19$, $P < 0.001$; Figure 4.3b).

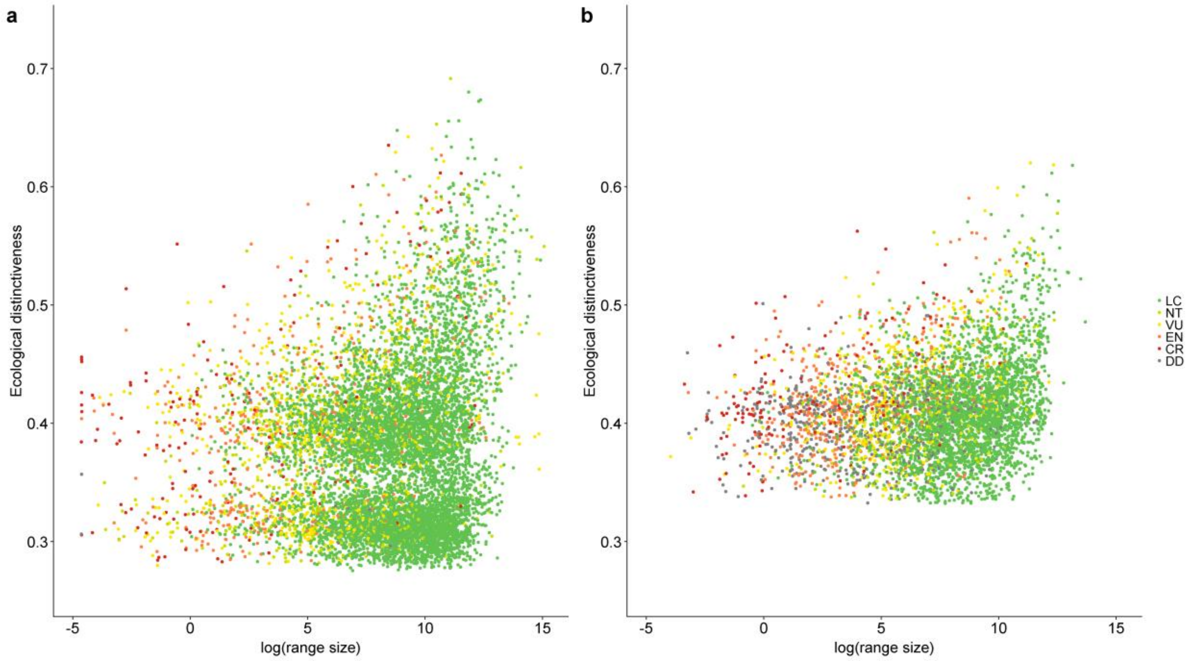

Figure 4.3 The relationship between log range size and ecological distinctiveness for (a) birds and (b) mammals. Points represent mean ecological distinctiveness across 25 imputed trait datasets for each species for 9,032 bird species and 4,984 mammal species. Colours depict IUCN Red List status.

4.4.5 Ecological distinctiveness by dimension

Ecological distinctiveness for the top twenty bird species is predominantly driven by large body mass, long generation length and high habitat breadth (Figure 4.4a). For mammals, the primary drivers of distinctiveness for the top twenty species are large body mass, high habitat breadth and a carnivorous diet (Figure 4.4b).

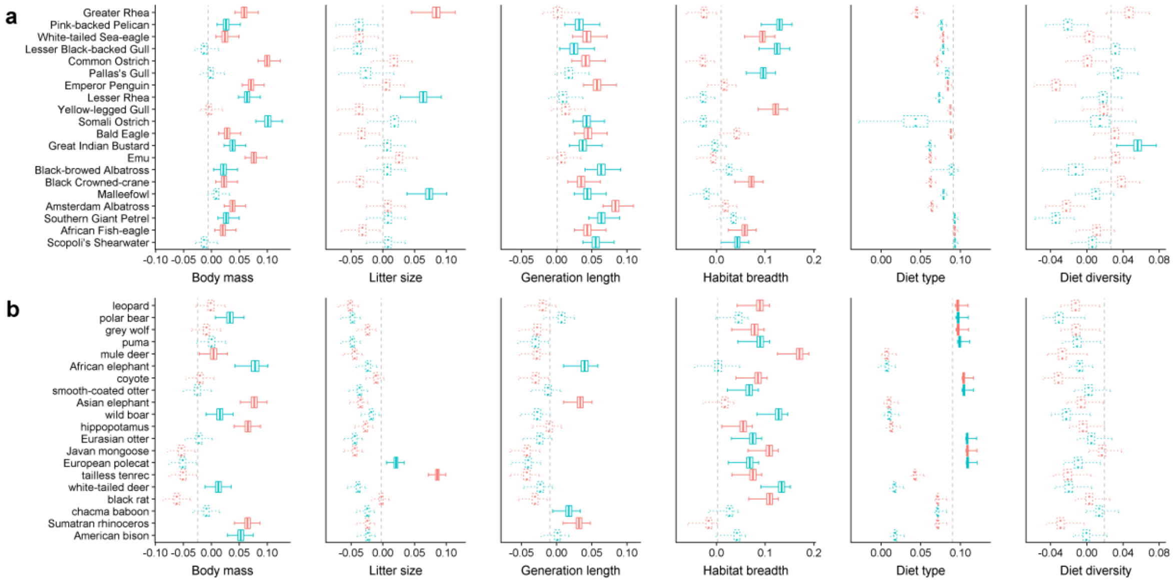

Figure 4.4 The difference between ecological distinctiveness for all six traits together and for each trait removed individually for the top 20 ecologically distinct (a) birds and (b) mammals. The difference between ecological distinctiveness for all six traits together and for each trait removed individually for the top 20 ecologically distinct (a) bird and (b) mammal species. Boxplots show the mean (centre line), 95% confidence intervals around the mean (box), minimum and maximum (whiskers) for ecological distinctiveness per species across 25 imputed trait datasets, according to Rubin's rules. Positive values indicate a decrease in a species distinctiveness when we removed the trait, while negative values indicate an increase in distinctiveness when we removed the trait. Alternate rows are coloured red and blue to ease comparison across the plots. The long dashed lines represent the global mean difference for each trait. Boxes with 95% confidence intervals not overlapping the global mean have solid outlines (i.e., a greater than average decrease in the species distinctiveness when we removed the trait) and those with overlapping confidence intervals have dotted outlines.

4.5 Discussion

We find, as predicted, that on average, threatened birds and mammals are the most ecologically distinct. Continuing to conserve threatened species should therefore simultaneously reduce extinction and support ecological diversity, thus maintaining nature's variability.

However, our findings also support the need for a balanced consideration of both non-threatened (i.e., common) and threatened (i.e., rare) species (Gaston, 2011; Chapman, Tunnicliffe and Bates, 2018). Most of the top twenty ecologically distinct birds and mammals are non-threatened, including ubiquitous species, such as Lesser Black-backed Gull (*Larus fuscus*), wild boar (*Sus scrofa*), coyote (*Canis latrans*) and black rat (*Rattus rattus*). We therefore demonstrate that, although threatened birds and mammals are more ecologically distinct on average, non-threatened species can have extremely distinct ecological strategies, contrary to our predictions. Thus, we find that both common and rare species make unique contributions to ecological diversity (as reported in other ecosystems; Chapman, Tunnicliffe and Bates, 2018).

We find that these ecologically distinct non-threatened species are generally large-bodied, habitat generalists, which are often widespread and successful in multiple environments - in other words, hyper-generalists. For example, we observe a positive correlation between range size and ecological distinctiveness. Yet a common ecological tenet is that generalist species are at a disadvantage when competing with specialists - a ‘jack of all trades is a master of none’ mechanism (Marvier, Kareiva and Neubert, 2004; Büchi and Vuilleumier, 2014; Burin *et al.*, 2016). For instance, when a specialist and a generalist species compete for the specialist’s preferred resource, the specialist species should ecologically outperform the other (Burin *et al.*, 2016). Instead, here we suggest that the evolution of distinct ecological strategies could allow some generalist species to separate themselves from direct competitors and reduce interspecific competition, via negative frequency-dependence selection, allowing them to successfully colonise and occupy a diversity of environments (Levine and HilleRisLambers, 2009; Violle *et al.*, 2017; Chapman, Tunnicliffe and Bates, 2018).

We also suggest that it is ecologically difficult to be a hyper-generalist, hence it is rare to be common (Gaston, 2011). Thus, hyper-generalists are distinctive - while this is counter-intuitive, we suggest that generalists require specialist traits to survive in a diverse set of environmental conditions and habitats. In addition, these species could be promoted by human assisted dispersal and/or human impacts (human commensals; e.g., black rat, Lesser Black-backed Gull), as generalists can often take advantage of disturbed or heterogeneous landscapes, such as human-dominated systems (Marvier, Kareiva and Neubert, 2004; Büchi and Vuilleumier, 2014; Monnet *et al.*, 2014). Moreover, these hyper-generalist species are ecologically important, as they are often involved in engineering environments and interact with many other species (Gaston, 2011). If unchecked, a decline of these distinctive hyper-generalists could lead to cascading ecological effects. The evolutionary and ecological adaptations of these species therefore require greater research, to understand why these species are so successful in different environments and how they contribute to ecosystem processes and function across scales. Overall, we suggest that high ecological distinctiveness is associated with either high extinction risk or successful hyper-generalism.

The most ecologically distinct species, as quantified here, often have unique roles in their environment. For example, predators, such as White-tailed Sea-eagle (*Haliaeetus albicilla*), leopard (*Panthera pardus*), Bald Eagle (*Haliaeetus leucocephalus*), grey wolf (*Canis lupus*) and puma (*Puma concolor*) can effect grazing and mesopredation pressure, productivity, disease dynamics and carbon sequestration (Ritchie and Johnson, 2009; Estes *et al.*, 2011; Ritchie *et al.*, 2012; Ripple *et al.*, 2014; O'Bryan *et al.*, 2018); while African (*Loxodonta africana*) and Asian elephants (*Elephas maximus*), and hippopotamus (*Hippopotamus amphibius*) can alter vegetation structure and composition, fundamentally restructuring ecosystems (Bakker, Pagès, *et al.*, 2016; Terborgh *et al.*, 2016, 2018). Thus, the ecologically distinct species highlighted here, have critical roles in ecosystems across the globe. The loss of these ecologically distinct species could therefore potentially disrupt species interactions, and undermine the integrity of ecological processes and functions (Duffy, 2002; Larsen, Williams and Kremen, 2005).

The analyses we have performed are based on the best available data, however greater trait data and the inclusion of abundance data could reveal further insights into the ecological distinctiveness and ecological importance of birds and mammals. For example, the low average ecological distinctiveness for Data Deficient species could potentially be due to insufficient ecological information for these species. Thus, here our conservation implications focus on threatened and non-threatened species. While the incorporation of abundance data could reveal ecologically rare, as well as ecologically distinct, species and species with crucial ecological roles at the local scale (Grime, 1998; Grenié *et al.*, 2017). Thus we recommend further conservation assessment of Data Deficient species (Bland *et al.*, 2015) and future inclusion of abundance in ecologically-focussed conservation prioritisation.

We also find that ecologically distinct species are generally charismatic. For example, six (elephant, panther, polar bear, wolf, hippo and rhino) of the top twenty most charismatic animals, based on public perceptions of charisma (Albert, Luque and Courchamp, 2018), correspond to species in the top twenty most ecologically distinct mammals. Public preferences for charismatic bird and mammal species (Morse-Jones *et al.*, 2012; Smith *et al.*, 2012) are reflected in greater willingness-to-pay for conservation focusing on these species (Martín-López, Montes and Benayas, 2007; Colléony *et al.*, 2017; Albert, Luque and Courchamp, 2018). We therefore highlight a conservation opportunity, where the protection of ecologically distinct species can be facilitated through the public support of charismatic species. The use of charismatic species to elicit funding is controversial, as it can divert focus to species that are not the most threatened or ecologically important (Restani and Marzluff, 2002; Brodie, 2009; Colléony *et al.*, 2017; Albert, Luque and Courchamp, 2018). However, here we show that charismatic species may be deserving of their elevated attention, due to their often-distinct ecological strategies and therefore potentially unique ecological roles. In addition, funding for charismatic species can result in additional benefits (e.g., flagship species), via conservation actions shared with other species (Bennett, Maloney and Possingham, 2015), because these species tend to be broad ranging and thus lead to conservation of the habitats encompassing many other species. Flagship marketing remains a key fund raising tool for international agencies (e.g., IUCN and United Nations), non-governmental organisations, local governments, and the scientific community (Bennett, Maloney and Possingham, 2015). Thus, capitalizing on the appeal of charismatic and/or flagship species will help to conserve the most ecologically distinct species and maintain a diversity of ecological strategies across the globe, supporting and maintaining ecosystem processes and functions (Hector and Bagchi, 2007).

4.6 Conclusions

We demonstrate that, although previously suggested as a proxy (Redding and Mooers, 2015), evolutionary distinctiveness is a poor surrogate for ecological distinctiveness. We therefore suggest that joint consideration of a species' ecological and evolutionary distinctiveness could better summarise the irreplaceability of a species and inform species prioritization. However conservation actions must be timely, as well as targeted (Gumbs *et al.*, 2018). Hence, species at imminent risk of extinction are widely considered to be the first priority for immediate conservation action (Gumbs *et al.*, 2018). We therefore propose that highly threatened species that are also ecologically and evolutionarily distinct require urgent attention, as the loss of these species could result in disproportionate ecological consequences (Chapter 3) (Cooke, Eigenbrod and Bates, 2019) and an over-proportional loss of evolutionary history (Isaac *et al.*, 2012; Davis, Faurby and Svenning, 2018). Ecological distinctiveness, as quantified here, is therefore not an alternative to existing conservation prioritization frameworks, e.g., the EDGE approach (Isaac *et al.*, 2007), but provides a complementary perspective on the potential ecological costs of species loss and supports the overall goal of biodiversity conservation to maintain living variation. We therefore add to the growing consensus that, beyond focusing on the number of species or on those with major extinction risks, other facets of biodiversity need to be considered (Isaac *et al.*, 2007; Thuiller *et al.*, 2015; Brum *et al.*, 2017). Overall, we suggest that our quantification of ecological distinctiveness could better inform species prioritization and the direction of conservation actions, highlighting species with irreplaceable ecological strategies.

4.7 Acknowledgements

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Chapter 5 Global relationships between multiple dimensions of mammalian predator and prey diversity

5.1 Abstract

Relationships between trophic levels play critical roles in structuring biotic communities, but their importance across multiple dimensions of mammalian diversity (species richness, functional diversity, phylogenetic diversity) is poorly understood. Here we used structural equation models to quantify effect strengths of environmental predictors and relationships between mammalian predator (species that predominantly consume vertebrates) and prey (species not classified as predators) diversity. We predict that there will be strong links between global predator and prey diversity across multiple dimensions, that this effect will be top-down for functional and phylogenetic diversity and that environmental predictors will particularly important for functional diversity. Contrary to our predictions, we find very weak links between predators and prey for functional diversity and phylogenetic diversity. However, we do confirm the previously described strong link, particularly bottom-up, between predator and prey species richness. In addition, we detect a strong role for environmental predictors, especially temperature, precipitation and temperature seasonality, for predator and prey functional diversity, confirming our prediction; yet much remains unexplained. Thus, we highlight a potential research avenue to identify the primary drivers and mechanisms for mammalian functional diversity and phylogenetic diversity. Overall, our results support the idea that relationships between trophic levels can be important drivers of species richness gradients, but that this influence does not extend to functional diversity and phylogenetic diversity.

5.2 Introduction

Communities are assembled from species that evolve or colonise a given geographic region, and persist in the face of abiotic conditions and biotic interactions (Speed *et al.*, 2019). Biotic interactions, such as predator-prey dynamics, can alter community composition and reshape biodiversity patterns by affecting immigration, extinction and speciation processes (Schemske *et al.*, 2009; Gravel *et al.*, 2011; Faurby and Svenning, 2016). Moreover, relationships between trophic levels underpin the functioning and stability of ecosystems (Estes *et al.*, 2011). Thus, trophic relationships, in combination with environmental effects, play critical roles in structuring biotic communities and hence shape broad-scale species richness gradients (Sandom *et al.*, 2013; Zhang *et al.*, 2018; Speed *et al.*, 2019).

Although considerable effort has been applied to understanding the mechanisms and determinants of diversity patterns, most studies have focused on species richness, the number of species within a specified geographic area, as ‘biodiversity’ (Field *et al.*, 2009; Sandom *et al.*, 2013; Zhang, Kissling and He, 2013; Zhang *et al.*, 2018). Yet by ranking each species as one unit of richness, each species is equally different, thereby ignoring the ecological and evolutionary attributes of each individual species (Brum *et al.*, 2017). In contrast, integrating species richness with information on species’ ecological strategies, e.g. functional diversity, and the evolutionary relationships among species, e.g. phylogenetic diversity, can determine the mechanisms underlying community assembly (Petchey and Gaston, 2006; Safi *et al.*, 2011; Swenson, 2014). Thus, species richness, functional diversity and phylogenetic diversity offer the potential for complementary and synergistic perspectives, advancing our understanding of biodiversity patterns (Safi *et al.*, 2011; Cadotte, Albert and Walker, 2013; Hao *et al.*, 2018). However the influence of trophic relationships on the functional and phylogenetic dimensions of biodiversity remains uncertain (Speed *et al.*, 2019), especially at global scales.

Here we explore diversity patterns and predator-prey dynamics by quantifying the importance of trophic relationships globally for multidimensional biodiversity (species richness, functional diversity, phylogenetic diversity) across mammals. We focus on mammals, as they are a diverse group of organisms spanning a broad range of body masses and exploiting a variety of habitats and niches using a wide range of ecological strategies and feeding modes (Chapter 3) (Smith *et al.*, 2011; Tucker and Rogers, 2014; Cooke, Eigenbrod and Bates, 2019).

Understanding the interplay between predators and prey, and between top-down (trophic regulation) and bottom-up (resource extraction) relationships, has strong implications for ecosystem structure and function. Specifically, mammalian predators can have disproportionate impacts on ecosystem function, structure and stability through top-down control along the trophic chain (Estes *et al.*, 2011; Ripple *et al.*, 2014). For example, predators can modify the abundance, richness, behaviour and functioning of their prey through predation, and mesopredators through intraguild competition; suppressing grazing and mesopredation pressure, and enhancing biodiversity and productivity (Ritchie and Johnson, 2009; Ritchie *et al.*, 2012; O’Bryan *et al.*, 2018). By contrast, mammalian prey influence vegetation growth, plant composition and plant diversity, nutrient cycling, and seed dispersal, in turn affecting ecosystem functioning (Ripple *et al.*, 2015, 2017; Bakker, Gill, *et al.*, 2016). In addition, prey route basal energy and biomass into food webs, and therefore have a crucial role as bottom-up inputs (Ripple *et al.*, 2017).

Here we classify mammalian predators and prey based on their dietary composition, with predators defined as those that predominantly consume vertebrates (> 50% vertebrate diet; i.e., carnivores; 184 species) and potential prey as those not classified as predators (≤ 50% vertebrate diet; 3,985 species), *sensu* Sandom *et al.* (2013). We acknowledge that prey classified here often also predate species (e.g., mesopredators), however we suggest that the predator species we have defined occupy high trophic levels (e.g., top predators). Moreover, Sandom *et al.* (2013) found similar trophic relationships when dividing prey into finer categories of herbivores and insectivores. Thus, here we compare species of a high trophic level (predators) to those at lower trophic levels (prey). For simplicity, hereafter we refer to predators and prey.

To disentangle the complexity of factors that determine multidimensional diversity we require methods to account for both direct and indirect environmental drivers. For instance, species may respond to the environment directly in terms of their performance or characteristics, or indirectly through their interactions with other species (Gaston, 2003). Accounting for both direct and indirect effects is therefore key, as any apparent trophic correlation could simply arise from responses of both predators and prey to the same environmental drivers (Kissling, Field and Böhning-Gaese, 2008; Sandom *et al.*, 2013). By employing a Structural Equation Modelling (SEM) approach, we attempt to make reasonable and meaningful generalizations - simplifying spatial associations based on a multifactor research framework, whilst evaluating the mediating role of both top-down and bottom-up trophic relationships. Moreover, SEMs unite multiple predictor and response variables in a single causal network (Grace, 2006), enabling the evaluation of hypothesized causal relationships among interacting trophic groups (Zhang *et al.*, 2018). Because variables can be both predictors and responses, SEM is also a useful tool for simultaneous testing of direct and indirect effects (Grace, 2006).

There are numerous potential explanations for the relationships between predator and prey diversity, and between species richness, functional diversity and phylogenetic diversity. Here we explore *a priori* modelled relationships derived from the literature, but acknowledge that competing hypotheses exist and require further investigation.

We make the following predictions:

(1) There will be a strong role for trophic interactions across multiple dimensions of global predator and prey diversity. We make this prediction based on previous global richness-focused analyses (Sandom *et al.*, 2013; Zhang *et al.*, 2018), and a biogeographic-scale analysis that suggested biotic interactions were important for functional and phylogenetic diversity (Speed *et al.*, 2019). Moreover, there is evidence that functional diversity within trophic levels can shape food webs, and bottom-up and top-down dynamics (Gravel,

Albouy and Thuiller, 2016; Schmitz, 2017), and phylogenetic diversity can cascade between trophic levels (Brodersen, Post and Seehausen, 2018). Furthermore, greater niche diversification, which relates to both functional and phylogenetic diversity, at one trophic level would be expected to lead to greater niche diversification at the other trophic level (Brodersen, Post and Seehausen, 2018)

(2) Top-down trophic interactions will be of greater importance for functional and phylogenetic diversity than for richness. Top-down forcing reduces competition from dominant species at lower trophic levels, promoting (species, functional and/or phylogenetic) diversification among lower trophic levels (Terborgh, 2015). Moreover, there is experimental evidence that predation promotes divergence for insects (Nosil and Crespi, 2006). In addition, it has been suggested that top-down trophic interactions can shape the phylogenetic structure of communities by the amplification of environmental limitation (Cavender-Bares *et al.*, 2009). Plus, strong top-down forcing by high trophic levels may affect the processes of species immigration (Loreau and Holt, 2004), extinction (Johnson, Isaac and Fisher, 2007; Sanders *et al.*, 2018) and speciation (Schemske *et al.*, 2009), and thus reshape biodiversity patterns across space and time even across broad scales (Zhang *et al.*, 2018). Yet, there is also theory to suggest that prey diversification could lead to greater predator diversification (i.e., bottom-up trophic interactions could be equally or more important) (Brodersen, Post and Seehausen, 2018).

(3) There will be a strong relationship between the environment and predator/prey functional diversity. Functional diversity has a more direct and mechanistic link to ecosystem processes (Diaz and Cabido, 2001; Hooper *et al.*, 2005), and thus we expect it to be strongly associated with environmental drivers.

5.3 Methods

In brief, we quantified species richness, functional diversity and phylogenetic diversity for mammalian predators (184 species) and prey (3,985 species), and coupled this with environmental variables in a Structural Equation Modelling (hereafter, SEM) framework.

All data handling and analyses were performed in R version 3.5.1 (R Core Team, 2018).

5.3.1 Species distributions

We extracted current range maps for all 4,203 extant terrestrial non-volant mammal species from the PHYLACINE database (Faurby *et al.*, 2018), excluding extinct species, marine mammals and bats (Chiroptera). We excluded volant species as we were focussed on the impacts of terrestrial predation. The PHYLACINE taxonomy employed follows the IUCN Version 2016-3 (IUCN, 2016), with minor adjustments (Faurby *et al.*, 2018). The maps consist of individual geoTIFF files for each species in a Behrman cylindrical equal area projection with a resolution of 96.5 km by 96.5 km at 30° North and 30° South (Faurby *et al.*, 2018), approximately equal to 1°. We used an equal area projection as different diversity measures should represent similar areas independent of their latitudinal position. Given that data on species distributions are inexact and our analysis was global, we opted for a relatively coarse resolution; a higher resolution would only increase spatial autocorrelation without a real gain in analytical performance. We transformed all range maps into presence/absence grids and compiled species assemblages for each grid cell, excluding grid cells with < 50% land area, as well as cells with missing predictor data and cells with no predator or prey species. The result was a total of 13,569 grid cells for subsequent analyses. We then excluded species that were not present in any cell, resulting in a total of 4,169 extant terrestrial non-volant mammal species.

5.3.2 Phylogenetic data

We used a pruned version (pruned to only extant terrestrial non-volant mammal species) of the complete mammalian phylogeny from the PHYLACINE database (Faurby *et al.*, 2018), where branch lengths were proportional to time since divergence. The phylogenetic information from PHYLACINE consists of 1000 random trees, due to uncertainties in branching time and topology (Faurby *et al.*, 2018). We ran all phylogenetic analyses across the first 100 trees, due to computational demands (Mazel *et al.*, 2018). Additionally, previous work has demonstrated that pairwise distance metrics, which we use here, are not generally biased by small differences in phylogenetic topology (Swenson, 2009). By repeating our analyses across a distribution of phylogenetic trees, we account for phylogenetic uncertainty (Mazel *et al.*, 2018) and we find that 100 trees is sufficient (Figure D.1).

5.3.3 Trait data

We selected five traits (body mass, diet, litter size, generation length and habitat breadth) to calculate functional diversity, which reflect the resource acquisition, utilisation and release by species (Flynn *et al.*, 2009; Newbold *et al.*, 2013), and thus together summarize a species' form, function and ecological strategy (Chapter 3) (Cooke, Eigenbrod and Bates, 2019). We extracted body mass and diet data from the PHYLACINE database (Faurby *et al.*, 2018); litter size and habitat breadth were extracted from Cooke, Bates and Eigenbrod (2019) (Chapter 2); and generation length was obtained from Pacifici *et al.* (2013). For 122 species that were missing litter size data from Cooke, Bates and Eigenbrod (2019) (Chapter 2) we obtained litter size data from the Amniote (Myhrvold *et al.*, 2015) and PanTHERIA (Jones *et al.*, 2009) databases.

Trait data were transformed where it improved normality: log10 for body mass, generation length and litter size; square root for habitat breadth; and all numeric traits were standardized to zero mean and unit variance (z-transformation) to eliminate the effects of differences in the dimensions and magnitudes of the trait data (Villéger, Mason and Mouillot, 2008).

5.3.3.1 Missing trait data

Functional approaches are sensitive to missing values as the interpretation of the data depends on multiple trait values. We had complete trait data for body mass and diet, however litter size, habitat breadth and generation length had missing values. To avoid excluding species, which can lead to reduced statistical power and introduce bias (Penone *et al.*, 2014; Taugourdeau *et al.*, 2014; Kim, Blomberg and Pandolfi, 2018), we estimated missing data using Multivariate Imputation with Chained Equations (MICE). MICE has been shown to have greater accuracy, improved sample size and smaller error and bias than single imputation methods and the data deletion approach (Penone *et al.*, 2014; Taugourdeau *et al.*, 2014). Phylogenetic data can improve the estimation of missing trait values in the MICE process (Kim, Blomberg and Pandolfi, 2018), because closely related species tend to be more similar to each other. Phylogenetic information was therefore summarised by eigenvectors extracted from a principal coordinate analysis for each of the 100 phylogenetic trees from the PHYLACINE database (Faurby *et al.*, 2018), using the MPSEM package (Guénard, 2015). We calculated the mean eigenvector values across the 100 trees, representing the mean phylogenetic distances among species. We then implemented MICE based on the functional (all five transformed traits) and phylogenetic (the first 10 phylogenetic eigenvectors) relationships between species (Chapter 2) (Cooke, Bates and Eigenbrod, 2019), using the mice() function in the mice package (Van Buuren and Groothuis-Oudshoorn, 2011). We imputed missing data for litter size (38% imputed), habitat breadth (8% imputed) and generation length (5% imputed), and repeated the imputations to generate 25 trait datasets (Figure D.2). These imputed datasets are based on the same input trait data, but differ in their estimations for the missing-data.

We calculated variance inflation factors (VIF) to estimate collinearity (after imputation) among the traits. VIFs ranged from 1.06 to 3.09, indicating low collinearity among the traits (Fox, 2002). The highest collinearity was between generation length and habitat breadth (see Figure B.16), however we decided that these traits represent different ecological features, so we kept all the traits in our analyses.

5.3.4 Predator and prey classification

Diet was quantified in the PHYLACINE database (Faurby *et al.*, 2018) as the percentage use of three dietary categories: plants (including plant material, fruits, nectar and seeds), invertebrates and vertebrates (including endotherms, ectotherms, fish and carrion). We classified predators and prey according to the major fraction of their diet based on these dietary categories. We defined predators as species that predominantly consume vertebrates (> 50% vertebrate diet; i.e., carnivores; 184 species) and prey as all species not classified as predators (≤ 50% vertebrate diet; 3,985 species) (Sandom *et al.*, 2013).

5.3.5 Diversity metrics

We quantified all three dimensions of biodiversity (species richness, functional diversity and phylogenetic diversity) for each grid cell for each dietary group of mammals. Species richness was calculated as the number of species per cell. Functional diversity and phylogenetic diversity were both calculated using Rao's quadratic entropy, Q, (Rao, 1982) and thus use the same mathematical framework (de Bello *et al.*, 2010). Rao's Q sums pairwise distances between species in a community, and therefore reflects the functional or phylogenetic divergence between species. To summarize functional distances between species we used a Euclidean distance matrix of four continuous traits: body mass, litter size, generation length and habitat breadth. We extracted phylogenetic distances between species from the 100 trees described previously (Faurby *et al.*, 2018). We then used these distance matrices to calculate Rao's Q via the divc() function in the ade4 package (Dray and Dufour, 2007).

Rao's Q is not mathematically constrained to be positively correlated with species richness (Botta-Dukát, 2005), and thus allows unbiased tests of the relationships between species richness, functional diversity and phylogenetic diversity (Stuart-Smith *et al.*, 2013). Still, phylogenetic diversity and functional diversity are often positively related to species richness (Safi *et al.*, 2011; Oliveira *et al.*, 2016). The models tested reflect this dependency, and were constructed to assess the relationships between the diversity dimensions (i.e., the interrelationships between species richness, functional diversity and phylogenetic diversity) (Flynn *et al.*, 2011).

5.3.6 Predictor variables

We obtained data on climatic and anthropogenic predictor variables and aggregated all spatial data to the same resolution and projection as the range maps. The environmental predictors summarize energy and resource availability, seasonality and climate, landscape heterogeneity, and human pressure; and have previously been shown to predict vertebrate diversity (Field *et al.*, 2009; Safi *et al.*, 2011; Sandom *et al.*, 2013; Zhang, Kissling and He, 2013; Zhang *et al.*, 2018). The climatic predictors included annual mean temperature (TEMP), temperature seasonality (TSEAS), annual precipitation (PREC) and precipitation seasonality (PSEAS), all from the WorldClim database (v1.4, 1960-1990; (Hijmans *et al.*, 2005)), as well as topographical complexity (TOPO). We calculated topographical complexity as the standard deviation in elevation per grid cell using data from the Shuttle Radar Topography Mission (SRTM30; Farr *et al.*, 2007), reflecting landscape heterogeneity and topographical barriers to dispersal. These five environmental variables were combined using a principal components analysis. We used the first three principal components (PC), capturing 89.2% of the variation (PC1 = 44.0%, representing positive TEMP and PREC, and negative TSEAS; PC2 = 25.0%, representing positive PSEAS and negative PREC; PC3 = 20.2%, representing negative TOPO). We also calculated mean Normalized Difference Vegetation Index (NDVI) for the period 1982-2015, to characterize net primary productivity. NDVI per year was extracted from ECOCAST (https://ecocast.arc.nasa.gov/data/pub/gimms/3g.v1/) and then averaged. For the anthropogenic predictor we used the human influence index, which is made up of 4 variables representing human disturbance: population density, land transformation, accessibility, and electrical power infrastructure (Sanderson *et al.*, 2002). The human influence index was obtained from the Socioeconomic Data and Applications Center (http://sedac.ciesin.columbia.edu/data/collection/wildareas-v2). We used the human influence index instead of the human footprint index, because we were interested in a globally comparable measure of human influence, not the relative human influence in different biomes as measured by the human footprint index.

To improve normality the following transformations were applied: square-root transformations of TSEAS, PREC, PSEAS, human influence index, predator richness and prey richness, and log-transformation of TOPO, predator phylogenetic diversity (+ 1) and prey phylogenetic diversity (+ 1). All variables were further standardized (z-transformed) before the analyses to make the ranges of all variables comparable and similarly scaled, so that the SEMs could be fitted (Hao *et al.*, 2018).

5.3.7 Statistical analyses

We used SEMs to investigate the relationship between predator and prey diversity, when accounting for environmental effects. SEMs are a powerful statistical approach for disentangling the relative importance of numerous direct and indirect effects (Grace and Bollen, 2005, 2008). First theoretical frameworks (informed by knowledge) are translated into explicit multivariate hypotheses, and then the SEM is used to evaluate whether the theory is consistent with empirical data (Grace and Bollen, 2005, 2008; Grace, 2006; Sandom *et al.*, 2013; Lee *et al.*, 2019). Although

SEMs cannot replace experimental manipulations, this approach is one of the few methods to test ecological hypotheses at broad spatial scales (Kissling, Field and Böhning-Gaese, 2008).

Based on hypothesized relationships (Flynn *et al.*, 2011; Sandom *et al.*, 2013; Naeem, 2016; Hao *et al.*, 2018; Zhang *et al.*, 2018) among our predictor variables we constructed *a priori* theoretical SEMs (Figure 5.1). We first constructed an 'environment SEM', where each predator and prey diversity dimension (species richness, functional diversity, phylogenetic diversity) is predicted by environmental variables only (i.e., excluding any trophic interactions). We then built two alternative SEMs: a 'bottom-up SEM' - adding paths from prey diversity to predator diversity to the environment SEM; and a 'top-down SEM' - adding paths from predator diversity to prey diversity to the environment SEM. For these two SEMs we treated the three diversity metrics as independent dimensions, i.e., for the bottom-up SEM we specified paths between prey species richness and predator species richness, between prey phylogenetic diversity and predator phylogenetic diversity, and between prey functional diversity and predator functional diversity.

We then hypothesised alternative paths between the diversity dimensions, including: richness-driven phylogenetic and functional diversity (Flynn *et al.*, 2011; Hao *et al.*, 2018) and phylogenetic-driven richness and functional diversity (Webb *et al.*, 2002; Naeem, 2016). For these SEMs, we constructed environment, bottom-up and top-down versions.

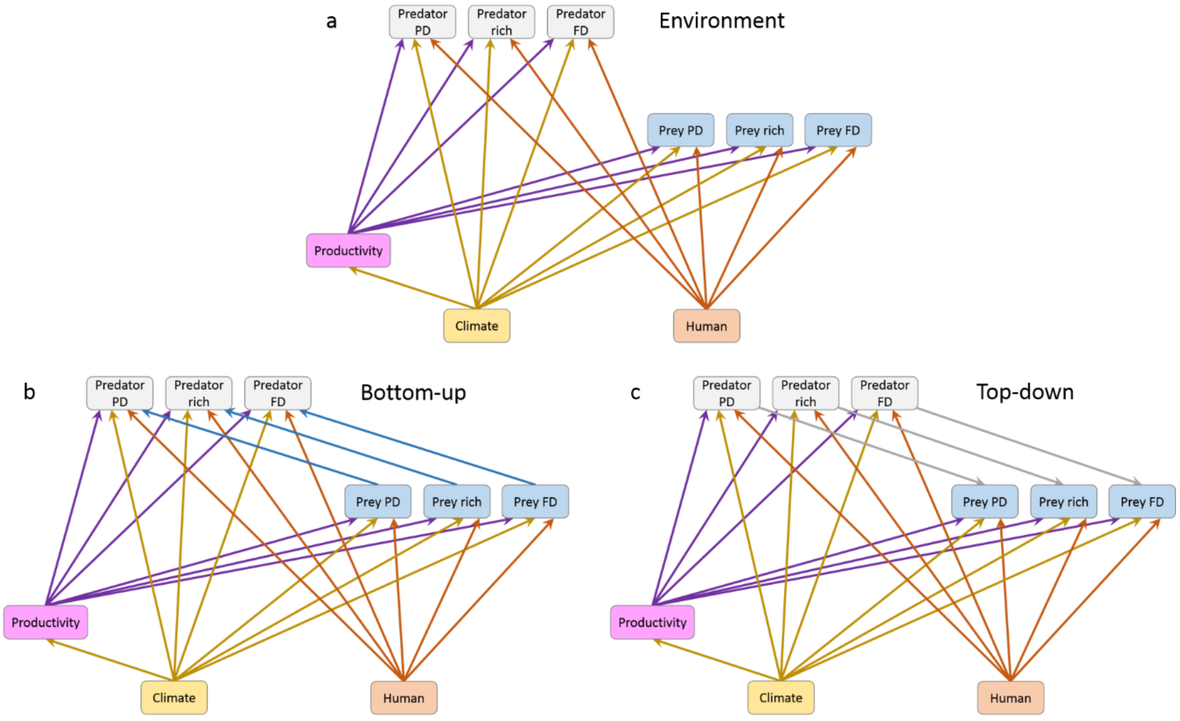

Figure 5.1 *A priori* theoretical Structural Equation Models (SEMs). Three SEMs are shown: (a) environment SEM - each predator and prey diversity dimension (phylogenetic diversity: PD, richness: rich, functional diversity: FD) is predicted by environmental

variables only (i.e., excluding any trophic interactions); (b) bottom-up SEM - adding paths from prey diversity to predator diversity; (c) top-down SEM - adding paths from predator diversity to prey diversity. In the modelling framework, 'Climate' relates to three climate principal components (represented together as a concept for simplicity), 'Human' relates to the human influence index and 'Productivity' relates to the normalized difference vegetation index. Paths are coloured according to the variable from which they originate.

In all analyses, we included direct effects of climate (PCs) and productivity (NDVI), as well as indirect effects of climate via productivity on diversity. Standardized coefficients for each path were calculated and used to compare the relative importance of trophic interactions and environmental effects for species richness at each trophic level.

The SEMs were fitted using a maximum likelihood approach and evaluated using the Bentler's comparative fit index (CFI) and standardized root mean square residual (SRMR) (Hu and Bentler, 1999; Hoyle, 2012; Hao *et al.*, 2018). We did not focus on chi-square values as they can be influenced by sample size (Hooper, Coughlan and Mullen, 2008). After assessing modification indices and residuals for the SEMs, we identified that error covariances between all diversity dimensions were required; this also helped to account for the non-independence between the diversity dimensions. All subsequent models had sufficient fit, CFI > 0.95 and SRMR < 0.08, and all modification indices were below 1000 and all residuals were < 0.1, suggesting no important paths were missing (Hu and Bentler, 1999; Hooper, Coughlan and Mullen, 2008; Hoyle, 2012).

5.3.7.1 Trait and phylogenetic uncertainty

To account for both the trait (25 imputation datasets) and phylogenetic uncertainty (100 phylogenetic trees) in our data we ran SEMs for every combination of imputation dataset and phylogenetic tree, resulting in 2,500 SEMs for each hypothesized SEM structure. We then calculated the mean of the parameter estimates (e.g. the standardized coefficients, R^2) and the associated total variance (and total standard error) of the parameter estimates, according to Rubin's rules (Rubin, 1987), across the 2,500 SEMs, capturing the uncertainty in the trait imputation process (Vink and van Buuren, 2014) and the phylogenetic tree construction (Mazel *et al.*, 2018). Total variance accounts for the within dataset variance, between dataset variance and the number of datasets (Rubin, 1987). Although each dataset combination is not independent from the others, there is currently no method to incorporate two types of between dataset variances. However, here we attempt to approximate and account for between dataset variance, which is preferable to just accounting for within dataset variance, as is commonly applied (Mazel *et al.*, 2018). We only report the associated uncertainty, as the standard error, for parameter estimates that have both within and between dataset variance, e.g., standardized coefficients, as between dataset variance was very low.

5.3.7.2 Spatial autocorrelation

The presence of spatial autocorrelation violates the assumption of independently distributed errors in regression models (Legendre, 1993; Kissling, Field and Böhning-Gaese, 2008). There was moderate spatial autocorrelation in the endogenous variables (Moran's I ranged from 0.14 for NDVI to 0.30 for predator phylogenetic diversity). To account for the spatial autocorrelation we used the function 'lavSpatialCorrect' (https://github.com/jebyrnes/spatial_correction_lavaan). This function addresses the problem of correcting sample sizes and standard errors in SEMs with spatial structure in the autocorrelation of endogenous variables (Zhang *et al.*, 2018). All standard errors (SE) reported have been corrected for spatial autocorrelation.

5.4 Results

5.4.1 Spatial patterns of predator and prey diversity

Species richness of both predators and prey show similar patterns (Figure 5.2a, Figure 5.2b). Mean predator species richness was 10.0 ±0.04 SE per grid cell and mean prey species richness was 39.1 ±0.19 SE. By contrast, predator functional diversity and prey functional diversity (Fig. 2c, d), and predator phylogenetic diversity and prey phylogenetic diversity (Figure 5.2e, Figure 5.2f) differ markedly. Predator functional diversity was highest across northern high latitudes and South America (Figure 5.2c), whereas prey functional diversity was highest across western North America, South Asia and Indonesia (Figure 5.2d). Predator phylogenetic diversity peaked across the Americas (Figure 5.2e), while prey phylogenetic diversity peaked in Australia and New Guinea (Figure 5.2f).

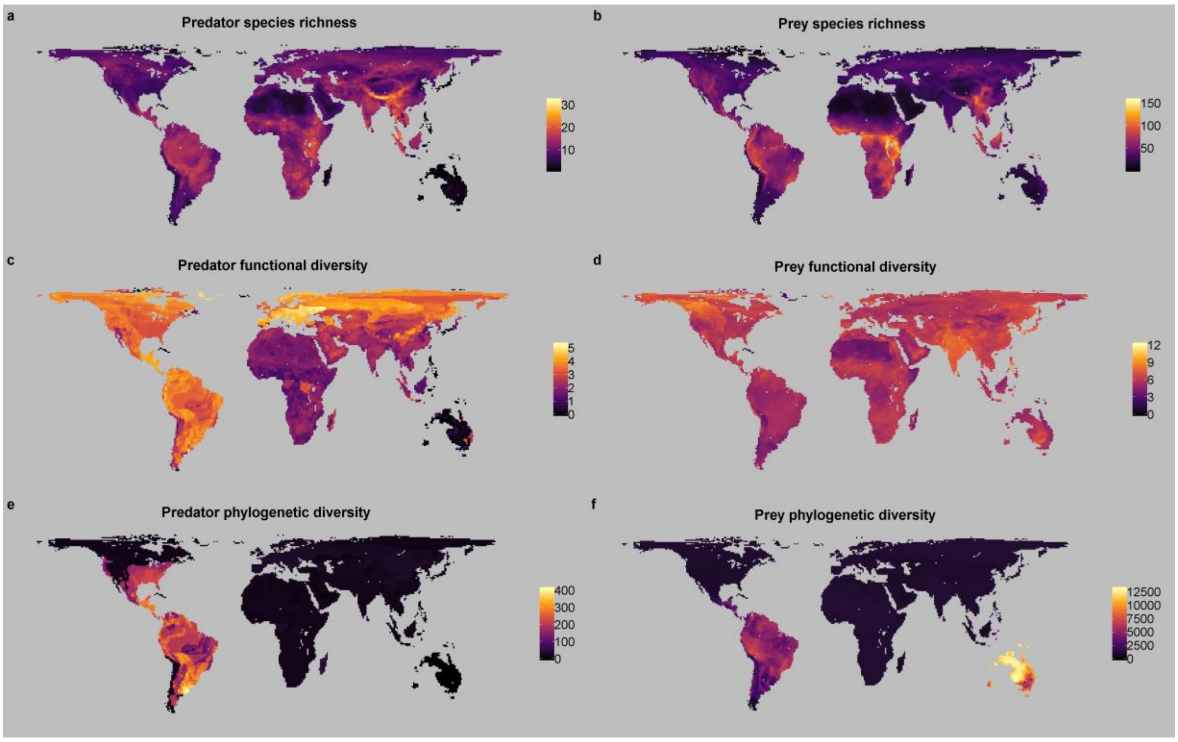

Figure 5.2 Spatial patterns of species richness, functional diversity and phylogenetic diversity for mammalian predators and prey. In total, there are 184 predator species and 3,985 prey species (out of 4,169 extant terrestrial non-volant mammal species investigated). Functional and phylogenetic diversity are measured as Rao's Q. The projection is Behrman cylindrical equal area with a resolution of ~1°, 13,569 grid cells are included (cells with < 50% land area, missing predictor data and/or no predator/prey species were excluded).

5.4.2 Structural equation models

The environment SEM excludes trophic interaction (Figure 5.3a) and indicated that the combined effect of climate, productivity and human influence explains a large amount of the variation in prey richness (R^2 = 0.53) and predator functional diversity (R^2 = 0.38), but less for prey phylogenetic diversity (R^2 = 0.26), predator richness (R^2 = 0.24), predator phylogenetic diversity (R^2 = 0.17) and prey functional diversity (R^2 = 0.16). The strongest path coefficients were: a negative effect of climate PC1 (positive temperature and precipitation, and negative temperature seasonality) on predator functional diversity (path coefficient = -0.66 ±0.02 SE), a negative effect of PC2 (positive precipitation seasonality and negative precipitation) on NDVI (-0.61 ±0.01), a positive effect of PC1 on NDVI (0.56 ±0.01), a positive effect of PC1 on prey functional diversity (0.52 ±0.02), a positive effect of NDVI on prey richness (0.48 ±0.02) and a positive effect of NDVI on predator richness (0.46 ±0.03) (Figure 5.3a; Table D.1).

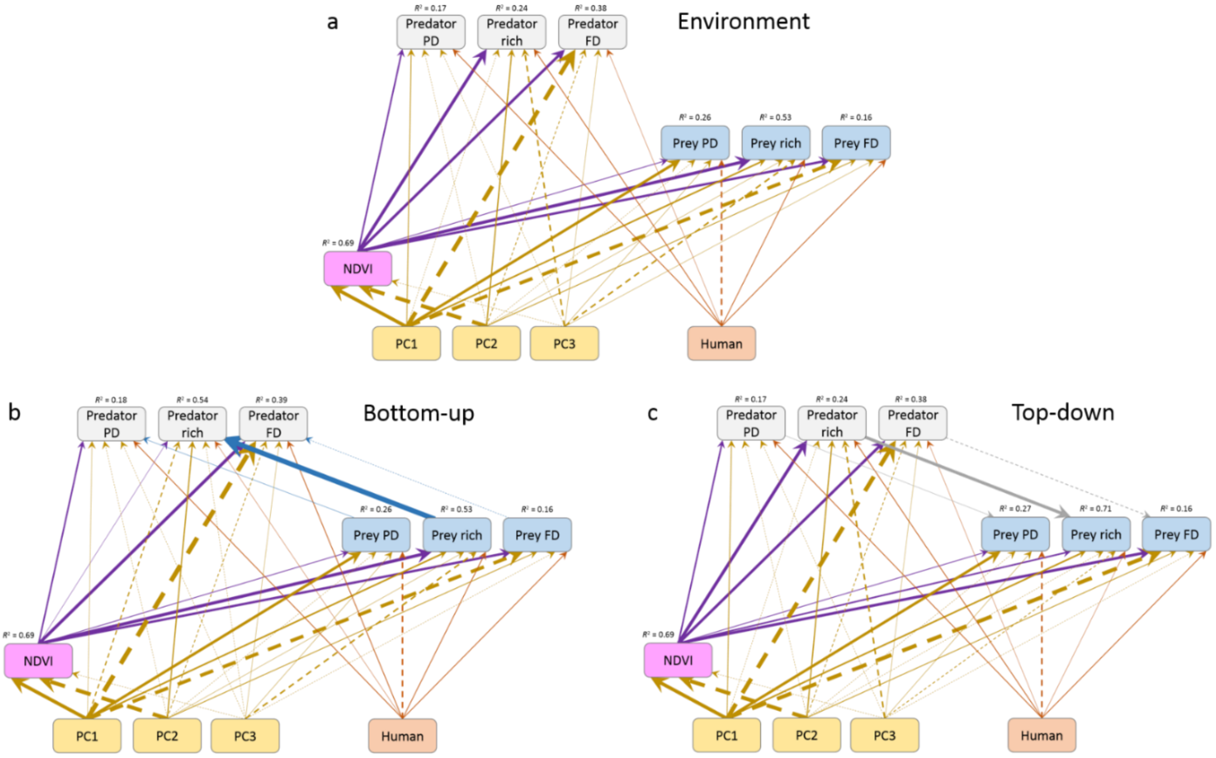

Figure 5.3 Empirical Structural Equation Models (SEMs). Three SEMs are shown: (a) environment SEM - each predator and prey diversity dimension (phylogenetic diversity: PD, richness: rich, functional diversity: FD) is predicted by environmental variables only (i.e., excluding any trophic interactions); (b) bottom-up SEM - adding paths from prey diversity to predator diversity; (c) top-down SEM - adding paths from predator diversity to prey diversity. ‘PC1’ is the first principal component from the climate principal components analysis, reflecting positive temperature and precipitation, and negative temperature seasonality. ‘PC2’ reflects positive precipitation seasonality and negative precipitation. ‘PC3’ reflects negative topographic complexity. ‘Human’ represents the human influence index and ‘NDVI’ represents the normalized difference vegetation index. Arrows represent path coefficients (solid lines positive coefficients, dashed lines negative coefficients), with line thickness proportional to coefficient strength. For all coefficient estimates, including error covariances, with total uncertainty see Table D.1, Table D.2 and Table D.3. In total, there are 184 predator species and 3,985 prey species (out of 4,169 extant terrestrial non-volant mammal species investigated). Paths are coloured according to the variable from which they originate.

When bottom-up trophic interactions were included (Figure 5.3b), there was a strong positive direct effect of prey richness on predator richness (path coefficient = 0.78 ±0.01; Table D.2), with a strong increased explained variance for predator richness (R^2 = 0.54, ΔR^2 = 0.29 [calculated before rounding]), supporting previous findings (Sandom *et al.*, 2013). However, contrary to prediction 1, we found weak bottom-up roles for prey-to-predator functional diversity (path coefficient = -0.08 ±0.01, R^2 = 0.39, ΔR^2 = 0.006) and prey-to-predator phylogenetic diversity (path coefficient = 0.08 ±0.02, R^2 = 0.18, ΔR^2 = 0.005) (Figure 5.3b; Table D.2). The direct path between NDVI and predator richness decreases in strength when accounting for bottom-up interactions, suggesting the effect of NDVI on predator richness is mediated via prey richness (Figure 5.3a, Figure 5.3b; Table D.1 and Table D.2).

There was also a strong role for top-down trophic interactions from predator richness to prey richness (path coefficient = 0.49 ±0.01; Table D.3), with an increased explained variance for prey richness compared to the environment SEM (R^2 = 0.71, ΔR^2 = 0.18; Figure 5.3c). However, the bottom-up richness connection was stronger than the top-down richness connection (Figure 5.3b, Figure 5.3c; Table D.2 and Table D.3). We also found weak top-down roles for predator-to-prey functional diversity (path coefficient = -0.12 ±0.02, R^2 = 0.16, ΔR^2 = 0.008) and predator-to-prey phylogenetic diversity (path coefficient = 0.08 ±0.02, R^2 = 0.27, ΔR^2 = 0.005) (Figure 5.3c; Table D.3), contrary to prediction 2.

When modelling alternative paths between the diversity dimensions, trophic interactions were generally found to be weak (all path coefficients ≤ +/- 0.20, Figure D.3 and Figure D.4; Table D.4-Table D.8), except for a negative effect of predator richness on prey phylogenetic diversity for the top-down phylogenetic-driven model (path coefficient = -0.38 ±0.02; Figure D.4c; Table D.9). Within the trophic levels (i.e., modelling the relationship between the diversity dimensions), predator richness was a moderate driver of predator functional diversity (path coefficient = 0.41 ±0.01) and predator phylogenetic diversity (path coefficient = 0.39 ±0.02), but prey richness showed much weaker effects (Figure D.3a; Table D.4). Predator phylogenetic diversity showed a strong effect on predator functional diversity (path coefficient = 0.63 ±0.01) and a moderate effect on predator richness (path coefficient = 0.36 ±0.01), but prey phylogenetic diversity showed very weak effects (Figure D.4a; Table D.7).

Predator richness was best explained by the bottom-up independent SEM (R^2 = 0.54; Figure 5.3b) and the strongest direct driver within that model was prey richness (path coefficient = 0.78; Table D.2). Predator functional diversity was best explained for the phylogenetic-driven models (R^2 = 0.71; Figure D.4) and the strongest driver across these models was climate PC1 (path coefficient = -0.74; Table D.7, Table D.8 and Table D.9). Predator phylogenetic diversity was best explained for the richness-driven models (R^2 = 0.29; Figure D.3) and the principal driver across these models was predator richness (path coefficient = 0.39-0.48; Table D.4, Table D.5 and Table D.6). Prey richness was best explained by the top-down independent SEM (R^2 = 0.71; Figure 5.3c) and the strongest direct driver was predator richness (path coefficient = 0.49; Table D.3). Prey functional diversity was poorly explained by all models (all R^2 = 0.16). Prey phylogenetic diversity was best explained by the top-down phylogenetic-driven SEM (R^2 = 0.34; Figure D.4) and the primary driver within that model was climate PC1 (path coefficient = 0.52; Table D.9). Thus, there were strong links between predator and prey species richness, but the bottom-up (prey-predator) richness connection was stronger than the top-down (predator-prey) richness connection (Figure 5.3b, Figure 5.3c; Table D.2 and Table D.3).

The strongest path coefficient across all models was the bottom-up effect of prey richness on predator richness (path coefficient = 0.78 ±0.01; Figure 5.3b; Table D.2). Climate PC1 had a consistently strong negative effect on predator functional diversity (all path coefficients ≥ -0.65; Table D.1-Table D.9) and prey functional diversity (all path coefficients ≥ -0.48; Table D.1-Table D.9); confirming prediction 3, that functional diversity of both predators and prey is strongly associated with environmental drivers. The effect of humans, represented by the human influence index, was consistently low across all models. The strongest effect of humans was a negative effect on prey phylogenetic diversity (path coefficient = -0.25 ±0.02), when including top-down trophic interactions (Figure 5.3c; Table D.3).

5.5 Discussion

In this study, we tested hypothesized environmental and trophic drivers of global spatial patterns of predator and prey species richness, functional diversity and phylogenetic diversity. We looked to understand the nature and strength of interactions between mammals and their environment, and the strength and specificity of trophic interactions between predators and prey.

Contrary to our prediction 1, theoretical hypotheses (Brodersen, Post and Seehausen, 2018) and results for the Arctic tundra biome (Speed *et al.*, 2019), we find a very weak global role of trophic interactions for patterns of functional and phylogenetic diversity. However, we do confirm the strong effect of trophic interactions, especially bottom-up trophic interactions, for predator and prey richness (Sandom *et al.*, 2013). Thus, despite theory that suggests top-down trophic interactions could be more important for species diversity (Terborgh, 2015), we add further evidence that bottom-up trophic effects are more important globally than top-down trophic effects for mammal species richness (Sandom *et al.*, 2013).

The lack of importance of trophic interactions for patterns of predator and prey functional and phylogenetic diversity at global scales, although surprising, could have multiple explanations. Firstly, our result could suggest that processes other than trophic interactions are more important for phylogenetic and functional diversity. We previously suggested that different processes generate species richness and functional diversity (Chapter 2) (Cooke, Bates and Eigenbrod, 2019), and here we provide further evidence for this. For instance, species richness shows a strong role of trophic interactions, while functional diversity of both predators and prey is more strongly associated with environmental drivers. Yet other historical (e.g. historic ranges, historic human impacts; Losos and Glor, 2003; Sandom *et al.*, 2014; Faurby and Svenning, 2015), geological (e.g. historic distribution of glaciers; Speed *et al.*, 2019), ecological (e.g. interspecific competition, Great American Biotic Interchange; Mooers and Heard, 1997; Webb, 2006; Godsoe, Murray and Plank, 2015; Faurby and Svenning, 2016), evolutionary (e.g. lineage age; Wiens and Donoghue, 2004; Oliveira *et al.*, 2016) and environmental processes (e.g. long-term climate stability, habitat diversity; Keppel *et al.*, 2012; Stein, Gerstner and Kreft, 2014; Voskamp *et al.*, 2017) could influence diversification and patterns of predator and prey functional and phylogenetic diversity, and thus require further investigation. Secondly, natural trophic relationships between predator and prey functional and phylogenetic diversity might have been distorted by previous human impacts. For example, species richness, functional diversity and phylogenetic diversity patterns have been drastically modified by humans (Faurby and Svenning, 2015), and human impacts on predators, in particular, have been severe (Ripple *et al.*, 2014). Human impacts could therefore have diluted or modified previous, potentially strong, trophic effects. While we find weak effects of humans on mammalian diversity, based on the human influence index, we suggest that our finding of the low importance of human influence could indicate that the human influence index does not account for the multiple complex relationships between humans and predators/prey, especially at the relatively coarse scale of our global analysis. For example, there is abundant evidence that several large carnivore species strongly avoid humans and change their activity and foraging patterns in areas of human activity (Rogala *et al.*, 2011; Kuijper *et al.*, 2016), sometimes at fine spatiotemporal scales (Carter *et al.*, 2012). Thus, further analysis that better accounts for the effect of humans, for example by comparing and contrasting current (human-impacted) and ‘natural’ species distributions (Faurby and Svenning, 2015) or by including fine-grain human impact data, could reveal a stronger role of trophic interactions for functional and phylogenetic diversity than we have shown. Thirdly, the relatively coarse grain of the data used might not reflect the scale-of-effect of trophic interactions for functional and phylogenetic diversity (Belmaker and Jetz, 2013; Graham *et al.*, 2019). Thus, future analysis that identifies the appropriate scale-of-effect could find a stronger role for trophic interactions on functional and phylogenetic diversity (Graham *et al.*, 2019).

Despite the growing recognition that the phylogenetic diversity of interacting predator and prey species influences the structure and functioning of ecological communities (Hairston *et al.*, 2005; Schmitz, 2017; Pringle *et al.*, 2019), we do not find a strong influence of phylogenetic-driven trophic interactions at the global scale for mammals. We did, however, identify a strong within-trophic-level connection between predator phylogenetic diversity and predator functional diversity, which indicates that changes in predator phylogenetic composition broadly correspond to changes in the functional composition of predators (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009; Winter, Devictor and Schweiger, 2013; Naeem, 2016; Bovendorp *et al.*, 2019). However we did not find a strong connection between phylogenetic diversity and functional diversity for mammalian prey, potentially due to the higher numbers of prey species, as phylogenetic diversity levels-off with increasing species richness for mammals (Safi *et al.*, 2011). Thus, evolutionary dissimilarity might generate trait dissimilarity within mammalian predators but not within mammalian prey. In addition, there was moderate support that greater species richness leads to greater functional and phylogenetic diversity for predators (Flynn *et al.*, 2011; Hao *et al.*, 2018), reflecting the suggestion that species richness can drive diversification (Emerson and Kolm, 2005).

We add further evidence that the importance of environmental variables as drivers of species richness patterns could be overstated when trophic interactions are omitted (Kraft *et al.*, 2015). For instance, the effect of NDVI on predator richness is reduced when bottom-up trophic interactions are included, compared to when they are not included; suggesting the effect of productivity on predator richness is mediated by prey richness. Hence, we encourage consideration of trophic interactions when modelling predictors of mammalian species richness patterns. We do, however, demonstrate a strong role for environmental predictors, especially temperature, precipitation and temperature seasonality, on predator and prey functional diversity, confirming prediction 3.

While our study includes all mammalian predators and prey, to understand fully the trophic interactions between predators and prey additional taxa might need to be included in future analyses. For example, other prey, such as birds or reptiles, could be important for predators. Moreover, avian or reptilian predators could be important predators of mammalian prey; although, the majority of large-bodied predators are mammals and are therefore included in our analyses. Thus, ideally all taxa that contribute to broad-scale predator-prey interactions would be included in future analyses (Dehling and Stouffer, 2018). Furthermore, we classified predators and prey based on their major dietary preferences (Sandom *et al.*, 2013), but species' interactions between trophic groups are more complex in the real world. Thus, species-specific data on predator-prey interactions (Wolf and Ripple, 2016) could allow more accurate evaluation of broad-scale and potentially global-scale predator and prey biodiversity.

In addition, for the trophic relationships between predators and prey, a positive association between both groups might be expected simply because predators and prey are a division of one taxonomic group into two subgroups (Sandom *et al.*, 2013). However, Sandom *et al.* (2013) previously used null models to show that the trophic relationship for richness remains even when accounting for an expected covariation between both mammal groups, with path coefficients being stronger than expected from random associations. These null models could be further applied in the future to test if the weak functional and phylogenetic trophic relationships differ from random, although this would not account for the small magnitude of the coefficients for functional and phylogenetic diversity.

5.6 Conclusion

In the face of increasing human pressure, understanding how communities assemble and the forces that influence their dynamics, diversity and ecosystem function will prove critical to managing and restoring the world's biodiversity (Cavender-Bares *et al.*, 2009). Moreover, understanding the variation in trophic interactions in particular can provide important insights into biodiversity maintenance, conservation and the interdependence between trophic levels (Schemske *et al.*, 2009; Edgar *et al.*, 2017; Zhang *et al.*, 2018). Here we provide initial tests of hypothesized relationships between multiple dimensions of mammalian diversity across trophic levels, which together can increase our understanding of large-scale biodiversity patterns (Pavoine *et al.*, 2011; Cadotte, Albert and Walker, 2013); yet, much remains unexplained. Thus, we advocate for further research to unpick the processes and mechanisms driving the global diversity of mammals, building upon our primary analyses, which highlight the importance of trophic interactions in shaping taxonomic diversity patterns and the lack of explanatory power for functional and phylogenetic diversity.

Chapter 6 Conclusion

Biodiversity is essential for maintaining the evolutionary potential for species to evolve and adapt, and the diversity of ecological roles and functions performed by species (Pineda-Munoz and Alroy, 2014; Brum *et al.*, 2017). Biodiversity in all its dimensions is therefore crucial for the persistence of ecosystems (Hooper *et al.*, 2005; Gamfeldt, Hillebrand and Jonsson, 2008). Taken together, my results summarize the ecological diversity of the world's mammals and birds, highlight spatial and species priorities for conservation and identify drivers of multiple dimensions of biodiversity.

6.1 Research findings, limitations and future research directions

6.1.1 Mammals and birds are ecologically comparable

In Chapter 2 I establish a common currency of traits, which demonstrates the ecological comparability of mammals and birds. I have therefore made an initial step to bring together the mammal (Safi *et al.*, 2011; Oliveira *et al.*, 2016; Brum *et al.*, 2017) and bird (Luck, Carter and Smallbone, 2013; Newbold *et al.*, 2013; Barbet-Massin and Jetz, 2015; Schipper *et al.*, 2016) functional literatures. Moreover, I believe that I provide a valuable framework, as well as a database of traits to implement analyses, for taxonomically broader studies that can account for the similar ecological roles performed by divergent taxa and can reveal strong generalities. For instance, in Chapter 3 I built upon my finding of ecological comparability by distilling the diversity of terrestrial mammals and birds across the world into an ecological strategy surface. The overlap identified between mammals and birds across the ecological strategy surface and across ecological strategy space (31% overlap) again confirms the ecological comparability between mammals and birds. Moreover, I show that the diversity of form and function of mammals and birds is structured by two major axes, reflecting life-history and body mass as one major axis, and diet and habitat breadth as the other; highlighting that cross-taxa traits can reveal generalizable ecological patterns. These axes could potentially structure all vertebrate life, and with the increasing availability of amphibian (Oliveira *et al.*, 2017), lizard (Meiri, 2018) and fish (http://www.fishbase.org/) trait data, an inventory of the ecological diversity of vertebrates is becoming more achievable, ultimately leading to a wider understanding of ecological strategy differentiation across vertebrates (Pianka *et al.*, 2017). For instance, although previous studies suggested that mammals with larger bodies are more vulnerable to decline and extinction than smaller mammals (Cardillo *et al.*, 2005; Davidson *et al.*, 2009; Fritz, Bininda-Emonds and Purvis, 2009), Ripple *et al.* (2017) showed that, when including all vertebrates, extinction risk is most acute for the world's largest and smallest vertebrates. Thus, extending our analyses for other taxonomic groups could be an interesting research avenue.

In addition, I show that performing analyses on mammals and birds separately, as well as together, can highlight taxon-specific differences, which can help to better understand the pattern and process of ecological diversity across taxonomic groups. For instance, in Chapter 2 I find different contributions of mammals and birds to functional redundancy and functional dispersion, potentially due to differences in the mobility of these taxa. Moreover, in Chapter 3 I show that birds occupy a third less strategy space than mammals, despite around double the number of species. While, in Chapter 4 I quantified ecological distinctiveness separately for mammals and birds to ensure comparability to previous prioritization frameworks, such as the EDGE framework (Isaac *et al.*, 2007; Gumbs *et al.*, 2018), as well as reflecting the separation of taxon-focussed conservation organisations for mammals (e.g., Global Mammal Assessment programme) and birds (e.g., BirdLife). I find that ecological distinctiveness showed similar relationships between ecological distinctiveness and threat status for mammals and birds, emphasizing generalities between the two groups. In Chapter 5, I evaluated the importance of terrestrial predation and prey availability for biodiversity patterns, and therefore focussed on non-volant mammals. Although, I acknowledge that the incorporation of other predators and particularly prey, such as birds and reptiles could be important for future research. Thus, comparing and contrasting multiple taxonomic groups, both separately and combined, can elucidate novel and important findings. I therefore agree with Dehling and Stouffer (2018) that ideally - where possible and comparable - the investigation of ecological diversity should include all taxa that contribute to the ecological process(es) of interest. Overall, to achieve greater taxonomic inclusion in ecological analyses we need greater trait availability, greater comparability of trait data and greater communication between taxonomic research fields.

The traits I used throughout my thesis summarise species' ecological strategies and generally reflect the spatiotemporal distribution of resource capture, utilisation and release by species (Flynn *et al.*, 2009; Safi *et al.*, 2011; Luck, Carter and Smallbone, 2013). The selected traits are recognized as some of the most important traits for birds and mammals, underlying many of their physiological, ecological and evolutionary processes, and therefore their contribution to various functions (Flynn *et al.*, 2009; Luck *et al.*, 2012; Newbold *et al.*, 2012, 2013; Luck, Carter and Smallbone, 2013; Rapacciuolo *et al.*, 2017). However, without additional trait data our knowledge is incomplete. Thus, I recognize that there are a number of potentially important traits that are, at this point in time, unavailable for analysis (see Table A.1). For instance, I would suggest home range size (indicating the area of effect of a species), a species' natal dispersal distance (relating to the ability of a species to disperse between isolated habitats) or migratory behaviour (relating to the temporal changes in a species ecological influence) potentially crucial traits that could have unknown influence on my results. Thus, novel, ecologically important traits could reveal further insights into species' ecological differentiation and could form additional important axes of ecological variation. These potentially important traits would therefore benefit from further data acquisition and compiling efforts and future analysis.

Moreover, my analyses could be extended to incorporate finer-scale traits or finer-scale differences between species, sometimes referred to as tactics (Southwood, 1988), such as behavioural features (e.g., predator avoidance tactics) or micro-habitat preferences (e.g., foraging stratum) (Brandl and Bellwood, 2014). Future analyses could therefore help to elucidate the interplay between fine-scale tactics and the broader strategies implemented throughout my thesis. The inclusion of fine-scale features or the comparison between coarse- and fine-scale ecological variation could highlight regions or taxa that potentially differentiate at finer scales. For instance, I might hypothesize that the Neotropics has high trait redundancy but low tactic redundancy, or that volant species differentiate at finer-scales, reflecting the high taxonomic diversity and low ecological strategy diversity observed for volant species (Chapter 3). There are therefore several research questions that would benefit from analyses at multiple trait scales. Still, the coarse resolution I use avoids a potential pitfall, where including too many traits or too many fine scale features leads to a metric that simply reflects taxonomy (every species is unique) and thus is equivalent to species richness - and this should be considered when incorporating fine-scale trait or tactic data.

To maximise the use of available trait data I employed trait imputation procedures. Imputation can often be beneficial, as many ecological analyses are sensitive to or restricted by missing values (Blonder *et al.*, 2014; Keyel, Wiegand and Orme, 2016). In addition, the common practice of using only species with complete data (data-deletion approach) not only reduces sample size and consequently the statistical power of any analysis, but may also introduce bias that can lead to incorrect conclusions (due to the bias in the missing data) (Penone *et al.*, 2014; Taugourdeau *et al.*, 2014; Kim, Blomberg and Pandolfi, 2018). Yet, imputation might also lead to biased estimates (Schafer and Graham, 2002) - although, Penone *et al.* (2014) showed that the bias was lower when missing data were imputed rather than deleted. Here I treat imputation and data-deletion as alternative approaches and, for all analyses where applicable, I performed both the imputation and data-deletion approach, with strong agreement between them. Thus, the handling of missing data did not have a major effect on my conclusions. To impute missing values I used the ecological (traits) and phylogenetic (phylogenetic eigenvectors) relationships between species. Phylogenetic data can improve the estimation of missing trait values in the imputation process (Guénard, Legendre and Peres-Neto, 2013; Penone *et al.*, 2014; Kim, Blomberg and Pandolfi, 2018), because related species tend to be more similar to each other (Pagel, 1999). However, the use of phylogenetic information can amplify phylogenetic autocorrelation (see below 6.1.4 for the issues with phylogenetic autocorrelation). To reduce the effect of amplifying phylogenetic autocorrelation only the first 10 phylogenetic eigenvectors were used in the imputation process, these represent divergences closer to the root of the phylogeny, so they do not include fine-scale differences among species (Diniz-Filho *et al.*, 2012).

6.1.2 Ecological responses to disturbance and species' extinctions

It is crucial to understand how variation in biodiversity may influence the sensitivity of communities and ecoregions to environmental change (Oliver, Heard, *et al.*, 2015; Barros *et al.*, 2016; Segan, Murray and Watson, 2016; Nolan *et al.*, 2018; McLean *et al.*, 2019). Based on theory, in Chapter 2 I identify ecoregions that are potentially more vulnerable to disturbance events (high functional redundancy, low functional dispersion, e.g., the Neotropics), as well as those that are potentially more vulnerable to species loss (low functional redundancy, high functional dispersion, e.g., Madagascar). I therefore summarize the potential responses of ecoregions to current and future pressures. Moreover, ongoing human intervention will likely be needed to ensure delivery of ecosystem functions across most of the world (Hooper *et al.*, 2012; Newbold *et al.*, 2016). I therefore highlight regions that could potentially benefit more from habitat-focussed management - regions of high functional redundancy, low dispersion, and those that could potentially benefit more from species-focussed management - regions of high functional dispersion, low redundancy. Habitat-focussed conservation should maintain the resources required for complementary species to support ecosystem multifunctionality, i.e., via insurance and portfolio effects (Oliver, Heard, *et al.*, 2015; Leitão *et al.*, 2016), in the face of disturbance events that could cause population fluctuations and local extinctions (Yachi and Loreau, 1999). Moreover, habitat management should aim to improve connectivity so that species can recolonize after disturbance, thus giving ecosystems greater potential to recover from present and future disturbances (Standish *et al.*, 2014). By contrast, species-focussed conservation could help prevent local extinctions, which could be crucial for ecoregions with low functional redundancy, as regions of low functional redundancy are predicted to show accelerating declines in function with species loss (Larsen, Williams and Kremen, 2005; Laliberté *et al.*, 2010; Hooper *et al.*, 2012). In comparison, in Chapter 3, I hypothesized the potential ecological consequences of future predicted extinctions and the loss of ecological diversity. For instance, I forecast a substantial ecological downsizing, which could lead to the loss of unique ecological functions (Estes *et al.*, 2011; Boyer and Jetz, 2014; Dirzo *et al.*, 2014) and changes in ecosystem structure, function, and biogeochemical cycles (Rule *et al.*, 2012; Berzaghi *et al.*, 2018), while the loss of scavenging birds could impact widespread scavenging and spread of disease (Ogada *et al.*, 2012). However, explicit tests of connections between ecological strategies, functional metrics and measurable contributions to ecosystem processes and ecological resilience are still needed (Dee *et al.*, 2019)

To date, experimental and small-scale observational studies have shown that higher redundancy can maintain community stability in the face of environmental change (Rosenfeld, 2002; Loreau, 2004; Wohl, Arora and Gladstone, 2004) and a recent temporal analysis from large, natural ecosystems (McLean *et al.*, 2019) has shown support for the theory that greater redundancy can lead to greater stability (Walker, 1992; Rosenfeld, 2002; Elmqvist *et al.*, 2003). While Correia *et al.* (2018) demonstrate that pre-disturbance response diversity of deciduous trees results in increased post-disturbance productivity. Still, further local and particularly broad-scale studies are needed to test the relationships between functional metrics, such as redundancy and dispersion, and ecosystem function, especially for mammals and birds. Moreover, identifying the environmental drivers of redundancy and dispersion should be prioritized in future studies and resilience assessments (McLean *et al.*, 2019). Linking gradients in environmental condition, including human stressors, to redundancy and dispersion could be particularly informative for resource management, as management strategies could be adapted to enhance redundancy and dispersion for increased resilience against future disturbances (Laliberté *et al.*, 2010; Oliver, Isaac, *et al.*, 2015; McLean *et al.*, 2019).

Temporally-explicit investigation of ecological changes and ecosystem processes could help frame the implications of our spatial approach in Chapter 2 and our projected approach in Chapter 3. With the increasing availability of temporally-explicit biological data (e.g., Dornelas *et al.*, 2018), the analysis of large-scale ecosystem responses to disturbance events and species extinctions through time should become more practicable. Furthermore, the tools to investigate temporal changes in ecosystem state and processes are increasingly being developed and implemented. For example, Barros *et al.* (2016) propose a framework that uses n-dimensional hypervolumes to define ecosystem states and assess how they shift after environmental changes have occurred. Whereas, McLean *et al.* (2018) quantify the shifts in trait structure in response to disturbance, and show that two connected marine ecosystems underwent a rapid shift in functional structure triggered by a climate oscillation. Thus, I believe that the approaches I have applied, as well as temporally-explicit approaches, could help us better understand biodiversity responses to disturbance and extinctions, and underpin improved biological forecasting.

The lack of accurate biological projections, compared to climate projections, has recently been highlighted (Urban, 2019). I believe that biological forecasting is essential to inform practitioners of future impacts and to prevent the worst future ecological outcomes, such as species defaunation, loss of ecosystem function and ecosystem collapse (Estes *et al.*, 2011; Dirzo *et al.*, 2014; Oliver, Heard, *et al.*, 2015). Biological forecasting of extinctions, in particular, is essential, as extinctions do not happen immediately (Halley *et al.*, 2016). Thus, past and present pressures have generated an extinction debt (Tilman *et al.*, 1994; Kuussaari *et al.*, 2009), which I show has the potential to non-randomly restructure the ecological diversity of mammals and birds on Earth (Chapter 3). These ecological changes could, in turn, generate biodiversity-dependent debts in ecosystem functioning and ecosystem services of local and global importance (Isbell, Tilman, *et al.*, 2015; Isbell *et al.*, 2017). Yet, the probabilistic extinction framework I employed does not account for future secondary extinctions - initial species loss can lead to secondary extinctions, due to the interconnectedness of species in an ecosystem (Sanders *et al.*, 2018). For example, predators can be driven extinct by the loss of their prey (Sanders *et al.*, 2018; Zhang *et al.*, 2018); although, species can also become more abundant due to extinctions of negatively interacting species, e.g., competitor, or predator release (Ritchie and Johnson, 2009; Dee *et al.*, 2019). Sanders *et al.* (2018) found that biodiversity loss, leading to a decrease in redundant interactions, can increase the vulnerability of ecosystems to secondary extinctions, which, when they occur, can then lead to extinction cascades. Thus, incorporation of secondary extinctions could be an important research direction for biological forecasting. The inclusion of secondary extinctions in my extinction framework, for example, could magnify the predicted shifts in global ecological composition that I outline in Chapter 3.

I highlight that the potentially pervasive restructuring of mammal and bird ecological strategies in the next century (Chapter 3), could at least partly be driven by human impacts (Rapacciuolo *et al.*, 2017; Ripple *et al.*, 2019). Yet further research is needed to unpick how human actions will propagate into the future, including both the extent of human pressures and the intensification of existing pressures (Di Marco *et al.*, 2018). Consequently, I recommend greater biological forecasting, with increasingly sophisticated approaches that account for complex human impacts (Visconti *et al.*, 2016; Di Marco *et al.*, 2018; Powers and Jetz, 2019) and secondary extinctions (Sanders *et al.*, 2018).

On top of the global pool-level changes I predict in Chapter 3, individual species can modify their ecological strategies in response to environmental change, via phenotypic plasticity and evolutionary responses (Davis, Shaw and Etterson, 2005; Van Buskirk, Mulvihill and Leberman, 2010; Charmantier and Gienapp, 2014; Sandel, 2019). For example, the wing span of cliff swallows *Petrochelidon pyrrhonota* has evolved to be shorter near roads, with road killed swallows having longer wings, consistent with selection for increased manoeuvrability in the face of traffic (Brown and Bomberger Brown, 2013). While in a meta-analysis of 72 studies, Gaynor *et al.* (2018) showed a 36% increase in nocturnality among mammals, essentially a human-avoidance mechanism, with an even stronger effect in cities, but whether genetic changes have occurred causing (or responding to) this shift towards nocturnality is unknown. Thus, I suggest that local trait measurements (Carmona *et al.*, 2017), temporally-explicit trait measurements (Edeline *et al.*, 2007; Bjorkman *et al.*, 2018), and intraspecific trait measurements (Bolnick *et al.*, 2011; González-Suárez and Revilla, 2013; Albert, 2015), could build on my interspecific analyses and provide a different, potentially more detailed, perspective on the ecological diversity of mammals and birds and the ecological consequences of species loss. However, it has been suggested that the relative importance of considering local trait values decreases at the regional scale (Cordlandwehr *et al.*, 2013; Carmona *et al.*, 2017). Intraspecific trait variation can influence extinction risk and ecological resilience (Liow, 2007; González-Suárez and Revilla, 2013; Oliver, Heard, *et al.*, 2015), via effects on adaptation, acclimation, genetic diversity and biological interactions (Albert *et al.*, 2011; Bolnick *et al.*, 2011; Albert, 2015; Siefert *et al.*, 2015). For example, González-Suárez and Revilla (2013) found that mammalian species with more variable adult body masses, litter sizes, sexual maturity ages and population densities were less vulnerable to extinction, suggesting that intraspecific variation acts as a buffer against extinction in mammals. Thus, I advocate greater development and curation of local, temporal and intraspecific trait data, as well as greater integration of these data in studies of ecological diversity.

6.1.3 Conservation prioritization

There is increasing pressure to identify conservation priorities to maximize returns on limited conservation funding (Murdoch *et al.*, 2007; McCarthy *et al.*, 2012). In addition, there has been considerable debate on whether conservation goals are best achieved by promoting species-focussed management or ecosystem function-focussed management (Ducarme, Luque and Courchamp, 2013). I highlight both approaches in my thesis. For example, in Chapter 2 I indicate how habitat conservation could buffer ecosystems from environmental disturbance, while in Chapter 3 I highlight that the conservation of species at high risk of extinction could help to preserve ecological diversity, avoiding future potential ecological and functional loss. Building on the species-focussed approach, in Chapter 4 I directly investigated ecological distinctiveness and found that threatened birds and mammals are, on average, more ecologically distinct. However, I also identify a number of ecologically distinct widespread, generalists. I therefore advocate appropriate consideration of both threatened and non-threatened ecologically distinct species, as these species could have potentially irreplaceable ecological roles and their loss could undermine the integrity of ecological processes and functions (Duffy, 2002; Larsen, Williams and Kremen, 2005). Moreover, these ecologically distinct species could play key roles in the future, as when facing novel conditions, ecologically distinct species might thrive (Chapin *et al.*, 2000; Mouillot, Bellwood, *et al.*, 2013; Dee *et al.*, 2019). Yet further tests of the relationships between mammal and bird ecological distinctiveness and measurable contributions to ecosystem processes and function are still needed (Dee *et al.*, 2019). As well as which species could emerge as significant contributors to function under which conditions, given global change (Dee *et al.*, 2019).

In addition, inclusion of the direct interactions between species and their effects on each other could improve or complement my approach (Dehling and Stouffer, 2018), as species with high numbers of interactions could act as hubs, while species that bind different modules of a network together could act as connectors (Mello *et al.*, 2015). Thus, species' interactions can influence a species' ecological irreplaceability and functional role, and the loss of key species in a network can lead to disproportionate impacts on ecosystems (Sekercioglu, 2011; Mello *et al.*, 2015; Bender *et al.*, 2018). Across my thesis I have not directly accounted for species' interactions, known as the 'Eltonian shortfall' (Peterson *et al.*, 2011), and this is a major limitation of my work; however the data and methods to quantify species' interactions are currently limited (Dehling and Stouffer, 2018). Instead, I see the quantification of species' interactions as a future research goal for conservation biology, utilizing the increasing availability of ecological network data (e.g., Web of Life dataset www.web-of-life.es).

Moreover, species' relative abundances effect their contributions to ecological processes. For example, species' ecological effects are often assumed to be proportional to their abundance or biomass (Grime, 1998) and the abundance of common/dominant species can have strong implications for ecosystem functionality (Winfree *et al.*, 2015). Thus, abundance-weighted ecological diversity could reveal ecologically rare, as well as ecologically distinct, species (Grenié *et al.*, 2017, 2018), and species with potentially dominant ecological roles (Winfree *et al.*, 2015). Although, there is also evidence that rare species can have important ecological roles (Mouillot, Bellwood, *et al.*, 2013; Leitão *et al.*, 2016), especially across time and under disturbance (Violle *et al.*, 2017). For instance, even at low abundance, predators can have disproportionate impacts on ecosystem functioning through top-down control along the trophic chain (Ripple *et al.*, 2014; Violle *et al.*, 2017). Yet the inclusion of abundance data in future ecologically-focussed analyses, such as abundance-weighted ecological distinctiveness, could provide a different conservation perspective and highlight alternative priority species. Still, there are practical considerations, such as the paucity of data on the local abundance of species at global scales (Newbold *et al.*, 2012), and the variation in reported abundances among species due to differences in detectability (Thornton, Branch and Sunquist, 2011). Thus, incorporating comparable abundance data into global analyses for multiple taxa is currently challenging, but is an important research frontier.

Practically, based on Chapter 4, I suggest that ecologically distinct threatened species could benefit from increased conservation prioritization, similar to how evolutionarily distinct species have received conservation investment (Gumbs *et al.*, 2018). Moreover, I highlight that increased resources for ecologically distinct species could be mobilized via greater willingness-to-pay for conservation focusing on charismatic species, which are often ecologically distinct (Martín-López, Montes and Benayas, 2007; Colléony *et al.*, 2017; Albert, Luque and Courchamp, 2018). By contrast, ecologically distinct non-threatened species, which were generally hyper-generalists, could benefit from increased research focus to better understand how they contribute to ecosystem processes and function across scales, how they become successful and how they interact with co-occurring species and humans (Gaston, 2011). Overall, conservation is fundamentally about the maintenance of diversity. In Chapter 4 I have highlighted the potential of ecological distinctiveness as a conservation prioritization tool to maintain ecological diversity, which is not directly prioritized in current conservation frameworks. Thus, I recommend the joint consideration of ecological distinctiveness, evolutionary distinctiveness and extinction risk when prioritizing species for conservation, complemented by the quantification of species' interactions in the future.

6.1.4 Mechanistic understanding

Across Chapters 2, 3 and 4 I suggest possible mechanistic explanations for my results. For example, in Chapter 2 I find that Neotropical ecoregions are composed of many ecologically similar species. There are a number of potential, non-mutually exclusive, mechanisms for the finding of greater redundancy than expected across the Neotropics, such as high environmental stability, relaxed competition, low environmental heterogeneity, strong environmental filtering, high productivity and/or slow trait evolution (Safi *et al.*, 2011; Lamanna *et al.*, 2014; Belmaker and Jetz, 2015; Oliveira *et al.*, 2016). I put forward that the high functional redundancy in the Neotropics could simply be the result of rapid accumulation of species with little time for ecological divergence (Currie *et al.*, 2004; Mittelbach *et al.*, 2007; Rolland *et al.*, 2014; Belmaker and Jetz, 2015). While in Chapter 3 I suggest that rapid mammalian diversification during the Cenozoic led to high mammal ecological diversity (Alroy, 1998; Smith *et al.*, 2010), but limited taxonomic diversity and in Chapter 4 I suggest that hyper-generalist species require specialist traits to survive in a diverse set of environmental conditions and habitats. Yet these suggestions and hypotheses need further mechanistic evaluation.

Thus, in Chapter 5 I used structural equation models to begin to evaluate mechanistic relationships between dimensions of mammalian predator and prey diversity and environmental predictors. I show that trophic interactions, in combination with environmental drivers, explain a large proportion of the variation in mammalian predator and prey species richness. By contrast, much of the variation in functional and phylogenetic diversity remains unexplained. I therefore add further evidence to my suggestion from Chapter 2 that different processes generate species richness and functional diversity. Although surprising, I believe the weak trophic interactions and low explained variance for functional and phylogenetic diversity found in Chapter 4 offer an interesting avenue for research, as the primary drivers of these diversity dimensions remain unclear. In addition, there are multiple plausible candidates, including historical, geological, ecological, evolutionary and environmental processes across both space and time (Davies Jonathan and Buckley, 2011; Faurby and Svenning, 2015; Oliveira *et al.*, 2016; Voskamp *et al.*, 2017).

The reciprocal interplay between ecology and evolution complicates interpretations of causality (Harmon *et al.*, 2019). In Chapter 4, I tested multiple hypotheses to understand the interrelationships between the dimensions of diversity, however it is still not clear which process is the driving force and which the effect. Thus, I highlight a persistent issue in eco-evolutionary studies, where it can be difficult, using current methods, to untangle the causes from the effects of speciation, trait evolution and community assembly (Harmon *et al.*, 2019). Although, structural equation modelling is a promising potential approach (Kissling, Field and Böhning-Gaese, 2008; Sandom *et al.*, 2013; Oliveira *et al.*, 2016; Lee *et al.*, 2019), as are general ecosystem models (Harfoot *et al.*, 2014; Enquist *et al.*, 2019). I therefore recommend further consideration of additional processes, and in particular better accounting of the temporal effects that lead to contemporary patterns, such as historic impacts (Davies Jonathan and Buckley, 2011; Faurby and Svenning, 2015) and evolutionary time (Oliveira *et al.*, 2016). Yet, some interactions are weak or rapidly fluctuate over time or space (Emmerson and Yearsley, 2004; Wootton and Emmerson, 2005; Turcotte, Corrin and Johnson, 2012), and therefore, when summed over many generations and locations, might not leave a consistent signature (Eldredge *et al.*, 2005; Harmon *et al.*, 2019). Thus, the variability in interactions across space and time could be another potential cause for the unexplained variance in functional and phylogenetic diversity in Chapter 4.

Mechanistic understanding can be further complicated by phylogeny - species are phylogenetically non-independent, as they share many characteristics due to common ancestry (Freckleton, 2000). Hence, many traits exhibit phylogenetic signal (Freckleton, Harvey and Pagel, 2002). Some authors therefore argue the importance of removing phylogenetic autocorrelation in trait data (Diniz-Filho *et al.*, 2009; Pavoine *et al.*, 2011; Fountain-Jones, Baker and Jordan, 2015), with phylogenetic comparative methods used to control for the lack of statistical independence among species (Pagel and Harvey, 1989; Freckleton, Harvey and Pagel, 2002). Phylogenetic autocorrelation can be problematic, as it can lead to underestimation of standard errors and increased variability among the estimates, resulting in increased rate of Type I errors, when data exhibit phylogenetic dependence (Freckleton, Harvey and Pagel, 2002; Rohlf, 2006). Thus, the lack of phylogenetic correction is a major limitation of my work. Yet there is debate on if and when to apply phylogenetic comparative methods (Harvey, Read and Nee, 1995a, 1995b; Westoby, Leishman and Lord, 1995a, 1995b; Freckleton, 2000; Freckleton, Harvey and Pagel, 2002; de Bello *et al.*, 2015). Throughout my thesis I did not correct for phylogeny, based on the view that my focus was not on evolutionary questions and evolutionary mechanisms (de Bello *et al.*, 2015) and the argument that across-species patterns of trait variation primarily reflect the immediate ecological factors operating on species rather than evolutionary factors (Westoby, Leishman and Lord, 1995a, 1995b). These patterns are, however, descriptive and cannot be used to infer either the number of times the pattern has arisen independently or underlying mechanisms (Harvey, Read and Nee, 1995a, 1995b; Harvey, 1996). Thus, not correcting for phylogenetic autocorrelation gives priority to ecological interpretations, whereas correcting for phylogenetic autocorrelation gives priority to evolutionary interpretations, as phylogenetic correction allocates the maximum possible variation in a trait to phylogeny, considering only the residual as potentially attributable to ecology (Westoby, Leishman and Lord, 1995b). Yet, overall I take a pluralist view (Westoby, Leishman and Lord, 1995a) and suggest that both correcting and not correcting for phylogeny can be informative and can provide different perspectives. In fact, I suggest that the analysis of data within a phylogenetic framework allows a broader set of questions to be asked about the data (Westoby, Leishman and Lord, 1995a) and can reveal patterns of association of ecological characters that would be masked by simple across-species comparisons (Harvey, 1996). Thus, phylogenetic analyses that build upon the work here could reveal comparative, novel insights into the structure, form and mechanism of the patterns I describe across mammals and birds. Consequently, I recommend future research that could provide a phylogenetic perspective, potentially using the data and frameworks I have assembled, allowing phylogenetic and non-phylogenetic comparisons (Price, 1997; Blackburn and Gaston, 1998; Garland, Midford and Ives, 1999).

Research on ecological diversity at global extents, as I have performed here, offers important insights into potential worldwide transformations and responses, however, the spatial grain is too coarse to account for the localized changes that must precede global-scale change (Howard, Flather and Stephens, 2019). By contrast, smaller scale studies can help to uncover the drivers of finer-resolution diversity patterns and changes, and potentially tease apart multiple mechanisms. Yet, conclusions drawn from small-scale studies can also lack generality and wider conservation application (Bonnot *et al.*, 2013; Baldwin *et al.*, 2018). Thus, both broad- and local-scale approaches are needed for conservation. I therefore suggest that the approaches I have used throughout my thesis could be developed, extended and further applied globally, as well as down-scaled and applied to local or regional data-rich systems. Overall, identifying and conserving the mechanisms driving taxonomic, evolutionary and ecological diversity, as we all as ecological stability and resilience will be critical to maintaining ecosystem services.

6.2 Next step research questions

Overall, the outstanding research questions and opportunities from my research are:

- Are the results I find for mammals and birds generalizable to other taxonomic groups, such as reptiles and amphibians?
- How do functional redundancy and functional dispersion relate to ecosystem processes, ecosystem function and ecological resilience, through space and time?
- What are the environmental drivers of functional redundancy and functional dispersion?
- How have ecosystems responded to disturbance and species' extinctions in the past, and how does this impact future predictions?
- What are the ecological consequences of future secondary extinctions?
- How do patterns of intraspecific ecological diversity compare to interspecific analyses?
- How does the inclusion of fine-scale trait data and tactics compare to coarse analyses?
- How do species' ecological strategies and ecological distinctiveness relate to measurable contributions of ecosystem function?
- Which species have crucial roles in their ecological network, and are potentially irreplaceable?
- What drives a species to become ecologically distinct?
- How do species become hyper-generalists, and why are they so successful? How do hyper-generalists contribute to ecosystem processes and function across scales, and how do they interact with co-occurring species and humans?
- How did the evolutionary history of mammals and birds lead to contemporary ecological diversity?
- What are the principal drivers of mammalian predator and prey functional and phylogenetic diversity?

6.3 Concluding remarks

In this thesis, I analyzed the ecological diversity of the world's mammals and birds. I summarized the role of mammals and birds for ecoregional functional redundancy and functional dispersion (Chapter 2), examined mammal and bird ecological strategies (Chapter 3), quantified their ecological distinctiveness (Chapter 4) and modelled predator-prey interactions (Chapter 5). Together, my research shows that ecological diversity can provide novel and complementary perspectives for macroecological patterns and can be utilised to inform conservation prioritization. Thus, I advocate the use of an ecological lens to help understand the complexity of mammal and bird diversity on Earth.

Appendix A Supporting information for Chapter 2

A.1 The ecological role of functional redundancy and functional dispersion

We recognise two key mechanisms as characterising an ecoregion's functional state (Walker, 1992; Elmqvist *et al.*, 2003; Laliberté *et al.*, 2010). First, multiple species can play similar ecological and functional roles - functional redundancy (Walker, 1992; Naeem, 1998; Fonseca and Ganade, 2001; Laliberté *et al.*, 2010). Second, species can respond differently to disturbance - functional dispersion (more broadly recognized as response diversity) (Chapin *et al.*, 1997; Yachi and Loreau, 1999; Elmqvist *et al.*, 2003; Laliberté *et al.*, 2010).

A.1.1 Functional redundancy

Functional redundancy is fundamental to the support of ecological processes when disturbances are strong enough to deplete or remove species from assemblages (Yachi and Loreau, 1999). Ecosystems with high functional redundancy are expected to be able to lose species without great decreases in ecosystem function (Yachi and Loreau, 1999; McCann, 2000; Fonseca and Ganade, 2001; Mayfield *et al.*, 2010; Carmona *et al.*, 2016). Whereas ecosystems with low functional redundancy are predicted to show accelerating declines in function with species loss (Larsen, Williams and Kremen, 2005; Laliberté *et al.*, 2010). Functions performed by many species thus benefit from an insurance against biodiversity erosion (Yachi and Loreau, 1999; Fonseca and Ganade, 2001; Luck, Carter and Smallbone, 2013; Mouillot, Bellwood, *et al.*, 2013; Oliver, Isaac, *et al.*, 2015), while functions with low redundancy are more prone to local threats and associated extinctions (Boyer and Jetz, 2014; Parravicini *et al.*, 2014). Moreover, the insurance hypothesis proposes that ecosystem function is more stable over time when multiple species contribute to, and therefore safeguard, each ecosystem process (Walker, 1992; Naeem, 1998; Yachi and Loreau, 1999; Mouillot, Graham, *et al.*, 2013; Oliver, Isaac, *et al.*, 2015; Carmona *et al.*, 2016).

Thus, ecosystems with greater redundancy should be more resistant to species extinctions and provide more constant levels of function (the 'portfolio effect' - the statistical effect whereby averaging across independently fluctuating species populations results in lower variance) (Naeem, 1998; Mouillot, Graham, *et al.*, 2013; Oliver, Isaac, *et al.*, 2015).

A.1.2 Functional dispersion

Here, we employ functional dispersion as an indicator of response diversity (Laliberté *et al.*, 2010), where a greater spread of species in trait space implies a greater diversity of responses. Response diversity occurs when some species increase, while others decrease, in response to the same environmental change (Walker, 1992; Elmqvist *et al.*, 2003; Winfree and Kremen, 2009). Higher levels of response diversity across species should therefore help to buffer ecosystems, providing greater capacity to successfully respond to a broader range of environmental perturbations (Luck, Carter and Smallbone, 2013).

Although more direct measures of response diversity exist (Winfree and Kremen, 2009; Cariveau *et al.*, 2013), they generally relate to single disturbance types (e.g., natural land cover), whereas we look to summarise the diversity of species responses to a diversity of disturbance types. In addition, these response diversity metrics (Winfree and Kremen, 2009; Cariveau *et al.*, 2013) require detailed abundance data and are therefore not yet possible at global scales.

Functional dispersion can also be considered as a weighted version of functional richness, where more dispersed assemblages should support a greater range of ecosystem functions or greater differential supply of particular functions (Luck, Carter and Smallbone, 2013). Moreover ecosystem trait dissimilarity, favoured by the presence of species with distinct trait combinations, increases ecological process rates (Hedde *et al.*, 2010; Mouillot *et al.*, 2011).

Functional dispersion, via response diversity, therefore represents the first safeguard against the loss of ecosystem functions in a changing world and is considered crucial for ecosystem renewal and reorganisation following disturbances (Chapin *et al.*, 1997; Elmqvist *et al.*, 2003; Folke *et al.*, 2004; Laliberté *et al.*, 2010).

A.2 Ecological relevance of the selected traits

Birds and mammals play important roles in controlling how nutrients are vectored across or cycled within ecosystems, how propagules like seeds are distributed, and how well component habitats within ecosystems are interactively connected (Ripple *et al.*, 2017). Thus birds and mammals contribute to multiple processes, such as pollination, predation, herbivory, seed dispersal and food-web structure (Sekercioğlu, 2006; Luck *et al.*, 2012; Newbold *et al.*, 2012; Díaz *et al.*, 2013). The contribution of each species to these ecosystem processes depends on biological traits related to the spatiotemporal distribution of resource capture, utilisation and release (Flynn *et al.*, 2009; Safi *et al.*, 2011; Chillo and Ojeda, 2012; Luck *et al.*, 2012; Luck, Carter and Smallbone, 2013; Mouillot, Bellwood, *et al.*, 2013; Newbold *et al.*, 2013). Here, we selected six traits that summarise a species' form, function and ecological strategy, and thus dictate both their influence on ecological and biogeochemical processes (effect) and how species respond to change (response). The ability to predict the implications of environmental change is enhanced when the same traits dictate both a species effect and response (Lavorel and Garnier, 2002; Suding *et al.*, 2008; Luck *et al.*, 2012).

We define a trait as any morphological, physiological, phenological or behavioural feature affecting fitness or performance in a given environment measurable at the individual level (Lavorel and Garnier, 2002; Violle *et al.*, 2007). Properties measurable at the population/community/ecosystem level, such as geographic range size, population abundance, climatic niche or population density were not considered to be traits (Violle *et al.*, 2007).

A.2.1 Body mass

Body mass reflects the type and amount of resources that species consume and release (Chillo and Ojeda, 2012). Body mass is arguably the most important trait of birds and mammals, underlying many of their physiological, ecological and evolutionary processes, and therefore their contribution to various functions (Brown, Calder and Kodric-brown, 1978; Flynn *et al.*, 2009; Smith *et al.*, 2011; Luck, Carter and Smallbone, 2013; Smith and Lyons, 2013; Rapacciuolo *et al.*, 2017). For example, body mass influences a species' contribution to pollination (Sekercioğlu, Daily and Ehrlich, 2004; Ghanem and Voigt, 2012; Luck *et al.*, 2012), predation (Sekercioğlu, 2006; Roemer, Gompper and Van Valkenburgh, 2009; Wenny *et al.*, 2011; Ripple *et al.*, 2014), herbivory (Ripple *et al.*, 2015), food-web structure (Williams and Purves, 2011) and seed-dispersal (Sekercioğlu, Daily and Ehrlich, 2004; Jordano *et al.*, 2007) (effect).

Additionally, body mass relates to the scale at which species respond to their environment, to species' dispersal ability and their susceptibility to disturbance (Fischer *et al.*, 2007; Fritz, Bininda-Emonds and Purvis, 2009; Luck *et al.*, 2012; Newbold *et al.*, 2013; Standish *et al.*, 2014; Nash *et al.*, 2016) (response).

A.2.2 Diel activity (diurnal/nocturnal)

A species' activity pattern reflects the temporal distribution of their resource use, characterising whether a species is trophically coupled to the day or night (effect).

Plus, diel activity relates to the magnitude of time-specific disturbances a species will be subject to and its ability to avoid or react to these disturbances (Flynn *et al.*, 2009; Chillo and Ojeda, 2012; Díaz *et al.*, 2013), such as solar-driven temperature anomalies (daytime), some types of anthropogenic hunting (daytime), changes in the composition of day or night flowering plants (daytime/nighttime) or removal of day active or night active predators (daytime/nighttime) (response).

A.2.3 Diet

Diet is a fundamental trait, because all organisms must acquire and assimilate resources for maintenance, growth and reproduction (Simberloff and Dayan, 1991; Winemiller *et al.*, 2015). Thus the impact of birds and mammals on ecosystem function is related primarily to what they eat and how they procure their food (Sekercioğlu, 2006; Chillo and Ojeda, 2012). Moreover, diet constrains metabolic rates of organisms (Brown *et al.*, 2004) and defines the functional roles and trophic interactions of species in ecosystems (Duffy, 2002). For instance, diet determines mammalian and avian impact on ecosystem functioning through trophic interactions with other food web components (Burin *et al.*, 2016) and, consequently, on nutrient cycling (Sekercioğlu, 2006; Ripple *et al.*, 2017). Diet is therefore related to functions such as pollination, seed dispersal, predation, herbivory and scavenging (Sekercioğlu, 2006; Wenny *et al.*, 2011; Ghanem and Voigt, 2012; Ripple *et al.*, 2014, 2015) (effect).

In addition, the diet type and diet breadth (e.g., omnivores have wider diet breadth) of a species will dictate how they respond to changes in resource availability (i.e., disturbances that impact the resources they consume) (Luck, Carter and Smallbone, 2013; Newbold *et al.*, 2013) (response).

A.2.4 Habitat breadth

Habitat use strongly influences the spatial distribution and extent of resources intake and release by species, and thus the functional influence of a species across habitat types (Flynn *et al.*, 2009; Chillo and Ojeda, 2012). For example, a species may have a habitat-specific functional role, or may share its functional contribution across a variety of habitats (effect).

Plus the habitat breadth of a species should confer its capacity to adapt to environmental change, especially changes in land cover (Luck, Carter and Smallbone, 2013) (response).

A.2.5 Litter/clutch size

Litter/clutch size relates to a species' reproductive strategy and output (fecundity) and therefore their contribution to trophic processes, such as herbivory (routing basal energy into food-webs via many offspring) and predation (some predators rely on highly fecund prey species) (Newbold *et al.*, 2013) (effect).

Litter/clutch size also reflects the ability of a species to recover after perturbations, where species with high litter/clutch size may repopulate or recolonize more quickly after disturbance (Newbold *et al.*, 2013). A diversity of reproductive strategies across an ecosystem may be important for coping with change (Larsen, Williams and Kremen, 2005) (response).

A.2.6 Volancy (flight ability)

Volancy shapes the spatial dimensionality of resource use, for example, by providing greater access to vertical environmental gradients (e.g., arboreal and aerial resources, including flying invertebrates (Sekercioğlu, 2006)) and greater access between isolated landforms (e.g., oceanic islands, islands of habitat). Volancy also characterises the dispersal abilities of species (Munguía, Townsend Peterson and Sánchez-Cordero, 2008) and thus their contribution to spatial insurance (the dispersal-dependent maintenance of ecosystem processes within a community) of processes, including pollination and seed-dispersal (Gonzalez, 2009; Oliver, Heard, *et al.*, 2015) (effect).

Plus, volancy is a key factor in a species' ability to respond to disturbance, via greater mobility leading to the capacity to escape adverse disturbance events (Berg *et al.*, 2010) (response).

A.3 Supporting methods

A.3.1 Spatial data

We assessed mammal and bird functional redundancy and functional dispersion for all 825 terrestrial ecoregions, according to the WWF ecological regionalisation of the world (Olson *et al.*, 2001). We used ecoregions for a number of reasons. Firstly, ecoregions - areas of relatively homogeneous species composition, clearly distinct from adjacent systems - although somewhat subjective, are the most relevant and ecologically distinct spatial unit at the global scale (Olson and Dinerstein, 2002). Ecoregions act as spatially bounded complex systems, each of which interacts with others, therefore changes in ecoregions can propagate across the entire biosphere (Peters *et al.*, 2009; Barnosky *et al.*, 2012). In addition, ecoregions are widely used to guide global conservation investments, assessments and action (Funk and Fa, 2010; Watson, Iwamura and Butt, 2013), represent similar specific ecological continuums, disturbance regimes, and often similar underlying drivers (Olson *et al.*, 2001; Bonnot, Thompson and Millspaugh, 2011; Farias and Svensson, 2014; González-Maya *et al.*, 2017), and have close relationships with taxonomic and functional compositions (Belmaker and Jetz, 2013; González-Maya *et al.*, 2017).

Plus, ecoregions have practical benefits, as they are less arbitrary and have greater biological relevance than grid-based analyses. For instance, ecoregions allow us to directly evaluate the influence of environmental areas (e.g., the Pontic steppe will be counted only once and not multiple times as in grid-based analyses; therefore we treat ecoregion area as an inherent system property) or wide-ranging species found in multiple grid cells, thus reducing pseudoreplication and spatial-autocorrelation (Jetz and Fine, 2012; Belmaker and Jetz, 2015; Buschke *et al.*, 2015). Moreover, species lists generated at the ecoregion scale are less affected by the geographical heterogeneity of species range sizes and weigh occurrences independent of grid cell occupancy within a region (Kreft and Jetz, 2010).

Birds and mammals were selected as they fill a diverse range of ecological niches, act as connecting nodes among ecological processes and are among the best studied taxonomic groups at the global scale (Sekercioğlu, 2006; Kreft and Jetz, 2010; Newbold *et al.*, 2012). The analysis of birds and mammals together is crucial as species from any taxonomic group may provide redundancy in trait space (redundancy is taxon-unspecific). The ultimate assessment of the functional redundancy and/or functional dispersion of an ecoregion would therefore include all its component species, but this is currently unachievable due to limitations on data availability.

To produce a species list for each ecoregion, we used expert-based species' range maps for 15,485 species - 5,232 terrestrial mammals (IUCN, 2016) and 10,253 birds (BirdLife International and NatureServe, 2015). 15,489 species maps were available, but we excluded: one erroneous subspecies *Pseudois nayaur schaeferi*; one species - *Melomys rubicola* - that has gone extinct since the maps were produced; and two species that were not present in any ecoregion (endemic to very small islands): *Pteropus howensis* and *Acrocephalus rehsei*. These species distributions - plus the shapefiles for each of the 825 ecoregions (we excluded 'Lake' and 'Rock and Ice' ecoregions, because they are not coherent systems, i.e., they occur at multiple locations across the globe) (Olson *et al.*, 2001) - were loaded in to R using the *readOGR* function ('rgdal' package (Bivand, Keitt and Rowlingson, 2016)).

The distribution data were then converted to a presence-absence matrix (PAM) via a polygon-to-grid procedure at 0.5° resolution, a grain size that should yield satisfactory accuracy (Hurlbert and Jetz, 2007), using the *lets.presab* function ('letsR' package (Vilela and Villalobos, 2015)). Species polygons were filtered to include only those coded by the IUCN as presence: 'extant'; origin: 'native', 'reintroduced', 'introduced' or 'origin uncertain'; and seasonality: 'resident', 'breeding season', 'non-breeding season' or 'seasonal occurrence uncertain'. We therefore treat originally present (native) and novel (introduced) species as functionally equivalent, as in previous global analyses (Gibson *et al.*, 2011; Newbold *et al.*, 2015, 2016). We clipped the global PAM to each ecoregion to obtain species composition using the *lets.pamcrop* function ('letsR' package (Vilela and Villalobos, 2015). Finally, we converted the composition data to a site by species matrix (ecoregions in rows, species in columns) using the *create.matrix* function ('fossil' package (Vavrek, 2011)).

The distributions upon which our analyses were based represent the best available data, but have limitations, in particular because they are maps of range boundaries, which overestimate species' occurrences and are therefore susceptible to commission errors (i.e., false presences) (Hurlbert and Jetz, 2007; Kreft and Jetz, 2010; Tracewski *et al.*, 2016). Although, as stated earlier, using ecoregions reduces the impacts of possible pseudoreplication. The alternative is point data, which may be oversampled in easily accessed regions and undersampled in regions that are more difficult to access, as well as being influenced by species' detectability. For example, distribution estimates of species based on GBIF primary data are probably biased (Yesson *et al.*, 2007; Mesibov, 2013; García-Roselló *et al.*, 2015) and cannot provide reliable predictions of the extent of ranges (Beck *et al.*, 2013; García-Roselló *et al.*, 2015).

Our indices of function were purposefully not weighted by species abundances because of the rapid changes in species population sizes and dominance over time, and the disproportional influence of rare species upon ecosystem functions (Walker, Kinzig and Langridge, 1999; Mouillot, Bellwood, *et al.*, 2013; Leitão *et al.*, 2016). Instead, we look to summarise the variety of functional roles within an ecoregion based on species composition, and therefore also do not consider intraspecific trait variation. We thus make the assumption that interspecific insurance, as represented by functional metrics, outweighs the influence of intraspecific insurance, characterised by species abundances or intraspecific trait variability (Westoby *et al.*, 2002; McGill *et al.*, 2006; Auger and Shipley, 2013; Carmona *et al.*, 2015; Díaz *et al.*, 2016). In addition, recent findings in terrestrial grasslands showed that functional metrics that did not incorporate relative abundance were better predictors of ecosystem processes than those that did (Mouillot *et al.*, 2011; Cadotte, Dinnage and Tilman, 2012). There were also practical considerations, given the scale of our study, such as the paucity of data on the local abundance of species (Newbold *et al.*, 2012) and intraspecific trait values, and the variation in reported abundances among species due to differences in detectability (Thornton, Branch and Sunquist, 2011).

A.3.2 Trait data

We followed a systematic three-step trait selection process, as the results of functional analyses rest heavily on the traits included (Luck *et al.*, 2012). We began (1) by compiling a list of potential traits, as extensive as possible based on current knowledge, which may relate birds and mammals to their environment (Table A.1). Specifically, we aimed to identify traits that relate to ecosystem function (effect) and the possible differential responses to multiple disturbance types (response) (Cadotte, Carscadden and Mirotchnick, 2011); although, our understanding of the dynamic relationships between traits and functioning is not complete and requires further study. We then (2) further reduced this trait set by excluding traits with low coverage (>50% missing values (Laliberté *et al.*, 2010)) for our species list (following the IUCN taxonomy). This produced the traits: body mass, litter/clutch size, diel activity, diet, generation length, volancy and habitat breadth. However, if these selected traits are highly correlated with each other, then the 'true' functional value, which may become evident if other traits or combinations of traits were considered, can be obscured (Violle *et al.*, 2017). Thus we (3) reduced multicollinearity by regressing each trait against all other traits using regression and assessing variance inflation factors (VIF; *vif* function - 'car' package (Fox and Weisberg, 2011)). Traits were then removed based on their summed VIF values, until VIF values were <3 for all remaining traits (Zuur, Ieno and Elphick, 2010; Luck *et al.*, 2012). For our data-set this lead to the removal of generation length, due to high collinearity with body mass and litter/clutch size.

Our trait selection process resulted in six traits that summarise a species' ecological strategy and its position in trait space: body mass, litter/clutch size, diel activity, diet, volancy and habitat breadth (Appendix A.2). These traits reflect the spatiotemporal distribution of resource capture, utilisation and release by species (Flynn *et al.*, 2009; Safi *et al.*, 2011; Chillo and Ojeda, 2012; Luck, Carter and Smallbone, 2013; Schipper *et al.*, 2016). We outline how the selected traits summarise both the functional *effect* and *response* of the focal species (Appendix A.2); and suggest that the strict response-effect dichotomy is more applicable to plants (Laughlin, 2014). Furthermore, the selected traits relate to multiple processes, such as pollination, predation, seed dispersal and food-web structure, and influence a species' susceptibility and response to environmental threats (Davidson *et al.*, 2009; Fritz, Bininda-Emonds and Purvis, 2009; Williams and Purves, 2011; Luck *et al.*, 2012; Newbold *et al.*, 2012, 2013; Murray *et al.*, 2014). These nominated traits are widely applicable to vertebrates in general, summarising their form and function, and therefore these 'cross-taxa' traits can be applied to further groups when data become available.

Body mass data were sourced from three databases for mammals: Amniote (Myhrvold *et al.*, 2015), EltonTraits (Wilman *et al.*, 2014) and Pacifici (Pacifici *et al.*, 2013). The Pacifici database builds on PanTHERIA (Jones *et al.*, 2009), but for species that lacked body mass data (1,047 species) they calculated the average body mass of congeneric or confamilial species, we extended this for the 11 species from our global list that were missing data. We took the median across these databases, with 84% of species having values from all three datasets and all species having at least one value (this was required so that all species overlapped in at least one trait dimension). For birds, we calculated the median across two databases: Amniote and EltonTraits. We sourced estimates of body mass values for 573 birds that were missing data, using the average from congeners, as we recognized body mass as a key trait that is strongly related to many aspects of a species' ecology and therefore their contribution to various functions (Brown, Calder and Kodric-brown, 1978; Flynn *et al.*, 2009; Smith *et al.*, 2011; Luck, Carter and Smallbone, 2013) (Appendix A.2). Therefore all species had at least one estimate of body mass and 72% received the average from two estimates. Diel activity was obtained from the EltonTraits database for both mammals and birds. Diet information was available as both semi-quantitative records (percentage use of different dietary categories) or as an aggregated score (assignment to the dominant diet category based on the summed scores of constituent individual diets). We chose to use the more coarse representation, as the semi-quantitative diet data have been shown to differ between databases (Olalla-Tárraga *et al.*, 2016). Thus species were classified into five groups according to their primary diet (Wilman *et al.*, 2014): plant/seed, fruit/nectar, invertebrates, vertebrates (including carrion), and omnivore (score of ≤50 in the four other diet categories). Habitat breadth was coded using the IUCN Habitats Classification Scheme (http://www.iucnredlist.org/technical-documents/classification-schemes/habitats-classification-scheme-ver3) and was quantified as the number of habitats listed for each species. These habitat affinities were extracted via the IUCN Red List Application Programming Interface (API) using the *rl_habitats* function ('rredlist' package (Chamberlain, 2016)). Litter size was calculated as the median across the Amniote and PanTHERIA databases (46% had values from both databases), whereas clutch size was only available from the Amniote database. Data on volancy (flight capability) were compiled from the literature, where it is established that bats (Chiroptera) are the only true flying mammals and that most extant birds - apart from ratites, penguins and some flightless rails and waterfowl - are volant (Findley, 1993; Healy *et al.*, 2014). The volancy of birds was validated using two key sources (del Hoyo *et al.*, 2013; BirdLife International, 2018).

Trait data were transformed where it improved normality, as recommended by Villéger *et al.*, (2008): log10 for body mass and litter/clutch size; square root for habitat breadth; and all traits were standardised to zero mean and unit variance (z-transformation - which is considered appropriate for data with different measurement scales (Jongman, Ter Braak and Van Tongeren, 1995)).

Unfortunately taxonomies often vary, due to name revisions at the generic or specific levels, lumping or splitting lower taxa (genera, species) among higher taxa (families), and name spelling changes (Chamberlain, Szoecs and Boettiger, 2012); this was the case across the multiple datasets we used. To ensure the trait data required for the species listed in the composition data were extracted if available, we built a function in R that wrapped around the 'taxize' (Chamberlain, Szoecs and Boettiger, 2012) and 'rredlist' (Chamberlain, 2016) packages. This function sourced possible synonyms for missing-data species (i.e., those species unmatched between the composition data and trait data) from the Integrated Taxonomic Information System and the

IUCN databases via their APIs, using the *synonyms* (‘taxize’ package (Chamberlain, Szoecs and Boettiger, 2012)) and *rl_synonyms* (‘rredlist’ package (Chamberlain, 2016)) functions, respectively. This process generated up to a possible 12 synonyms per species. In addition, the function collapsed any trinomial synonyms produced into binomial names, as matching was executed at the species level. For example the trinomial synonym *Puma yagouaroundi cacomitli* was reduced into both *Puma yagouaroundi* and *Puma cacomitli*. This created up to an additional 12 synonyms per species. These synonyms were then used to match the trait data to the composition data under its original taxonomic framework (for our dataset: IUCN). This generated data for many species that would otherwise have been missing data. For example, species matched by synonyms for mammals: PanTHERIA 234, Amniote 225, EltonTraits 234, Pacifici 90; and for birds: Amniote 253, EltonTraits 536, BirdLife 90. This R programmatic approach is more efficient, reproducible and accurate than manually sourcing names through a web interface (Chamberlain, Szoecs and Boettiger, 2012). The creation and implementation of this function therefore ensured the traits selected had high coverage of our global species list (Table A.2).

Functional approaches are sensitive to missing values as the interpretation of the data depends on multiple trait values (Keyel, Wiegand and Orme, 2016). Therefore, to ensure consistency in the calculations across all methods we needed to deal with missing data. The common practice of using only species with complete data (data-deletion approach) not only reduces sample size and consequently the statistical power of any analysis, but may also introduce bias that can lead to incorrect conclusions (Penone *et al.*, 2014; Taugourdeau *et al.*, 2014; Kim, Blomberg and Pandolfi, 2018). We therefore chose to implement Multivariate Imputation with Chained Equations (MICE) to account for missing data (the data deletion approach was performed for comparative purposes; Figure A.1; Table A.3). MICE was chosen as it has been found to have smaller error and bias compared to other multiple imputation approaches (Ambler, Omar and Royston, 2007; Penone *et al.*, 2014). MICE is also the most frequently used technique in previous imputations of trait data (Fisher, Blomberg and Owens, 2003; Baraloto *et al.*, 2010; Paine *et al.*, 2011; Di Marco *et al.*, 2012). The pattern of missing data throughout our dataset lends itself to multiple imputation, with the majority of species having complete data (54% overall; 61% for mammals; 50% for birds) or only one trait value missing (31% overall; 34% for mammals; 29% for birds). Only 15% of species (5% for mammals; 21% for birds) suffer from missing data in more than one trait.

Phylogenetic data can improve the estimation of missing trait values in the imputation process (Fisher, Blomberg and Owens, 2003; Cardillo *et al.*, 2008; Guénard, Legendre and Peres-Neto, 2013; Swenson, 2014; Kim, Blomberg and Pandolfi, 2018), because closely related species tend to be more similar to each other (Pagel, 1999) and many traits display high degrees of phylogenetic signal (Blomberg, Garland and Ives, 2003). Phylogenetic information was therefore summarized by eigenvectors extracted from a principal coordinate analysis, representing the variation in the phylogenetic distances among species (Diniz-Filho, Bini, *et al.*, 2012; Diniz-Filho, Rangel, *et al.*, 2012). To do this, a supertree of mammals (Bininda-Emonds *et al.*, 2008) with updates (Fritz, Bininda-Emonds and Purvis, 2009) and a tree of birds (Prum *et al.*, 2015) were read into R - *read.tree/read.nexus* functions ('ape' package (Paradis, Claude and Strimmer, 2004)) - and decomposed into a set of orthogonal phylogenetic eigenvectors using the *PVRdecomp* function ('PVR' package (Santos *et al.*, 2013)).

It has been shown that error is minimised when including the first 10 eigenvectors as variables in the imputations (Penone *et al.*, 2014). Note, however, that these eigenvectors are more representative of divergences closer to the root of the phylogeny so they do not include fine-scale differences among species (Diniz-Filho, Bini, *et al.*, 2012). Here, we also used the first 10 eigenvectors, ensuring a balance between including detailed phylogenetic information and diluting the information contained in the other traits. The first 10 eigenvectors in our data represented 49% of the variation in the phylogenetic distances among mammals and 45% for birds.

To generate imputed values, we used the *mice* function ('mice' package (Van Buuren and Groothuis-Oudshoorn, 2011)). We specified the method as: predictive mean matching for continuous traits, which preserves non-linear relationships (Van Buuren and Groothuis-Oudshoorn, 2011) often present in trait datasets (Santini *et al.*, 2013); logistic regression for binary traits; and polytomous regression for the categorical traits (Van Buuren and Groothuis-Oudshoorn, 2011) (Table A.2). The variables included were the transformed traits (log-transformed and square-root transformed where applicable - trait data with more balanced distributions perform better under imputation (Taugourdeau *et al.*, 2014)) and the first 10 phylogenetic eigenvectors. This was consistent with the recommendations of the authors of mice who suggest including fewer than 15-25 variables in the imputation (Van Buuren and Groothuis-Oudshoorn, 2011). We extracted 25 imputed datasets and repeated the imputations 100 times per dataset (i.e., 2,500 imputed values per missing value). There was very strong agreement between the imputed datasets (Figure A.2; all pairwise correlations $\text{rho}_{823} > 0.97$). Thus for all analyses (excluding Figure A.3) we used a single, randomly selected, imputation dataset (see https://figshare.com/articles/Global_trade-offs_of_functional_redundancy_and_functional_dispersion_for_birds_and_mammals/5616424), due to the high computational costs associated with running the null models for all the imputed datasets. For completeness we also present the mean results (correlation between single, randomly selected, imputation dataset and mean imputation values: functional redundancy $\text{rho}_{823} = 0.99$, $P < 0.001$, functional dispersion $\text{rho}_{823} > 0.99$, $P < 0.001$) across the 25 imputed datasets

(Figure A.3). We also calculated the associated total variance according to Rubin's rules (Vink and van Buuren, 2014); showing that the continental patterns of functional redundancy and functional dispersion are robust to the imputation of missing-data, while the highest variance is recorded for island ecoregions and areas of Antarctica (Figure A.3).

To test the sensitivity of the results to the inclusion of the number and the identity of traits, we reran all analyses with all combinations of five out of six traits (Mouillot *et al.*, 2014; Toussaint *et al.*, 2016). We did not reduce the number of traits lower than five because we might have missed important dimensions of the functional space (Mouillot *et al.*, 2014). The results were robust to this procedure (Figure A.1; Table A.3). Thus, our findings show low sensitivity to functional trait selection (Toussaint *et al.*, 2016). Although, the addition of novel, functionally important traits could have unknown influence on the results. Yet there are few traits, not selected here, for birds and mammals with strong hypothesised functional relationships identified in the literature. For instance, we would suggest home range size (indicating the area of effect of a species) or a species' natal dispersal distance (relating to the ability of a species to disperse between isolated habitats) as possible candidates that therefore require further data acquisition and compiling efforts, but are, at this point in time, unavailable for analysis.

A.3.3 Functional metrics

The above steps generated a matrix of ecoregion species composition (825 ecoregions in rows, 15,485 species in columns, values = presence/absence) and a matrix of trait data (15,485 species in rows, six traits in columns, values = trait values [empirical and imputed]). We then utilised these matrices to calculate functional redundancy and functional dispersion.

Here, functional redundancy and functional dispersion are not intended to relate directly to specific ecological functions or processes, but instead to describe species' ecological strategies and thus the functional roles (redundancy) and breadth of functions (dispersion) performed by species.

Functional redundancy is defined as the number of species contributing similarly to an ecosystem function (Walker, 1992) and therefore relates to the insurance of an ecosystem to species declines or extinctions (Mouillot, Bellwood, *et al.*, 2013; Carmona *et al.*, 2016). In practical terms, two species can be deemed as functionally redundant if they have the same trait values - in other words, if they occupy the same portion of trait space (Carmona *et al.*, 2016).

To determine functional redundancy we applied the Unique Trait Combination (UTC) approach, which can accommodate continuous and categorical traits and account for holes in the trait space (Keyel, Wiegand and Orme, 2016). The UTC approach is also intuitive, easy to calculate and easy to interpret; it does not require ordination, clustering techniques, convex hulls or use of a dendrogram - all of which have their issues (Keyel, Wiegand and Orme, 2016). For instance, clustering depends upon the choice of clustering algorithm and selecting the ‘correct’ number of functional groups, both of which can significantly affect the outcome of a functional analysis (Wright *et al.*, 2006; Mouchet *et al.*, 2008; Carmona *et al.*, 2016). Whereas, convex hulls are sensitive to outliers and do not detect gaps in functional space (Blonder *et al.*, 2014; Carmona *et al.*, 2016). Functional dendrograms tend to bias the initial distribution of functional distances towards overestimating the functional dissimilarity between species pairs (Maire *et al.*, 2015). Plus, functional dendrograms are sensitive to the species included in the pool (Huang, Stephens and Gittleman, 2012).

To perform the UTC approach, first the continuous traits (body mass, litter/clutch size and habitat breadth) were binned using Sturges algorithm (Sturges, 1926) - a data-driven approach, which accounts for the variation present in the trait across the species pool. Binning traits based on their distribution reflects previous advice that researchers should consider the degree of variability likely to occur in trait values (Violle *et al.*, 2007). Sturges algorithm breaks the data into classes based on the sample size and distribution of the trait (Sturges, 1926). Sturges algorithm was chosen as it provided the best compromise between loss of resolution of the data (too few bins) and a ‘broken comb look’ (too many bins leading to gaps in the data distribution). The binning procedure produced 14 bins for body mass, 17 bins for litter/clutch size and 10 bins for habitat breadth. While it may be argued that binning leads to information loss, we are using mean trait values, which do not account for intraspecific variability, and therefore coarse categorisation may actually represent a more accurate treatment of these data (Keyel, Wiegand and Orme, 2016). For example, two species may differ in their average trait values by a small amount (e.g., many species differ by < 0.1 g for body mass) but the intraspecific variation may be larger than the difference and therefore the ranges of the two species may almost entirely overlap. Treating these two species as unique - by using continuous trait values or broken comb binning - would therefore not make biological sense. After binning, we sorted species into functional units based on their trait combinations to produce UTCs using the *mvfd* function (‘multirich’ package (Keyel, Wiegand and Orme, 2016)). Functional redundancy was then simply the number of species per UTC per ecoregion.

Our characterization of functional redundancy has a broad resolution and we therefore do not expect species in the same UTC to fully compensate for the loss of group members. Instead, we propose that species with similar traits have similar ecological strategies, and hence can be considered as functionally redundant (Laliberté *et al.*, 2010; Carmona *et al.*, 2016). Our broad resolution also avoids a potential pitfall, where including too many traits or too many fine scale features leads to a metric that simply reflects taxonomy (every species is unique) and thus is equivalent to species richness.

Functional dispersion relates to response diversity, where a higher diversity of responses in a ecoregion should, in theory, provide greater resistance against environmental perturbations because of an enhanced capacity to respond to various types of perturbations (Luck, Carter and Smallbone, 2013). Mathematically defined, functional dispersion is the mean distance of individual species to the assemblage multidimensional trait space centroid (Laliberté *et al.*, 2010).

To estimate functional dispersion, a species by species trait-distance matrix was generated for all traits together (transformed where applicable) using Gower distances, *gowdis* function (‘FD’ package (Laliberté, Legendre and Shipley, 2014)), which allows mixed trait types (Table A.2) while giving them equal weight (Villéger, Mason and Mouillot, 2008). To calculate functional dispersion we used the *fdisp* function (‘FD’ package (Laliberté, Legendre and Shipley, 2014)), with the inputs being the Gower dissimilarity matrix and the ecoregion composition matrix. If an ecoregion contained no species or only one species (in which case no multivariate dispersion can be computed), it was assigned a functional dispersion value of zero (Laliberté *et al.*, 2010).

The previous steps generated raw values for functional redundancy and functional dispersion (i.e., including the effects of species richness) across ecoregions. However, to test whether observed functional values differed from the expected distribution of functional values given the observed species richness of an ecoregion, we used a null model based on global randomisation of species composition (Villéger, Mason and Mouillot, 2008). To implement the null model, for each ecoregion, we constructed 999 randomised assemblages drawn from a global species pool (all 15,485 species) (Oliveira *et al.*, 2016), while holding species richness constant (the R and bash scripts to run the null models on a High Performance Computer are available from the author upon request). Using a global pool makes the assumption that any combination of traits that exists globally can be found in any ecoregion, acknowledging convergent evolution. In contrast to this assumption, we also implemented a null model based on biome-scale randomisation of species composition, i.e., using biome species pools, to potentially better account for the spatial filtering of trait combinations due to biogeographic and historical processes. Results were qualitatively very similar when using a global or biome null model (Figure A.1; Table A.3; Figure A.4), so here we present the global null model, to allow functional contributions across biomes to be assessed (Figure 2.3). For each of the simulated assemblages, we then computed the functional metrics (functional redundancy and functional dispersion). To assess the magnitude of the difference for functional redundancy and dispersion between the observed (Fobs) and null (Fnull) results we calculated the standardised effect size (Toussaint *et al.*, 2016): SES = [Fobs –

mean(Fnull)]/SD(Fnull). We also carried out one-tailed permutation tests, where the null hypothesis was that the observed and null functional values were equivalent and the alternative hypothesis was that observed functional values were greater (or less) than the expected value under the null model assumptions. If the alternative hypothesis was greater, a p-value was estimated as: (number of Fnull ≥ Fobs + 1)/(999 + 1). If the alternative hypothesis was less, a p-value was estimated as: (number of Fnull ≤ Fobs + 1)/(999 + 1). Our rarefied analysis therefore maps functional patterns independently of differences in species richness, allowing us to assess the degree to which the observed functional values differ from the null distribution of functional values, revealing regions with higher (positive SES; permutation test [H1 = greater]) or lower (negative SES; permutation test [H1 = less]) functional values than expected at random (Villéger, Mason and Mouillot, 2008; Maire *et al.*, 2015), as well as allowing us to compare functional values across taxonomic groups with greatly different species richness (10,253 bird and 5,232 mammal species). We also performed the functional analyses for birds and mammals independently (Figure A.5; Figure A.6). We assessed differences in the functional metrics between birds and mammals using two-tailed Kolmogorov-Smirnov tests via the *ks.test* function. We calculated Spearman’s rho correlation coefficients between each pair of functional metrics, using the *cor.test* function.

Overall our results and conclusions were similar (i) with and without imputed data (compare Figure 2.1 and Figure A.1; Table A.3; Figure A.2; Figure A.3), (ii) with all combinations of five out of six traits (Figure A.1; Table A.3), and (iii) with a null model based on a global or biome species pool (Figure A.1; Table A.3; Figure A.4).

Appendix A

Table A.1 A list of potential traits which may be important in influencing the relationships between birds/mammals and their environment.

Trait	**Description**	**Data source(s)**	**Selection**
Age at maturity	Age when individuals are first physically capable of reproducing	(Jones *et al.*, 2009; Myhrvold *et al.*, 2015)	No (>50% missing values)
Basal metabolic rate	The amount of energy expended while at rest in a neutrally temperate environment, in the post-absorptive state	(Jones *et al.*, 2009)	No (>50% missing values)
Body mass	Average adult body mass in grams	(Pacifici *et al.*, 2013; Wilman *et al.*, 2014; Myhrvold *et al.*, 2015)	Yes
Diel activity	Foraging activity at night or during the day (nocturnal vs. diurnal species)	(Wilman *et al.*, 2014)	Yes
Diet	Utilisation of different dietary categories (e.g. invertebrates, vertebrates, scavenge, fruit, nectar, seed, plant)	(Kissling *et al.*, 2014; Wilman *et al.*, 2014)	Yes
Dispersal age	Age at which young permanently leave the parent, parental group, social group or any associated territories	(Jones *et al.*, 2009)	No (>50% missing values)
Foraging stratum	The stratum primarily used for foraging (e.g. ground-level, scansorial, arboreal, aerial)	(Jones *et al.*, 2009; Wilman *et al.*, 2014)	No (>50% missing values)
Generation length	The time required for a population to increase by the replacement rate. Reflects the turnover rate of breeding individuals in a population.	*, (Pacifici *et al.*, 2013)	No (high multicollinearity with body mass and litter/clutch size)
Gestation length	Length of time of non-inactive foetal growth	(Jones *et al.*, 2009;	No (>50% missing values)

		Myhrvold *et al.*, 2015)	
Habitat breadth	Number of habitat types occupied	†	Yes
Home range size	Size of the area within which everyday activities are typically restricted	(Jones *et al.*, 2009)	No (>50% missing values)
Litter/clutch size	Number of offspring per litter/clutch	(Jones *et al.*, 2009; Myhrvold *et al.*, 2015)	Yes
Litters/clutches per year	Number of litters/clutches per female per year	(Jones *et al.*, 2009; Myhrvold *et al.*, 2015)	No (>50% missing values)
Maximum longevity	Maximum adult age	(Jones *et al.*, 2009; Myhrvold *et al.*, 2015)	No (>50% missing values)
Migratory behaviour	Migratory status (e.g. non-migrants, nomads, altitudinal migrants)	∗	No (no data available for mammals)
Natal dispersal distance	Distances moved by juvenile animals during natal dispersal	(Sutherland *et al.*, 2000)	No (>50% missing values)
Volancy	The capacity to fly	(Findley, 1993; del Hoyo *et al.*, 2013; Healy *et al.*, 2014)	Yes

∗ birdlife@birdlife.org

† http://www.iucnredlist.org/technical-documents/classification-schemes/habitats-classification-scheme-ver3

Table A.2 Traits selected, their data type and the number and percent of species covered (before imputation) out of 15,485 bird and mammal species.

Trait	**Type**	**Species covered**
Body mass	Continuous	15,485 (100%)
Diel activity (diurnal/nocturnal)	Nominal (binary)	14,100 (91%)
Diet	Categorical (plat/seed; fruit/nectar; invertebrates; vertebrates; omnivore)	14,307 (92%)
Habitat breadth	Continuous	14,013 (90%)
Litter/clutch size	Continuous	9,040 (58%)
Volancy (flight ability)	Nominal (binary)	15,485 (100%)

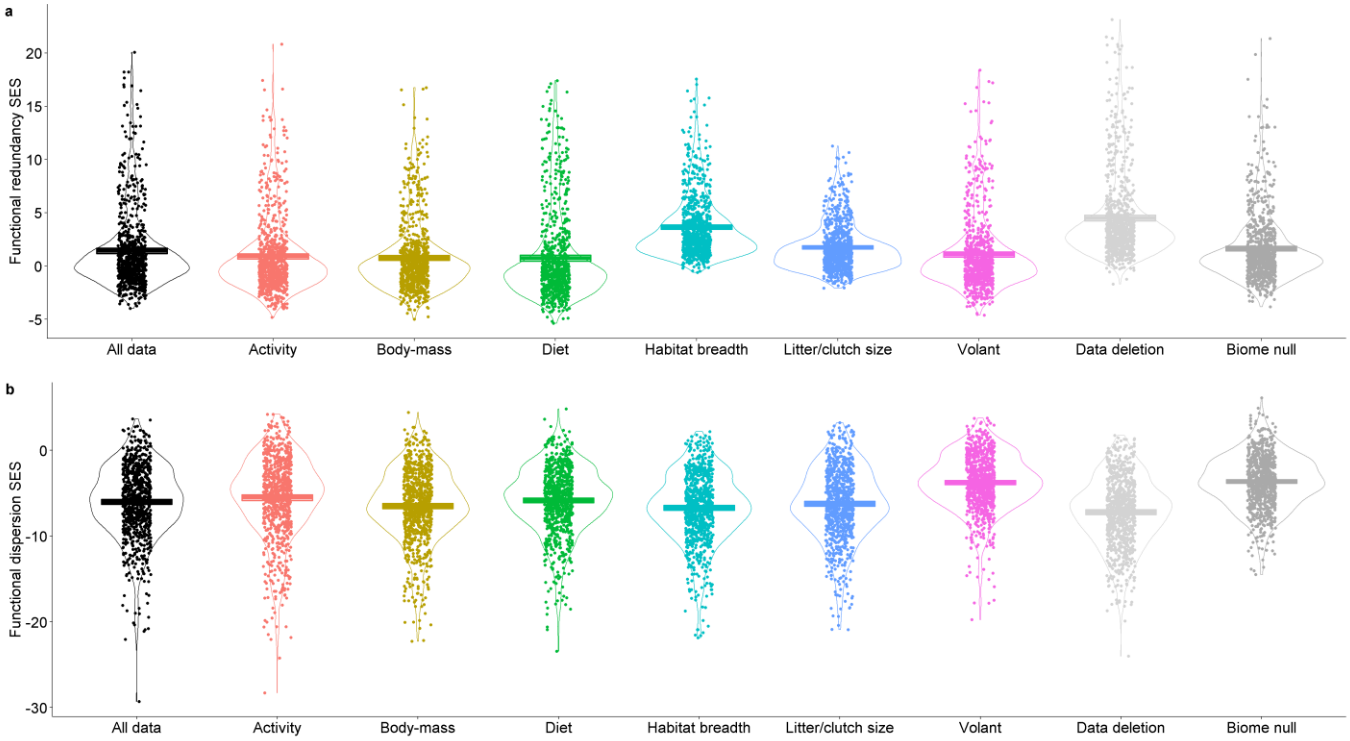

Figure A.1 Comparison of (a) functional redundancy SES (standardized effect size; calibrating against species richness) and (b) functional dispersion SES for all data (black) and for each trait removed individually (coloured), plus the data deletion approach (light grey) and when using a null model based on a biome species pool (dark grey). Included are the values for each ecoregion as jittered points, violins of data density and crossbars where the central thick line is the mean and the edges of the rectangle are the 95% confidence intervals around the mean.

Table A.3 Correlations (Spearman's rho_{823}; all significant $P < 0.05$) between functional metrics for all six traits included and for each trait removed individually (n-1 traits), plus the data deletion approach and when using a null model based on a biome species pool.

Sensitivity	**Functional metrics**			
	Functional redundancy	**Functional dispersion**	**Functional redundancy SES**	**Functional dispersion SES**
Body mass	0.98	1.00	0.85	0.93
Diel activity (diurnal/nocturnal)	0.99	0.96	0.94	0.93
Diet	0.98	0.99	0.88	0.94
Habitat breadth	0.96	1.00	0.73	0.94
Litter/clutch size	0.96	1.00	0.69	0.95
Volancy (flight ability)	0.99	0.96	0.95	0.90
Data deletion approach	0.95	0.95	0.78	0.85
Biome null	NA	NA	0.65	0.76

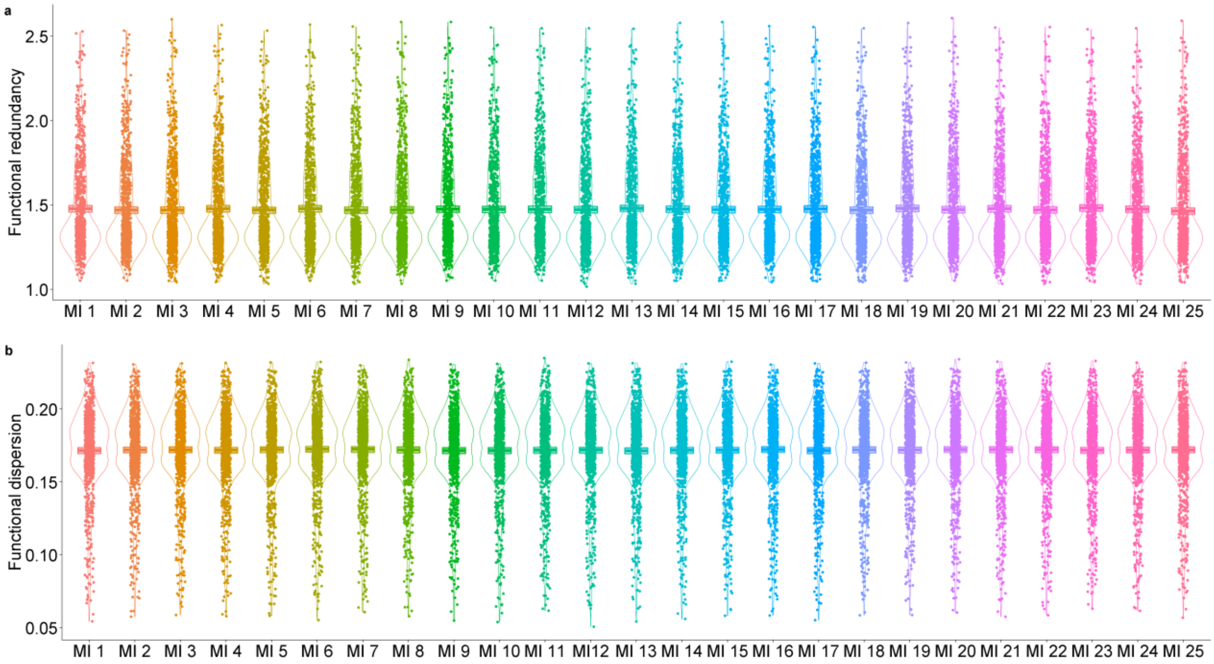

Figure A.2 Comparison of (a) functional redundancy and (b) functional dispersion for all 25 imputed datasets (see Appendix A.3). Included are the values for each ecoregion as jittered points, violins of data density and crossbars where the central thick line is the mean and the edges of the rectangle are the 95% confidence intervals around the mean. All pairwise correlations rho$_{823}$ > 0.97.

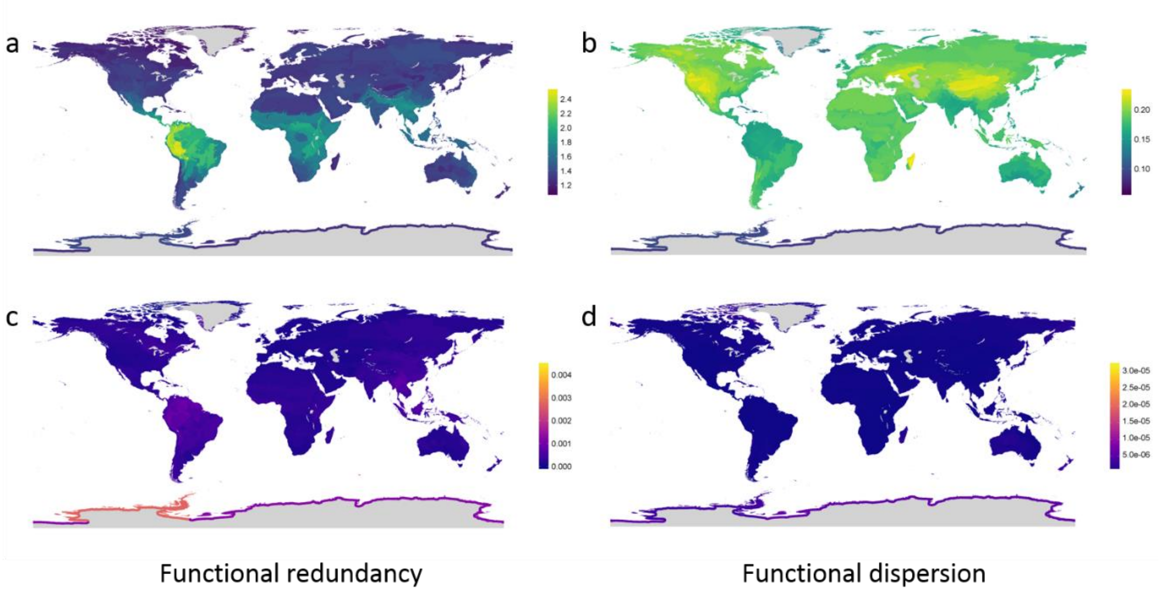

Figure A.3 Functional redundancy and functional dispersion according to Rubin's rules across 825 terrestrial ecoregions for 15,485 bird and mammal species. (a) mean functional redundancy across 25 imputed datasets, (b) mean functional dispersion across 25 imputed datasets, (c) total variance of functional redundancy across the imputations, and (d) total variance of functional dispersion across the imputations.

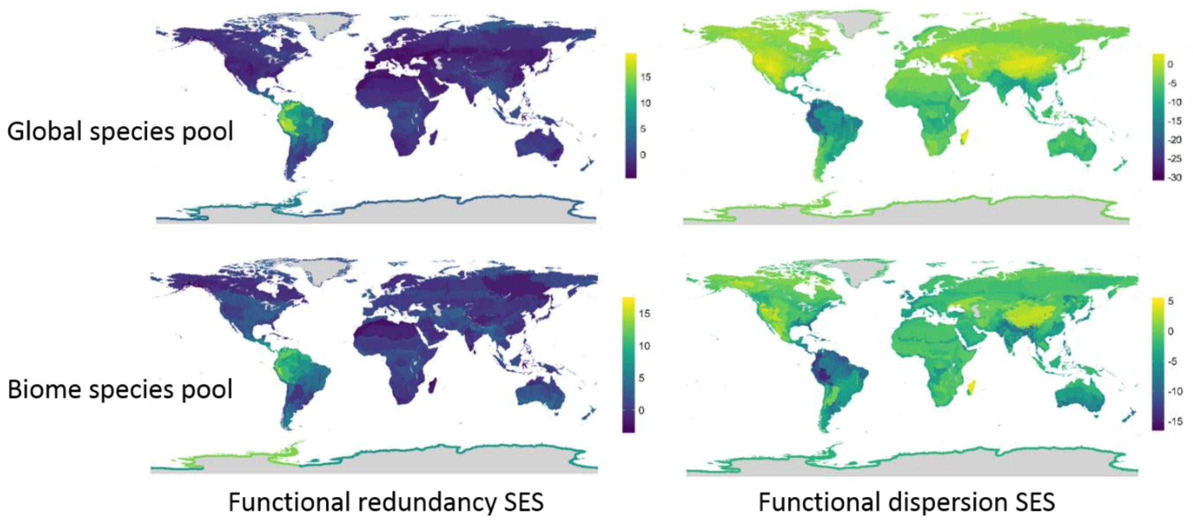

Figure A.4 Functional redundancy SES (standardized effect size; calibrating against species richness) and functional dispersion SES across 825 terrestrial ecoregions for 15,485 bird and mammal species based on a global or biome species pool null model. Ecoregions in grey were not considered in the analyses (‘Lake’ and ‘Rock and Ice’ ecoregions, because they are not coherent systems, i.e., they occur at multiple locations across the globe).

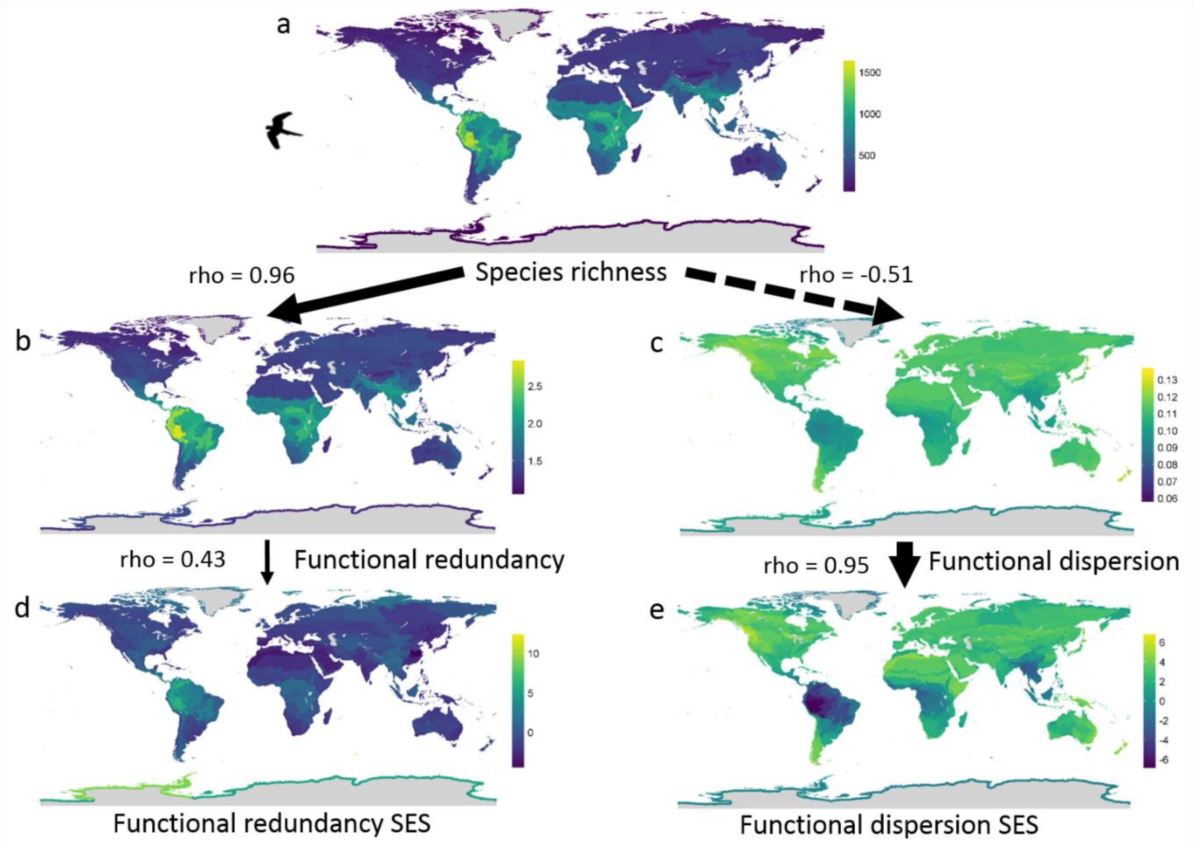

Figure A.5 Functional redundancy and functional dispersion across 825 terrestrial ecoregions for 10,253 extant bird species. (a) species richness, (b) functional redundancy, (c) functional dispersion, (d) functional redundancy SES (standardized effect size;

calibrating against species richness), (e) functional dispersion SES. Arrows are proportional to Spearman’s rho correlation coefficients (all correlations are significant; rho_{823}, $P < 0.001$). Ecoregions in grey were not considered in the analyses (‘Lake’ and ‘Rock and Ice’ ecoregions, because they are not coherent systems, i.e., they occur at multiple locations across the globe).

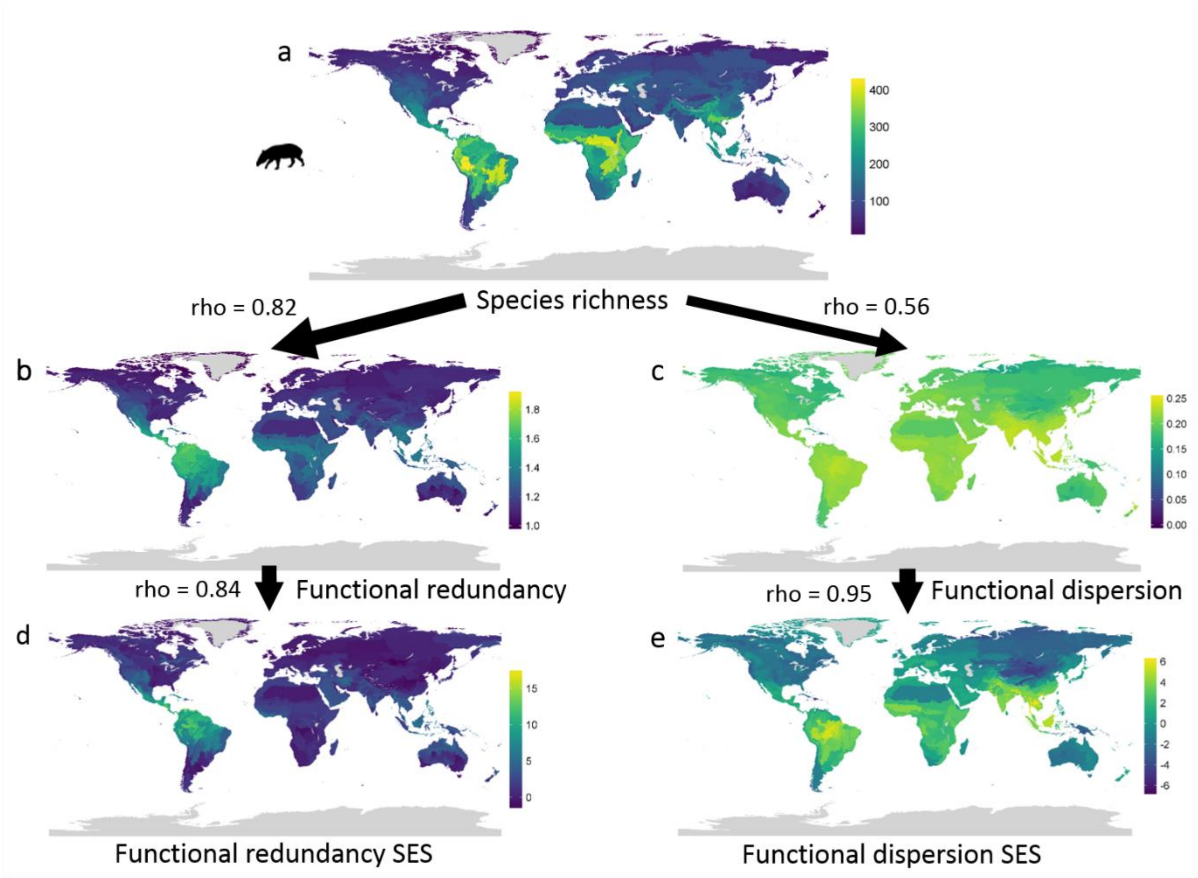

Figure A.6 Functional redundancy and functional dispersion across 825 terrestrial ecoregions for 5,232 extant mammal species. (a) species richness, (b) functional redundancy, (c) functional dispersion, (d) functional redundancy SES (standardized effect size; calibrating against species richness), (e) functional dispersion SES. Arrows are proportional to Spearman’s rho correlation coefficients (all correlations are significant; rho_{823}, $P < 0.001$). Ecoregions in grey were not considered in the analyses (‘Lake’ and ‘Rock and Ice’ ecoregions, because they are not coherent systems, i.e., they occur at multiple locations across the globe).

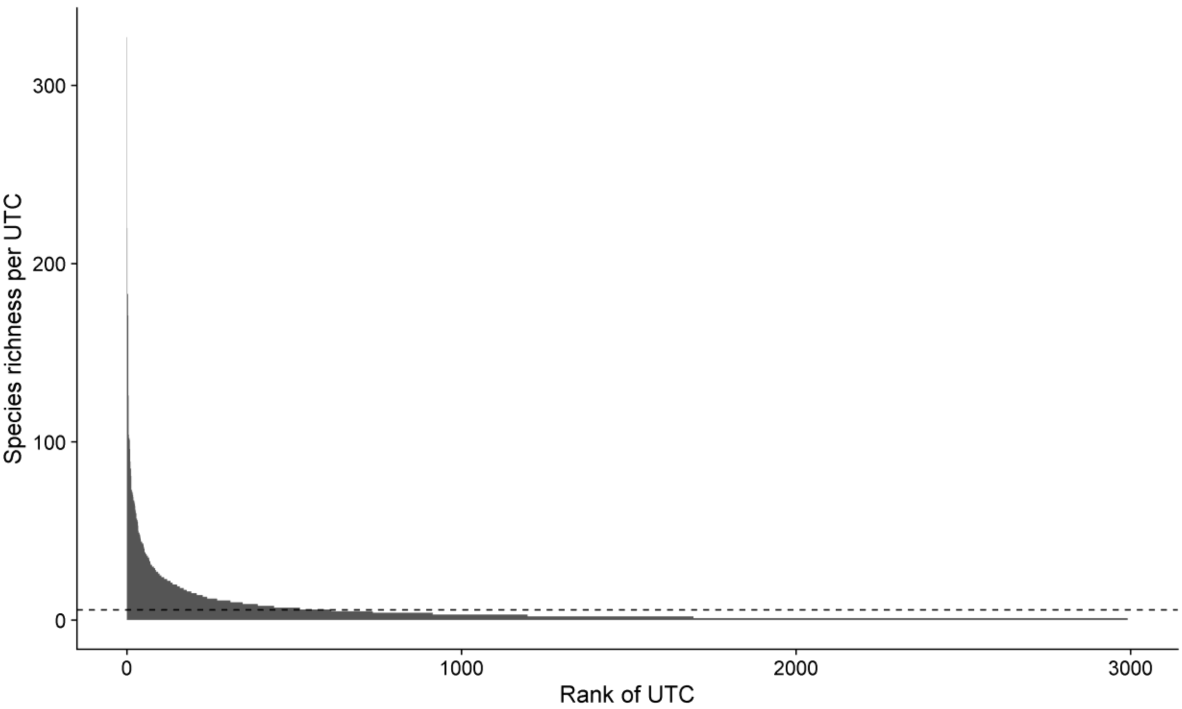

Figure A.7 The distribution of species across 2,991 Unique Trait Combinations (UTCs) for 15,485 bird and mammal species. On average there are 5.2 species per UTC (dashed line). The most speciose UTC contains 327 species, while 1,297 UTCs contain only one species. Reflecting previous results for fish (Mouillot *et al.*, 2014).

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Appendix B Supporting information for Chapter 3

B.1 Supplementary methods

B.1.1 Traits

We extracted three categorical traits for post-analysis interpretations (Chapter 2) (Cooke, Bates and Eigenbrod, 2019): flight capability (volant/non-volant), diel activity (diurnal/nocturnal) and diet guild (an aggregated diet score) (Figure B.5). For diet guild, species were classified into five groups according to their primary diet (Wilman *et al.*, 2014): plant/seed, fruit/nectar, invertebrates, vertebrates (including carrion), and omnivore (score of ≤ 50 in the four other diet categories).

B.1.2 Ecological strategy surface

We used only the first principal component from the diet PCoA for our main analyses, so that each trait dimension had equal weight. However, for comparison we provide the ecological strategy surface when including two synthetic diet traits (first and second principal components from diet PCoA; Figure B.4) (Figure B.11), which is very similar to when we only include one synthetic diet trait (Figure 3.1). Moreover, diet guild showed clear patterning across the ecological strategy surface (Figure B.5d), indicating that the use of a single diet axis sufficiently captured the variation in species diets. For instance, carnivores show distinct separation on the ecological strategy surface (Figure B.5d, see marginal plot on PC1), despite the low importance of carnivory in the PCoA (Figure B.4). We also generated ecological strategy surfaces for mammals (Figure B.16) and birds (Figure B.17) separately.

Overall our results and conclusions for the ecological strategy surface were similar (i) with and without imputed data (compare Figure 3.1 and Figure B.8; Figure B.2), and (ii) with one or two synthetic diet traits (compare Figure 3.1 and Figure B.11).

B.1.3 Extinction scenarios

For simplicity, in the main extinction analyses we treated DD species as LC (Purvis, Gittleman, *et al.*, 2000; Veron *et al.*, 2016). However, in reality, an unknown proportion of DD species are not at risk of extinction whilst others are likely to be threatened. To evaluate the impact of the extinction probability for DD species we implemented two alternative scenarios: excluding DD species (Figure B.12; Figure B.13) and assigning an average predicted extinction probability to DD species (Figure B.14; Figure B.15), based on previous research (Bland *et al.*, 2015). To calculate an extinction probability for DD species we first calculated the average extinction probability of threatened species at the same ratio of CR:EN:VU (380:863:1254 species) as for the set of species for which threat categories are known (Isaac *et al.*, 2012). Thus, the average extinction probability for threatened species was 0.433 = ((380 CR species * 0.999) + (863 EN species * 0.667) + (1254 VU species * 0.1)) / (380 + 863 + 1254). We then did the same for non-threatened species ((1300 NT species * 0.01) + (10963 LC species * 0.0001)) / (1300 + 10963) = 0.001. 64% of DD mammal species were previously predicted to be threatened, using machine learning tools (Bland *et al.*, 2015). As the majority of our DD species were mammals (665 DD mammal species, 59 DD bird species) we applied this value across our 724 DD species. So we multiplied the average extinction probability for threatened species (0.433) by the proportion of DD species predicted to be threatened (0.64) (Bland *et al.*, 2015) and multiplied the average extinction probability for non-threatened species (0.001) by the proportion of DD species predicted to be non-threatened (0.36), and then summed the total extinction probability, resulting in an extinction probability of 0.277 for DD species. Thus, DD species were assigned an average predicted extinction probability that falls between VU and EN.

The IUCN Red List is, of course, not a perfect predictor of the future state of the biosphere, but it represents our best and most comprehensive assessment of the probability that any given species will go extinct in the near future (Smith *et al.*, 2018). Here we consider extinction only (disregarding possible speciation), because our focus is on the impact of current high rates of extinction over relatively short time frames (100 years), for which little speciation may be expected.

Overall our results and conclusions for the extinction analyses were similar (i) with and without imputed data (compare Figure 3.3 and Figure B.9; plus, compare Figure B.7 and Figure B.10), (ii) with and without DD species (compare Figure 3.3 and Figure B.12; plus, compare Figure B.7 and Figure B.13), and (iii) when assigning DD species an extinction probability of 0.0001 or 0.277 (compare Figure 3.3 and Figure B.14; plus, compare Figure B.5 and Figure B.15).

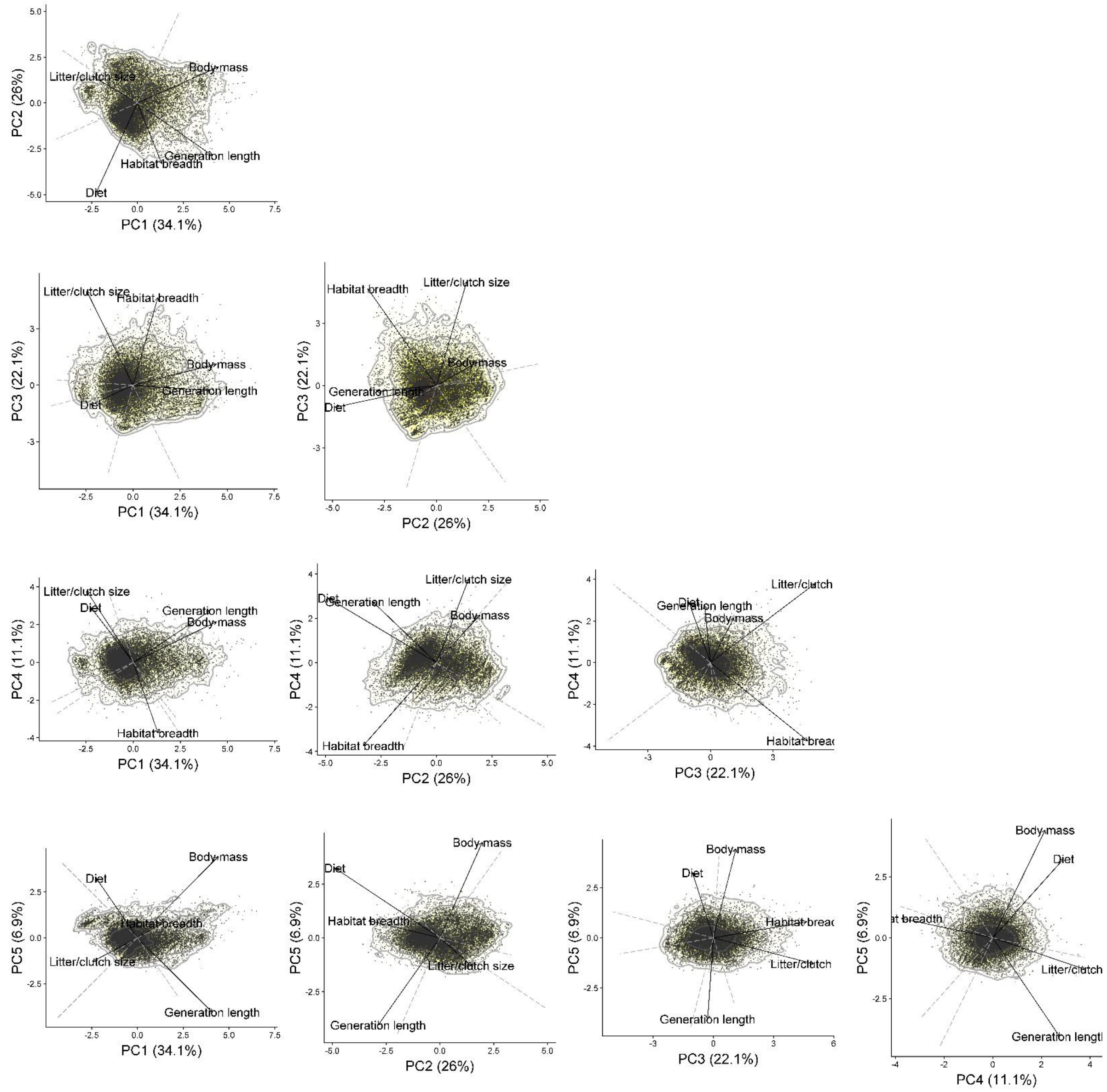

Figure B.1 Ecological strategy surfaces for mammals and birds (15,484 species) for each pairwise combination of the five principal components. Percentage values represent proportion of the total variation explained by each PC.

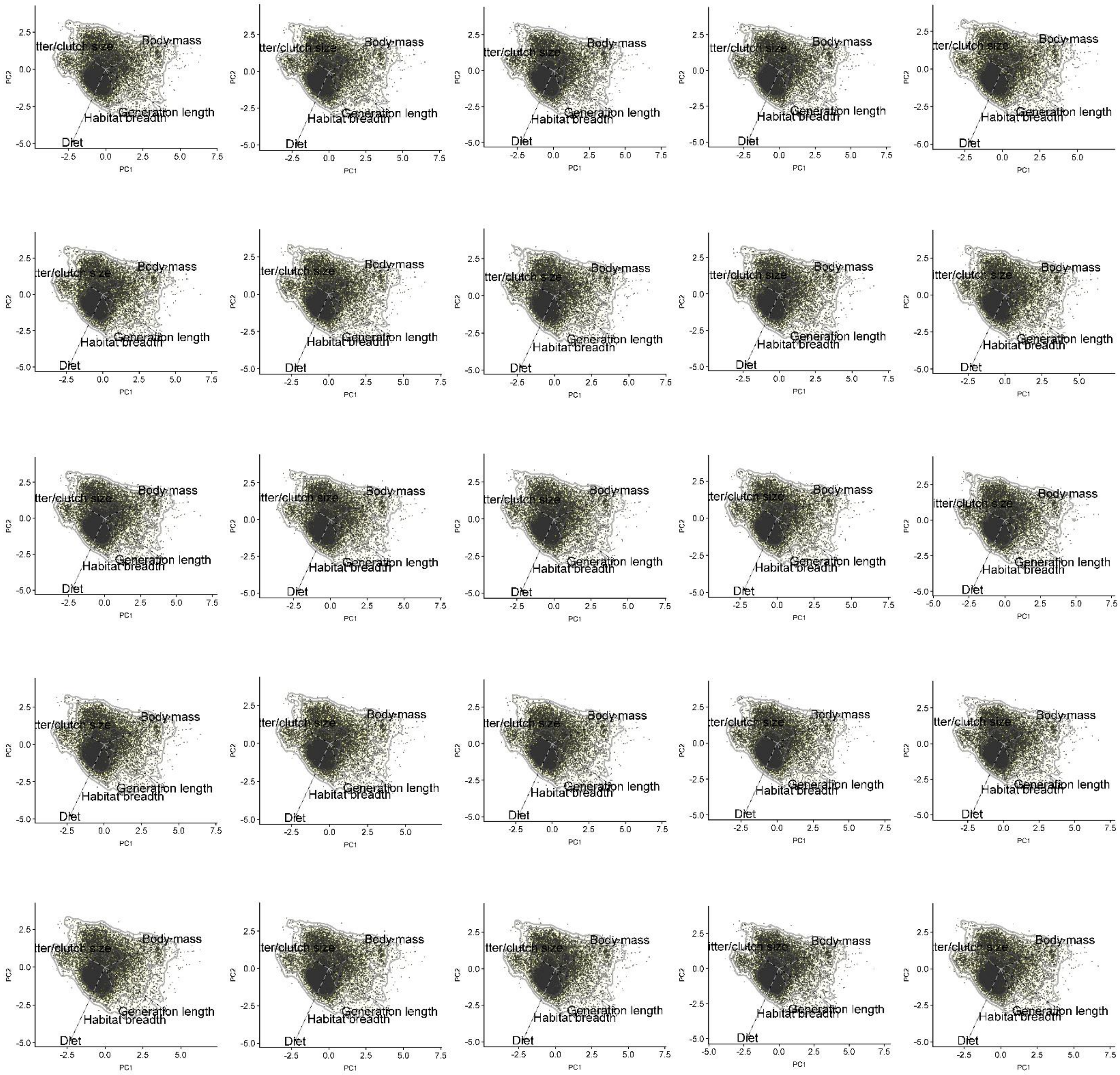

Figure B.2 Ecological strategy surfaces for mammals and birds (15,484 species) for each of the 25 imputed datasets (Appendix B.1). The plots show very high similarity across the imputed datasets.

Table B.1 Mean variable loadings (across 25 imputed datasets) resulting from the principal components analysis (PCA; Figure 3.1). Positive loadings are shown in increasingly dark shades of blue with increasing magnitude, and negative loadings in increasingly dark red. The proportion of variance of a given trait accounted for can be obtained by squaring the loading.

Trait	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
Body mass	0.63	0.28	0.16	0.31	0.63
Diet	-0.32	-0.70	-0.15	0.42	0.46
Generation length	0.58	-0.41	-0.04	0.39	-0.58
Habitat breadth	0.19	-0.47	0.66	-0.54	0.11
Litter/clutch size	-0.35	0.21	0.71	0.54	-0.18

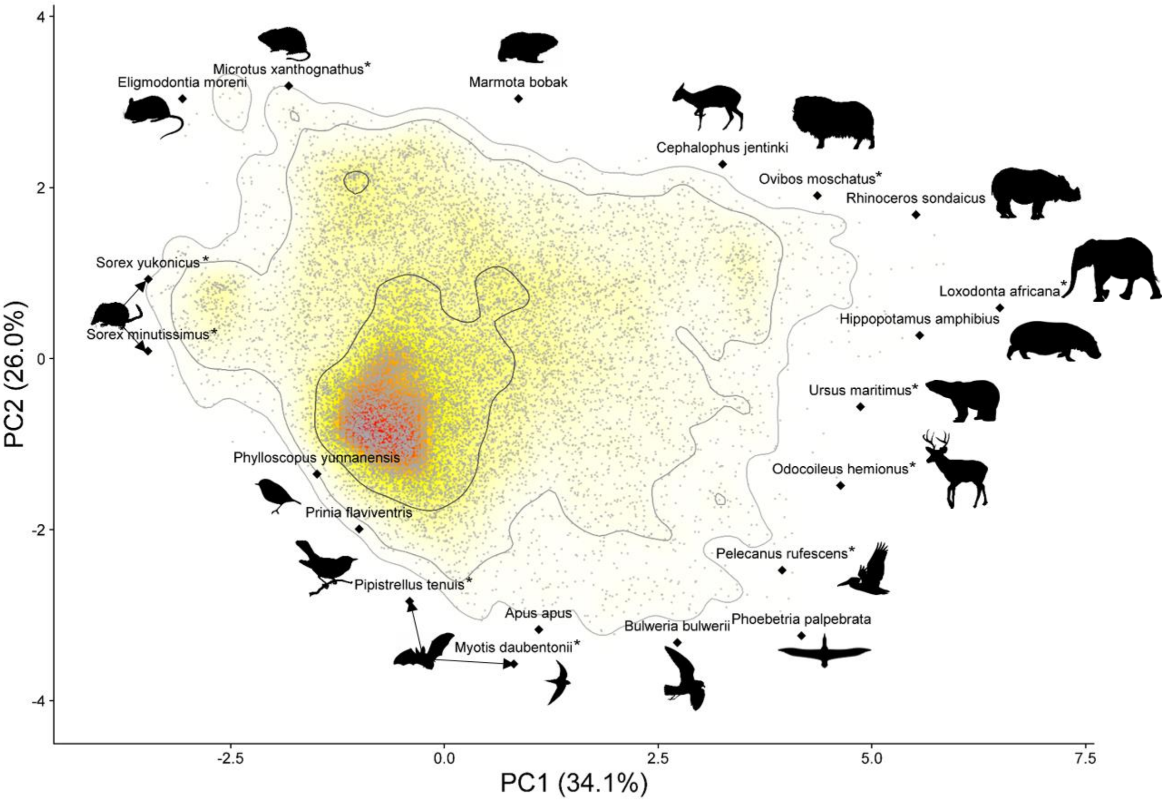

Figure B.3 The ecological strategy surface for mammals and birds (15,484 species) with species locations, scientific names and image sources. Projection of extant terrestrial mammal and bird species (grey dots) on the surface defined by principal components (PC) 1 and 2 (mean values across 25 imputed datasets; Appendix B.1). Silhouettes show a selection of species characterising the edges of trait space, with their locations represented by black diamonds and scientific names labelled. Silhouettes with scientific names followed by an * were freely downloaded from PhyloPic (www.phylopic.org), under CC0 1.0 Public Domain Dedication. The rest of the silhouettes were created by the authors in Inkscape. The silhouette of a bat is used to represent the location of two ecological outliers: *Pipistrellus tenuis* and *Myotis daubentonii* and the silhouette of the shrew for *Sorex minutissimus* and *Sorex yukonicus*.

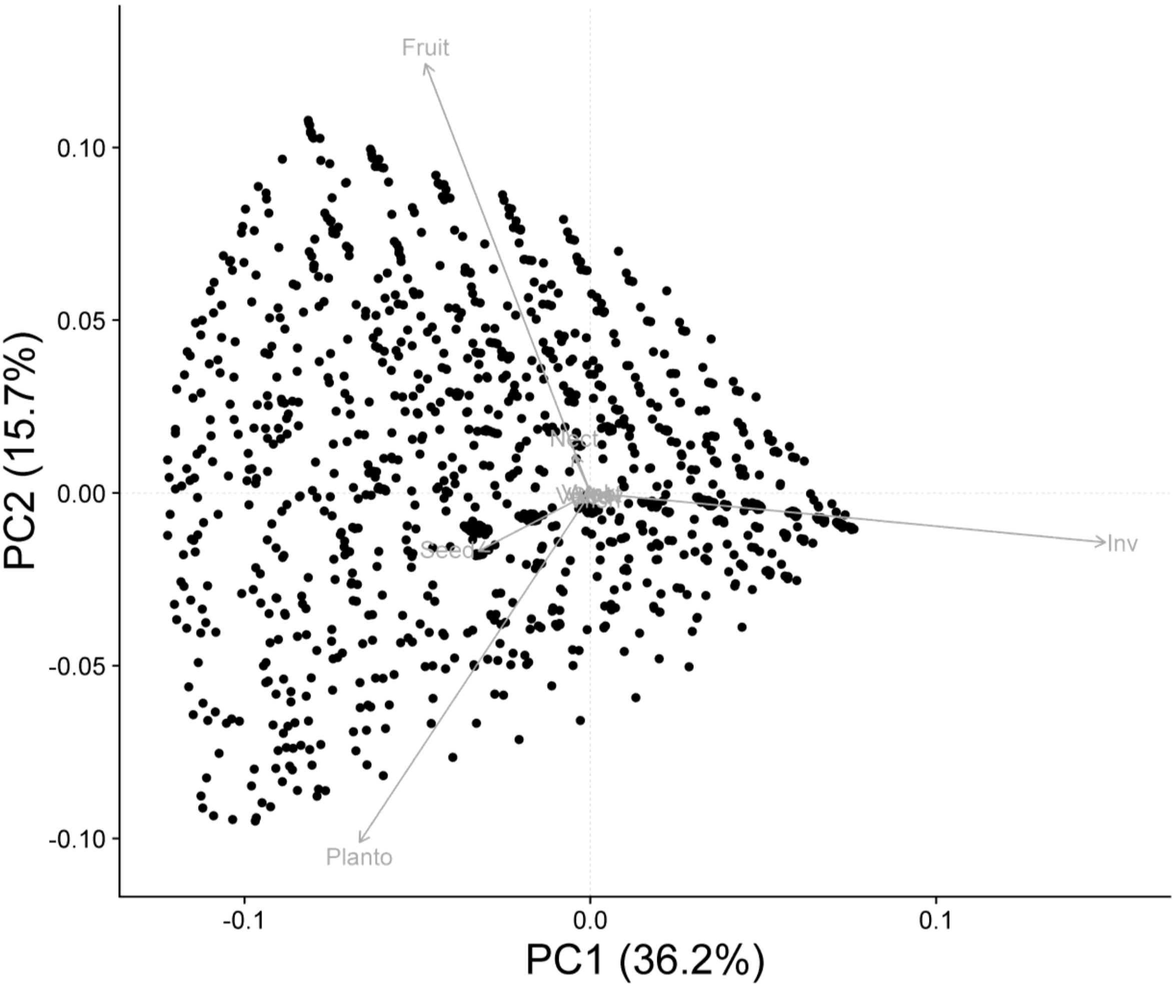

Figure B.4 Principal coordinates analysis (PCoA) of diet categories for mammals and birds (15,484 species). Arrows indicate direction and weighting of vectors representing the ten diet categories: Inv (invertebrates); Planto (other plant material); Fruit (fruit and drupes); Seed (seed, nuts); Nect (nectar, pollen, gum); Vend (vertebrate endotherms); Vect (vertebrate ectotherms); Vfish (fish); Vunk (vertebrate unknown); Scav (scavenge) - for full descriptions see the EltonTraits 1.0 metadata (Wilman *et al.*, 2014). Percentage values represent proportion of the total variation explained by each PC.

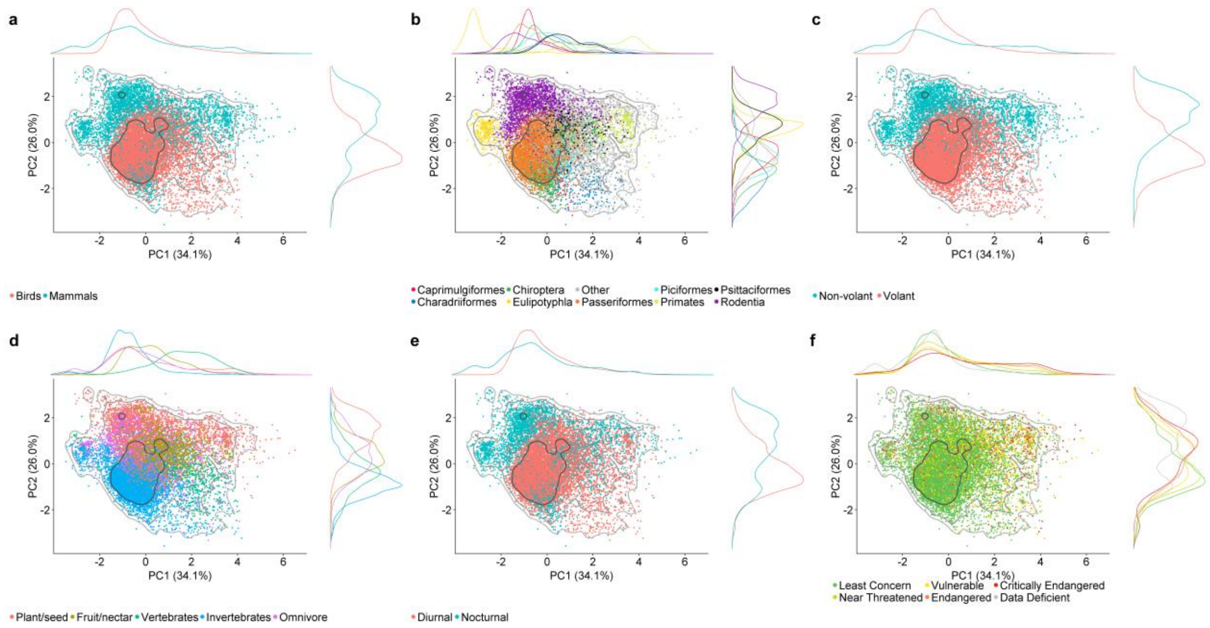

Figure B.5 The ecological strategy surface for mammals and birds (15,484 species) with categorical divisions. Differentiating categories include (a) Class, (b) the most speciose Orders, (c) flight capability, (d) dietary guild, (e) diel activity and (f) IUCN Red List category. Contours indicate 0.5 (hotspots), 0.95 and 0.99 quantiles of occurrence probability of species across the ecological strategy surface. Marginal plots indicate density distributions of the categories along the principal component axes. The most speciose Orders: Passeriformes - perching birds (5,903 species), Rodentia - rodents (2,206 species), Chiroptera - bats (1,104 species), Caprimulgiformes - nightjars, swifts, hummingbirds, and relatives (586 species), Piciformes - woodpeckers, toucans, puffbirds, and relatives (482 species), Eulipotyphyla - shrews, moles, hedgehogs and solenodons (441 species), Primates - apes, monkeys, lemurs, and relatives (414 species), Psittaciformes - parrots (397 species), and Charadriiformes - waders, gulls, auks, and relatives (374 species); the ‘Other’ category is a group comprised of 52 less speciose Orders.

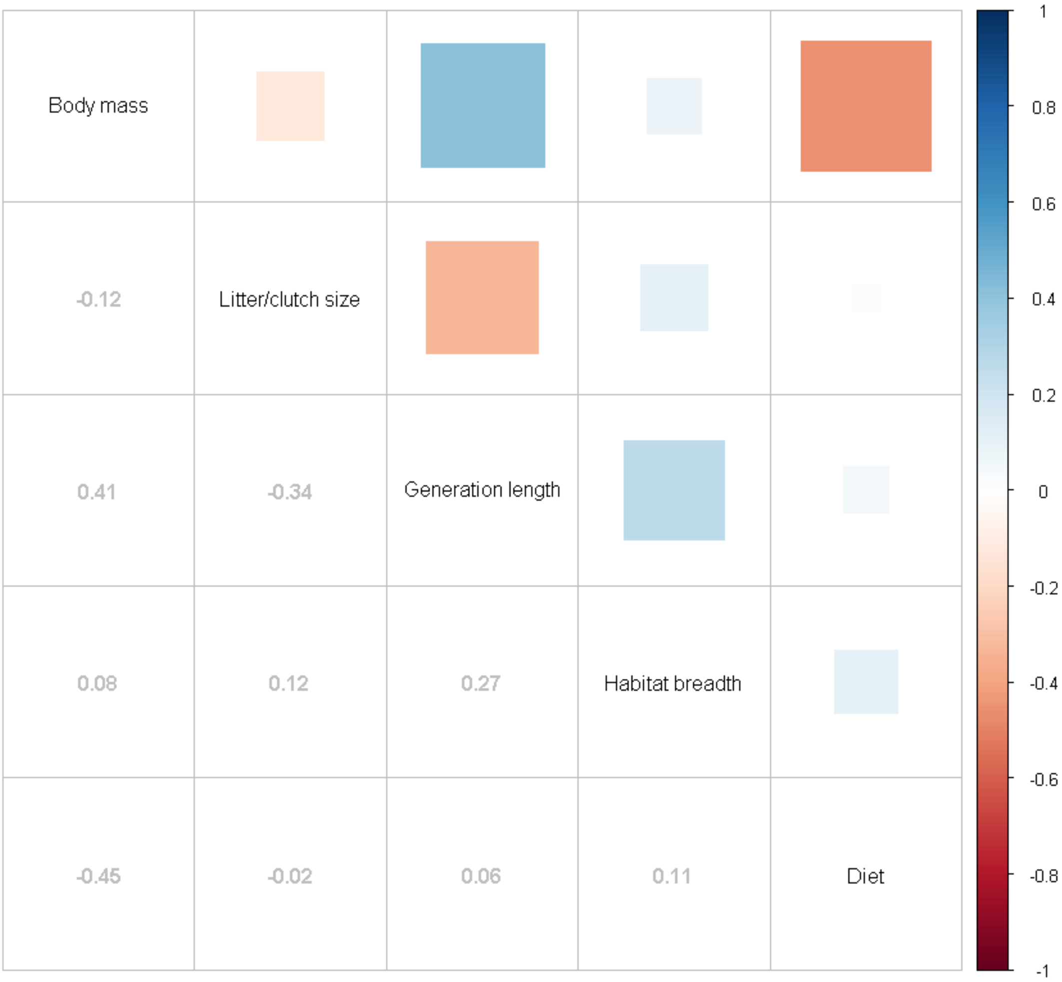

Figure B.6 Pairwise correlations between five traits for mammals and birds (15,484 species). Values are Pearson's correlation coefficients, with blue shades representing positive correlations and red shades reflecting negative correlations.

Table B.2 Percentage occupation by the observed ecological strategy space of the mean of 999 null strategy spaces generated from the assumptions of each null model, for each taxonomic group (all $P \leq 0.001$). We also tested across taxonomic groups, i.e., birds within mammal null strategy space. We found that birds are not completely nested within the null strategy space for mammals (and vice versa), due to extreme trait values that fall outside of the range of trait values for the other taxa (e.g., maximum generation length and litter/clutch size is greatest for birds, whereas maximum body mass and habitat breadth is greatest for mammals). Thus the different taxonomic groups do not completely share the same potential suite of trait combinations. In multi-dimensional space we find that 2.6% of the observed bird strategy space is unique compared to the null 1 mammal space, whereas 22.8% of the observed mammal space falls outside the null 1 bird space.

Null model*	**Taxonomic group**		
	Combined	**Mammals**	**Birds**
1: Traits uniformly distributed and independent from each other (approximately a hypercube)	9%	11%	11%
2: Traits normally distributed and independent from each other (approximately a hypersphere)	37%	43%	20%
3: Traits distributed as observed and independent from each other	62%	53%	71%
4: Traits normally distributed and correlated as observed (approximately a hyperellipsoid)	51%	74%	27%

* See Díaz *et al.* (2016) for full description and illustration of the null models

Table B.3 Contributions of different taxonomic and morphological groups to ecological strategy space. Volant mammals (bats [Chiroptera]; 1,103 species) may be expected to extend the mammalian ecological strategy space, due to strong ecomorphological differences to non-volant mammals. However we find that only 1.3% of the ecological strategy space occupied by mammals is attributable to bats. Thus, although bats may occupy a distant region of the ecological strategy surface compared to non-volant mammals, the ability of the hypervolume approach to model holes and disjunctions accounts for this separation. In addition, bats are densely packed in ecological strategy space, suggesting high convergence among strategies - reflecting previous spatial results, where bats showed high phylogenetic divergence but low ecological divergence (Mazel *et al.*, 2018). In contrast, non-volant birds (predominantly ratites, penguins and flightless rails; 57 species) had a much lower density of 1.0 species SD^{-5}, implying high strategy divergence among flightless birds.

Group	**No. of species**	**Volume (SD^5)**	**Unique volume**	**Density (species SD^{-5})**
Mammals	5232	881	51% (unique component of all mammals and birds)	5.9
Birds	10252	534	19% (unique component of all mammals and birds)	19.2
Volant mammals (bats; Chiroptera)	1103	27	1.3% (unique component of all mammals)	40.4
Non-volant birds (predominantly ratites, penguins and flightless rails)	57	58	1.7% (unique component of all birds)	1.0

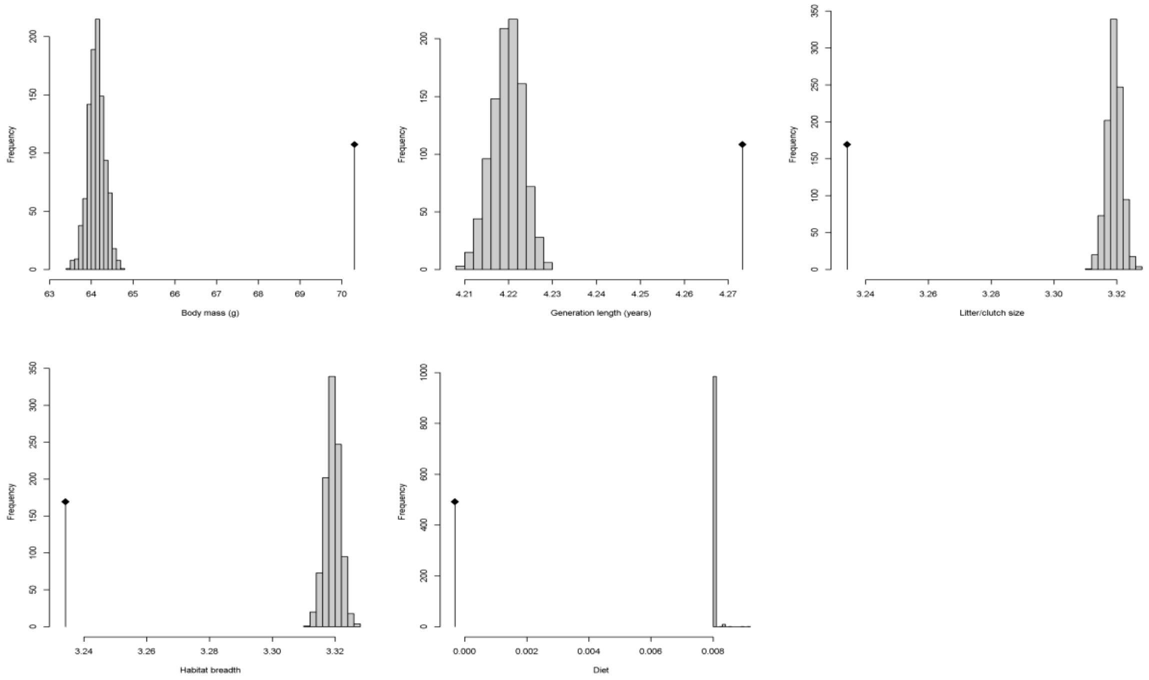

Figure B.7 Plots showing the results of the permutation tests, with histograms of the projected mean values (across 999 runs) and lollipops of the observed mean value per trait. When the lollipop is on the right of the histogram the trait is projected to decrease, whereas when the lollipop is on the left the trait is projected to increase.

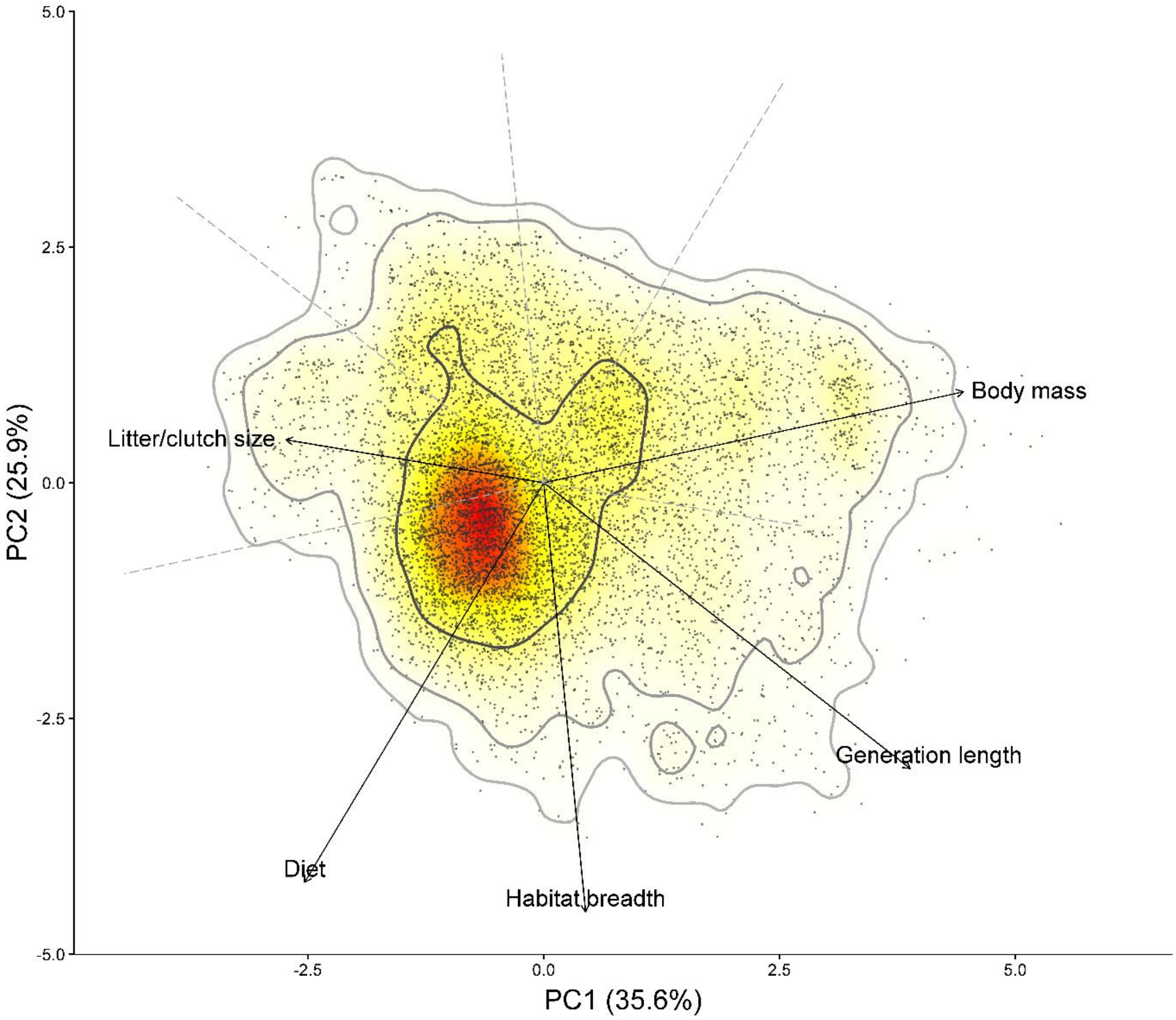

Figure B.8 The ecological strategy surface for mammals and birds (8,294 species) under the data deletion approach. Projection of extant terrestrial mammal and bird species with complete trait data (dots) on the surface defined by principal components (PC) 1 and 2.

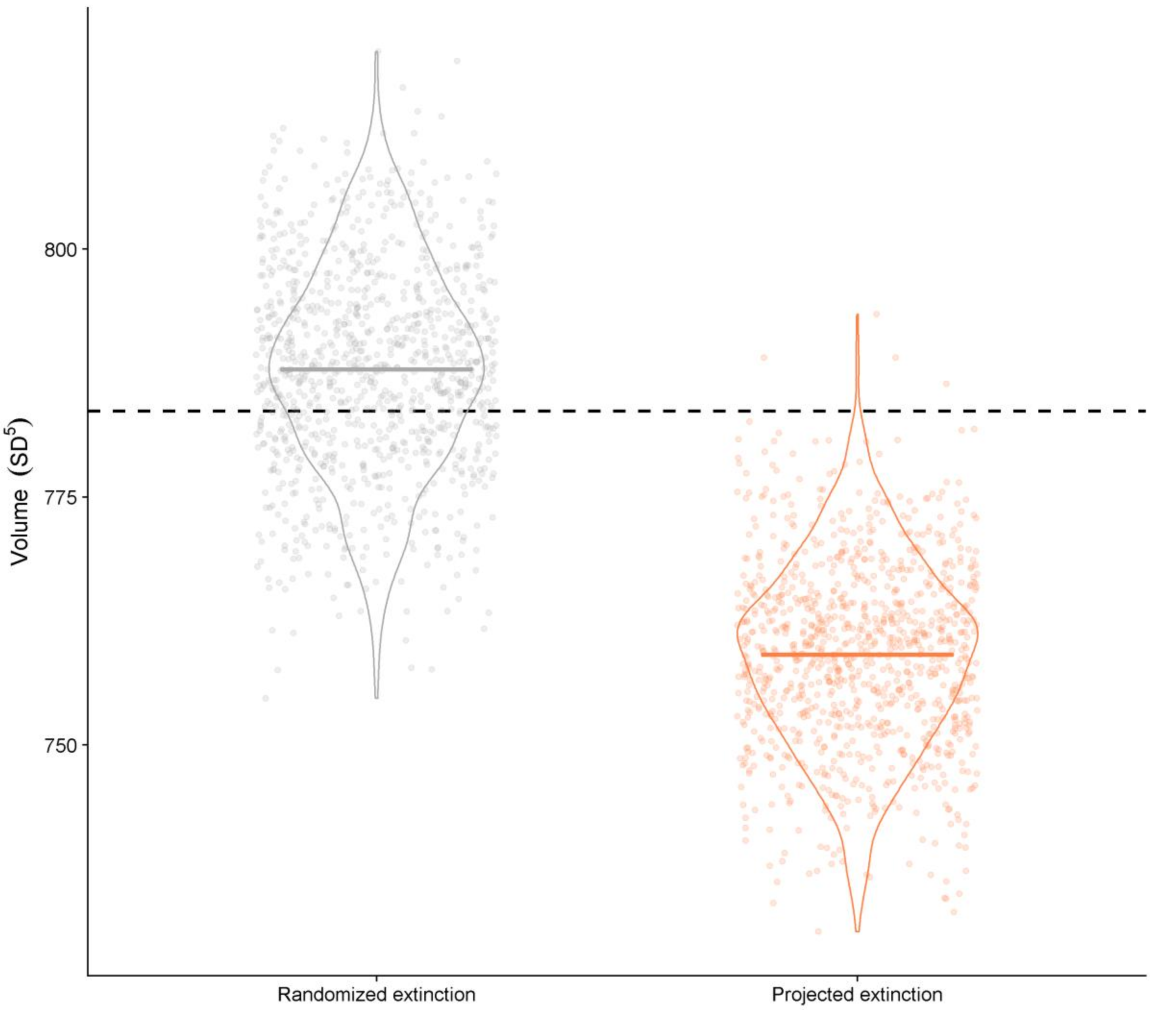

Figure B.9 The ecological strategy space for mammals and birds under 100-year extinction scenarios under the data deletion approach (8,294 species). The dashed horizontal line indicates the observed ecological strategy space (hypervolume), excluding missing-data species. 514 mammal and bird species are lost under both the projected and randomized extinction scenarios for the data deletion approach. Kolmogorov-Smirnov test: observed extinction mean under the data deletion approach = 784 SD^5, randomized extinction mean under the data deletion approach = 788 SD^5, projected extinction mean under the data deletion approach = 759 SD^5; $D = 0.85$, $P < 0.001$. Randomized compared to observed, effect size = +4.2 [95% CI: +23.9, -16.9] SD^5, projected compared to observed, effect size = -24.5 [-6.4, -43.8] SD^5.

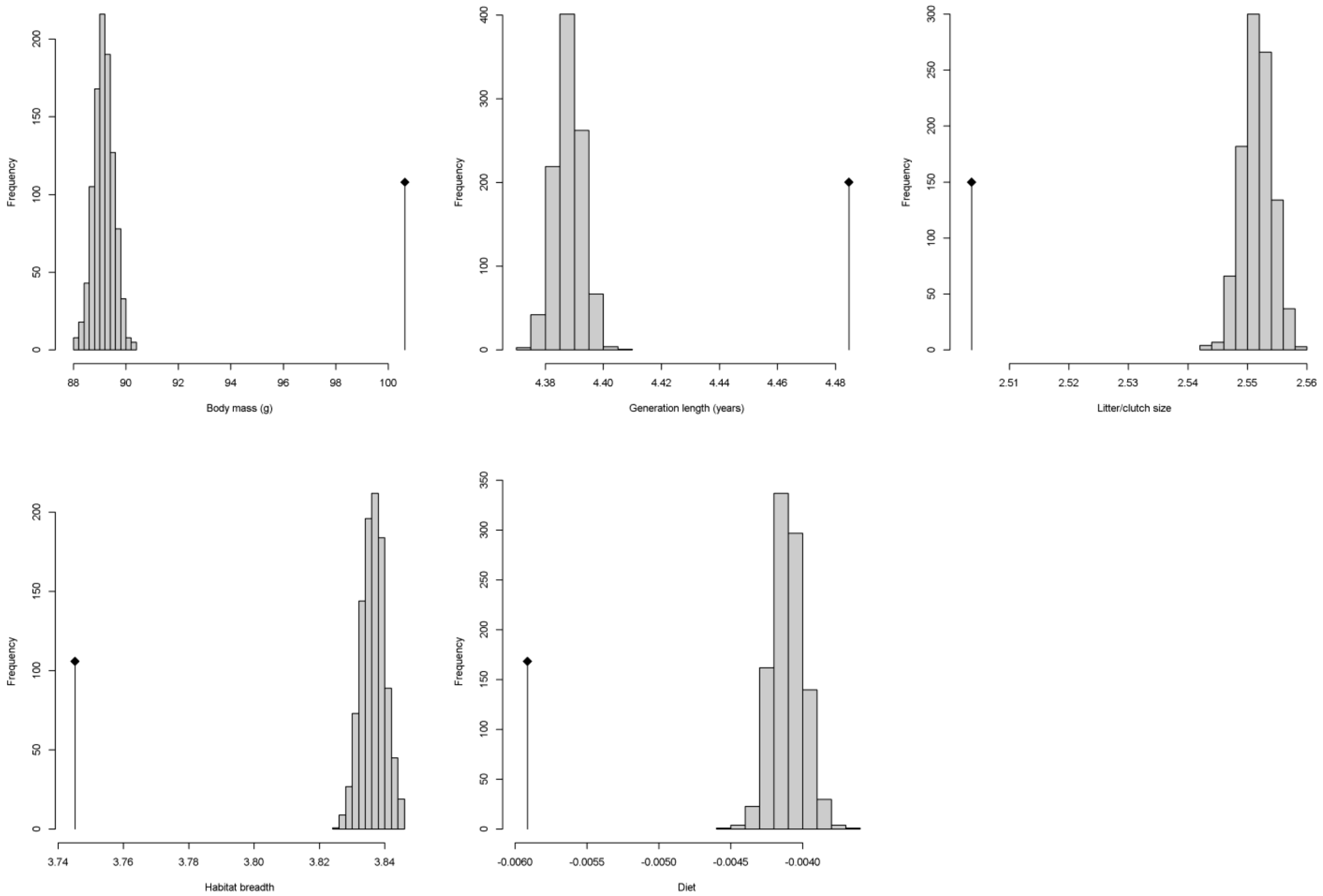

Figure B.10 Plots showing the results of the permutation tests under the data deletion approach (8,294 species), with histograms of the projected mean values (across 999 runs) and lollipops of the observed mean value per trait.

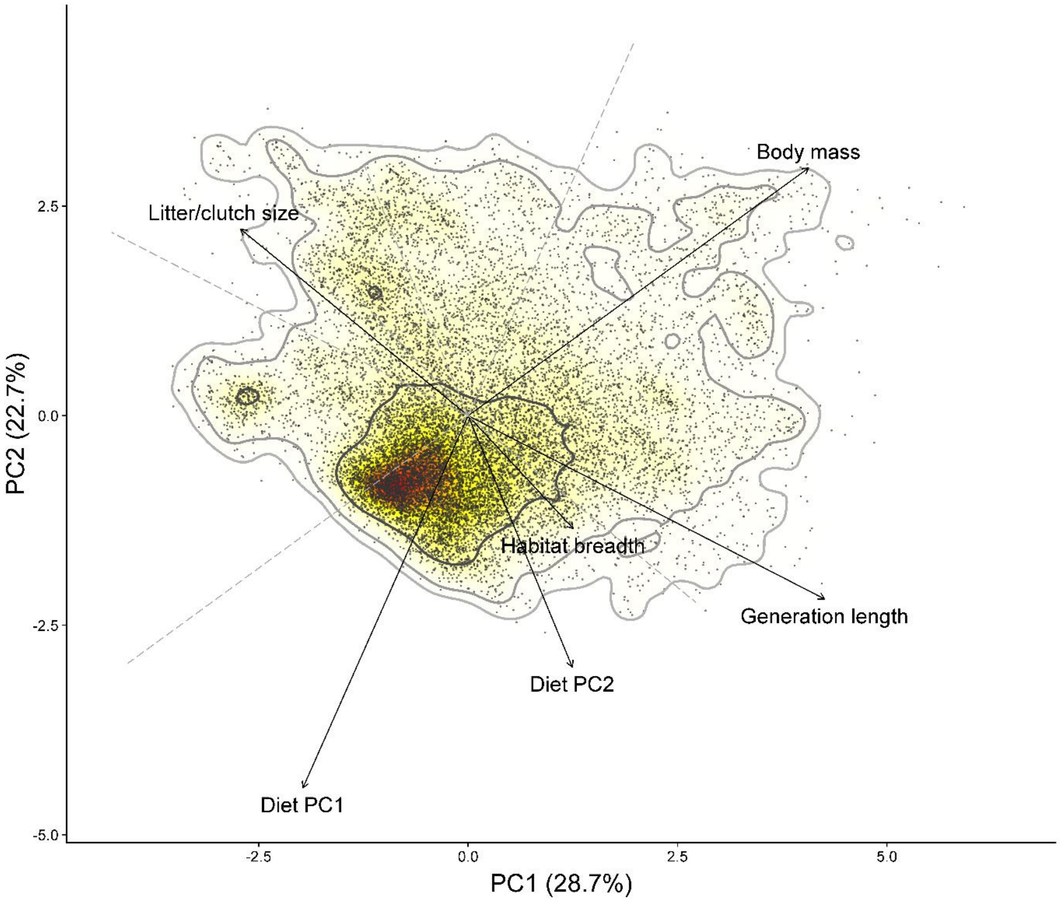

Figure B.11 The ecological strategy surface for mammals and birds (15,484 species) when including two synthetic diet traits (Figure B.4; Appendix B.1).

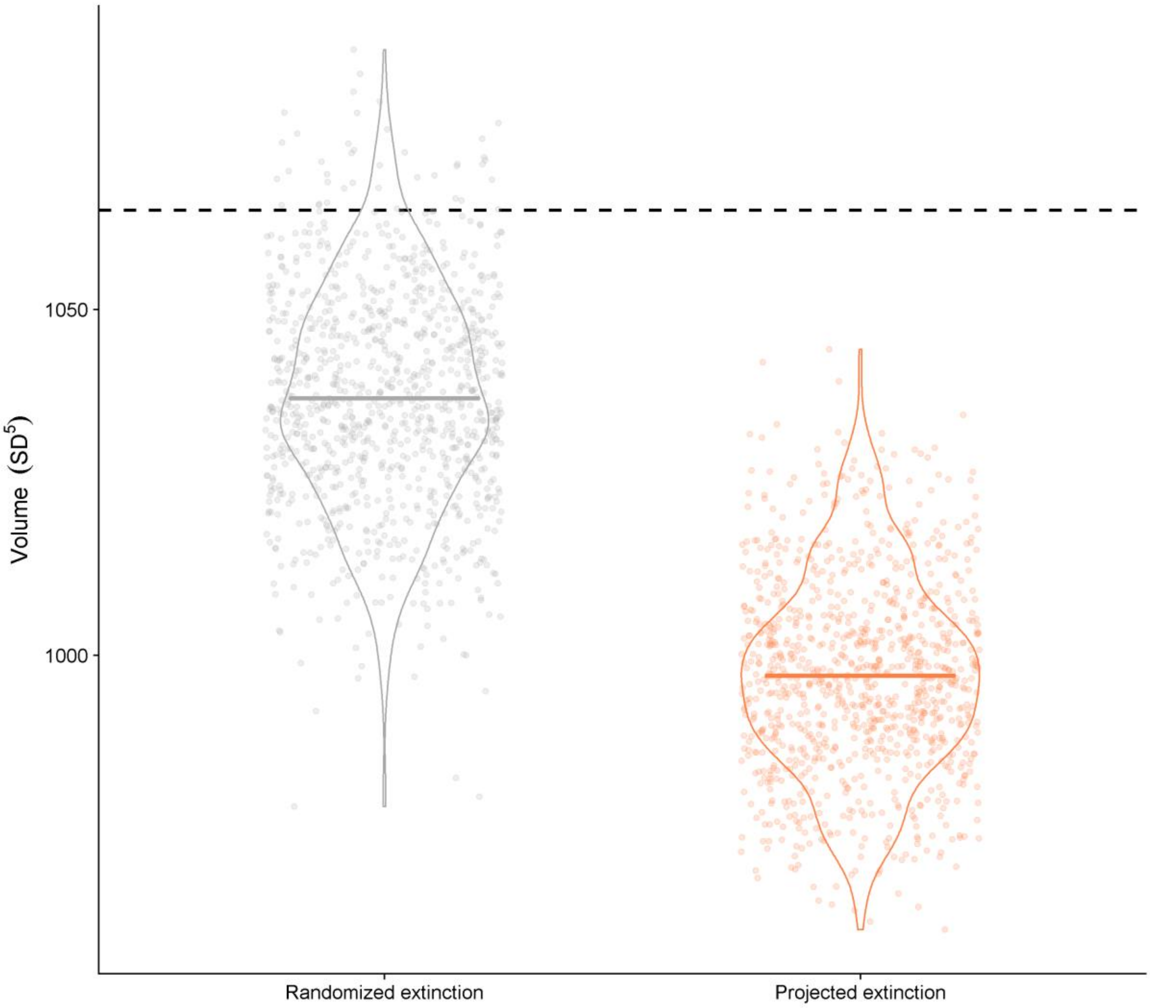

Figure B.12 The ecological strategy space for mammals and birds under 100-year extinction scenarios when excluding DD species (14,760 species). The dashed horizontal line indicates the observed ecological strategy space (hypervolume), excluding DD species. Kolmogorov-Smirnov test: observed extinction mean excluding DD species = 1064 SD^5, randomized extinction mean excluding DD species = 1037 SD^5, projected extinction mean excluding DD species = 997 SD^5; $D = 0.81$, $P < 0.001$. Randomized compared to observed, effect size = -27.2 [95% CI: +4.7, -56.9] SD^5, projected compared to observed, effect size = -67.3 [-38.1, -93.2] SD^5.

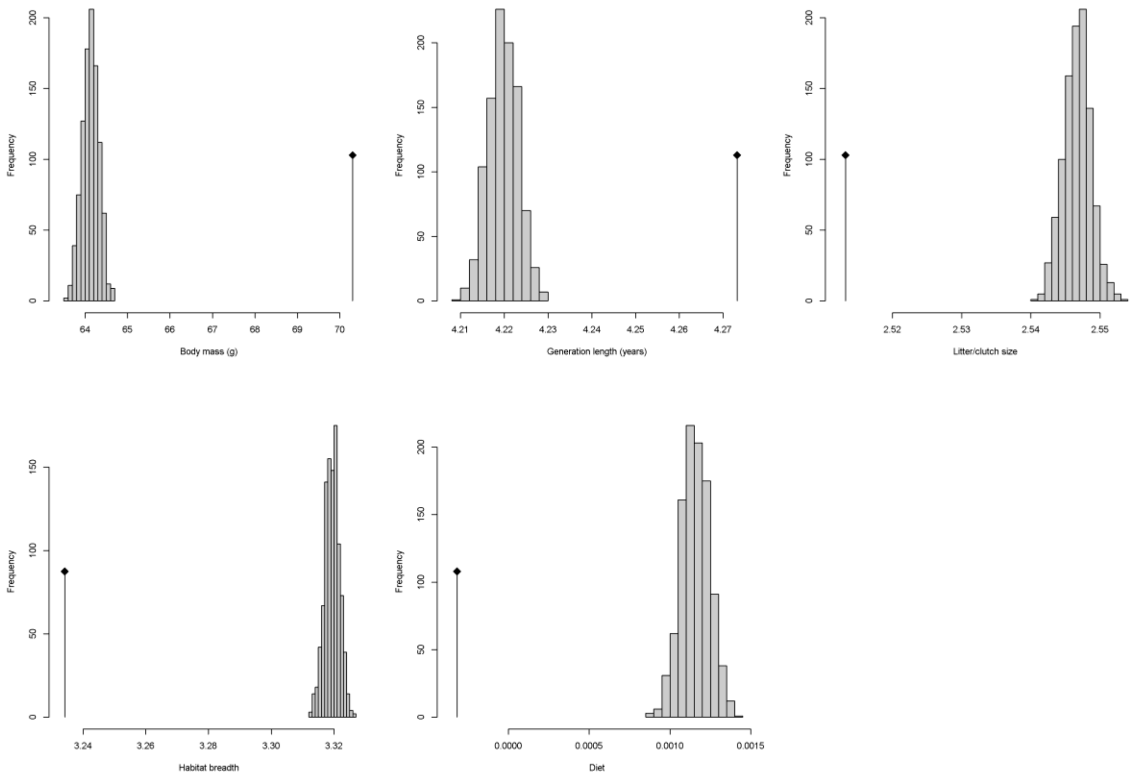

Figure B.13 Plots showing the results of the permutation tests when excluding DD species (14,760 species), with histograms of the projected mean values (across 999 runs) and lollipops of the observed mean value per trait.

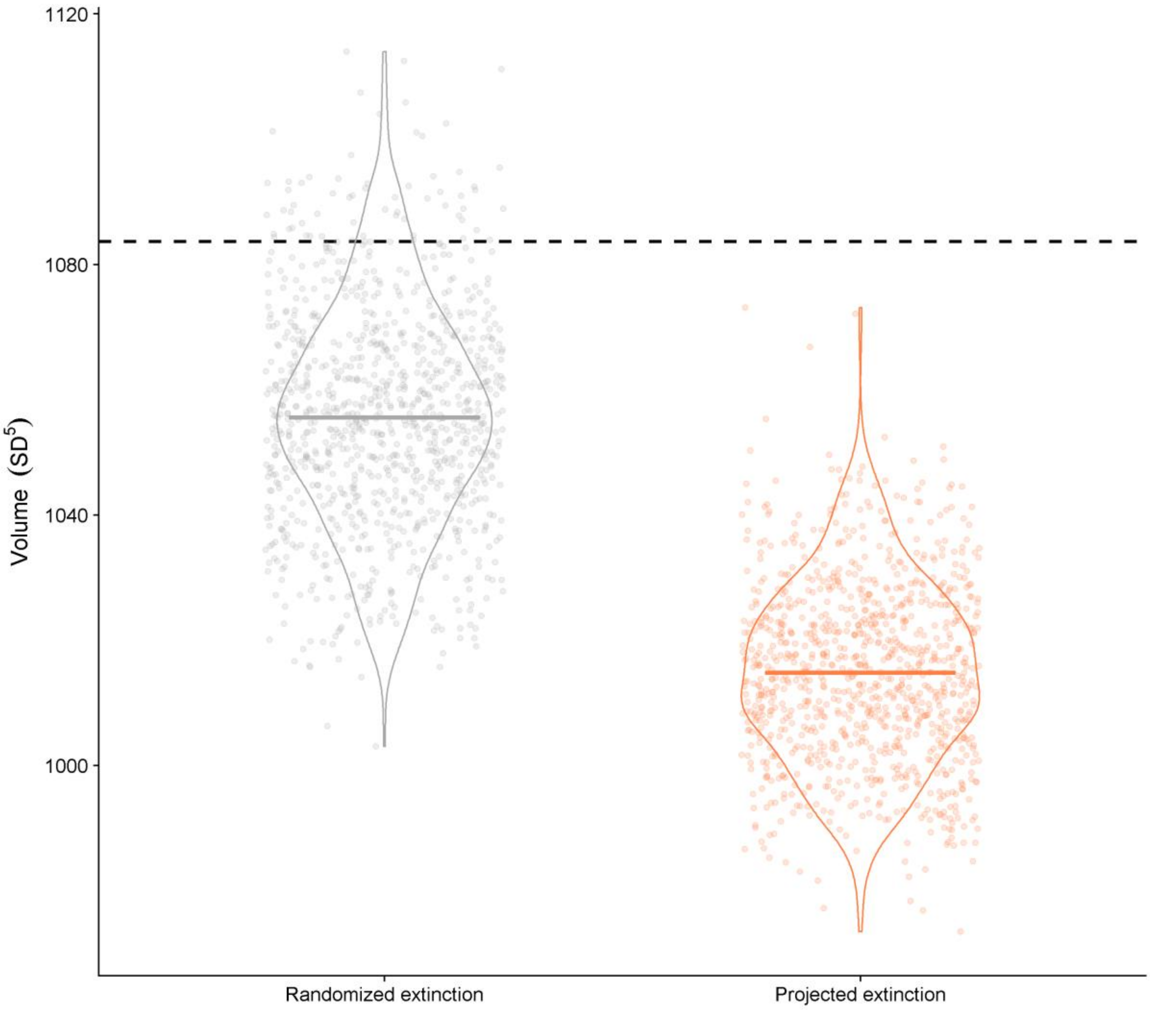

Figure B.14 Plots showing the results of the permutation tests when excluding DD species (14,760 species), with histograms. The dashed horizontal line indicates the observed ecological strategy space (hypervolume). 1,296 mammal and bird species are lost under both the projected and randomized extinction scenarios for the predicted DD species approach. Kolmogorov-Smirnov test: observed extinction mean for the predicted DD species approach = 1084 SD^5, randomized extinction mean for the predicted DD species approach = 1056 SD^5, projected extinction mean for the predicted DD species approach = 1015 SD^5; $D = 0.80$, $P < 0.001$. Randomized compared to observed, effect size = -28.1 [95% CI: +7.9, -61.6] SD^5, projected compared to observed, effect size = -68.9 [-39.5, -94.6] SD^5.

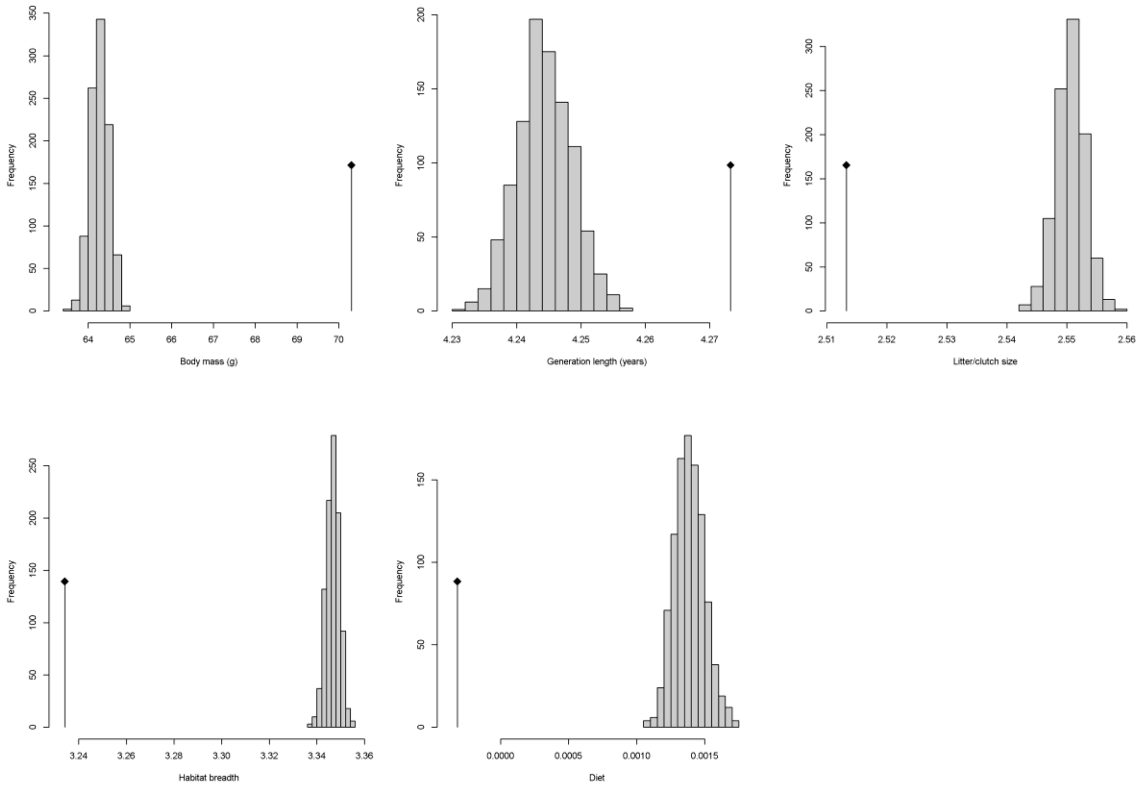

Figure B.15 Plots showing the results of the permutation tests when predicting extinction probability for DD species (15,484 species), with histograms of the projected mean values (across 999 runs) and lollipops of the observed mean value per trait.

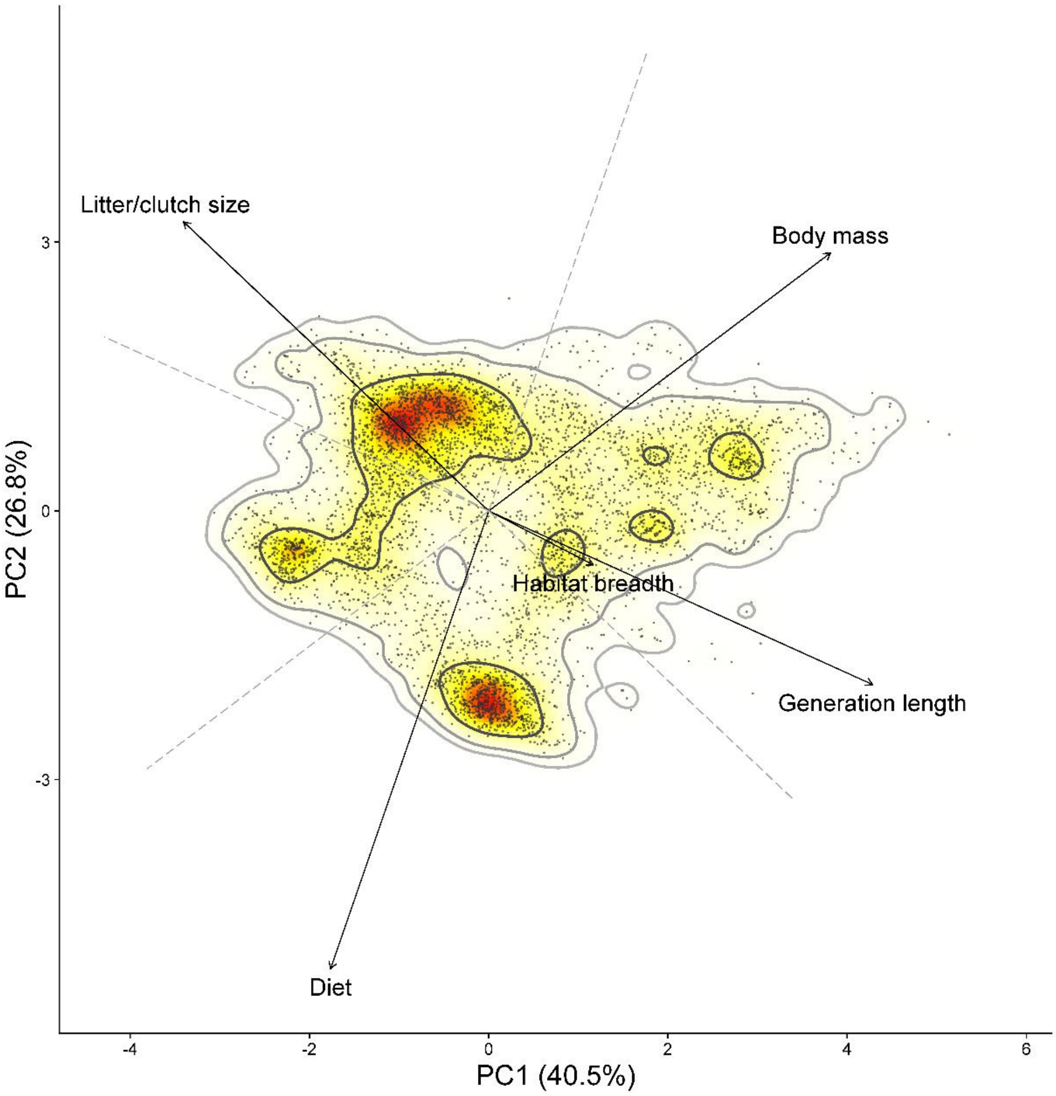

Figure B.16 Ecological strategy surface for mammals (5,232 species). Projection of extant terrestrial mammal species (grey dots) on the surface defined by principal components (PC) 1 and 2 (mean values across 25 imputed datasets; Appendix B.1).

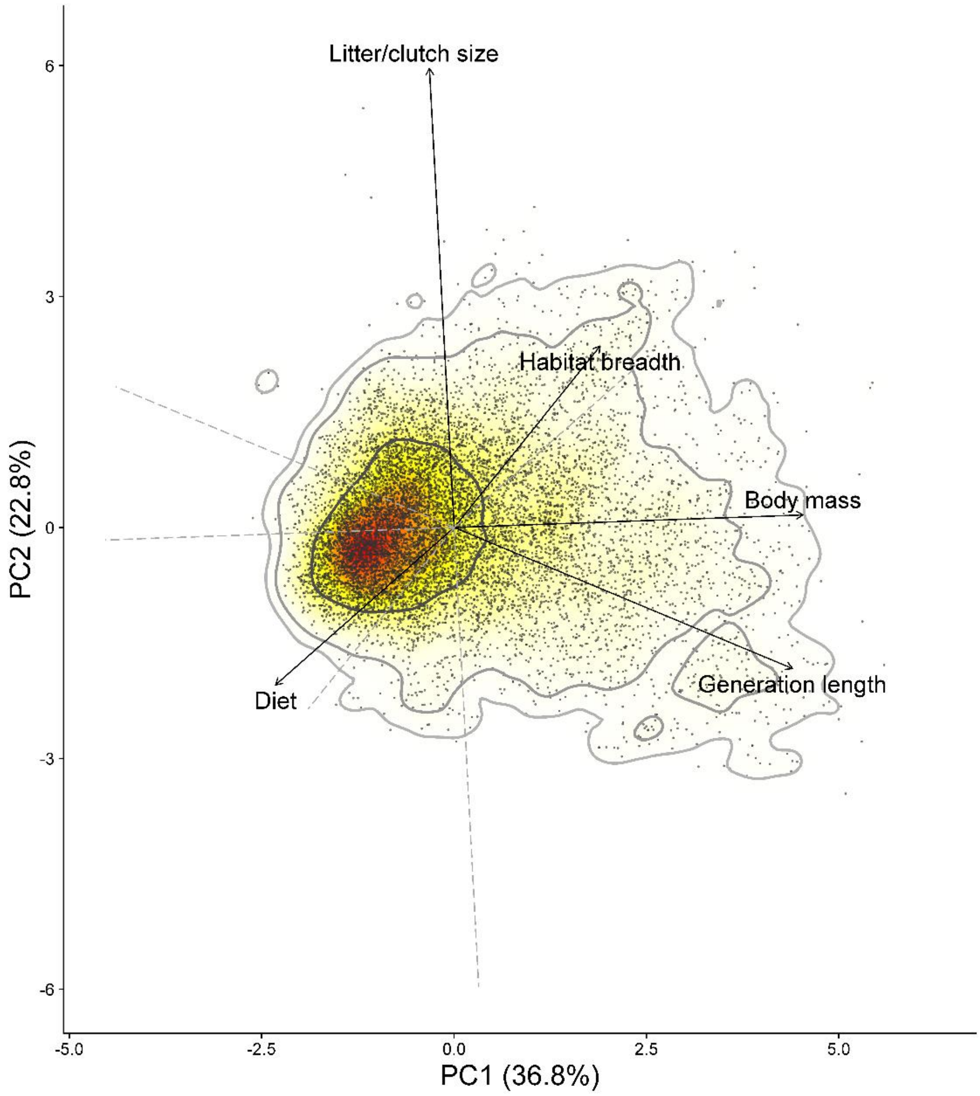

Figure B.17 Ecological strategy surface for birds (10,252 species). Projection of extant bird species (grey dots) on the surface defined by principal components (PC) 1 and 2 (mean values across 25 imputed datasets; Appendix B.1).

B.2 Supplementary references

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Appendix C Supporting information for Chapter 4

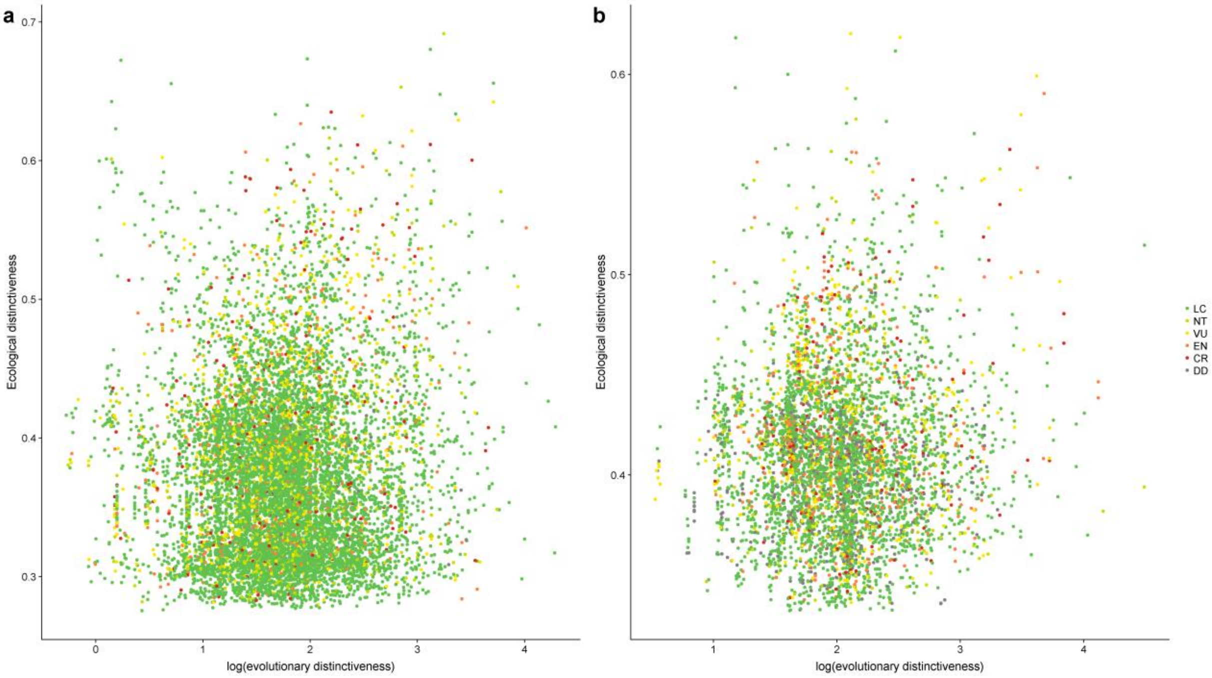

Figure C.1 The relationship between log evolutionary distinctiveness and ecological distinctiveness for (a) 10,960 bird species and (b) 5,278 mammal species. Points represent mean ecological distinctiveness across 25 imputed trait datasets for each species. Colours depict IUCN Red List status.

Appendix D Supporting information for Chapter 5

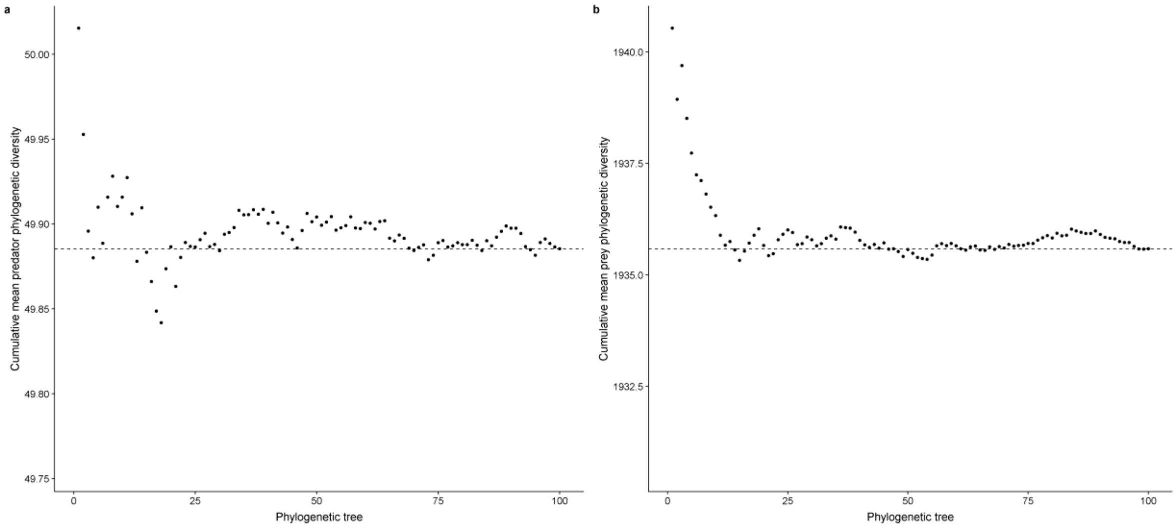

Figure D.1 Cumulative mean phylogenetic diversity for predators (a) and prey (b) across 100 phylogenetic trees. The first 100 trees from the PHYLACINE database (Faurby *et al.*, 2018).

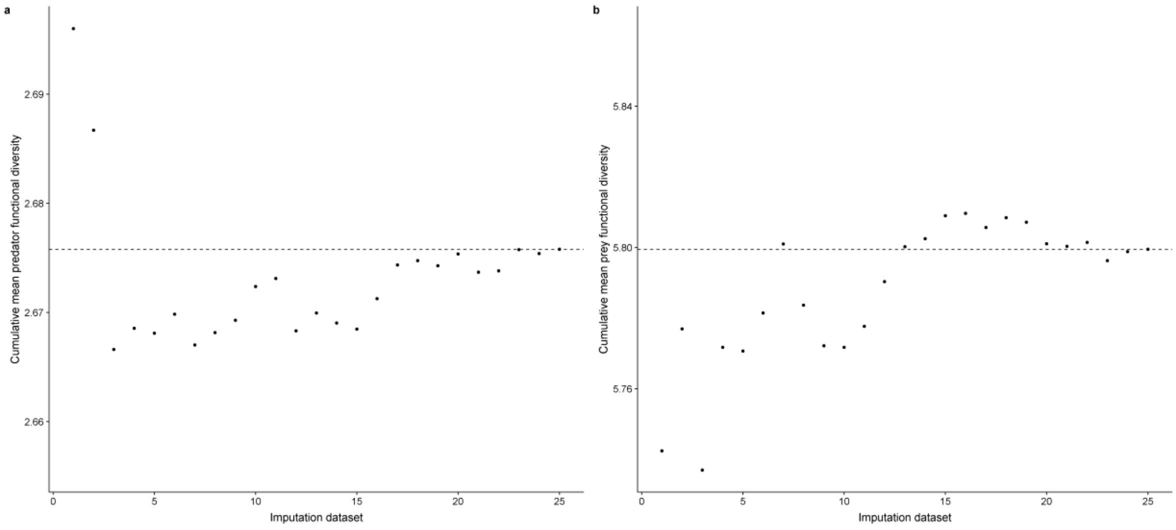

Figure D.2 Cumulative mean functional diversity for predators (a) and prey (b) across 25 trait imputation datasets.

Table D.1 Mean coefficient estimates for all paths, including error covariances (~~), for the environment structural equation model, i.e., excluding any trophic interactions. Mean coefficient estimates across all combinations (2,500) of trait imputation datasets (25) and phylogenetic trees (100); standard error, corrected for spatial autocorrelation, calculated according to Rubin's rules. Diversity abbreviations are 'PD', phylogenetic diversity; 'FD', functional diversity; 'rich', richness.

Response		Predictor	Mean coefficient	Standard error
Predator rich	~	Human	0.14	0.02
Predator rich	~	NDVI	0.46	0.03
Predator rich	~	PC1	-0.02	0.02
Predator rich	~	PC2	0.20	0.02
Predator rich	~	PC3	-0.21	0.01
Predator FD	~	Human	0.09	0.01
Predator FD	~	NDVI	0.42	0.02
Predator FD	~	PC1	-0.66	0.02
Predator FD	~	PC2	-0.13	0.02
Predator FD	~	PC3	0.02	0.01
Predator PD	~	Human	0.10	0.02
Predator PD	~	NDVI	0.25	0.03
Predator PD	~	PC1	0.12	0.02
Predator PD	~	PC2	-0.08	0.02
Predator PD	~	PC3	-0.02	0.02
Prey rich	~	Human	0.11	0.01
Prey rich	~	NDVI	0.48	0.02
Prey rich	~	PC1	0.24	0.02
Prey rich	~	PC2	0.01	0.02
Prey rich	~	PC3	-0.23	0.01
Prey FD	~	Human	0.13	0.02
Prey FD	~	NDVI	0.36	0.03
Prey FD	~	PC1	-0.52	0.02
Prey FD	~	PC2	0.15	0.02
Prey FD	~	PC3	-0.08	0.02
Prey PD	~	Human	-0.24	0.02

Prey PD	~	NDVI	0.12	0.03
Prey PD	~	PC1	0.44	0.02
Prey PD	~	PC2	-0.07	0.02
Prey PD	~	PC3	0.01	0.02
NDVI	~	PC1	0.56	0.01
NDVI	~	PC2	-0.61	0.01
NDVI	~	PC3	-0.06	0.01
Predator FD	~~	Predator PD	0.73	0.01
Predator rich	~~	Predator FD	0.45	0.01
Predator rich	~~	Predator PD	0.38	0.01
Prey FD	~~	Prey PD	-0.09	0.02
Prey rich	~~	Prey FD	0.00	0.02
Prey rich	~~	Prey PD	-0.13	0.02
Predator rich	~~	Prey rich	0.62	0.01
Predator rich	~~	Prey FD	0.16	0.02
Predator rich	~~	Prey PD	-0.28	0.02
Predator FD	~~	Prey rich	0.13	0.02
Predator FD	~~	Prey FD	-0.10	0.02
Predator FD	~~	Prey PD	0.04	0.02
Predator PD	~~	Prey rich	0.14	0.02
Predator PD	~~	Prey FD	-0.20	0.02
Predator PD	~~	Prey PD	0.08	0.02

Table D.2 Mean coefficient estimates for all paths, including error covariances (~~), for the bottom-up structural equation model, i.e., including trophic interactions from prey to predator diversity. Mean coefficient estimates across all combinations (2,500) of trait imputation datasets (25) and phylogenetic trees (100); standard error, corrected for spatial autocorrelation, calculated according to Rubin's rules. Diversity abbreviations are 'PD', phylogenetic diversity; 'FD', functional diversity; 'rich', richness.

Response		**Predictor**	**Mean coefficient**	**Standard error**

Predator rich	~	Human	0.06	0.01
Predator rich	~	NDVI	0.09	0.02
Predator rich	~	PC1	-0.20	0.02
Predator rich	~	PC2	0.19	0.02
Predator rich	~	PC3	-0.03	0.01
Predator FD	~	Human	0.10	0.01
Predator FD	~	NDVI	0.45	0.02
Predator FD	~	PC1	-0.70	0.02
Predator FD	~	PC2	-0.12	0.02
Predator FD	~	PC3	0.02	0.01
Predator PD	~	Human	0.12	0.02
Predator PD	~	NDVI	0.24	0.03
Predator PD	~	PC1	0.09	0.02
Predator PD	~	PC2	-0.07	0.02
Predator PD	~	PC3	-0.02	0.02
Prey rich	~	Human	0.11	0.01
Prey rich	~	NDVI	0.47	0.02
Prey rich	~	PC1	0.24	0.02
Prey rich	~	PC2	0.01	0.02
Prey rich	~	PC3	-0.23	0.01
Prey FD	~	Human	0.13	0.02
Prey FD	~	NDVI	0.36	0.03
Prey FD	~	PC1	-0.52	0.02
Prey FD	~	PC2	0.15	0.02
Prey FD	~	PC3	-0.08	0.02
Prey PD	~	Human	-0.24	0.01
Prey PD	~	NDVI	0.12	0.03
Prey PD	~	PC1	0.44	0.02
Prey PD	~	PC2	-0.07	0.02
Prey PD	~	PC3	0.01	0.01

NDVI	~	PC1	0.56	0.01
NDVI	~	PC2	-0.61	0.01
NDVI	~	PC3	-0.06	0.01
Predator rich	~	Prey rich	0.78	0.01
Predator FD	~	Prey FD	-0.08	0.01
Predator PD	~	Prey PD	0.08	0.02
Predator FD	~~	Predator PD	0.71	0.01
Predator rich	~~	Predator FD	0.50	0.01
Predator rich	~~	Predator PD	0.39	0.01
Prey FD	~~	Prey PD	-0.09	0.02
Prey rich	~~	Prey FD	0.00	0.02
Prey rich	~~	Prey PD	-0.13	0.02
Predator rich	~~	Prey FD	0.20	0.02
Predator rich	~~	Prey PD	-0.25	0.02
Predator FD	~~	Prey rich	0.13	0.02
Predator FD	~~	Prey PD	0.03	0.02
Predator PD	~~	Prey rich	0.15	0.02
Predator PD	~~	Prey FD	-0.20	0.02

Table D.3 Mean coefficient estimates for all paths, including error covariances (~~), for the top-down structural equation model, i.e., including trophic interactions from predator to prey diversity. Mean coefficient estimates across all combinations (2,500) of trait imputation datasets (25) and phylogenetic trees (100); standard error, corrected for spatial autocorrelation, calculated according to Rubin's rules. Diversity abbreviations are 'PD', phylogenetic diversity; 'FD', functional diversity; 'rich', richness.

Response		**Predictor**	**Mean coefficient**	**Standard error**
Predator rich	~	Human	0.14	0.02
Predator rich	~	NDVI	0.46	0.03
Predator rich	~	PC1	-0.02	0.02

Predator rich	~	PC2	0.20	0.02
Predator rich	~	PC3	-0.21	0.01
Predator FD	~	Human	0.09	0.01
Predator FD	~	NDVI	0.42	0.02
Predator FD	~	PC1	-0.66	0.02
Predator FD	~	PC2	-0.13	0.02
Predator FD	~	PC3	0.02	0.01
Predator PD	~	Human	0.10	0.02
Predator PD	~	NDVI	0.25	0.03
Predator PD	~	PC1	0.12	0.02
Predator PD	~	PC2	-0.08	0.02
Predator PD	~	PC3	-0.02	0.02
Prey rich	~	Human	0.04	0.01
Prey rich	~	NDVI	0.25	0.02
Prey rich	~	PC1	0.25	0.01
Prey rich	~	PC2	-0.09	0.01
Prey rich	~	PC3	-0.12	0.01
Prey FD	~	Human	0.14	0.02
Prey FD	~	NDVI	0.41	0.03
Prey FD	~	PC1	-0.60	0.02
Prey FD	~	PC2	0.13	0.02
Prey FD	~	PC3	-0.08	0.02
Prey PD	~	Human	-0.25	0.02
Prey PD	~	NDVI	0.11	0.03
Prey PD	~	PC1	0.43	0.02
Prey PD	~	PC2	-0.07	0.02
Prey PD	~	PC3	0.01	0.01
NDVI	~	PC1	0.56	0.01
NDVI	~	PC2	-0.61	0.01
NDVI	~	PC3	-0.06	0.01

Prey rich	~	Predator rich	0.49	0.01
Prey FD	~	Predator FD	-0.12	0.02
Prey PD	~	Predator PD	0.08	0.02
Predator FD	~~	Predator PD	0.73	0.01
Predator rich	~~	Predator FD	0.45	0.01
Predator rich	~~	Predator PD	0.38	0.01
Prey FD	~~	Prey PD	-0.08	0.02
Prey rich	~~	Prey FD	-0.15	0.02
Prey rich	~~	Prey PD	0.07	0.02
Predator rich	~~	Prey FD	0.21	0.02
Predator rich	~~	Prey PD	-0.31	0.01
Predator FD	~~	Prey rich	-0.19	0.01
Predator FD	~~	Prey PD	-0.01	0.01
Predator PD	~~	Prey rich	-0.12	0.02
Predator PD	~~	Prey FD	-0.13	0.01

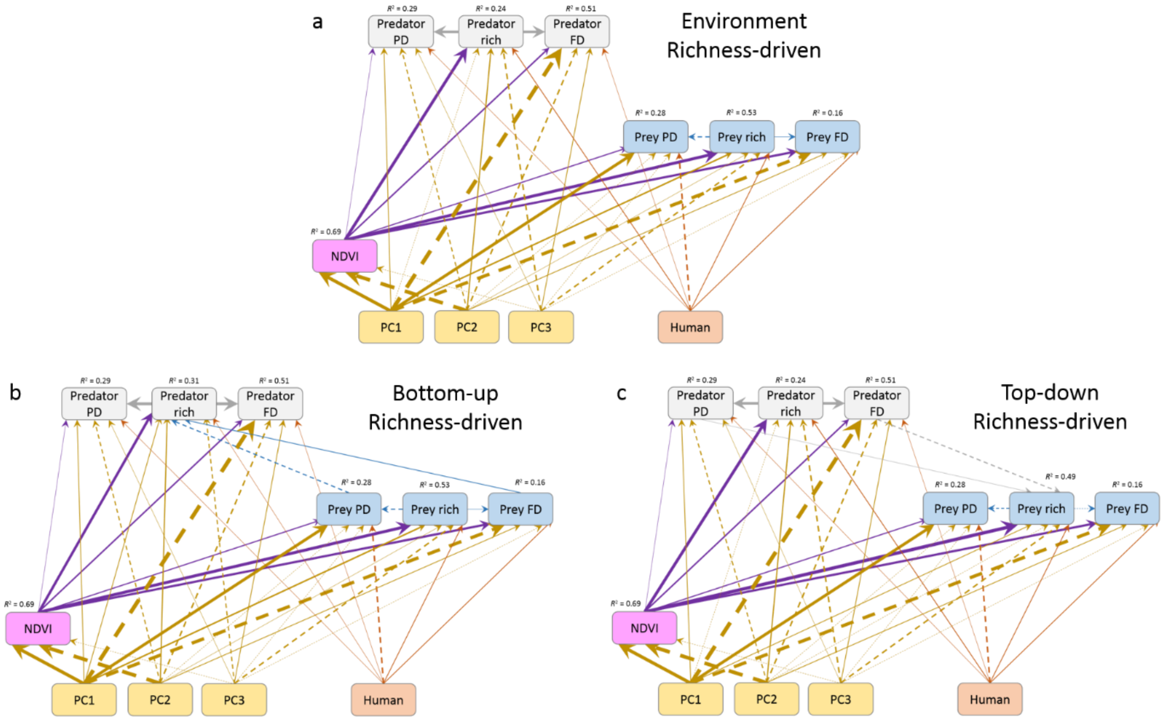

Figure D.3 Richness-driven empirical Structural Equation Models (SEMs). Three SEMs are shown: (a) environment SEM - each predator and prey diversity dimension (phylogenetic diversity: PD, richness: rich, functional diversity: FD) is predicted by environmental variables only (i.e., excluding any trophic interactions); (b) bottom-up SEM - adding paths from prey diversity to predator diversity; (c) top-down SEM - adding paths from predator diversity to prey diversity. 'PC1' is the first principal component from the climate principal components analysis, reflecting positive TEMP and PREC, and negative TSEAS. 'PC2' reflects positive PSEAS and negative PREC. 'PC3' reflects negative TOPO. 'Human' represents the human influence index and 'NDVI' represents the normalized difference vegetation index. Arrows represent path coefficients (solid lines positive coefficients, dashed lines negative coefficients), with line thickness proportional to coefficient strength. For all coefficient estimates, including error covariances, with total uncertainty see Table D.4, Table D.5 and Table D.6. In total, there are 184 predator species and 3,985 prey species (out of 4,169 extant terrestrial non-volant mammal species investigated). Paths are coloured according to the variable from which they originate.

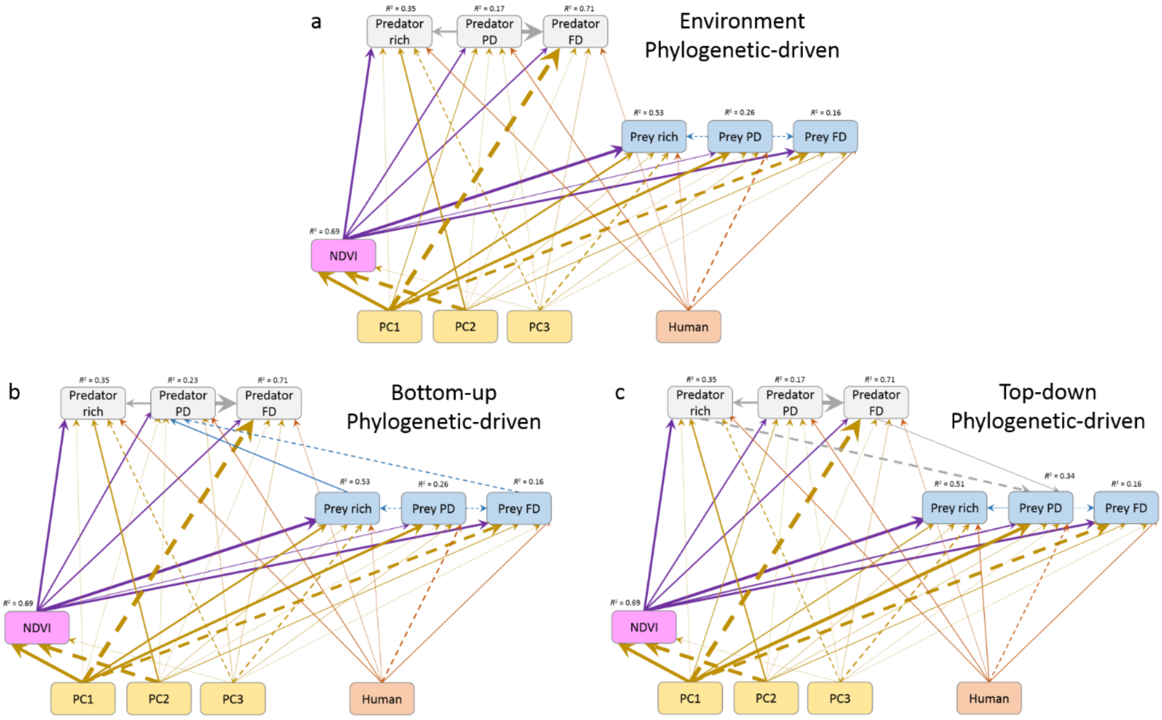

Figure D.4 Phylogenetic-driven empirical Structural Equation Models (SEMs). Three SEMs are shown: (a) environment SEM - each predator and prey diversity dimension (phylogenetic diversity: PD, richness: rich, functional diversity: FD) is predicted by environmental variables only (i.e., excluding any trophic interactions); (b) bottom-up SEM - adding paths from prey diversity to predator diversity; (c) top-down SEM - adding paths from predator diversity to prey diversity. 'PC1' is the first principal component from the climate principal components analysis, reflecting positive TEMP and PREC, and negative TSEAS. 'PC2' reflects positive PSEAS and negative PREC. 'PC3' reflects negative TOPO. 'Human' represents the human influence index and 'NDVI' represents the normalized difference vegetation index. Arrows represent path coefficients (solid lines positive coefficients, dashed lines negative coefficients), with line thickness proportional to coefficient strength. For all coefficient estimates, including error covariances, with total uncertainty see Table D.7, Table D.8 and Table D.9. In total, there are 184 predator species and 3,985 prey species (out of 4,169 extant terrestrial non-volant mammal species investigated). Paths are coloured according to the variable from which they originate. Notice that the dimensions of diversity have been rearranged.

Table D.4 Mean coefficient estimates for all paths, including error covariances (~~), for the richness-driven environment structural equation model, i.e., excluding any trophic interactions. Mean coefficient estimates across all combinations (2,500) of trait imputation datasets (25) and phylogenetic trees (100); standard error, corrected for spatial autocorrelation, calculated according to Rubin's rules. Diversity abbreviations are 'PD', phylogenetic diversity; 'FD', functional diversity; 'rich', richness.

Response		**Predictor**	**Mean coefficient**	**Standard error**
Predator rich	~	Human	0.14	0.02
Predator rich	~	NDVI	0.46	0.03
Predator rich	~	PC1	-0.02	0.02
Predator rich	~	PC2	0.20	0.02
Predator rich	~	PC3	-0.21	0.01
Predator FD	~	Human	0.03	0.01
Predator FD	~	NDVI	0.24	0.02
Predator FD	~	PC1	-0.65	0.02
Predator FD	~	PC2	-0.22	0.02
Predator FD	~	PC3	0.11	0.01
Predator PD	~	Human	0.04	0.02
Predator PD	~	NDVI	0.07	0.03
Predator PD	~	PC1	0.13	0.02
Predator PD	~	PC2	-0.16	0.02
Predator PD	~	PC3	0.06	0.01

Prey rich	~	Human	0.11	0.01
Prey rich	~	NDVI	0.47	0.02
Prey rich	~	PC1	0.24	0.02
Prey rich	~	PC2	0.01	0.02
Prey rich	~	PC3	-0.23	0.01
Prey FD	~	Human	0.13	0.02
Prey FD	~	NDVI	0.36	0.03
Prey FD	~	PC1	-0.52	0.02
Prey FD	~	PC2	0.15	0.02
Prey FD	~	PC3	-0.08	0.02
Prey PD	~	Human	-0.23	0.02
Prey PD	~	NDVI	0.20	0.03
Prey PD	~	PC1	0.48	0.02
Prey PD	~	PC2	-0.07	0.02
Prey PD	~	PC3	-0.03	0.02
NDVI	~	PC1	0.56	0.01
NDVI	~	PC2	-0.61	0.01
NDVI	~	PC3	-0.06	0.01
Predator FD	~	Predator rich	0.41	0.01
Predator PD	~	Predator rich	0.39	0.02
Prey FD	~	Prey rich	0.00	0.02
Prey PD	~	Prey rich	-0.16	0.02
Predator FD	~~	Prey rich	-0.17	0.01
Predator PD	~~	Prey rich	-0.10	0.01
Predator FD	~~	Predator PD	0.68	0.01
Prey FD	~~	Prey PD	-0.09	0.02
Predator rich	~~	Prey rich	0.62	0.01
Predator rich	~~	Prey FD	0.16	0.01
Predator rich	~~	Prey PD	-0.20	0.01
Predator FD	~~	Prey FD	-0.19	0.02

Predator FD	~~	Prey PD	0.17	0.02
Predator PD	~~	Prey FD	-0.28	0.02
Predator PD	~~	Prey PD	0.19	0.02

Table D.5 Mean coefficient estimates for all paths, including error covariances (~~), for the richness-driven bottom-up structural equation model, i.e., including trophic interactions from prey PD and FD to predator richness. Mean coefficient estimates across all combinations (2,500) of trait imputation datasets (25) and phylogenetic trees (100); standard error, corrected for spatial autocorrelation, calculated according to Rubin’s rules. Diversity abbreviations are ‘PD’, phylogenetic diversity; ‘FD’, functional diversity; ‘rich’, richness.

Response		**Predictor**	**Mean coefficient**	**Standard error**
Predator rich	~	Human	0.08	0.02
Predator rich	~	NDVI	0.44	0.02
Predator rich	~	PC1	0.14	0.02
Predator rich	~	PC2	0.17	0.02
Predator rich	~	PC3	-0.20	0.01
Predator FD	~	Human	0.02	0.01
Predator FD	~	NDVI	0.21	0.02
Predator FD	~	PC1	-0.65	0.02
Predator FD	~	PC2	-0.23	0.02
Predator FD	~	PC3	0.12	0.01
Predator PD	~	Human	0.03	0.02
Predator PD	~	NDVI	0.03	0.03
Predator PD	~	PC1	0.13	0.02
Predator PD	~	PC2	-0.18	0.02
Predator PD	~	PC3	0.08	0.01
Prey rich	~	Human	0.11	0.01
Prey rich	~	NDVI	0.47	0.02

Prey rich	~	PC1	0.24	0.02
Prey rich	~	PC2	0.01	0.02
Prey rich	~	PC3	-0.23	0.01
Prey FD	~	Human	0.13	0.02
Prey FD	~	NDVI	0.36	0.03
Prey FD	~	PC1	-0.52	0.02
Prey FD	~	PC2	0.15	0.02
Prey FD	~	PC3	-0.08	0.02
Prey PD	~	Human	-0.23	0.02
Prey PD	~	NDVI	0.20	0.03
Prey PD	~	PC1	0.48	0.02
Prey PD	~	PC2	-0.07	0.02
Prey PD	~	PC3	-0.03	0.02
NDVI	~	PC1	0.56	0.01
NDVI	~	PC2	-0.61	0.01
NDVI	~	PC3	-0.06	0.01
Predator FD	~	Predator rich	0.46	0.01
Predator PD	~	Predator rich	0.48	0.02
Predator rich	~	Prey FD	0.13	0.01
Predator rich	~	Prey PD	-0.19	0.01
Prey FD	~	Prey rich	0.00	0.02
Prey PD	~	Prey rich	-0.16	0.02
Predator FD	~~	Predator PD	0.68	0.01
Prey FD	~~	Prey PD	-0.09	0.02
Predator rich	~~	Prey rich	0.62	0.01
Predator FD	~~	Prey rich	-0.21	0.01
Predator PD	~~	Prey rich	-0.15	0.01
Predator FD	~~	Prey FD	-0.20	0.02
Predator PD	~~	Prey FD	-0.30	0.02
Predator FD	~~	Prey PD	0.18	0.02

Predator PD	~~	Prey PD	0.20	0.02

Table D.6 Mean coefficient estimates for all paths, including error covariances (~~), for the richness-driven top-down structural equation model, i.e., including trophic interactions from predator PD and FD to prey richness. Mean coefficient estimates across all combinations (2,500) of trait imputation datasets (25) and phylogenetic trees (100); standard error, corrected for spatial autocorrelation, calculated according to Rubin's rules. Diversity abbreviations are 'PD', phylogenetic diversity; 'FD', functional diversity; 'rich', richness.

Response		**Predictor**	**Mean coefficient**	**Standard error**
Predator rich	~	Human	0.14	0.02
Predator rich	~	NDVI	0.46	0.03
Predator rich	~	PC1	-0.02	0.02
Predator rich	~	PC2	0.20	0.02
Predator rich	~	PC3	-0.21	0.01
Predator FD	~	Human	0.03	0.01
Predator FD	~	NDVI	0.24	0.02
Predator FD	~	PC1	-0.65	0.02
Predator FD	~	PC2	-0.22	0.02
Predator FD	~	PC3	0.11	0.01
Predator PD	~	Human	0.04	0.02
Predator PD	~	NDVI	0.07	0.03
Predator PD	~	PC1	0.13	0.02
Predator PD	~	PC2	-0.16	0.02
Predator PD	~	PC3	0.06	0.01
Prey rich	~	Human	0.12	0.01
Prey rich	~	NDVI	0.55	0.02
Prey rich	~	PC1	0.11	0.02
Prey rich	~	PC2	-0.01	0.02

Prey rich	~	PC3	-0.22	0.01
Prey FD	~	Human	0.13	0.02
Prey FD	~	NDVI	0.37	0.03
Prey FD	~	PC1	-0.52	0.02
Prey FD	~	PC2	0.15	0.02
Prey FD	~	PC3	-0.09	0.02
Prey PD	~	Human	-0.23	0.02
Prey PD	~	NDVI	0.19	0.03
Prey PD	~	PC1	0.48	0.02
Prey PD	~	PC2	-0.07	0.02
Prey PD	~	PC3	-0.02	0.02
NDVI	~	PC1	0.56	0.01
NDVI	~	PC2	-0.61	0.01
NDVI	~	PC3	-0.06	0.01
Predator FD	~	Predator rich	0.41	0.01
Predator PD	~	Predator rich	0.39	0.02
Prey rich	~	Predator FD	-0.19	0.02
Prey rich	~	Predator PD	0.02	0.01
Prey FD	~	Prey rich	-0.02	0.02
Prey PD	~	Prey rich	-0.15	0.02
Predator FD	~~	Predator PD	0.68	0.01
Prey FD	~~	Prey PD	-0.09	0.02
Predator rich	~~	Prey rich	0.68	0.01
Predator rich	~~	Prey FD	0.17	0.01
Predator rich	~~	Prey PD	-0.21	0.01
Predator FD	~~	Prey FD	-0.19	0.02
Predator FD	~~	Prey PD	0.17	0.02
Predator PD	~~	Prey FD	-0.29	0.02
Predator PD	~~	Prey PD	0.19	0.02

Table D.7 Mean coefficient estimates for all paths, including error covariances (~~), for the phylogenetic-driven environment structural equation model, i.e., excluding any trophic interactions. Mean coefficient estimates across all combinations (2,500) of trait imputation datasets (25) and phylogenetic trees (100); standard error, corrected for spatial autocorrelation, calculated according to Rubin's rules. Diversity abbreviations are 'PD', phylogenetic diversity; 'FD', functional diversity; 'rich', richness.

Response		**Predictor**	**Mean coefficient**	**Standard error**
Predator rich	~	NDVI	0.37	0.02
Predator rich	~	PC1	-0.06	0.02
Predator rich	~	PC2	0.23	0.02
Predator rich	~	PC3	-0.20	0.01
Predator FD	~	Human	0.02	0.01
Predator FD	~	NDVI	0.27	0.02
Predator FD	~	PC1	-0.74	0.01
Predator FD	~	PC2	-0.08	0.01
Predator FD	~	PC3	0.04	0.01
Predator PD	~	Human	0.10	0.02
Predator PD	~	NDVI	0.25	0.03
Predator PD	~	PC1	0.12	0.02
Predator PD	~	PC2	-0.08	0.02
Predator PD	~	PC3	-0.02	0.02
Prey rich	~	Human	0.08	0.01
Prey rich	~	NDVI	0.49	0.02
Prey rich	~	PC1	0.28	0.02
Prey rich	~	PC2	0.00	0.02
Prey rich	~	PC3	-0.22	0.01
Prey FD	~	Human	0.10	0.02
Prey FD	~	NDVI	0.37	0.03
Prey FD	~	PC1	-0.48	0.02

Prey FD	~	PC2	0.14	0.02
Prey FD	~	PC3	-0.08	0.02
Prey PD	~	Human	-0.24	0.01
Prey PD	~	NDVI	0.12	0.03
Prey PD	~	PC1	0.44	0.02
Prey PD	~	PC2	-0.07	0.02
Prey PD	~	PC3	0.01	0.01
NDVI	~	PC1	0.56	0.01
NDVI	~	PC2	-0.61	0.01
NDVI	~	PC3	-0.06	0.01
Predator FD	~	Predator PD	0.63	0.01
Predator rich	~	Predator PD	0.36	0.01
Prey FD	~	Prey PD	-0.10	0.02
Prey rich	~	Prey PD	-0.10	0.01
Predator FD	~~	Prey PD	-0.02	0.02
Predator rich	~~	Prey PD	-0.33	0.02
Predator rich	~~	Predator FD	0.28	0.02
Prey rich	~~	Prey FD	-0.01	0.02
Predator PD	~~	Prey PD	0.08	0.02
Predator PD	~~	Prey FD	-0.20	0.02
Predator PD	~~	Prey rich	0.15	0.02
Predator FD	~~	Prey FD	0.07	0.02
Predator FD	~~	Prey rich	0.04	0.02
Predator rich	~~	Prey FD	0.23	0.02
Predator rich	~~	Prey rich	0.57	0.01

Table D.8 Mean coefficient estimates for all paths, including error covariances (~~), for the phylogenetic-driven bottom-up structural equation model, i.e., including trophic interactions from prey richness and FD to predator PD. Mean coefficient estimates across all combinations (2,500) of trait imputation datasets (25) and phylogenetic trees (100); standard error, corrected for spatial autocorrelation, calculated according to Rubin's rules. Diversity abbreviations are 'PD', phylogenetic diversity; 'FD', functional diversity; 'rich', richness.

Response		**Predictor**	**Mean coefficient**	**Standard error**
Predator rich	~	Human	0.11	0.01
Predator rich	~	NDVI	0.38	0.02
Predator rich	~	PC1	-0.05	0.02
Predator rich	~	PC2	0.23	0.02
Predator rich	~	PC3	-0.21	0.01
Predator FD	~	Human	0.02	0.01
Predator FD	~	NDVI	0.26	0.02
Predator FD	~	PC1	-0.74	0.01
Predator FD	~	PC2	-0.08	0.01
Predator FD	~	PC3	0.04	0.01
Predator PD	~	Human	0.10	0.02
Predator PD	~	NDVI	0.23	0.03
Predator PD	~	PC1	-0.03	0.02
Predator PD	~	PC2	-0.05	0.02
Predator PD	~	PC3	0.01	0.02
Prey rich	~	Human	0.08	0.01
Prey rich	~	NDVI	0.49	0.02
Prey rich	~	PC1	0.28	0.02
Prey rich	~	PC2	0.00	0.02
Prey rich	~	PC3	-0.22	0.01
Prey FD	~	Human	0.10	0.02
Prey FD	~	NDVI	0.37	0.03
Prey FD	~	PC1	-0.48	0.02
Prey FD	~	PC2	0.14	0.02
Prey FD	~	PC3	-0.08	0.02

Prey PD	~	Human	-0.24	0.01
Prey PD	~	NDVI	0.12	0.03
Prey PD	~	PC1	0.44	0.02
Prey PD	~	PC2	-0.07	0.02
Prey PD	~	PC3	0.01	0.01
NDVI	~	PC1	0.56	0.01
NDVI	~	PC2	-0.61	0.01
NDVI	~	PC3	-0.06	0.01
Prey FD	~	Prey PD	-0.10	0.02
Prey rich	~	Prey PD	-0.10	0.01
Predator PD	~	Prey FD	-0.19	0.02
Predator PD	~	Prey rich	0.20	0.02
Predator FD	~	Predator PD	0.63	0.01
Predator rich	~	Predator PD	0.32	0.01
Predator rich	~~	Predator FD	0.28	0.02
Prey rich	~~	Prey FD	-0.01	0.02
Predator PD	~~	Prey PD	0.08	0.02
Predator rich	~~	Prey PD	-0.33	0.02
Predator FD	~~	Prey PD	-0.02	0.02
Predator FD	~~	Prey FD	0.07	0.02
Predator rich	~~	Prey FD	0.22	0.02
Predator FD	~~	Prey rich	0.03	0.02
Predator rich	~~	Prey rich	0.58	0.01

Table D.9 Mean coefficient estimates for all paths, including error covariances (~~), for the phylogenetic-driven top-down structural equation model, i.e., including trophic interactions from predator richness and FD to prey PD. Mean coefficient estimates across all combinations (2,500) of trait imputation datasets (25) and phylogenetic trees (100); standard error, corrected for spatial autocorrelation, calculated according to Rubin’s rules. Diversity abbreviations are ‘PD’, phylogenetic diversity; ‘FD’, functional diversity; ‘rich’, richness.

Response		Predictor	Mean coefficient	Standard error
Predator rich	~	Human	0.11	0.01
Predator rich	~	NDVI	0.37	0.02
Predator rich	~	PC1	-0.06	0.02
Predator rich	~	PC2	0.23	0.02
Predator rich	~	PC3	-0.20	0.01
Predator FD	~	Human	0.02	0.01
Predator FD	~	NDVI	0.27	0.02
Predator FD	~	PC1	-0.74	0.01
Predator FD	~	PC2	-0.08	0.01
Predator FD	~	PC3	0.04	0.01
Predator PD	~	Human	0.10	0.02
Predator PD	~	NDVI	0.25	0.03
Predator PD	~	PC1	0.12	0.02
Predator PD	~	PC2	-0.08	0.02
Predator PD	~	PC3	-0.02	0.02
Prey rich	~	Human	0.13	0.01
Prey rich	~	NDVI	0.46	0.02
Prey rich	~	PC1	0.20	0.02
Prey rich	~	PC2	0.02	0.02
Prey rich	~	PC3	-0.23	0.01
Prey FD	~	Human	0.12	0.02
Prey FD	~	NDVI	0.37	0.03
Prey FD	~	PC1	-0.51	0.02
Prey FD	~	PC2	0.15	0.02
Prey FD	~	PC3	-0.08	0.02
Prey PD	~	Human	-0.20	0.01
Prey PD	~	NDVI	0.24	0.03
Prey PD	~	PC1	0.52	0.03

Prey PD	~	PC2	0.02	0.02
Prey PD	~	PC3	-0.07	0.01
NDVI	~	PC1	0.56	0.01
NDVI	~	PC2	-0.61	0.01
NDVI	~	PC3	-0.06	0.01
Predator FD	~	Predator PD	0.63	0.01
Predator rich	~	Predator PD	0.36	0.01
Prey PD	~	Predator FD	0.13	0.03
Prey PD	~	Predator rich	-0.38	0.02
Prey FD	~	Prey PD	-0.02	0.02
Prey rich	~	Prey PD	0.09	0.01
Predator rich	~~	Predator FD	0.28	0.02
Prey rich	~~	Prey FD	0.01	0.02
Predator PD	~~	Prey PD	0.15	0.02
Predator PD	~~	Prey FD	-0.20	0.02
Predator PD	~~	Prey rich	0.13	0.02
Predator FD	~~	Prey FD	0.07	0.02
Predator FD	~~	Prey rich	0.04	0.02
Predator rich	~~	Prey FD	0.25	0.02
Predator rich	~~	Prey rich	0.64	0.01

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