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Traits influence responses to land-use and climate change in terrestrial vertebrates

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Declaration

I, Adrienne Etard, confirm that the work presented in this thesis is my own. Some parts have been conducted in collaboration with other researchers, and the contributions of co-authors to specific Chapters are described in the *Thesis outline of contents* on page 6. All else is appropriately referenced, and where information has been derived from other sources, I confirm that this has been indicated in the Thesis.

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Abstract

Human activities have profoundly impacted global biodiversity. Currently, anthropogenic land-use and climate change figure among the major threats to the world's fauna. However, not all species respond similarly to these pressures. Interspecific variability in responses to human threats is notably underpinned by the fact that different species possess different ecological characteristics, some of them allowing species to cope with environmental changes, while others confer a disadvantage to species in modified environments. Understanding what renders species sensitive to anthropogenic pressures is vital to inform and prioritise conservation efforts. Yet, in terrestrial vertebrates, a group for which ecological data is the most abundant, it remains unclear which traits are associated with higher sensitivity to human pressures. The aims of my thesis are to investigate whether and which traits are associated with land-use responses and climate-change sensitivity in terrestrial vertebrates, and to highlight some of the consequences for ecosystem functioning. I first assess the global availability of ecological trait data for terrestrial vertebrates, identifying understudied groups and regions (e.g., Central-African reptiles). I then show that, at global scales, disturbed land uses negatively impact the functional diversity of vertebrate assemblages. Further, I find that in all classes, higher sensitivity to land-use and climate change is associated with narrower ranges, smaller habitat breadth and inability to use human-modified habitats. Both land-use responses and climate-change sensitivity are unevenly distributed among dietary groups, highlighting potential food-web disruptions in assemblages under pressure. Finally, I show that land-use responses are influenced by species' energetic requirements, so that energetic fluxes within vertebrate assemblages are likely modified under human-driven land-use change. Although the large-scale consequences of biodiversity changes for ecosystem functioning remain to be fully understood, my thesis highlights a compositional reshaping of vertebrate assemblages under human pressure and furthers our understanding of anthropogenic impacts on biodiversity.

Impact statement

As anthropogenic pressures on the world's biota keep increasing, it is vital to put into place conservation measures to prevent and reverse further species loss. Beyond ethical and moral considerations, there is an urgent need to protect biodiversity because it sustains a range of ecological processes essential to human well-being and planetary health. Effectively managing biodiversity and related ecosystem processes in a changing world requires an understanding of how different species respond to anthropogenic disturbances. My thesis integrates various data sources to investigate the influence of traits on species' land-use responses and on species' climate-change sensitivity – two of the most pressing threats to biodiversity – at global scales and comparatively across the four terrestrial vertebrate classes. By asking whether interspecific trait variation is associated with species' land-use responses and with climate-change sensitivity, my work consolidates our understanding of what renders species sensitive to environmental change, which can help prioritise conservation efforts.

Chapter 2 presents a trait data collection for terrestrial vertebrates, targeting seven commonly-used traits. I highlight the global taxonomic, geographical, and phylogenetic biases in the trait data, revealing knowledge gaps which could guide future data collection efforts. Chapter 2 was published in *Global Ecology and Biogeography*. The compiled data were made available and have since been used by other ecologists (e.g., Capdevila et al. (2022a)) and downloaded 272 times as of May 2022. Chapter 3 uses the collected trait data and reveals profound effects of land-use change on vertebrate functional diversity, which contributes to documenting global human impacts on vertebrates and also underlines the possible threats posed by land-use change to ecosystem processes sustained by vertebrates. Chapter 3 was published in *Ecology Letters*. In Chapter 4, I ask whether traits are associated with species' land-use responses and with species' climate-change sensitivity, comparatively across the four vertebrate classes. Chapter 4 thus puts into perspective the usefulness of trait data for understanding how species respond to these anthropogenic changes, which is valuable for conservation planning and prioritisation. In Chapter 5, I ask whether species' energetic requirements, estimated from metabolic rates, influence species persistence in disturbed land uses. Chapter

5 thus integrates physiological data to further our fundamental understanding of how vertebrate species respond to land-use change and of the potential consequences for ecosystem functioning.

Beyond publishing two of my PhD Chapters, I have been able to disseminate my work at various international conferences (BES annual meetings in 2019, 2020 and 2021; BES Macroecology conference in 2019; IBS early-career conference in 2021). I will also present my PhD work at the IBS conference (June 2022, 10th Biennial meeting), and at the BES Macroecology conference (July 2022). I have contributed to the Living Planet Report 2020 (WWF, 2020) and to other published papers (Newbold et al., 2019, 2020b). Overall, my PhD work consolidates our knowledge of the role of vertebrate traits for understanding species responses to human pressures and highlights the value of trait data, and more widely, of ecological knowledge, for preserving vertebrate species in a changing world.

Thesis outline of contents, authorship and collaborations

Chapter 1: General introduction

Chapter 1 presents the background for this thesis, exposes the fundamental concepts, and highlights the research questions I investigated in the different Chapters.

Chapter 2: Global gaps and biases in trait data for terrestrial vertebrates

In Chapter 2, I present an analysis of the global gaps and biases in terrestrial vertebrate trait data. To this end, I collate data on seven traits commonly measured in terrestrial vertebrates. I then evaluate the availability of these trait data across the vertebrate classes, assessing whether there are taxonomic, phylogenetic and spatial biases. This chapter was published in *Global Ecology and Biogeography* in 2020 (DOI: 10.1111/geb.13184; Etard et al. (2020)). The paper was co-authored by Sophie Morrill who collated some of the data on reptile traits as part of an MRes project at UCL, and by Tim Newbold, who participated in the development of the research questions, provided detailed feedback on the analyses, and contributed to the writing of the paper.

Chapter 3: Intensive human land uses negatively affect vertebrate functional diversity

In this Chapter, I investigate how land-use change affects the functional composition and functional diversity of local vertebrate assemblages. This Chapter was published in *Ecology Letters* in 2022 (DOI: 10.1111/ele.13926; Etard et al. (2022)) and co-authored by Alex Pigot and Tim Newbold, who helped construct the hypotheses, provided detailed feedback on the work, and took part in the writing of the paper.

Chapter 4: Geographical range area, habitat breadth and specialisation on natural habitats are associated with land-use responses and climate-change sensitivity more consistently than life-history and dietary traits in terrestrial vertebrates

In this Chapter, I assess whether ecological traits as well as geographical range area are associated with species' land-use responses and species' estimated climate-change sensitivity, comparatively among terrestrial vertebrate classes. Rhiannon Osborne-Tonner contributed to this Chapter by collecting data on amphibian and reptile diet during her MSci project at UCL, which I used to complement my datasets. This Chapter was conducted in collaboration with Tim Newbold who helped develop the research questions and provided detailed feedback on the work and on the writing.

Chapter 5: Energetic constraints and trophic group explain species persistence in disturbed land uses

In Chapter 5, I evaluate the impacts of land-use change on community-level energetic requirements, and I assess whether species' energetic requirements influence species persistence in disturbed land uses. To this end, I use physiological data, compiling species resting metabolic rates (used as a proxy for energetic requirements) from the literature. Meghan Hayden and Laura Dee of the University of Colorado, Boulder, as well as Tim Newbold, contributed to the elaboration of the research questions for this Chapter. Meghan Hayden further contributed to this Chapter by retrieving information on net primary productivity for PREDICTS sites, using data from MODIS satellite imagery. All collaborators also provided feedback on the work and participated in writing the manuscript. This Chapter was submitted to a scientific journal and underwent a round of peer-review. I am preparing this Chapter for resubmission.

Chapter 6: General discussion

This final Chapter summarises the main findings of my thesis and assesses their contributions to the field.

Data and code access

Code access

The main pieces of R code for Chapters 2, 3, 4 and 5 are available at: https://github.com/AdrienneEtard/PhD_thesis_code.

This document was compiled with L^AT_EX; the source code and files are available at: <https://github.com/AdrienneEtard/Thesis>

Data

The data used in this thesis are freely accessible and sources are referenced throughout. In particular:

- the PREDICTS database (Hudson et al., 2014, 2017) can be downloaded from: <https://data.nhm.ac.uk/dataset/the-2016-release-of-the-predicts-database>;
- the trait datasets I compiled in Chapter 2 are available at: https://figshare.com/articles/dataset/Global_gaps_in_terrestrial_vertebrate_trait_data/10075421.

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¹ 1 | General introduction

² Humans have been modifying Earth's ecosystems for thousands of years. Archaeological and palaeontological evidence suggest that human activities may have played a major role in the extinction of Australia's megafauna as early as fifty thousand years ago (Johnson et al., 2016; Miller et al., 2016; van der Kaars et al., 2017). The subsequent arrival of modern humans in other parts of the world has also been associated with extinctions, of the megafauna in particular (Broughton and Weitzel, 2018; Sandom et al., 2014). However, the global signature of human presence on Earth has never been as prominent as in recent decades. The past two hundred years have been characterised by a sharp increase in the rates of human-driven changes at the planetary scale, a phenomenon that has been termed 'the Great Acceleration' (Steffen et al., 2015).

¹⁰ To emphasize the recent impacts of human activities on the Earth's systems, Crutzen and Stoermer (2000) proposed that we have entered a new geological epoch, which they called 'the Anthropocene'. Although the formal acceptance of this epoch and the timing of its start are still debated within the stratigraphic community (Lewis and Maslin, 2015; Monastersky, 2015), the coined term reflects the profound effects of humans on planetary processes and on the biosphere, such that its use has largely surpassed the geological field (Malhi, 2017).

¹⁶ The Anthropocene can be characterised by Earth-system and socio-economic indicators (Biermann et al., 2016; Steffen et al., 2011). Two of the major signatures are the human-driven transformations of the land surface, and changes to atmospheric composition, which have led to the onset of anthropogenic climate change (Lewis and Maslin, 2015). Altogether, the development of human activities at unprecedented scales and magnitude has led to the alteration of many ecosystems. As a result of combined anthropogenic pressures, the world's biodiversity has been changing (Daru et al., 2021; Dirzo et al., 2014; Johnson et al., 2017; McGill et al., 2015). Decreases in a range of biodiversity indicators have been reported for many taxonomic groups (Butchart et al., 2010). Human-mediated invasions and translocations of species, coupled with local declines in native species, have promoted biotic homogenisation (Daru et al., 2021; Finderup Nielsen et al., 2019; Newbold et al., 2018). In addition, species have gone extinct at rates higher than expected from natural

26 background variability, with current extinction rates estimated to exceed those inferred from fossil records by
27 a hundred to a thousand times (Barnosky et al., 2011; De Vos et al., 2015). Biodiversity loss and ecosystem
28 change have become such major issues in the 21st century that the prevention of biodiversity erosion and
29 the protection of ecosystems have become priority goals on international agendas (Convention on Biological
30 Diversity, 2022; Hoban et al., 2020). Indeed, it is now well established that biodiversity is tightly linked
31 with ecosystem functioning and ecosystem services delivery (Hooper et al., 2005; Millennium Ecosystem
32 Assessment, 2005; Oliver et al., 2015), and thus ultimately with human well-being (Millennium Ecosystem
33 Assessment, 2005). However, the difficulty in achieving global conservation goals – such as the failure to
34 reach the Aichi targets (Buchanan et al., 2020) – highlights the need to strengthen global conservation efforts
35 if we are to protect biodiversity and related ecosystem services from global threats (Butchart et al., 2016).

36 **1.1 Major drivers of global biodiversity change**

37 Currently, land-use change is the primary driver of global biodiversity loss, and is responsible for causing
38 global declines in species richness and abundance through habitat modification (Chaudhary et al., 2018;
39 Maxwell et al., 2016; Newbold et al., 2015; Nowakowski et al., 2018; Powers and Jetz, 2019). Although
40 climate change is not currently the main driver of biodiversity change, the negative effects of climate change
41 on biodiversity could equate those of land-use change in their magnitude by 2070 (Newbold, 2018). Other
42 major drivers of biodiversity loss include overexploitation, pollution and the spread of non-native species. In
43 this thesis, my focus is on land-use and climate change as global drivers of biodiversity change.

44 **1.1.1 Land-use change**

45 Land cover describes the physical aspect and composition of the land surface from dominant biotic and
46 abiotic features, typically classifying the Earth's surface into determined sets of natural and artificial ensem-
47 bles (e.g., grasslands, forests, man-made structures, waterbodies, etc; Grekousis et al. (2015)). Land cover
48 can notably be characterised with satellite imagery (Wulder et al., 2018). Land use, however, describes the
49 human intent behind a particular land cover (Lambin et al., 2001). Land-use change thus refers the pro-
50 cess by which humans transform the landscape to achieve socio-economic needs. Land-use change includes
51 transitions from natural to anthropogenic landscapes, as exemplified by agricultural-driven deforestation in
52 tropical areas (Jayathilake et al., 2021). It also describes transitions between different forms of human-
53 dominated land uses, such as the expansion of urban areas over agricultural lands (Ustaoglu and Williams,
54 2017). Land-use change can also include transitions from anthropogenic land uses to natural habitats, for

example with the restoration of human-degraded landscapes (Banks-Leite et al., 2020). Land-use and land-cover classifications may overlap, and these two terms have often been used interchangeably (Comber et al., 2008). Although humans have been modifying terrestrial ecosystems for millennia – between 75% and 95% of the total land surface could have been altered by human activities at some point in history (Ellis et al., 2013, 2021) – it is only during the past three centuries that the terrestrial surface made the transition from mostly wild to mostly human-dominated (Ellis et al., 2010). The most important driver behind this transition has been agricultural expansion, with major increases in cropland and grazing areas from the mid-18th century onward (Figure 1.1a). In recent decades, the expansion of grazing areas and animal feed crops, fuelled by the rising demand for animal products, has been identified as the most important driver of land-use change (Alexander et al., 2015).

The effects of land-use change on biodiversity have been characterised at local, regional and global scales – although global-scale studies represent a small proportion of the published research (Davison et al., 2021). Overall, land-use change has a negative impact on species richness and abundance (Foley et al., 2005; Newbold et al., 2015). For example, urban areas, which have been expanding at faster rates than urban populations themselves (Seto et al., 2010), can have a considerable negative impact on biodiversity and ecosystem services, despite currently representing a small proportion of the terrestrial surface (about 1%; Goldewijk et al. (2017)). In particular, the expansion of impervious surfaces, which characterizes urban development, has been linked to a reduction in species richness (Souza et al., 2019; Yan et al., 2019) and to increases in environmental risks (e.g., due to flooding, Hou et al. (2022); or to heat-island effects). Another important aspect of land-use change for biodiversity outcomes and ecosystem service delivery is the level of intensity at which the land is used to fulfil its purpose. For instance, management practices in agricultural areas are a major determinant of local biodiversity and related ecosystem services such as pollination and pest control (Foley et al., 2005; Kehoe et al., 2015; Millard et al., 2021). In urban areas, introducing and managing green spaces can lead to positive biodiversity outcomes (Aronson et al., 2017; Ives et al., 2016), and can also help mitigate flooding risks and heat islands (Livesley et al., 2016). Yet, land-use intensity has not been explicitly considered by a majority of past studies investigating impacts of land-use change on biodiversity (Davison et al., 2021; Dullinger et al., 2021).

1.1.2 Climate change

According to the World Meteorological Organization, climate change is defined as long-term changes (i.e., over at least several decades) to the mean state or to the variability of the climate, attributable to human activity or to natural causes. There is a strong scientific consensus that current climate change (from ap-

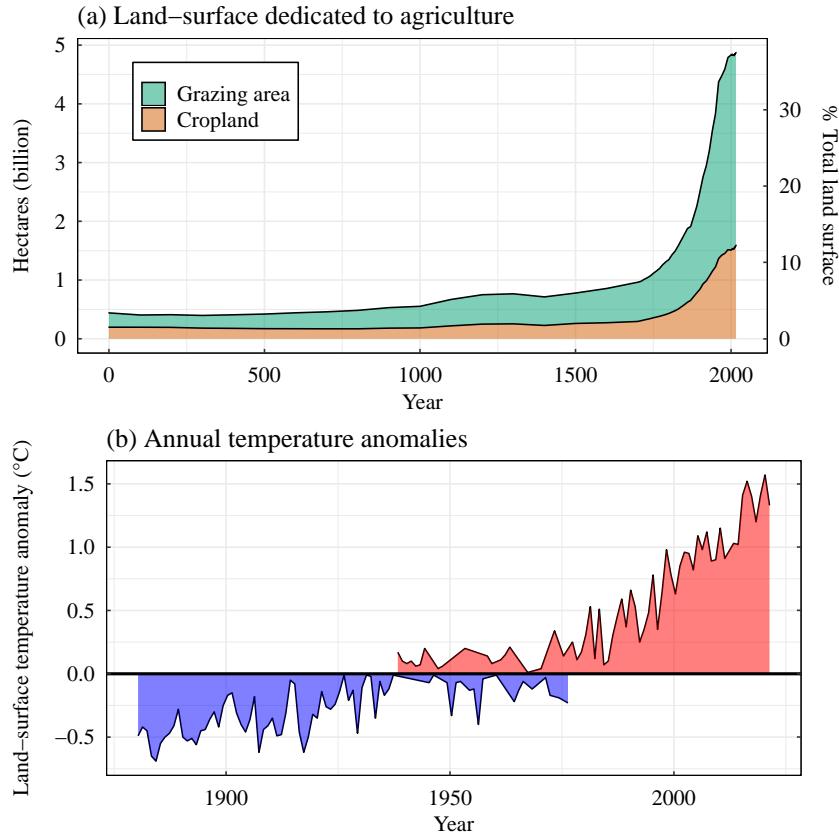


Figure 1.1: Characteristics of the ‘Great Acceleration’. (a) Land surface (and % land-surface) used for agricultural purposes between year 0 and 2016. Data from the HYDE database (Goldewijk et al., 2017), downloaded from <https://ourworldindata.org/land-use> (24/01/2022). (b) Annual land-surface temperature anomaly between 1880 and 2021. Data retrieved from the National Oceanic and Atmospheric Administration – National Centers for Environmental Information, Climate at a Glance: Global Time Series, published April 2022, retrieved 06/05/2022 from <https://www.ncdc.noaa.gov/cag/>. The anomalies are calculated with reference to the global temperature average for the 20th century.

proximately 1850) is the result of human-driven changes to atmospheric composition (Crowley, 2000; Intergovernmental Panel on Climate Change, 2013; Maibach et al., 2014). Current manifestations of climate change include rising average temperatures (Valipour et al. (2021); Figure 1.1b), increases in the frequency of extreme events (Seneviratne et al., 2012), and changes in global rainfall patterns (Dore, 2005; Trenberth, 2011).

There is accumulating empirical evidence that climate change affects biodiversity globally, with documented changes in phenology (Inouye, 2022), in the geographical distributions of species (Chen et al., 2011; Lenoir and Svenning, 2015; Soroye et al., 2020), and in species physiology (Chown et al., 2010; Pörtner and Farrell, 2008). Climate-change impacts on individual species have consequences for whole communities, through disruptions of species interactions, which can in turn exacerbate impacts on individual species (Cahill et al., 2013; Kharouba et al., 2018).

97 **1.1.3 The future of biodiversity in the Anthropocene**

98 Projecting future land-use and climate-change impacts on biodiversity highlights the key role of human-
99 development scenarios for global biodiversity outcomes (Newbold, 2018; Powell and Lenton, 2013), for the
100 long-term viability of animal populations (Spooner et al., 2018), and for ecosystem processes and services
101 (Lawler et al., 2014). As the world's population continues to grow and as the demand for food, energy and
102 other commodities keeps rising, rates of global land-use and climate change are unlikely to slow without
103 the implementation of strong international regulations and consumption changes (Intergovernmental Panel
104 on Climate Change, 2022; Stehfest et al., 2019). Under current development scenarios ('business as usual'),
105 future projections show that biodiversity will likely be negatively impacted overall, with decreases in species
106 abundance, increases in extinction rates, and shifts in the distribution of species (Newbold, 2018; Pereira
107 et al., 2010; Schipper et al., 2020). In this context, evaluating the effects of land-use and climate change
108 on biodiversity and associated ecosystem services has become vital in order to put into place mitigation
109 measures. Understanding how species have responded to past and current pressures can help assess how they
110 are likely to respond to future pressures. In particular, understanding what makes species more sensitive to
111 land-use and climate change can help conservation efforts and mitigate global human impacts on biodiversity.

112 **1.2 Ecological importance of terrestrial vertebrates and current threats**

113 In this thesis, I focus on terrestrial vertebrates, a group of more than 30,000 species that has been particu-
114 larly well sampled and studied (Titley et al., 2017), and for which there is available ecological information
115 for many species (such as geographical distributions, traits, occurrence, etc.), allowing for large-scale bio-
116 diversity assessments (e.g., Jenkins et al. (2013)). Terrestrial vertebrates play significant roles in ecosystem
117 functioning and support a wide range of processes, most notably as pollinators (Ratto et al., 2018), seed
118 dispersers (Tiffney, 2004), regulators of lower trophic levels (Lin et al., 2018; Luck et al., 2012; Mooney
119 et al., 2010; Salo et al., 2010; Zhang et al., 2018a), nutrient cyclers (Cunningham et al., 2018; Inger et al.,
120 2016; Wilson and Wolkovich, 2011) and ecosystem engineers (Severtsov, 2012). Vertebrates are also impor-
121 tant for human societies, both culturally and as sources of proteins (Albert et al., 2018; Alves et al., 2018;
122 H irons et al., 2016), and feature among the most charismatic species in the public's eye (Albert et al., 2018;
123 Courchamp et al., 2018).

124 Despite their cultural and ecological importance, terrestrial vertebrates are highly threatened by hu-
125 man activities. The latest Living Planet Report revealed that vertebrate populations have decreased by
126 70% on average since 1970 (WWF, 2020). According to the IUCN Red List of Threatened Species,

about 41% of assessed amphibian species, 26% of mammals, 21% of reptiles and 13% of birds are classified as threatened with extinction (IUCN 2022, <https://www.iucnredlist.org/resources/summary-statistics>). A recent assessment of vertebrates listed in the IUCN Red List of Threatened Species highlights habitat destruction as the predominant human threat (Cox et al., 2022), but direct exploitation also features among the major factors of decline (Monastersky, 2014). Although climate change is not the principal driver of current population declines (Caro et al., 2022), the first extinction of a mammal (the Bramble Cay melomys, *Melomys rubicola*) attributed to anthropogenic climate was reported in 2016 (Watson, 2016). Future projections highlight that between 10% and 30% of vertebrate species could be locally lost by 2070 depending on climate-change scenarios (Newbold, 2018), and that up to one in six species could face extinction under current climate change (Urban, 2015). Further, despite having been well sampled and studied compared to other groups, there still remain important gaps and biases in our ecological knowledge of terrestrial vertebrates and of their responses to human threats (Hevia et al., 2017; Meiri and Chapple, 2016; Meyer et al., 2015; Oliver et al., 2021).

1.3 Using trait-based approaches to understand global biodiversity change

1.3.1 Traits as common currencies across species

Despite the global average declines reported for vertebrate populations, not all species respond similarly to environmental changes (Dornelas et al., 2019; Leung et al., 2020): while some species are impacted negatively, others benefit from global environmental changes (Newbold et al., 2018; Thomas, 2013). One of the reasons why species differ in their ability to cope with disturbances is that species present different characteristics, or traits. In my thesis, I use the term ‘traits’ to refer to *intrinsic* characteristics, i.e. measurable at the level of an individual. Thus, although the formal definition of a trait can vary depending on studies, I adopt the definition of McGill et al. (2006), considering traits to be characteristics that are measurable at an organismal level, comparable across different species, and that likely influence organismal fitness and performance. I further make a distinction between ‘traits’ and ‘ecological characteristics’, notably in Chapter 4, where I refer to ‘ecological characteristics’ as encompassing traits and geographical range area (as geographical range area does not meet the strict definition of a trait).

The idea that species traits mediate species’ responses to environmental change was formalised in the ‘response-effect’ framework, developed in the field of plant ecology (Lavorel and Garnier, 2002), where traits that influence species’ responses to environmental change were termed ‘response traits’ (and those that underpin ecological processes were termed ‘effect traits’). One of the appeals of trait-based approaches is

157 that individual species are no longer the fundamental unit of biodiversity investigations. Rather, traits become
158 the focus and act as ‘common currencies’ across species, which is of particular interest for conservation when
159 long-term population data are lacking. If species’ responses to human threats consistently relate to certain
160 traits, it may be possible to generalise patterns, and estimate the responses of species for which population
161 data are not available (Verberk et al., 2013).

162 **1.3.2 Using ecological traits to assess which species are at most risk from human-driven
163 changes**

164 Vertebrate ecological traits (which I distinguish from physiological traits, and which I define here as traits
165 relating to the life-history, diet, morphology, and habitat use of species) have been used to explain species’
166 responses to global changes. Past studies have notably investigated whether species extinction risk is associ-
167 ated with species traits (Chichorro et al., 2019; Lebreton, 2011; Ripple et al., 2017), which is of high interest
168 for conservation, but often lacks a consideration of specific threats (González-Suárez et al., 2013).

169 Other studies have focused on the influence of traits on species’ responses to particular human pressures.
170 For example, a range of correlative trait-based approaches have been used to understand whether traits are
171 associated with species’ responses to climate change. One the one hand, past work has made use of spatial
172 data to investigate species’ responses to climate change. For instance, some studies have focused on explain-
173 ing interspecific variation in past or projected range shifts with traits (Di Marco et al., 2021; McCain and
174 King, 2014; Pacifici et al., 2017; Schloss et al., 2012). However, studying observed responses to climate
175 change may be complicated by the fact that this requires to disentangle the effects of climate change from
176 that of other drivers of change on observed responses (MacLean and Beissinger, 2017). Thus, other studies
177 have used proxies instead of observed responses, which may provide complementary insights into the rela-
178 tionships between traits and species’ ability to track climate change. For instance, Estrada et al. (2018) used
179 a ‘range-filling’ approach as a proxy for species’ ability to shift their distributions under climate change.
180 The ‘range-filling’ approach consists in investigating interspecific differences between the realised and po-
181 tentially suitable climatic niche of species, differences which are interpreted as being driven by intrinsic (i.e.,
182 traits) and/or extrinsic factors (e.g., non-climatic environmental factors, biotic interactions, etc.) limiting the
183 realised distribution of the species (Estrada et al., 2018; Svenning and Skov, 2004). On the other hand, de-
184 mographic approaches relying on long-term population data have also been employed to explain population-
185 and species’ responses to recent climate change (Spooner et al., 2018). These approaches may suffer from
186 similar complications regarding the disentangling of climatic and non-climatic effects on observed responses
187 (Williams et al., 2022). Finally, ecological traits have been used in a predictive fashion, notably with frame-

188 works aiming to assess species' vulnerability to climate change (Foden et al., 2013; Pacifici et al., 2015),
189 assuming that given traits confer higher sensitivity to climate change.

190 Past studies have also investigated whether traits are associated with species' responses to habitat dis-
191 turbance. Most of these studies have used spatial data, inferring effects of land-use change on biodiversity
192 from 'space-for-time' substitutions (Davison et al., 2021; De Palma et al., 2018), such as in Newbold et al.
193 (2013), Quesnelle et al. (2014) or Nowakowski et al. (2017).

194 Further, trait-based approaches have also been employed to understand the signature of human impacts
195 on the diversity and variability of traits within ecological communities. To this end, a range of functional
196 diversity indices have been developed (Legras et al., 2018; Schleuter et al., 2010). Functional diversity
197 indices have been employed to evaluate the effects of land-use disturbance on the trait diversity of vertebrate
198 assemblages (most often at local and regional scales; Flynn et al. (2009), La Sorte et al. (2018), and Tinoco
199 et al. (2018)), or to assess the projected effects of climate change on the trait diversity of vertebrate species
200 (Stewart et al., 2022).

201 Although trait-based approaches using ecological traits have been widely employed to understand the
202 effects of human-driven changes on vertebrate species, past studies have mostly been conducted at local to
203 regional scales (Davison et al., 2021), and have tended to focus on given taxa among the vertebrate classes
204 (Hevia et al., 2017). Thus, global comparative assessments of the relationships between ecological traits
205 and species' responses to human pressures across terrestrial vertebrates are lacking. Because of the diver-
206 sity of approaches used to investigate associations between species traits and human pressures in past work,
207 and because of the different spatial scales and taxonomic focus of past studies, identifying a set of traits
208 that emerge as important determinants of sensitivity to both land-use and climate change across terrestrial
209 vertebrates remains challenging. For instance, Quesnelle et al. (2014) found that reproductive rates, as es-
210 timated from litter or clutch sizes, were significantly associated with sensitivity to habitat loss in wetland
211 vertebrates; however, Nowakowski et al. (2017) did not find any effect of clutch size on amphibian sensi-
212 tivity to habitat modification. The meta-analysis by MacLean and Beissinger (2017) highlights the lack of
213 consensus in published studies on the associations between traits and species' range shifts on under recent
214 climate change. Thus, there remains a need to assess whether and which traits are associated with species'
215 responses to human pressures in terrestrial vertebrates.

216 **1.3.3 Using physiological traits to understand land-use impacts on biodiversity and ecosys-**
217 **tem functioning**

218 Physiological traits are typically measured to capture aspects of species' metabolism, performance or bio-
219 chemistry. Recent decades have seen advances in large-scale studies linking physiological traits to macroe-
220 cological patterns of species existence across levels of organisation (Burger et al., 2021; Chown et al., 2004),
221 as exemplified by the development of the 'metabolic theory of ecology' (Brown et al., 2004; Gillooly et
222 al., 2001). In particular, metabolic rates reflect the amount of energy used at the organismal level (I define
223 metabolic rates here as the rates at which an organism processes available energy, which is often measured
224 in the lab by estimating the amount of consumed O₂ by a whole organism over a period of time (Auer et al.,
225 2017; Sadowska et al., 2015)). As energy is a fundamental currency across all living organisms, metabolic
226 rates can be employed comparatively across species to investigate interspecific variation in energetic expen-
227 diture. Thus, past studies have focused on understanding intraspecific variation in metabolic rates (Auer
228 et al., 2017; Burton et al., 2011) as well as interspecific variation (such as variation in metabolic rates with
229 temperature; Clarke and Fraser (2004); or variation in metabolic rates with longevity – e.g., testing the 'pace
230 of life' theory; Stark et al. (2020)).

231 How species allocate their energy impacts almost all aspects of their persistence. Energetic expenditure
232 relates to food intake, which itself is constrained by the amount of available energy in the environment. Thus,
233 species' energetic requirements are ultimately constrained and influenced by trade-offs between energetic-
234 expenditure allocation and resource intake (Auer et al., 2020). As land-use change profoundly modifies the
235 amount and the types of resources available, it follows that land-use change should impact the total amount
236 of energy processed by vertebrate assemblages. Further, the amount of energy required by species could
237 also be an important predictor of species' ability to cope with a disturbed resource landscape. However,
238 to my knowledge, no study has yet investigated how land-use change affects the energetic requirements of
239 vertebrate assemblages, or whether species' energetic requirements influence how species respond to land-
240 use change.

241 **1.3.4 Thesis aims**

242 As discussed above, studies investigating relationships between ecological traits and environmental change
243 have mostly been conducted at local to regional scale (Davison et al., 2021; Hevia et al., 2017), and have
244 mostly focused on single vertebrate classes or sub-taxa within particular classes. Thus, although response
245 traits to land-use and climate change have been identified in various vertebrate taxa, whether the effects of

246 such traits can be generalised geographically and taxonomically remains largely uncertain, emphasising the
247 need for global comparative assessments of the relationships between traits and species' responses to human
248 threats.

249 In this thesis, I set out to fill in this gap by asking whether interspecific variation in ecological traits is as-
250 sociated with species' land-use responses and with estimated climate-change sensitivity, at global scales, and
251 comparatively across the four terrestrial vertebrate classes. Such an assessment helps to understand which
252 species are at most risk from global changes, and may be useful for the prioritisation of conservation efforts.
253 My thesis also aims to highlight some of the consequences of land-use change for ecosystem functioning,
254 by investigating relationships between species energetic requirements (estimated from metabolic rates) and
255 land-use differences.

256 Throughout my thesis, assemblage-level and species-level responses to land use and land-use intensity
257 are assessed using a 'space-for-time' approach (De Palma et al., 2018). To this end, I use one of the most
258 comprehensive databases recording species occurrence and abundance in different land uses (the PREDICTS
259 database, Hudson et al. (2014, 2017)). I estimate sensitivity to climate change from properties of species'
260 climatic niche space, and thus it is important to emphasize that this does not allow a consideration of species'
261 *responses* to climate change. Indeed, it is difficult to capture the responses of many species to climate change,
262 given that this requires disentangling the effects of climate change from that of other drivers of change over
263 the considered time period (which can be complex; MacLean and Beissinger (2017)), and also requires
264 gathering data on the occurrence or abundance of species over several decades (which may be particularly
265 challenging when working at large taxonomic scales).

266 **1.4 Detailed aims, hypotheses and outline of the following Chapters**

267 The overarching aims of my thesis are to investigate whether species traits are associated with species' land-
268 use responses and species' estimated climate-change sensitivity in terrestrial vertebrates, and to highlight
269 some of the consequences of global changes for ecosystem processes sustained by terrestrial vertebrates.
270 One of the obstacles that has hindered the application of trait-based approaches at large scales in animal
271 taxa is the lack of a centralised repository for readily available trait data, as emphasized by the recent calls
272 to compile and release trait data for animals (Junker et al., 2022; Kissling et al., 2018). Thus, collecting
273 trait data and investigating the current availability of the data for terrestrial vertebrates is an important and
274 necessary prerequisite to any analysis. In Chapter 2, I present a data collection of ecological traits for
275 terrestrial vertebrates. Because using similar traits in the different vertebrate classes is necessary to be able

276 to make comparisons among vertebrate classes, I target seven classes of traits that are commonly used across
277 taxonomic groups: body mass/size, lifespan, litter/clutch size, trophic level, diel activity, habitat breadth,
278 and habitat specialisation (characterising whether a species is able to use artificial habitats). I am not able
279 to consider intraspecific variation in the data compilation, since multiple measurements of trait values do
280 not exist for many vertebrate species. Chapter 2 also assesses the availability of the trait data across the
281 terrestrial vertebrate classes, and investigates whether the trait data present global taxonomic, phylogenetic
282 and spatial biases. On the basis of past work (Titley et al., 2017), I predict that amphibians and reptiles are
283 under-sampled compared to mammals and birds. Further, I hypothesize that trait data are less abundant for
284 the narrower-ranging species and in species-richer regions.

285 At the assemblage level, the diversity of species traits can be summarised with functional diversity indices
286 (Legras et al., 2018; Schleuter et al., 2010; Villéger et al., 2008). Past research has shown that land-use
287 disturbances affect the functional composition of vertebrate assemblages (Flynn et al., 2009; Tinoco et al.,
288 2018). However, to the best of my knowledge, a global assessment of how the functional diversity of local
289 terrestrial vertebrate assemblages respond to land use and land-use intensity, within and across taxonomic
290 classes, has not yet been undertaken. In Chapter 3, I aim to fill in this gap. To this end, I combine the trait
291 data collected in Chapter 2 with the PREDICTS database, after imputing missing trait values (as described
292 in Chapter 2). I hypothesize that the functional diversity of vertebrate assemblages in disturbed land uses is
293 lower than in undisturbed areas. I further predict that decreases in functional diversity in disturbed land uses
294 are driven by high levels of functional loss and that observed declines in functional diversity exceed those
295 expected from random species loss.

296 Chapter 3 highlights the effects of land-use change on the functional composition of vertebrate assem-
297 blages, but does not allow an assessment of the effects of particular traits on species' land-use responses,
298 as multidimensional interspecific trait variation is summarised into single indices of functional diversity.
299 Chapter 4 aims at assessing such effects, by investigating whether species traits are associated with species'
300 land-use responses and species' climate-change sensitivity. In addition to the traits considered in Chapter 3,
301 Chapter 4 includes dietary traits and species geographical range area. Although geographical range area is
302 not a trait *per se*, it has been shown to influence species' responses to land-use and climate change (Newbold
303 et al., 2018; Thuiller et al., 2005), and it is likely an important determinant of climate-change sensitivity.
304 Thus, in Chapter 4, I define 'ecological characteristics' as encompassing both traits and geographical range
305 areas. I investigate whether these ecological characteristics are associated with species' land-use responses
306 on the one hand and with species' estimated climate-change sensitivity on the other hand, comparatively
307 among the terrestrial vertebrate classes. To the best of my knowledge, Chapter 4 constitutes the first global

308 comparative assessment, across terrestrial vertebrate classes, of associations between species' ecological
309 characteristics and both land-use responses and estimated climate-change sensitivity.

310 Chapter 5 develops our understanding of the impacts of land-use change on ecosystem functioning by
311 focusing on species' energetic requirements, which is interesting for at least two reasons: first, because en-
312 ergetic requirements relate to resource intake, and as such reflect the amount of energy that is processed by
313 different trophic groups, which can inform about ecosystem functioning; second, because species persistence
314 is constrained by trade-offs in energy allocation among diverse processes (e.g., maintenance, growth, repro-
315 duction), such that energetic requirements are likely important determinants of species' ability to cope with
316 disturbances. Yet, there has been no study so far investigating relationships between energetic requirements
317 and land-use differences in terrestrial vertebrates. In Chapter 5, I collect resting metabolic rate estimates for
318 vertebrates, that is, the estimated minimum amount of energy necessary for organismal maintenance (esti-
319 mated at the species level), and I combine these estimates with the PREDICTS database. I then assess the
320 effects of land use on the total energetic requirements of vertebrate assemblages (conceptually comparable
321 to 'community metabolism'; Migné et al. (2015)). Second, I assess whether species' energetic requirements
322 influence species persistence in disturbed land uses (after controlling energetic requirements for the effects of
323 body mass and taxonomy, which explain most of the interspecific variation in metabolic rates; White (2011)).
324 Assuming that there is less energy available in disturbed land uses, I hypothesize that the assemblage-level
325 energetic requirements of vertebrates are lower in disturbed land uses compared to natural habitats, and that
326 species with lower mass-independent energetic requirements are favoured over species with higher mass-
327 independent energetic requirements in disturbed land uses. Chapter 5 highlights the impacts of land-use
328 change on vertebrate community metabolism and develops our understanding of the factors that shape how
329 species respond to changes in land use.

330 Finally, in Chapter 6, I summarise the findings of my thesis, I highlight some of the limitations, and I ex-
331 amine the relevance of my findings for the field. By investigating whether traits are associated with species'
332 land-use responses and climate-change sensitivity across the terrestrial vertebrates, my thesis furthers our
333 understanding of what could render species more sensitive to human threats, underlines possible modifica-
334 tions to ecosystem functioning, and stresses the role and usefulness of vertebrate trait data and ecological
335 knowledge for understanding species- and community-level responses to human pressures.

³³⁶ **2 | Global gaps and biases in trait data for**
³³⁷ **terrestrial vertebrates**

³³⁸ **Keywords**

³³⁹ Terrestrial vertebrates; traits; coverage; completeness; taxonomic biases; spatial biases; phylogenetic biases.

³⁴⁰ **Abstract**

³⁴¹ Trait data are increasingly used in studies investigating the impacts of global changes on the structure and
³⁴² functioning of ecological communities. Despite a growing number of trait data collations for terrestrial
³⁴³ vertebrates, there is to date no global assessment of the gaps and biases the data present. Here, I assess
³⁴⁴ whether terrestrial vertebrate trait data are taxonomically, spatially and phylogenetically biased. I compile
³⁴⁵ seven ecological traits and quantify coverage as the proportion of species for which an estimate is available.
³⁴⁶ For a species, I define completeness as the proportion of non-missing values across traits. I assess whether
³⁴⁷ coverage and completeness differ across classes and examine phylogenetic biases in trait data. To investi-
³⁴⁸ giate spatial biases, I test whether wider-ranging species have more complete trait data than narrow-ranging
³⁴⁹ species. Additionally, I test whether species-rich regions, which are of most concern for conservation, are
³⁵⁰ less well-sampled than species-poor regions. My results show that mammals and birds are well-sampled
³⁵¹ even in species-rich regions. For reptiles and amphibians (herptiles), only body size presents a high cov-
³⁵² erage (>80%), as well as habitat related variables (for amphibians). Herptiles are poorly sampled for other
³⁵³ traits. The shortfalls are particularly acute in some species-rich regions and for certain clades. Across all
³⁵⁴ classes, geographically rarer species have less complete trait information. Hence, trait information is less
³⁵⁵ available on average in some of the most diverse areas and in geographically rarer species, both critical for
³⁵⁶ biodiversity conservation. Gaps in trait data may impede our ability to conduct large scale analyses, while

357 biases can impact the validity of extrapolations. A short-term solution to the problem is to estimate missing
358 trait data using imputation techniques, while a longer-term and more robust filling of existing gaps requires
359 continued data collection efforts.

360 **2.1 Introduction**

361 Species traits are fundamental to ecological and evolutionary research. Comparative studies regularly use
362 trait data across organisms to understand evolutionary processes and species coexistence (Escudero and
363 Valladares, 2016; Zamudio et al., 2016), to investigate global patterns of life forms and functions (Díaz et
364 al., 2016), or to assess species' vulnerability to environmental changes (Böhm et al., 2016; Pacifici et al.,
365 2015; Pearson et al., 2014). Because traits influence species' ability to cope with environmental changes
366 (Newbold et al., 2013) and underpin species' contributions to ecosystem processes (Lavorel and Garnier,
367 2002; Violle et al., 2007; Wong et al., 2018), they play an increasingly important role in functional and
368 conservation ecology.

369 Past and recent efforts to collate and release trait data in the public domain have facilitated the develop-
370 ment of trait-based research. For instance, a global trait database has been published for plants (Kattge et al.,
371 2011). As of May 2020, data from this database had been used in 297 publications since its release (Ac-
372 tivity report, 18/06/2020, <https://www.try-db.org/TryWeb/Home.php>). Such databases hence
373 constitute invaluable research tools and have the potential to greatly advance the field.

374 Vertebrates are one of the most studied taxa (Titley et al., 2017). There are now diverse sources of eco-
375 logical traits for vertebrate groups (primates: Galán-Acedo et al., 2019; mammals: 'PanTHERIA', Jones et
376 al., 2009; amniotes: Myhrvold et al., 2015; amphibians: 'AmphiBIO', Oliveira et al., 2017). These datasets
377 stem from important efforts to collate published estimates of trait data and make them readily available. Trait
378 data have also been made available on online platforms (for instance, the Global Assessment of Reptile Dis-
379 tribution initiative: <http://www.gardinitiative.org/>; the IUCN Red List of Threatened Species:
380 <https://www.iucnredlist.org/>; BirdLife data zone: <http://datazone.birdlife.org/>
381 home).

382 Nevertheless, despite the importance of vertebrate species in global research outputs, there is no single
383 source for vertebrate ecological traits. Consequently, researchers wishing to conduct comparative studies
384 across vertebrate groups may have to collate trait data from a range of sources (such as in Cooke et al.
385 (2019a,b) or in González-Suárez et al. (2018)), a time-consuming prerequisite which may be a limiting
386 step of the research process. Indeed, collating data from heterogeneously-formatted sources presents many

387 challenges (Schneider et al., 2019), particularly when working across a large number of species. For instance,
388 traits may be measured differently across datasets; units may be inconsistent; and taxonomic resolution and
389 nomenclature may vary.

390 The lack of a curated, readily available global database for vertebrate ecological traits impedes our ability
391 to conduct cross-taxon comparative studies at global scales. However, efforts to collate data into a single
392 database are limited by the availability of underlying data. Because there exist important gaps in biodiversity
393 knowledge (Hortal et al., 2015), trait datasets are often incomplete, with many species lacking estimates for
394 many traits. The incompleteness of ecological trait data at the species level has been termed the ‘Raunkiær
395 shortfall’ by Hortal et al. (2015). Furthermore, incomplete trait data are likely to be biased. Biases in trait data
396 may be the consequence of uneven taxonomic and spatial collection effort, with a set of charismatic or easily
397 detectable species being more completely sampled. For instance, González-Suárez et al. (2012) investigated
398 biases in global trait information in mammals. They notably found that the availability of mammalian trait
399 data was geographically and phylogenetically biased, with larger and more widely distributed species being
400 better sampled. In addition, data availability also differed across IUCN Red List extinction risk categories,
401 with threatened species (Critically Endangered, Endangered or Vulnerable) being less well sampled for traits
402 than non-threatened species (Least Concern or Near Threatened).

403 A major issue with incomplete, biased data is the introduction of bias in subsequent analyses. Assessing
404 the amount of missing data as well as the so-called ‘missingness mechanism’ – whether missing data are
405 missing at random, as opposed to there being systematic biases in the way missing values are distributed, see
406 Baraldi and Enders (2010) – is an important prerequisite. Indeed, there exist diverse techniques to deal with
407 data missingness. The simplest one consists of retaining complete cases only by filtering out missing values
408 (case deletion, see Nakagawa and Freckleton (2008)). Nevertheless, case deletion may lead to biased param-
409 eter estimates and erroneous conclusions when values are not missing at random (González-Suárez et al.,
410 2012). Therefore, it is critical to determine the most appropriate way to deal with data incompleteness. For
411 instance, previous studies using terrestrial vertebrate trait data have employed multiple imputation techniques
412 to fill in the gaps (Cooke et al., 2019a; González-Suárez et al., 2012). Yet, imputation techniques could be
413 sensitive to non-randomness in trait data. Phylogenetic biases (where some clades are under-sampled com-
414 pared to other clades) could notably impact the performance of several imputation approaches. It is thus
415 vital to characterise the gaps in trait data prior to any analysis. However, there has been no study to date
416 investigating global patterns in the availability of trait data across terrestrial vertebrates.

417 Here, I aim to assess the global state of trait data in terrestrial vertebrates. I focus on a set of traits that are
418 available across the four classes and that are commonly used by ecologists: body size; litter or clutch size;

419 longevity; trophic level; activity time; habitat breath; and a measure of habitat specialisation. I quantify and
420 compare the gaps in trait data across classes by calculating the coverage of each trait across species, and the
421 completeness of trait estimates for each species (Box 1). I investigate taxonomic, spatial and phylogenetic
422 biases in trait coverage and completeness.

423 Given that biodiversity research is globally biased towards birds and mammals (Titley et al., 2017),
424 I hypothesise that herptiles are less well sampled for traits than mammals and birds, having both lower
425 coverage and completeness.

426 Furthermore, building upon previous studies conducted on mammals (González-Suárez et al., 2012), I
427 hypothesize that species rarity influences completeness, focusing on species geographical range size as one
428 aspect of rarity. Widely distributed species could be better sampled than narrowly distributed species because
429 their ranges overlap with more study sites, regardless of their abundance. As such, I test whether species
430 geographical range size explains trait completeness.

431 It is well established that global research effort is distributed unequally (United Nations Educational
432 Scientific and Cultural Organization, 2015), with patterns underpinned by various geographical and so-
433 cieconomic factors. For instance, countries with higher gross domestic product tend to host a larger number
434 of research institutions (Martin et al., 2012). The proximity of research infrastructures and the accessibility
435 of survey sites play an important part in explaining the global distribution of knowledge (Hortal et al., 2015).
436 As a result of these factors, biodiversity data gaps tend to be greater in tropical areas (Collen et al., 2008).
437 Tropical areas have the greatest species richness, and so these data biases are of great concern for biodiversity
438 conservation. Whether species-rich regions are systematically under-sampled for traits compared to species-
439 poor regions is thus important to assess, given the significance of species-rich areas for global conservation.
440 Here, I investigate spatial biases in trait completeness, hypothesizing that species-rich areas are on average
441 less well sampled than species-poor areas.

442 Finally, I investigate phylogenetic biases in the trait data. I assess whether particular clades have received
443 more attention than others by looking for patterns in the distribution of trait completeness across the terminal
444 branches of phylogenetic trees in each class.

Box 1. Definitions

Trait: Sensu stricto, a characteristic measurable at the level of an individual and that influences organismal fitness or performance (Violle et al., 2007). In this thesis, I broaden this definition to include ‘ecological’ traits (e.g., the number of habitats used by a species), where the relationship of a species to the surrounding environment needs to be considered. Ecological traits may be estimated by aggregating data across multiple individuals.

Trait completeness: For a given species, the proportion of traits for which an estimate is available.

Trait coverage: For a given trait, the proportion of species for which an estimate is available.

445 2.2 Methods

446 I produced class-specific trait datasets that were made available on figshare (https://figshare.com/articles/dataset/Global_gaps_in_terrestrial_vertebrate_trait_data/10075421/)
447 2). Data compilation and all analyses were conducted with R version 3.5.1 (R Core Team, 2018). Distribu-
448 tion maps were processed using both R and the ‘ArcPy’ package available in ArcGIS v.10.6 (ESRI, 2011)
449 (implemented in Python 2.7; van Rossum, G. (1995)).
450

451 2.2.1 Trait data collection

452 Sources and taxonomic matching

453 I used freely accessible secondary sources in my compilation (Table 2.1), selected for their broad taxonomic
454 coverage and/or for their frequent use in macroecological studies. Across sources, similar species could
455 appear under synonymous names. This was a potential problem for matching sources by binomial names.
456 Indeed, synonymy can artefactually decrease trait coverage, when trait information is not available across
457 all synonyms. Notably, difficulties arise when species have been divided into several subspecies or when
458 different subspecies are clumped together. Systematic manual checks could not be applied considering the
459 scale of the data collection (there were >39,000 unique binomial names across sources). I developed a
460 procedure aiming at identifying one accepted name for each of the binomial names found across sources.
461 When I could not find an accepted name, I used the original name. Figure 2.1 summarizes the main steps;
462 similar solutions have been used in other large-scale studies (Cooke et al., 2019a).

463 Briefly, the procedure consisted of extracting synonyms from the IUCN (IUCN, 2020) or from the In-
464 tegrated Taxonomic Information System (ITIS; <https://www.itis.gov/>), using the ‘rredlist’ (Cham-
465 berlain, 2018) and ‘taxize’ (Chamberlain and Szöcs, 2013) R packages. One accepted name was assigned to

466 each synonym. I produced a "Synonym" dataset that I have also made available. I then normalized taxonomy
467 across sources by replacing binomial names with their identified accepted name where applicable.

468 Given that different taxonomic backbones could be used to correct for taxonomy, I make two versions
469 of the trait compilations available (corrected and not corrected for taxonomy), meaning that users are free to
470 apply their own corrections; for example, taxonomy could be aligned to that of class-specific sources, such
471 as The Reptile Database, the American Museum of Natural History's Amphibian Species of the World, the
472 Mammal Diversity Database or the International Ornithological Congress World Bird List. Datasets cor-
473 rected for taxonomy contain 11,634 species of birds, 5,381 mammals, 10,612 reptiles and 6,990 amphibians.
474 Where no taxonomic correction was applied when matching sources, the compiled datasets contain 13,501
475 birds, 5,791 mammals, 11,012 reptiles and 8,583 amphibians. For more information, see Appendix 1 (S2.1:
476 'Taxonomic corrections'; Figure S2.1).

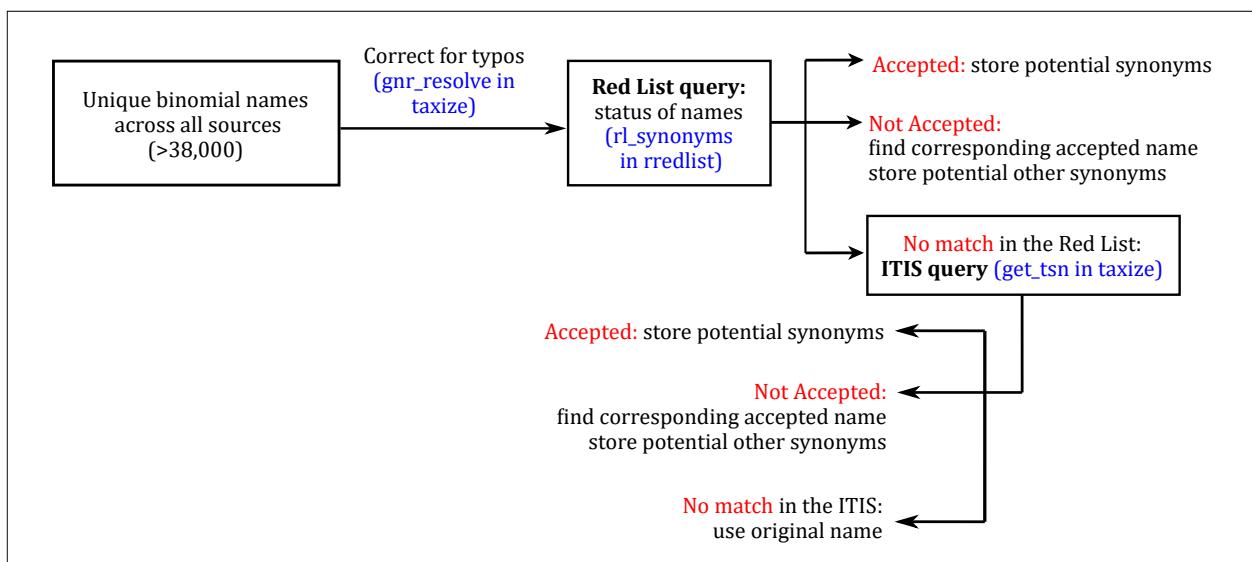


Figure 2.1: Procedure used to identify the accepted names of species. I extracted, where possible, the accepted names of species from either the IUCN Red List or the Integrated Taxonomic Information System (ITIS). Figure reproduced from Etard et al. (2020).

477 Compilation methods

478 For continuous traits, I took the median value within species when multiple estimates were available from
479 different sources, after removal of any repeated values, which were assumed to represent estimates duplicated
480 across secondary compilations and derived from the same underlying primary sources. Although intraspe-
481 cific variation is increasingly being recognized to have important effects on ecological systems (Bolnick
482 et al., 2011; Des Roches et al., 2018; González-Suárez and Revilla, 2012; Siefert et al., 2015), it was not

Table 2.1: Data sources for each trait. Abbreviations: A = amphibians; B = birds; BL = body length; BM = body mass; DA = diel activity time; GL = generation length; H = habitat data; LCS = litter or clutch size; L/ML = longevity or maximum longevity; M = mammals; MA = age at sexual maturity; R = reptiles; RS = range size; TL = trophic level. Note. Data sources may contain more traits than shown here. Tick marks in parentheses indicate that the trait was present in the data source but that another closely related trait with a better coverage was used instead. The tilde character (~) before a tick mark indicates that I derived trophic levels from species diet. ¹ <http://datazone.birdlife.org/home>; ² <https://www.iucnredlist.org/resources/spatial-data-download>; ³ <http://apiv3.iucnredlist.org/api/v3/docs##general>. Table reproduced from Etard et al. (2020).

Sources	Taxa	Traits									
		BM	BL	L/ML	MA	GL	LCS	TL	DA	RS	H
Oliveira et al. (2017)	Amphibians	(✓)	✓	(✓)	✓		✓	~✓	✓		
Cooper et al. (2008)							✓				
Sodhi et al. (2008)			✓								
Wilman et al. (2014)	Birds	✓						~✓	✓		
BirdLife ¹		✓				✓					✓
Jones et al. (2009)	Mammals	✓	(✓)	(✓)	(✓)		✓		✓		
Kissling et al. (2014)								✓			
Gainsbury et al. (2018)								✓			
Wilman et al. (2014)		✓							✓		
Pacifici et al. (2015)		✓				✓					
Scharf et al. (2015)	Reptiles	✓		✓	(✓)		✓	✓	✓		
Vidan et al. (2017)										✓	
Stark et al. (2018)		✓		✓			✓		✓		
Schwarz and Meiri (2017)								✓			
Novosolov et al. (2017)		✓						✓			
Novosolov et al. (2013)							✓				
Slavenko et al. (2016)		✓									
Feldman et al. (2016)		✓									
Meiri (2018)					✓		✓	✓	✓		
Meiri et al. (2015)								✓	✓		
Roll et al. (2017)										✓	
Myhrvold et al. (2015)	B, M, R	✓	✓	✓	(✓)		✓				
IUCN (2020) ²	A, B, M										✓
IUCN (2020) ³	All										✓

483 feasible to obtain measures of intraspecific variability from all sources; therefore, estimates were provided
 484 as a single measure for each species. For some species and some traits, measures were provided separately
 485 for females and males. In such cases, I first obtained the mean of these two measures.

486 Across sources, there were multiple traits related to each of body size and lifespan. For instance, body
 487 mass and/or body length information could be provided. Different proxies were also available for lifespan,

488 such as the age at sexual maturity or generation length. In such cases, I focused on the trait presenting the
489 highest coverage.

490 • **Body size**

491 Adult body mass estimates were compiled for mammals, birds and reptiles. Body length information
492 was compiled for amphibians, because the coverage for body length was higher than that for body
493 mass. Body mass and body length are known to scale allometrically, although the allometric rela-
494 tionship differs across amphibian clades (Santini et al., 2018). In the amphibian dataset, Pearson's
495 correlation coefficient between log(Body mass) and log(Body length) was 0.71 (data points shown in
496 Appendix 1, S2.2:‘Additional information for trait compilation’, Figure S2.2).

497 • **Longevity**

498 I defined longevity as the lifespan of an individual and maximum longevity as the longest lifespan
499 reported. I used closely related traits when longevity/maximum longevity was not available or when
500 longevity/maximum longevity had a poorer coverage than a related trait. I selected the age at sexual
501 maturity for amphibians; Pearson's correlation coefficient between log(Age at sexual maturity) and
502 log(Maximum longevity) was 0.55 (Appendix 1, Figure S2.2). I compiled the generation length for
503 mammals and birds. The correlation between log(Generation length) and log(Longevity) was 0.74 for
504 mammals and 0.70 for birds (data points shown in Appendix 1, S2.2, Figure S2.3). Finally, I used
505 maximum longevity directly for reptiles.

506 • **Litter or clutch size**

507 The number of offspring (litter size) or eggs (clutch size) was compiled directly from the sources and
508 treated as equivalent across classes. I reported measures of central tendencies provided by the sources
509 where applicable; otherwise, I calculated range midpoints (mean of smallest and largest reported lit-
510 ter/clutch sizes).

511 • **Trophic level**

512 In all classes, species were described as omnivores, carnivores or herbivores. For reptiles and mam-
513 mals, this information was compiled directly from the sources. For amphibians and birds, trophic
514 levels were not provided. For these two classes, I inferred trophic levels from dietary information
515 (Table 2.1). For birds, I used the primary diet (based on food items recorded as composing $\geq 50\%$
516 of the diet of a species). Diet for amphibians was described without respect to the percentage use of
517 food items; simply as a binary record of whether or not food items were used. In both cases, species

518 recorded to only consume plant-based resources (seeds, nectar, fruit or other plant material) were
519 classified as herbivores. Species consuming only animal resources (invertebrates or vertebrates) were
520 classified as carnivores. Species consuming a mixture of plant and animal resources were classified as
521 omnivores.

522 • **Activity time**

523 Species were described as being either nocturnal or non-nocturnal. Despite a higher resolution of ac-
524 tivity time information in some of the sources (e.g., species being described as cathemeral, crepuscular
525 or diurnal), I adopted the classification of the source with the lowest resolution (EltonTraits: Wilman
526 et al. (2014), for birds), in order to have consistent information across classes. As such, all species
527 defined as diurnal, cathemeral or crepuscular were classified as non-nocturnal, as opposed to species
528 classified as strictly nocturnal.

529 • **Habitat breadth**

530 I used IUCN habitat data (IUCN, 2020), which describe species habitat preferences and the suitabil-
531 ity and importance of each habitat. I defined habitat breadth as the number of habitats a species was
532 known to use, using level 2 of the IUCN Habitat Classification Scheme for description of habitat
533 types (divided into: Forest, Savanna, Shrubland, Grassland, Wetland, Rocky areas, Caves and subter-
534 ranean, Desert, Marine, Marine intertidal or coastal/supratidal, Artificial, Introduced vegetation, and
535 Other/Unknown.) Note that the total number of habitats, determined by including those that qualify as
536 artificial, correlates positively with the number of natural habitats used (Figure 2.2).

537 • **Use of artificial habitats**

538 For a species, I recorded whether any artificial habitat was reported to be suitable in the IUCN habitat
539 data.

540 Finally, the compiled datasets contain an additional column, ‘Note’, where I reported species found to
541 be extinct or extinct in the wild (EW). I used species Red List status and information from Meiri (2018) to
542 flag such species. I reported 75 extinct/EW species for mammals, 160 for birds, 34 for amphibians and 53
543 for reptiles. It is likely that the datasets contain extinct species that I could not flag, because they were not
544 recorded as extinct in the sources I used.

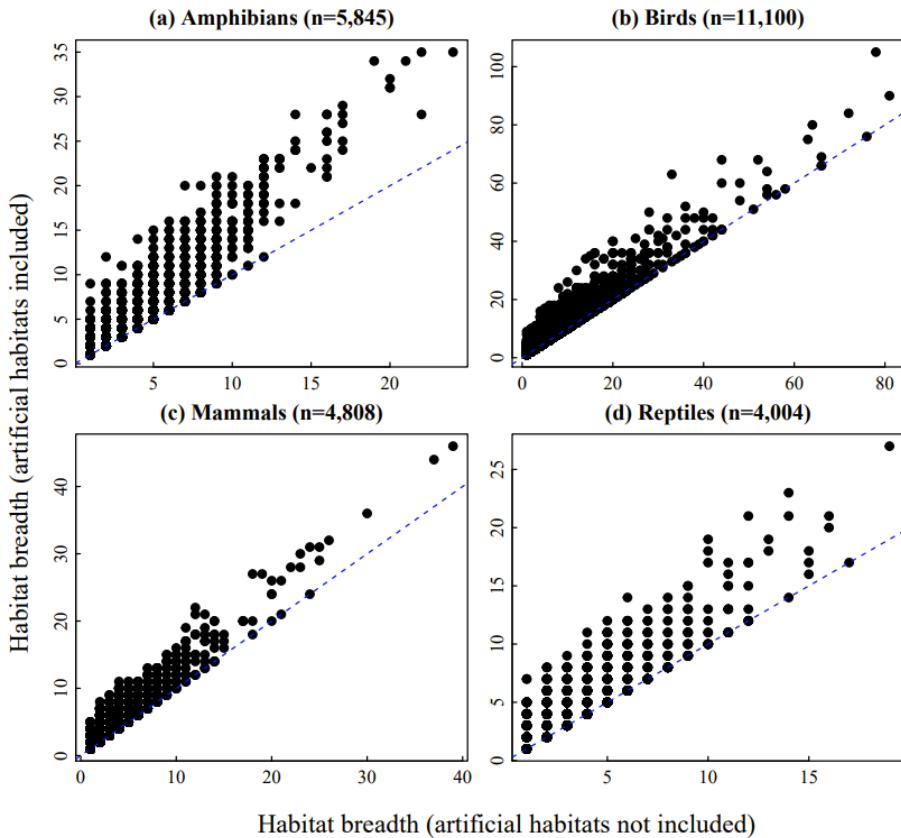


Figure 2.2: Number of natural and artificial habitats used by species against number of strictly natural habitats used by species. Pearson's correlation coefficients show a high positive correlation between these two metrics of habitat breadth in all terrestrial vertebrate classes: 0.92 for amphibians (a), 0.95 for birds (b), 0.94 for mammals (c), and 0.90 for reptiles (d).

545 Phylogenies

546 I used class-specific phylogenetic trees downloaded on 13 April 2020. For mammals, I used ‘complete’
 547 trees from Faurby et al. (2018, 2020), downloaded from <https://zenodo.org/record/3690867#.Xyc5wyhKhPZ>. For amphibians, birds and squamates, I obtained trees from <https://data.vertlife.org/>. The original sources were as follows: Jetz et al. (2012) for birds; Jetz and Pyron (2018) for amphibians; and Tonini et al. (2016) for squamates. For each class, a distribution of 1,000 trees was available.
 548
 549 For plotting purposes, I obtained consensus trees using the TreeAnnotator program of the BEAST software
 550
 551 (Bouckaert et al., 2019).

553 Species distributions

554 I obtained extent-of-occurrence distribution maps for reptiles from Roll et al. (2017), available at: <https://datadryad.org/stash/dataset/doi:10.5061/dryad.83s7k> (downloaded 13 April 2020).
 555
 556 For mammals and amphibians, species distribution maps were obtained from the IUCN Red List (IUCN

557 (2020), downloaded 13 April 2020); for birds, they were obtained from BirdLife International (<http://datazone.birdlife.org/species/requestdis>, downloaded 17 April 2020).

559 For amphibians, mammals and birds, I selected areas of extant or probably extant presence only. Addi-
560 tionally, I selected areas where species were resident or present during the breeding season, and I excluded
561 areas occupied during the non-breeding season or where species were considered vagrant.

562 In addition, for all classes, I excluded occupied areas that fell outside the known elevational limits of
563 species, where such data were available. Lower and upper elevational limits were retrieved from the IUCN
564 Red List (queried using the ‘rredlist’ package) and were available for approximately half of the species
565 (Appendix 1, S2.3: ‘Cutting distribution maps by altitudinal limits’, Figure S2.4). Decreases in range sizes
566 were observed after cutting distribution maps by the known elevational limits (Appendix 1, Figure S2.5).

567 **2.2.2 Investigating gaps and biases in trait data**

568 I used trait coverage and completeness to investigate taxonomic, phylogenetic and spatial biases in the trait
569 data. Table 2.2 summarizes the sample sizes (number of species) in each of the following analyses. Note
570 that species for which completeness was 0% were included in all analyses (for more details, see Figure 2.3).
571 Also note that I did not filter out species identified as extinct or extinct in the wild, because they represented
572 a small proportion of the datasets (0.48% for amphibians, 1.4% for both birds and mammals, and 0.50% for
573 reptiles) and also because I could not exclude such species systematically, because it is likely that I did not
574 flag them all.

Table 2.2: Number of species for each analysis. All species represented in the trait datasets were included in (1). All species from the class-specific phylogenetic trees or from the distribution maps that matched with species in the trait datasets were included in (2) and (3). *Table reproduced from Etard et al. (2020).*

	(1) Taxonomic biases	(2) Phylogenetic biases	(3) Spatial biases
Amphibians	6,990	6,170	5,650
Birds	11,634	8,315	10,802
Mammals	5,381	5,171	5,046
Reptiles	10,612	9,404	9,382

575 **Taxonomic biases**

576 I tested whether completeness varied across taxonomic class using pairwise Wilcoxon rank sum tests. I
577 tested for the extent and performance of the taxonomic corrections by looking at trait coverage when taxo-
578 nomic corrections are applied and when no correction is applied (Appendix 1, S2.4: ‘Impact of taxonomic
579 corrections on trait coverage’, Figure S2.6).

580 **Phylogenetic biases**

581 Initially, to assess whether more closely related species were more likely to be similar in trait completeness,
582 I estimated the phylogenetic signal in completeness with Pagel’s λ (Pagel, 1999) in each class. I used a boot-
583 strapping approach, calculating λ for each of 50 trees randomly sampled in each class (using the ‘phylosig’
584 function of the ‘phytools’ R package; Revell, 2012). I then estimated the mean and 95% confidence intervals
585 (95% CIs) of λ . Sample sizes for computing λ (number of species represented in both the phylogenies and
586 trait datasets) are shown in Table 2.2.

587 I then plotted within-family median completeness in phylogenetic trees built at the family level, using
588 the consensus trees. Within-family median completeness was calculated using taxonomic information in the
589 trait datasets (sample sizes shown in Table 2.2).

590 **Spatial biases**

591 I first investigated whether wider-ranging species were more likely to be better sampled than narrow-ranging
592 species. I tested for a relationship between species range size and trait completeness. I fitted a generalized
593 linear model with a Poisson error distribution (directly using the number of sampled traits, ‘N_{traits}’, rather
594 than the proportion (completeness)). Class was added as a predictor interacting with range size; thus the
595 model was:

$$596 N_{traits} \sim \log(\text{Range size}) * \text{Class.}$$

597 Second, I mapped assemblage-level median completeness. Assemblages were characterized at the pixel level
598 at 50 km² resolution. I determined pixel-level composition and richness by stacking species geographical
599 distributions. I then calculated median completeness across species in each pixel. I show the resulting maps
600 for herptiles in the main text, and for mammals and birds in Appendix 1 (Figure S2.7; median completeness
601 was very high across most pixels for mammals and birds). In addition, I provide maps of assemblage-
602 level mean completeness and standard deviation for all classes in Appendix 1 (Figures S2.8 and S2.9 show
603 corresponding maps; Figure S2.10 shows standard deviation against species richness).

I then tested for a spatial correlation between species richness and median completeness. Given that median completeness was very high across most pixels for mammals and birds, I fitted such models for herptiles only. I fitted spatial autoregressive lag models to explain assemblage-level median completeness as a function of species richness (using the function ‘lagsarlm’ of the ‘spatialreg’ package (Bivand and Piras, 2015; Bivand et al., 2013a; Bivand et al., 2013b)). Given that responses could vary geographically, I included the biogeographical realm as an interacting factor (using the World Wide Fund for Nature (WWF) ecoregion shapefile to characterise realms, obtained from <https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world>); the considered realms were Afrotropics, Australasia, Indo-Malayan, Nearctic, Neotropics and Palaearctic. To improve normality, I arc-sin square-root transformed completeness values and log-transformed species richness. The ‘lagsarlm’ function allows for a consideration of spatial autocorrelation in the dependent variable by estimating the autoregressive lag coefficient, ρ , associated with an n-by-n matrix of spatial weights, W . The final model was:

$$\text{arcsin}(\sqrt{\text{Completeness}}) \sim \log(\text{Species richness}) * \text{realm} + \rho \cdot W \cdot \text{arcsin}(\sqrt{\text{Completeness}}).$$

The value of W was estimated using the functions ‘tri2nb’ and ‘nb2listw’ of the ‘spdep’ package (Bivand and Wong, 2018; Bivand et al., 2013b). Fitting the model using all grid cells was computationally intractable; therefore, I randomly sampled cells for this analysis (using 30% of the grid cells in each realm). I selected grid cells where species richness was higher than three to avoid sampling issues. I fitted separate models for amphibians and reptiles, because when adding class as an interacting predictor, the same cells (with the same coordinates) might be sampled for multiple classes, whereas the ‘tri2nb’ function does not tolerate duplicated coordinates.

2.3 Results

2.3.1 Taxonomic biases in trait information

Trait coverage for mammals and birds was overall high (Figure 2.3a; mean and median coverage across traits: 89% and 95% for mammals; 84% and 85% for birds). In both cases, litter/clutch size was the trait with the poorest coverage (61% for mammals and 59% for birds). Coverage exceeded 80% for all other traits (except trophic level for birds, at 75% coverage).

Conversely, trait coverage was more variable for herptiles, and poorer overall (Figure 2.3a; mean and median trait coverage: 47% and 32% for amphibians, 46% and 38% for reptiles). Coverage exceeded 80% only for body size in both reptiles and amphibians and for habitat related traits in amphibians only. In all

633 other cases coverage was <55%, with very little information available for longevity-related traits.
 634 Trait completeness (proportion of non-missing trait values for a species) reflected similar biases (Figure
 635 2.3b). The distribution of trait completeness varied significantly among classes (pairwise Wilcoxon rank sum
 636 test: p-value<0.0001 in all cases). Distributions were highly left skewed in mammals and birds (skewness:
 637 -2 and -1.6). 84% of all mammalian species and 80% of avian species fell in the 80–100% completeness
 638 range. Moreover, the completeness distribution was moderately right skewed for reptiles (skewness: 0.4),
 639 and slightly right skewed for amphibians (skewness: 0.02). 56% of all reptiles and 57% of amphibians fell
 640 in the 0-50% completeness range.

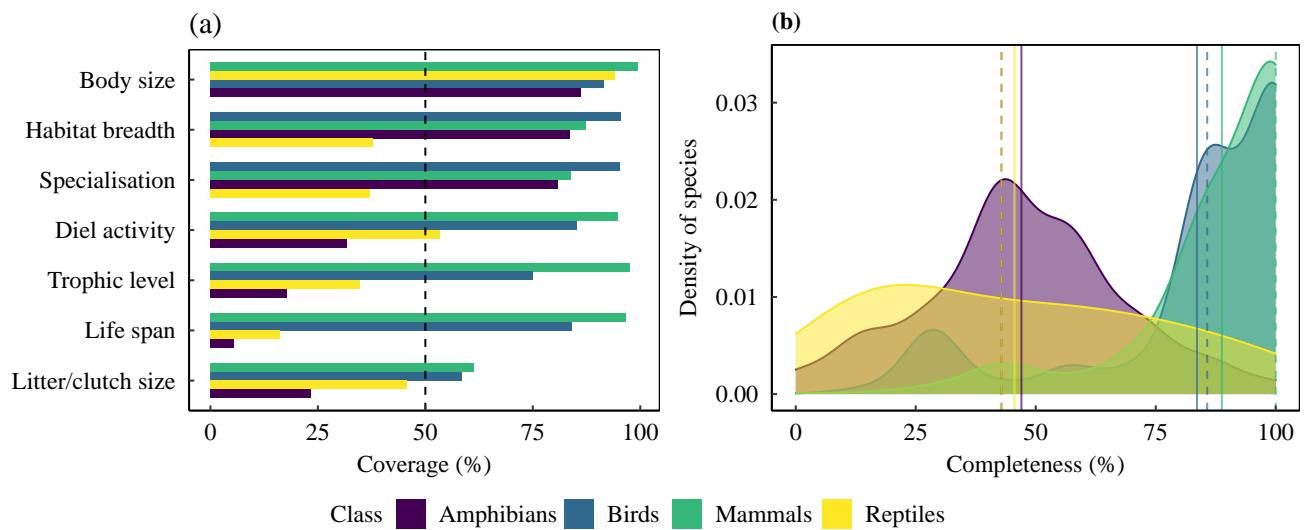


Figure 2.3: Trait coverage and completeness across species. (a) I defined coverage as the proportion of species for which an estimate is available for a given trait. The dashed line represents 50% coverage. (b) Trait completeness is the proportion of estimated traits for a species. Here, I show the distribution of completeness. Continuous lines represent the mean trait completeness for each class, whereas dashed lines represent the median trait completeness. Note that there were species with 0% completeness (230 species for amphibians – 3.3% of amphibian species in the trait dataset; 9 for birds – 0.077% of species; 7 for mammals – 0.13% of species; and 161 for reptiles – 1.5% of species). Species with 0% completeness were retained in the datasets when there was information for traits I did not select in the analyses, but no known value for the traits I did select. For instance, the body mass of the amphibian species *Rhinella centralis* was known, but other trait values (including body length) were missing, meaning that *Rhinella centralis* had 0% completeness for the set of traits I considered. *Figure reproduced from Etard et al. (2020).*

641 2.3.2 Phylogenetic biases in trait completeness

642 As expected from the distribution of trait completeness in mammals and birds (Figure 2.3), within-family
 643 median trait completeness was high across most tips of the phylogenetic trees (Appendix 1, Figures S2.11
 644 and S2.12; I present the avian and mammalian phylogenies in Appendix 1 because there was little variation
 645 in completeness across tips). For birds, λ was 0.71 (± 0.0053). For mammals, λ was 0.78 (± 0.0035). This
 646 indicated that, despite completeness generally being high across tips, the sampling was not evenly distributed
 647 across the phylogeny.

648 In herptiles, clusters of families with similar median trait completeness appeared (Figure 2.4). In am-
649 phibians, groups of families belonging to the order *Anura* (frogs) showed both the best and worst median
650 completeness (Figure 2.4a). The best-sampled families included the tailed frogs of the family *Ascaphidae*
651 (two species) and species of the family *Leiopelmatidae* (four species endemic to New Zealand). The family
652 *Ceratobatrachidae* (containing c. 90 species occurring in Southeast Asia and in some Pacific islands), the
653 family *Ranidae* (true frogs, 450 species considered here) and the family *Rhacophoridae* (shrub frogs, 382
654 species considered here) figured among the worst-sampled families. For amphibians, λ was $0.63 (\pm 0.0039)$.
655 In reptiles, most snakes were poorly sampled, whereas families in other suborders appeared to be sampled
656 better overall (Figure 2.4b). Within snakes, the pythons, boas, the three species of the family *Acrochordidae*
657 and the python-like species of the family *Loxocemidae* were better sampled than other snake families. In
658 reptiles, λ was $0.69 (\pm 0.0032)$. The sampling in herptiles was thus also uneven with regard to the phylogeny.

659 It is important to underline that Figure 2.4 shows within-family median completeness, masking the con-
660 siderable variation in species richness across families, hence masking potential important variation in com-
661 pleteness across species within families. For example, in the amphibian family *Allophrynididae* (three recog-
662 nized species), the within-family median completeness was 50%; but the dataset comprised two species of
663 completeness 14% and 86%, respectively. I present similar plots to those in Figure 2.4 showing the within-
664 family standard deviation in completeness in Appendix 1 (Figure S2.13). Within-family standard deviation
665 tended to increase with within-family species richness (Appendix 1, Figure S2.14).

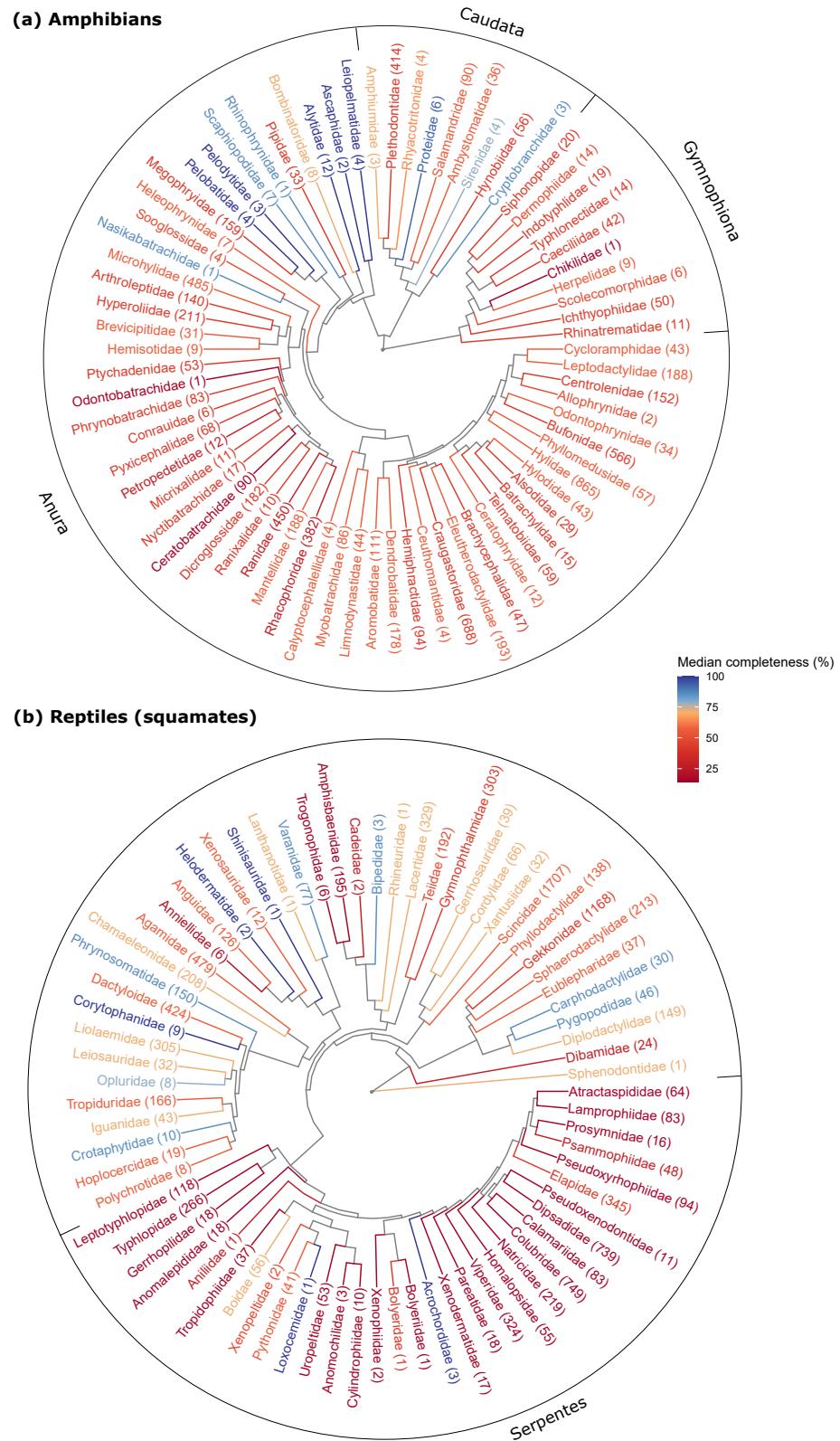


Figure 2.4: Within-family median trait completeness in herptiles. The number next to each family name represents the number of species included in the calculation of the median. *Figure reproduced from Etard et al. (2020).*

666 2.3.3 Spatial biases in trait completeness

667 Range size was significantly correlated with the number of sampled traits. Larger range sizes were associated
668 with a higher number of sampled traits (i.e., with higher completeness; Figure 2.5; Appendix 1, Table S2.1).
669 Similar results were obtained when using distribution maps not cut by elevational limits (Appendix 1, Table
670 S2.2; Figure S2.15). The rate of increase was steepest for reptiles, then for amphibians, then for birds and
671 mammals (slope estimates for birds and mammals were not significantly different from each other; Appendix
672 1, Table S2.1).

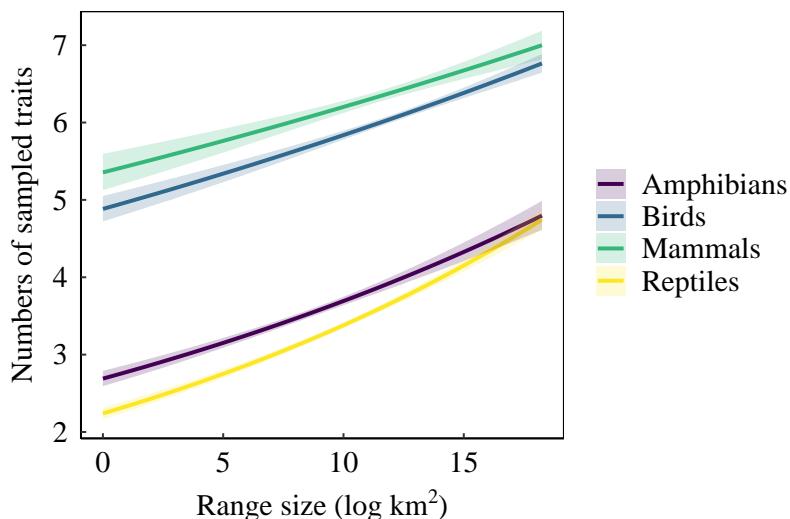
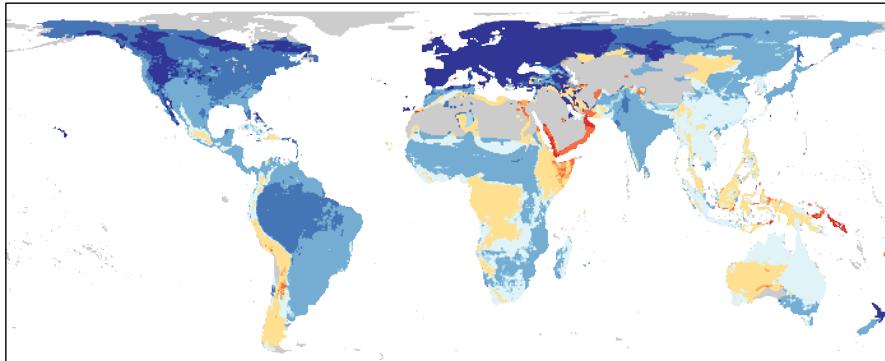


Figure 2.5: Relationship between number of sampled traits and geographical range size. The model was fitted using a Poisson error distribution. Class was added as a predictor interacting with range size. Rates of increase in number of sampled traits with range size were not significantly different for mammals and birds but differed for reptiles and amphibians, with the steepest rates of increase for reptiles. *Figure reproduced from Etard et al. (2020).*

673 There were marked spatial variations in median trait completeness in herptiles (Figure 2.6). North Amer-
674 ica and Europe were well sampled for both amphibians and reptiles. However, Southeast Asia and the Congo
675 basin were on average less well sampled. In other regions, contrasting patterns emerged between amphibians
676 and reptiles. For instance, median completeness was poorer for amphibians than for reptiles in Australia,
677 but opposite patterns were observed in South America. As in the phylogenetic analyses, assemblage-level
678 median completeness could mask potential important variation in completeness within species of a given
679 assemblage. Assemblage-level mean and standard deviation maps are shown in Appendix 1 (Figures S2.8
680 and S2.9). There was a trend for increasing standard deviation with increasing species richness, with a larger
681 spread in standard deviation at lower species richness (Appendix 1, Figure S2.10).

(a) Amphibians



Median completeness:

NA
0 – 10%
10 – 20%
20 – 30%
30 – 40%
40 – 50%
50 – 60%
60 – 70%
70 – 80%
80 – 90%
90 – 100%

(b) Reptiles

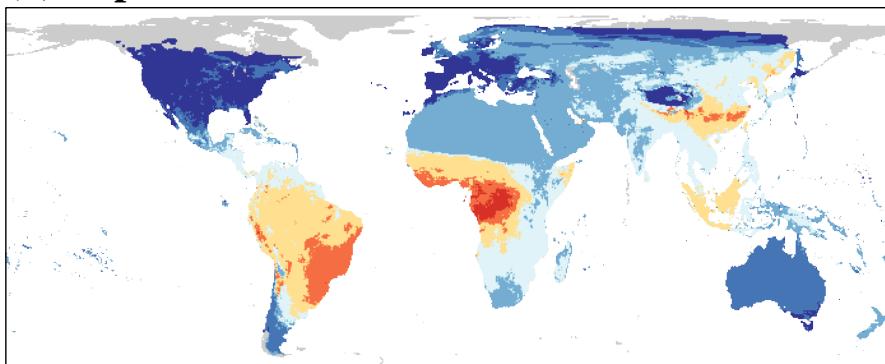


Figure 2.6: Spatial distribution of assemblage-level median trait completeness in herptiles. Similar maps for birds and mammals are shown in Appendix 1 (Figure S2.7). *Figure reproduced from Etard et al. (2020).*

682 Spatial models showed that species richness explained median trait completeness in herptiles in most
683 realms (Figure 2.7; Appendix 1, Tables S2.3 and S2.4); including spatial lags improved the models (am-
684 phibians: $\rho = 0.92$, p-value < 0.0001; reptiles: $\rho = 0.91$, p-value < 0.0001). For reptiles, completeness was
685 negatively correlated with species richness in the most species-rich realms (Afrotropics, Indo-Malayan and
686 Neotropics) and in the Palaearctic; the relationship was steepest in the Afrotropics and shallowest in the
687 Palaearctic. In the Australasian and Nearctic realms, completeness tended to increase with species richness.
688 For amphibians, negative relationships were observed in the Indo-Malay and Nearctic realms, whereas pos-
689 itive trends were observed in the Neotropics and the Palaearctic. The opposite trends between reptiles and
690 amphibians observed in the Australasian and Neotropical realms reflected patterns observed on the maps.
691 The Indo-Malayan was the only realm where median completeness tended to decrease with species richness
692 for both reptiles and amphibians.

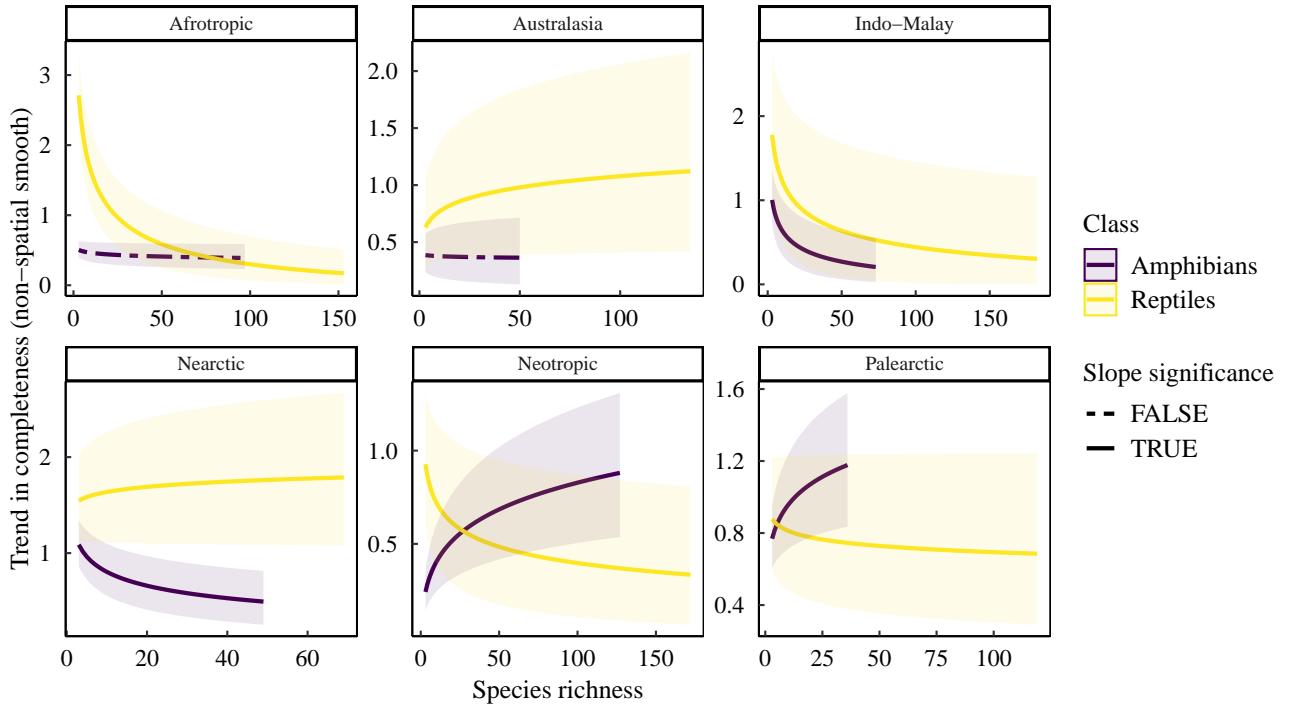


Figure 2.7: Spatial model trends for herptiles. The lines represent in-sample predictions (\pm standard error) for the trend components of the spatial models (trends after accounting for spatial autocorrelation). *Figure reproduced from Etard et al. (2020).*

693 2.4 Discussion

694 The results of this Chapter illustrate the taxonomic, spatial and phylogenetic dimensions of the knowledge
 695 gaps in trait data, termed the Raunkiær shortfall by Hortal et al. (2015). To the best of my knowledge,
 696 this work constitutes the first comparative assessment of global gaps for terrestrial vertebrate trait data,
 697 despite their use in numerous studies. I showed that the trait data present important taxonomic, spatial and
 698 phylogenetic biases, with contrasts in the availability of trait information between, on the one hand, herptiles
 699 and, on the other hand, birds and mammals.

700 Birds and mammals are globally well sampled for the set of traits I considered, even in the most species-
 701 rich assemblages. However, the availability of trait information for herptiles is lower overall and phyloge-
 702 netically and geographically biased. Several factors could interplay to shape these patterns. For instance,
 703 species that are more easily detectable (for example, wider ranging) and more charismatic are likely to be
 704 better sampled. Diverse socio-economic predictors could also contribute to geographical biases in trait data
 705 sampling; global biases in primary data collection are likely to be one of the most important contributors to
 706 the patterns I highlighted. Nevertheless, biases in the data could have been introduced at later stages, notably
 707 with the selection of sources and traits. The global compilation I obtained in this Chapter reflects, in part, the

708 interest and focus of the secondary data sources I used. It is possible that the addition of new sources from
709 regional journals or other authorities could diminish spatial biases in the data by increasing coverage for
710 certain areas. Nevertheless, I argue that by focusing on widely used traits, these results are likely to reflect
711 the “true” availability of the data in primary sources and that the shortfalls for other, less used traits would
712 be more pronounced.

713 I believe that the results presented here are robust to taxonomic uncertainty, although taxonomic match-
714 ing might potentially be improved further using class-specific sources, such as the Reptile Database or Am-
715 phibiaWeb, for identification of synonyms (but see Appendix 1, Figure S2.16). I have made two versions of
716 the data compilations available, one in which my own corrections were applied and one using the original
717 binomial names of the sources, meaning that users are free to use their own taxonomic backbones and iden-
718 tify synonyms within the compilations. I believe that taxonomic matching is a recurring issue when working
719 across thousands of species. Taxonomic synonymy artefactually inflates the numbers of identified species,
720 potentially lowering trait coverage (whereas clumping subspecies together can have the opposite effect).
721 Tackling this problem is difficult (Isaac et al., 2004; Jones et al., 2012), notably because there is no global
722 curated database recording the status of species names, and also because of the nature of taxonomy and the
723 debates around the species concept (May, 2011). Nevertheless, taxonomic uncertainty can have important
724 consequences. For instance, Cardoso et al. (2017) showed that inaccuracies and errors in species checklists
725 contributed to the overestimation of plant diversity in the Amazon (but see Freeman and Pennell (2021): the
726 relative underdescription of species in tropical areas compared to temperate areas –‘taxonomic debt’, also
727 referred to as ‘latitudinal taxonomic gradient’ by the authors– may lead to the underestimation of species
728 richness at low latitudes).

729 Biases in trait data have important implications for conservation planning. Past studies have shown that
730 narrow-ranging species, for which fewer trait data are available on average, have higher extinction risks
731 (Collen et al., 2016; Purvis et al., 2000; Ripple et al., 2017) and are more negatively impacted by anthro-
732 pogenic pressures than wider-ranging species (Newbold et al., 2018). Trait information is also less available
733 for herptiles in tropical regions such as the Congo basin, Southeast Asia and South America, which are some
734 of the most diverse areas of crucial importance for worldwide conservation (Barlow et al., 2018). Conse-
735 quently, trait information is on average less available where potentially more crucial to conservation plan-
736 ning. Indeed, trait information can be incorporated into vulnerability assessments and, as such, can help to
737 prioritize conservation efforts. Species traits have been found to mediate species responses to environmental
738 changes across diverse taxonomic groups, and thus can inform on the sensitivity of species to anthropogenic
739 pressures (Flynn et al., 2009; Newbold et al., 2013; Nowakowski et al., 2017). Traits are now commonly

740 used to estimate species vulnerability or extinction risks (Pacifici et al., 2015; Ramírez-Bautista et al., 2020).
741 As opposed to trend-based approaches, which rely on historical population trends (changes in abundance
742 or shifts in distributions) to predict species' vulnerability and extinction risks, trait-based approaches rely
743 on species' intrinsic sensitivity to particular threats. The appeal of trait-based approaches to extinction risk
744 estimation is that, by providing mechanistic insights, they diminish the amount of population information
745 needed. If the responses of species to a threat consistently relate to certain traits, it is possible to generalize
746 patterns across species for which population data are less available (Verberk et al., 2013). Integrating traits
747 into vulnerability assessments is hence of particular interest when field monitoring of species population
748 sizes or distributions is difficult to achieve, but biases in the data could mean that such information is lacking
749 for some of the most vulnerable species.

750 Traits that influence species responses to environmental changes have been termed 'response traits' (or
751 'response-mediating traits'; Luck et al. (2012)), as opposed to 'effect traits' that underpin ecosystem func-
752 tioning (Lavorel and Garnier, 2002). For instance, relative brain size and longevity have been characterized
753 as response traits in birds (Newbold et al., 2013; Sayol et al., 2020), whereas dietary characteristics (e.g.,
754 trophic levels or guilds) are both response and effect traits. Hortal et al. (2015) highlighted that, for plants,
755 both response and effect traits have been investigated, whereas for vertebrates the research has been more
756 focused on understanding species responses. This could be because the way vertebrate traits interact to shape
757 some ecosystem processes has not yet been characterized well.

758 Ecosystem processes sustained by animals might be harder to quantify and might be influenced by a com-
759 bination of traits. The traits compiled in this work are likely to have a role in diverse processes. Nevertheless,
760 there was one important omission, in that I did not compile species diet in this Chapter, potentially the most
761 straightforward trait to link with diverse processes, such as grazing, pollination, scavenging and seed dis-
762 persal. From a practical perspective, I chose traits that had been estimated at least for some of the species
763 in each class, and that were readily available. Diet was excluded because although estimates were available
764 for amphibians, birds and mammals, there was no readily available database for reptilian diet. Movement or
765 dispersal abilities were also excluded because information was not readily available for any class. Although
766 I expect that species diet and dispersal abilities would present similar sampling biases to the ones presented
767 in this work, the addition of such traits to the compilation would represent a valuable contribution and would
768 notably facilitate studies looking at the functional roles of reptiles.

769 For practical reasons, I did not consider intraspecific trait variation. Intraspecific variation has been
770 shown to have important effects on ecological systems, and a growing body of literature encourages trait-
771 based research to include intraspecific variability (Guralnick et al., 2016). There have been several calls to

772 produce open-access, global trait datasets (Weiss and Ray, 2019), including a representation of intraspecific
773 trait variation (Kissling et al., 2018). Notably, Schneider et al. (2019) designed a framework to store and
774 share inter- and intraspecific trait data, accompanied by an R package to standardize the data in a proposed
775 format. Such a proposition could constitute an important step towards the unification of individual datasets
776 into a single, comprehensive database for ecological trait data.

777 The current spatial and taxonomic gaps in trait data might limit our ability to scale studies up, whereas
778 biases in the data can affect the validity of extrapolations to groups or areas that are undersampled. More gen-
779 erally, biases and gaps in biodiversity data can have important implications for ecological studies. Data gaps
780 can hinder our ability to draw conclusions on observed macroecological patterns. For example, Chaudhary
781 et al. (2016) proposed that marine species richness follows a bimodal distribution, peaking at mid-latitudinal
782 locations, and argued that these patterns were not underpinned by knowledge gaps in species distributions.
783 However, Menegotto and Rangel (2018) attributed the tropical dip in marine species richness to a lack of
784 species distribution data, explained by lower sampling efforts in tropical areas ('Wallacean' shortfall; Hor-
785 tal et al. (2015)). Biases and gaps in trait data could also affect studies in closely related fields, such as
786 functional ecology – for instance, past studies have shown that functional diversity indices are sensitive to
787 missing data (Májeková et al., 2016; Pakeman, 2014) – or community assembly (Perronne et al., 2017).

788 Ecologists should, therefore, take particular care when designing trait-based studies, because both data
789 quality and data gaps are likely to influence the results and the generality of the conclusions. There exist
790 diverse methods to deal with missing trait values, should data missingness be problematic. Complete removal
791 of missing values ('case deletion') is commonly used but presents several issues, because it reduces sample
792 size and statistical power and introduces potential bias in data subsamples (Nakagawa and Freckleton, 2008).
793 For example, retaining complete cases only from the trait datasets would generate trait data disproportionately
794 representative of mammals and birds, which would be problematic for conducting cross-taxon analyses in
795 terrestrial vertebrates. As such, it is recommended that case deletion be applied only when data are missing
796 completely at random, which is rarely the case (Peugh and Enders, 2004).

797 Alternatives to case deletion consist of filling in the gaps. In recent years, the development of imputation
798 techniques has provided robust methods to handle missing data. Such imputation techniques have been used
799 to complete trait datasets in recent studies (Cooke et al., 2019a). Penone et al. (2014) used a simulation ap-
800 proach to evaluate the performance of four of these techniques, namely PhyloPars (Bruggeman et al., 2009),
801 random forest algorithms as implemented in R with missForest (Stekhoven, 2016; Stekhoven and Bühlmann,
802 2012), multivariate imputation by chained equations (MICE; van Buuren and Groothuis-Oudshoorn (2007))
803 and k-nearest neighbour (kNN; Troyanskaya et al. (2001)). Penone et al. (2014) introduced missing values

804 (10%–80%) in a complete trait dataset of carnivorans and measured imputation performance in different
805 scenarios. Given that phylogenetic non-randomness in missing trait values can impact imputation accuracy,
806 Penone et al. (2014) removed values in three different ways (completely at random; with a phylogenetic
807 bias; and with a body mass bias). Out of the four techniques, missForest and PhyloPars performed best when
808 species phylogenetic position was included as a predictor of missing trait values. Such imputations appeared
809 to be robust even when trait coverage was as low as 40%, which might be relevant for many reptilian and
810 amphibian traits. The performance was not significantly affected by phylogenetic non-randomness of the
811 data. Hence, missForest and PhyloPars appear to be well suited when traits are phylogenetically conserved,
812 because they allow species phylogenetic position to be included as a predictor of missing trait values. The
813 study by Penone et al. (2014) highlights that there are robust imputation techniques allowing to deal with
814 incomplete trait data where biases might otherwise be problematic. Nevertheless, it is important to highlight
815 that some imputation techniques, such as single or mean imputation, can be problematic because they do
816 not allow an estimation of uncertainty and suffer from a lack of accuracy (Nakagawa and Freckleton, 2008);
817 indeed, imputation techniques sometimes perform no better than case deletion. More work should be con-
818 ducted to assess imputation performance in various contexts (e.g., Johnson et al. (2021)), and the datasets
819 compiled in this Chapter might provide an opportunity for such studies.

820 Although robust imputation techniques can be useful for filling gaps in trait datasets, they are no substi-
821 tute for continued data collection efforts. The results of this Chapter show that data are particularly lacking
822 in herptiles, notably in the Afrotropics, the Neotropics and the Indo-Malayan realms. For these areas, incor-
823 porating regional databases into existing datasets could contribute to the reduction of global gaps. I believe
824 that both primary research and subsequent efforts to integrate new data and existing databases are required
825 if we are to collectively strive towards the unification of trait databases.

826 To conclude, this work constitutes, to my knowledge, the first assessment of the global gaps and biases
827 in terrestrial vertebrate trait information. I show that herptiles are undersampled compared with mammals
828 and birds, with important spatial and phylogenetic variability in the availability of trait information. Impu-
829 tation techniques are one possible solution to these problems. Nevertheless, I believe that primary research,
830 combined with efforts to complete existing datasets, is the only way to fill the current data gaps genuinely
831 and robustly. I hope that the compiled trait dataset and these findings can prove useful for guiding further
832 data collection efforts and for conducting macroecological analyses.

833 **3 | Intensive human land uses negatively af-**

834 **fect vertebrate functional diversity**

835 **Keywords**

836 Land use; land-use intensity; terrestrial vertebrates; functional diversity; traits.

837 **Abstract**

838 Land-use change is the leading driver of global biodiversity loss, thus characterising its impacts on the func-

839 tional structure of ecological communities is an urgent challenge. Using a database describing vertebrate

840 assemblages in different land uses, I assess how the type and intensity of land use affect the functional di-

841 versity of vertebrates globally. I find that human land uses alter local functional structure by driving declines

842 in functional diversity, with the strongest effects in the most disturbed land uses (intensely used urban sites,

843 cropland and pastures), and among amphibians and birds. Both tropical and temperate areas experience im-

844 portant functional losses, which are only partially offset by functional gains. Tropical assemblages are more

845 likely to show decreases in functional diversity that exceed those expected from species loss alone. These re-

846 sults indicate that land-use change non-randomly reshapes the functional structure of vertebrate assemblages,

847 raising concerns about the continuation of ecological processes sustained by vertebrates.

848 **3.1 Introduction**

849 Anthropogenic activities are profoundly transforming global biodiversity. Although multiple pressures act

850 in combination, land-use change currently poses the greatest threat to biodiversity (Maxwell et al., 2016;

851 Newbold et al., 2015). However, not all species respond similarly to land-use change. Traits have been found

852 to explain species' sensitivity to land-use change in diverse groups (Newbold et al., 2013; Nowakowski et

al., 2017; Quesnelle et al., 2014; Todd et al., 2017). Previous work has also shown that land-use change leads to non-random modification of assemblage trait composition (or functional diversity) (Chapman et al., 2018; Colin et al., 2018; Flynn et al., 2009; La Sorte et al., 2018; Newbold et al., 2013; Tinoco et al., 2018). Since it is widely acknowledged that biodiversity, and in particular trait diversity, may promote ecosystem functioning and stability, modification to the trait composition of assemblages could have far-reaching and adverse impacts on ecological processes (Hooper et al., 2012; Magioli et al., 2021; Oliver et al., 2015; Tilman and Downing, 1994).

Terrestrial vertebrates support many processes, ranging from pollination (Ratto et al., 2018), to seed dispersal to the regulation of lower trophic levels (Letnic et al., 2012; Mooney et al., 2010; Salo et al., 2010; Zhang et al., 2018a). However, we lack a global understanding of how the functional diversity of entire vertebrate assemblages responds to changes in land use. Most previous studies have been conducted at regional or local scales (Davison et al., 2021), but these may not be representative of global patterns. Indeed, recent global syntheses have highlighted how biodiversity responses can differ substantially between regions and across latitudes, with higher sensitivity reported for the tropics (Matuoka et al., 2020; Millard et al., 2021; Newbold et al., 2020b). Another key issue is the taxonomic coverage of past work. Few studies investigating effects of land use on functional diversity have considered several vertebrate classes together, and comparative studies remain rare. Thus, how land-use change affects the functional diversity of local vertebrate assemblages at global scales, and the potential geographical and taxonomic variation in the effects, still largely remains to be explored.

Here, I aim to assess how human land use and land-use intensity affect the functional diversity of vertebrate assemblages, across and within taxonomic classes. Building on recent work (Matuoka et al., 2020; Millard et al., 2021; Newbold et al., 2020b), I investigate differences in response between tropical and temperate regions. I use multiple response metrics to quantify functional diversity. First, functional richness measures the breadth and variety of trait combinations represented in an assemblage (Legras et al., 2018). Second, functional dispersion quantifies how similar species in a given assemblage are in terms of their traits (Laliberté and Legendre, 2010). These metrics can mask important alterations of assemblage composition if functional losses are compensated for by functional gains. To address this, I consider pairwise measures between assemblages, to explore levels of functional loss and functional gain across land uses (Figure 3.1).

To this end, I combine (1) the trait data across terrestrial vertebrates collected in Chapter 2 with (2) global records of species occurrence in eight land-use types of differing intensity of use (the PREDICTS database: Hudson et al. (2014, 2017); Figure 3.1; Appendix 2, Table S3.1). The PREDICTS database is currently the most comprehensive database of sampled species occurrence, and for most records also

885 abundance, across multiple land uses of different land-use intensity. Using the PREDICTS database allows
886 me to contrast biodiversity metrics among intact land uses (primary-vegetation sites, considered to be the
887 undisturbed reference condition), and all other human land-use types. Specifically, I test the following
888 hypotheses, both across and within taxonomic classes:

- 889 1. I expect decreases in functional diversity in human land uses compared to primary vegetation, caused
890 by contractions of occupied trait space. I expect such effects to be more pronounced where land is
891 used more intensively by humans. This hypothesis builds upon evidence that species with certain
892 traits are more sensitive to land-use disturbance (Newbold et al., 2013), meaning that disturbed land
893 uses will retain only disturbance-tolerant species, more functionally similar to one another. Given the
894 reported higher sensitivity of tropical assemblages to land-use disturbance, I predict that such effects
895 are stronger in the tropics.
- 896 2. I hypothesise that decreases in functional diversity in disturbed land uses exceed decreases expected
897 by chance, given local species loss. Thus, I expect disturbed land uses to promote functional under-
898 dispersion. Functional under-dispersion occurs when species within an assemblage are more similar,
899 in term of their traits, than expected by chance (Cadotte and Tucker, 2017; Wong et al., 2018) – or,
900 in other words, when functional dispersion is lower than expected given local species richness. I
901 predict that under-dispersion is more likely to occur in the highly disturbed sites, in both temperate
902 and tropical areas. This hypothesis is based on the idea that species are being removed non-randomly
903 from sensitive areas of the trait space, and increasingly so with higher disturbance level.
- 904 3. Finally, I expect decreases in functional diversity in human land uses to be driven by high functional
905 loss, whereby species are being removed from previously occupied areas of the trait space; I expect
906 no functional gain. This hypothesis is based on the idea that the functional trait space in undisturbed
907 land uses represents all of the possible regional trait combinations and that species with functional
908 attributes rendering them unable to persist in altered conditions will be filtered out (Cornwell et al.,
909 2006).

910 **3.2 Methods**

911 **3.2.1 Vertebrate assemblages**

912 I used vertebrate occurrence data from the PREDICTS database (Hudson et al., 2014, 2017), a collection of
913 studies that recorded species occurrence across multiple land uses and land-use intensities. In PREDICTS,

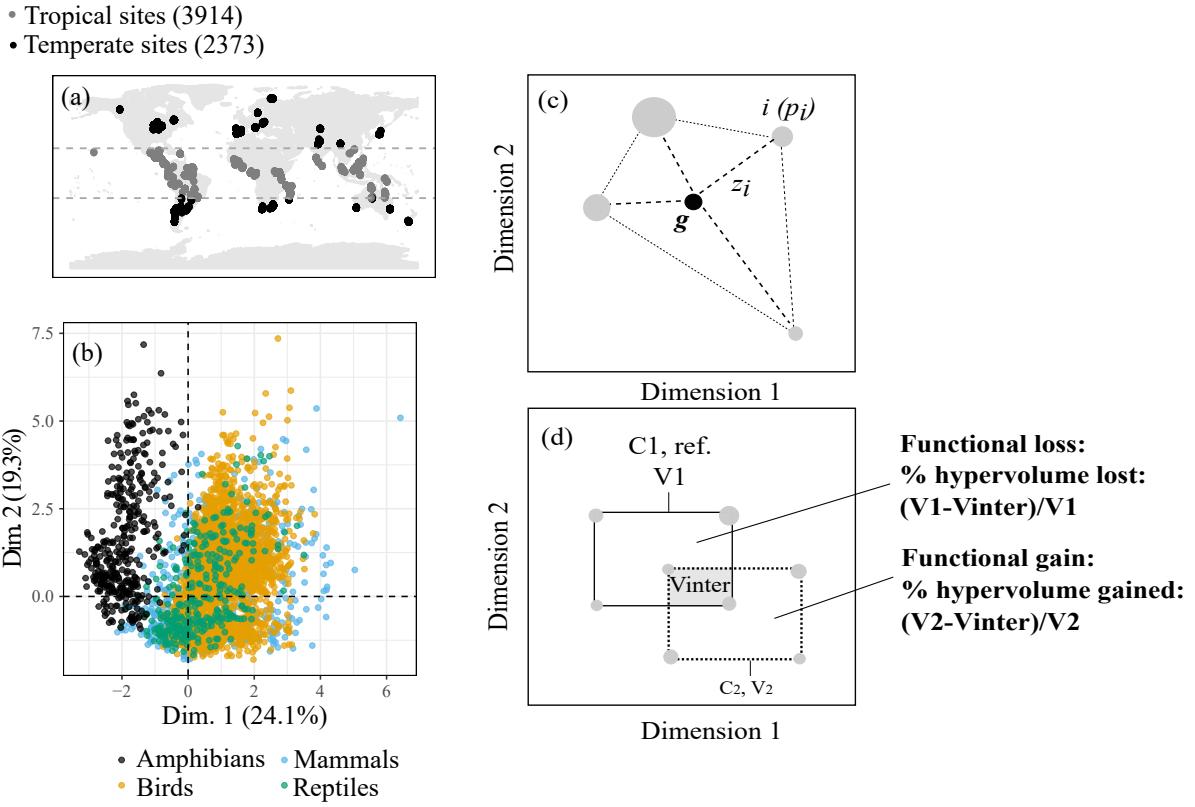


Figure 3.1: Overview of the study design and functional diversity metrics. I used occurrence data for vertebrate species from the PREDICTS database ((Hudson et al., 2014, 2017); 180 studies; 431,170 records; 4,339 species; 6,758 sampled sites). (a) shows the spatial distribution of sites I consider. I combine occurrence data with trait data compiled in Chapter 2 to calculate functional diversity metrics. (b) is a representation of the trait data in two dimensions, plotted across PREDICTS vertebrates. Traits that contributed most to dimension 1 were lifespan (29%) and litter/clutch size (22%), while traits that contributed most to dimension 2 were habitat breadth (47%) and use of artificial habitats (35%). (c) and (d) present the conceptual framework for the calculation of the functional diversity metrics: local measures (c) and pairwise metrics (d). (c) Given a trait space, functional richness is calculated as the hypervolume occupied by the minimum convex hull encompassing all species (Villéger et al., 2008). Functional dispersion is calculated as the mean distance of the species to the centroid, g (Laliberté and Legendre, 2010). (d) I compute functional loss as the proportion of hypervolume lost from the reference assemblage, and I define functional gain as the proportion of hypervolume of the disturbed assemblage that was gained (proportion of novel trait space in the disturbed assemblage). *Figure reproduced from Etard et al. (2022).*

914 each study contains several sites, which may be clustered into spatial blocks. Assemblage and land-use
915 data are available at the site level: one site is characterised by a unique land use of given land-use intensity
916 and provides occurrence data for a set of sampled taxa (and the same set of taxa is sought at all other sites
917 within a study). Sites located between 23.5°N and 23.5°S of latitude were considered tropical, and otherwise
918 temperate (Figure 3.1).

919 Land uses in PREDICTS were assigned to the following categories, based on the descriptions of the
920 habitat given by the original collectors of the data: primary vegetation (considered to be the undisturbed ref-
921 erence); secondary vegetation; plantation forest; pasture; cropland; urban (considered human, or disturbed;
922 Appendix 2, Table S3.1; Hudson et al., 2014, 2017). Secondary vegetation is further divided into three cat-

923 egories: mature, intermediate and young, depending on the stage of recovery of the vegetation. Land-use
924 intensity is reported as minimal, light or intense, according to criteria that depended on the land-use type in
925 question (e.g., crop diversity, degree of mechanisation and chemical inputs in cropland, or bushmeat harvest-
926 ing and selective logging in primary vegetation; Hudson et al., 2014). I excluded sites for which the land use
927 could not be characterised or for which the stage of recovery of secondary vegetation was unclear. As the
928 PREDICTS database is a collection of independent studies, the design of this study was not balanced: the
929 sample size varied across land uses (Appendix 2, Figures S3.1 & S3.2), and across taxonomic groups (3,103
930 species of birds; 531 mammals; 379 amphibians; 326 reptiles).

931 **3.2.2 Functional traits and diversity metrics**

932 Trait choice is a critical step when calculating functional diversity metrics, which are highly sensitive to
933 trait selection (Mouillot et al., 2021). However, trait selection trades off with data availability. Here, a
934 constraint was to use similar traits across the different classes. Thus, I used the seven traits compiled in
935 Chapter 2 across terrestrial vertebrates. Most of these traits were available for at least 50% of the species
936 in each class (except trophic level in amphibians and lifespan in herptiles; Appendix 2, Figure S3.4). In
937 addition, I chose traits that were ecologically relevant, broadening the biological definition of traits (i.e.,
938 a characteristic measurable at the level of an individual) to include measures of habitat breadth and habitat
939 specialisation (still theoretically measurable at the level of an individual). The final set constituted seven traits
940 that influence species' responses to environmental change: body mass, trophic level, lifespan, litter/clutch
941 size, diel activity, habitat breadth and use of artificial habitats. These traits related to life-history, habitat
942 specialisation and use of geographical space (e.g., habitat breadth significantly explains geographical range
943 size in all classes; Appendix 2, Figure S3.3). Here, I did not consider estimations of dispersal abilities or
944 home range size as these were available for a small fraction of the species (<3%, Paradis et al., 1998; Smith
945 and Green, 2005; Sutherland et al., 2000; Whitmee and Orme, 2013), neither did I include geographical
946 range size which is measured across many individuals, and hence cannot be considered a trait. As in Chapter
947 2, I did not consider intraspecific trait variation, thus assuming no effect of the environment on trait values.

948 Trait coverage was variable among classes and traits, with important gaps for reptiles and amphibians
949 (Appendix 2, Figures S3.4 & S3.5; Chapter 2). I imputed missing trait values using random forest algorithms
950 ('missForest' package: Stekhoven and Bühlmann (2012), Stekhoven (2016)), including traits, taxonomic
951 order and phylogenetic eigenvectors as predictors (Debastiani et al., 2021; Penone et al., 2014). To further
952 assess the sensitivity of the results to imputation (see next section), I imputed missing trait values eight times,
953 thereby obtaining eight sets of imputed traits. I randomly selected one imputed trait set for the calculation of

functional metrics. Imputations of missing trait values & imputation performance are detailed in Appendix 2, S3.2: ‘Trait data & imputation of missing trait values’ and S3.4: ‘Imputation performance’ (and Figures S3.6-S3.8). Post-imputation, continuous traits were \log_{10} -transformed (except habitat breadth which was square-rooted) and z-scored (standardised to unit variance and zero mean). In addition, I assessed whether the results were robust to imputation error using a subset of the PREDICTS data considering only species for which I had complete trait information (see next section).

Correlation among traits can be a safeguard against high sensitivity of functional metrics to trait omission, notably where omitted traits correlate strongly with traits that are already included in the calculation (Mouillot et al., 2021). Nevertheless, high multicollinearity among traits has been reported as potentially problematic for the calculation of functional diversity (Cadotte et al., 2011). Thus, I verified that the degree of multicollinearity among traits was not problematically high (with a threshold of 5 for variance inflation factors, Appendix 2, Table S3.3). Furthermore, I tested the sensitivity of the results to trait omission, by investigating whether adding geographical range size in the calculation of functional metrics was likely to affect the results.

3.2.3 Effects of land use and land-use intensity on FRic and FDis (Hypothesis 1)

For each assemblage, I measured functional richness using ‘FRic’ (Villéger et al., 2008), and functional dispersion using ‘FDis’ (Laliberté and Legendre (2010); Figure 3.1), from the ‘FD’ package (Laliberté and Legendre (2010); Laliberté et al. (2014)). I assessed the effects of land use, land-use intensity, and region (temperate versus tropical) on FRic and FDis across and within taxonomic classes using linear mixed-effects models (‘lme4’ package, Bates et al. (2015)). Land use and land-use intensity were not ranked in the models. A random intercept of study identity accounted for variation in experimental design across studies, while a random intercept representing spatial blocks of sampled sites, nested within study, accounted for spatial structuring within studies. To improve normality and bound predictions between 0 and 1, I transformed FRic and FDis using an arcsin-square-root transformation. The best-fitting model was sought using backwards stepwise model selection, starting with the most complex model that included all two-way interactions among the specified main effects. Model fits were compared using likelihood-ratio tests at each iteration of the selection procedure.

Across vertebrates, the starting models included the effects of land use, land-use intensity and region (temperate versus tropical). The best-fitting model for FRic was:

983 $\text{arcsin}(\sqrt{\text{FRic}}) \sim \text{Land use} + \text{Land-use intensity} + \text{Region} + \text{Land use : Land-use intensity} + \text{Land use : Region}$.

985 (Model 1a)

986 For FDis, the best-fitting model did not include interactions between land use and region, but the main
987 effect of region was retained:

988 $\text{arcsin}(\sqrt{\text{FDis}}) \sim \text{Land use} + \text{Land-use intensity} + \text{Region} + \text{Land use : Land-use intensity}$.

989 (Model 1b)

990 To investigate differences in responses across classes, I pooled some of the land uses together, because
991 otherwise, sample sizes would have been too low. Mature, intermediate and young secondary vegetation were
992 grouped together as ‘Secondary vegetation’, and cropland and pasture were grouped together as ‘Agricultural
993 land uses’. The starting models included the effects of land use, land-use intensity, region and taxonomic
994 class. For FRic, the best model was:

995 $\text{arcsin}(\sqrt{\text{FRic}}) \sim \text{Land use} + \text{Land-use intensity} + \text{Region} + \text{Class} + \text{Land use : Land-use intensity} + \text{Land use : Class} + \text{Land-use intensity : Region} + \text{Class : Region}$.

997 (Model 2a)

998 For FDis, regional effects were dropped:

999 $\text{arcsin}(\sqrt{\text{FDis}}) \sim \text{Land use} + \text{Land-use intensity} + \text{Class} + \text{Land use : Land-use intensity} + \text{Land use : Class} + \text{Land-use intensity : Class}$.

1001 (Model 2b)

1002 To assess whether the results were robust to imputation error, I used a subset of the PREDICTS data
1003 considering only species for which there were complete trait information (6,212 sites; 442 mammals; 1,975
1004 birds; 78 reptiles; 9 amphibians), and I fitted models again to this data subset. I did not have enough complete
1005 trait data among amphibians to be able to consider this class separately, so I first considered amphibians and
1006 reptiles together (herptiles), and reptiles only. In addition, I complemented this validation with a sensitivity
1007 analysis to variation in imputed values. I calculated FDis and FRic using each of the eight imputed trait
1008 datasets and fitted the previous models to each set. I then qualitatively evaluated the congruence of the
1009 estimates from the different models. Finally, because there tended to be more sites sampled in primary
1010 vegetation than in other land uses (Appendix 2, Figures S3.1 & S3.1), I ran additional sensitivity tests to
1011 assess whether the results were robust to resampling primary vegetation sites to a number equal to 50 (a
1012 sample size close to the median number of sites sampled in land uses other than primary vegetation in both
1013 regions (median = 37 for the temperate subset and 57 for the tropical subset, Appendix 2, Figure S3.1)).

1014 **3.2.4 Investigating functional under-dispersion (Hypothesis 2)**

1015 To assess whether effects of land use and land-use intensity on FDis differed from what would be expected
1016 by chance given changes in local species richness, I generated null expectations of FDis at each site. I
1017 randomised assemblage composition 500 times, drawing species from the corresponding study's species
1018 pool while maintaining local species richness. For each site, I thus obtained a null distribution for FDis.
1019 Then, I tested whether FDis differed from null expectations using Wilcoxon signed-rank tests. I created
1020 a binary variable which was assigned 1 if FDis was significantly lower than null expectations at a given
1021 site (significant under-dispersion), and 0 otherwise. I investigated how land use, land-use intensity, region
1022 and taxonomic class affected the probability of occurrence of under-dispersion using a generalised linear
1023 mixed-effects model with a binomial distribution of errors. The best-fitting model did not retain any effect
1024 of taxonomic class:

1025 $P_{\text{under-dispersion}} \sim \text{Land use} + \text{Land-use intensity} + \text{Region} + \text{Land use : Land-use intensity} + \text{Land use :}$
1026 Region.

1027 (Model 3)

1028 **3.2.5 Functional loss and functional gain (Hypothesis 3)**

1029 I calculated the proportion of trait space that was lost in disturbed land uses compared to reference land uses
1030 (functional loss) and the proportion of trait space that was gained in disturbed land uses (functional gain)
1031 (Figure 3.1c), across and within taxonomic classes. I selected studies where at least one site was sampled in
1032 primary vegetation. I then made within study pairwise comparisons between reference assemblages, sampled
1033 in primary vegetation, and disturbed assemblages. In addition, I considered all comparisons between pairs
1034 of primary-vegetation sites, to create reference pairs. I then investigated how land use, land-use intensity
1035 and region affected functional loss and gain across and within taxonomic classes using linear mixed-effects
1036 models, controlling for study identity in the random effects. Across vertebrates, the best-fitting model for
1037 functional loss was:

1038 $\text{arcsin}(\sqrt{\text{loss}}) \sim \text{Land use} + \text{Land-use intensity} + \text{Region} + \text{Land use : Land-use intensity} + \text{Land use :}$
1039 Region.

1040 (Model 4a)

1041 For functional gain, one interaction term (land use with region) was dropped:

1042 $\text{arcsin}(\sqrt{\text{gain}}) \sim \text{Land use} + \text{Land-use intensity} + \text{Region} + \text{Land use : Land-use intensity}.$

1043 (Model 4b)

1044 When considering the effects of taxonomic class, the best-fitting model for functional loss was:

1045 $\text{arcsin}(\sqrt{\text{loss}}) \sim \text{Land use} + \text{Land-use intensity} + \text{Class} + \text{Region} + \text{Land use :}$

1046 $\text{Land-use intensity} + \text{Land use : Class} + \text{Land use : Region} + \text{Land-use intensity : Class}.$

1047 (Model 5a)

1048 For functional gain (Model 5b), the fitted effects were the same as those of Model 2b. More details about
1049 the calculation of functional loss and gain can be found in Appendix S3.5.

1050 All data analyses were conducted using R version 3.5.1 (R Core Team, 2018). I made the code available
1051 on figshare (DOIs: <https://doi.org/10.6084/m9.figshare.14161883> and <https://doi.org/10.6084/m9.figshare.15163926>), as well as the main result datasets (<https://doi.org/10.6084/m9.figshare.15163971>).

1054 3.3 Results

1055 3.3.1 Effects of land use on FRic and FDis

1056 Across all vertebrates, land use and land-use intensity significantly affected FRic and FDis (Figure 3.2).
1057 FRic tended to decrease with increasing disturbance level and higher intensity of land use. For FRic, relative
1058 effects differed between regions (Figure 3.2a). Although declines were overall more important for disturbed
1059 tropical assemblages, significant declines were observed for the temperate assemblages (e.g., a 37% average
1060 decline in intensely used urban areas; a 49% decline in pastoral areas of high land-use intensity). Never-
1061 theless, tropical assemblages typically showed more important reductions in FRic. For instance, declines
1062 averaged 63% for intensely used tropical cropland and 76% for urban areas. For FDis, relative effects were
1063 similar in both regions (Figure 3.2b). The most important average declines were observed for urban assem-
1064 blages of intense use (20% decline), and for lightly- and intensely used cropland (by 15% and 26%). Note
1065 that confidence intervals around the estimated average declines were large in some cases, highlighting some
1066 heterogeneity in the responses.

1067 Fitting the same models to the subset of species with complete trait data, I detected important declines in
1068 functional diversity in a number of land uses, showing that the conclusions are robust to trait imputation un-
1069 certainty (for example, FRic declined on average by 75% in intensely used temperate pastoral assemblages;
1070 by 48% for intensely used tropical cropland; and FDis declined by an average 37% in intensely used tropical

Use intensity • Minimal use ▲ Light use * Intense use

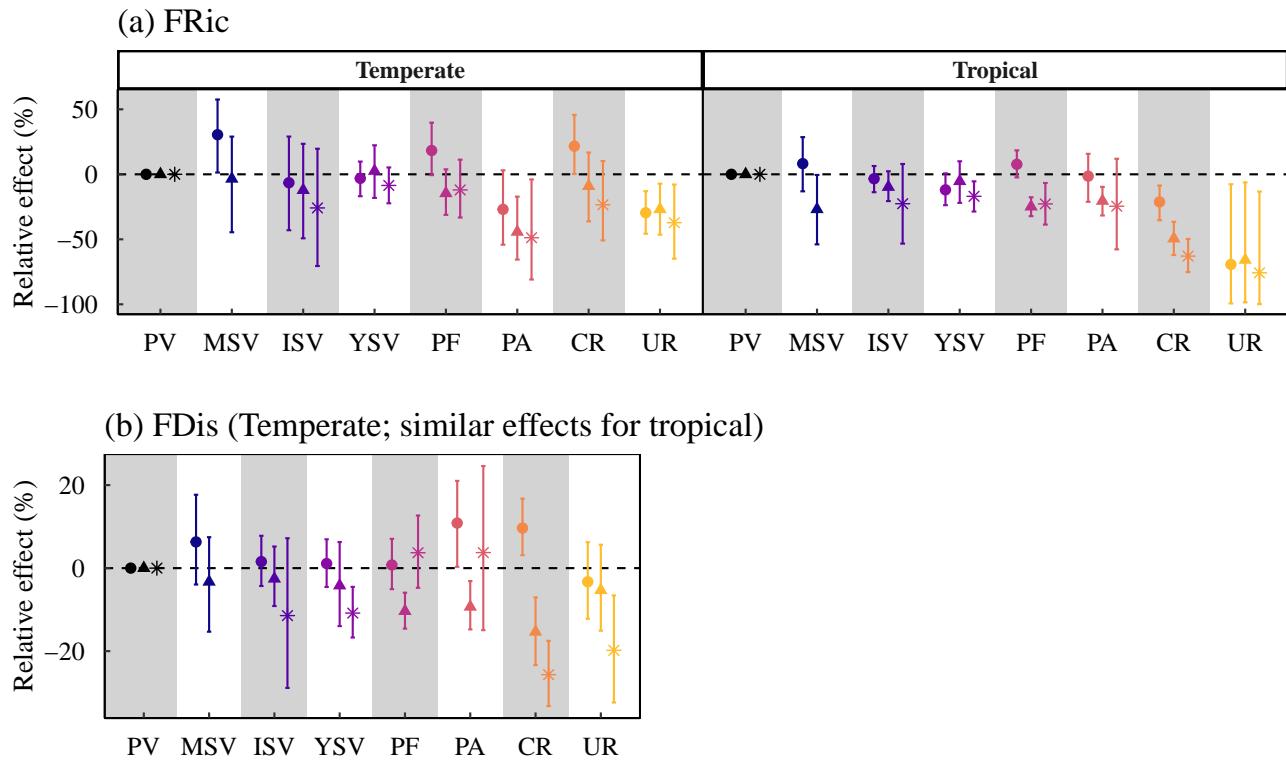


Figure 3.2: Effects of land use, land-use intensity and region on FRic (a) and on FDis (b) across all PREDICTS vertebrates. Effects were rescaled with reference to primary vegetation (PV) and are plotted as a % difference relative to PV within each land-use intensity. For FRic, the best-fitting model included interactions between land use and region, while these interactions were dropped for FDis, explaining the similar relative effects in both regions. Error bars represent 95% confidence intervals. MSV: mature secondary vegetation; ISV, intermediate secondary vegetation; YSV, young secondary vegetation; PF, plantation forest; PA, pasture; CR, cropland; UR, urban. Effects for intense use in MSV could not be estimated as there were not enough sampled sites. *Figure reproduced from Etard et al. (2022).*

1071 urban assemblages; Appendix 2, Figure S3.18). Furthermore, using the subset of species with complete trait
 1072 data, I found that the results were not sensitive to the inclusion of geographical range size as an additional
 1073 trait (Appendix 2, Figure S3.19). Finally, the results were not sensitive to variation across imputed trait val-
 1074 ues (Appendix 2, Figure S3.20) and were also robust to resampling in primary-vegetation sites (Appendix 2,
 1075 Figure S3.21).

1076 Responses of FRic and FDis to land use and land-use intensity differed among taxonomic classes (Figure
 1077 3.3). Within-class effects for FDis were similar between regions. The most notable decreases were observed
 1078 in lightly- and intensely used agricultural land uses in amphibians, birds and reptiles; and in intensely used
 1079 urban land uses for birds and mammals. For FRic, the effects in tropical and temperate regions were qual-
 1080 itatively similar in three out of four classes (birds, mammals and reptiles), although effect sizes tended to be
 1081 bigger for tropical assemblages. Birds and reptiles showed reductions in disturbed land uses in both tropical

and temperate regions, whereas I detected few significant effects for mammals. For birds, the most important average decline, of 50%, was observed in intensely used tropical urban land uses, while for reptiles I detected significant decreases in lightly- and intensely used agricultural sites (but I could not estimate effects for urban land uses due to the small sample size). Finally, the effects differed between tropical and temperate regions for amphibians, with no significant effects detected across temperate assemblages, but important reductions across tropical agricultural and urban assemblages.

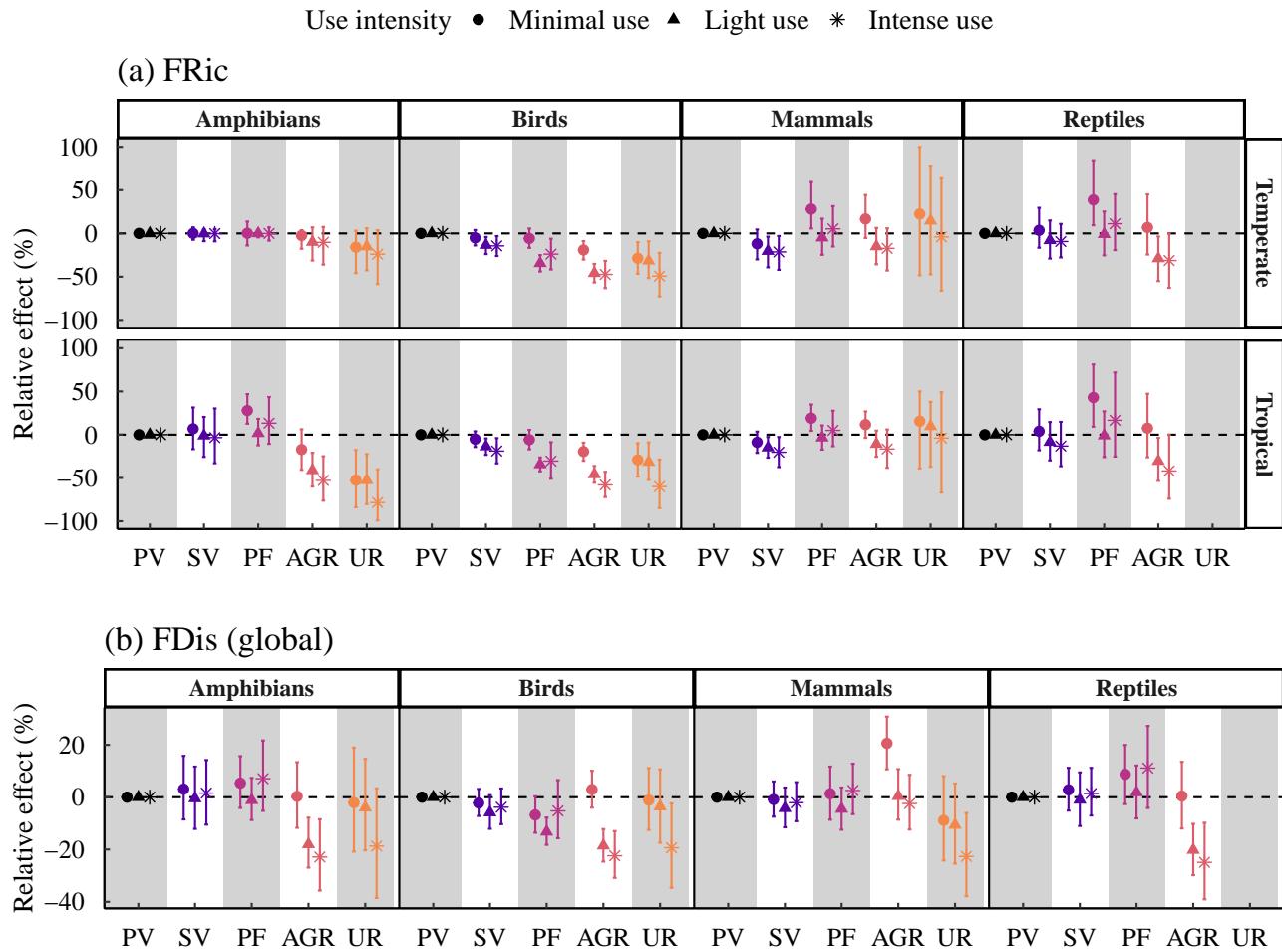


Figure 3.3: Effects of land use, land-use intensity, region and taxonomic class on FRic (a) and FDis (b). Effects were rescaled with reference to primary vegetation (PV) and are plotted as a % difference relative to PV within each land-use intensity. Error bars represent 95% confidence intervals. Effects for FRic were estimated from Model 2a, and from Model 2b for FDis. SV, secondary vegetation; PF, plantation forest; AGR, agricultural land uses (pasture and cropland); UR, urban. Effects for reptiles in urban land uses could not be estimated as there were not enough sampled sites. *Figure reproduced from Etard et al. (2022).*

Fitting similar models only for species with complete trait data showed that these patterns are unlikely to be affected by imputation uncertainty for birds; for mammals and reptiles, the main results could even be conservative (Appendix 2, Figures S3.22, S3.23). Indeed, although confidence intervals around the estimates

1091 were large, I typically observed larger decreases in functional diversity when using the complete data subset,
 1092 including an 86% decline in FRic for mammals in intensely used tropical agricultural areas. The results were
 1093 also unaffected by variation across replicate sets of imputed trait values (Appendix 2, Figure S3.24).

1094 **3.3.2 Changes in the probability of occurrence of functional under-dispersion**

1095 Land use, land-use intensity and region significantly affected the probability of occurrence of functional
 1096 under-dispersion across vertebrates. Functional under-dispersion was more likely to occur in tropical crop-
 1097 land of all land-use intensities (Figure 3.4b), as well as in some of the lightly-used land uses (notably urban
 1098 and plantation forest). Contrary to my expectations, and with the exception of tropical cropland, functional
 1099 under-dispersion was not more likely to occur in intensely-used land uses. For minimally-used sites, changes
 1100 in FDis were mostly consistent with changes expected given local species richness.

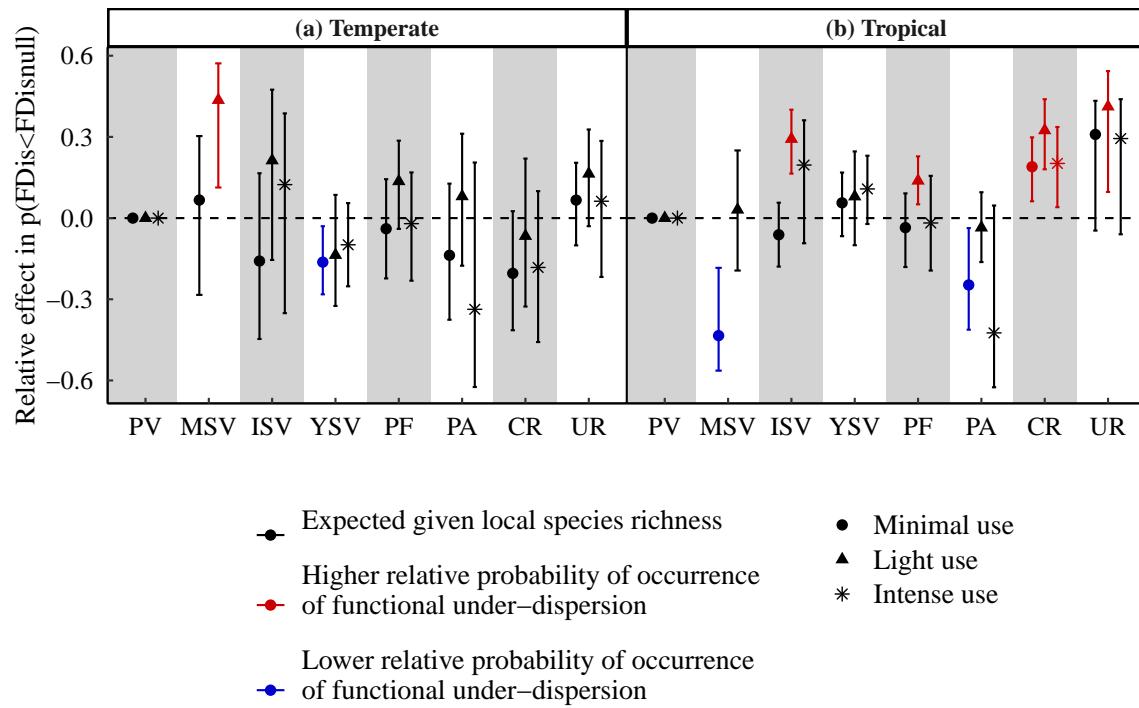


Figure 3.4: Effects of land use, land-use intensity and region on the probability of occurrence of functional under-dispersion. Error bars represent 95% confidence intervals. PV: primary vegetation; MSV, mature secondary vegetation; ISV, intermediate secondary vegetation; YSV, young secondary vegetation; PF, plantation forest; PA, pasture; CR, cropland; UR, urban. Effects are rescaled and represent the average difference in the probability of occurrence of functional under-dispersion between the reference (PV, probability of functional under-dispersion set at 0 within each land-use intensity) and the disturbed land uses. *Figure reproduced from Etard et al. (2022).*

3.3.3 Functional loss and gain

Across and within vertebrate classes, I detected high levels of functional loss, exceeding the natural turnover between primary-vegetation sites, both in temperate and tropical regions. Across vertebrates (Figure 3.5a), functional loss was notably high in temperate pastures (+27% above reference for minimal use; +73% for intense use), temperate urban sites (+27% for light use; +50% for intense use; effects for tropical urban sites could not be estimated), temperate and tropical cropland (+44% and +56% respectively for light use; effects for intense use could not be estimated). Important levels of functional loss were also observed in tropical plantation forest of light use intensity (+51%; effects for the intense use could not be estimated). High levels of functional loss were also observed within each class (Figure 3.6a) (although not all effects could be estimated because of limited sample sizes, Appendix 2, Table S3.5). The highest losses were observed in agricultural areas for amphibians and reptiles, with important losses also observed in temperate urban areas for both birds and amphibians (+35% for minimal use; effects for tropical urban areas could not be estimated).

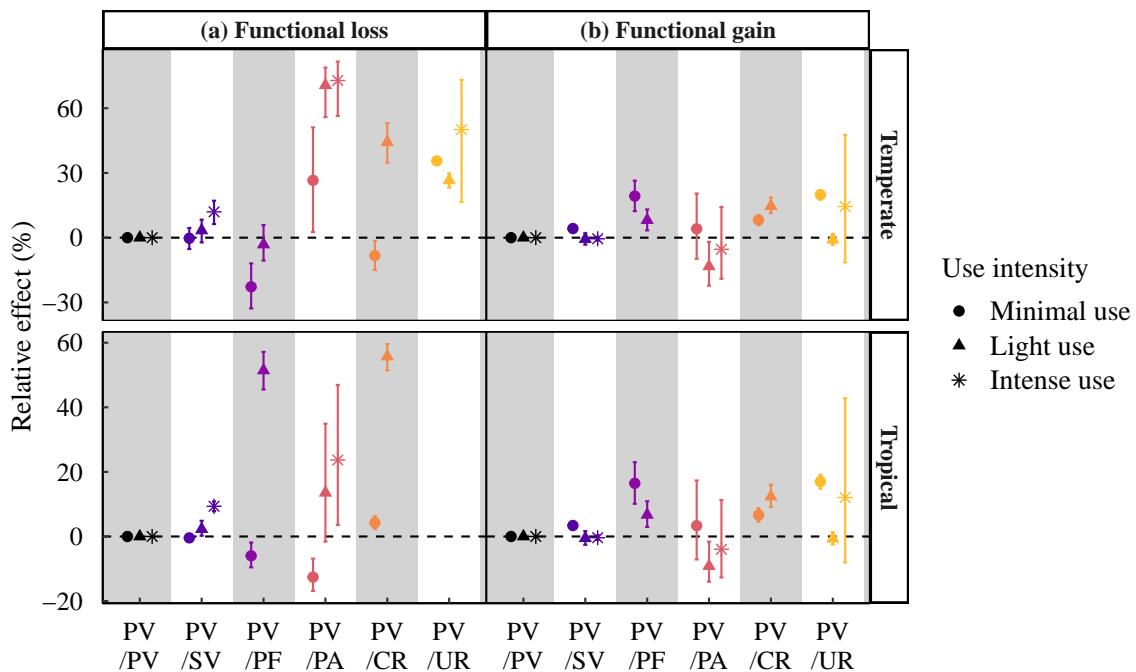


Figure 3.5: Effects of land use and land-use intensity on (a) functional loss and (b) functional gain across pairs of sites in temperate areas and tropical areas. PV: primary vegetation; SV, secondary vegetation; PF, plantation forest; PA, pasture; CR, cropland; UR, urban. Error bars represent 95% confidence intervals. Effects are rescaled and represent the average difference in functional loss and gain between the reference pairs (PV/PV, with loss and gain set at 0% within each land-use intensity), and pairs of primary vegetation with disturbed land uses. Negative effects mean that, on average, levels of functional loss (or gain) were lower than functional loss (or gain) observed between pairs of primary-vegetation sites, and not that there were absolute ‘negative losses’ or ‘negative gains’. *Figure reproduced from Etard et al. (2022).*

1114 Across vertebrates, average functional gain (average proportion of novel trait space in the disturbed
 1115 assemblage) was moderate and on average did not exceed 20% in any disturbed land uses (Figure 3.5b).
 1116 Patterns of functional gain were similar in both regions. The highest functional gains were observed for
 1117 minimally-used urban sites and plantation forest (range: +16% to +20%). On the other hand, important
 1118 levels of functional gain were observed in some classes (Figure 3.6b), with the highest functional gain for
 1119 mammals (+80% in intensely used urban sites).

1120 Diagnostic plots (qq-plots and residual distributions) for the models are shown in Appendix 2, Figures
 1121 S3.9–S3.17. Overall, the model residuals were appropriately distributed (but with some leptokurtic residual
 1122 distributions, to which mixed-effect models are generally robust (Schielzeth et al., 2020)).

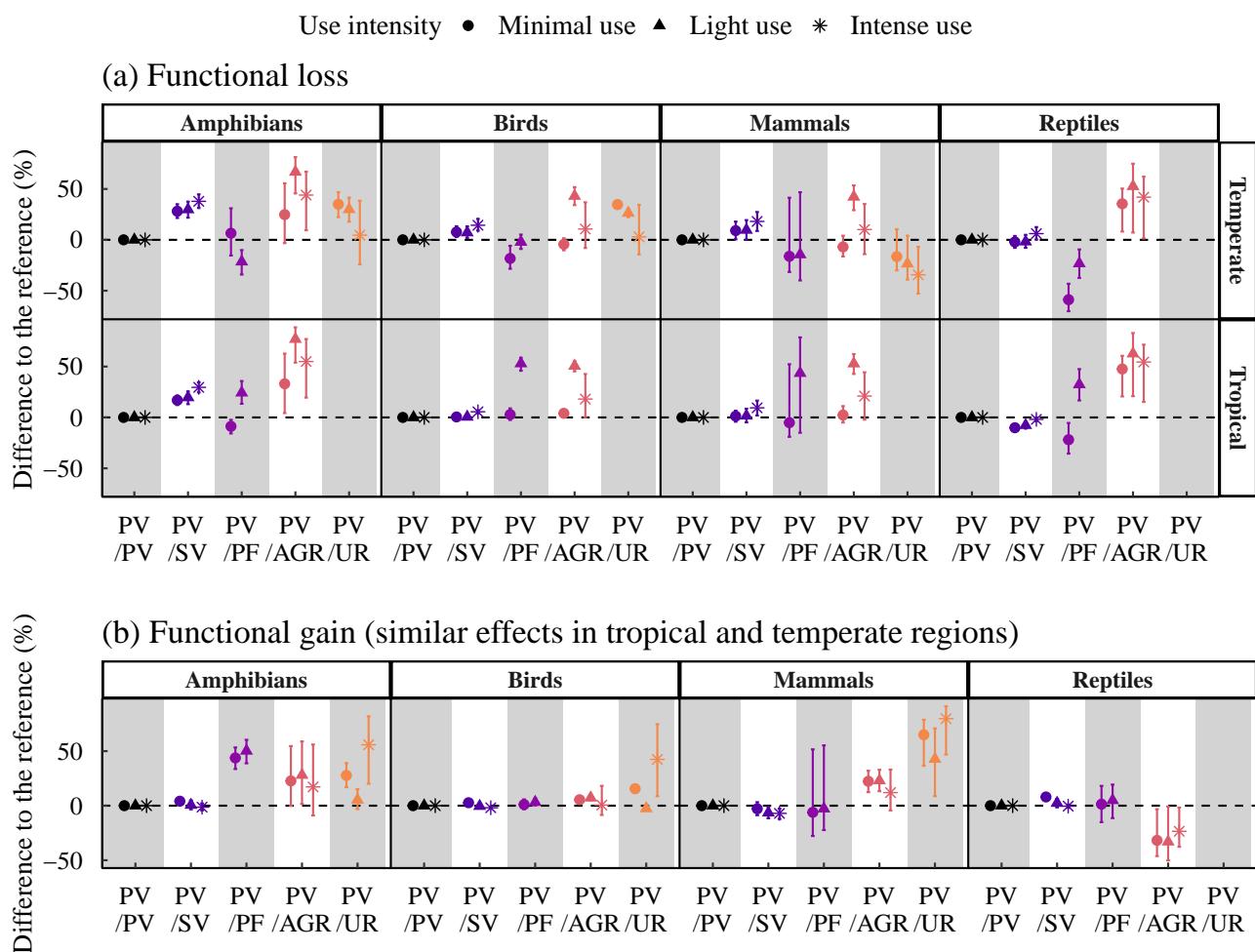


Figure 3.6: Effects of land use, land-use intensity, region and taxonomic class on functional loss (a) and functional gain (b) across pairs of sites. PV: primary vegetation; SV: secondary vegetation; PF: plantation forest; AGR: agricultural land uses (pasture and cropland); UR: urban. Error bars represent 95% confidence intervals. Effects are rescaled and represent the average difference in functional loss and gain between the reference pairs (PV/PV, with loss and gain set at 0% within each land-use intensity), and pairs of primary vegetation with disturbed land uses. Negative effects mean that, on average, levels of functional loss (or gain) were lower than functional loss (or gain) observed between pairs of primary-vegetation sites, and not that there were absolute ‘negative losses’ or ‘negative gains’. Figure reproduced from Etard et al. (2022).

1123 **3.4 Discussion**

1124 Here, I showed that the functional diversity of vertebrate assemblages is negatively impacted in human land
1125 uses, particularly in the most intensely used land types. The results of this Chapter extend previous studies
1126 that have been more taxonomically or geographically restricted (Flynn et al., 2009; Matuoka et al., 2020).
1127 Matuoka et al. (2020) found that the functional diversity of tropical bird assemblages was negatively affected
1128 by human disturbance, a pattern that did not appear in temperate assemblages. Yet, I found that functional
1129 diversity was negatively affected in both tropical and temperate areas, with important functional losses in all
1130 four vertebrate classes.

1131 Using multiple metrics allowed me to explore different facets of functional diversity. For instance, func-
1132 tional gain could locally offset functional loss in some disturbed land uses. This could indicate that despite
1133 no apparent negative effect on FRic, some disturbed land uses (e.g. lightly-used temperate cropland) could
1134 experience important functional loss, and highlights the importance of using a variety of indicators. This
1135 mechanism could be at play in mammalian assemblages, for which important levels of functional gain were
1136 observed in agricultural and urban sites. Further, functional gain in disturbed land uses could indicate that
1137 disturbances facilitate the introduction of functionally novel species, falling into previously unoccupied parts
1138 of the trait space. This may be because non-native species are more likely to become established in disturbed
1139 assemblages. Previous work has shown that land-use disturbance facilitates biological invasions in island
1140 ecosystems (Jesse et al., 2018; Sánchez-Ortiz et al., 2019), but to my knowledge, this has not been tested
1141 specifically across continental areas for invasive vertebrates (but see Pyšek et al. (2010)). It is also pos-
1142 sible that disturbed areas harbour synanthropic species that do not occur in primary vegetation, leading to
1143 substantial functional gain.

1144 Overall, the negative effects of land use on functional richness tended to be more pronounced in the
1145 tropics. This is congruent with past studies that have found tropical biodiversity to be disproportionately
1146 sensitive to human pressures (Martins and Pereira, 2017; Newbold et al., 2020b). There are a number of
1147 potential explanations for this. First, it could be that a long history of intense land-use disturbance at large
1148 scales in many temperate regions (e.g. Western Europe; Stephens et al. (2019)) means that biodiversity is
1149 now less sensitive to new disturbances, because the most sensitive species have been filtered out (Balmford,
1150 1996; “Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic lev-
1151 els” 2010; Le Provost et al., 2020; Munteanu et al., 2020). Species unable to cope with such disturbances
1152 may have gone extinct in the past, while the remaining species would be more disturbance-tolerant (Betts
1153 et al., 2019). Tropical regions, historically less disturbed at large scales, would then contain a higher pro-

portion of disturbance-sensitive species than temperate regions. Consequently, the functional richness in undisturbed tropical sites could be less resilient to new disturbances. This also highlights that time since land-use conversion could have important impacts on local functional diversity. Although I did not consider the effects of time since land-use conversion in this work (notably because PREDICTS contained data on time since land-use conversion only for about 22% of the sites), I expect that time since land-use conversion may affect assemblage composition, and thus, functional diversity, with potentially land-use-specific relationships between time since conversion and functional diversity (e.g., a positive relationship for recovering secondary vegetation or a negative relationship for urban areas; but I did not detect such effects when using the data subset for which there were information on time since land-use conversion [see Appendix 2, S3.8: ‘Model robustness – time since land-use conversion’]).

Second, it could be that tropical species are intrinsically more sensitive to disturbances than temperate species because of their evolutionary history. Natural climatic variability experienced by species as well as species history of exposure to disturbances have been proposed to influence sensitivity to disturbance. For instance, tropical species are, on average, nearer to their climatic limits than temperate species (Deutsch et al., 2008; Sunday et al., 2014). Tropical species could therefore experience more deleterious effects from interacting drivers of change, with land-use change bringing about novel climatic conditions pushing them beyond their tolerance limits (Frishkoff et al., 2016; Williams and Newbold, 2020).

In addition to filtering out sensitive species, land-use change is also expected to modify interactions among species, thereby influencing species persistence (Tylianakis et al., 2008; Valiente-Banuet et al., 2015). Although I detected a signal of functional under-dispersion (particularly in tropical cropland), which indicates that assemblages may be locally structured by environment filtering (Bregman et al., 2015), it is likely that several assembly rules underpin assemblage composition (Fournier et al., 2016). For instance, land-use changes could enhance competition among species, promoting over-dispersion by removing species that share similar resources. Such opposite signatures of environmental filtering and enhanced competition on functional dispersion could explain why I did not detect stronger effects of land use on functional under-dispersion occurrence.

Studies looking at impacts of global land use on functional diversity computed with species from all four terrestrial vertebrate classes remain rare. Lack of availability of standardised trait data across terrestrial vertebrates may have hindered such studies from being conducted in the past. To overcome this problem, I based the analyses on a large-scale collation of trait data (Chapter 2; Etard et al. (2020)), and I imputed missing trait values to obtain complete trait datasets in each class. I used random forest algorithms, currently thought to be one of the most robust technique for missing value imputations in trait datasets (Debastiani

et al., 2021; Johnson et al., 2021; Penone et al., 2014). Replicating the analyses on complete trait data subsets showed that imputation uncertainty did not affect the main conclusions of this work and that the negative effects of human land uses were in some cases even stronger when using the complete data subsets. Furthermore, the results were highly consistent across imputed datasets and so insensitive to variation across imputed values. Although missing value imputation can offer a robust filling of missing entries, this study highlights the existing taxonomic biases both in trait data availability and in PREDICTS studies, and thus stresses the need to pursue data compilation efforts, particularly for the least-sampled classes (reptiles and amphibians).

Another implication of trait data availability for vertebrates is that the choice of traits was constrained. Mouillot et al. (2021) showed that functional diversity metrics are sensitive to trait omission and that the sensitivity to trait omission decreases with increasing levels of correlation among traits. Here, I chose seven traits that were available across all classes at least for a subset of the species and that have been implicated in shaping species responses to environmental change. A notable omission was any metric of dispersal ability, which is likely to influence species' ability to respond to land-use change but is difficult to obtain for most species. In fact, past studies have shown that dispersal abilities can be predicted from ecological correlates, such as body mass, diet or geographical range size (Schloss et al., 2012; Sutherland et al., 2000). Since the results were robust to the omission of geographical range size, I am confident that the omission of dispersal abilities also does not affect the conclusions of this work.

Functional diversity metrics are often used as a proxy for ecosystem functioning because of the conceptual and mechanistic link between functional 'effect' traits and ecosystem processes (Lavorel and Garnier, 2002; Violle et al., 2007). In many studies focused on vertebrates, however, functional diversity metrics do not correlate with a given ecosystem function (Hatfield et al., 2018). Here, I did not explicitly target given ecosystem functions, but I argue that evidence of functional loss of vertebrate assemblages indicates that processes sustained by vertebrates are put at risk by land-use change. My results further show that some disturbed land uses are more likely to experience functional under-dispersion, particularly tropical cropland and tropical urban areas, which again indicates a potential imperilment of ecological processes. Indeed, in such cases, decreases in functional dispersion exceed changes expected from the chance removal of species; such non-random modifications indicate that certain areas of the functional trait space are more sensitive to land-use disturbance. Future work could investigate the impacts of land-use change on particular ecosystem functions. The integration of trophic information (beyond the trophic levels I used here) to the species-trait dataset could be an interesting step in that direction, as dietary traits relate to resource use and are, as such, probably the most straightforward traits to link with ecosystem functions. Furthermore, my results suggest

1218 that the functional loss experienced within a class is unlikely to be compensated for by the persistence of
1219 functionally similar species in other classes. Indeed, I detected negative effects of human land use on func-
1220 tional richness in at least three out of four vertebrate classes (amphibians, birds, and reptiles), in accordance
1221 with past studies focusing on each of these groups (Gallmetzer and Schulze, 2015; Marcacci et al., 2021;
1222 Riemann et al., 2017; Sol et al., 2020). Although overall mammalian functional richness was less affected,
1223 high levels of functional gain suggest that the functional composition of mammalian assemblages is heavily
1224 modified in disturbed land uses.

1225 To conclude, the results of this Chapter highlight the negative impacts of human land uses on multiple
1226 dimensions of functional diversity, within and across terrestrial vertebrate classes, at a global scale. In
1227 many disturbed sites, decreases in functional diversity exceed changes expected from species loss alone,
1228 showing that human activities non-randomly reshape ecological assemblages. By intensifying functional
1229 loss and promoting functional under-dispersion, land-use change could have deleterious effects on ecosystem
1230 functioning, highlighting the necessity of putting into place effective conservation measures in the face of
1231 anthropogenic change.

1232 **4 | Geographical range area, habitat breadth**

1233 **and specialisation on natural habitats**

1234 **are associated with land-use responses**

1235 **and climate-change sensitivity more con-**

1236 **sistently than life-history and dietary traits**

1237 **in terrestrial vertebrates**

1238 **Keywords**

1239 Land use; land-use intensity; climate change; sensitivity; CENFA; dietary traits ; life-history traits; speciali-

1240 sation; geographical range area; terrestrial vertebrates.

1241 **Abstract**

1242 Land-use and climate change are two of the most important pressures on terrestrial biodiversity, however the

1243 factors that explain interspecific variation in responses to these pressures remain unclear. Although it is well

1244 established that extinction risk and some species' responses to human pressures relate to species traits, we

1245 lack large-scale comparative assessments across multiple clades linking traits to multiple human pressures.

1246 Here, I investigated whether a set of ecological characteristics that are commonly measured across terrestrial

1247 vertebrates (that is, ecological traits and geographical range area) are associated with (1) species' responses

1248 to different land-use types and (2) species' sensitivity to climate change. My aim was to test whether general-

1249 isable patterns in species' response to these pressures arise with regards to species' ecological characteristics,
1250 which helps assess the global signature of human pressures on vertebrate biodiversity and is also of inter-
1251 est for the prioritisation of conservation efforts. Among the set of characteristics I considered, I found that
1252 only three were consistently associated with both land-use responses and climate-change sensitivity across
1253 terrestrial vertebrate classes: geographical range area, habitat breadth and specialisation on natural habitats.
1254 The association of other traits with species' land-use responses and with climate-change sensitivity often de-
1255 pended on class and land-use type. My work highlights that narrow-ranged species with small habitat breadth
1256 and natural habitat specialism are typically more sensitive to human pressures. Further, in all classes, I found
1257 that invertebrate eaters and fruit/nectar eaters tended to be negatively affected in disturbed land uses, and that
1258 invertebrate- and plant/seed- eating birds had higher climate-change sensitivity, raising concerns about the
1259 continuation of ecological processes sustained by these species under global changes. My work stresses the
1260 need for putting into place conservation and mitigation measures to protect biodiversity and related services
1261 from human impacts.

1262 **4.1 Introduction**

1263 Land-use change is currently the most important driver of global biodiversity loss (Newbold et al., 2015)
1264 and is likely to continue to cause species loss in the coming decades (Li et al., 2022; Powers and Jetz, 2019;
1265 Stehfest et al., 2019). However, biodiversity faces multiple pressures acting in combination (Maxwell et al.,
1266 2016). In particular, the impacts of climate change on biodiversity are projected to equate or even surpass
1267 those of land-use change in their magnitude by 2070 (Newbold, 2018). Thus, it has become more vital than
1268 ever to put into place mitigation and conservation measures to protect biodiversity from human pressures.

1269 It is now well established that species differ in their ability to cope with environmental changes (Fer-
1270reira et al., 2022; Matich and Schalk, 2019; Newbold et al., 2013). As such, global average declines in
1271 biodiversity indices mask substantial interspecific variation in responses to disturbances (Leung et al., 2020).
1272 Such interspecific variation has important consequences for the prioritisation of conservation efforts and the
1273 definition of protected areas (Morelli et al., 2021). Mitigating land-use and climate-change impacts on the
1274 world's biota requires to understand which species are put at most risk by these pressures, in other words to
1275 understand the factors that are associated with species' sensitivity to land-use and climate change.

1276 By capturing key aspects of species' morphology, life-history, ecological strategies or demography, traits
1277 can inform on species' use of resources and space, as well as on some community and population-level
1278 processes (Capdevila et al., 2022b). As such, traits can help understand what drives species' responses

1279 to environmental change. Thus, to explain interspecific differences in responses to human disturbance, a
1280 number of studies have investigated whether species traits influence species' responses to human pressures,
1281 in particular to land-use change (Newbold et al., 2013; Nowakowski et al., 2017; Quesnelle et al., 2014;
1282 Tinoco et al., 2018) and climate change (Angert et al., 2011; Di Marco et al., 2021; Estrada et al., 2018;
1283 McCain and King, 2014; Pacifici et al., 2017; Pearson et al., 2014; Schloss et al., 2012).

1284 From these past studies, several traits have been identified as important correlates of species' responses
1285 to land-use and climate change within vertebrate taxa (for example, body mass and generation length were
1286 found to influence bird responses to land-use change in Newbold et al. (2013); and body mass and activity
1287 time were found to be associated with mammal responses to climate change in McCain and King (2014)).
1288 However, past work has mostly been conducted at local to regional scales (Davison et al., 2021; Hevia et
1289 al., 2017), such that it remains unclear whether the effects of traits on species' responses to environmental
1290 change can be generalised across vertebrate taxa and regions. Yet, at least two meta-analyses have inves-
1291 tigated whether traits explained responses to human pressures across diverse taxa, one focused on climate-
1292 change responses (MacLean and Beissinger, 2017), and one on species extinction risk (Chichorro et al.,
1293 2019). MacLean and Beissinger (2017) found that habitat breadth and historic range limit were consistently
1294 associated with interspecific variation in range shifts under contemporary climate change across a range of
1295 taxa (including plants, birds and butterflies), but they did not detect any effect of life-history traits, such as
1296 body size or fecundity. Similarly, Chichorro et al. (2019) highlighted the effects of geographical range area
1297 and habitat breadth on species extinction risks in different taxa (including terrestrial vertebrates), with other
1298 traits having inconsistent effects. However, as underlined by Chichorro et al. (2019), the studies included in
1299 the meta-analysis often considered extinction risk without an explicit consideration of the pressures to which
1300 the species were exposed. Yet, a given trait could be associated with opposite responses depending on the
1301 pressure in consideration (González-Suárez et al., 2013).

1302 Further, previous studies have often been restricted in their taxonomic coverage, with very few studies
1303 considering several vertebrate classes together, so that comparative investigations among vertebrate classes
1304 remain rare. In addition, there has not yet been a global assessment of the association between vertebrate
1305 traits and both land-use responses and climate-change sensitivity. Here, I test whether general patterns in
1306 species' land-use responses and climate-change sensitivity arise with regards to species traits. I include
1307 species geographical range area in the analysis, as it is one aspect of rarity that has been shown to influence
1308 species' responses to land use and to climate change (Newbold, 2018; Thuiller et al., 2005). Since geo-
1309 graphical range area does not meet the strict definition of a trait, I henceforth refer to all traits and range
1310 area as 'ecological characteristics'. Thus, I examine associations with a set of ecological characteristics that

1311 are commonly measured across terrestrial vertebrates, at global scales (Figure 4.1a). Considering ecological
1312 characteristics that are available at least for a subset of the species in each class allows for a cross-taxon
1313 comparative assessment. Further, it also allows me to ask whether such commonly measured ecological
1314 characteristics show consistent associations with species' land-use responses and climate-change sensitivity.
1315 I ask two questions: (1) are any ecological characteristics associated with interspecific variation in responses
1316 to land use and with climate-change sensitivity? (2) If so, are these ecological characteristics similar across
1317 classes; are they similar between land-use responses and climate-change sensitivity; and are associations in
1318 the same direction, such that I can identify a set of characteristics that are associated with a high sensitivity
1319 of species to human pressures? Conversely, are such associations both taxon- and pressure- dependent?

1320 Given the different nature of the threats I consider, I use two independent approaches, one for land-use
1321 change and one for climate-change sensitivity. Thus, I do not consider interactive effects between these
1322 pressures. To infer species' responses to land-use change, I use a space-for-time substitution approach,
1323 modelling occurrence probability across different land-use types (Figure 1b). I estimate species' expected
1324 sensitivity to future climate change from properties of species' climatic niches (Figure 1c); species niche
1325 properties have been shown to be strong indicators of species' climate-change sensitivity (Thuiller et al.
1326 2005), and are also straightforward to use at large scales given the availability of species distribution data,
1327 from which climatic niche spaces can be constructed. I then bring these two approaches together to look for
1328 any emerging pattern in species' responses to land use or in their climate-change sensitivity, with regards to
1329 species' ecological characteristics.

1330 Among the characteristics I consider (Figure 4.1a), some may directly influence species survival by me-
1331 diating resource acquisition and use. These characteristics are body mass, diet, and diet breadth. Other
1332 characteristics (e.g., lifespan and litter/clutch size) may indirectly affect species persistence over time by
1333 influencing species reproductive output and demographic processes (Capdevila et al., 2022b). Finally, re-
1334 sponds to human pressures are known to be dependent on species' degree of specialisation, which I capture
1335 with characteristics reflecting specialisation in time (i.e., diel activity) and reflecting use of space (e.g., habi-
1336 tation breadth and geographical range area).

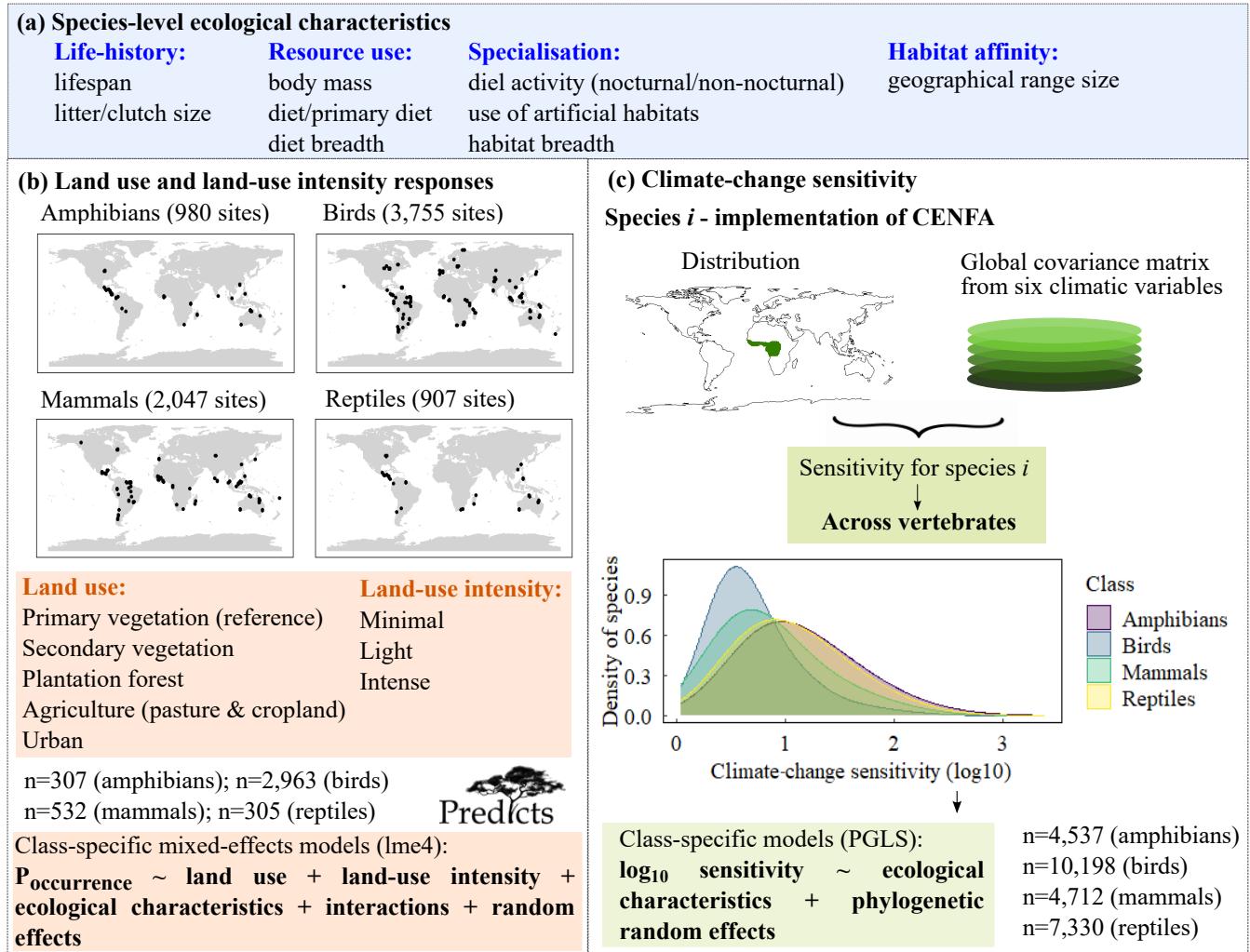


Figure 4.1: Framework of the study. (a) I collected ecological trait data and geographical range areas across terrestrial vertebrates (termed ‘ecological characteristics’). I then used two independent approaches to assess the influence of these characteristics on species’ responses to land use and on species’ climate-change sensitivity. (b) To assess the influence of traits on responses to land use and land-use intensity in each vertebrate class, I combined the ecological characteristics with the PREDICTS database. (c) To estimate species’ sensitivity to climate change, I used the CENFA framework (Rinnan and Lawler, 2019), which relies on the combination of species’ distributions with climatic variables to estimate sensitivity from properties of the species’ climatic niche space. I then built class-specific models to assess whether the ecological characteristics were associated with species’ sensitivity to climate change.

1337 **4.2 Methods**

1338 **4.2.1 Ecological characteristics (Figure 4.1a)**

1339 **Traits**

1340 I obtained the six following traits from Chapter 2 (in which I presented a trait data compilation across
1341 terrestrial vertebrates): body size (body mass and/or length, depending on the class); a proxy for species
1342 lifespan (generation length for mammals and birds; age at sexual maturity for amphibians; and maximum
1343 longevity for reptiles); litter or clutch size; diel activity; habitat breadth; and use of artificial habitats. I
1344 chose these traits because 1) they were available across all vertebrate classes, at least for a subset of species,
1345 allowing for a comparative assessment; and 2) they relate to species life-history, ecology, and resource use,
1346 such that they might influence species' land-use responses and climatic niche properties (and thus expected
1347 climate-change sensitivity). I couldn't capture intraspecific variation in trait values, and instead I used single
1348 mean values for all traits.

1349 I enhanced the trait data from Chapter 2 with species-level estimates of diet, lacking in the published
1350 database but likely important for understanding species' sensitivity to human pressures. For birds and mam-
1351 mals, I collected estimates of species primary diet (i.e., the diet inferred from the combination of food items
1352 totalling more than 50% of species' consumption), from the EltonTraits database (Wilman et al., 2014). For
1353 amphibians and reptiles, obtaining species *primary* diet was not possible, as there were no data available
1354 on the relative consumption of different food items. For amphibians, the AmphiBIO database (Oliveira
1355 et al., 2017) provided information on species consumption of different food items (just in terms of pres-
1356 ence/absence in the diet, but without estimation of their percent use), so I inferred diet on the basis of these
1357 reported food items (however the coverage was low, with more than 75% of the species missing diet infor-
1358 mation; Appendix 3, Figure S4.1). For reptiles, there was no available data collection describing diet. For
1359 both reptiles and amphibians, I supplemented the existing datasets with data on species consumption from
1360 published sources (recording the presence/absence of different food items in species consumption; compiled
1361 by Rhiannon Osborne-Tonner), for an additional 108 amphibians and for 239 reptiles (see Appendix 3, S4.1:
1362 'Compiling diet information').

1363 I standardised the diet data across the vertebrate classes, by grouping species in five different diet cate-
1364 gories: vertebrate eaters; invertebrate eaters; plant/seed eaters; fruit/nectar eaters; and omnivores (for mam-
1365 mals and birds, species were classified as omnivores when all food items had a percent use $\leq 50\%$; and for
1366 amphibians and reptiles, when species were known to consume both plant and animal matter, or both in-

1367 vertebrates and vertebrates). I also calculated species diet breadth – the total number of recorded food items
1368 (in terms of presence/absence) known to be consumed by a species. More information on the compilation of
1369 dietary information can be found in Appendix 3, S4.1: ‘Compiling diet information’.

1370 **Geographical range area**

1371 I used extent-of-occurrence maps from BirdLife International for birds (<http://datazone.birdlife.org/species/requestdis>), from the IUCN Red List for mammals and amphibians (IUCN, 2020), and
1372 from Roll et al. (2017) for reptiles (all downloaded in April 2020). I excluded areas occupied during non-
1373 breeding seasons and areas falling outside species known elevational limits (following Chapter 2). The range
1374 maps were then converted to the raster format (‘raster’ package, version 3.5.15 Hijmans (2022)), and I esti-
1375 mated species geographical range areas using a resolution of 1 km² with Behrmann’s equal-area projection.
1376 Although range area cannot be considered a trait (which is a property measurable at the level of individual
1377 organisms), I included range area in the analyses because past work has shown that range area is an important
1378 correlate of species’ responses to land-use (Newbold et al., 2018) and climate change (Thuiller et al., 2005).
1379 In addition, range area may correlate with other aspects of species’ ecology that I could not include directly
1380 in the analysis because of limited data availability, such as dispersal ability (Capurucho et al., 2020).

1382 **Phylogenies**

1383 I used information on species’ phylogenetic position in the imputations of missing trait values (see next
1384 section), and also to control for phylogenetic relationships in the models investigating the association be-
1385 tween species’ ecological characteristics and species’ estimated climate-change sensitivity. Class-specific
1386 phylogenetic trees were downloaded April 2020 from <https://zenodo.org/record/3690867#.Xyc5wyhKhPZ> for mammals (Phylacine 1.2; Faurby et al. (2018, 2020)); and from <https://data.vertlife.org/> for amphibians (Jetz and Pyron, 2018), birds (Jetz et al., 2012) and squamates (Tonini
1388 et al., 2016). For each class, I used a consensus tree obtained with the TreeAnnotator programme of the
1389 BEAST software (Bouckaert et al. 2014), from an available distribution of 1000 trees.

1391 **4.2.2 Imputations of missing trait values**

1392 For some of the traits and classes, there was a substantial proportion of missing trait values (Figure S4.1).
1393 To fill these gaps, I imputed missing trait values using random forests, as implemented with the ‘missforest’
1394 function of the ‘missForest’ package in R (version 1.4, Stekhoven (2016) and Stekhoven and Bühlmann
1395 (2012)). ‘missforest’ is one of the best methods for missing-value imputations when working with continuous

1396 and categorical variables, and when including species phylogenetic position as a predictor (Debastiani et al.,
1397 2021; Penone et al., 2014). After showing that several traits were strongly phylogenetically conserved
1398 (Table S4.1), I included ten phylogenetic eigenvectors in the imputations (Penone et al., 2014), as well as
1399 taxonomic orders as a categorical variable (included to account for the taxonomic positions of species that
1400 were not represented in the phylogenies). Full details are given in Appendix 3 (S4.2: ‘Imputing missing
1401 trait values’). After imputation, continuous traits were \log_{10} -transformed to improve normality (except for
1402 habitat and diet breadth, which I square-root transformed; this transformation was more appropriate here
1403 because the distributions of habitat breadth and diet breadth tended to be less right-skewed than that of the
1404 other traits, and the range of values was smaller).

1405 4.2.3 Characterizing the influence of traits on species’ land-use responses (Figure 4.1b)

1406 Vertebrate assemblage composition

1407 To compare vertebrate assemblages in different land-use types, I used the PREDICTS database (Hudson
1408 et al., 2014, 2017). PREDICTS is a collection of independent studies that have sampled biodiversity in sites
1409 of varying land use and land-use intensity. Samples are mostly of species abundance, sometimes species
1410 occurrence, and rarely just overall species richness. It is one of the most comprehensive such databases
1411 to date, with 4,107 vertebrate species sampled across 7,689 sites considered in this work (Figure 4.1b). In
1412 PREDICTS, sites are assigned to one of the following land-use categories: primary vegetation (native vege-
1413 tation); secondary vegetation, plantation forest, pasture, cropland, and urban (disturbed land uses; see Table
1414 S4.2 and Hudson et al. (2014, 2017) for more details). Each site is also characterised in terms of land-use
1415 intensity based on land-use-specific criteria (such as mechanisation degree, crop diversity and agricultural
1416 inputs for cropland; Hudson et al. (2014)). Land-use intensity is divided into three categories to reflect the
1417 degree of human transformation and impacts on the land: minimal, light or intense. Here, I considered
1418 minimally-used primary vegetation to be the least-disturbed reference land use against which I compare all
1419 other land-use types. I grouped pasture and cropland together into a category I termed ‘agricultural’. As the
1420 design of the PREDICTS database is not balanced, sample sizes varied among classes and land-use types
1421 (Figure S4.3).

1422 Full models (all-predictor models)

1423 Within each vertebrate class, I investigated whether interactions among the ecological characteristics, land
1424 use and land-use intensity explained species occurrence probability. I fitted four binomial mixed-effects

models (one for each class), using the ‘lme4’ package (version 1.1-23; Bates et al. (2015)), with random effects accounting for study, site and species identity to account for the nested design of the database, taxonomic non-independence, and repeated observations among species. I did not consider interactions among the ecological characteristics, but I included interactions between land use and ecological characteristics, and between land-use intensity and ecological characteristics. Before fitting the models, I checked the degree of multicollinearity among explanatory variables using generalised variance inflation factors (GVIF; Fox and Monette (1992)), with a threshold of 5 for the detection of multicollinearity (Tables S4.3-S4.8). For amphibians and reptiles, including both diet and diet breadth was problematic, so I excluded diet from the set of predictors for these classes on the basis of the GVIF scores. Models investigating the effects of diet were built separately (see next section, ‘Partial models’).

I did not use phylogenetic random effects directly in the models because of the computational load required by such models when working with several hundred or thousands of species. However, I checked the phylogenetic signal in the models’ residuals using Pagel’s λ (Pagel, 1999). Thus, in each class, the model fitted was:

$P_{\text{occurrence}} \sim \text{land use} + \text{land-use intensity} + \text{species-level ecological characteristics} +$
 $\text{land use : species-level ecological characteristics} +$
 $\text{land-use intensity : species-level ecological characteristics} +$
 $(1|\text{sudy identity}) + (1|\text{site identity}) + (1|\text{species identity}).$

To verify that the models’ estimates were robust to any violation of distributional assumptions, I fitted the models again using a Bayesian framework (using the ‘MCMCglmm’ package version 2.32, Hadfield (2010)).

1448 **Partial models (single-predictor models)**

In addition to the full models, I fitted partial models for each class. These were fitted to visualise occurrence patterns for each trait independently of other traits. The structure of the models was similar to that of the full models, except that I included a single species-level characteristic at a time in each model.

1452 **Effects of categorical ecological characteristics on species’ occurrence probability (Figure 4.2a)**

The influence of categorical traits on species’ responses to land use and land-use intensity can be visualised in two ways: either by comparing occurrence probability in different land-use types relative to species with

1455 similar traits (I term such effects ‘among land-use type effects’, Figure 4.2a); or by comparing occurrence
1456 probability in a given land-use type relative to species with different traits (I term such effects ‘within land-
1457 use type effects’, Figure 4.2a).

- 1458 • Within land-use type effects (Figure 4.2a): from the full, all-predictor models fitted for each class, I
1459 focused on the interactive effects between land use and ecological characteristics (and between land-
1460 use intensity and ecological characteristics). These interactions indicated whether, in a given land-use
1461 type, there were any significant differences in occurrence probability between species with different
1462 traits. In other words, I looked at whether any trait level lowered or increased occurrence probability
1463 in each land-use type, compared to a reference trait level. I used this approach for all the categorical
1464 predictors, except diet (interpreting within land-use type effects for primary diet being complicated by
1465 the fact that there were more than two levels for this trait).
- 1466 • Among land-use type effects (Figure 4.2a): from a partial model, I predicted occurrence probability
1467 in the different land uses for all different levels of the trait. The partial models allowed to visualise
1468 occurrence patterns across land-use types for single explanatory variables, without having to account
1469 for the values of other variables. I used this approach to evaluate the influence of diet on species’
1470 land-use responses.

1471 Effects of continuous ecological characteristics on species’ occurrence probability (Figure 4.2b)

1472 For a given continuous ecological characteristic, any effect of land use or land-use intensity can be as-
1473 sessed through changes in the slope of the relationship between the ecological characteristic and occurrence
1474 probability (Figure 4.2b). When an ecological characteristic negatively impacts occurrence probability in a
1475 disturbed land use, I expect the slope of the relationship to be more negative than the slope for the reference
1476 land use (minimally-used primary vegetation). Focussing on slopes does not allow to infer absolute changes
1477 in occurrence probability across land-use types (e.g., a positive slope in a disturbed land use does not mean
1478 that there are absolute increases in occurrence probability in that land use, but only that higher values of the
1479 ecological characteristic are associated with relatively higher occurrence probability in that land-use type).
1480 This is because I do not assess changes in the mean occurrence probability here (which would require to
1481 consider the intercept of the relationship between the ecological characteristic and occurrence probability in
1482 different land-use types). Thus, I only capture ‘within land-use type’ effects for continuous predictors.

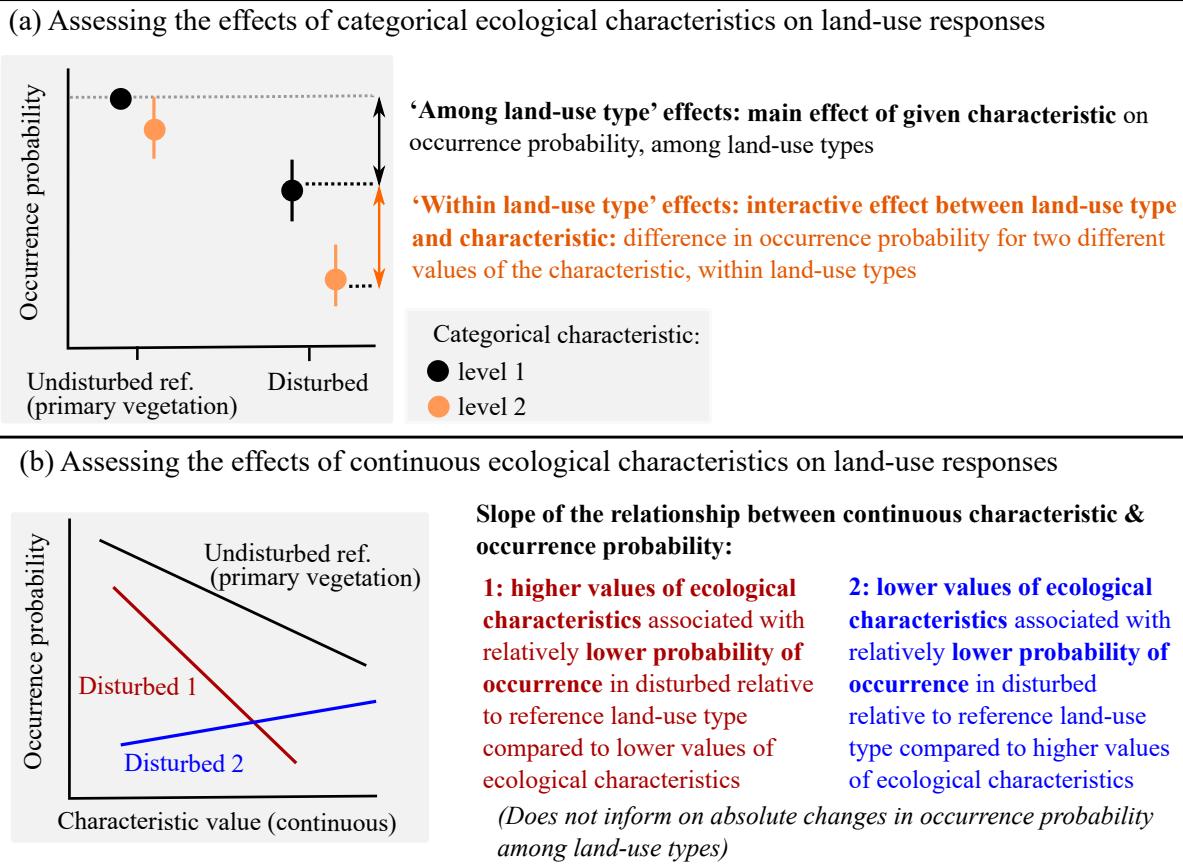


Figure 4.2: Assessing the effects of ecological characteristics on species' land-use responses: methodology for (a) categorical characteristics and (b) continuous characteristics. (a) For all categorical characteristics, except diet, I look at 'within land-use type' effects, asking whether there are significant differences in occurrence probability among species with different ecological characteristics in a given land-use type. For diet, I look at 'among land-use type' effects, comparing species occurrence probability in disturbed land uses versus that in primary vegetation (I chose this approach here because visualising 'within land-use type' effects for diet is complicated by the fact that there were more than two levels for this categorical trait). (b) For continuous characteristics, I focus on the relationship with occurrence probability, and I investigate how the slope of this relationship is affected by land-use type, i.e. a 'within land-use type' effect.

1483 Validation on complete trait data subset (no imputed trait values)

1484 To assess whether the results were robust to trait imputation uncertainty, I fitted the models again for the
 1485 subset of species for which I had complete, non-imputed data for all ecological characteristics. The models'
 1486 structure was unchanged for birds and mammals. For amphibians, I excluded both diet and litter/clutch size
 1487 because of multicollinearity issues, and I also excluded lifespan proxy and body mass (as there were too
 1488 many missing values in the dataset, 85% and 59% respectively). For reptiles, I excluded both diet and body
 1489 mass because of multicollinearity issues.

1490 **4.2.4 Characterizing the influence of traits on species' sensitivity to climate change (Figure**
1491 **4.1c)**

1492 I estimated climate-change sensitivity across vertebrate species using the ‘Climate-niche Factor Analysis’
1493 (CENFA) approach developed by Rinnan and Lawler (2019), implemented with the ‘CENFA’ R package
1494 version 1.1.1 (Rinnan, 2021). CENFA is a spatial approach for estimating species’ climate-change sensitivity,
1495 exposure, and vulnerability. CENFA combines distribution data with climatic variables to estimate sensitivity
1496 and vulnerability from properties of species’ climatic niches (see Rinnan and Lawler (2019) for details).
1497 CENFA has been used in previous studies focused on a small number of species or on a few taxonomic
1498 groups, but to my knowledge has not yet been applied across all terrestrial vertebrates.

1499 **Historical climate data**

1500 I used global climate data from WorldClim version 2.1 (Fick and Hijmans, 2017). I downloaded 19 climatic
1501 variables at a resolution of 2.5 arcminutes ($\sim 4.6 \text{ km}^2$ at the Equator). I removed variables that were strongly
1502 collinear with any other climatic variables (using a threshold of 0.65 for Spearman correlation coefficients).
1503 I obtained six groups of intercorrelated variables (using the ‘removeCollinearity’ function from the ‘virtu-
1504 alspecies’ R package version 1.5.1 (Leroy et al., 2015); Figure S4.4), and randomly selected one climatic
1505 variable in each group. The final set comprised six climatic variables: annual mean temperature (bio1), mean
1506 diurnal temperature range (bio2), maximum temperature of the warmest month (bio5), annual precipitation
1507 (bio12), precipitation seasonality (bio15), and precipitation of the coldest quarter (bio19).

1508 **Estimating climate-change sensitivity from CENFA**

1509 All climatic variables and distribution files were re-projected to a resolution of 5 km^2 in the Behrmann
1510 equal-area projection. I picked this resolution because the coarser the resolution, the more climate-change
1511 sensitivity tended to be underestimated for narrowly distributed species (Figures S4.5 & S4.6). However,
1512 finer resolutions demand a large amount of memory space when working at global scales across all terrestrial
1513 vertebrates. I found the 5-km^2 resolution to be an acceptable trade-off between computational load and
1514 accuracy of the sensitivity estimations. However, when working at 5-km^2 resolution, there were still some
1515 narrowly distributed species for which sensitivity was likely underestimated (Figure S4.6). Thus, I chose to
1516 exclude species with a range area $\leq 100 \text{ km}^2$ from further analyses (i.e., excluding narrow-ranging species
1517 whose distributions could intersect up to 4 grid cells). In doing so, the sample size was reduced by 660
1518 species for amphibians, by 142 species for birds, by 129 species for mammals, and by 615 species for

1519 reptiles (the final sample sizes were: n=4,537 for amphibians; n=10,198 for birds; n=4,721 for mammals;
1520 n=7,330 for reptiles). My results were overall robust to the exclusion of these species (see Results section).

1521 I then combined the climate data with the species' distributions to estimate sensitivity to climate change,
1522 applying the CENFA framework across terrestrial vertebrates (Figure 4.1c). Further details of the imple-
1523 mentation of the CENFA framework are given in Appendix 3 (S4.5: 'Implementing Climate-niche Factor
1524 Analysis across terrestrial vertebrates').

1525 **Climate-change sensitivity models**

1526 I used phylogenetic least-square (PGLS) regressions, implemented in the 'caper' R package version 1.0.1
1527 (Orme et al., 2018), to assess the effects of ecological characteristics on species' estimated sensitivity to
1528 climate change, while controlling for phylogenetic relationships among species. I combined the ecological
1529 characteristics and the phylogenies using the 'comparative.data' function from the 'caper' package, and then
1530 built class-specific models to explain climate-change sensitivity with the ecological characteristics (Figure
1531 4.1c). Before fitting the models, I checked for multicollinearity among the predictors using GVIF scores.
1532 Across all classes, the models included all the main effects of the ecological characteristics, except for am-
1533 phibians, for which I dropped diet breadth (which was strongly collinear with diet; Tables S4.9-S4.13). For
1534 the continuous predictors, I fitted third-order polynomials to allow for non-linearity of the responses (I in-
1535 cluded third order polynomials for the climate-change sensitivity models but not for the land-use models
1536 because the PGLS model had a simpler structure than the land-use models, were less computationally inten-
1537 sive, and also because the number of estimated parameters was already high for the land-use models without
1538 allowing for third-order polynomials). As such, the general form of the PGLS models was:
1539 $\log_{10}(\text{climate-change sensitivity}) \sim \text{poly}(\log_{10}(\text{continuous ecological characteristics}), 3) +$
1540 categorical ecological characteristics +
1541 phylogenetic random effects.

1542 **Models' robustness**

1543 To check whether the results were robust to the exclusion of species whose range area was $\leq 100 \text{ km}^2$, I
1544 repeated the models on all species (including those with range area $\leq 100 \text{ km}^2$: n=5,208 for amphibians;
1545 n=10,340 for birds; n=4,844 for mammals; n=7,951 for reptiles).

1546 Finally, to assess the degree to which the results were robust to trait imputation uncertainty, I fitted the
1547 models again for the subset of species for which I had empirical (i.e., non-imputed) trait estimates. Diet
1548 was excluded for amphibians and reptiles on the basis of high collinearity (GVIF>5). I fitted first-order

1549 polynomials here because of the substantially reduced sample size compared to the main models.

1550 4.3 Results

1551 4.3.1 Land-use responses

1552 ‘Within land-use type’ effects (Table 4.1a)

1553 Land-use, land-use intensity, species’ ecological characteristics and their interactions had significant effects
1554 on species occurrence probability. Significant interactive effects between land use and ecological charac-
1555 teristics (and between land-use intensity and ecological characteristics) reflected differences in the ability
1556 of species with different ecological characteristics to cope within the disturbed land-use types (Table 4.1a).
1557 Across all classes, species with narrower geographical range areas, smaller habitat breadth and inability to
1558 exploit artificial habitats showed greater decreases in occurrence probability within disturbed land uses, than
1559 species with larger range areas, larger habitat breadth and ability to exploit artificial habitats (the only ex-
1560 ceptions were opposite effects found for mammals and reptiles for habitat breadth in two of the land-use
1561 types). The effects of the other ecological characteristics differed in direction depending on class and land
1562 use, impeding any generalisation (Table 4.1a). For instance, I found that being smaller and longer-lived was
1563 associated with decreases in occurrence probability for birds found in agricultural areas, but with increases
1564 in occurrence probability for urban birds; and that longer-lived species tended to be more negatively affected
1565 for mammals and reptiles, whereas I found evidence of opposite trends for amphibians.

1566 I would like to highlight that the ‘within land-use type’ effects summarised in Table 4.1a do not nec-
1567 essarily reflect occurrence patterns among land-use types. For example, in all classes, ‘among land-use
1568 type’ effects derived from partial models showed that occurrence probability in disturbed land uses was
1569 strongly negatively affected for natural habitat specialists, compared with primary vegetation levels (Figure
1570 S4.7). On the other hand, in most classes and disturbed land uses, artificial habitat users either increased or
1571 showed no significant difference in occurrence probability. One exception was for reptiles, where the effect
1572 of habitat specialisation was mostly non-significant within land-use types (Table 4.1a), with both natural
1573 habitat specialists and artificial habitat users showing important declines in some disturbed land uses (e.g.,
1574 intensely-used agricultural areas, Figure S4.7d). Similarly, the occurrence probability of both nocturnal and
1575 non-nocturnal species was negatively impacted in disturbed land uses compared with primary vegetation
1576 (Figure S4.8), such that land-use responses were not distinguishable between nocturnal and non-nocturnal
1577 species for all classes and land-use types.

Table 4.1: Summary of the effects of the ecological characteristics (except for primary diet) on (a) species' responses to disturbed land uses ('within land-use type' effects) and (b) species' climate-change sensitivity, for each class of terrestrial vertebrates. The symbol - indicates where a characteristic has a significant negative effect on occurrence probability within a disturbed land-use type (within any of the land-use intensities), or where the characteristic renders species significantly more sensitive to climate change. A + indicates a significantly positive effect of a characteristic on occurrence probability in a land-use type (within any of the land-use intensities), or significantly lower sensitivity to climate change. For the land-use effects, I report 'within land-use type' effects here, that is, within a disturbed land use whether there were significant differences in occurrence probability among species with different trait values (see Figure 4.2). These effects were derived from the interactive terms of the full, all-predictor models.

(a) "Within land-use type" effects of the species-level characteristics on occurrence probability - <=> more sensitive; + <=> less sensitive																Predictors				(b) Climate-change sensitivity: - <=> more sensitive + <=> less sensitive				
-	-	-	-	(-)	-	0	-	0	-	-	-	-	0	-	0	NA	More narrowly-distributed		-	-	-	-	-	
0	-	0	+	-	-	-	0	-	-	0	-	0	0	-	+	NA	Smaller habitat breadth		-	-	-	-	-	
-	-	(-)	-	-	-	0	0	-	-	-	-	0	0	-	-	NA	Natural habitat specialist	(-)	-	-	-	-	-	
0	+	+	-	-	+	0	+	-	+	+	-	0	0	0	0	NA	Non-nocturnal		-	0	0	(+)		
-	0	+	(-)	-	0	+	+	-	0	0	+	0	-	0	NA	Narrower diet breadth		NA	0	-	0	0		
0	0	+	0	(+)	+	+	0	0	-	0	-	0	+	0	NA	Smaller body mass		-	+	-	-	-		
+	0	0	0	0	-	0	0	+	-	0	0	0	0	0	NA	Smaller litter/clutch size		-	+	+	0			
(-)	0	(+)	+	0	0	0	+	-	+	(+)	+	0	-	0	NA	Shorter-lived		(+)	-	0	-	-		

1578 **Effects of diet on species' occurrence probability (Figure 4.3)**

1579 In all classes, diet had significant effects on occurrence probability in disturbed land uses (Figure 4.3).
1580 Changes in occurrence probability in disturbed land uses differed among classes and dietary groups. Overall,
1581 invertebrate eaters tended to be negatively affected in disturbed land uses (e.g., -66% average declines in
1582 occurrence probability for amphibians in intensely used agricultural areas, compared with minimally-used
1583 primary vegetation). Omnivores were both negatively and positively impacted, showing both important
1584 decreases (e.g., -81% for reptiles in intensely used plantation forest) as well as strong increases (e.g., +43%
1585 for lightly used urban areas in birds). Overall, fruit/nectar eaters showed important declines in occurrence
1586 probability for mammals and birds, as opposed to plants/seeds eaters, whose occurrence probability tended
1587 to be strongly positively affected for birds, and dependent on land-use intensity for mammals (with increases
1588 in minimally-used land-types, but not in more intensely-used land-types). Finally, I also detected significant
1589 changes in occurrence probability for vertebrate eaters, with some declines for mammals in agricultural areas
1590 (-75% on average in intense uses), but also some increases (e.g., +43% on average for birds in lightly used
1591 agricultural areas).

1592 **Explanatory power for the full models & variance explained by each characteristic (Figure 4.4)**

1593 Overall, land use, land-use intensity and the ecological characteristics explained a small amount of the total
1594 variation in species' occurrence probability (marginal R²: 0.15 for amphibians; 0.054 for birds; 0.15 for
1595 mammals; 0.13 for reptiles), in part because the random effects explained a substantial proportion (condi-
1596 tional R²: 0.59 for amphibians; 0.61 for birds; 0.72 for mammals; 0.57 for reptiles). The relative importance
1597 of traits explaining the most variation differed among classes, with interactions between land use and habitat
1598 breadth explaining the most variation in amphibians and birds, but interactions between land use and body
1599 mass explaining the most variation for mammals, and interactions between land use and lifespan explaining
1600 the most variation for reptiles (Figure 4.4a).

1601 Finally, the models' diagnostics showed evidence of deviations from distributional assumptions (diag-
1602 nistic plots for the full models are shown in Figures S4.9-S4.12). However, when estimated from a Bayesian
1603 framework, the models' estimates were mostly congruent (results not shown), so the frequentist approach I
1604 used with 'lme4' was robust despite the deviations from distributional assumptions. The phylogenetic sig-
1605 nals in the models' residuals were low and not significant (Pagel's $\lambda < 0.01$ for amphibians and reptiles, $p \approx$
1606 1; $\lambda = 0.13$ for mammals, $p = 0.09$; $\lambda = 0.01$ for birds, $p = 0.56$), despite not having included phylogenetic
1607 random effects.

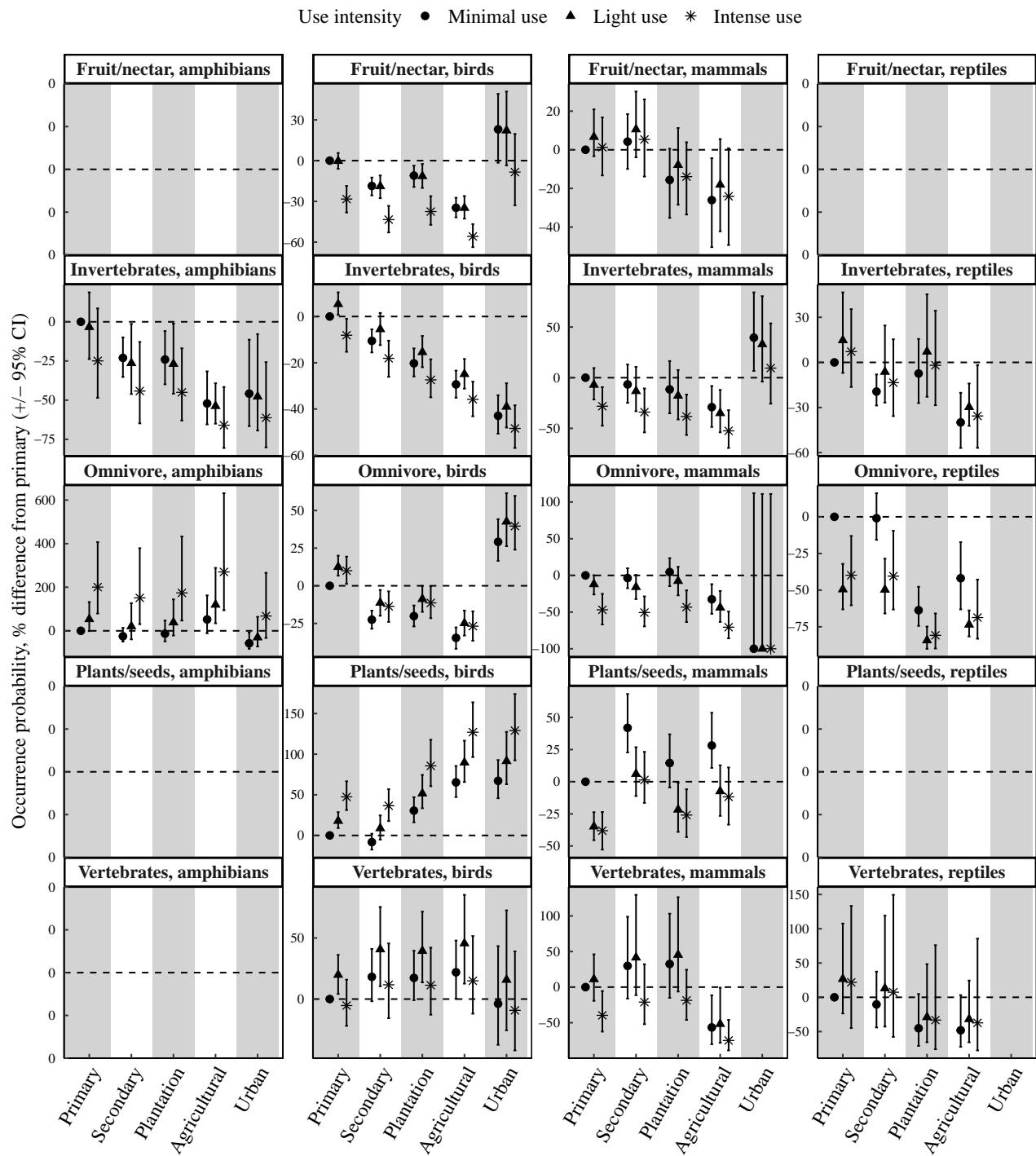


Figure 4.3: Predicted occurrence probability as a function of land use, land-use intensity, diet and their interactions, for each class of terrestrial vertebrates (mean \pm 95% confidence interval; the predictions are rescaled with reference to minimally-used primary vegetation). The predictions were obtained from the partial models fitted for each class, considering only diet among the ecological characteristics. Empty plots are drawn where there were no data for a diet category for a given class. Effects could not be estimated for urban reptiles, as well as for urban vertebrate, fruit/nectar and plant/seed eaters for mammals because there were no sampled species. Primary: primary vegetation; Secondary: secondary vegetation; Plantation: plantation forest; Agricultural: cropland and pasture.

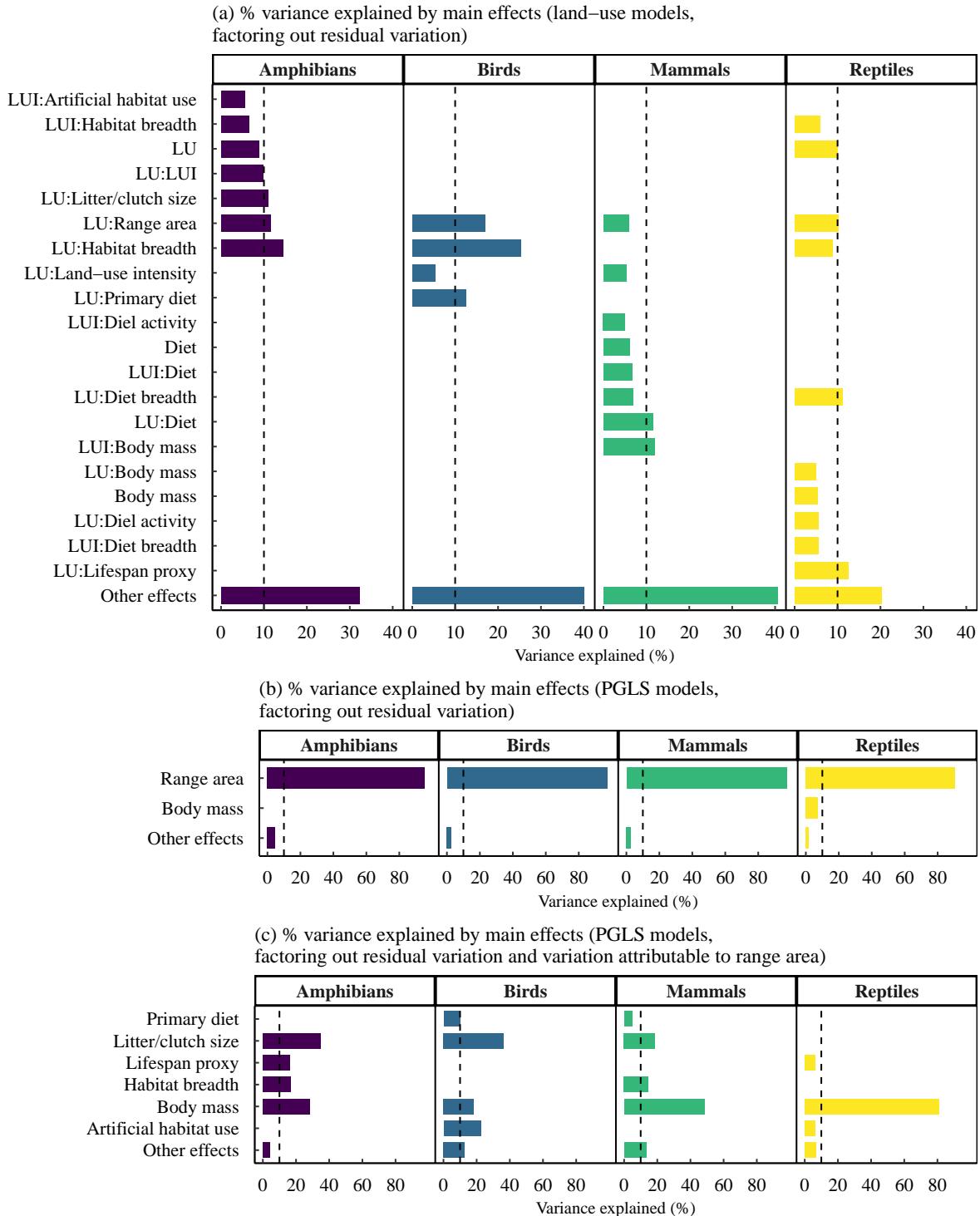


Figure 4.4: Proportion of the explained variance attributable to each of the main effects for (a) the mixed-effects models fitting the effects of land use, land-use intensity, and ecological characteristics on species occurrence probability (after factoring out residual variation); (b) for the phylogenetic least-squares regressions investigating whether the ecological characteristics explained climate-change sensitivity (after factoring out residual variation); and (c) for the phylogenetic least-squares regressions investigating whether the ecological characteristics explained climate-change sensitivity (after factoring out the variance explained by geographical range area and the residual variation). The dashed vertical lines mark 10% explained variance (for visualisation purposes). I individually show all the effects that explain more than 5% of the overall variation. Effects that individually explain less than 5% of the overall variation are grouped together as ‘Other effects’. LU: land use; LUI: land-use intensity.

1608 **4.3.2 Climate-change sensitivity**

1609 The ecological characteristics were significantly associated with climate-change sensitivity in all classes
1610 (Tables 4.1b & 4.2, Figures 4.5 & 4.6); models' coefficients shown in Tables S4.14-S4.17). Overall, climate-
1611 change sensitivity was highest for amphibians (median \log_{10} -sensitivity: 1.1; 95% interpercentile range:
1612 0.40-2.2), then reptiles (median \log_{10} -sensitivity: 1.0; 95% interpercentile range: 0.32-2.1), then mammals
1613 (median \log_{10} -sensitivity: 0.76; 95% interpercentile range: 0.22-2.0) and birds (median \log_{10} -sensitivity:
1614 0.62; 95% interpercentile range: 0.21-1.77). In all classes, narrower geographical range area, smaller habitat
1615 breadth and being specialised on natural habitats were consistently associated with higher climate-change
1616 sensitivity (Table 4.1b). However, other characteristics did not have consistent associations with climate-
1617 change sensitivity across classes, in different cases varying in both significance and direction. For instance,
1618 I found opposite associations between body mass and climate-change sensitivity for mammals, amphibians
1619 and reptiles on the one hand, and birds on the other hand.

1620 The PGLS models explained an important proportion of the overall variation in estimated climate-change
1621 sensitivity (adjusted $R^2 = 0.64$ for amphibians; 0.62 for birds; 0.63 for mammals and reptiles). Geographical
1622 range area explained the majority of this variation in climate-change sensitivity (about 60% in all classes;
1623 Figure 4.4b), which largely reflects the design of the CENFA approach. When factoring out residual variation
1624 and variation explained by geographical range area, the relative importance of the traits as correlates of
1625 climate-change sensitivity varied among classes (Figure 4.4c), with body mass explaining the most variation
1626 for mammals and reptiles, and litter/clutch size explaining the most variation for amphibians and birds.

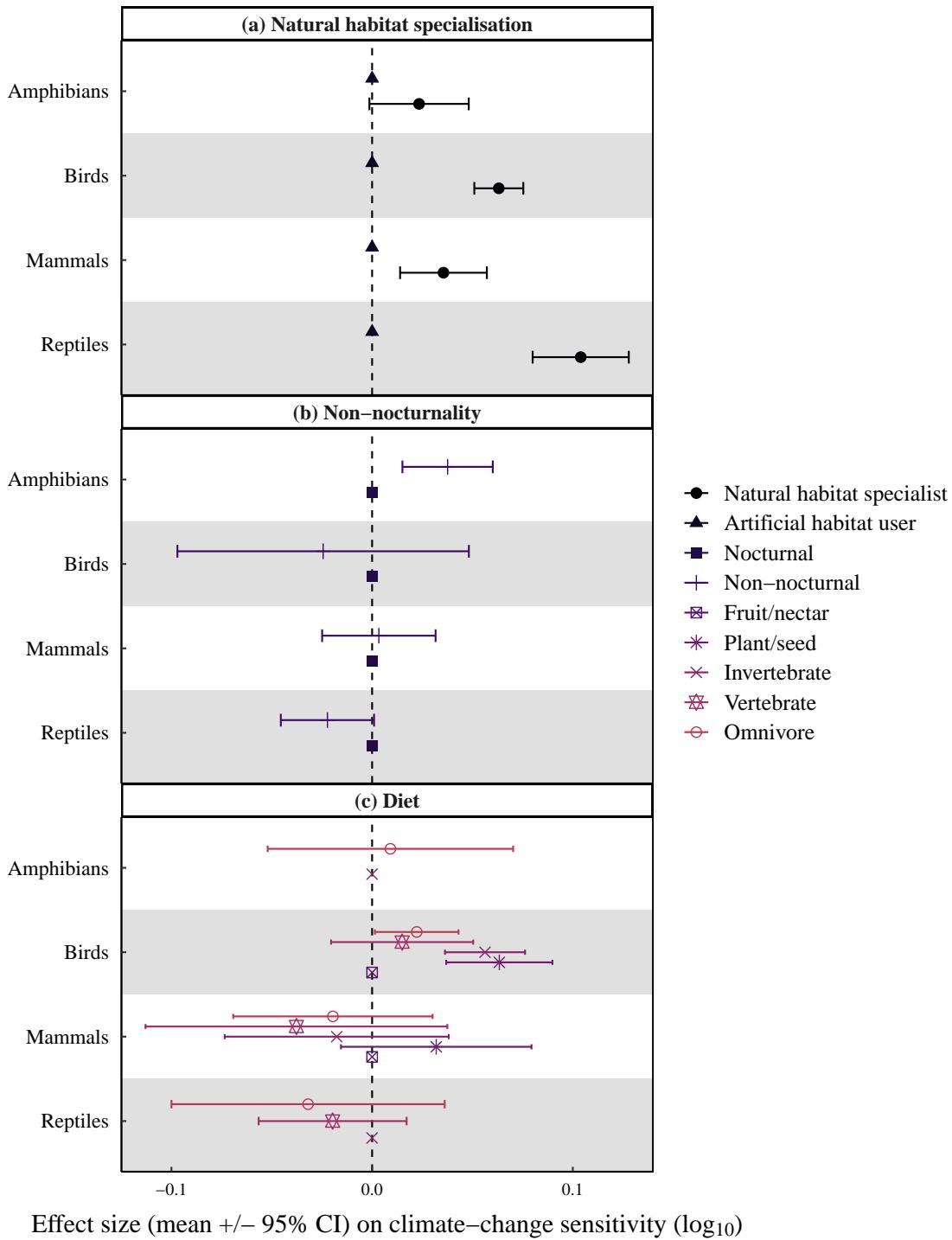


Figure 4.5: Estimated effects of the categorical traits on climate-change sensitivity, from the PGLS models fitted in each class (mean effect \pm 95% confidence interval). For each categorical trait, I show the effect size for all levels referring to the reference level (vertical dashed line). (a) For artificial habitat use, the reference level is ‘Artificial habitat user’; (b) for diel activity, the reference level is ‘Nocturnal’; (c) for diet, the reference level for mammals and birds is ‘Fruit/nectar’ eaters, but it is ‘Invertebrate’ eaters for amphibians and reptiles.

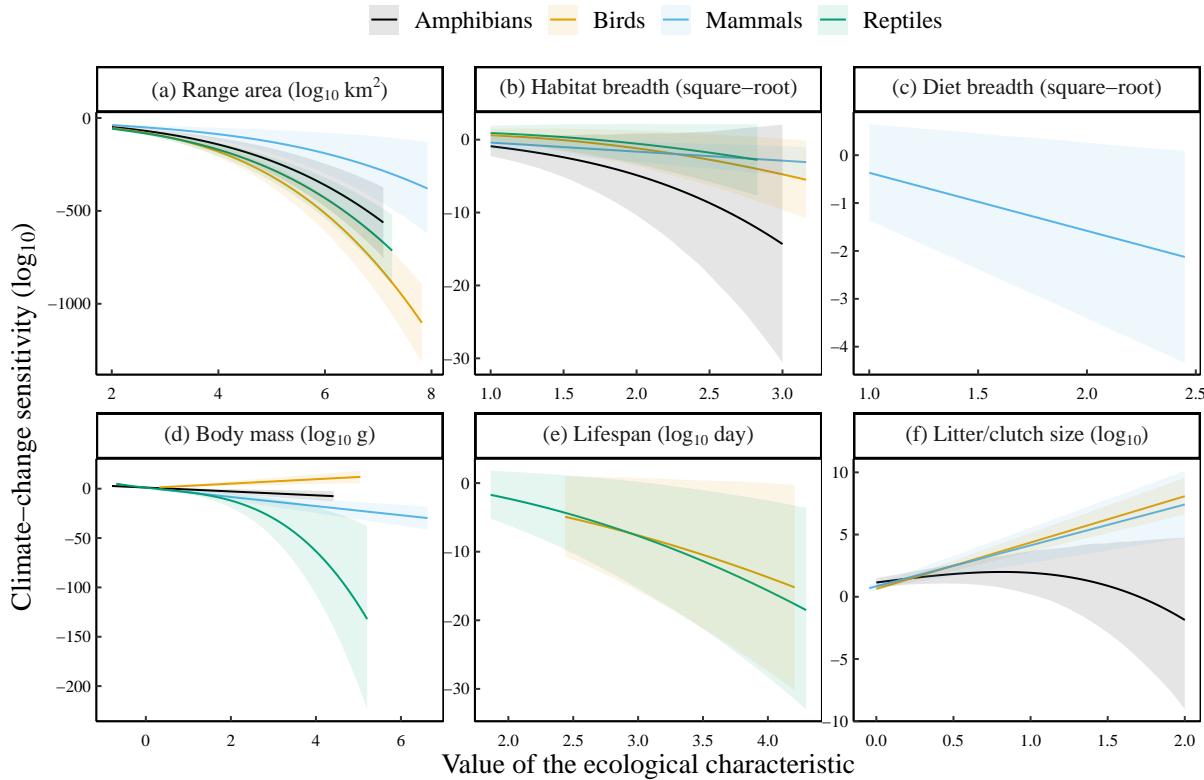


Figure 4.6: Effects of the continuous ecological characteristics on climate-change sensitivity, estimated from the PGLS models in each class. The lines represent the estimated relationships between climate-change sensitivity and ecological characteristics; the shaded areas are 95% confidence intervals. I plotted the estimated relationships only when they were found to be significant.

1627 Robustness of the PGLS models

1628 The PGLS models were robust to distributional assumptions (Figures S4.13-S4.16). When fitting the models
 1629 on all species (including those with range area $\leq 100 \text{ km}^2$), I found that the relationship between climate-
 1630 change sensitivity and geographical range area was reversed in all classes (with smaller-ranging species
 1631 estimated to be less sensitive). This result is likely an artefact caused by the underestimation of climate-
 1632 change sensitivity for the most narrow-ranging species, which would support the exclusion of such species
 1633 from the analysis. Other results were generally not sensitive to the exclusion of species whose range area
 1634 was $\leq 100 \text{ km}^2$ (Figure S4.17).

Table 4.2: ANOVA summaries for the PGLS models investigating the associations between the species-level ecological characteristics and species' estimated climate-change sensitivity.

Class	Model terms	Df	Sum Square	Mean Square	F-value	Pr(>F)
Amphibians	poly(log ₁₀ (Body mass, 3))	3	9.85E-02	3.28E-02	3.41E+01	9.03E-22 ***
	poly(log ₁₀ (Lifespan proxy), 3)	3	5.62E-02	1.87E-02	1.94E+01	1.60E-12 ***
	poly(log ₁₀ (Litter/clutch size), 3)	3	1.22E-01	4.07E-02	4.22E+01	6.68E-27 ***
	poly(log ₁₀ (Range area), 3)	3	7.30E+00	2.43E+00	2.52E+03	0.00E+00 ***
	poly(sqrt(Habitat breadth), 3)	3	5.86E-02	1.95E-02	2.03E+01	4.69E-13 ***
	Specialisation	1	3.17E-03	3.17E-03	3.29E+00	6.96E-02 .
	Diel activity	1	1.03E-02	1.03E-02	1.07E+01	1.07E-03 **
	Diet	3	8.61E-04	2.87E-04	2.98E-01	8.27E-01
Birds	poly(log ₁₀ (Body mass, 3))	3	5.78E-02	1.93E-02	2.87E+01	1.87E-18 ***
	poly(log ₁₀ (Lifespan proxy), 3)	3	1.55E-02	5.18E-03	7.70E+00	3.87E-05 ***
	poly(log ₁₀ (Litter/clutch size), 3)	3	1.15E-01	3.83E-02	5.70E+01	1.63E-36 ***
	poly(log ₁₀ (Range area), 3)	3	1.10E+01	3.66E+00	5.45E+03	0.00E+00 ***
	poly(sqrt(Habitat breadth), 3)	3	1.29E-02	4.30E-03	6.39E+00	2.53E-04 ***
	poly(sqrt(Diet breadth), 3)	3	1.01E-02	3.38E-03	5.02E+00	1.77E-03 **
	Specialisation	1	7.10E-02	7.10E-02	1.06E+02	1.15E-24 ***
	Diel activity	1	1.58E-03	1.58E-03	2.34E+00	1.26E-01
Mammals	Primary diet	4	3.15E-02	7.88E-03	1.17E+01	1.70E-09 ***
	poly(log ₁₀ (Body mass, 3))	3	9.00E-02	3.00E-02	3.44E+01	5.41E-22 ***
	poly(log ₁₀ (Lifespan proxy), 3)	3	7.32E-03	2.44E-03	2.80E+00	3.85E-02 *
	poly(log ₁₀ (Litter/clutch size), 3)	3	3.46E-02	1.15E-02	1.32E+01	1.33E-08 ***
	poly(log ₁₀ (Range area), 3)	3	6.83E+00	2.28E+00	2.61E+03	0.00E+00 ***
	poly(sqrt(Habitat breadth), 3)	3	2.73E-02	9.11E-03	1.05E+01	7.50E-07 ***
	poly(sqrt(Diet breadth), 3)	3	8.64E-03	2.88E-03	3.31E+00	1.94E-02 *
	Specialisation	1	8.99E-03	8.99E-03	1.03E+01	1.33E-03 **
Reptiles	Diel activity	1	6.08E-06	6.08E-06	6.98E-03	9.33E-01
	Primary diet	4	9.32E-03	2.33E-03	2.67E+00	3.04E-02 *
	poly(log ₁₀ (Body mass), 3)	3	8.53E-01	2.84E-01	3.18E+02	3.24E-194 ***
	poly(log ₁₀ (Lifespan proxy), 3)	3	6.40E-02	2.13E-02	2.39E+01	2.25E-15 ***
	poly(log ₁₀ (Litter/clutch size), 3)	3	4.55E-02	1.52E-02	1.70E+01	5.50E-11 ***
	poly(log ₁₀ (Range area), 3)	3	1.03E+01	3.42E+00	3.83E+03	0.00E+00 ***
	poly(sqrt(Habitat breadth), 3)	3	1.34E-02	4.48E-03	5.01E+00	1.81E-03 **
	poly(sqrt(Diet breadth), 3)	3	6.37E-03	2.12E-03	2.38E+00	6.79E-02 .
	Specialisation	1	6.58E-02	6.58E-02	7.36E+01	1.13E-17 ***
	Diel activity	1	2.76E-03	2.76E-03	3.09E+00	7.89E-02 .
	Diet	2	1.34E-03	6.69E-04	7.48E-01	4.73E-01

1635 **4.3.3 Validations on complete trait data**

1636 Running the land-use and PGLS models again using data subsets for which I had empirical, non-imputed
1637 values only for the ecological characteristics showed that the conclusions of this work are likely robust
1638 to imputation uncertainty. Overall, across all classes, the associations of geographical range area, habitat
1639 breadth and use of artificial habitats with sensitivity to climate change and land-use responses were consistent
1640 with the main models (Table S4.10, Figure S4.18).

1641 **4.4 Discussion**

1642 Here, I investigated whether species' ecological characteristics were associated with species' sensitivity to
1643 two human pressures (climate change and land-use change), across terrestrial vertebrate classes. Overall, I
1644 found that geographical range area, habitat breadth and specialisation on natural habitats were consistently
1645 associated with sensitivity to both pressures across terrestrial vertebrate classes: narrower ranges, narrower
1646 habitat breadth and inability to exploit artificial habitats were associated with more negative land-use re-
1647 sponds and with higher climate-change sensitivity. My results are in line with previous meta-analyses that
1648 have found species' extinction risks to be associated with habitat breadth and range area (Chichorro et al.,
1649 2019), range shifts under contemporary climate change to be associated with species' historical range limits
1650 and habitat breadth (MacLean and Beissinger, 2017), and with many other studies on land-use responses or
1651 extinction risks (Newbold et al., 2018; Nowakowski et al., 2017; Purvis et al., 2000; Ripple et al., 2017).
1652 However, to the best of my knowledge, this work constitutes the first global study to compare patterns among
1653 vertebrate classes and between the two major human pressures of climate change and land use. The results
1654 of this Chapter have important implications for conservation, as they mean that land-use and climate change
1655 are non-randomly affecting all terrestrial vertebrates, with a consistently higher risk for geographically rarer
1656 species and habitat specialists. Geographical rarity has been employed by the IUCN for many years in vul-
1657 nerability assessments (Rodrigues et al., 2006), and this work provides further support for its integration in
1658 large-scale assessments. My results also lend support to the idea that habitat specialisation is a likely indica-
1659 tor of species' sensitivity to both land-use and climate change across all vertebrates, thus indices reflecting
1660 habitat specialisation should be highly relevant to consider in large-scale vulnerability assessments, as done
1661 by Foden et al. (2013).

1662 This work further highlights the class-specific associations between most traits and likely responses to
1663 human-driven environmental changes, but again highlighting a non-random reshaping of vertebrate biodi-
1664 versity under global changes. In the case of land use, I find that the directionality of the responses not only

often depends on taxonomic class but also on land-use type, further complicating the patterns. In line with past work highlighting the low explanatory power of traits when used to explain species' responses to human pressures (Angert et al., 2011; Cannistra and Buckley, 2021; Verberk et al., 2013), I found that most traits explained a small proportion of the interspecific variation in land-use responses and in climate-change sensitivity. The only exception was range area, which explained a large proportion of the interspecific variation in climate-change sensitivity. Given that the estimates of climate-change sensitivity were based on properties of species' climatic niches (Rinnan and Lawler, 2019), it was not surprising that range area explained such an important part of the interspecific variation in sensitivity, as it is likely that broader range areas are associated with broader climatic tolerances, and thus with lower estimated climate-change sensitivity on average.

Despite their generally low explanatory power, traits have been used to assess species vulnerability to human threats, in particular to climate change (Böhm et al., 2016; Foden et al., 2013). One of the conceptual appeals behind the use of traits is that if clear patterns in responses to environmental change can be identified across taxa, then it could be possible to generalize their effects in space and time (Hamilton et al., 2020; Verberk et al., 2013), which is of interest for conservation -- notably for data-deficient species and/or those lacking estimates of abundance or population sizes. This work does not provide support for the generalisation at large scales of the effects of life-history and dietary traits on sensitivity to either land-use or climate change. The class-specific influence of traits on climate-change sensitivity, coupled with their low explanatory power, could be one of the reasons why trait-based approaches have been shown to perform less well and show less congruence than trend-based approaches (which rely on the use of long-term population data) for climate-change vulnerability assessments (Wheatley et al., 2017). Indeed, low explanatory power is likely to be particularly problematic for drawing inferences and predictions on species' responses to environmental change from traits. I would like to emphasize that this does not mean that life-history and dietary traits are unimportant for understanding species' responses; it means, however, that the effects of traits and their relative importance and predictive power could depend on interactions between the considered taxa and the pressures affecting them.

Further, it is possible that general underlying patterns remain undetected or are being masked by interactions and trade-offs among traits, which I did not consider here. For instance, larger species tend to have larger dispersal distances and movement abilities (Jenkins et al., 2007), which could be beneficial to resource acquisition in disturbed areas (Hillaert et al., 2018); however, such species also tend to have higher energetic requirements (White, 2011) and lower reproductive output, which could be detrimental to their persistence in the face of environmental change. Interactions and trade-offs among traits have been shown to be important for understanding which species are likely to persist in disturbed environments (Sayol et al., 2020), but little

1697 is known about their potential effects at large scales and for different types of pressure. Thus, developments
1698 of my work could focus on the effects of trait interactions on species' sensitivity to climate change and
1699 land-use responses. I was also unable to consider intraspecific variation in this work. Intraspecific variation
1700 and the potential for acclimation and evolutionary adaptation are likely important determinants of species'
1701 ability to cope with human disturbance (Carlson et al., 2014; Rohr et al., 2018), but considering such effects
1702 at large scales is challenging because of the lack of available data.

1703 Moreover, I investigated climate-change sensitivity and land-use responses separately, meaning that I
1704 did not consider the combined effects of these pressures. However, human pressures act in combination
1705 (Capdevila et al., 2022a; Harfoot et al., 2021; Segan et al., 2016), and a number of confounding factors and
1706 threats that I could not account for could possibly influence species' sensitivity. For example, larger species
1707 might be more sensitive to warming than smaller species (Hantak et al., 2021; Merckx et al., 2018), but larger
1708 species could also be better able to persist in fragmented landscapes, such that habitat fragmentation and cli-
1709 mate warming may have opposite effects on the responses of such species. Further, larger species might also
1710 be disproportionately exposed to other threats such as overexploitation and human-wildlife conflicts (Rip-
1711 ple et al., 2014, 2017). Interactions among traits, among types of pressure, and among traits and pressures
1712 should ideally be considered together to understand species' responses to human disturbances (Hantak et al.,
1713 2021). However, considering all these effects simultaneously may be challenging because of data-limitation
1714 issues, model complexity, and difficulty in assessing and disentangling individual and interactive effects. In
1715 addition, I would like to emphasize that my results, based on correlative assessments of the associations be-
1716 tween ecological characteristics and species' sensitivity to climate change and species' land-use responses,
1717 do not allow to infer any causal links between traits and species' responses to global changes. Reinforcing
1718 our mechanistic understanding of how traits influence species' ability to cope with different disturbances
1719 may help understand opposite signatures of human impacts on vertebrate trait diversity (e.g., on body mass
1720 (Hantak et al., 2021; Merckx et al., 2018; Rapacciulo et al., 2017; Ripple et al., 2014, 2017)). Further work
1721 could help elucidate the mechanistic links between species traits and responses to environmental change,
1722 perhaps supported by long-term population data and demographic models (Hernández-Yáñez et al., 2022).

1723 To conclude, the results of this Chapter indicate that land-use and climate change are likely to impact
1724 terrestrial vertebrates non-randomly with respect to their ecological characteristics, which could have impor-
1725 tant consequences for ecosystem functioning (Duffy, 2003; Luck et al., 2012). I found that narrow-ranging
1726 species, species with smaller habitat breadth and species with natural habitat specialisation are disproportio-
1727 nately sensitive to both land-use and climate change. Further, I detected substantial declines in occur-
1728 rence probability of certain dietary groups in disturbed land-use types, most notably invertebrate eaters

1729 and fruit/nectars eaters in all classes. I also found higher climate-change sensitivity for invertebrate- and
1730 plant/seed-eating birds. My findings thus highlight the potential risks from global changes for ecosystem
1731 processes and services sustained by those species, such as pest control, seed dispersal or pollination (Civan-
1732 tos et al., 2012; Fricke et al., 2022; González-Varo et al., 2013), highlighting the need to put into place
1733 mitigation and conservation measures in the face of global changes.

5 | Energetic constraints and trophic group explain species persistence in disturbed land uses

Keywords

Land use; land-use intensity; metabolic rates; energetic constraints; energetic requirements; terrestrial vertebrates; trophic group; occurrence.

Abstract

Land-use change is the primary driver of global biodiversity loss. In terrestrial vertebrates, previous work has shown that sensitivity to land-use change depends on species traits, but the extent to which energetic constraints explain species' responses to disturbed land uses remains largely unexplored. Here, I investigate relationships between the energetic requirements of terrestrial vertebrates (estimated from resting metabolic rates) and land-use change, at two levels of organisation. First, at the assemblage level I hypothesize that total energetic requirements in disturbed land uses are lower than in undisturbed land uses, assuming that there is less energy available in these areas overall. Second, after controlling for the effects of body mass and taxonomy on metabolic rates, I predict that species with relatively lower energetic expenditure are favoured over species with relatively higher energetic expenditure in disturbed land uses, as resource efficiency will be beneficial in these resource-poor environments. Because trophic group influences species' ability to assimilate various types of food, I investigate whether my predictions are consistent among trophic groups (here, omnivores, carnivores or herbivores). The results challenged both hypotheses. I found that total assemblage-level energetic requirements did not systematically decrease in disturbed land uses. For instance,

1754 I detected significant increases for urban areas in all trophic groups, highlighting that disturbed areas may not
1755 be as energy-poor as I initially assumed. Second, I found a positive effect of metabolic rates (after controlling
1756 for body mass and taxonomy) on species probability of occurrence across all trophic groups for at least one
1757 of the most disturbed land uses I considered (pasture, cropland and urban). Species for which there are
1758 exploitable resources in disturbed environments may benefit from having larger mass-independent energetic
1759 expenditure: they may display a set of characteristics rendering them more able to cope with disturbances
1760 and more able to acquire available resources, such as higher activity levels or bigger brain sizes. The findings
1761 of this Chapter highlight that land-use change has substantial impacts on vertebrate community metabolism.

1762 **5.1 Introduction**

1763 Land-use change is currently the strongest driver of global biodiversity declines (Maxwell et al., 2016;
1764 Newbold et al., 2015), with major and long-lasting impacts on the structure and functioning of ecological
1765 communities (Bregman et al., 2016; Fukasawa and Akasaka, 2019; Magioli et al., 2021; Marcacci et al.,
1766 2021). With land-use change likely to continue to intensify (Stehfest et al., 2019), it is vital to put into
1767 place conservation and mitigation measures to minimise future losses of biodiversity and negative impacts
1768 on ecosystem functioning. To this end, pressing questions remain as to what renders species able or unable
1769 to cope with human disturbance, and how losses of sensitive species might influence ecosystem functioning
1770 (Dirzo et al., 2014; Young et al., 2016).

1771 Land-use change acts as an environmental filter affecting species persistence (Edwards et al., 2021;
1772 Evans et al., 2018). Past studies have shown that sensitivity to land-use change is distributed unevenly across
1773 the tree of life (Nowakowski et al., 2018), and across behavioural (Lowry et al., 2013; Samia et al., 2015)
1774 and ecological strategies (De Palma et al., 2015; Møller, 2009; Newbold et al., 2013). For instance, long-
1775 lived and large forest specialist birds respond more negatively to land-use change than generalist species
1776 (Newbold et al., 2013). In addition, human land uses impose energetic constraints on species, by modifying
1777 the amount and type of available resources (Inger et al., 2016; Zuñiga-Palacios et al., 2021). Consequently,
1778 land-use change brings about modifications in dietary and foraging strategies (Møller, 2009; Ramesh et al.,
1779 2017; Sévèque et al., 2020), which can have cascading effects on local trophic structure (e.g., mesopredator
1780 release; Crooks and Soulé (2010)). The impacts of land-use change on biodiversity also depend on land-
1781 use intensity (Davison et al., 2021; Newbold et al., 2015), that is, the magnitude of human disturbance in
1782 a given land-use type, which can vary importantly according to local practices and management (Dullinger
1783 et al., 2021). In particular, land-use intensity affects the types and availability of resources (by homogenising

1784 resources for example), which in turn may affect biodiversity patterns (Weiner et al., 2011).

1785 Energetic requirements are likely to be important predictors of species' ability to cope with a disturbed
1786 environment where resource availability and resource types are strongly impacted (Auer et al., 2020). Past
1787 research has shown that metabolic rates (the amount of energy required for organismal maintenance and for
1788 other processes such as growth and reproduction) are heritable and subject to selection, for instance with
1789 species in energy-rich environments having evolved faster metabolic rates than species in less energy-rich
1790 environments (Mueller and Diamond, 2001). However, metabolic rates have received less attention than
1791 other life-history traits in studies aiming to understand different species' responses to land-use change. Body
1792 mass, known to explain much of the variation in metabolic rates (Bushuev et al., 2018; Hudson et al., 2013;
1793 White and Seymour, 2003), has been considered in past studies examining effects of land-use disturbance on
1794 assemblage composition (Hevia et al., 2017). Since metabolic rates correlate positively with body mass, the
1795 effects of land-use change on local energetic requirements have been indirectly assessed through investiga-
1796 tions of changes in body-mass composition along land-use gradients (Newbold et al., 2020a; Tinoco et al.,
1797 2018). However, to the best of my knowledge, no study has yet directly reported the effects of land-use
1798 change on assemblage-level energetic requirements.

1799 Thus, the first objective of this Chapter is to investigate how land-use change impacts assemblage-level
1800 energetic requirements in terrestrial vertebrates. To this end, I use metabolic rates as a proxy for maintenance
1801 energetic requirements at the species level. I predict that, at the assemblage level, total energetic requirements
1802 in disturbed land uses are lower than in undisturbed land uses. This prediction relies on the assumption that
1803 there is less energy available overall in disturbed land uses than in undisturbed land uses (Figure 5.1c), with
1804 disturbed land uses being characterised by human appropriation of net primary productivity (Krausmann et
1805 al., 2013). Because species' ability to exploit particular resources and meet energetic demands also depends
1806 on food types and diet (McNab, 1986; Mendoza and Araújo, 2019), I test whether this prediction holds
1807 true within trophic groups (i.e., within herbivores, omnivores, and carnivores). Here, I consider energetic
1808 requirements at the assemblage level, not controlling for species' body mass, to obtain estimates of total
1809 energy expenditure in different land-use types (Figure 5.2a). Thus, any changes in assemblage-level energetic
1810 requirements could be ultimately driven by shifts in the size-spectrum of local assemblages.

1811 Body mass explains much of the variation in metabolic rates, but species with similar body masses still
1812 display important variation in metabolic rates (Mueller and Diamond, 2001). Some of this variation can
1813 be explained by taxonomic position (which also accounts for differences in thermoregulatory strategy be-
1814 tween endotherms and ectotherms). However, there remains substantial interspecific variation in metabolic
1815 rates even after accounting for body mass and taxonomic affiliation (Mueller and Diamond, 2001; White

1816 and Kearney, 2013). Food availability and food type might explain this residual variation in metabolic rates
1817 among species (Mueller and Diamond, 2001). Species that evolved in areas with abundant resources assim-
1818 ilate and burn calories at high rates, regardless of their body mass – while species that evolved with limiting
1819 resources could process resources at lower rates, irrespectively of their body mass (Mueller and Diamond,
1820 2001). Building upon this idea and the ‘allocation’ principle (i.e., the trade-offs in resource allocation; Auer
1821 et al. (2020)), species with lower energetic expenditure (than expected from body mass and taxonomy) may
1822 be able to cope with food scarcity better than those with larger energy expenditure (than expected from
1823 body mass and taxonomy). Indeed, regardless of their body mass, such species should need fewer resources
1824 to meet energetic demands (Clarke and Fraser, 2004). Thus, as land-use disturbance modifies the types and
1825 abundance of resources, I expect species energetic requirements –after removing the effects of body mass and
1826 taxonomic position– to influence responses to land-use change. Yet, whether energetic constraints explain
1827 species’ responses to land-use change in terrestrial vertebrates has not been investigated before (Hevia et al.,
1828 2017). Thus, the second objective of this Chapter is to characterise the influence of energetic constraints
1829 on species occurrence probability in disturbed land uses, compared to undisturbed land uses. I approximate
1830 energetic constraints at the species level from residual variation in metabolic rates, that is, the variation not
1831 explained by body mass or taxonomy. I predict that species with negative deviations (lower rates than ex-
1832 pected from body mass and taxonomy) are more likely to persist in disturbed land uses than species with
1833 positive deviations (higher rates than expected from body mass and taxonomy; Figure 5.2b). Given that
1834 trophic group can influence resource acquisition and species’ ability to assimilate various types of food, I
1835 investigate whether this prediction is consistent among trophic groups.

1836 To test both predictions, I use a space-for-time substitution approach, obtaining vertebrate assemblage
1837 composition data from the PREDICTS database (Hudson et al., 2014, 2017). I combine this database with
1838 trophic-group information (characterising species as either omnivores, herbivores, or carnivores), and with
1839 species-level estimates of resting metabolic rates and body mass.

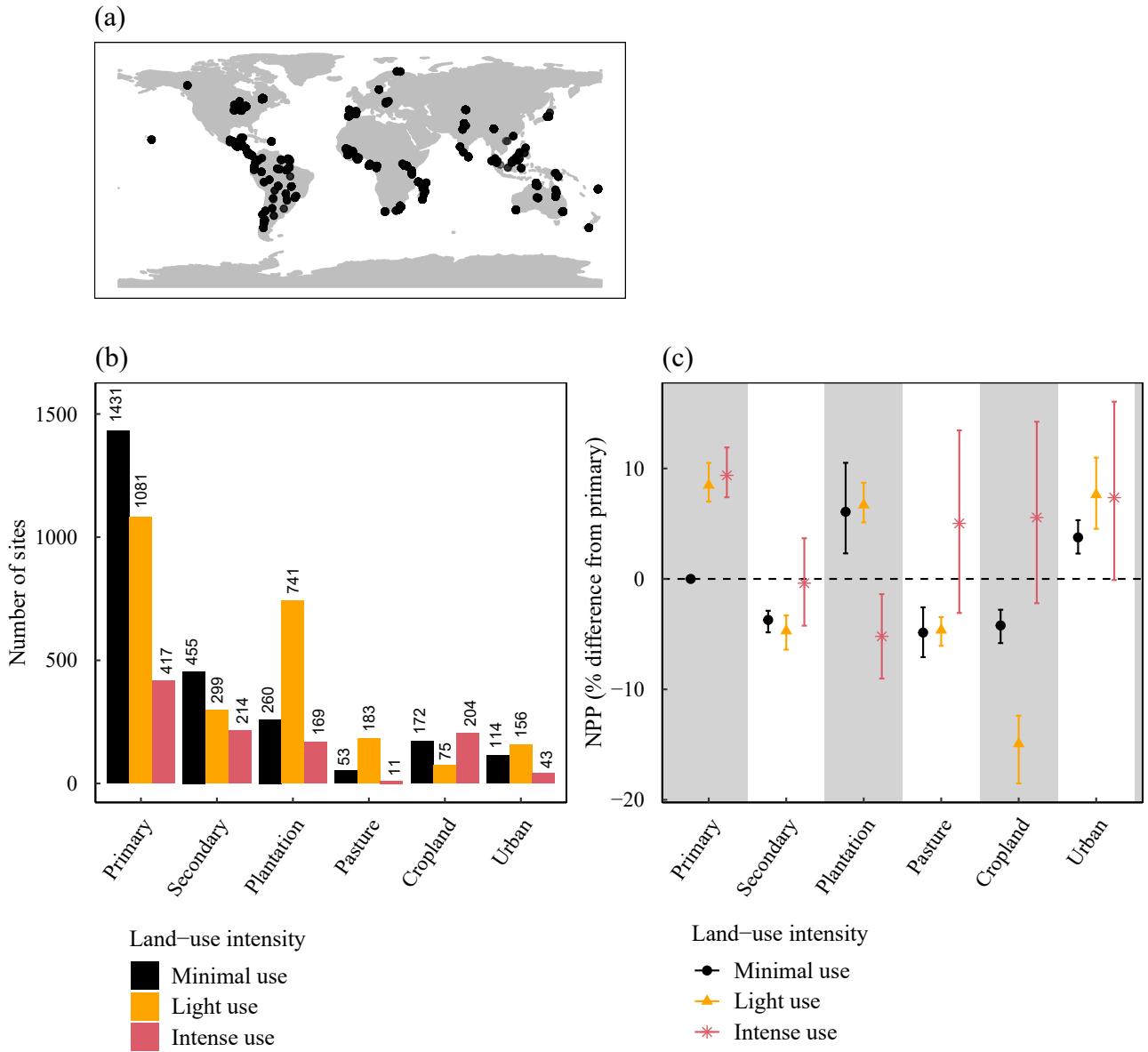
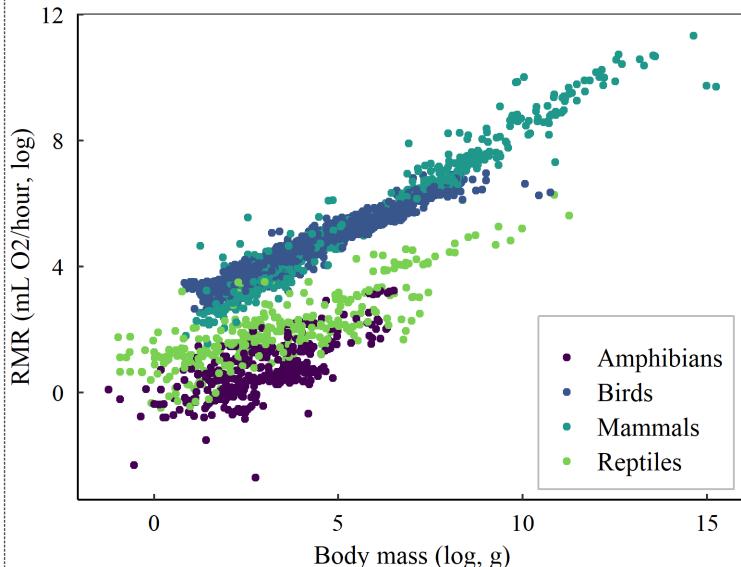


Figure 5.1: (a) Spatial distribution of the sampled sites from the PREDICTS database for terrestrial vertebrates (6,484 sites); (b) Number of sites in each land-use and land-use-intensity category; (c) Net primary productivity by land use and land-use intensity (derived from MODIS satellite imagery), with model predictions plotted relative to minimally used primary vegetation (and rescaled with reference to that land-use type). Primary: primary vegetation; secondary: secondary vegetation; plantation: plantation forest.

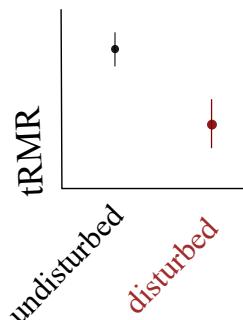
(a) Assemblage-level: there is less energy available to utilize by vertebrate assemblages in disturbed land uses than in undisturbed land uses.



Prediction 1: within all trophic groups, total assemblage-level **mass-dependent** metabolic rates decrease in disturbed land uses compared to undisturbed land uses.

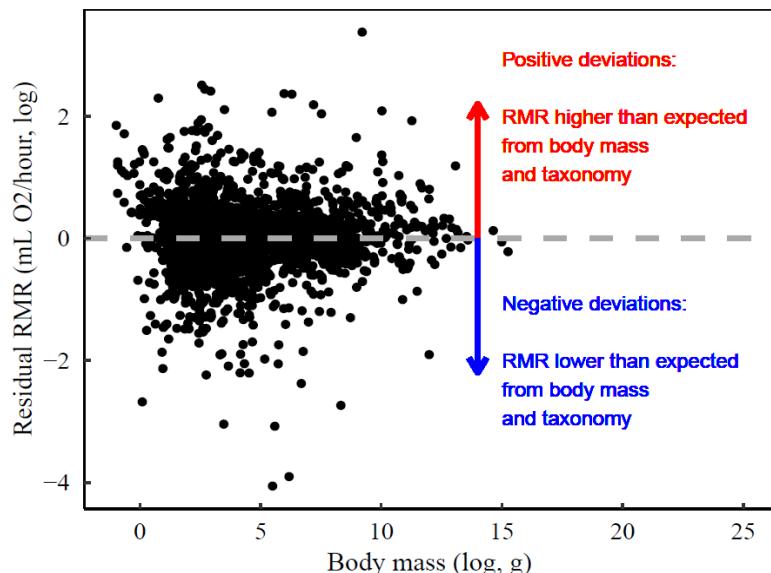
$$\text{Assemblage level:} \\ t\text{RMR} = \sum_i (\text{RMR}_i * a_i)$$

$$\text{Across assemblages - model 1:} \\ \log(t\text{RMR}) \sim \text{LU} + \text{LUI} + \text{TG} + \\ \text{LU:LUI} + \text{LU:TG} + \text{LUI:TG} + \\ \text{LU:LUI:TG} + RE$$



(b) Species-level: species with lower energetic expenditure than expected from body mass and taxonomy (negative deviations) do better in disturbed land uses than species with higher energetic expenditure than expected from body mass and taxonomy (positive deviations).

residuals of
 $\log(\text{RMR}) \sim \log(\text{BM}) + (1|\text{Class/Order/Family})$



Prediction 2: within all trophic groups, species occurrence probability in disturbed land uses is negatively affected by **residual RMR**. The slope of the relationship between occurrence probability and residual RMR is significantly lower than the slope estimate for the undisturbed land uses.

Across species - model 2:

$$\text{P}_{\text{occurrence}} \sim \text{LU} + \text{LUI} + \text{resRMR} + \text{TG} + \\ \text{LU:LUI} + \text{LU:TG} + \text{LU:resRMR} + \\ \text{LUI:TG} + \text{LUI:resRMR} + \text{TG:resRMR} + \\ \text{LU:TG:resRMR} + \text{LUI:TG:resRMR} + RE$$

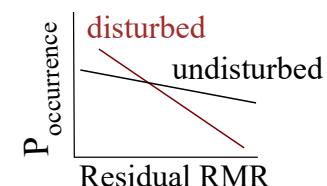


Figure 5.2: Framework for the predictions and models. I use resting metabolic rates (RMR) as a proxy for the amount of energy processed by vertebrate species. **(a)** I hypothesize that there is less energy overall that can be utilized by vertebrate species in disturbed land uses compared to undisturbed land uses. As such, I expect decreases in assemblage-level total metabolic rates ($t\text{RMR}$). $t\text{RMR}$ is calculated as the sum, over all species occurring at a site, of species RMR (RMR_i) weighted by species abundance (a_i). **(b)** After removing the effects of body mass and taxonomy, I expect species with lower energy expenditure than expected to do better than species with higher energy expenditure than expected. I predict that the slope of the relationship between residual RMR and occurrence probability is more negative in disturbed land uses than in undisturbed land uses. For both (a) and (b), I test whether the predictions are consistent among trophic groups. LU: Land use; LUI: land-use intensity; TG: trophic group; RE: random effects. In *model 1*, random effects include the identity of the PREDICTS studies from which the assemblages are derived. In *model 2*, random effects include study, site, and species identity.

1840 **5.2 Methods**

1841 **5.2.1 Vertebrate assemblage composition**

1842 I obtained vertebrate assemblage composition in different land uses from the PREDICTS database (Hudson
1843 et al., 2014, 2017). The PREDICTS database is a large collection of published studies that measure bio-
1844 diversity across different land uses and is one of the most comprehensive global databases of its type. In
1845 each PREDICTS study, species occurrence and often abundance were recorded across different sites. Each
1846 site was assigned to one of the following land-use types: primary vegetation (natural, undisturbed vegeta-
1847 tion), secondary vegetation (recovering after complete destruction of primary vegetation), plantation forest
1848 (woody crops), pasture (areas grazed by livestock), cropland (herbaceous crops) and urban (built-up areas).
1849 The land-use categories were assigned based on habitat descriptions from the original studies (Hudson et al.,
1850 2014), sometimes in consultation with the original study authors. Each site was also classified in terms of
1851 land-use intensity as either minimal, light or intense. The land-use-intensity assignment was also made on
1852 the basis of the habitat description in the original studies, and depended on criteria specific to each land use
1853 (such as degree of mechanisation, yield or chemical inputs for cropland; or the amount of green space in
1854 urban areas; Hudson et al. (2014)).

1855 I subset the PREDICTS database for studies that sampled terrestrial vertebrates, and for which both land
1856 use and land-use intensity had been characterised. I thus obtained 181 studies for 4,238 species sampled
1857 across 6,484 sites (Figure 5.1a). Sample sizes varied across land uses and land-use intensities (Figure 5.1b).

1858 **5.2.2 Energy availability by land-use type and land-use intensity**

1859 The predictions of this Chapter rely on the assumption that resource types and abundance are modified in
1860 disturbed environments, with less energy available in disturbed compared to undisturbed land uses overall.
1861 To test this assumption, I used terrestrial net primary productivity (NPP) across land uses as a proxy for
1862 available energy. NPP quantifies the amount of atmospheric carbon fixed by plants and accumulated as
1863 biomass. NPP estimates were derived by Meghan Hayden, using imagery from the Moderate Resolution
1864 Imaging Spectroradiometer (MODIS) on board NASA's Terra satellite. NPP estimates were based on a
1865 yearly composite of measures made at 8-day intervals, captured at 500-m spatial resolution (Running and
1866 Zhao, 2015). Meghan Hayden obtained NPP for 4,062 of the PREDICTS sites used in the analysis (matching
1867 the sites to the NPP data using the sampling year available in PREDICTS). I fit a linear mixed-effects model
1868 ('lme4' package, version 1.1-23, Bates et al. (2015)) explaining site-level NPP by land use and land-use

intensity, with a random intercept accounting for study identity, to control for differences in experimental design across studies. Model predictions showed that NPP decreased significantly in several land uses (e.g., pasture and cropland) compared with the primary vegetation reference level, although the strength and in some cases direction of the difference varied among land-use and land-use intensity combinations (e.g., increases in urban land uses; Figure 5.1c).

5.2.3 Resting Metabolic Rates (RMR) & imputations of missing RMR values

As a proxy for species-level energetic expenditure, I used estimates of the minimum amount of energy required for organismal maintenance, i.e., basal metabolic rates (BMR) for endotherms, and resting metabolic rates (RMR) for ectotherms. From the literature, I obtained estimates of BMR for 719 species of birds and 685 mammals, and estimates of RMR for 126 amphibians and 173 reptiles (Appendix 4, Table S5.1). For endotherms, BMR are measured when species are in their thermoneutral zone, that is, when there is little to no energy expenditure allocated to thermoregulation. Thus, BMR estimates were derived from lab studies that mostly measured oxygen consumption of the organisms at rest under controlled conditions and in the thermoneutral zone of the species. For an ectotherm, there is no ‘basal’ metabolic rate, as body temperature mainly depends on environmental temperature. Their metabolic rates follow a hump-shaped relationship with environmental temperature, highest at an optimal temperature which corresponds to a performance peak. To be able to compare endotherms’ BMR with ectotherms’ RMR, Stark et al. (2020) used the metabolic rates that correspond to a performance peak for both groups (i.e., BMR in the thermoneutral zone for endotherms, and metabolic rates at optimal temperature for ectotherms). Thus, I used the data compiled in Stark et al. (2020) for ectotherms, and from the sources specified in Table S5.1 for endotherms. The units for BMR and RMR were standardized to mL of dioxygen consumed per hour (mLO₂/h). As in Stark et al. (2020), I henceforth refer to both basal and resting metabolic rates as RMR.

For the species occurring in PREDICTS, initial data coverage for RMR was poor (Table S5.1), necessitating imputation of missing values. To do so, I first measured the phylogenetic signal in BMR and RMR (\log_e -transformed), using Pagel’s λ (Pagel, 1999), to assess whether metabolic rates were sufficiently phylogenetically conserved to be estimated from species’ phylogenetic position. I obtained class-specific phylogenetic trees from Jetz et al. (2012) for birds, from Faurby et al. (2018, 2020) for mammals, from (Tonini et al., 2016) for reptiles (squamates), and from Jetz and Pyron (2018) for amphibians (all downloaded in April 2020). For each class, I randomly sampled 100 trees. To account for phylogenetic uncertainty, I calculated Pagel’s λ for each sampled tree and reported the median value, as well as the 2.5th and 97.5th percentiles (Table S5.1).

1900 In addition to being highly phylogenetically conserved (Table S5.1), RMR correlate strongly with body
1901 mass (Figure 5.2a). Thus, I imputed missing values using body-mass information (see next section), phy-
1902 logenetic relationships and taxonomic orders as predictors (Penone et al., 2014). For each class, I used a
1903 consensus phylogenetic tree from which I summarised phylogenetic relationships in the form of five phy-
1904 logenetic eigenvectors. Including more eigenvectors had little impact on the imputed values (results not
1905 shown). Consensus trees were obtained with the TreeAnnotator programme of the BEAST software (Bouck-
1906 aert et al., 2014). Missing RMR values were imputed using random forests algorithms implemented in R
1907 using the ‘missForest’ package (version 1.4; Stekhoven (2016) and Stekhoven and Bühlmann (2012)).

1908 **5.2.4 Trophic group and body mass information**

1909 I used body mass and trophic group information for terrestrial vertebrates compiled in Chapter 2. Body
1910 mass was compiled as a single measure at the species level, meaning I was unable to consider intraspecific
1911 variation. Trophic group described species as either carnivores, omnivores, or herbivores. Because there
1912 were gaps in the availability of the data, more so for trophic group than for body mass (Chapter 2), I imputed
1913 the missing trait values (independently of RMR imputations), then used both imputed and empirical body
1914 mass values for imputations of missing RMR values. To impute missing body mass and trophic groups, I
1915 used random forests algorithms (again, using the ‘missForest’ R package), including as additional predictors
1916 phylogenetic information, added in the form of 10 phylogenetic eigenvectors (Diniz-Filho et al., 2012) fol-
1917 lowing Penone et al. (2014), and also taxonomic order. I considered a wider set of life-history traits in the
1918 missing values imputations: lifespan, litter/clutch size, habitat breadth and use of artificial habitats (compiled
1919 in Chapter 2). Phylogenetic eigenvectors were extracted from the class-specific phylogenies using the ‘PVR’
1920 package (Santos, 2018).

1921 **5.2.5 Effects of land use, land-use intensity and trophic group on assemblage-level total 1922 RMR (prediction 1; Figure 5.2a)**

1923 Assemblage-level total RMR (tRMR) was obtained by summing abundance-weighted RMR for the species
1924 occurring in each site; abundance data were available for 125 of the 181 PREDICTS studies I considered
1925 (sampling 3,487 species across 4,644 sites). I fitted a linear mixed-effects model to explain \log_e -tRMR as
1926 a function of land use, land-use intensity and trophic group, with a random intercept accounting for study
1927 identity to control for differences in experimental design across studies. I started with a model allowing all
1928 two-way interactions among the predictors. I then tested whether adding the three-way interaction among
1929 land use, land-use intensity and trophic group improved the fit of the model, using a likelihood-ratio test.

1930 The model that included the three-way interaction was retained ($P \ll 0.01$; *model 1*, Figure 5.2). In addition,
1931 because it is well established that resting metabolic rates are influenced by temperature (Clarke and
1932 Fraser, 2004), I checked whether including annual mean temperature in the model affected the conclusions.
1933 Annual mean temperature at each PREDICTS site was estimated from WorldClim version 2.1 (Fick and
1934 Hijmans, 2017), using a 2.5 arc-minute resolution. Adding annual mean temperature did not improve model
1935 fit (likelihood-ratio test: $P=0.113$), thus I did not consider its effects any further.

1936 **Model validation.**

1937 To ensure that imputation uncertainty did not affect the conclusions, I refitted *model 1* using the subset of
1938 species ($n = 426$) from PREDICTS for which there were empirical RMR information (i.e., excluding imputed
1939 RMR values).

1940 **Disentangling the effects of body mass and abundance on tRMR.**

1941 Since RMR correlates strongly with body mass, changes in tRMR are likely to be driven in part by changes
1942 in the size-spectrum of ecological assemblages. I fitted an additional model to explain changes in species'
1943 abundance (given presence) by land use, land-use intensity, trophic group, body mass and their interactions,
1944 to understand the role of shifts in the body mass of species on observed changes in tRMR (Appendix 4,
1945 Figure S5.1).

1946 **5.2.6 Effects of land use, land-use intensity, trophic group and residual RMR on species
1947 occurrence probability (prediction 2; Figure 5.2b)**

1948 To control for the effects of body mass and taxonomy on RMR, I used the residual variation in RMR after
1949 accounting for these variables, from a linear mixed-effects model fitting \log_e -RMR as a function of \log_e -
1950 body mass with nested random taxonomic effects (1|Class/Order/Family; Figure 5.2). Hence, I used a metric
1951 that describes how much more energy (positive deviations) or less energy (negative deviations) than expected
1952 from body mass and taxonomic position a species spends for organismal maintenance. Similar approaches
1953 have been used in previous papers (Furness and Speakman, 2008; Naya et al., 2013). As detailed earlier, I
1954 expect species with lower residual RMR to do better in disturbed land uses than species with higher residual
1955 RMR (prediction 2; Figure 5.2b) because, given any body mass, investing less energy in maintenance could
1956 contribute to persistence in a context of resource scarcity.

1957 To test the second prediction, I fitted a binomial mixed-effects model explaining species occurrence
1958 with land use, land-use intensity, trophic group and residual RMR. I started with a complete model that

1959 included all two-way interactions among the main effects. Because I wanted to test whether the second
1960 prediction was valid for each trophic group, I needed to account for potential differences in the slope of the
1961 relationships between occurrence probability and residual RMR among trophic groups. Thus, I performed
1962 a forward stepwise selection procedure to test whether adding three-way interactions among (1) land use,
1963 trophic group and residual RMR and (2) among land-use intensity, trophic group and residual RMR improved
1964 model fit, using likelihood-ratio tests. The final model included both three-way interactions (Figure 5.2b;
1965 *model 2*). I fitted random effects that accounted for species identity, as well as for study and site identity
1966 within PREDICTS.

1967 **Model validation.**

1968 I checked the phylogenetic signal in the model residuals using Pagel's λ (Pagel, 1999). Non-significant
1969 phylogenetic signal in the residuals would indicate that fitting species identity in the model's random effects
1970 was sufficient to account for residual phylogenetic variation in RMR. Further, to assess the potential effects
1971 of imputation uncertainty on the results, I again fitted *model 2* on the data subset for the 489 species with
1972 collected empirical RMR values, across 5,948 sites in 151 studies (i.e., excluding imputed values).

1973 **5.3 Results**

1974 **5.3.1 Effects of land use, land-use intensity and trophic group on assemblage-level total
1975 RMR**

1976 Land use, land-use intensity, trophic group and their interactions had significant effects on assemblage-level
1977 total RMR (Figure 5.3). Overall, and contrary to my expectations, assemblage-level total RMR did not
1978 show systematic decreases in disturbed land uses. In fact, urban land uses were associated with strong
1979 significant increases in tRMR in all trophic groups (e.g., a 200% average increase in tRMR in lightly-used
1980 urban areas for carnivores, compared with primary vegetation levels; +207% on average in lightly-used urban
1981 areas for herbivores; +107% for minimally-used urban areas for omnivores). In other land uses, responses
1982 depended on trophic group and land-use intensity. Whilst for herbivores, disturbed land uses were typically
1983 associated with increases in tRMR, I detected decreases in tRMR for omnivores and carnivores in several
1984 land uses, most notably in intensely-used pasture for carnivores (-84%). Such effects could reflect changes
1985 in the size-spectrum of local assemblages (Appendix 4, Figure S5.2). For instance, in minimally-used urban
1986 areas, larger herbivores tended to occur at higher abundances compared to primary vegetation level; and in
1987 intensely-used pastures, carnivores tended to occur at lower abundances overall (Figure S5.2).

1988 The model residuals were appropriately distributed (see diagnostic plots in Appendix 4, Figure S5.3).
 1989 Investigating the sensitivity of the results to imputation uncertainty showed that the conclusions were robust
 1990 to the removal of all imputed estimates of RMR (the correlation coefficient was 0.72 between the two sets of
 1991 model coefficients; Figure S5.4). Comparing model predictions showed that effects were mostly congruent,
 1992 although there were some differences (Figure S5.5). In particular, for herbivores, effect sizes tended to be
 1993 bigger for the model fitted on empirical data compared with the model that included imputed data. Thus, the
 1994 main results appear to be conservative if anything. The model fitted on empirical data had larger standard
 1995 errors, likely due to the reduction in sample size.

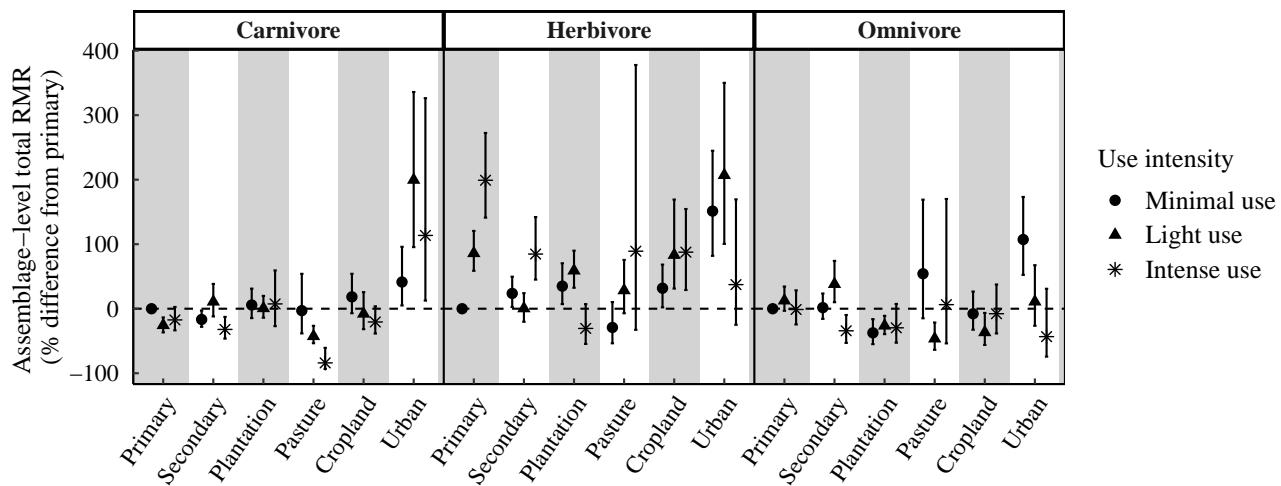


Figure 5.3: Effects of land use, land-use intensity and trophic group on assemblage-level total RMR (mean estimate $\pm 95\%$ confidence interval). Model predictions are rescaled with reference to minimally-used primary vegetation, considered to be the undisturbed baseline. Primary: primary vegetation; secondary: secondary vegetation; plantation: plantation forest.

1996 5.3.2 Effects of land use, land-use intensity, trophic group and residual RMR on species' occurrence probability

1998 Species' occurrence probability was significantly affected by land use, land-use intensity, trophic group,
 1999 residual RMR and their interactions (Figures 5.4, 5.5). Contrary to my expectations, species with higher
 2000 residual RMR (relative to their body mass and taxonomic position) tended to do better than species with lower
 2001 residual RMR in a number of disturbed land uses. Overall, land-use type was more important for determining
 2002 the relationship between occurrence probability and residual RMR than land-use intensity (Figure 5.4a).

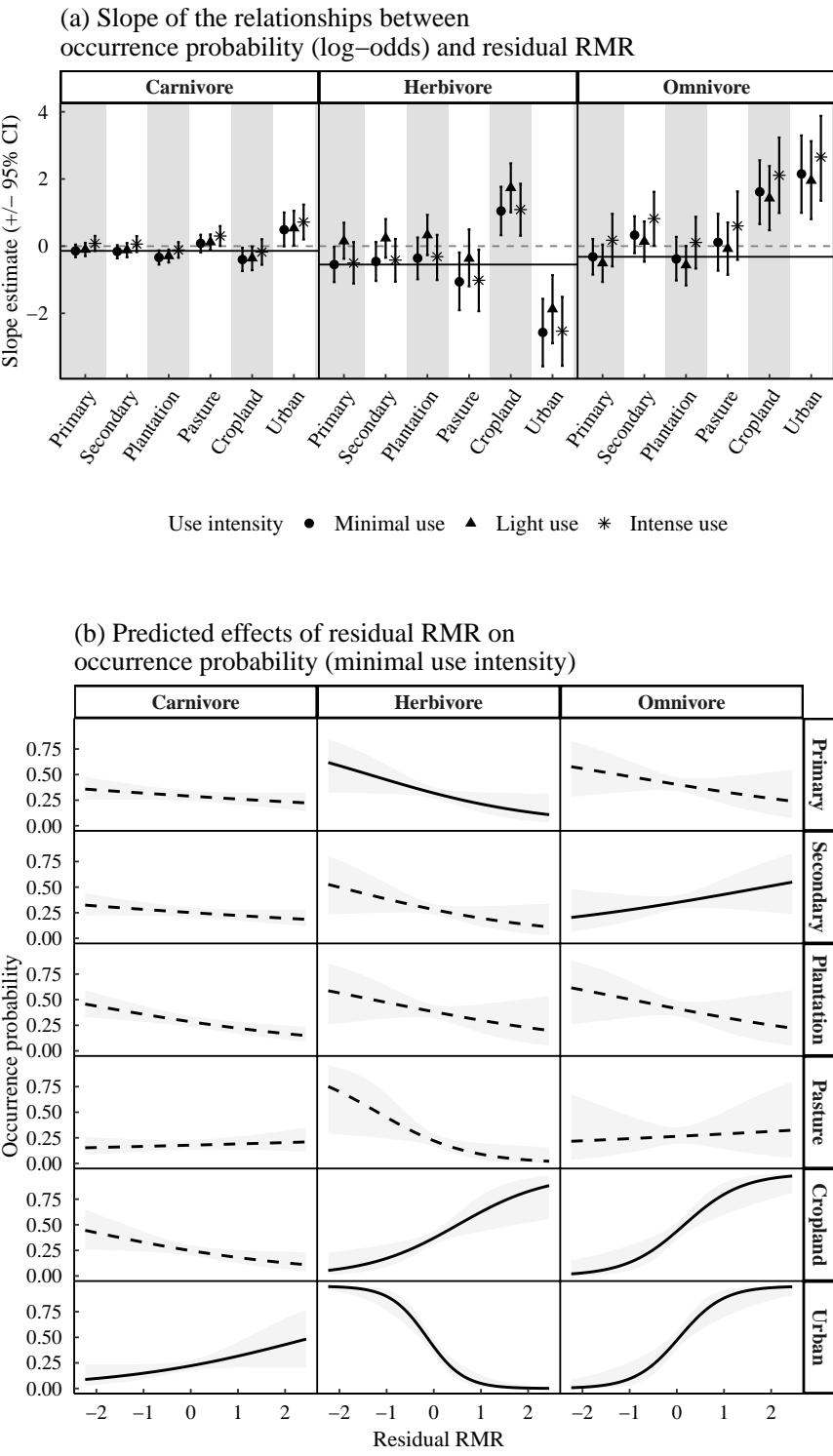


Figure 5.4: (a) Slope estimates for the relationship between residual RMR and occurrence probability in each land-use type and for the three levels of land-use intensity (mean estimate $\pm 95\%$ confidence interval). The black horizontal line indicates the slope for the reference level (primary vegetation) for minimal land-use intensity. The grey dashed line marks 0. (b) Effect of residual RMR on species probability of occurrence within each trophic group and for each land-use type. I plotted the predictions for minimal land-use intensity only. Solid lines represent significant relationships (with slopes significantly different from 0), and dashed lines are plotted where the slope was not significantly different from 0. Shaded areas represent 95% confidence intervals. Primary: primary vegetation; secondary: secondary vegetation; plantation: plantation forest.

2003 For minimally-used primary vegetation (reference), residual RMR tended to be negatively associated
 2004 with species occurrence probability in all trophic groups (but with a significant slope for herbivores only;
 2005 Figure 5.4a). However, the directionality of this relationship was reversed in some disturbed land uses in
 2006 all trophic groups (secondary vegetation, cropland and urban for omnivores; cropland for herbivores; urban
 2007 for carnivores), with significant positive slopes, also significantly higher than those observed for primary
 2008 vegetation (Figure 5.4a); in these land uses, residual RMR was thus positively associated with occurrence
 2009 probability. One notable exception was the opposite pattern for urban herbivores (Figure 5.4b), where resid-
 2010 ual RMR had a more negative effect on occurrence probability than in minimally-used primary vegetation.

2011 I would like to emphasize that positive effects of residual RMR on occurrence probability in some of the
 2012 most disturbed land uses (e.g., urban for carnivores) do not mean that there were absolute increases in species
 2013 occurrence probability in disturbed land uses compared to primary vegetation (and vice-versa). I illustrate
 2014 this point in Figure 5.5. For carnivores with a median value for residual RMR, occurrence probability was
 2015 reduced by an average 24% in urban land uses compared to primary vegetation (but there was a significant
 2016 positive association between residual RMR and occurrence probability for carnivores in urban areas; Figure
 2017 5.4).

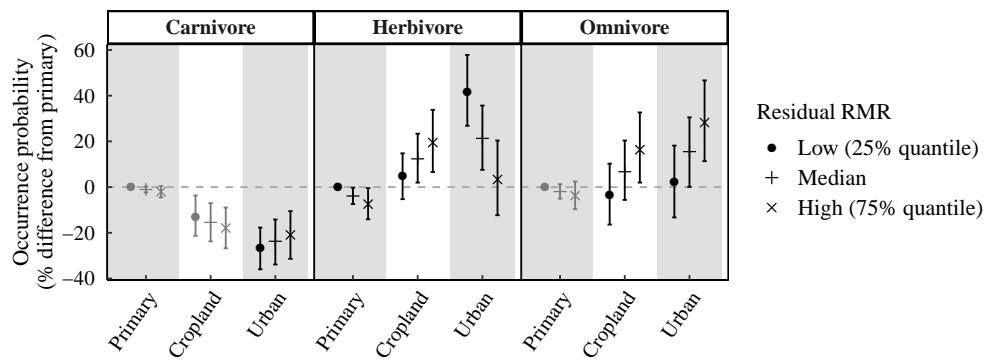


Figure 5.5: Predicted occurrence probabilities (mean effect \pm 95% confidence interval) in primary vegetation (primary) and for the most disturbed land uses where residual RMR was found to have a significant effect on occurrence probability. For visualisation purposes, I discretised residual RMR in three levels. The predicted probabilities of occurrence were rescaled with reference to primary vegetation for the lowest value of residual RMR (25% quantile). Here, the predictions are plotted for minimal land-use intensity (effects would be similar for light and intense land-use intensities). Black points and error bars are plotted where the relationship between occurrence probability and residual RMR was significant (and dark grey points and error bars represent non-significant trends).

2018 Finally, the model showed some degree of deviation from distributional assumptions (diagnostic plots,
 2019 Appendix 4, Figure S5.6). Nevertheless, the model's coefficients were similar when estimated with a
 2020 Bayesian framework, suggesting that the estimates were robust (Figure S5.7). The phylogenetic signal in
 2021 the model residuals was weak and non-significant ($\lambda=0.004$, $P=0.24$). Re-fitting the model using the com-

2022 plete data subset (i.e., excluding imputed RMR estimates) showed that the conclusions are likely robust to
2023 imputation uncertainty (Figure S5.8), with congruent results overall, although there were a few differences
2024 in the predictions between the two models – notably, for herbivores in urban land uses (Figure S5.8).

2025 **5.4 Discussion**

2026 The results of this Chapter provide insights into the relationship between land-use change and energetic
2027 requirements at two levels of organisation (at the assemblage level and the species level), and contradict
2028 both my initial predictions. I found that total energetic requirements did not show systematic decreases in
2029 disturbed land uses. On the contrary, there were strong increases in all trophic groups, most notably in urban
2030 land uses. Further, in all trophic groups, species with higher energetic expenditure (than expected from body
2031 mass and taxonomy) tended to do better in some of the most disturbed land uses (that is, cropland and urban)
2032 than species with lower energetic expenditure (than expected from body mass and taxonomy).

2033 At the assemblage level, the results first highlight the effects of land-use change on vertebrate com-
2034 munity metabolism. Contrary to my expectations, I found differing effects of land use on total energetic
2035 requirements among trophic groups, reflecting changes in the size-spectrum of ecological assemblages (i.e.,
2036 changes in the distribution of abundance along the body-mass gradient). On the one hand, decreases in total
2037 energetic requirements, such as observed for carnivores in intensely used pastures, are likely due to overall
2038 reductions in local abundance (with carnivorous species in pastures perceived as a threat to livestock (Eeden
2039 et al., 2018); or because of increased competition for fewer resources). On the other hand, increases in total
2040 energetic requirements could reflect higher levels of resource intake in some disturbed land-use types. On the
2041 basis of net primary productivity, I hypothesized that there would be fewer resources available in disturbed
2042 areas. However, it could be that the carrying capacity of some disturbed land-use types actually increases
2043 for some trophic groups compared to that of primary vegetation, because of the presence of novel or more
2044 abundant food sources. For instance, in urban areas, both wildlife feeding and the presence of anthropogenic
2045 food sources, such as human refusal or pet food, could lead to an increase in resource availability all year-
2046 round for species with a non-specialised diet that are able to exploit such food sources (Fischer et al., 2012).
2047 Past research on urban carnivores has shown that some species have adapted to urban environments by ex-
2048 ploiting anthropogenic food sources, and also benefit from physical protection (with some human structures
2049 providing shelter) and from reduced occurrence of natural enemies (Bateman and Fleming, 2012). Herbi-
2050 vores and omnivores could also benefit from increased resources in urban areas, notably where the urban
2051 matrix includes semi-natural habitats, which is congruent with observed increases in occurrence probability

2052 in minimally used urban areas for these trophic groups. Further, anthropogenic ‘bottom-up food forcing’ has
2053 been shown to affect food-web dynamics, with decreases in predation rates, loss of anti-predator abilities
2054 (Geffroy et al., 2020) and mesopredator release (Fischer et al., 2012). Thus, in urban areas, increases in
2055 anthropogenic food sources could provide support for a higher abundance of medium-sized species released
2056 from predation, increasing total energetic requirements.

2057 I hypothesized that resource availability would be the main driver behind changes in energetic require-
2058 ments. However, resource availability likely interacts with other factors to explain the patterns. In particular,
2059 past work has shown that brain size is an important determinant of species’ ability to cope with disturbance,
2060 notably in urban settings (Sayol et al., 2020). Since brain size scales allometrically with body mass, it is
2061 possible that I observe increases in total energetic requirements where having larger brains is advantageous
2062 for resource acquisition, and in turn where resources are both exploitable and abundant enough to sustain
2063 the larger energetic expenditures associated with bigger brain sizes. In addition, body size, which explains
2064 an important proportion of the interspecific variation in mobility, likely interacts with characteristics of the
2065 landscape (such as fragmentation) with consequences for species persistence in disturbed land uses (Merckx
2066 et al., 2018). Hence, the patterns I observe in this Chapter could emerge from interactions and trade-offs
2067 among resource availability, diet, body size and human management of the landscape.

2068 At the species level, the results underline the role of energetic constraints on species’ responses to land-
2069 use change. After controlling for the effects of body mass and taxonomy, I found that residual energetic
2070 expenditure was significantly associated with species occurrence probability in disturbed land uses. Con-
2071 trary to my expectations, in several disturbed land uses and in all trophic groups, species with higher residual
2072 energetic expenditure tended to have a higher occurrence probability than species with lower residual ener-
2073 getic expenditure. It could be that species with lower residual energetic requirements are less well equipped
2074 than species with higher residual energetic requirements at making use of the available food sources in dis-
2075 turbed land uses. Species in disturbed land uses may need to display higher levels of feeding innovation
2076 (Coogan et al., 2018), have larger brains (Sayol et al., 2020), or be bolder and more active to make use of
2077 the available resources. In mammals, past research has shown that larger brains are associated with larger
2078 residual energetic expenditure (Isler and Van Schaik, 2006). At the individual level, past research suggests
2079 that metabolic rates are linked to differences in behaviour, with bolder and more active individuals exhibiting
2080 higher metabolic rates than less active individuals, with consequences for food acquisition (Biro and Stamps,
2081 2010). Although I am not aware of similar evidence at the species level, I propose that residual metabolic
2082 rates interact with species’ ecological traits, behavioural traits and foraging strategy in influencing species’
2083 responses to land use. Among species with an adaptable diet, able to make use of the resources available in

2084 a disturbed landscape, those with higher residual metabolic rates could present a set of behavioural charac-
2085 teristics that render them better at acquiring the available resources, hence more able to cope with land-use
2086 disturbance. This could be the case for urban carnivores and omnivores, as well as herbivores in cropland.
2087 Thus, it is possible that disturbed land uses favour species with higher residual resting metabolic rates be-
2088 cause such species are overall better competitors when faced with disturbance. In addition, release from
2089 predation in some disturbed land uses – most notably in urban areas – could favour bolder species, as they
2090 become less exposed to predation risks. Conversely, and in accordance with my initial hypothesis, the re-
2091 sults suggest that when there are no or few exploitable resources in disturbed areas, spending less energy
2092 than expected from body mass and taxonomy might be beneficial for persistence (this could be the case for
2093 urban herbivores, which include species specialised on fruit, nectar, and other plant materials; some of these
2094 resources likely become less abundant and less substitutable in disturbed areas).

2095 To summarise, I propose that, for species with adaptable diets, increases in exploitable resources cou-
2096 pled with decreases in predation rates could lead to increases in overall energetic expenditure, associated
2097 with shifts towards assemblages composed of a higher abundance of medium-sized, bolder, more active and
2098 larger-brained species. On the other hand, species with specialised diets might be better able to persist and
2099 cope with resource scarcity when their energetic expenditure is lower than expected from body mass. These
2100 ideas could be further tested by considering more refined dietary groups (as those compiled in Chapter 4)
2101 rather than trophic groups, as diet should be easier to link with resource availability in a given land-use type.
2102 This could constitute a development for this work.

2103 Finally, I would like to emphasize that energetic budget allocation is a fundamental aspect of organismal
2104 fitness (Burger et al., 2021). Past studies suggest that individuals exposed to food scarcity can lower their
2105 energetic expenditure to increase their chances of survival. For instance, Zhang et al. (2018b) showed that,
2106 subjected to food restrictions, the Chinese bulbul (*Pycnonotus sinensis*) was able to lower its basal metabolic
2107 rate not only passively through body and organ mass reductions, but also by modifying enzymatic activity
2108 and metabolism in the muscles and liver. Other studies have also found that bird nestlings downregulate
2109 energetic costs allocated to maintenance when exposed to food shortage (Brzék and Konarzewski, 2001;
2110 Moe et al., 2004), or to disturbances such as urban noise (Brischoux et al., 2017). Intraspecific variation
2111 in energetic expenditure could affect individual responses to land-use change, which in turn could affect
2112 species' ability to adapt to human pressures. However, the lack of spatially explicit estimates of metabolic
2113 rates precluded its consideration in this Chapter.

2114 To conclude, the findings of this Chapter suggest important effects of land-use change on energetic
2115 fluxes, and thus potentially on ecosystem functioning. Further research is warranted as to the effects of these

2116 energetic patterns for ecosystem processes. Indeed, assemblage-level energy fluxes may serve as important
2117 indicators of change for ecosystem processes, such as decomposition (Barnes et al., 2014). Understanding
2118 these impacts is particularly important given increasing land-use change and biodiversity loss across the
2119 globe.

2120 **6 | General discussion**

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Appendix 1: Supporting information for Chapter 2

S2.1 Taxonomic corrections

Across the different sources of trait data, similar species could appear under different binomial names. This was a problem when matching datasets by species. Moreover, it is possible that within a source, a given species was appearing under two or more different, synonymous names. As such, taxonomic synonymy created duplicated rows for the same species, overall falsely increasing the total number of species and potentially inflating the number of missing trait values. Taxonomic synonymy was hence a major issue. Due to the large number of species across datasets, extensive manual checks could not be applied. The presence of typos in species names had the same effect as synonymy, erroneously duplicating species. I attempted to correct for taxonomy first by correcting for typos, and second by identifying species which were entered under non-accepted names and replacing these with the accepted name. To this end, I developed an automated procedure, complemented with a few manual entries where errors were opportunistically spotted. Such errors in taxonomy were notably spotted when attempting to retrieve trait data for subsets of species, for analyses not directly related to the work conducted here. Taxonomic synonymy was as such checked manually for 91 species (56 birds, 7 mammals and 28 reptiles); in that case, information was extracted from other diverse sources (such as the Reptile Database (<http://www.reptile-database.org/>); Avibase (<https://avibase.bsc-eoc.org/avibase.jsp?lang=EN&pg=home>); AmphibiaWeb (<https://amphibiaweb.org/>); and additional manual checks using the IUCN Red List for mammals). A column in the Synonym dataset mentions where manual checks were applied (in which case the Synonym dataset was manually corrected).

Automated procedure and outputs

Extracting names from the IUCN Red List and the Integrated Taxonomic Information System (ITIS)

The objectives of the automated procedure were to (1) extract species synonymous binomial names from the

IUCN Red List or from the ITIS, using the ‘rredlist’ (Chamberlain, 2018) and ‘taxize’ (Chamberlain and Szöcs, 2013) R packages; and (2) identify the status of each name (accepted or not accepted). I started by generating a list of all names featuring in any of the sources. These ‘original’ names were corrected for typos (using the ‘gnr_resolve’ function in the ‘taxize’ package). Then, the IUCN Red List was queried and any listed synonyms were stored, as well as the status of each synonym (accepted or not accepted). When species were not found in the IUCN Red List, synonyms were extracted from the ITIS. When species were not found in the ITIS either, corrected names (original names corrected for typos) were used. Family and order designations were extracted using the same procedure and some entries were retrieved from the Global Biodiversity Information Facility taxonomic backbone when not available in the IUCN Red List or in the ITIS (GBIF, <https://www.gbif.org/tools/species-lookup>).

NB: for species entered with the forms *Genus cf.*, *Genus aff.* or *Genus spp.*, the accepted binomial name was left empty.

Output. I generated a ‘Synonym’ dataset containing records of binomial names (14,124 recorded names for birds; 8,743 for amphibians; 6,090 for mammals; and 11,678 for reptiles), and for each I recorded their status and their potential synonyms.

Harmonising taxonomy in trait datasets. Taxonomy across datasets was finally homogenised by replacing synonyms with a uniquely identified accepted name. As a consequence, the total number of identified unique species decreased (Figure S2.1a). The species presenting the highest number of synonyms was the East African mole rat (*Tachyoryctes splendens*), for which I found 12 synonymous names (Figure S2.1b).

The automated procedure was not perfect, and taxonomic errors are likely to have persisted in the trait datasets. The IUCN Red List and the ITIS were not comprehensive taxonomic sources, and for clades with high degrees of synonymy in names, such as reptiles or amphibians, neither the IUCN Red List or the ITIS contained enough information. Taxonomy may be further improved by using class-specific sources in an automated procedure.

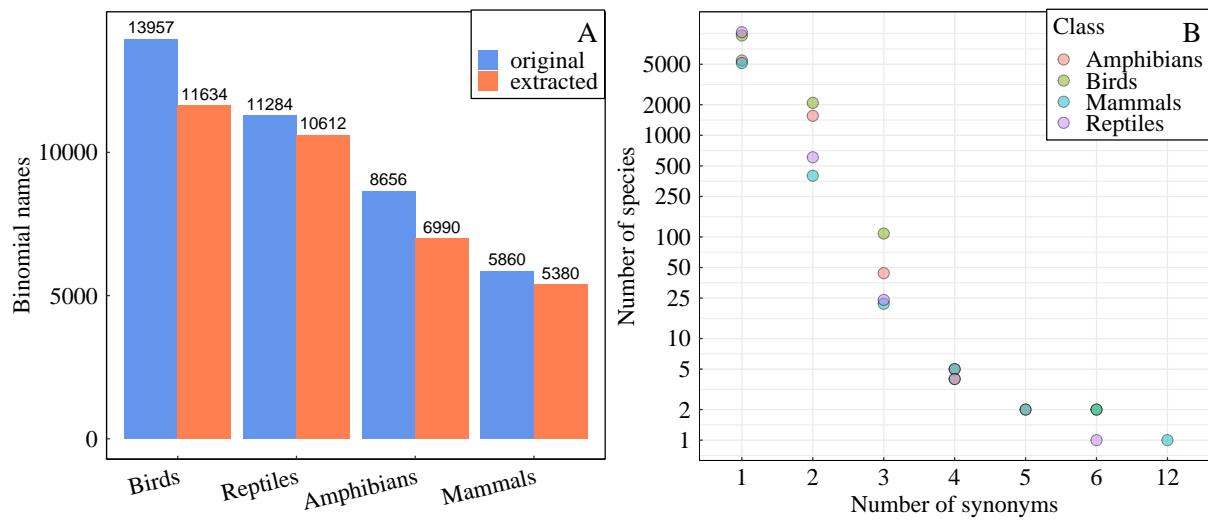


Figure S2.1: Difference in species number before and after taxonomic correction (A) and distribution of number of synonyms across datasets (B). (A) shows the number of species (binomial names) extracted from all sources (blue bars), and the number of uniquely identified accepted names (in red). Replacing non-accepted synonyms by one identified accepted name reduced the number of species in all classes, with the largest reduction for birds. (B) shows the distribution of the number of synonymous names. In all four classes, more than 5,000 species were known under one name only. Nevertheless, a large number of species had two identified synonyms (range: 400 species for mammals - 2086 for birds). The most potentially replicated species was the East African mole rat *Tachyoryctes splendens*, for which 12 synonyms were identified.

S2.2 Additional information for trait compilation

Correlations among closely related traits

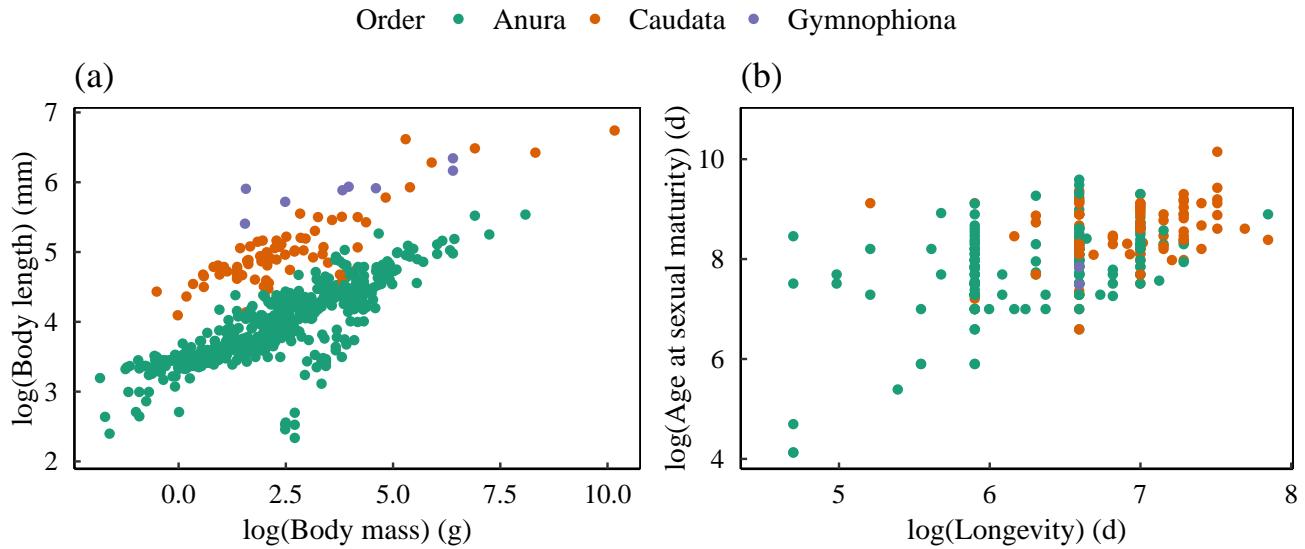


Figure S2.2: (a) Body mass versus body length and (b) longevity versus age at sexual maturity in amphibians. Pearson's correlation coefficient was 0.71 in (a) and 0.55 in (b) (taxonomic order was considered in these coefficients).

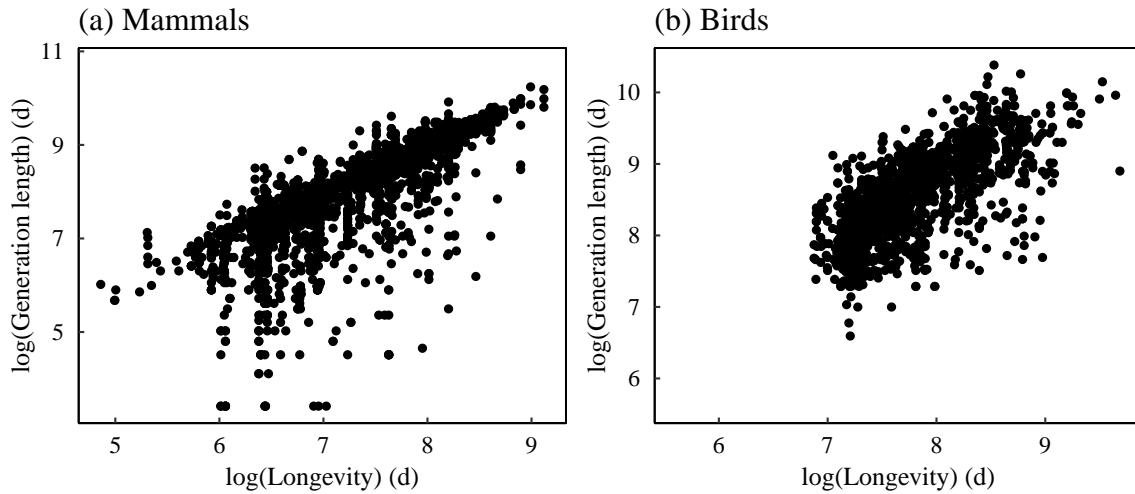


Figure S2.3: Generation length versus longevity data in (a) mammals and (b) birds. Pearson's correlation coefficient was 0.74 in (a) and 0.70 in (b).

S2.3 Cutting distribution maps by altitudinal limits

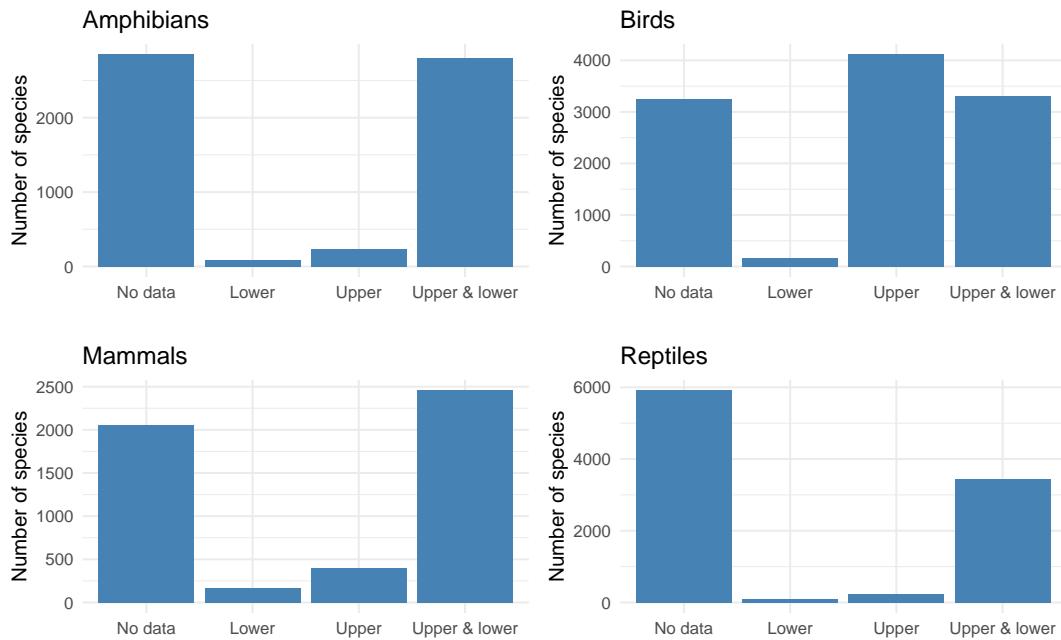


Figure S2.4: Availability of altitudinal limits across species. Upper and lower altitudinal limits were extracted from the IUCN Red List (IUCN, 2020).

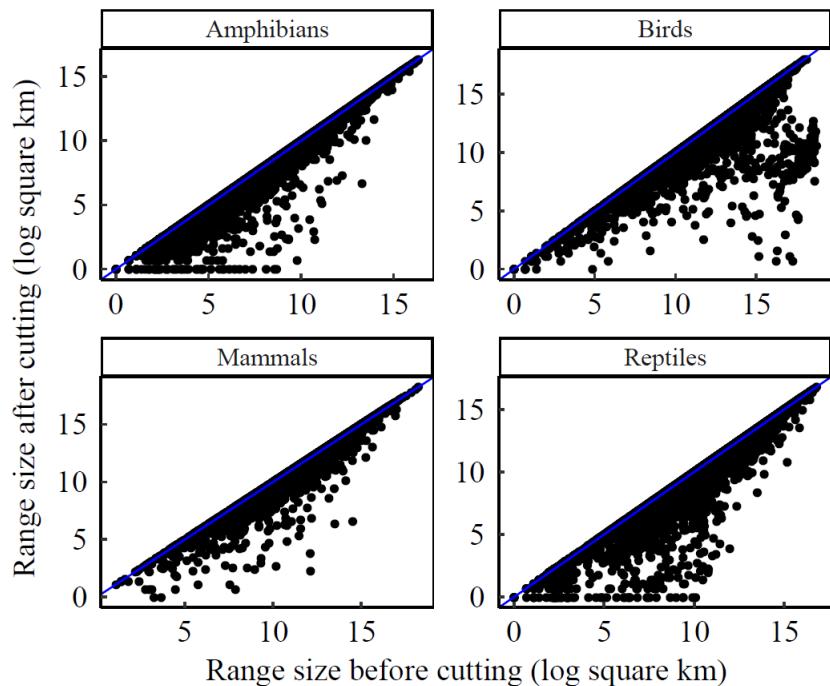


Figure S2.5: Range sizes before versus after cutting the range maps by altitudinal limits.

S2.4 Impact of taxonomic corrections on trait coverage

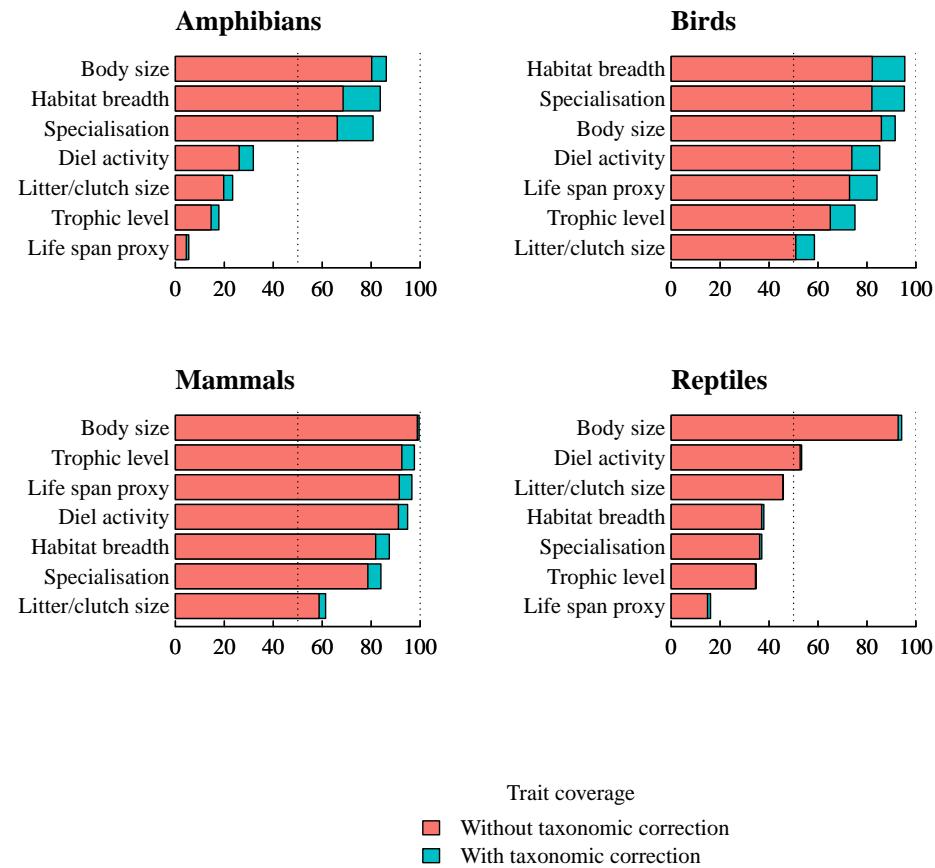
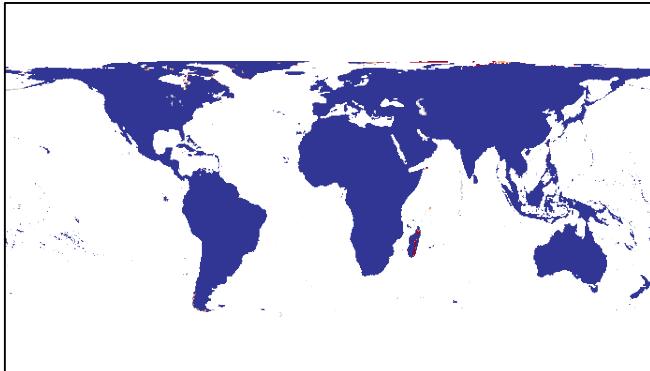


Figure S2.6: Trait coverage when no taxonomic correction is applied before matching sources by binomial names, versus when I applied the described procedure. The identification of synonymous names resulted in an increase in trait coverage in most cases.

S2.5 Assemblage-level median, mean and standard deviation of trait completeness (maps)

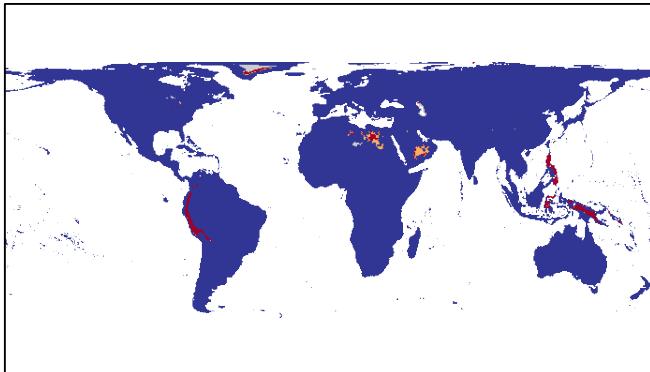
(a) Mammals



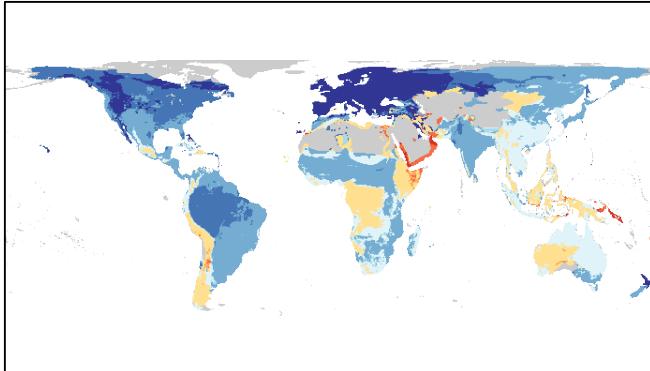
Median completeness
(birds and mammals):

- NA
- 80 – 90%
- 90 – 91%
- 91 – 92%
- 92 – 93%
- 93 – 94%
- 94 – 95%
- 95 – 96%
- 96 – 97%
- 97 – 98%
- 98 – 99%
- 99 – 100%

(b) Birds



(c) Amphibians



Median completeness
(herptiles):

- NA
- 0 – 10%
- 10 – 20%
- 20 – 30%
- 30 – 40%
- 40 – 50%
- 50 – 60%
- 60 – 70%
- 70 – 80%
- 80 – 90%
- 90 – 100%

(d) Reptiles

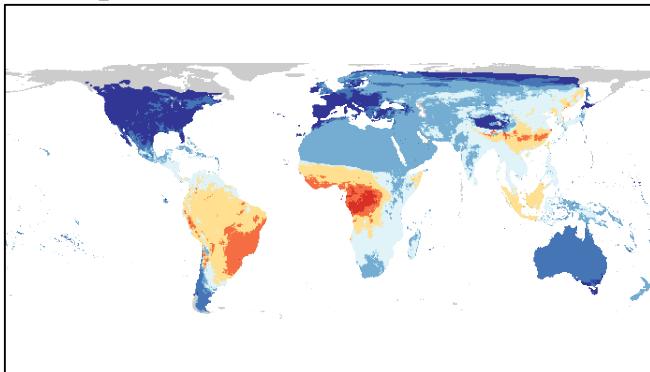
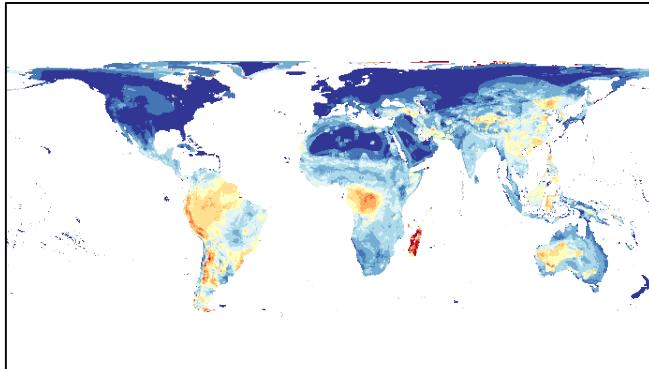


Figure S2.7: Spatial distribution of assemblage-level median trait completeness in each class. Note that the color breaks differ for mammals and birds and for herptiles.

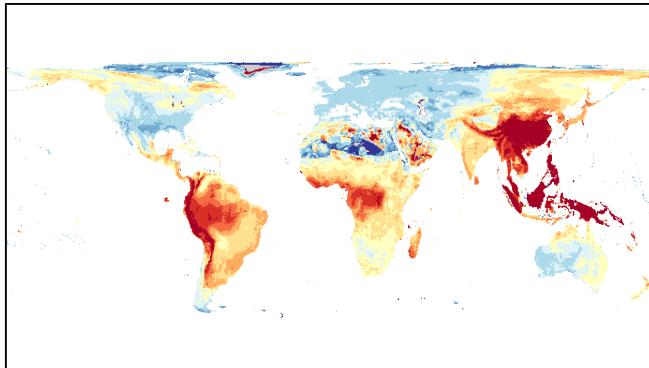
(a) Mammals



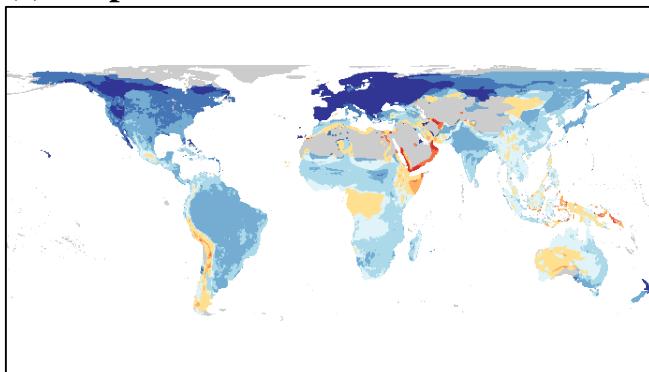
Mean completeness
(birds and mammals):

- NA
- 80 – 90%
- 90 – 91%
- 91 – 92%
- 92 – 93%
- 93 – 94%
- 94 – 95%
- 95 – 96%
- 96 – 97%
- 97 – 98%
- 98 – 99%
- 99 – 100%

(b) Birds



(c) Amphibians



Mean completeness
(herptiles):

- NA
- 0 – 10%
- 10 – 20%
- 20 – 30%
- 30 – 40%
- 40 – 50%
- 50 – 60%
- 60 – 70%
- 70 – 80%
- 80 – 90%
- 90 – 100%

(d) Reptiles

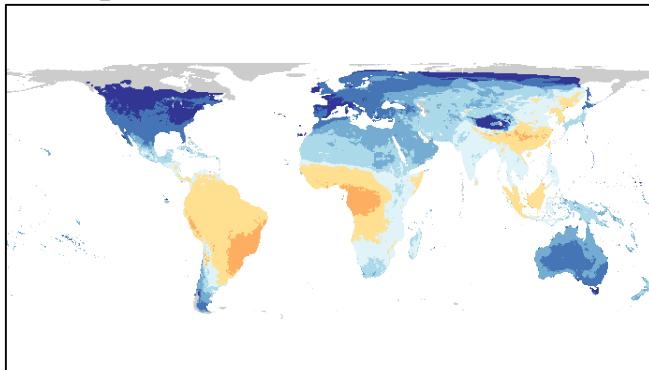
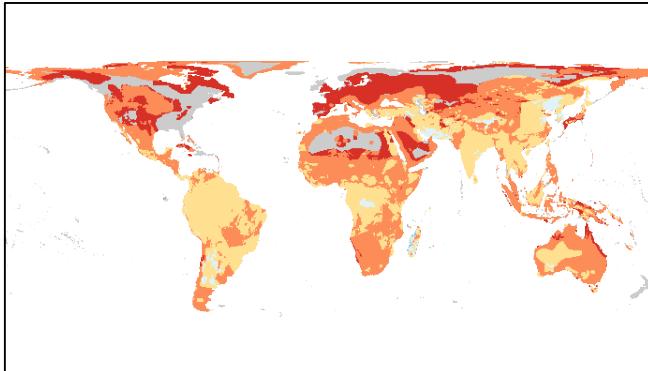


Figure S2.8: Spatial distribution of assemblage-level mean trait completeness in each class. Note that the color breaks differ for mammals and birds and for herptiles.

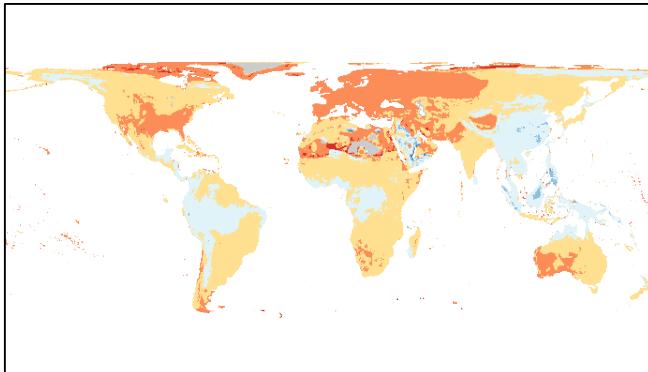
(a) Mammals



Standard deviation
of completeness
(birds and mammals):

- NA
- 0 – 5%
- 5 – 10%
- 10 – 15%
- 15 – 20%
- 20 – 25%
- 25 – 30%

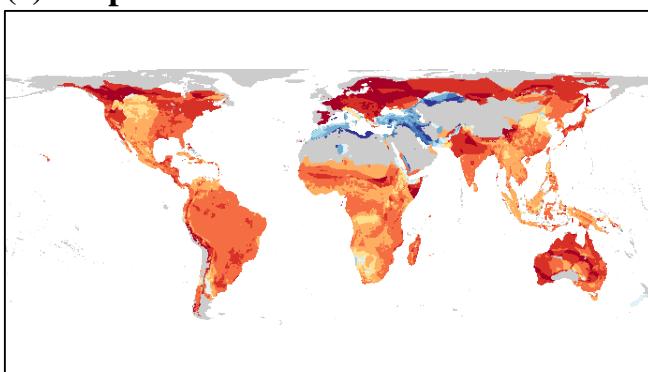
(b) Birds



Standard deviation
of completeness
(herptiles):

- NA
- 0– 10%
- 10 – 15%
- 15 – 20%
- 20 – 25%
- 25 – 30%
- 30 – 35%
- 35 – 40%
- 40 – 50%
- 50 – 60%
- 60 – 75%

(c) Amphibians



(d) Reptiles

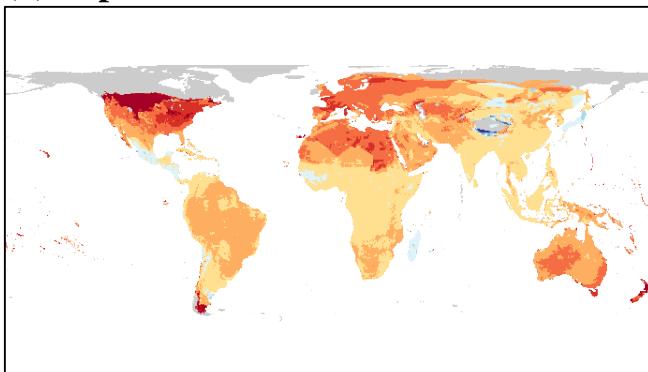


Figure S2.9: Spatial distribution of assemblage-level standard deviation of trait completeness in each class. Note that the color breaks differ for mammals and birds and for herptiles.

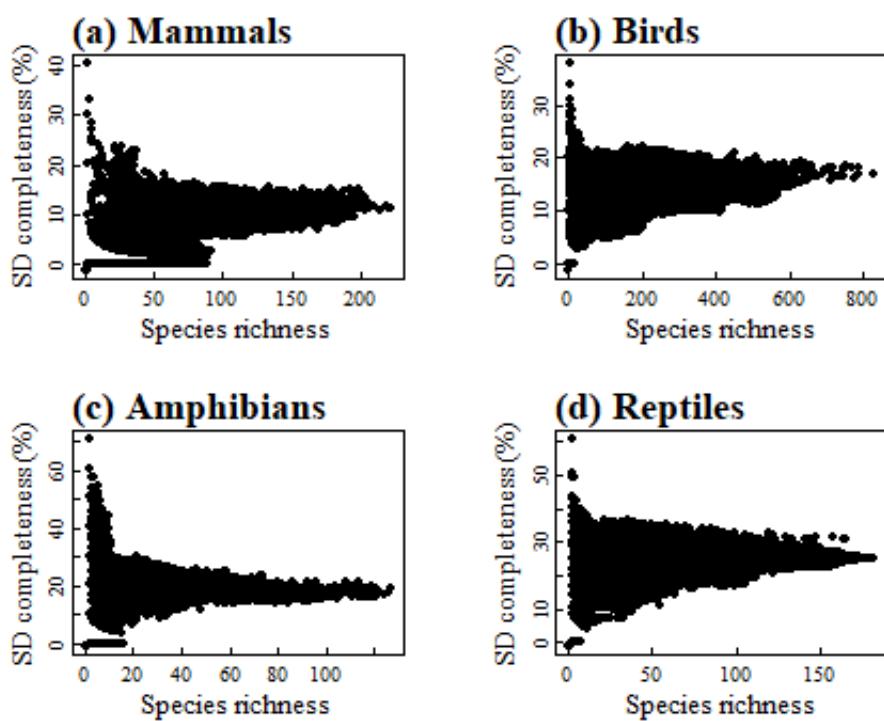


Figure S2.10: Assemblage-level species richness against standard deviation in trait completeness in each class.

S2.6 Phylogenetic patterns in trait completeness

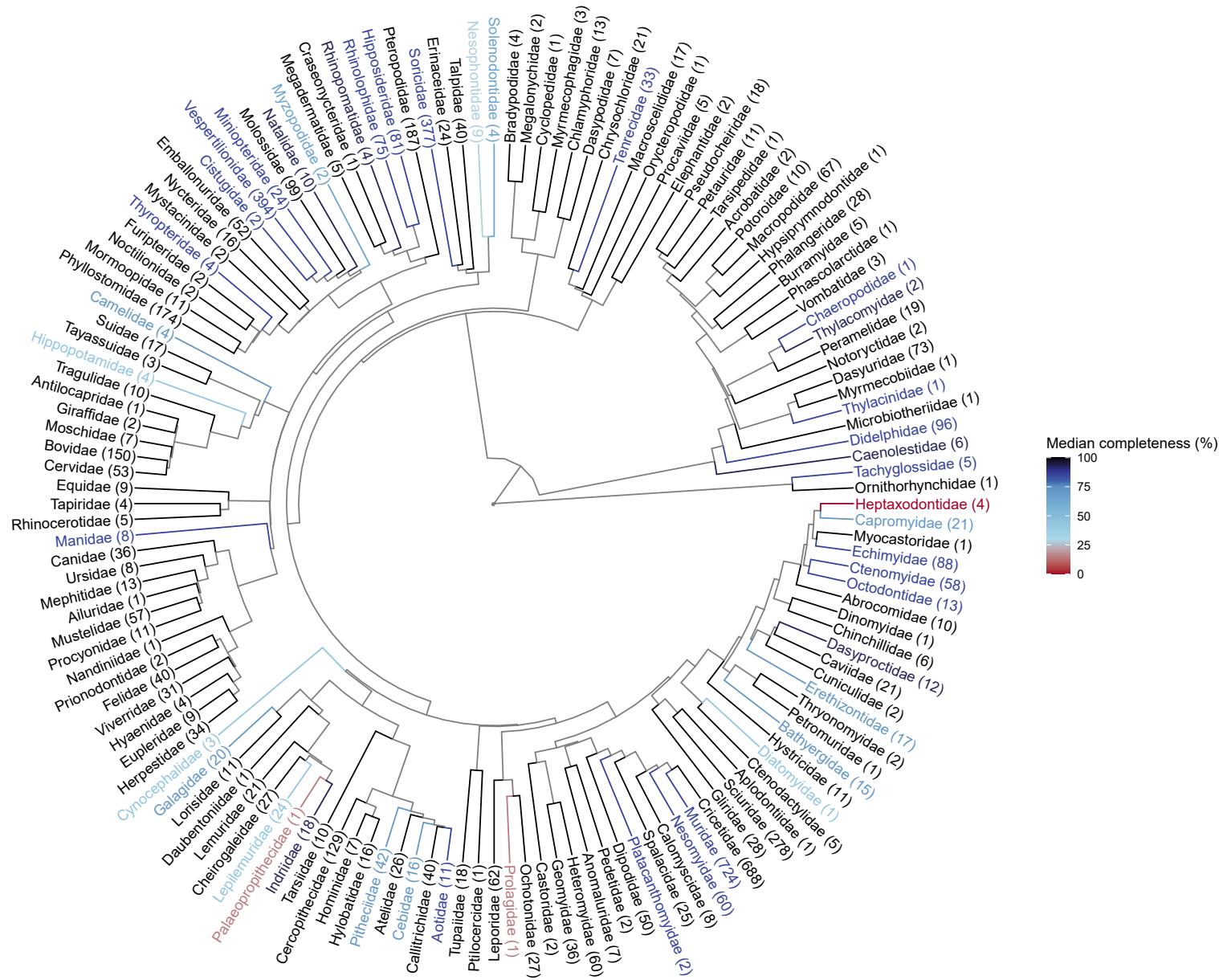


Figure S2.11: Within-family median trait completeness in mammals.

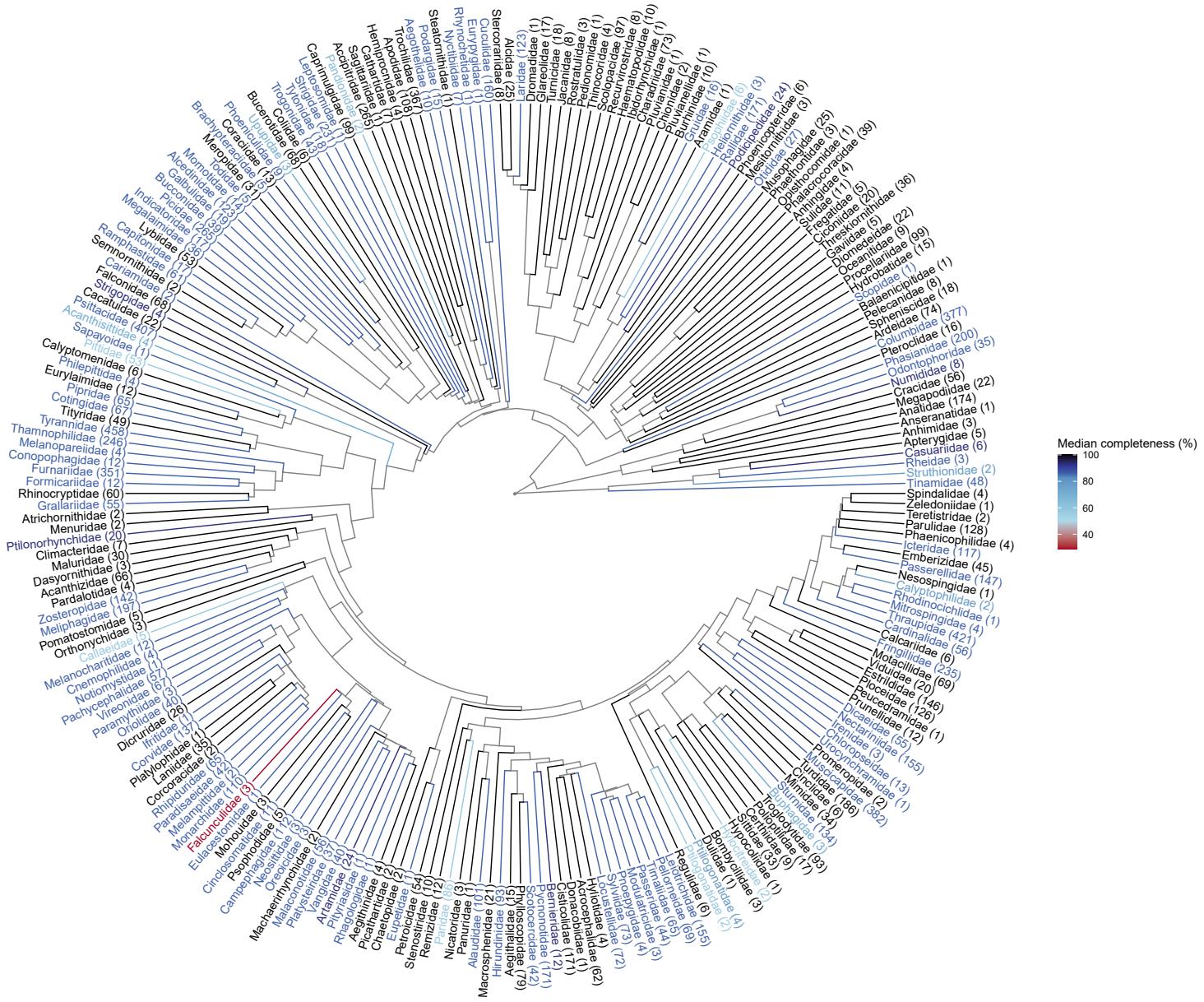


Figure S2.12: Within-family median trait completeness in birds.

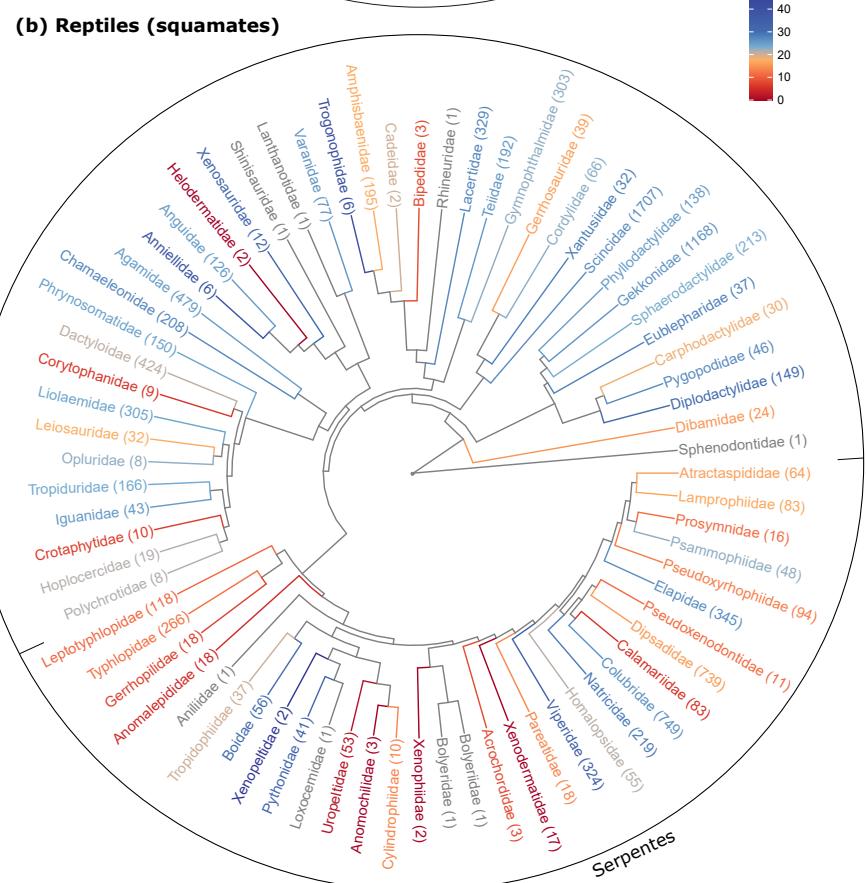
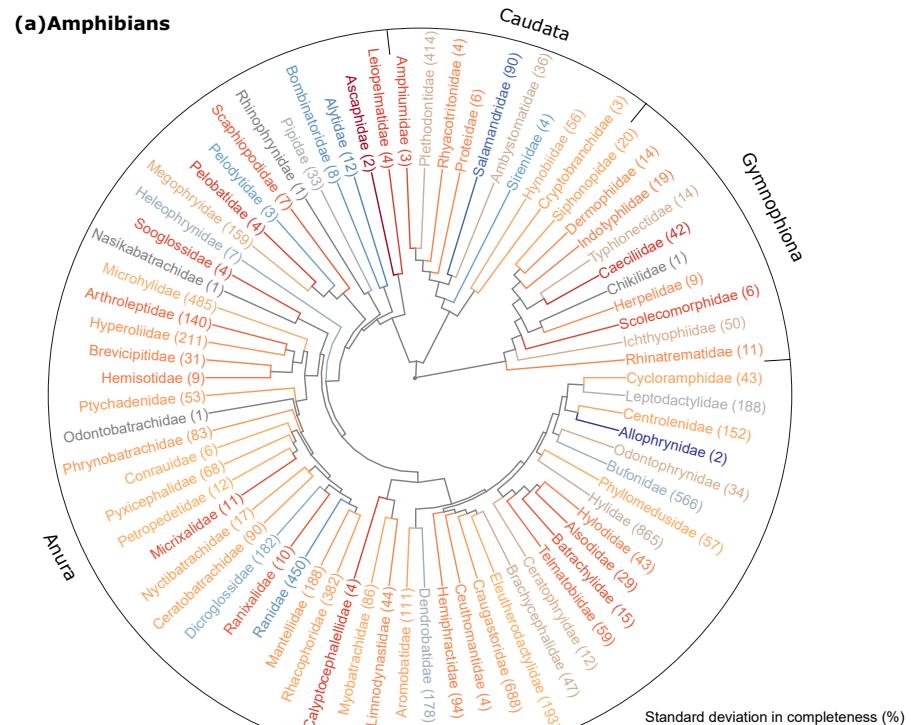


Figure S2.13: Within-family standard deviation in trait completeness (herptiles).

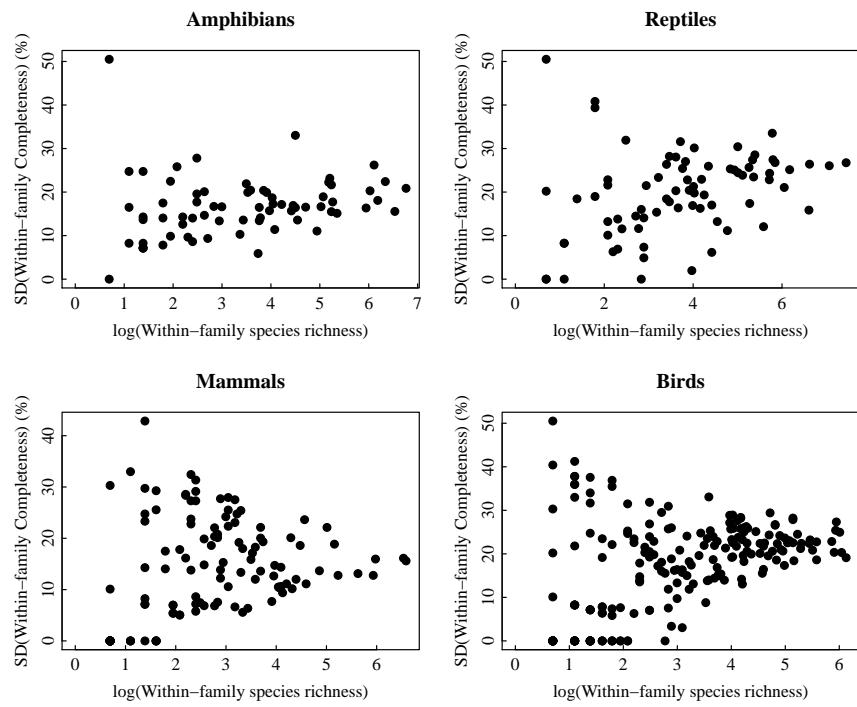


Figure S2.14: Within-family species richness against the within-family standard deviation of trait completeness.

S2.7 Poisson model summaries

Table S2.1: Coefficients of the model investigating whether species range size explained the number of sampled traits. Class was added as an interacting predictor. The reference level for class is mammals. The model was fitted using a Poisson error distribution.

	Estimate	Std. Error	z value	Pr(> z)
Intercept	1.678	0.022	76.809	< 2e - 16
log Range Size	0.015	0.002	8.086	6.16e - 16
Class Birds	-0.092	0.028	-3.350	0.000809
Class Amphibians	-0.689	0.029	-24.099	< 2e - 16
Class Reptiles	-0.872	0.027	-31.856	< 2e - 16
log Range Size:Class Birds	0.003	0.002	1.415	0.157
log Range Size:Class Amphibians	0.017	0.003	6.427	1.30e - 10
log Range Size:Class Reptiles	0.026	0.002	11.159	< 2e - 16

Table S2.2: Coefficients of the model investigating whether species range size explained the number of sampled traits, using range maps not cut by altitudinal limits. Class was added as an interacting predictor. The reference level for class is mammals. The model was fitted using a Poisson error distribution.

	Estimate	Std. Error	z value	Pr(> z)
Intercept	1.665	0.023	72.070	< 2e - 16
log Range Size	0.015	0.002	8.167	3.16e - 16
Class Birds	-0.110	0.029	-3.763	0.0002
Class Amphibians	-0.700	0.030	-23.721	< 2e - 16
Class Reptiles	-0.928	0.029	-32.403	< 2e - 16
log Range Size:Class Birds	0.004	0.002	1.840	0.066
log Range Size:Class Amphibians	0.018	0.003	6.564	5.24e - 11
log Range Size:Class Reptiles	0.031	0.002	12.630	< 2e - 16

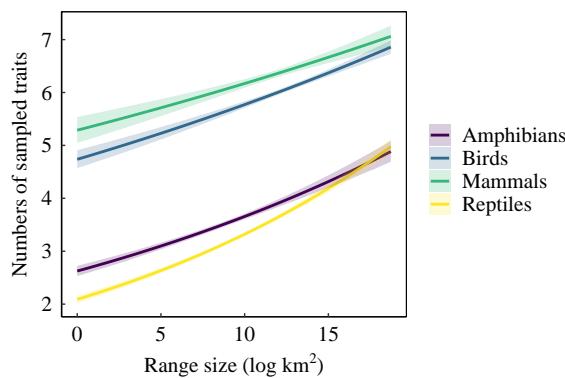


Figure S2.15: Relationship between number of sampled traits and geographical range size using distribution maps not cut by altitudinal limits. The model was fitted using a Poisson error distribution. Class was added as a predictor interacting with range size. Rates of increase were not significantly different for mammals and birds, but differed for reptiles and amphibians, with steeper rates of increase for reptiles overall.

S2.8 Spatial model summaries

Table S2.3: Spatial model summary for amphibians. The spatial model was fitted to explain assemblage-level median completeness with species richness. Biogeographic realm was added as an interacting explanatory variable.

	Estimate	Std. Error	z value	Pr(> z)
Intercept - Realm: Afrotropic	0.0738	0.0064	11.4908	0
log(Species richness)	-0.0025	0.0017	-1.4261	0.1538
Realm: Australasia	-0.0109	0.0095	-1.1453	0.2521
Realm: Indo-Malay	0.0455	0.0119	3.8294	0.0001
Realm: Nearctic	0.0441	0.0082	5.3905	0.000000
Realm: Neotropic	-0.0377	0.0083	-4.5538	0.00001
Realm: Palearctic	0.0047	0.0067	0.6992	0.4844
log(Species richness):Australasia	0.0018	0.0038	0.4789	0.6320
log(Species richness):Indo-Malay	-0.0147	0.0039	-3.7294	0.0002
log(Species richness):Nearctic	-0.0097	0.0030	-3.2003	0.0014
log(Species richness):Neotropic	0.0144	0.0026	5.6454	0.000000
log(Species richness):Palearctic	0.0109	0.0029	3.7358	0.0002

Table S2.4: Spatial model summary for reptiles. The spatial model was fitted to explain assemblage-level median completeness with species richness. Biogeographic realm was added as an interacting explanatory variable.

	Estimate	Std. Error	z value	Pr(> z)
Intercept - Realm: Afrotropic	0.2001	0.0144	13.9349	0
log(Species richness)	-0.0316	0.0031	-10.0547	0
Realm: Australasia	-0.1284	0.0189	-6.7851	0
Realm: Indo-Malay	-0.0453	0.0263	-1.7215	0.0852
Realm: Nearctic	-0.0788	0.0140	-5.6366	0.000000
Realm: Neotropic	-0.0932	0.0145	-6.4425	0
Realm: Palearctic	-0.1030	0.0131	-7.8787	0
log(Species richness):Australasia	0.0386	0.0046	8.4019	0
log(Species richness):Indo-Malay	0.0124	0.0061	2.0397	0.0414
log(Species richness):Nearctic	0.0346	0.0038	9.1601	0
log(Species richness):Neotropic	0.0220	0.0034	6.4231	0
log(Species richness):Palearctic	0.0286	0.0033	8.6153	0

S2.9 Trait coverage and taxonomic matching

Here, I briefly explore the robustness of my work to taxonomic uncertainty by comparing trait coverage obtained with the procedure I developed for taxonomic matching against trait coverage obtained when extracting synonyms from class-specific sources, which could potentially contain more taxonomic information than the ITIS or the IUCN Red List, notably for herptiles. I corrected the datasets for taxonomy again using the ‘rangeBuilder’ R package (Rabosky et al., 2016), which allows to extract accepted names from class-specific sources. Overall, my results are robust to the use of a different taxonomic backbone (Figure S2.16); the main conclusions of this work are likely unaffected by taxonomic uncertainty.

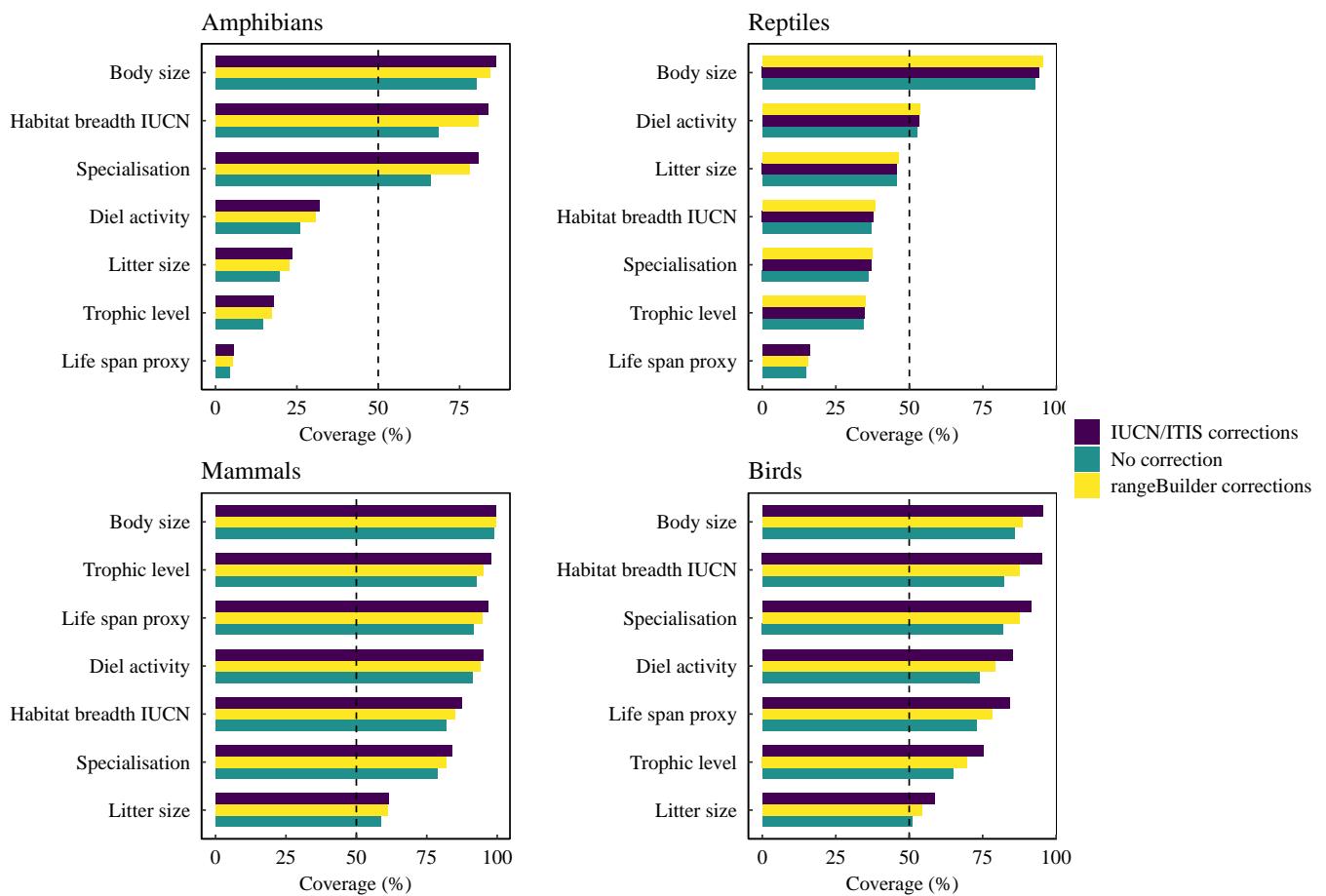


Figure S2.16: Comparison of trait coverage among datasets corrected for taxonomy in different ways: using the described procedure (purple bars); using datasets corrected for taxonomy with the ‘rangeBuilder’ package (yellow bars; Rabosky et al. (2016)); and using datasets uncorrected for taxonomy (green bars).

Appendix 2: Supporting information for Chapter 3

S3.1 Land-use categories in PREDICTS and sample sizes

Table S3.1: Land-use categories in the PREDICTS database. See Hudson et al. (2014, 2017) for more details.

Land-use category	Definition
Primary vegetation	Native vegetation, undisturbed since its establishment under current climatic conditions. No known alterations due to human activities or to extreme natural events.
Mature secondary vegetation	Vegetation recovering after complete destruction of primary vegetation & where succession is near complete – the structure approaches that of primary vegetation.
Intermediate secondary vegetation	Vegetation recovering after complete destruction of primary vegetation at a mid-successional stage.
Young secondary vegetation	Vegetation recovering after complete destruction of primary vegetation at an early successional stage.
Plantation forest	Previously cleared areas planted with crop trees or shrubs grown and harvested for human consumption or for commercial purposes (includes wood, fruit, oil, biofuel, rubber, etc).
Pasture	Areas grazed by livestock, permanently or regularly. Can be improved through cultivation techniques.
Cropland	Previously cleared areas planted with herbaceous crops and harvested for human or animal consumption (including animal feed and crops used in the food industry), or for commercial purposes (e.g., crops grown for the textile industry).
Urban	Previously cleared areas built up by humans. Vegetation is managed for civic or personal purposes.

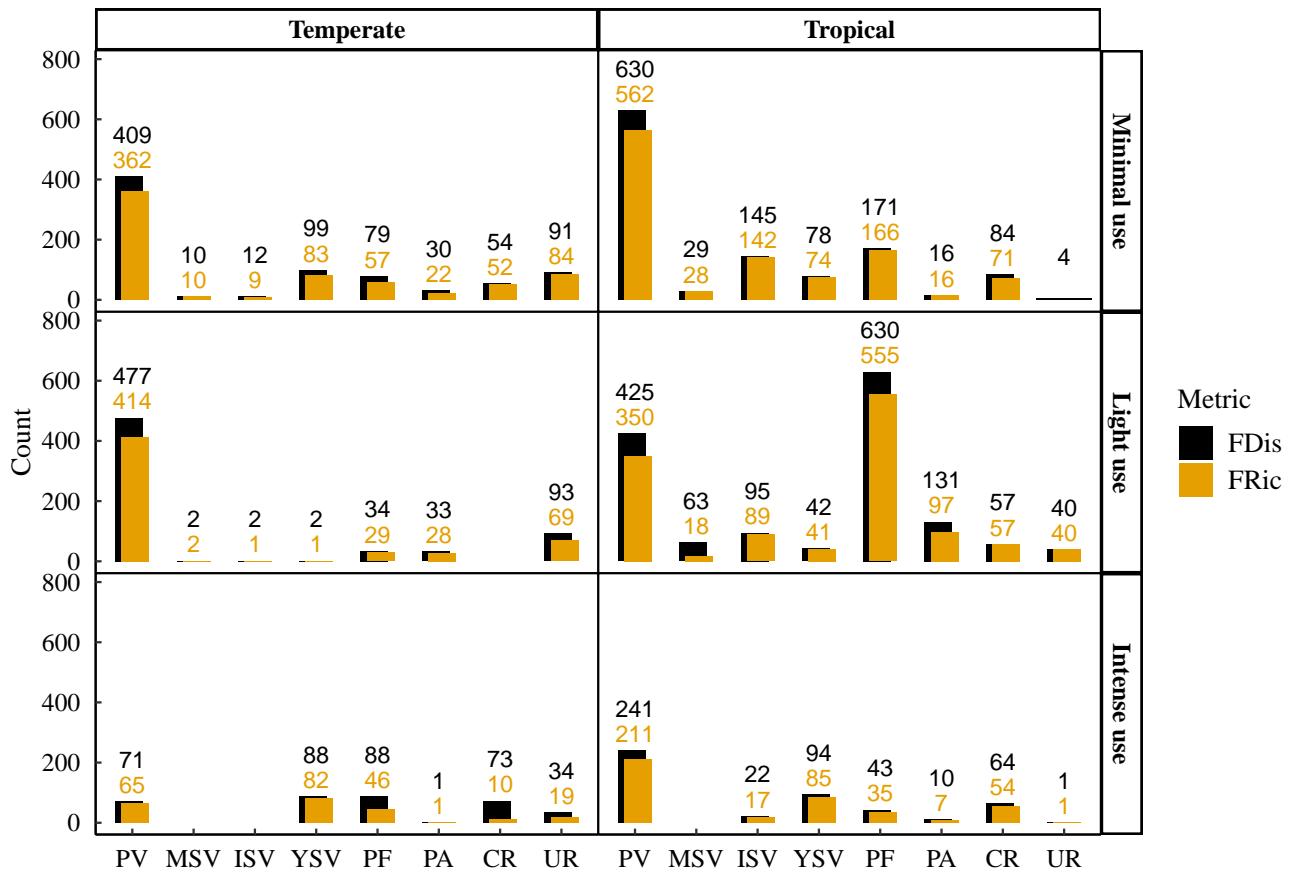


Figure S3.1: Number of sites in each land use and land-use intensity for which FRic and FDis were calculated, across all species. The number of sites for FRic can be smaller than the number of sites for FDis because FRic could not necessarily be computed for all assemblages in which FDis was estimated (in assemblages where species richness was 2 or 3, FRic could not be computed).

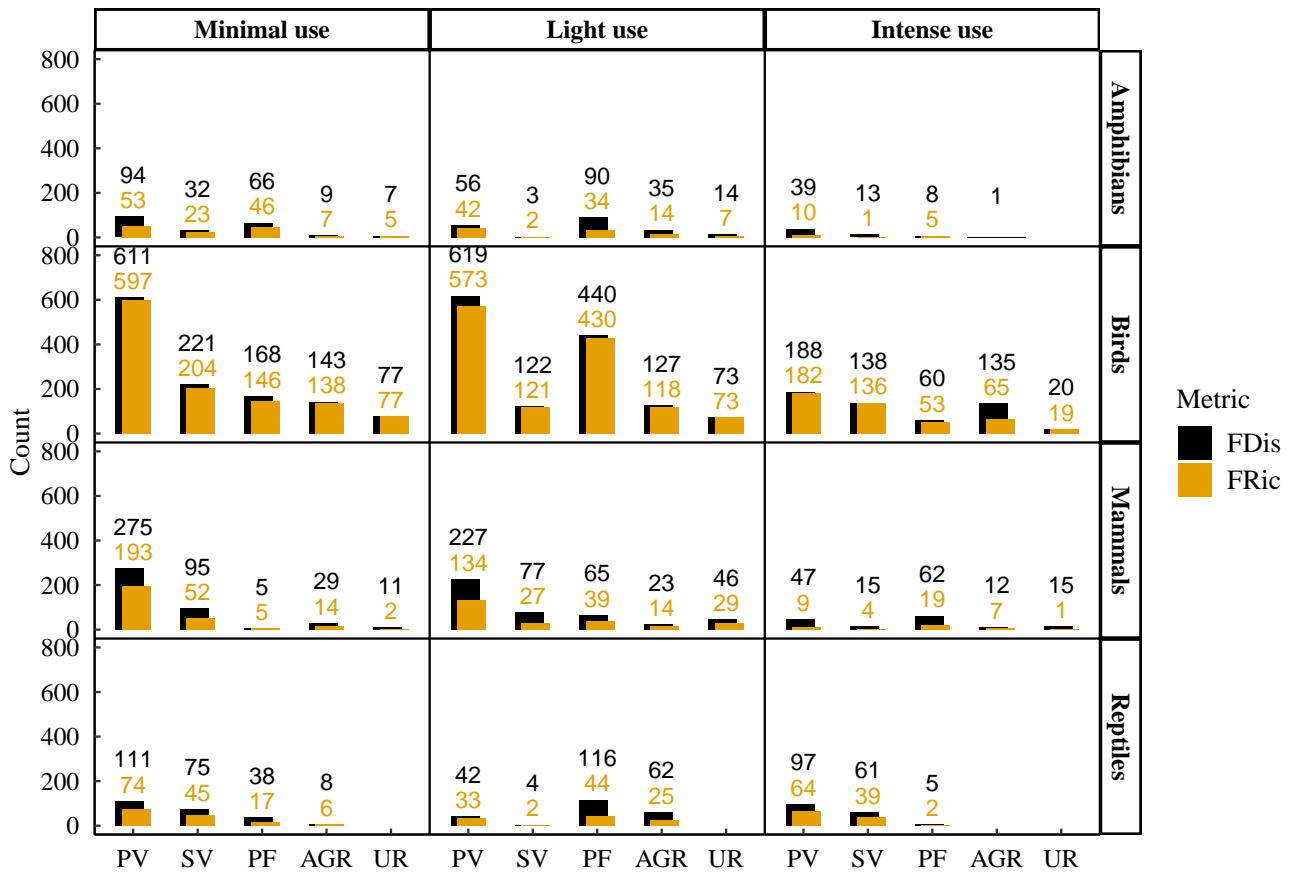


Figure S3.2: Number of sites in each land use, land-use intensity and for which FRic and FDis were calculated, within each class. The number of sites for FRic can be smaller than the number of sites for FDis because FRic could not necessarily be computed for all assemblages in which FDis was estimated (in assemblages where species richness was 2 or 3, FRic could not be computed).

S3.2 Trait data & imputation of missing trait values

I used the compilation of trait data across terrestrial vertebrates from Chapter 2. I selected seven traits that were available at least for a subset of the species in each class: body mass, trophic level, lifespan, litter/clutch size, diel activity, habitat breadth and use of artificial habitats. These traits related to life-history, habitat specialisation and use of geographical space (for instance, habitat breadth is a significant predictor of geographical range size in all classes, Figure S3.3).

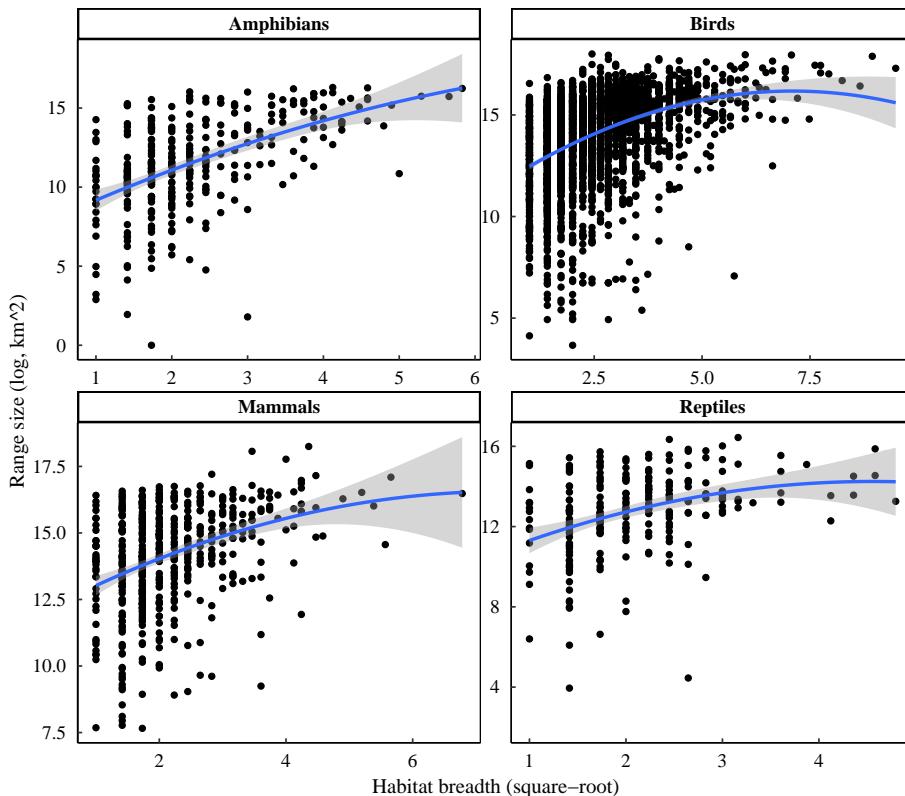


Figure S3.3: Relationship between habitat breadth and geographical range size across species in each class. The derivation of geographical range sizes is described in Chapter 2. The blue lines are the lines of best fit for the regression of geographical range size against habitat breadth in each class, allowing for a quadratic term in the models ($\text{range size} \sim \text{habitat breadth} + \text{habitat breadth}^2$); the shaded areas are the 95% confidence interval of the lines of best fit.

Trait-data coverage was highly variable among classes and traits, with important geographical and phylogenetic biases in trait data for reptiles and amphibians (Chapter 2; Figure S3.4, Figure S3.5). To obtain complete species-trait datasets, I imputed missing trait values. Further, in order to assess the sensitivity of the models to variation in imputed values, I imputed the missing trait values eight independent times. This allowed me to assess the congruence of the model predictions when using the different imputed trait datasets in the analyses.

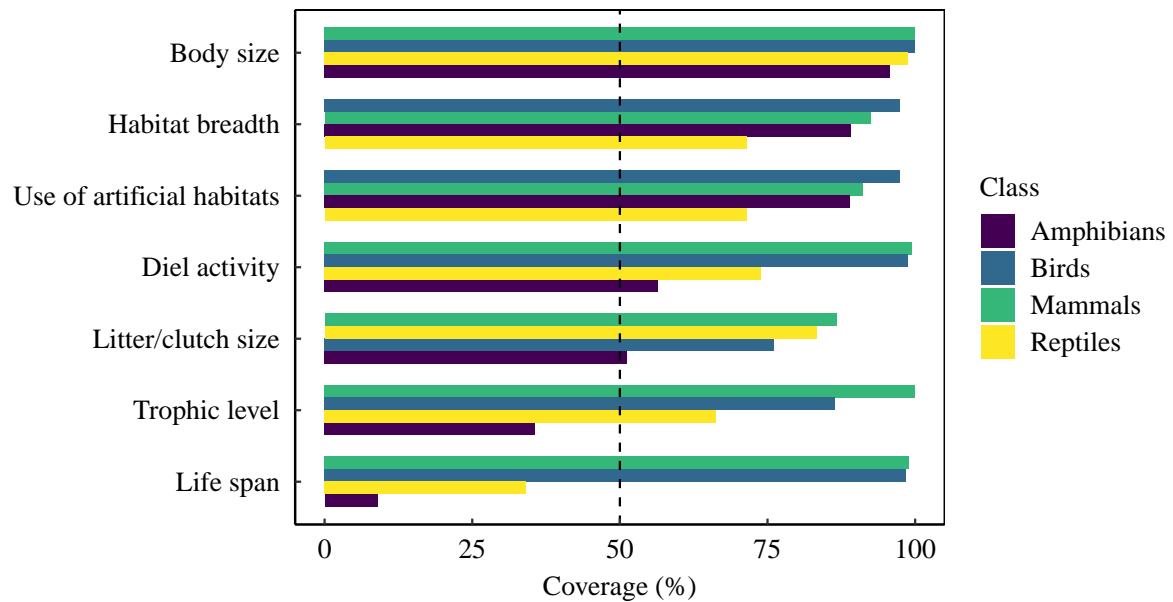


Figure S3.4: Trait coverage for the vertebrate species sampled in the PREDICTS database. For a given trait, coverage is calculated as the percentage of species for which an estimate was available.

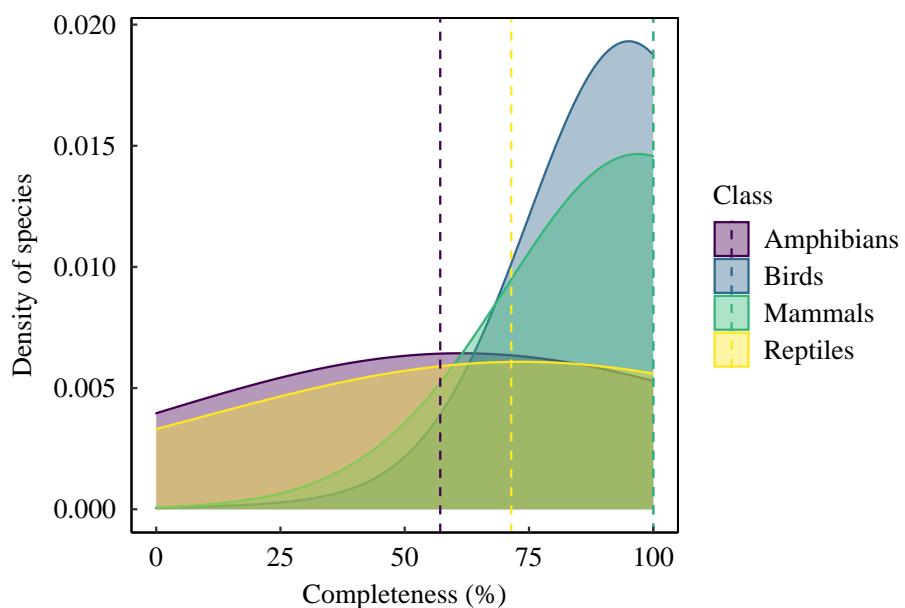


Figure S3.5: Distribution of trait completeness across the vertebrate species sampled in the PREDICTS database. For a given species, trait completeness is calculated as the proportion of traits for which an estimate was available. Dashed lines represent the median trait completeness.

S3.2.1 Choice of imputation technique

There exist several imputation techniques (Debastiani et al., 2021; Johnson et al., 2021; Penone et al., 2014), such as K-nearest neighbour (Troyanskaya et al., 2001), multivariate imputation by chained equations (van Buuren and Groothuis-Oudshoorn, 2007), random forest algorithms (implementable in R with the ‘missForest’ function from the ‘missForest’ package; Stekhoven, 2016; Stekhoven and Bühlmann, 2012), and phylogenetic imputations (implementable in R with PhyloPars, Bruggeman et al., 2009). Penone et al. (2014) assessed the performance of these four techniques and showed that ‘missforest’ and ‘PhyloPars’ performed better when traits were phylogenetically conserved, and when the species phylogenetic position was included as a predictor of missing trait values. ‘PhyloPars’ can only handle continuous data, while ‘missForest’ is compatible with mixed-type (including categorical) data. When no phylogenetic information was included, ‘mice’ was found to be the best method, with fast imputations of mixed-type data (Penone et al., 2014). Therefore, to assess whether ‘missForest’ or ‘mice’ was more appropriate here, I measured the phylogenetic signal in the traits. For continuous traits, I used Pagel’s λ (Pagel, 1999), and for categorical traits I used Borges’ δ (Borges et al., 2018). Strong phylogenetic signals would indicate that traits are phylogenetically conserved, and hence ‘missForest’ would be the most suited approach for imputing missing trait values, with the inclusion of species’ phylogenetic positions as a predictor.

S3.2.2 Phylogenetic signal in traits

Across all classes, similar traits were used for calculating functional diversity metrics: body mass, litter/clutch size, lifespan (using different proxies in different vertebrate classes: generation length for birds and mammals, longevity for reptiles, and age at sexual maturity for amphibians), trophic level, diel activity, habitat breadth and use of artificial habitats. In addition, I included some class-specific traits for the imputations, as certain class-specific traits could be useful predictors of other traits (such as body length for instance in amphibians (Santini et al., 2018)). Table S3.2 details the traits that were included for the imputations in each class and the phylogenetic signal for each of these traits. Continuous traits were log-10 transformed before assessing Pagel’s λ to improve normality. Pagel’s λ was estimated using the ‘phylosig’ function of the ‘phytools’ package (Revell, 2012), and Borges’ δ was assessed using code provided by Borges et al. (2018), available at : https://github.com/mrborges23/delta_statistic. To test for the significance of δ , I generated null distributions of δ for each categorical trait by randomising trait vectors 50 times, and calculating δ for each randomised vector – following the guidelines proposed by Borges et al. (2018). I then tested whether the observed medians were greater than the null distributions using one-sided Wilcoxon rank sum tests.

I used class-specific phylogenies to estimate phylogenetic signal, all downloaded on 13th April 2020. Trees from Faurby et al. (2018, 2020) were used for mammals (downloaded from <https://zenodo.org/record/3690867#.Xyc5wyhKhPZ>). For amphibians, birds and reptiles (squamates only), I downloaded trees from <https://data.vertlife.org/>. Trees were from Jetz et al. (2012) for birds, from Jetz and Pyron (2018) for amphibians and from Tonini et al. (2016) for squamates. For each class, I downloaded a distribution of 1,000 trees, from which I obtained consensus trees to estimate phylogenetic signal (to that end, I used the TreeAnnotator programme of the BEAST software (Bouckaert et al., 2014)).

Table S3.2: Phylogenetic signal in continuous and categorical traits. BM: body mass; BL: body length; GL: generation length; MA: age at sexual maturity; ML: maximum longevity; L: longevity; LCS: litter/clutch size; HB: habitat breadth; TL: trophic level; DA: diel activity; UA: use of artificial habitats. Continuous traits were log-10 transformed to improve normality before estimating Pagel's λ – except for habitat breadth which was square-rooted. A star indicates a significant signal (p-value<0.05 for the log-likelihood ratio test in the case of λ ; and a significant difference from the simulated null distribution of δ for categorical traits). 'NA' indicates traits that were not considered for a given class. All traits showed significant phylogenetic signal, with signals for BM, BL, L, GL, MA and LCS being particularly strong (above 0.8) across the four classes.

Class	Pagel's λ								Borges' δ		
	BM	BL	GL	MA	ML	L	LCS	HB	TL	DA	UA
Amphibians	0.98*	0.94*	NA	0.85*	0.82*	NA	0.93*	0.99*	18*	3.4*	4.5*
Birds	0.99*	NA	0.97*	NA	NA	NA	0.95*	0.60*	13*	32e3*	1.8*
Mammals	0.99*	NA	0.97	NA	NA	NA	0.99	0.71	26*	17*	1.3*
Reptiles	1.0*	NA	NA	NA	0.94*	0.98*	1.0*	0.52*	6.3*	6.4*	1.4*

S3.2.3 Implementation of ‘missforest’ imputations

As phylogenetic signals were strong in many categorical and continuous traits (Table S3.2), I imputed missing trait values using random forest algorithms, as implemented in R with ‘missforest’ from the ‘missForest’ package (Stekhoven, 2016; Stekhoven and Bühlmann, 2012). Another advantage of ‘missforest’ was that, being a non-parametric approach, no prior assumption about data distribution was required. The data were therefore not transformed prior to imputations. In addition, Penone et al. (2014) showed that including phylogenetic information did not decrease the accuracy of imputations for traits that were less phylogenetically conserved, such as habitat breadth in this work.

Phylogenetic relationships were included as additional predictors in the form of phylogenetic eigenvectors (Diniz-Filho et al., 2012), extracted from the phylogenies using the ‘PVR’ package (Santos, 2018). Following Penone et al. (2014), I included the first ten phylogenetic eigenvectors as additional predictors of missing trait values in each class, enough to minimise imputation error. As not all species were represented in the phylogenies, I also added taxonomic order as a predictor for all species. All traits in Table S3.2 were included in the imputations. Tuning parameters of ‘missforest’ were set to ten maximum iterations and to

one hundred trees grown in each forest.

S3.3 Degree of multicollinearity among traits

Multicollinearity among traits can be problematic when calculating functional diversity indices (Cadotte et al., 2011). After imputing missing trait values and before estimating functional metrics, I assessed whether the degree of multicollinearity among categorical and continuous traits was problematically high. To this end, I used generalised variance inflation factors (Fox and Monette, 1992). Given a regression model, variance inflation factors quantify the overestimation in the variance of estimated regression coefficients due to multicollinearity among the predictors. A GVIF value of 5 or 10 is commonly used as a threshold to select out collinear predictors (Dormann et al., 2013). I used the ‘stepwise.vif’ function of the ‘Rnalytica’ package (<https://github.com/awsm-research/Rnalytica>), with a threshold of 5, to determine the GVIF of each trait. I used the imputed traits from the 8th imputation iteration to assess whether multicollinearity was problematically high. Continuous traits were log-10 transformed (except for habitat breadth which was square-rooted). The degree of multicollinearity among traits was not detected to be problematically high, as all traits had a GVIF value below 2 (Table S3.3). As such, all seven traits were included in the calculation of the functional diversity indices.

Table S3.3: Variance inflation factors across considered (imputed) traits.

Trait	GVIF
Diel activity	1.1
Trophic level	1.3
Use of artificial habitats	1.4
Body mass (log10)	1.5
Habitat breadth (square-root)	1.5
Litter/clutch size (log10)	1.6
Lifespan proxy (log10)	1.7

S3.4 Imputation performance

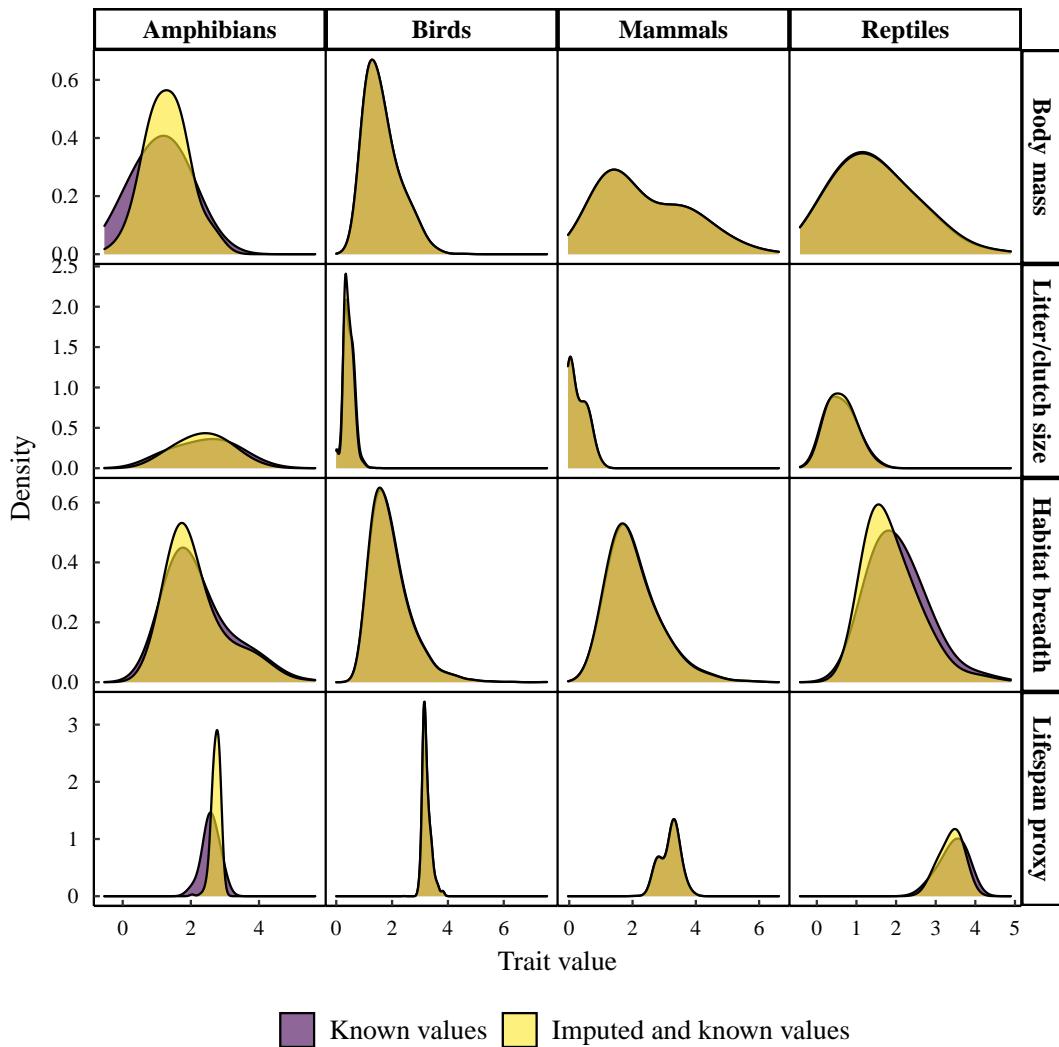


Figure S3.6: Distribution of continuous traits considered in the calculation of the functional diversity metrics (shown as density plots), before and after missing value imputations, in each class and for the species occurring in the PREDICTS database. All traits were log10-transformed, except habitat breadth, which was square-rooted.

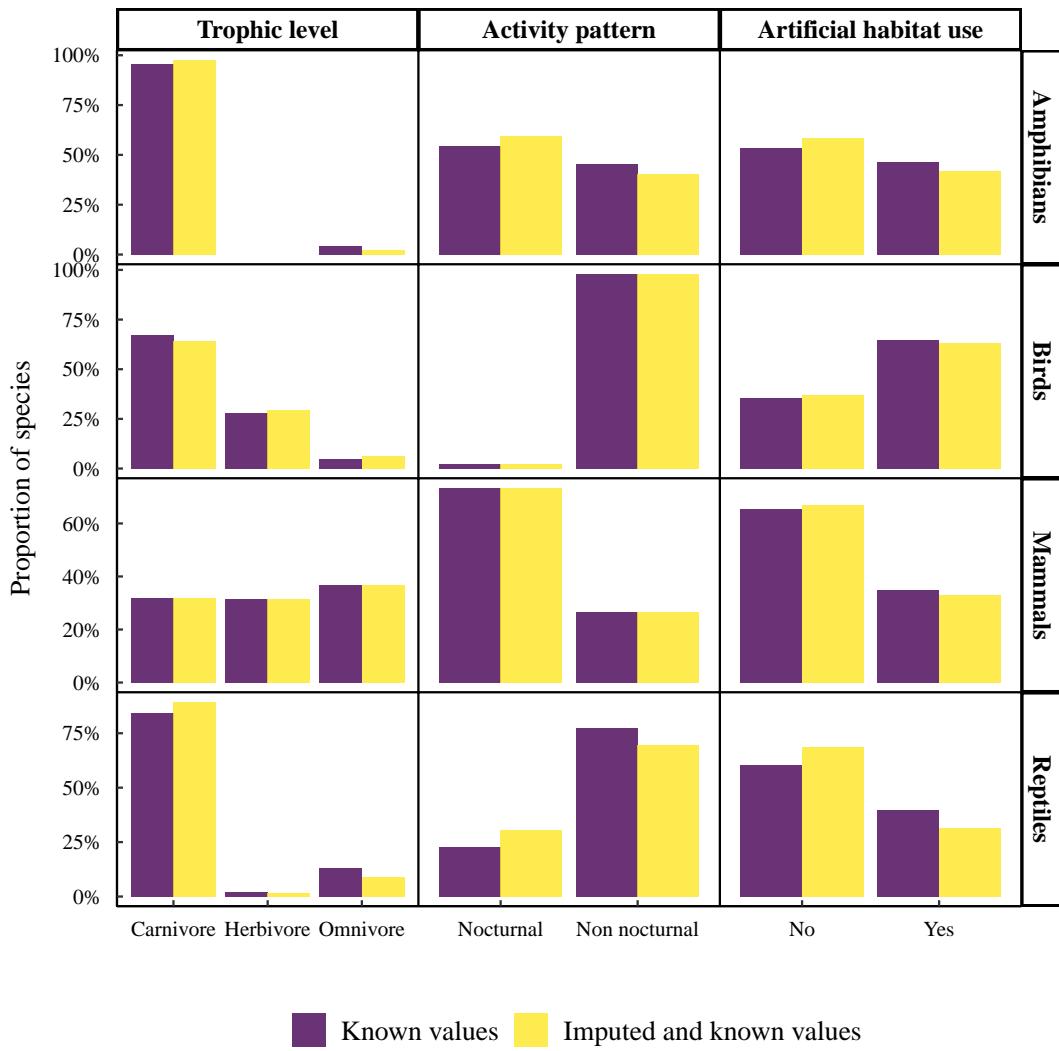


Figure S3.7: Frequency distribution for categorical traits considered in the calculation of the functional diversity metrics (shown as % of total species in each category) before and after missing value imputations, in each class, for the species occurring in the PREDICTS database.

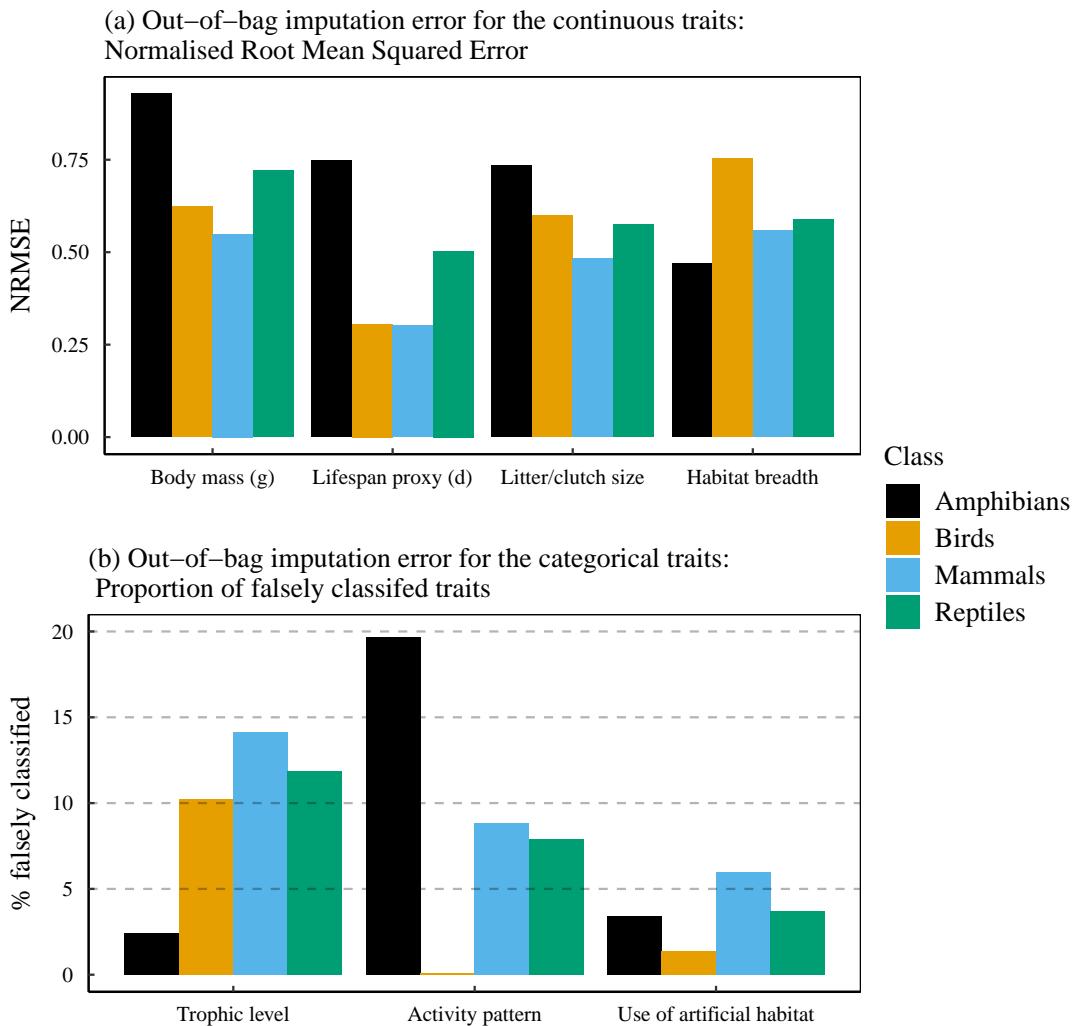


Figure S3.8: Out-of-bag imputation errors for the continuous traits (a) and categorical traits (b). For continuous traits, the Normalised Root Mean Squared Error (NRMSE) was obtained by dividing the Mean Squared Error (MSE) by the variance of the known trait distribution, then square-rooting the result. The MSE was returned for each trait by the ‘missForest’ function (‘missForest’ package, Stekhoven, 2016; Stekhoven and Bühlmann, 2012) and corresponds to an out-of-bag error. For categorical traits, the error was estimated as the out-of-bag proportion of falsely classified traits.

S3.5 Functional loss and functional gain

Across all vertebrates, I estimated functional loss and functional gain using 84 studies for the tropical subset and 39 studies for the temperate subset (51,514 and 30,470 pairwise comparisons between sites respectively, Table S3.4). Because of this large number of pairwise comparisons, I did not develop a null modelling approach (if I used 100 randomisations per pair of sites, I would need to compute functional loss and functional gain for more than 8 million pairs, which would be very computationally demanding). I grouped mature, intermediate and young secondary vegetation together in this analysis. I could not estimate the effects in all land uses (for instance, sample sizes for tropical urban sites were too small; Figure S3.1).

Within classes, I used 18 tropical studies and 1 temperate study for amphibians; 38 tropical studies and 21 temperate studies for birds; 28 tropical studies and 9 temperate studies for mammals; and 11 tropical studies and 7 temperate studies for reptiles. As sample sizes differed among pairs of land uses and land-use intensities (Table S3.5), I was not able to estimate all effects, notably for the intensely-used land uses.

To calculate functional loss and functional gain, the Gower distance matrix (obtained from the global species by trait dataset for the species occurring in PREDICTS) was first subsetted to the species occurring in a given pair of sites. Cailliez corrections were applied when the distance matrix was not Euclidian (Cailliez corrections consist of applying the smallest positive constant to the distances so as to make them Euclidian (Cailliez, 1983); ‘ade4’ R package (Dray et al., 2007)). I then performed a principal coordinates analysis on the (corrected) Gower distance matrix, retaining the first two axes to reduce the computational load in the calculation of convex hulls. Sites that contained fewer than three functionally different species were excluded (the computation of a convex hull requiring more species in the assemblage than PCoA axes). Then I estimated the hypervolume of trait space occupied by each assemblage of a given pair, as well as the volume of the shared trait space (intersection), from which I derived functional loss and functional gain.

Table S3.4: Sample sizes (number of pairs of sites) for the calculation of functional loss and functional gain across all species.

Region	Pairs	Minimal use	Light use	Intense use
Temperate	PV-PV	7626	22546	492
	PV-SV	511	72	–
	PV-PF	9	166	–
	PV-PA	8	40	–
	PV-CR	150	–	–
	PV-UR	6306	1197	7
Tropical	PV-PV	8547	4016	16722
	PV-SV	6584	1124	9713
	PV-PF	580	1378	–
	PV-PA	36	20	22
	PV-CR	1700	1088	–
	PV-UR	–	–	–

Table S3.5: Sample sizes (number of pairs of sites) for the calculation of functional loss and functional gain within each class.

Class	Region	Pair of land uses	Minimal use	Light use	Intense use
Amphibians	Temperate	PV/PV	–	45	–
Amphibians	Temperate	PV/SV	8	70	–
Amphibians	Temperate	PV/AGR	3	–	–
Amphibians	Temperate	PV/UR	6	100	–
Amphibians	Tropical	PV/PV	501	241	307
Amphibians	Tropical	PV/SV	838	–	90
Amphibians	Tropical	PV/PF	422	91	–
Amphibians	Tropical	PV/AGR	1	3	1
Birds	Temperate	PV/PV	7,382	19,300	491
Birds	Temperate	PV/SV	150	1	–
Birds	Temperate	PV/PF	9	166	–
Birds	Temperate	PV/AGR	145	40	–
Birds	Temperate	PV/UR	6,300	992	–
Birds	Tropical	PV/PV	5,059	3,117	9,014
Birds	Tropical	PV/SV	3,491	1,058	5,225
Birds	Tropical	PV/PF	156	994	–
Birds	Tropical	PV/AGR	1,626	1,085	–
Mammals	Temperate	PV/PV	110	3,030	–
Mammals	Temperate	PV/SV	25	–	–
Mammals	Temperate	PV/AGR	5	–	–
Mammals	Temperate	PV/UR	–	105	7
Mammals	Tropical	PV/PV	1,989	637	64
Mammals	Tropical	PV/SV	230	65	8
Mammals	Tropical	PV/PF	2	–	–
Mammals	Tropical	PV/AGR	109	20	21
Reptiles	Temperate	PV/PV	132	2	1
Reptiles	Temperate	PV/SV	250	1	–
Reptiles	Temperate	PV/AGR	5	–	–
Reptiles	Tropical	PV/PV	989	137	5,140
Reptiles	Tropical	PV/SV	1,760	1	3,456
Reptiles	Tropical	PV/PF	–	190	–

S3.6 Diagnostic plots

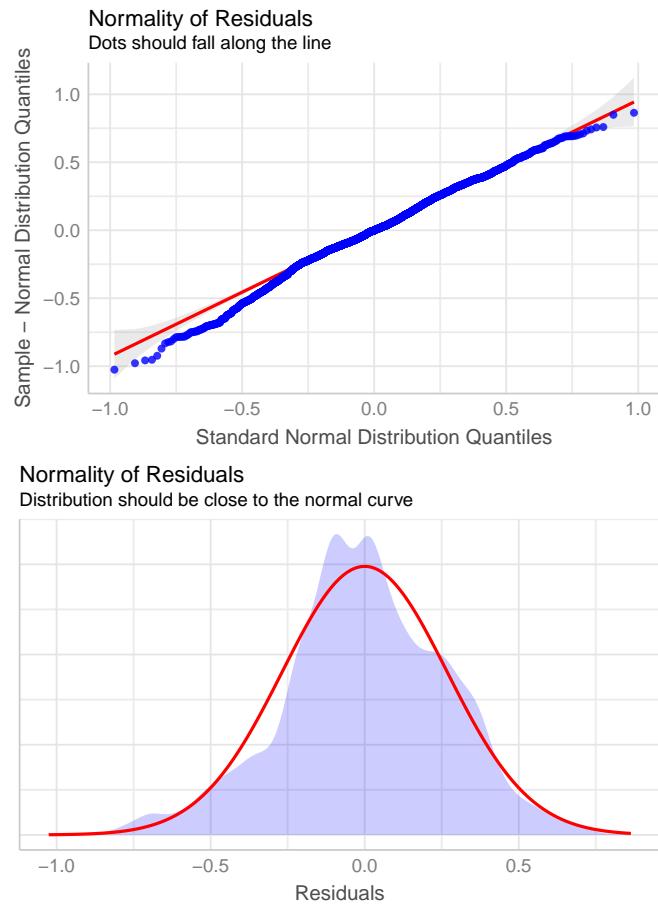


Figure S3.9: Diagnostic plots for Model 1a, obtained using the 'performance' R package (Lüdecke et al., 2021).

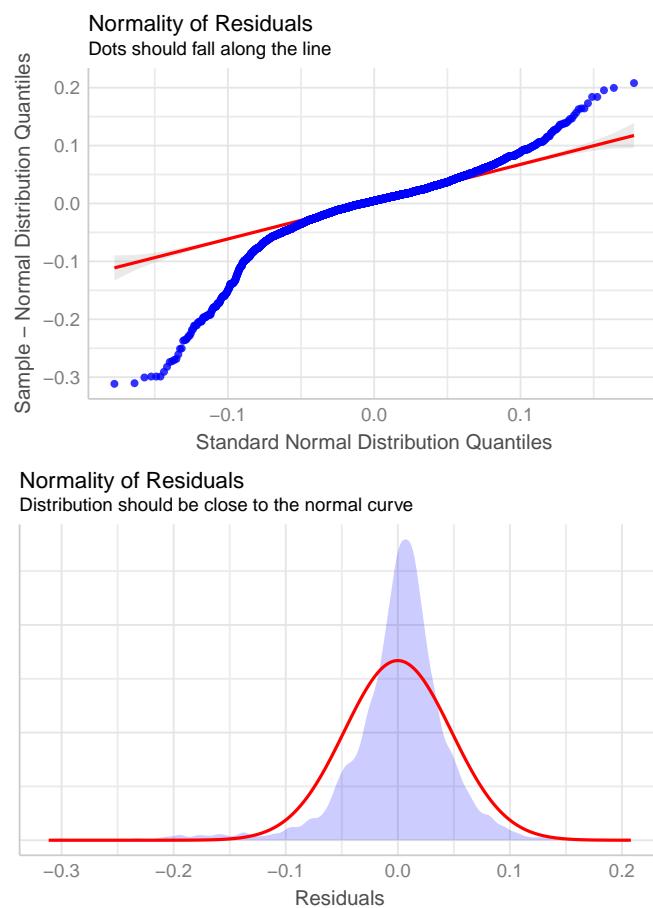


Figure S3.10: Diagnostic plots for **Model 1b**, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

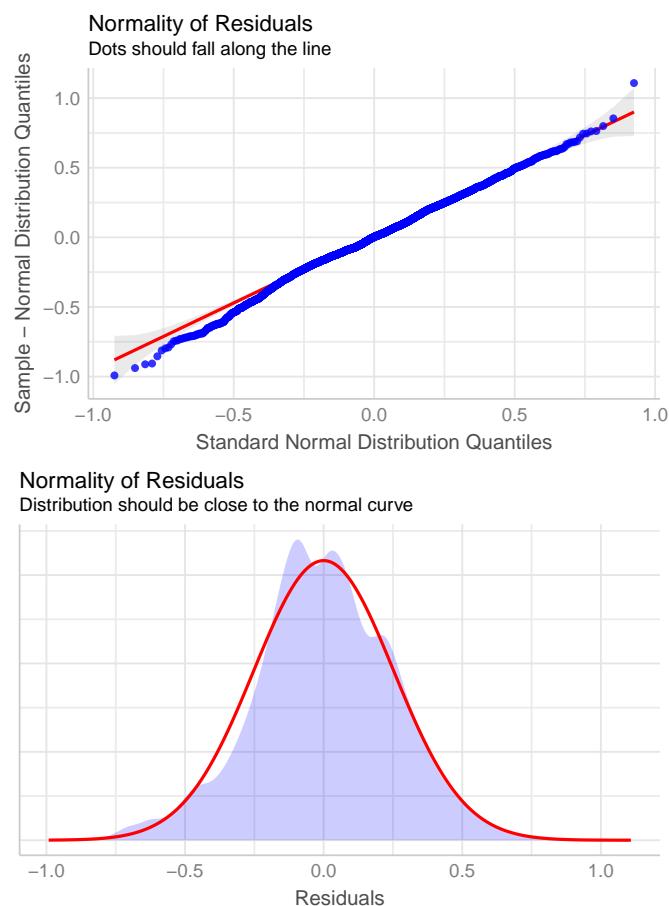


Figure S3.11: Diagnostic plots for Model 2a, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

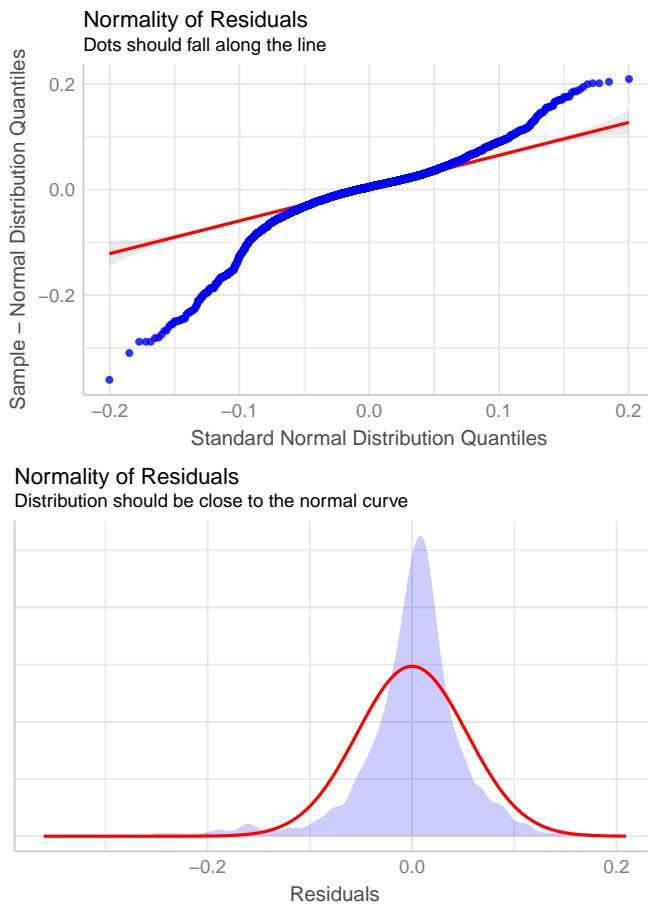


Figure S3.12: Diagnostic plots for Model 2b, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

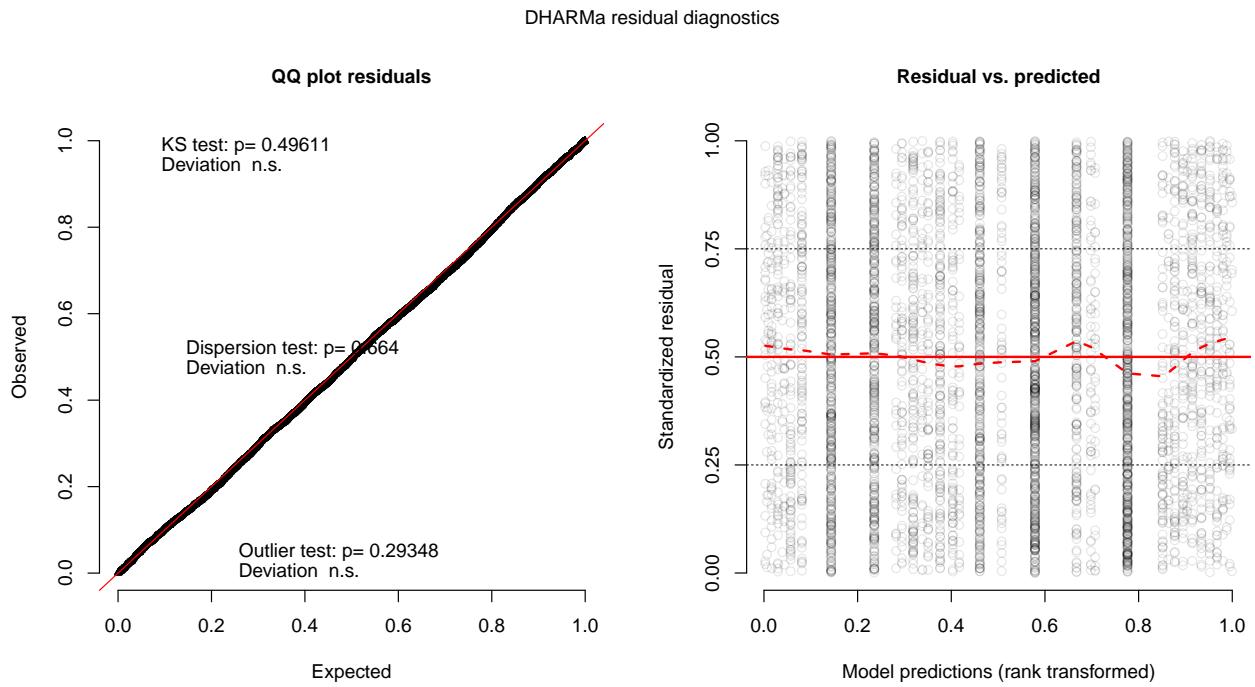


Figure S3.13: Diagnostic plots for Model 3, obtained using the ‘DHARMA’ R package (Hartig, 2021).

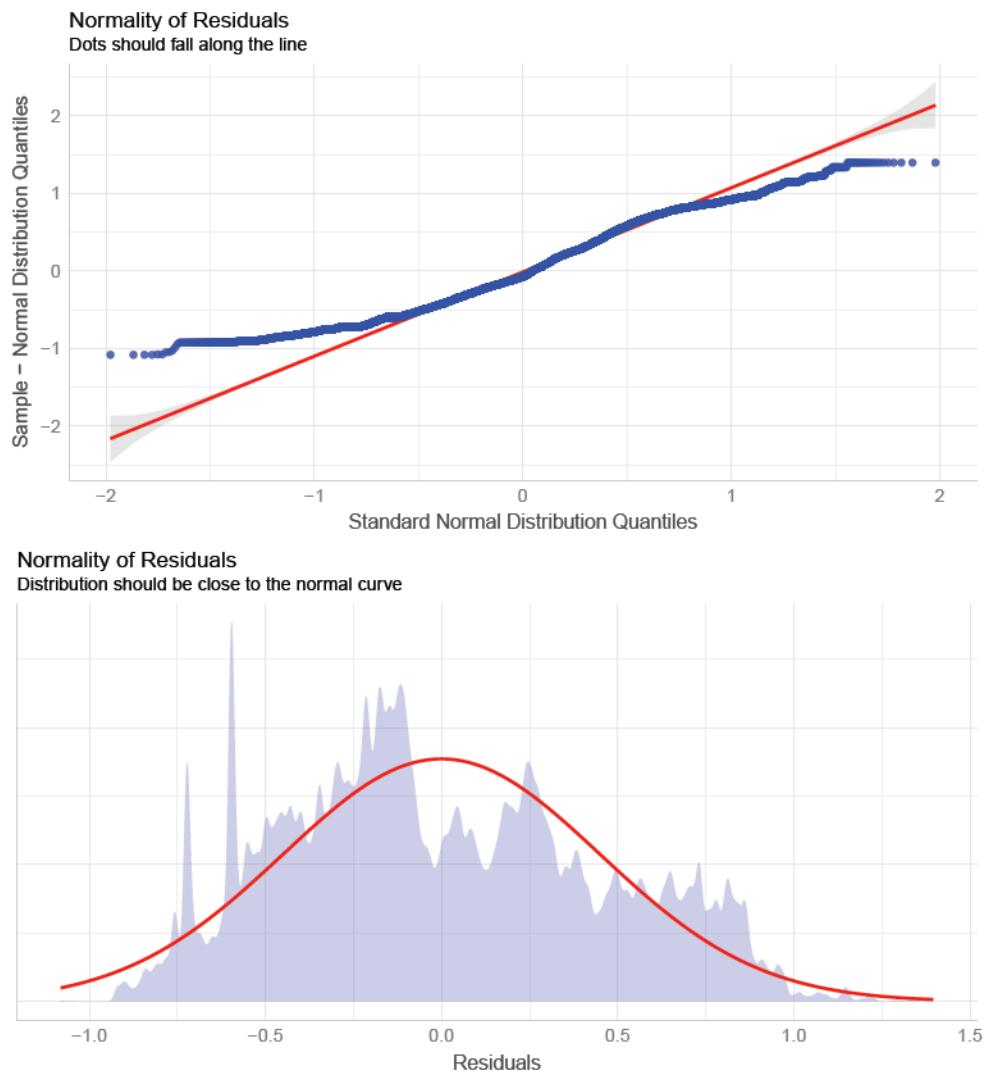


Figure S3.14: Diagnostic plots for Model 4a, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

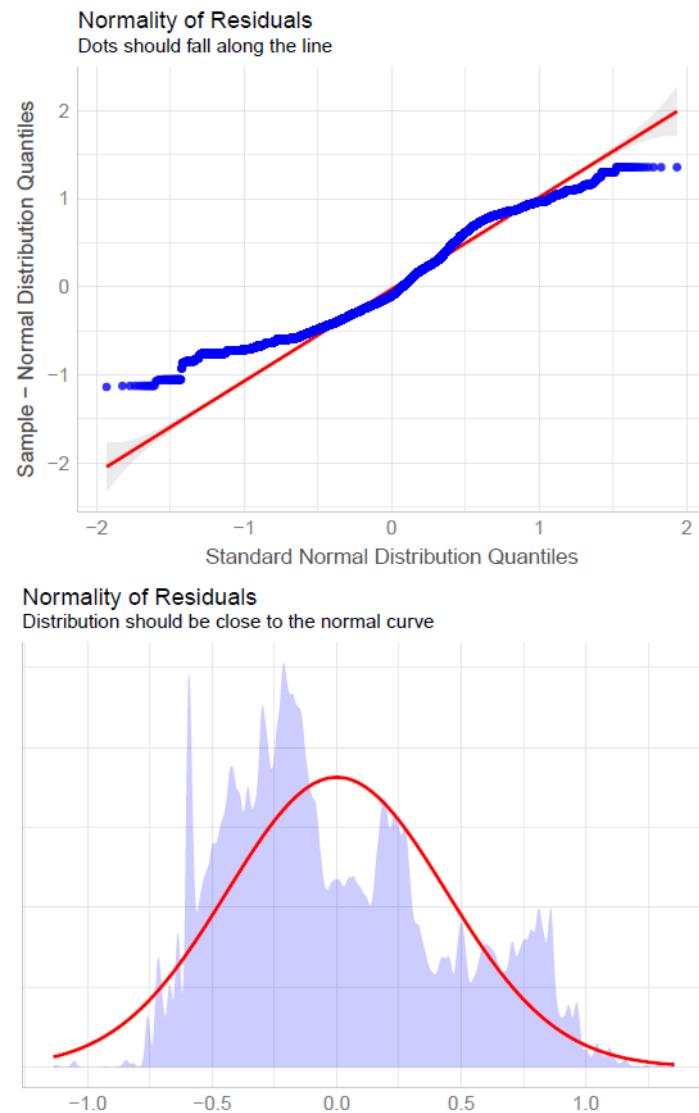


Figure S3.15: Diagnostic plots for Model 4b, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

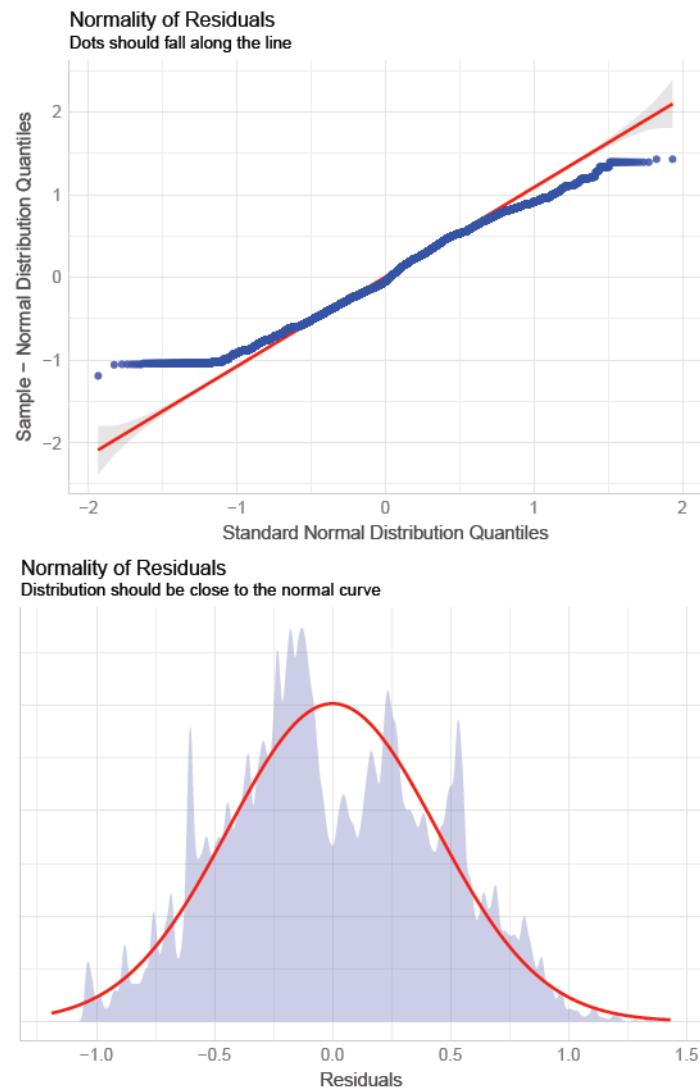


Figure S3.16: Diagnostic plots for Model 5a, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

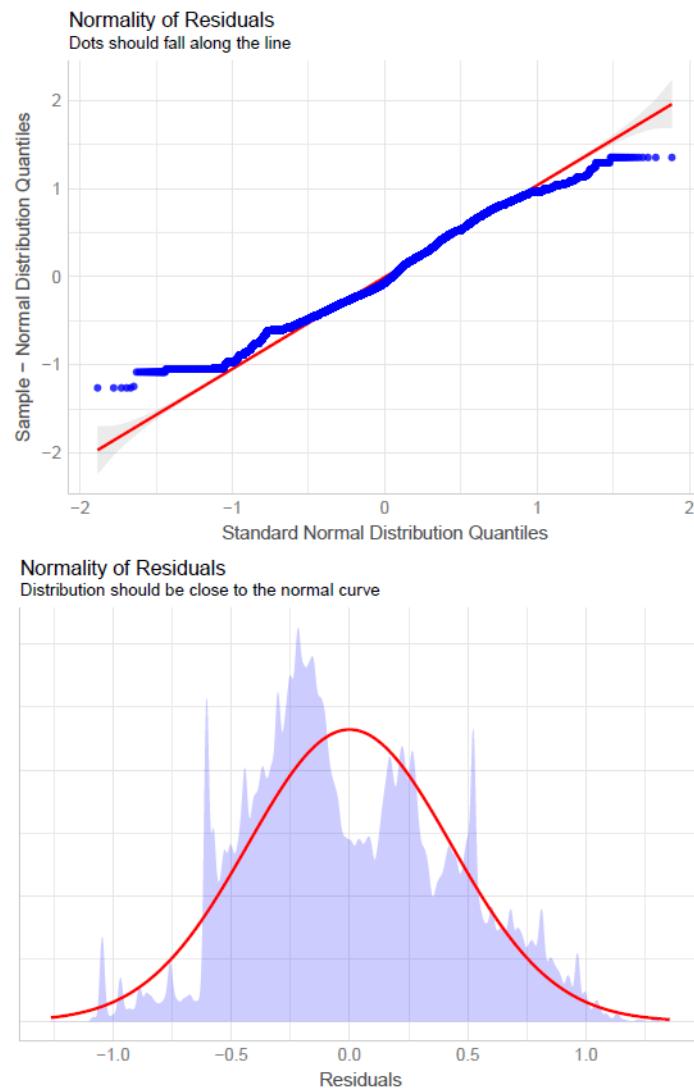


Figure S3.17: Diagnostic plots for **Model 5b**, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

S3.7 Model robustness

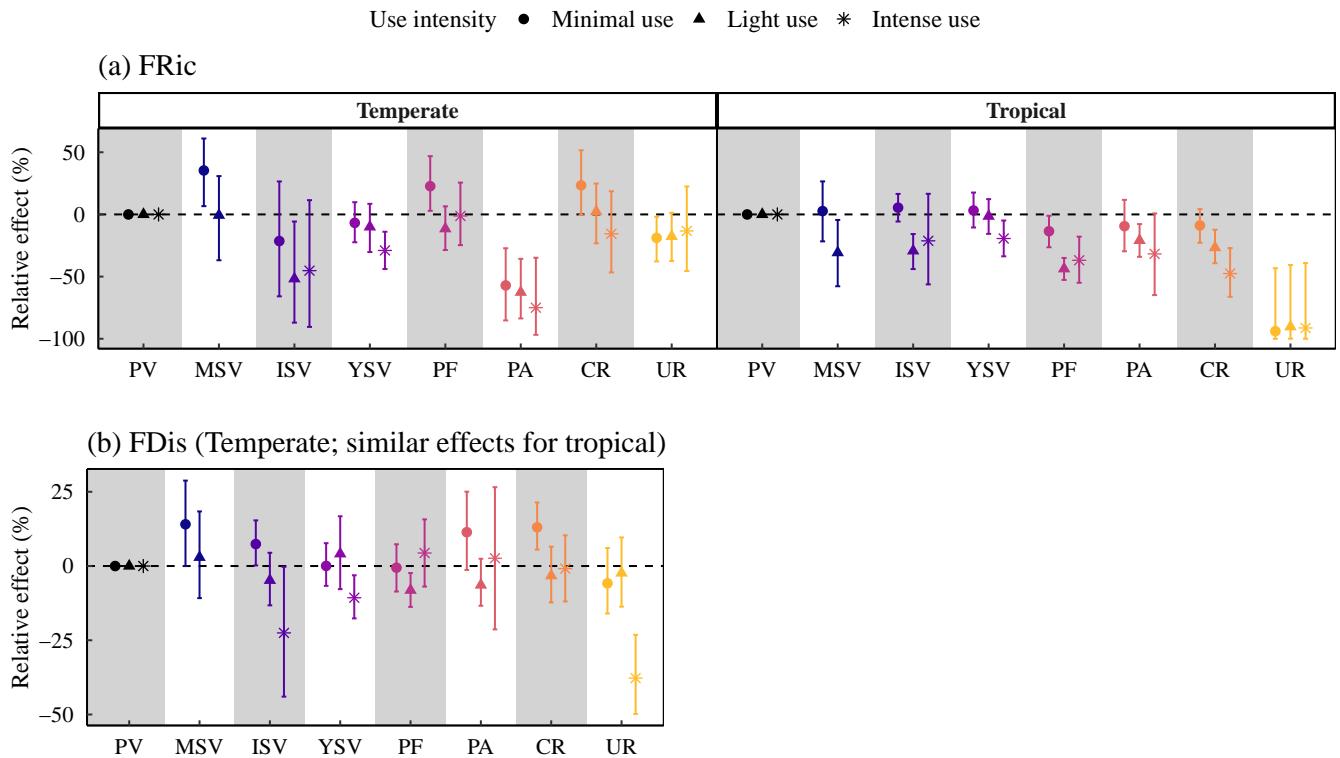


Figure S3.18: Effects of land use, land-use intensity and region on FRic (a) and FDis (b) across vertebrates, for the subset of species with complete trait data (i.e., excluding species with less than 100% trait completeness). Effects are plotted as a % difference relative to the reference land use (primary vegetation, PV). For FRic, I fitted **Model 1a**, which included the effects of land use, land-use intensity and region, as well as interactions between land use and land-use intensity and between land use and region. For FDis, I fitted **Model 1b**, which included effects of land use, land-use intensity and region, and interactions between land use and land-use intensity. Error bars represent 95% confidence intervals. MSV: mature secondary vegetation; ISV: intermediate secondary vegetation; YSV: young secondary vegetation; PF: plantation forest; PA: pasture; CR: cropland; UR: urban. Effects for Intense use in MSV could not be estimated as there weren't enough sampled sites.

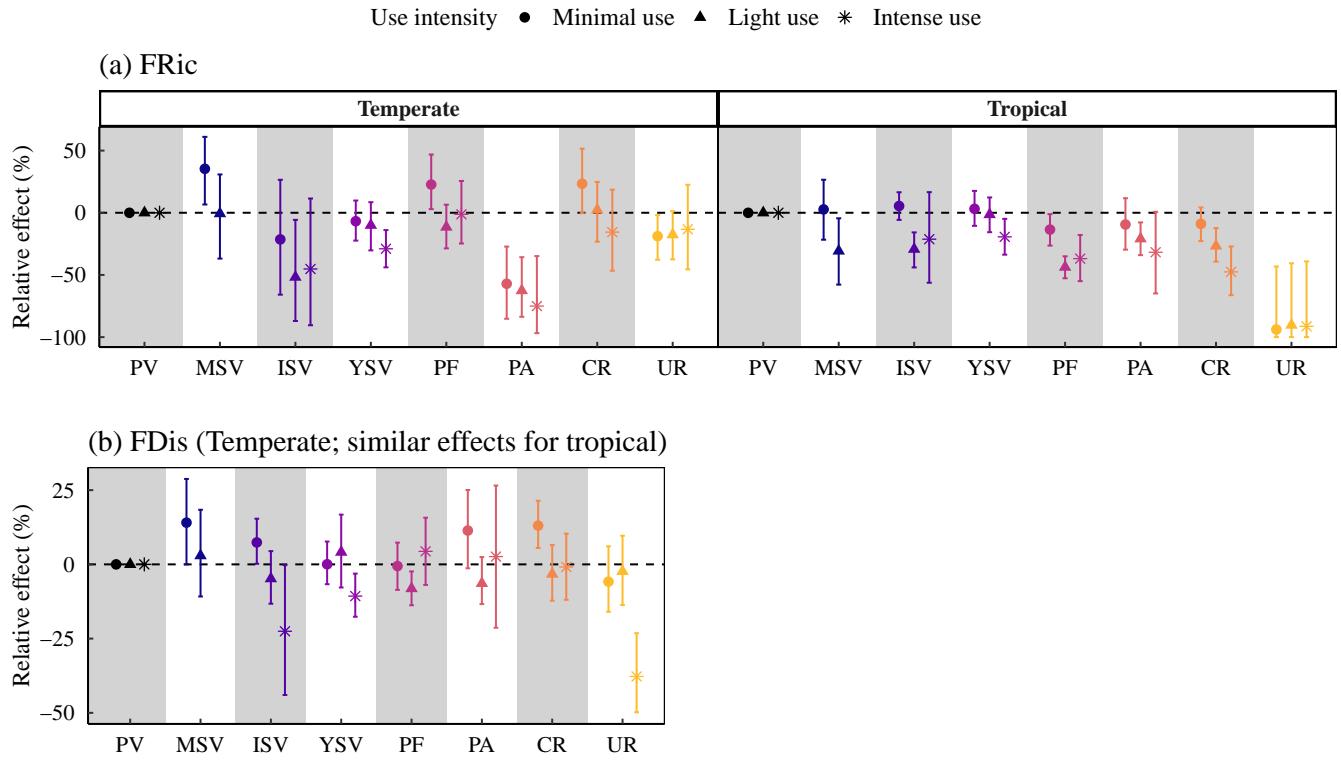


Figure S3.19: Effects of land use, land-use intensity and region on FRic (a) and FDis (b), for the subset of species with complete trait data (i.e., excluding species with less than 100% trait completeness), with geographical range size as an additional trait considered in the calculation of functional diversity metrics. Effects are plotted as a % difference relative to the reference land use (primary vegetation, PV). For FRic, I fitted **Model 1a**, which included the effects of land use, land-use intensity and region, as well as interactions between land use and land-use intensity and between land use and region. For FDis, I fitted **Model 1b**, which included effects of land use, land-use intensity and region, and interactions between land use and land-use intensity. Error bars represent 95% confidence intervals. MSV: mature secondary vegetation; ISV: intermediate secondary vegetation; YSV: young secondary vegetation; PF: plantation forest; PA: pasture; CR: cropland; UR: urban. Effects for Intense use in MSV could not be estimated as there weren't enough sampled sites.

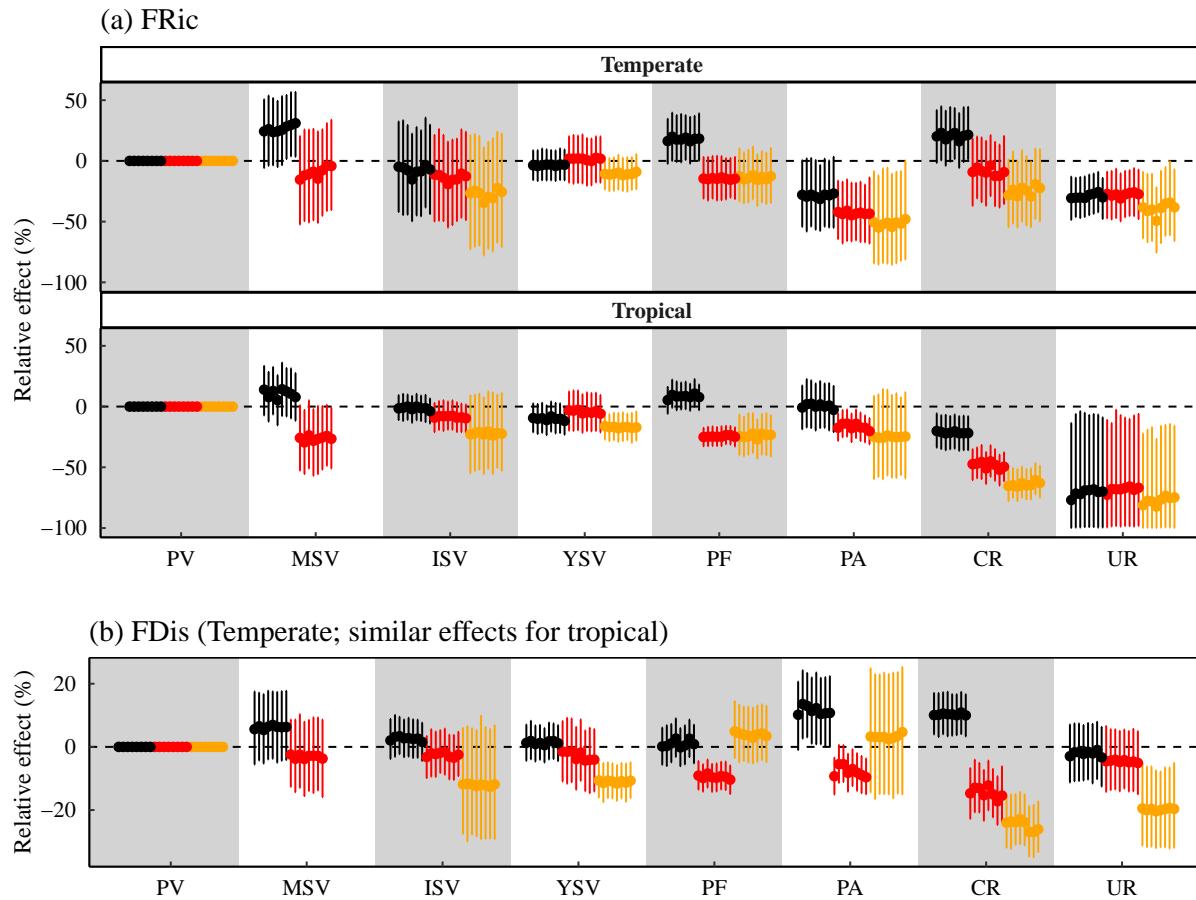


Figure S3.20: Effects of land use and land-use intensity on FRic (a) and FDis (b), obtained when calculating FRic and FDis with each set of imputed traits (eight in total). Effects are plotted as a % difference relative to the reference land use (primary vegetation, PV). For FRic, I fitted **Model 1a, which included the effects of land use, land-use intensity and region, as well as interactions between land use and land-use intensity and between land use and region. For FDis, I fitted **Model 1b**, which included effects of land use, land-use intensity and region, and interactions between land use and land-use intensity. Error bars represent 95% confidence intervals. MSV: mature secondary vegetation; ISV: intermediate secondary vegetation; YSV: young secondary vegetation; PF: plantation forest; PA: pasture; CR: cropland; UR: urban. Effects for Intense use in MSV could not be estimated as there weren't enough sampled sites.**

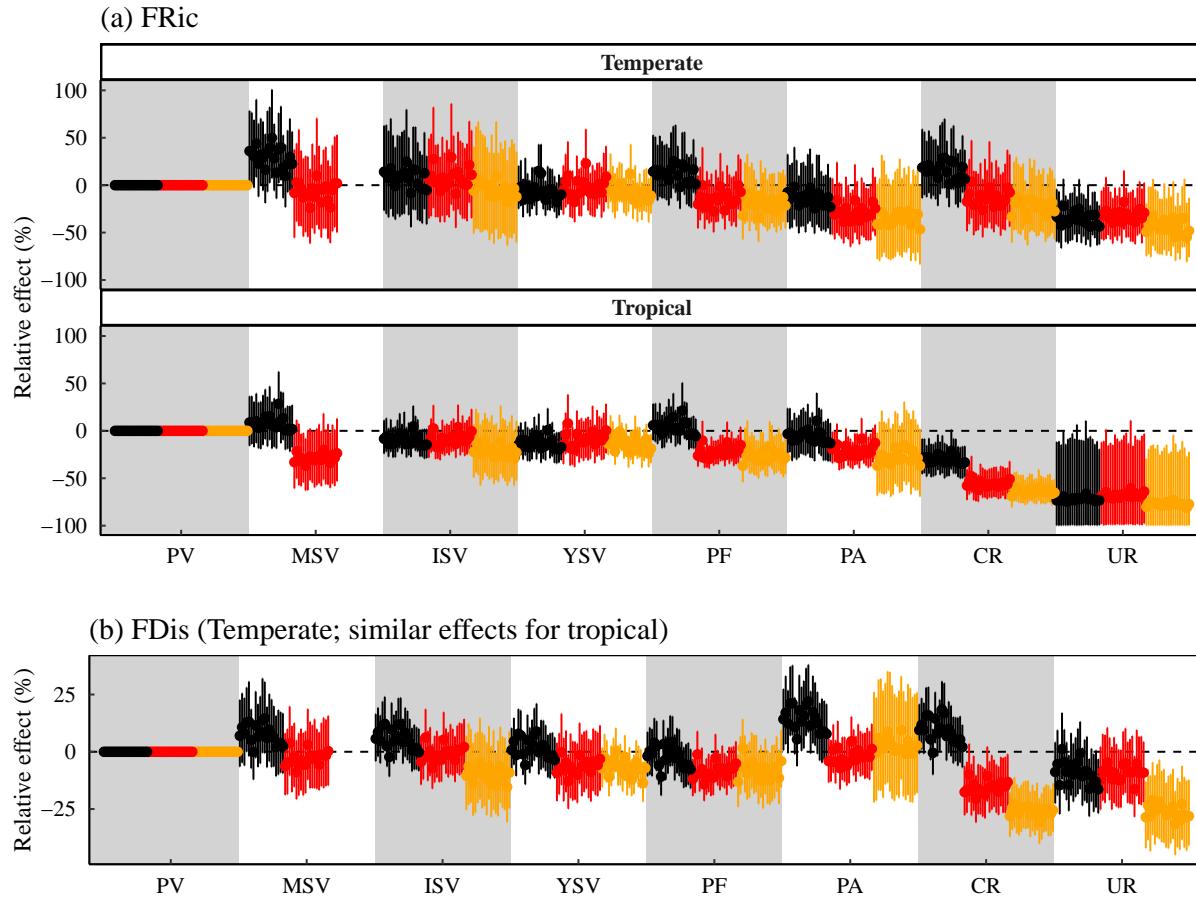


Figure S3.21: Effects of land use and land-use intensity on FRic (a) and FDis (b), obtained when re-sampling primary vegetation sites twenty independent times. I fixed the sample size for primary vegetation sites at 50. For FRic, we fitted **Model 1a**, which included the effects of land use, land-use intensity and region, as well as interactions between land use and land-use intensity and between land use and region. For FDis, I fitted **Model 1b**, which included effects of land use, land-use intensity and region, and interactions between land use and land-use intensity. Error bars represent 95% confidence intervals. MSV: mature secondary vegetation; ISV: intermediate secondary vegetation; YSV: young secondary vegetation; PF: plantation forest; PA: pasture; CR: cropland; UR: urban. Effects for Intense use in MSV could not be estimated as there weren't enough sampled sites.

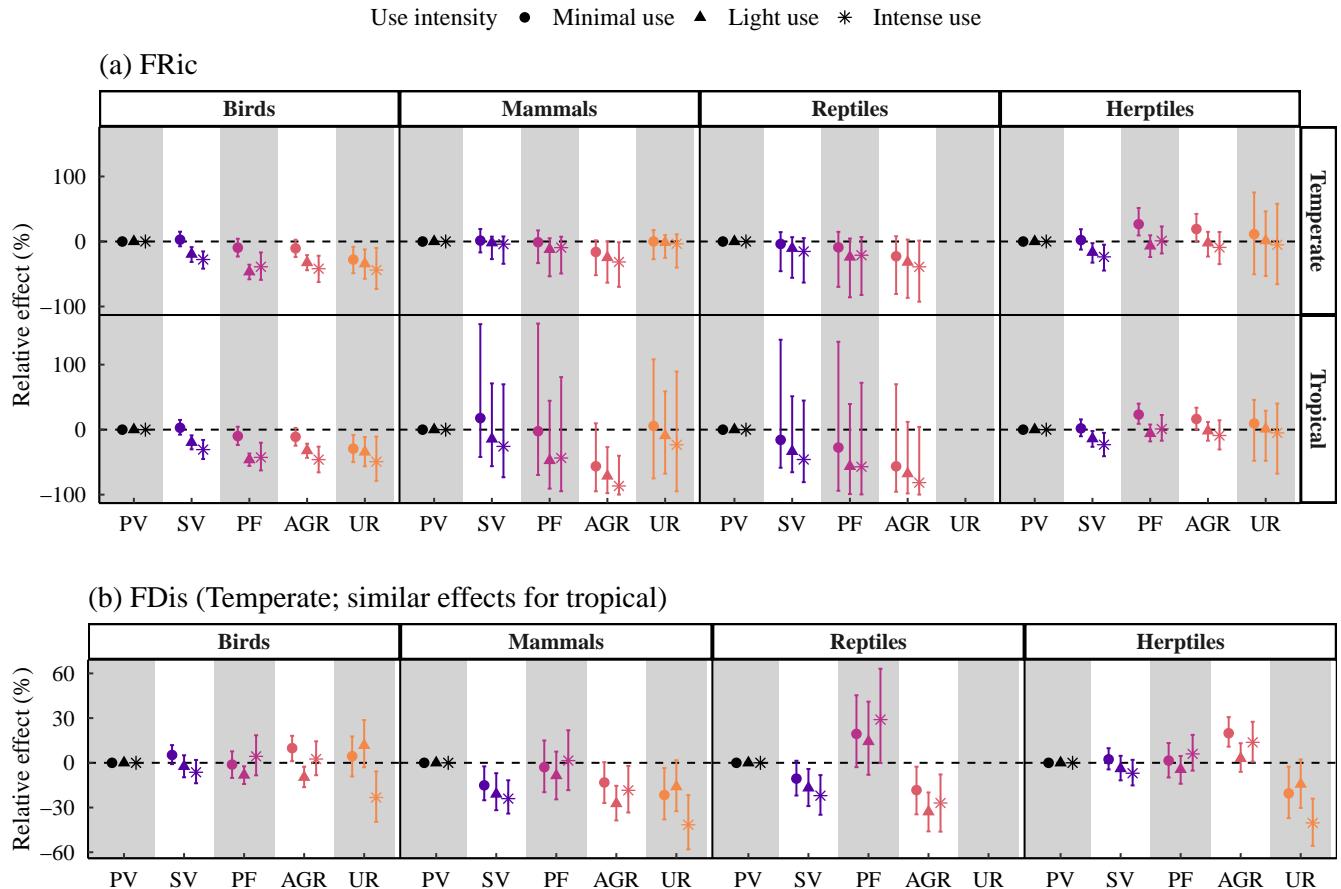
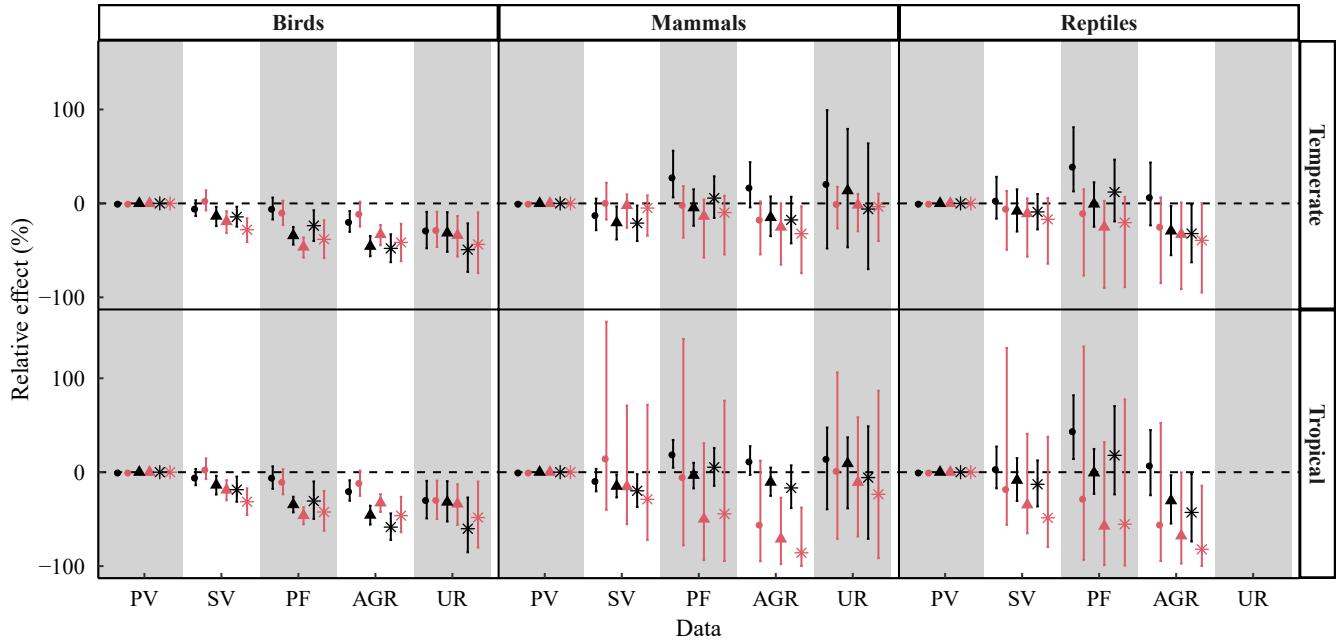


Figure S3.22: Effects of land use, land-use intensity and taxonomic class on FRic (a) and FDis (c), for the subset of species with complete trait data (i.e., excluding species with less than 100% trait completeness). Effects are plotted as a % difference relative to the reference land use (primary vegetation, PV). I did not include the effects of region here as sample sizes were not large enough for some classes. For FRic, the model included the effects of land use, land-use intensity and class, and interactions between land use and land-use intensity as well as land use and class. For FDis, the model included an additional interaction between land-use intensity and class. Error bars represent 95% confidence intervals. SV: secondary vegetation; PF: plantation forest; PA: pasture; CR: cropland; UR: urban. Effects for reptiles in urban land uses could not be estimated as there weren't enough sampled sites.

— complete and imputed trait data — complete trait data subset Use intensity • Minimal use ▲ Light use * Intense use

(a) FRic



(b) FDis

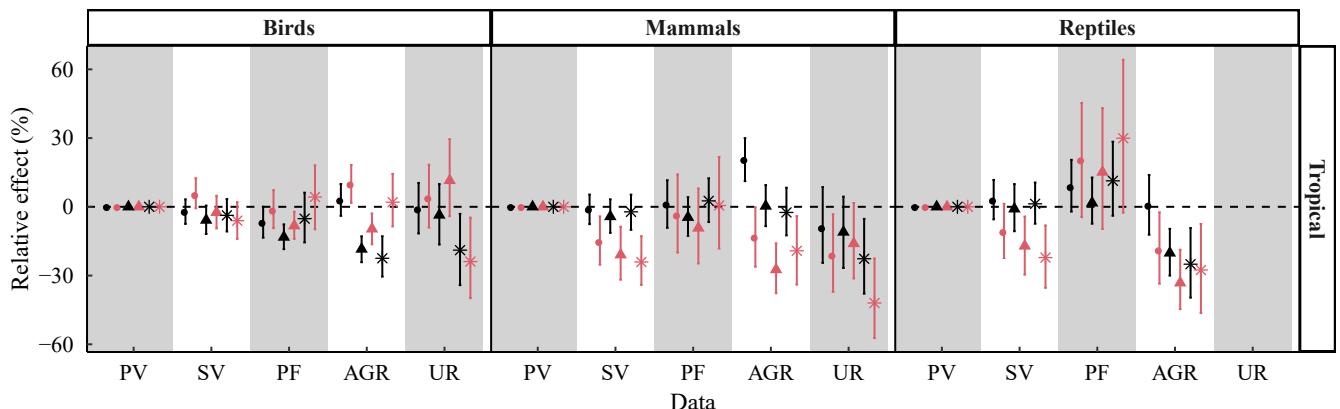


Figure S3.23: Effects of land use, region, land-use intensity and taxonomic class on FRic and FDis obtained with the imputed trait data (black points) or with the complete data subsets (red points). Effects are plotted as a % difference relative to the reference land use (primary vegetation, PV). For FRic, I fitted **Model 2a**, and I fitted **Model 2b** for FDis. Error bars represent 95% confidence intervals. SV: secondary vegetation; PF: plantation forest; AGR: agricultural (cropland and pasture); UR: urban. Effects for reptiles in urban land uses could not be estimated as there weren't enough sampled sites.

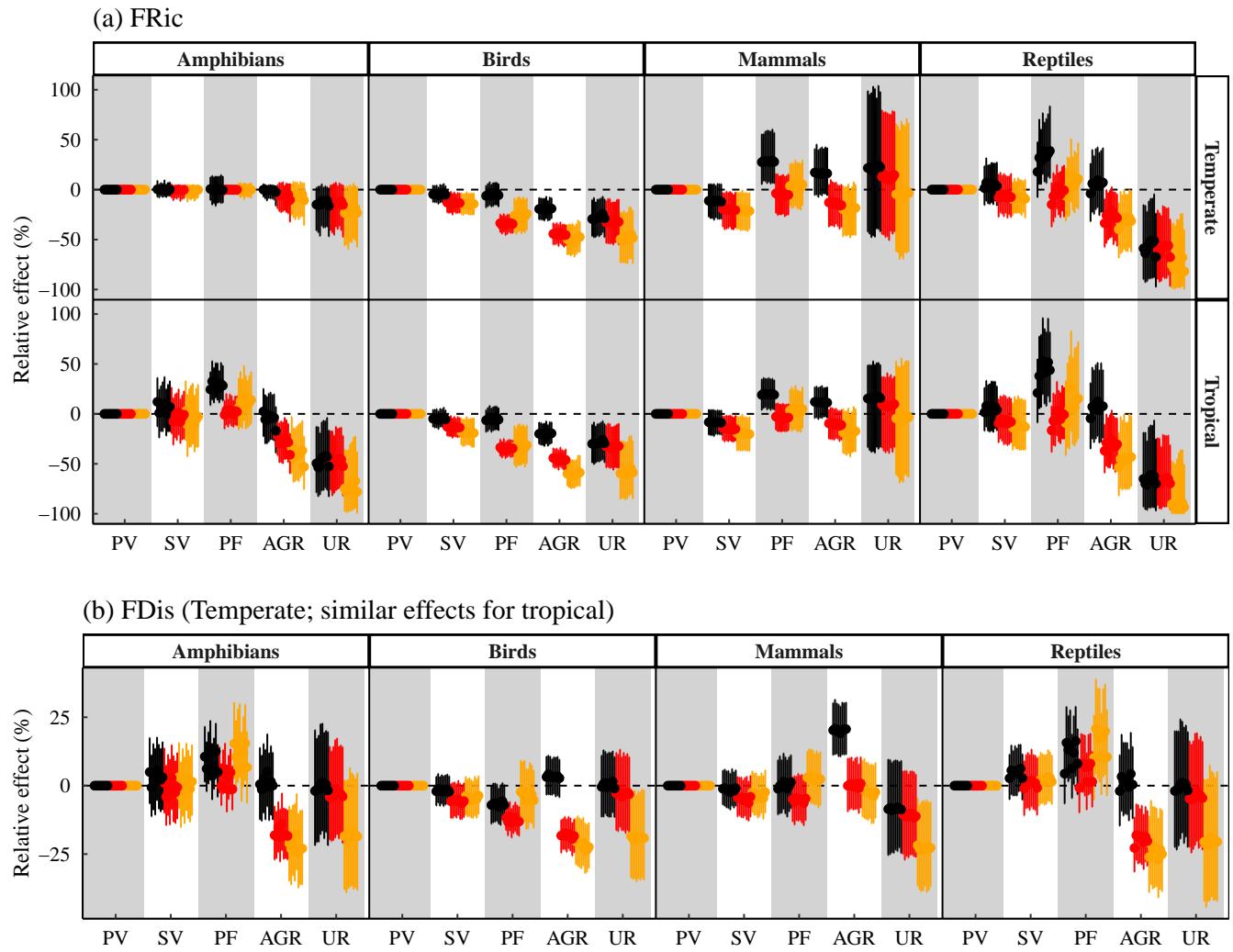


Figure S3.24: Effects of land use, region, land-use intensity and taxonomic class on FRic and FDis, obtained when calculating FRic and FDis with each set of imputed traits (eight in total). Effects are plotted as a % difference relative to the reference land use (primary vegetation, PV). For FRic, I fitted Model 2a, and Model 2b for FDis. Error bars represent 95% confidence intervals. SV: secondary vegetation; PF: plantation forest; AGR: agricultural (cropland and pasture); UR: urban. Effects for reptiles in urban land uses could not be estimated as there weren't enough sampled sites.

S3.8 Model robustness – time since land-use conversion

Time since land-use conversion could have important impacts on assemblage composition and thus, on local functional diversity. I did not investigate these effects because PREDICTS contained data on time since land-use conversion only for about 22% of the sites, considerably reducing samples sizes. Here, I investigated whether the results are likely robust to the inclusion of time since land-use conversion using the subset of sites for which time since land-use conversion was provided. To this end, I found the best-fitting models explaining FRic and FDis, using backwards stepwise selection, starting with complete models that included the effects of land use, time since land-use conversion, region, land-use intensity (for FRic only) and all two-way interactions among these predictors.

- For FRic, the best-fitting model included the main effects of land use and time since land-use conversion, but no interaction between these predictors. The model's summary (Table S3.6) showed that time since conversion had a significant negative effect on FRic, but the relationship between FRic and time since land-use conversion was similar in different land uses (as there were no interactions between land use and time since conversion retained in the best-fitting model, such that the slopes were similar in different land uses, and so the rate at which FRic decreased with time was similar in different land uses). The intercept was only different for urban land uses (significantly lower). Thus, based on this data subset, I expect time since land-use conversion to have a similar effect in different land-use types.

Table S3.6: Summary of the model explaining FRic by land use and time since land-use conversion, fitted on the subset of data for which there are information on time since land-use conversion.

	Estimate	Std. Error	t value
Intercept: Primary vegetation	1.156	0.073	15.921
Mature secondary vegetation	0.178	0.093	1.907
Intermediate secondary vegetation	0.018	0.072	0.249
Young secondary vegetation	-0.078	0.051	-1.532
Plantation forest	-0.018	0.082	-0.224
Pasture	-0.005	0.093	-0.054
Cropland	0.133	0.152	0.875
Urban	-0.316	0.133	-2.368
Time since conversion (log years)	-0.094	0.021	-4.566

I then compared this model's predictions with a simpler model that did not account for time since land-use conversion ($\text{FRic} \sim \text{Land use}$). The predictions (Figure S3.25) showed that including time since land-use

conversion did not bias the results, as I found a similar significant effect with both models in urban land uses, and elsewhere the effects were congruent. Thus, given this data subset, I argue that the results are robust to the inclusion of time since land-use conversion.

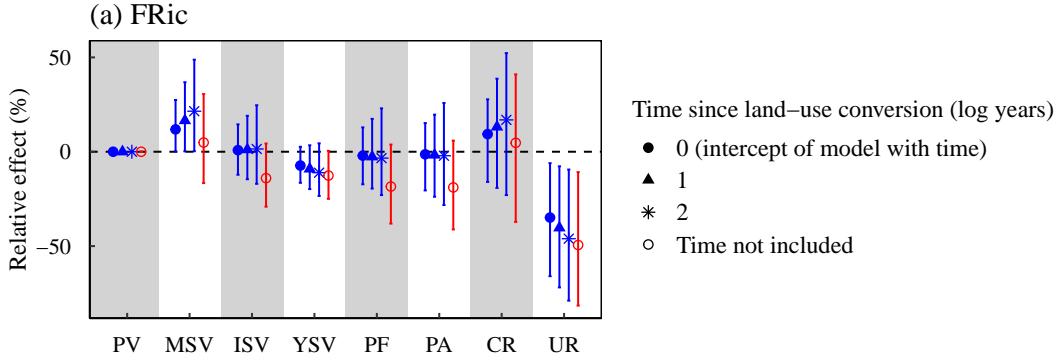


Figure S3.25: Effects of land use on FRic for the model that includes time since land-use conversion (blue points) versus the model that does not take time since land-use conversion into account (red points).

- For FDis, the best-fitting model included the main effects of land use, time since land-use conversion as well as interactions between land use and time since land-use conversion (I did not consider land-use intensity in the starting model because of sample size issues). Nevertheless, the main effect of time since land-use conversion was not significant (Table S3.7), and the relationship between time since land-use conversion and FDis was also not significant in most disturbed land uses (except for plantation forest). Thus, I argue the available data do not allow us to properly investigate the relationship between time since land-use conversion and FDis.

Table S3.7: Summary of the model explaining FDis by land use and time since land-use conversion, fitted on the subset of data for which I have information on time since land-use conversion.

	Estimate	Std. Error	t value
Intercept: Primary vegetation	0.366	0.011	32.219
Mature secondary vegetation	0.032	0.055	0.577
Intermediate secondary vegetation	-0.015	0.050	-0.298
Young secondary vegetation	0.020	0.015	1.386
Plantation forest	0.074	0.023	3.213
Pasture	-0.017	0.048	-0.346
Cropland	-0.013	0.042	-0.317
Urban	0.031	0.054	0.573
Time since conversion (years, log)	-0.004	0.004	-1.186
Mature secondary vegetation:Time since conversion (log years)	-0.005	0.015	-0.335
Intermediate secondary vegetation:Time since conversion (log years)	0.011	0.016	0.650
Young secondary vegetation:Time since conversion (log years)	-0.008	0.007	-1.170
Plantation forest:Time since conversion (log years)	-0.023	0.007	-3.077
Pasture:Time since conversion (log years)	0.010	0.015	0.688
Cropland:Time since conversion (log years)	0.007	0.012	0.620
Urban:Time since conversion (log years)	-0.016	0.022	-0.714

Appendix 3: Supporting information for Chapter 4

S4.1 Compiling diet information

For mammals and birds, diet information was obtained from the EltonTraits database (Wilman et al., 2014). Before processing the data, the taxonomy was aligned to that of the trait datasets compiled in Chapter 2. Primary diet – that is, the diet inferred from the combination of food items that represent more than 50% of species consumption – was directly available for birds, but not for mammals. For both classes, diet was described as the percent use of different food items (namely: invertebrates, vertebrates – either ectotherms, endotherms, fish or unknown –, carrion, fruit, nectar, seed or other plant material). In order to have a consistent classification scheme across mammals and birds, I chose not to use the provided primary diet for birds, and instead I applied my own procedure to infer primary diet from recorded food items across birds and mammals. I first grouped the different vertebrate food items together with carrion to create a single ‘vertebrate’ food item category. I then used the percent uses of the food items to infer primary diet, classifying species’ primary diet into the following categories: vertebrate eaters; invertebrate eaters; plant/seed eaters; fruit/nectar eaters; and omnivores [these categories are similar to those employed for birds’ primary diet in EltonTraits]. When all food items had a percent use below (or equal to) 50% percent, species were classified as omnivores. For each species, I calculated diet breadth as the number of consumed food items (regardless of the percent use of those items; I kept vertebrate food items grouped together in the calculation of diet breadth, such that I did not count carrion as a separate food item).

For amphibians, diet information was partly extracted from the AmphiBIO database (Oliveira et al., 2017), and partly compiled from the literature (see next paragraph). In AmphiBIO, diet information was recorded as the consumption of six food items (leaves, flowers, seeds, fruit, arthropods and vertebrates), but the percent use of these items was not recorded (only whether they were consumed or not). From AmphiBIO, I classified amphibians into the different diet categories, depending on the combinations of consumed food

items (with species consuming both plant and animal matter classified as omnivores; species consuming both vertebrates and invertebrates also classified as omnivores; and species consuming plant or seed only, fruit or nectar only, vertebrates only or invertebrates only classified into the corresponding groups).

To increase diet data coverage for amphibians, I used data compiled by Rhiannon Osborne-Tonner, collected during her MSci project at UCL. Rhiannon Osborne-Tonner collected data from published papers and from the grey literature, targeting species occurring in the PREDICTS database (which I used for inferring land-use responses). Using these data, I was able to supplement my datasets with diet information for an additional 108 amphibians from 26 published sources (all found to be invertebrate eaters; see below for the list of sources). For reptiles, there was no readily available diet information (except for trophic level information, see Chapter 2). Thus, I used diet data compiled by Rhiannon Osborne-Tonner, collected from the literature, again specifically targeting reptiles occurring in the PREDICTS database. I was thus able to add diet information for 239 reptiles. Finally, I calculated diet breadth across amphibians and reptiles from the recorded food items. The diet data compiled by Rhiannon Osborne-Tonner are available at: https://figshare.com/articles/Reptile_Diet_csv/12024309 (DOI: 10.6084/m9.figshare.12024309.v1) and https://figshare.com/articles/Untitled_Item/12024312 (DOI: 10.6084/m9.figshare.12024312.v4).

Complementary data sources for amphibians

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- Fonseca-Pérez, K. A., Molina, C., & Tárano, Z. (2017). Diet of *Dendropsophus microcephalus* and *Scarthyla vigilans* (Anura: Hylidae) at a locality in north-western Venezuela with notes on microhabitat occupation. *Papéis Avulsos De Zoologia*, 57(7), 93-104.
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- Yap, C.H. & Jaafar, I. (2011). Stomach Content Analysis of Tropical Forest Toads *Ingerophrynus parvus* and *Phrynoïdes aspera* (ANURA : BUFONIDAE) from Kedah, Malaysia. Taxonomist and Ecologist Conference 2011.

Complementary data sources for reptiles

The 148 sources are listed in the dataset available from https://figshare.com/articles/Reptile_Diet_csv/12024309 (DOI: 10.6084/m9.figshare.12024309.v1).

S4.2 Imputing missing trait values

S4.2.1 Trait data coverage

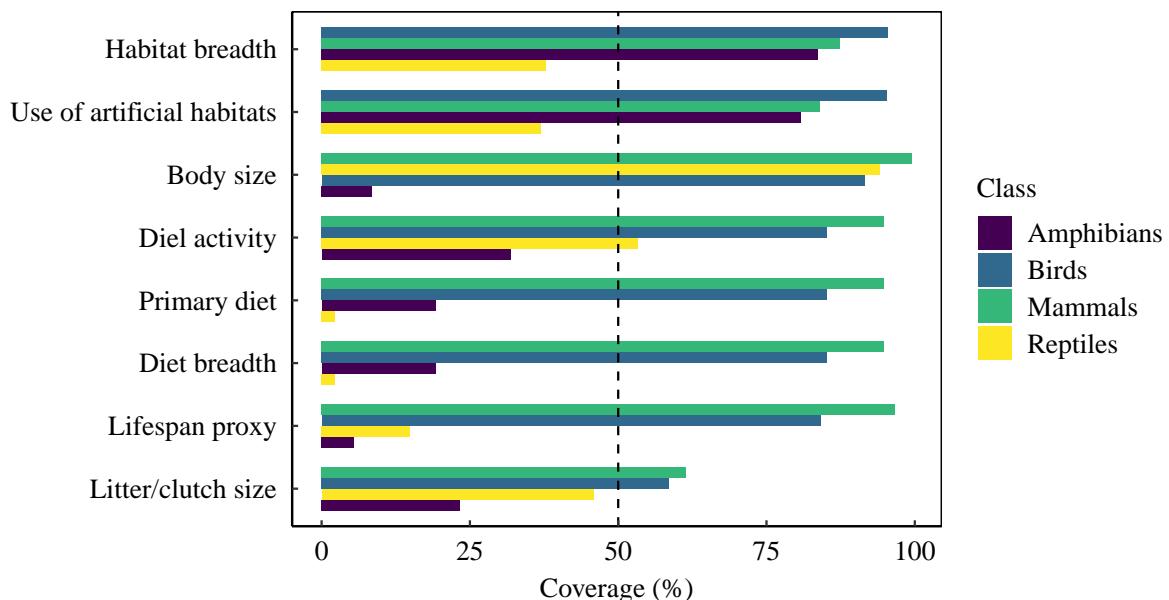


Figure S4.1: Trait coverage, including coverage for diet information, calculated as the proportion of species for which trait values are not missing. The dashed line represents 50% coverage.

S4.2.2 Phylogenetic signal in traits

I measured the phylogenetic signal in traits using Pagel's λ (for continuous traits) and Borges' δ (for categorical traits). I found evidence of phylogenetic conservatism in all traits.

Table S4.1: Phylogenetic signal in continuous and categorical traits. BM: body mass; BL: body length; GL: generation length; MA: age at sexual maturity; ML: maximum longevity; L: longevity; LCS: litter/clutch size; HB: habitat breadth; DA: diel activity; UA: use of artificial habitats. Continuous traits were log-10 transformed to improve normality before estimating Pagel's λ – except for habitat breadth and diet breadth which were square-rooted. A star indicates a significant signal ($P<0.05$ for the log-likelihood ratio test in the case of λ ; and a significant difference from the simulated null distribution of δ for categorical traits). 'NA' indicates traits that were not considered for a given class.

Class	Pagel's λ										Borges' δ		
	BM	BL	GL	MA	ML	L	LCS	HB	Diet breadth	Diet	DA	UA	
Amphibians	0.98*	0.94*	NA	0.85*	0.82*	NA	0.93*	0.99*	0.61*	3.4*	3.4*	4.5*	
Birds	0.99*	NA	0.97*	NA	NA	NA	0.95*	0.60*	0.72*	6.4*	32e3*	1.8*	
Mammals	0.99*	NA	0.97	NA	NA	NA	0.99	0.71	0.99*	26*	52*	1.3*	
Reptiles	1.0*	NA	NA	NA	0.94*	0.98*	1.0*	0.52*	0.84*	2.2*	6.4*	1.4*	

S4.2.3 Implementation of missing value imputations

I imputed missing trait values using random forest algorithms, as implemented in R with ‘missForest’ (Stekhoven, 2016; Stekhoven and Bühlmann, 2012). Phylogenetic relationships were included as additional predictors in the form of phylogenetic eigenvectors (Diniz-Filho et al., 2012), extracted from the phylogenies using the PVR package (Santos, 2018). I used class-specific phylogenetic trees from <https://zenodo.org/record/3690867#.Xyc5wyhKhPZ> for mammals (Phylacine 1.2; Faurby et al. (2018, 2020)); and from <https://data.vertlife.org/> for amphibians (Jetz & Pyron 2018), birds (Jetz et al. 2012) and squamates (Tonini et al. 2016). For each class, I used a consensus tree obtained with the TreeAnnotator programme of the BEAST software (Bouckaert et al. 2014), from an available distribution of 1000 trees.

Following Penone et al. (2014), I included the first ten phylogenetic eigenvectors as additional predictors of missing trait values in each class. As not all species were represented in the phylogenies, I also added taxonomic order as a predictor for all species. All traits in Table S4.1 were included in the imputations. Habitat & diet breadth were considered as categorical variables for the imputations (and so, discretised), in order to ensure that only integer estimates were obtained from the imputations for these traits. Tuning parameters of ‘missforest’ were set to ten maximum iterations and to one hundred trees grown in each forest.

S4.2.4 Imputation error

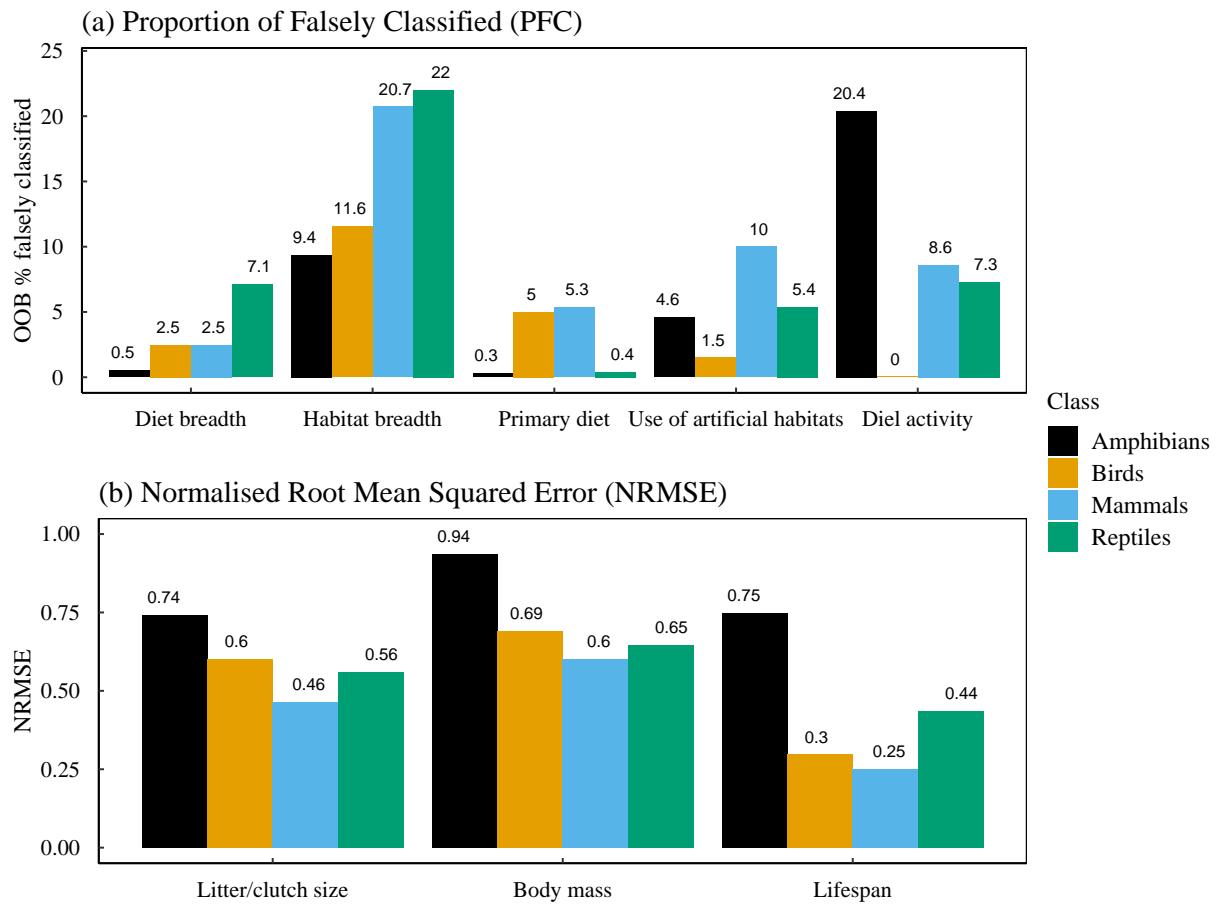


Figure S4.2: Out-of-bag estimation of imputation errors for the traits included in the analyses. (a) For the categorical traits, I show the proportion of falsely classified traits ('PFC', out-of-bag estimates); (b) For the continuous traits, I calculate the normalised root-mean-squared error (NRMSE), from the out-of-bag mean square error that I divide by the standard deviation of the known trait distribution. The lower the NRMSE, the lower the imputation error, with values close to 0 indicating lower imputation error and values close to 1 tending to indicate higher imputation error.

S4.3 Land-use types in PREDICTS and sample sizes (number of sampled sites across classes)

Table S4.2: Land-use categories in the PREDICTS database. See Hudson et al. (2014, 2017) for more details.

Land-use category	Definition
Primary vegetation	Native vegetation, undisturbed since its establishment under current climatic conditions. No known alterations due to human activities or to extreme natural events.
Mature secondary vegetation	Vegetation recovering after complete destruction of primary vegetation & where succession is near complete – the structure approaches that of primary vegetation.
Intermediate secondary vegetation	Vegetation recovering after complete destruction of primary vegetation at a mid-successional stage.
Young secondary vegetation	Vegetation recovering after complete destruction of primary vegetation at an early successional stage.
Plantation forest	Previously cleared areas planted with crop trees or shrubs grown and harvested for human consumption or for commercial purposes (includes wood, fruit, oil, biofuel, rubber, etc).
Pasture	Areas grazed by livestock, permanently or regularly. Can be improved through cultivation techniques.
Cropland	Previously cleared areas planted with herbaceous crops and harvested for human or animal consumption (including animal feed and crops used in the food industry), or for commercial purposes (e.g., crops grown for the textile industry).
Urban	Previously cleared areas built up by humans. Vegetation is managed for civic or personal purposes.

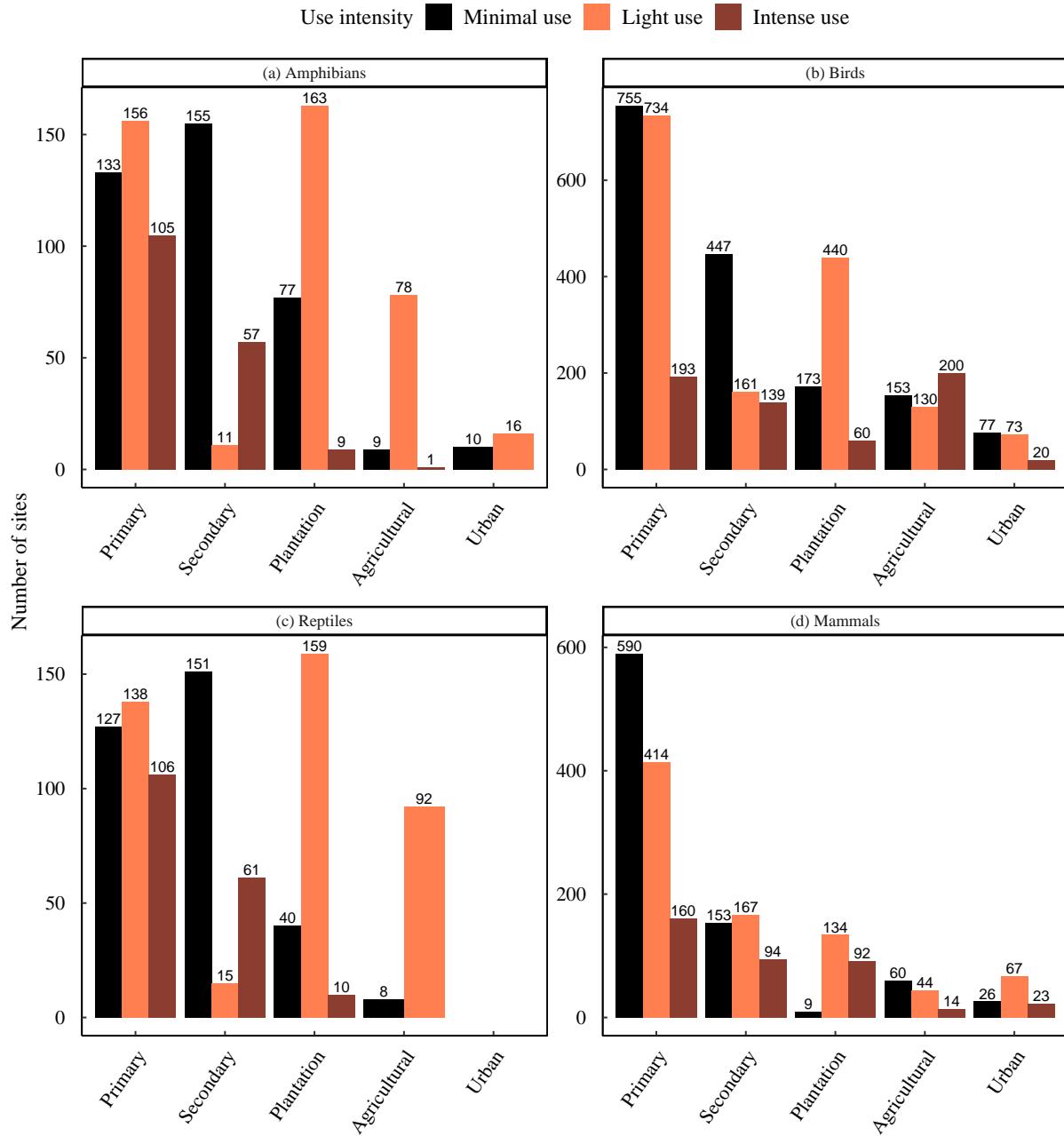


Figure S4.3: Sample sizes (number of PREDICTS sites) for the different land-use types, in each class.

S4.4 Land-use responses: multicollinearity checks among the models' explanatory variables

Table S4.3: Generalised Variance Inflation Factors among the candidate explanatory variables for the mixed-effects model fitted across amphibians, prior to the exclusion of diet. The model aimed at investigating the effects of land use, land-use intensity and the species-level ecological characteristics on species occurrence probability.

Predictor	GVIF
Diel activity	1.7
Lifespan proxy (\log_{10})	1.8
Specialisation	1.8
Range area (\log_{10})	2.0
Body mass (\log_{10})	2.0
Land use	2.0
Litter/clutch size (\log_{10})	2.5
Land-use intensity	2.6
Habitat breadth (square-root)	3.2
Diet breadth (square-root)	22.8
Primary diet	23.6

Table S4.4: Generalised Variance Inflation Factors among the explanatory variables for the mixed-effects model fitted across amphibians (after the exclusion of diet), looking at the effects of land use, land-use intensity and the species-level ecological characteristics on species occurrence probability.

Predictor	GVIF
Diel activity	1.6
Diet breadth (square-root)	1.7
Lifespan proxy (\log_{10})	1.8
Specialisation	1.8
Range area (\log_{10})	1.9
Land use	2.0
Body mass (\log_{10})	2.0
Litter/clutch size (\log_{10})	2.4
Land-use intensity	2.6
Habitat breadth (square-root)	3.1

Table S4.5: Generalised Variance Inflation Factors among the explanatory variables for the mixed-effects model fitted across birds, looking at the effects of land use, land-use intensity and the species-level ecological characteristics on species occurrence probability.

Predictor	GVIF
Diel activity	1.1
Land use	1.2
Land-use intensity	1.2
Litter/clutch size (\log_{10})	1.3
Range area (\log_{10})	1.4
Diet breadth (square-root)	1.5
Specialisation	1.6
Lifespan proxy (\log_{10})	1.7
Habitat breadth (square-root)	1.8
Body mass (\log_{10})	1.9
Primary diet	2.3

Table S4.6: Generalised Variance Inflation Factors among the explanatory variables for the mixed-effects model fitted across mammals, looking at the effects of land use, land-use intensity and the species-level ecological characteristics on species occurrence probability.

Predictor	GVIF
Diel activity	1.2
Range area (\log_{10})	1.2
Specialisation	1.4
Land-use intensity	1.4
Diet breadth (square-root)	1.7
Land use	1.8
Habitat breadth (square-root)	1.8
Litter/clutch size (\log_{10})	2.7
Body mass (\log_{10})	3.0
Lifespan proxy (\log_{10})	3.4
Primary diet	4.4

Table S4.7: Generalised Variance Inflation Factors among the candidate explanatory variables for the mixed-effects model fitted across reptiles, prior to the exclusion of diet. The model aimed at investigating the effects of land use, land-use intensity and the species-level ecological characteristics on species occurrence probability.

Predictor	GVIF
Diel activity	1.1
Specialisation	1.3
Range area (\log_{10})	1.3
Habitat breadth (square-root)	1.6
Lifespan proxy (\log_{10})	1.9
Litter/clutch size (\log_{10})	2.8
Land use	3.2
Land-use intensity	3.5
Body mass (\log_{10})	3.9
Diet breadth (square-root)	5.8
Primary diet	9.9

Table S4.8: Generalised Variance Inflation Factors among the explanatory variables for the mixed-effects model fitted across reptiles (*after the exclusion of diet*), looking at the effects of land use, land-use intensity and the species-level ecological characteristics on species occurrence probability.

Predictor	GVIF
Diel activity	1.1
Diet breadth (square-root)	1.2
Specialisation	1.2
Range area (\log_{10})	1.3
Habitat breadth (square-root)	1.6
Lifespan proxy (\log_{10})	1.9
Litter/clutch size (\log_{10})	2.7
Land use	3.2
Body mass (\log_{10})	3.2
Land-use intensity	3.4

S4.5 Implementing Climate-niche Factor Analysis across terrestrial vertebrates

S4.5.1 Historical climate data: groups of intercorrelated variables

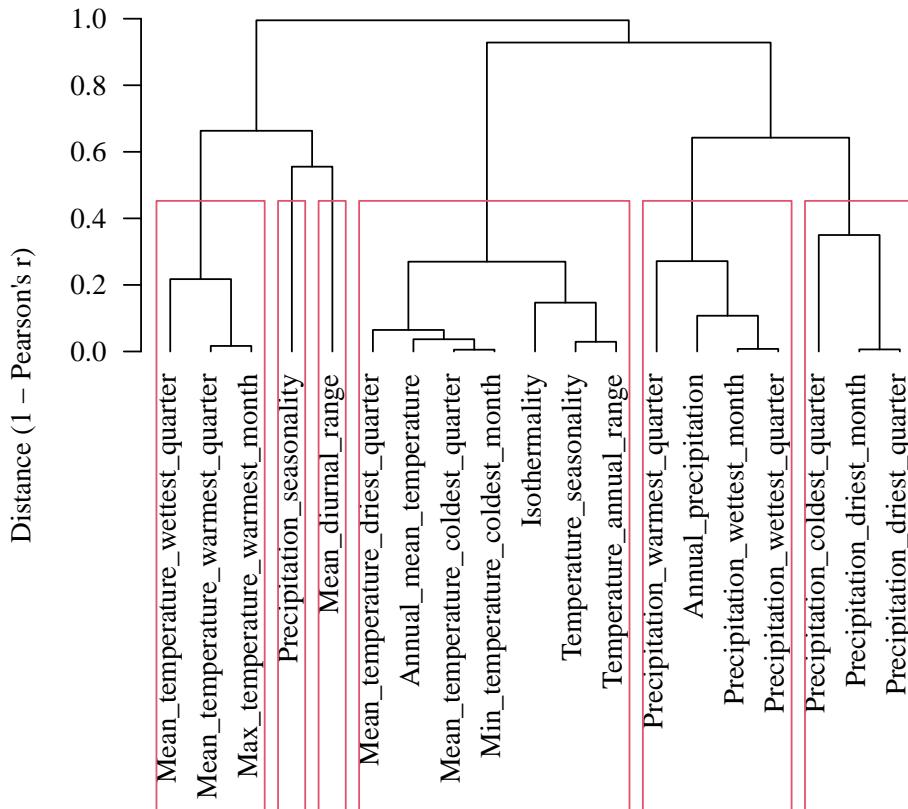


Figure S4.4: Groups of intercorrelated climatic variables using a cutoff of 0.65 for Pearson's correlation coefficient, obtained using the ‘removeCollinearity’ R function (‘virtualspecies’ package, Leroy et al. (2015)). Variables figuring in the same red boxes were correlated with Pearson's correlation coefficient > 0.65.

S4.5.2 CENFA estimation and resolution

I estimated climate-change sensitivity across terrestrial vertebrates with the CENFA framework using three different resolutions for the species distribution files and the climatic variables: 50 km², 10 km² and 5 km². The finer the resolution, the better the species' distribution is likely to be captured, particularly for narrow-ranging species (Figure S4.5). When working with coarser resolutions, the actual geographical distribution of a narrow-ranging species might be overestimated (Figure S4.5), such that the climatic niche breadth of the species might also be overestimated; consequently, its climate-change sensitivity may be underestimated. However, finer resolutions are more computationally demanding, which can be limiting when working across

several thousand species.

Thus, I looked for a resolution that provided the best compromise between accuracy of sensitivity estimation and computational load (Figure S4.6). Hence, I chose to work with a resolution of 5 km^2 . At this resolution, there were still some narrow-ranging species for which sensitivity was likely overestimated (Figure S4.6). To prevent any impact of these species on the analyses, I removed species with the smallest geographical range areas, using a conservative threshold of 100 km^2 for geographical range area (Figure S4.6).

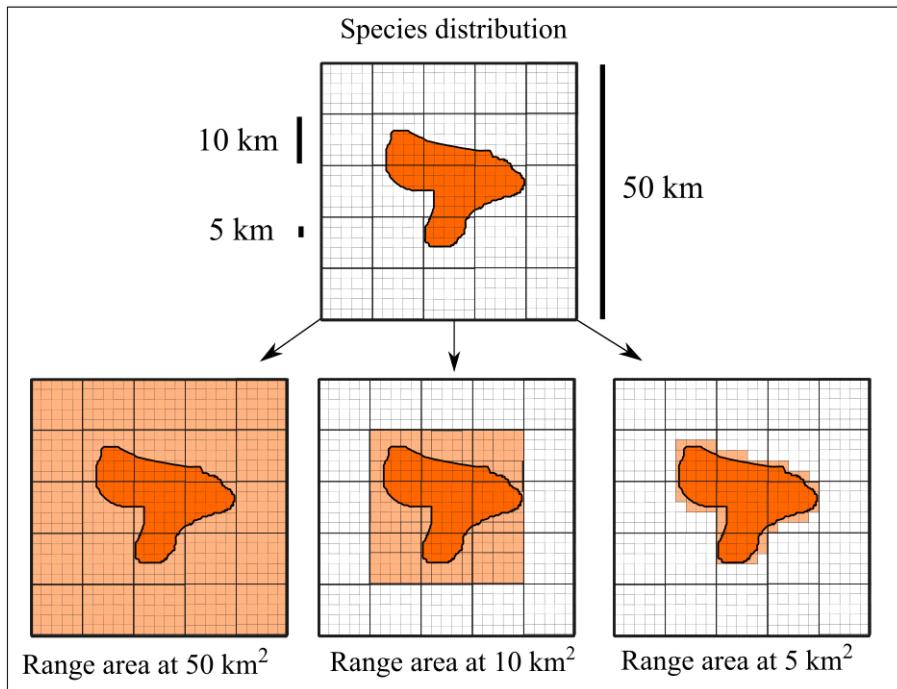


Figure S4.5: Possible impact of resolution on estimated geographical range area. I represent a virtual distribution for a species (orange shape). The species distribution is more accurately captured at finer resolutions (e.g., 5 km^2) than at coarser resolutions (e.g., 10 km^2 or 50 km^2). A possible consequence is that coarser resolutions can tend to disproportionately overestimate the geographical range area of narrow-ranging species, because the aggregation of grid cells where the species is found to be present can artificially augment the amount of occupied area at coarser resolutions, and relatively more so if the species is narrow-ranging.

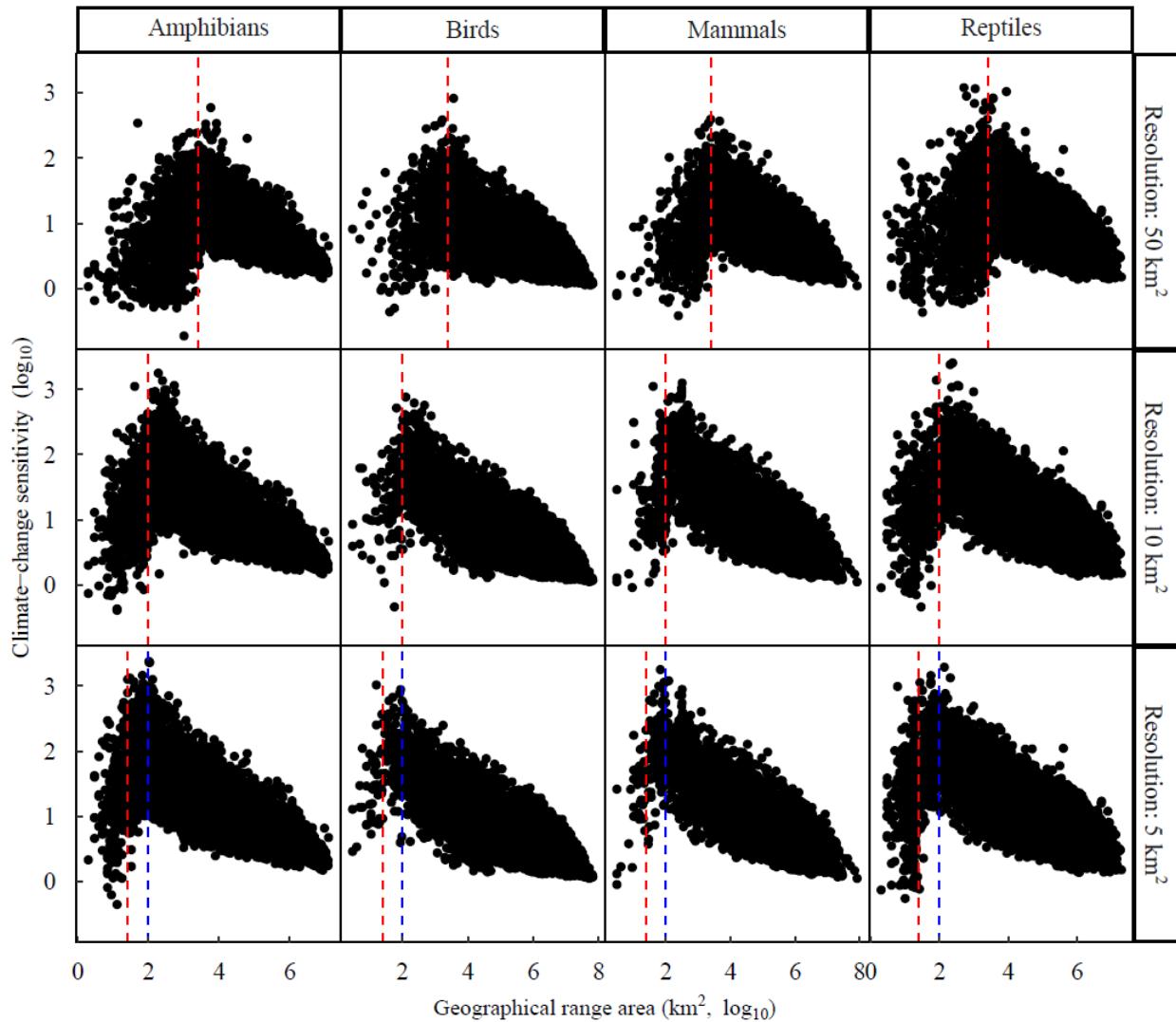


Figure S4.6: Estimated climate-change sensitivity estimations at three different resolutions (50 km^2 , 10 km^2 and 5 km^2) against geographical range area (estimated at 1 km^2). With the red dashed lines, I highlight the range areas that correspond to the surface area of one grid cell (i.e., $2,500 \text{ km}^2$, 100 km^2 and 25 km^2 respectively). Climate-change sensitivity was estimated using the CENFA framework (Rinnan and Lawler, 2019). I chose to work at a resolution of 5 km^2 and I excluded species whose range area was $\leq 100 \text{ km}^2$ (blue dashed line), that is, species whose distribution could intersect up to four grid cells at a resolution of 5 km^2 .

S4.6 Climate-change sensitivity models: multicollinearity checks among models' explanatory variables

Table S4.9: Generalised Variance Inflation Factors among the candidate explanatory variables for the phylogenetic least-square regression fitted across amphibians, prior to the exclusion of diet breadth. The model aimed at investigating the association between the species-level ecological characteristics and species climate-change sensitivity.

Predictor	GVIF
Diel activity	1.1
Lifespan proxy (\log_{10})	1.2
Range area (\log_{10})	1.3
Body mass (\log_{10})	1.4
Litter/clutch size (\log_{10})	1.5
Specialisation	1.6
Habitat breadth (square-root)	1.9
Primary diet	17.1
Diet breadth (square-root)	17.1

Table S4.10: Generalised Variance Inflation Factors among the explanatory variables for the phylogenetic least-square regression fitted across amphibians, after excluding diet breadth. The model aimed at investigating the association between the species-level ecological characteristics and species climate-change sensitivity.

Predictor	GVIF
Diel activity	1.1
Primary diet	1.1
Lifespan proxy (\log_{10})	1.2
Range area (\log_{10})	1.3
Body mass (\log_{10})	1.4
Litter/clutch size (\log_{10})	1.5
Specialisation	1.6
Habitat breadth (square-root)	1.9

Table S4.11: Generalised Variance Inflation Factors among the explanatory variables for the phylogenetic least-square regression fitted across birds. The model aimed at investigating the association between the species-level ecological characteristics and species climate-change sensitivity.

Predictor	GVIF
Diel activity	1.1
Range area (\log_{10})	1.2
Litter/clutch size (\log_{10})	1.3
Diet breadth (square-root)	1.5
Specialisation	1.6
Habitat breadth (square-root)	1.8
Lifespan proxy (\log_{10})	1.9
Body mass (\log_{10})	2.0
Primary diet	2.1

Table S4.12: Generalised Variance Inflation Factors among the explanatory variables for the phylogenetic least-square regression fitted across mammals. The model aimed at investigating the association between the species-level ecological characteristics and species climate-change sensitivity.

Predictor	GVIF
Range area (\log_{10})	1.2
Diel activity	1.3
Specialisation	1.3
Habitat breadth (square-root)	1.5
Diet breadth (square-root)	1.6
Body mass(\log_{10})	2.3
Litter/clutch size (\log_{10})	2.4
Primary diet	2.7
Lifespan proxy (\log_{10})	3.0

Table S4.13: Generalised Variance Inflation Factors among the explanatory variables for the phylogenetic least-square regression fitted across reptiles. The model aimed at investigating the association between the species-level ecological characteristics and species climate-change sensitivity.

Predictor	GVIF
Diel activity	1.1
Range area(\log_{10})	1.2
Specialisation	1.4
Habitat breadth (square-root)	1.5
Lifespan proxy (\log_{10})	1.6
Litter/clutch size (\log_{10})	2.0
Body mass (\log_{10})	2.9
Diet breadth (square-root)	2.9
Primary diet	3.6

S4.7 Land-use responses: occurrence probability predictions from the partial models for artificial habitat use and diel activity

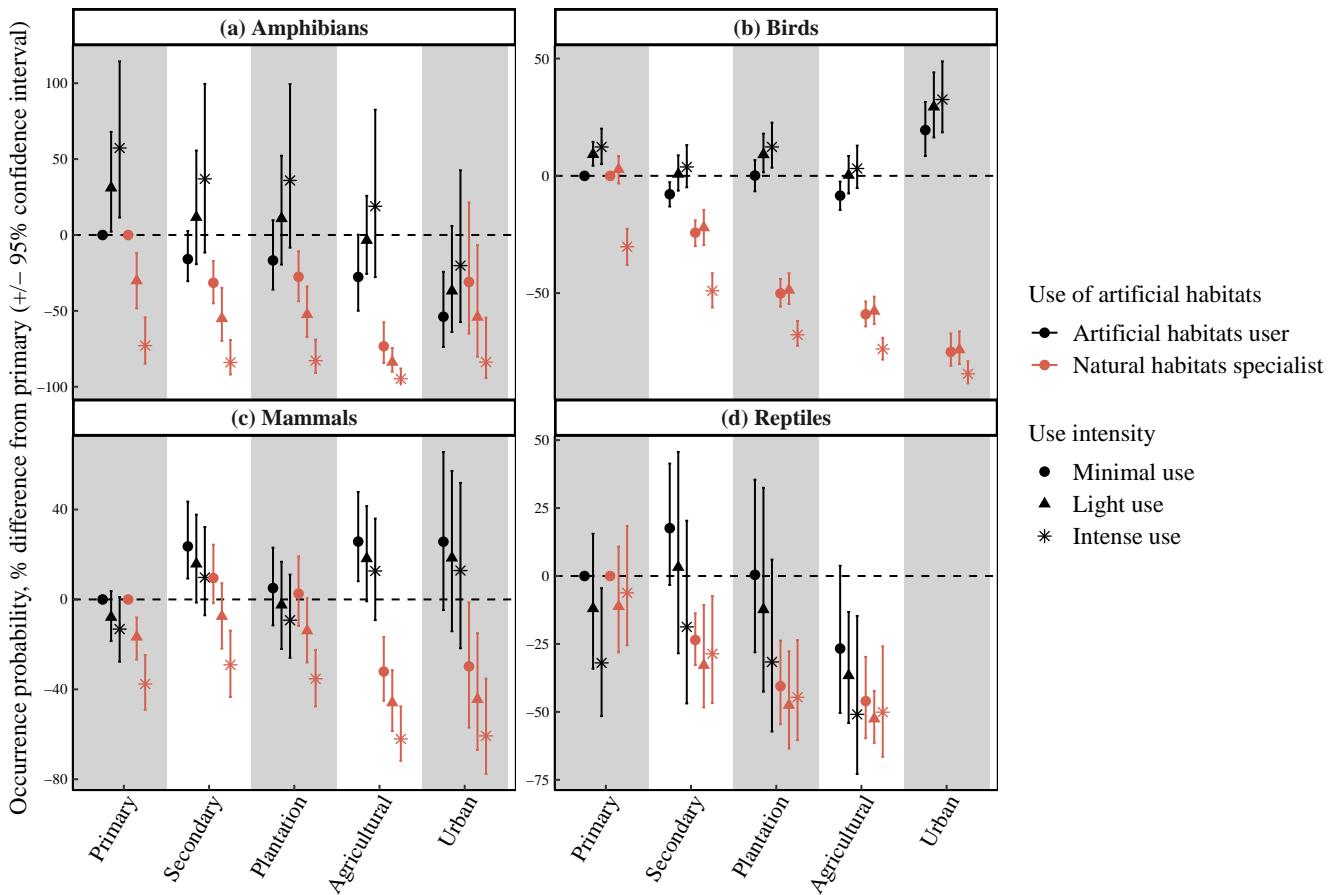


Figure S4.7: Predicted occurrence probability as a function of land use, land-use intensity, artificial habitat use and their interactions, for each class of terrestrial vertebrates (mean \pm 95% confidence interval; the predictions are rescaled with reference to minimally-used primary vegetation). The predictions were obtained from the partial models fitted in each class for artificial habitat use. Effects could not be estimated for urban reptiles, as there weren't any sampled sites. Primary: primary vegetation; Secondary: secondary vegetation; plantation: plantation forest; agricultural: cropland and pasture.

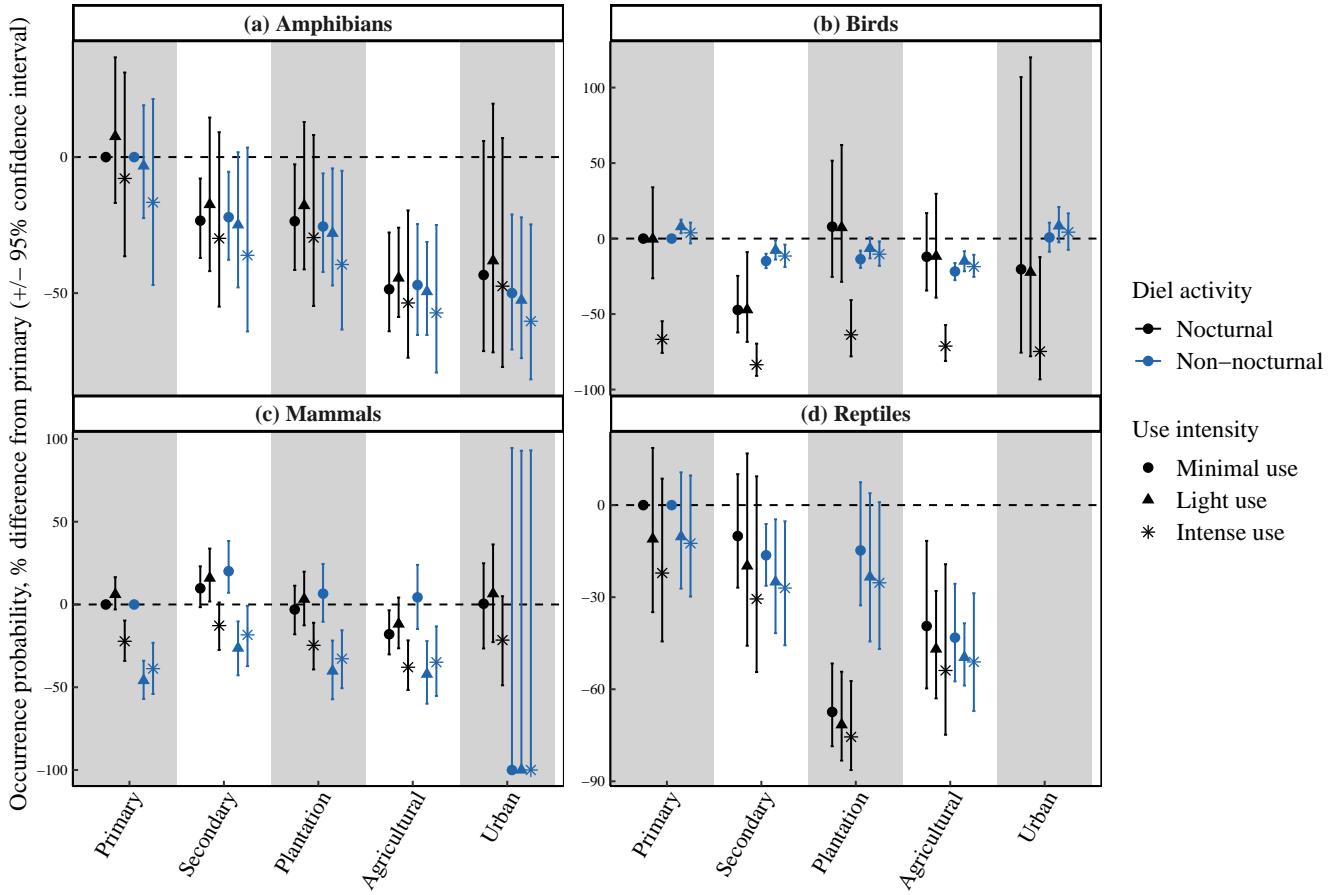


Figure S4.8: Predicted occurrence probability as a function of land use, land-use intensity, diel activity and their interactions, for each class of terrestrial vertebrates (mean $\pm 95\%$ confidence interval; the predictions are rescaled with reference to minimally-used primary vegetation). The predictions were obtained from the partial models fitted in each class for diel activity. Effects could not be estimated for urban reptiles, as there weren't any sampled sites. Error bars are large for non-nocturnal urban mammals because there were very few sampled species (only five). Primary: primary vegetation; Secondary: secondary vegetation; plantation: plantation forest; agricultural: cropland and pasture.

S4.8 Land-use responses: diagnostic plots for the full models

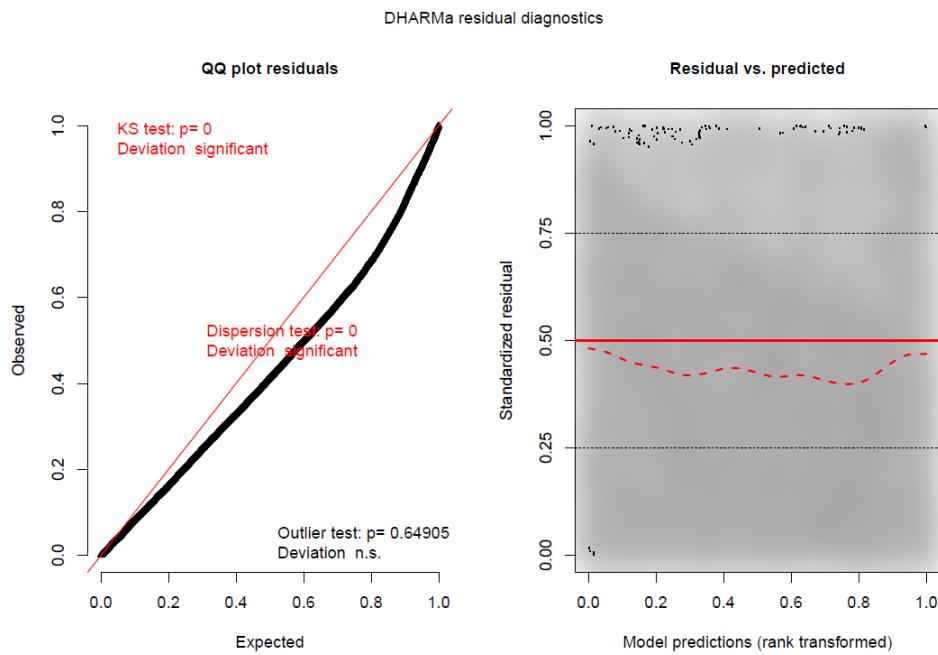


Figure S4.9: Diagnostic plots for the mixed-effects model fitted on amphibians, looking at the effects of land use, land-use intensity and the species-level ecological characteristics on species occurrence probability (full model). The diagnostic plots were obtained from the ‘DHARMA’ R package (Hartig, 2021).

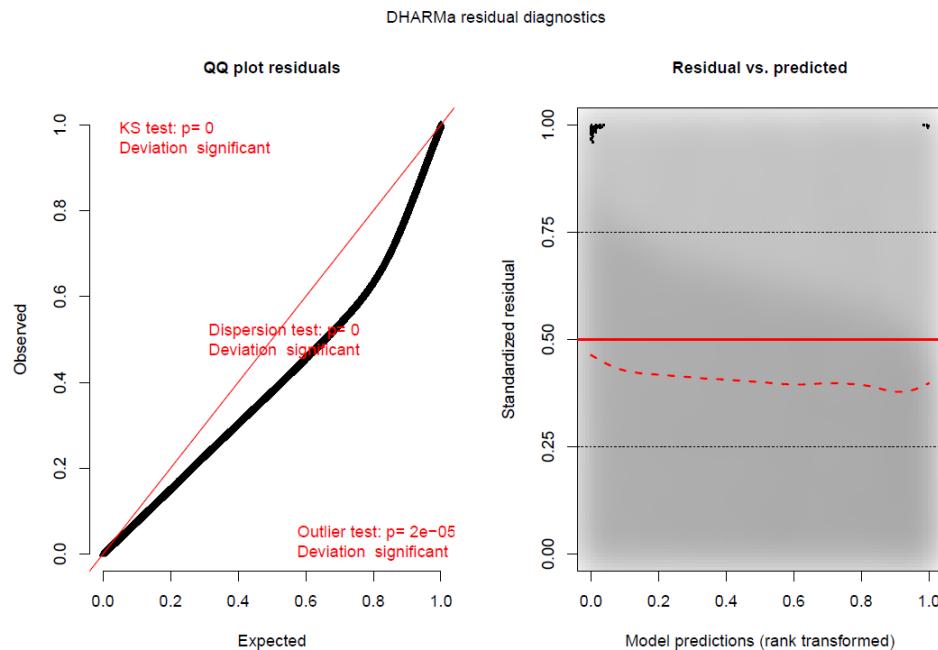


Figure S4.10: Diagnostic plots for the mixed-effects model fitted on birds, looking at the effects of land use, land-use intensity and the species-level ecological characteristics on species occurrence probability (full model). The diagnostic plots were obtained from the ‘DHARMA’ R package (Hartig, 2021).

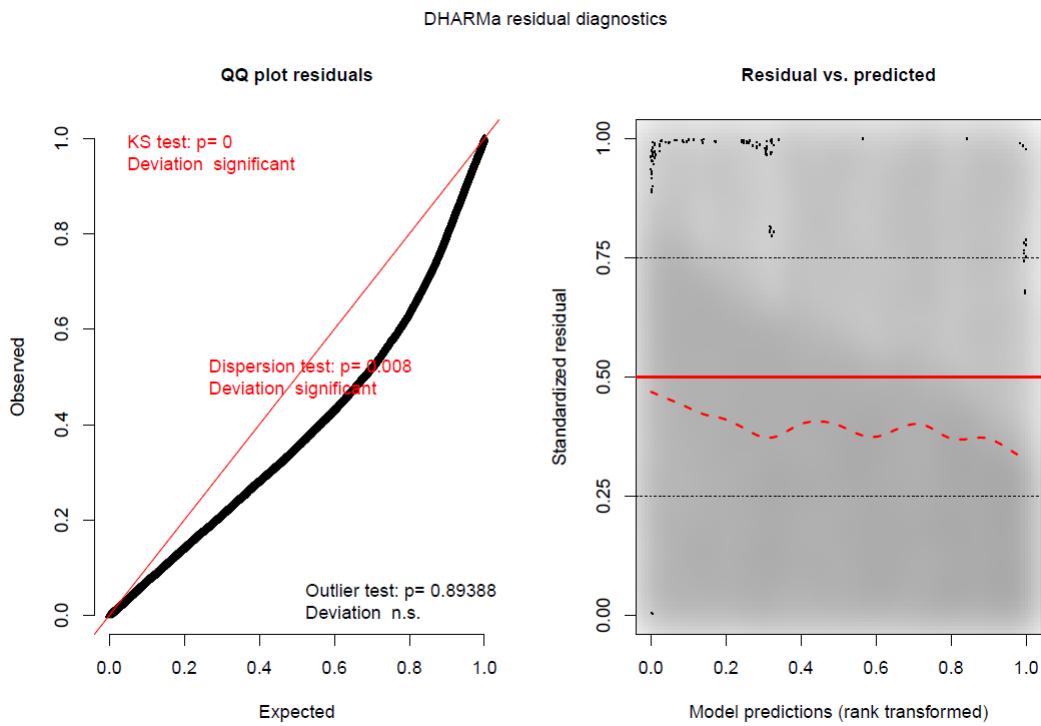


Figure S4.11: Diagnostic plots for the mixed-effects model fitted on mammals, looking at the effects of land use, land-use intensity and the species-level ecological characteristics on species occurrence probability (full model). The diagnostic plots were obtained from the ‘DHARMA’ R package (Hartig, 2021).

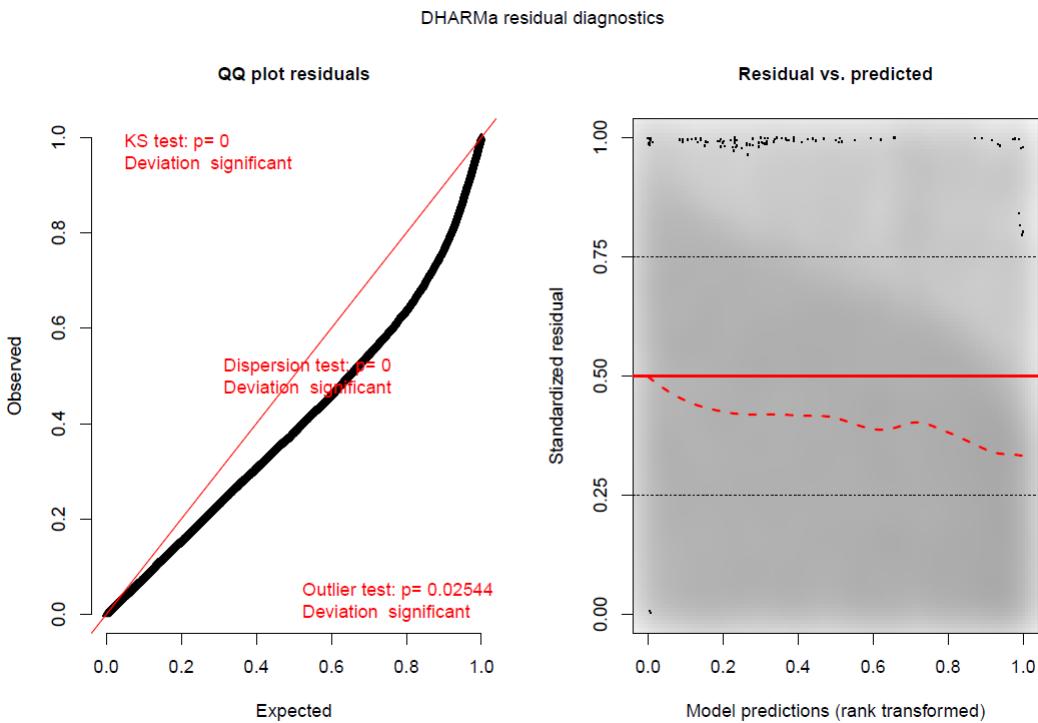


Figure S4.12: Diagnostic plots for the mixed-effects model fitted on reptiles, looking at the effects of land use, land-use intensity and the species-level ecological characteristics on species occurrence probability (full model). The diagnostic plots were obtained from the 'DHARMA' R package (Hartig, 2021).

S4.9 Climate-change sensitivity: model summaries and diagnostic plots

S4.9.1 Summaries & diagnostic plots for models fitted on species with range area $>100 \text{ km}^2$

Table S4.14: Summary for the PGLS model fitted on amphibians, investigating associations between species-level ecological characteristics and climate-change sensitivity, excluding species whose range area was $\leq 100 \text{ km}^2$ (sample size: n=4,537).

	Estimate	Std. Error	t value	Pr(> t)
Intercept	1.15	0.21	5.49	< 0.001
$\log_{10}(\text{Body mass})$	-1.97	0.61	-3.22	0.001
$\log_{10}(\text{Body mass})^2$	-0.26	0.42	-0.60	0.55
$\log_{10}(\text{Body mass})^3$	0.46	0.37	1.24	0.22
$\log_{10}(\text{Lifespan proxy})$	-0.21	0.59	-0.36	0.72
$\log_{10}(\text{Lifespan proxy})^2$	-0.14	0.43	-0.32	0.75
$\log_{10}(\text{Lifespan proxy})^3$	0.58	0.35	1.66	0.10
$\log_{10}(\text{Litter/clutch size})$	1.59	0.54	2.96	0.003
$\log_{10}(\text{Litter/clutch size})^2$	-0.06	0.38	-0.16	0.87
$\log_{10}(\text{Litter/clutch size})^3$	-0.74	0.31	-2.37	0.02
$\log_{10}(\text{Range area})$	-26.60	0.34	-77.15	< 0.001
$\log_{10}(\text{Range area})^2$	4.27	0.29	14.57	< 0.001
$\log_{10}(\text{Range area})^3$	-1.65	0.28	-5.96	< 0.001
square-root(Habitat breadth)	-2.26	0.43	-5.32	< 0.001
square-root(Habitat breadth) ²	0.81	0.30	2.67	0.01
square-root(Habitat breadth) ³	-0.59	0.28	-2.10	0.04
Specialisation: Natural habitat specialist	0.02	0.01	1.85	0.06
Diel activity: Non-nocturnal	0.04	0.01	3.28	0.001
Primary diet: Omnivore	0.01	0.03	0.29	0.77
Primary diet: Plants/seeds	0.04	0.13	0.31	0.76
Primary diet: Vertebrates	0.13	0.15	0.87	0.39

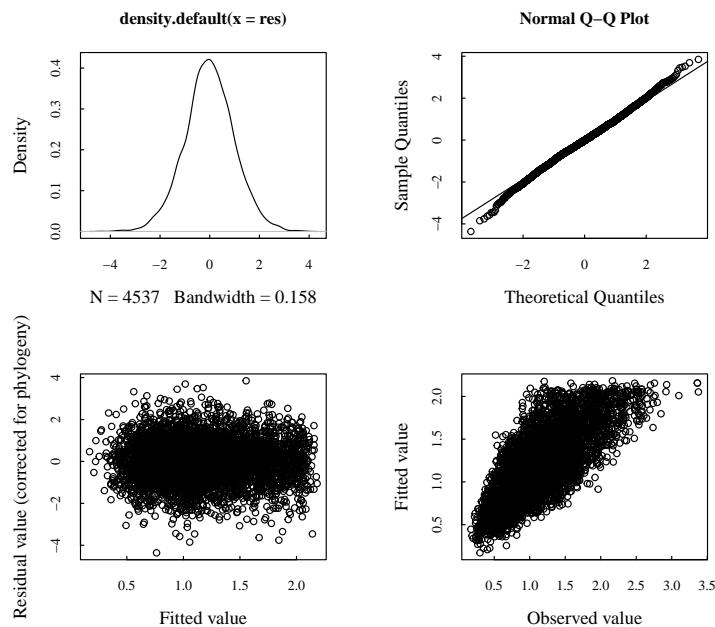


Figure S4.13: Diagnostic plots for the PGLS model fitted on amphibians, investigating associations between species-level ecological characteristics and climate-change sensitivity, excluding species whose range area was $\leq 100 \text{ km}^2$ (sample size: n=4,537).

Table S4.15: Summary for the PGLS model fitted on birds, investigating associations between species-level ecological characteristics and climate-change sensitivity, excluding species whose range area was $\leq 100 \text{ km}^2$ (sample size: n=10,198).

	Estimate	Std. Error	t value	Pr(> t)
Intercept	0.64	0.08	7.91	< 0.001
$\log_{10}(\text{Body mass})$	2.24	0.67	3.36	0.001
$\log_{10}(\text{Body mass})^2$	0.16	0.42	0.37	0.71
$\log_{10}(\text{Body mass})^3$	-0.22	0.37	-0.60	0.55
$\log_{10}(\text{Lifespan proxy})$	-0.23	0.59	-0.38	0.70
$\log_{10}(\text{Lifespan proxy})^2$	-0.84	0.39	-2.16	0.03
$\log_{10}(\text{Lifespan proxy})^3$	-0.10	0.28	-0.36	0.72
$\log_{10}(\text{Litter/clutch size})$	3.72	0.39	9.46	< 0.001
$\log_{10}(\text{Litter/clutch size})^2$	-0.42	0.33	-1.26	0.21
$\log_{10}(\text{Litter/clutch size})^3$	-0.40	0.27	-1.47	0.14
$\log_{10}(\text{Range area})$	-30.69	0.27	-113.09	< 0.001
$\log_{10}(\text{Range area})^2$	7.22	0.24	29.92	< 0.001
$\log_{10}(\text{Range area})^3$	-2.73	0.23	-11.74	< 0.001
square-root(Habitat breadth)	0.86	0.33	2.59	0.01
square-root(Habitat breadth) ²	-0.89	0.24	-3.63	< 0.001
square-root(Habitat breadth) ³	-0.22	0.23	-0.95	0.34
square-root(Diet breadth)	-0.50	0.31	-1.64	0.10
square-root(Diet breadth) ²	-0.11	0.25	-0.44	0.66
square-root(Diet breadth) ³	0.32	0.24	1.36	0.18
Specialisation: Natural habitat specialist	0.06	0.01	10.13	< 0.001
Diel activity: Non-nocturnal	-0.02	0.04	-0.66	0.51
Primary diet: Invertebrates	0.06	0.01	5.53	< 0.001
Primary diet: Omnivores	0.02	0.01	2.09	0.04
Primary diet: Plants/seeds	0.06	0.01	4.69	< 0.001
Primary diet: Vertebrates	0.01	0.02	0.83	0.41

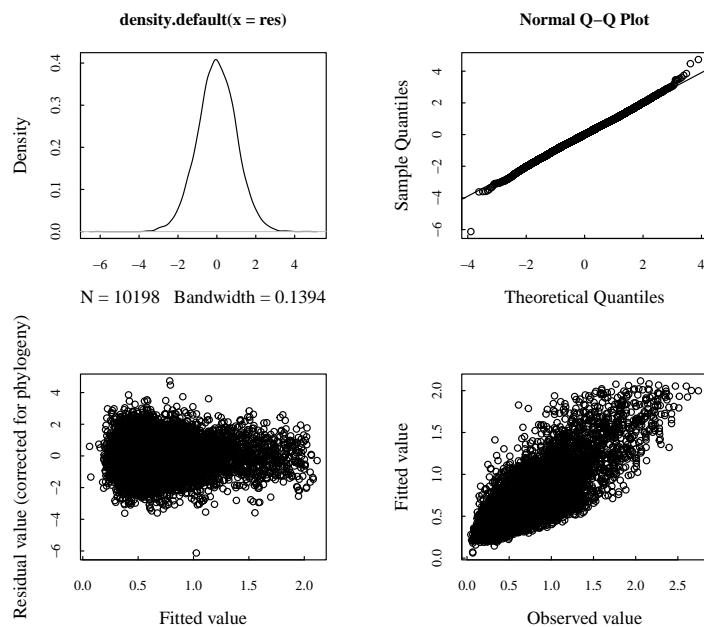


Figure S4.14: Diagnostic plots for the PGLS model fitted on birds, investigating associations between species-level ecological characteristics and climate-change sensitivity, excluding species whose range area was $\leq 100 \text{ km}^2$ (sample size: n=10,198).

Table S4.16: Summary for the PGLS model fitted on mammals, investigating associations between species-level ecological characteristics and climate-change sensitivity, excluding species whose range area was $\leq 100 \text{ km}^2$ (sample size: n=4,712).

	Estimate	Std. Error	t value	Pr(> t)
Intercept	0.84	0.16	5.37	< 0.001
$\log_{10}(\text{Body mass})$	-4.62	0.94	-4.93	< 0.001
$\log_{10}(\text{Body mass})^2$	0.40	0.56	0.72	0.47
$\log_{10}(\text{Body mass})^3$	0.59	0.44	1.33	0.18
$\log_{10}(\text{Lifespan proxy})$	1.60	1.03	1.55	0.12
$\log_{10}(\text{Lifespan proxy})^2$	-0.79	0.49	-1.60	0.11
$\log_{10}(\text{Lifespan proxy})^3$	-0.15	0.43	-0.35	0.73
$\log_{10}(\text{Litter/clutch size})$	3.29	0.71	4.63	< 0.001
$\log_{10}(\text{Litter/clutch size})^2$	0.06	0.42	0.14	0.89
$\log_{10}(\text{Litter/clutch size})^3$	-0.16	0.33	-0.47	0.64
$\log_{10}(\text{Range area})$	-24.17	0.31	-78.21	< 0.001
$\log_{10}(\text{Range area})^2$	4.15	0.28	15.09	< 0.001
$\log_{10}(\text{Range area})^3$	-0.90	0.26	-3.45	0.001
square-root(Habitat breadth)	-1.24	0.34	-3.60	< 0.001
square-root(Habitat breadth) ²	0.22	0.27	0.82	0.41
square-root(Habitat breadth) ³	-0.03	0.26	-0.10	0.92
square-root(Diet breadth)	-1.21	0.47	-2.55	0.01
square-root(Diet breadth) ²	0.33	0.36	0.91	0.36
square-root(Diet breadth) ³	0.11	0.34	0.33	0.74
Specialisation: Natural habitat specialist	0.04	0.01	3.22	0.001
Diel activity: Non-nocturnal	0.003	0.01	0.23	0.82
Primary diet: Invertebrates	-0.02	0.03	-0.62	0.54
Primary diet: Omnivores	-0.02	0.03	-0.77	0.44
Primary diet: Plants/seeds	0.03	0.02	1.32	0.19
Primary diet: Vertebrates	-0.04	0.04	-0.98	0.33

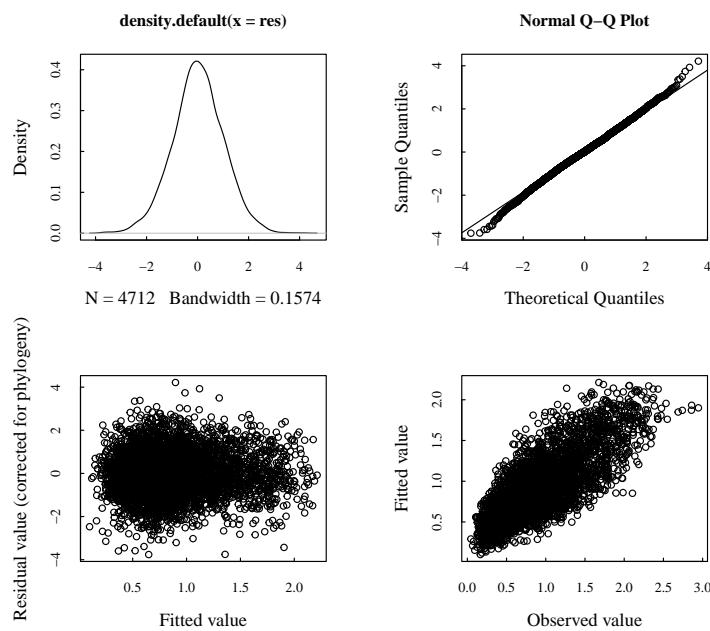


Figure S4.15: Diagnostic plots for the PGLS model fitted on mammals, investigating associations between species-level ecological characteristics and climate-change sensitivity, excluding species whose range area was $\leq 100 \text{ km}^2$ (sample size: n=4,712).

Table S4.17: Summary for the PGLS model fitted on reptiles, looking at the effects of species-level ecological characteristics on climate-change sensitivity, excluding species whose range area was $\leq 100 \text{ km}^2$ (sample size: n=7,330).

	Estimate	Std. Error	t value	Pr(> t)
Intercept	1.02	0.13	7.70	< 0.001
$\log_{10}(\text{Body mass})$	-4.62	0.62	-7.47	< 0.001
$\log_{10}(\text{Body mass})^2$	0.97	0.41	2.35	0.02
$\log_{10}(\text{Body mass})^3$	-0.96	0.33	-2.90	0.004
$\log_{10}(\text{Lifespan proxy})$	0.89	0.51	1.74	0.08
$\log_{10}(\text{Lifespan proxy})^2$	-1.27	0.39	-3.27	0.001
$\log_{10}(\text{Lifespan proxy})^3$	-0.29	0.33	-0.88	0.38
$\log_{10}(\text{Litter/clutch size})$	0.84	0.68	1.24	0.22
$\log_{10}(\text{Litter/clutch size})^2$	-0.34	0.45	-0.76	0.45
$\log_{10}(\text{Litter/clutch size})^3$	0.26	0.35	0.74	0.46
$\log_{10}(\text{Range area})$	-31.88	0.31	-101.48	< 0.001
$\log_{10}(\text{Range area})^2$	5.15	0.27	19.03	< 0.001
$\log_{10}(\text{Range area})^3$	-1.97	0.26	-7.53	< 0.001
square-root(Habitat breadth)	0.56	0.35	1.59	0.11
square-root(Habitat breadth) ²	-0.67	0.27	-2.49	0.01
square-root(Habitat breadth) ³	0.05	0.26	0.21	0.83
square-root(Diet breadth)	-0.33	0.37	-0.90	0.37
square-root(Diet breadth) ²	-0.02	0.27	-0.08	0.94
square-root(Diet breadth) ³	0.31	0.26	1.22	0.22
Specialisation: Natural habitat specialist	0.10	0.01	8.50	< 0.001
Diel activity: Non-nocturnal	-0.02	0.01	-1.88	0.06
Primary diet: Omnivore	-0.03	0.03	-0.92	0.36
Primary diet: Vertebrates	-0.02	0.02	-1.05	0.30

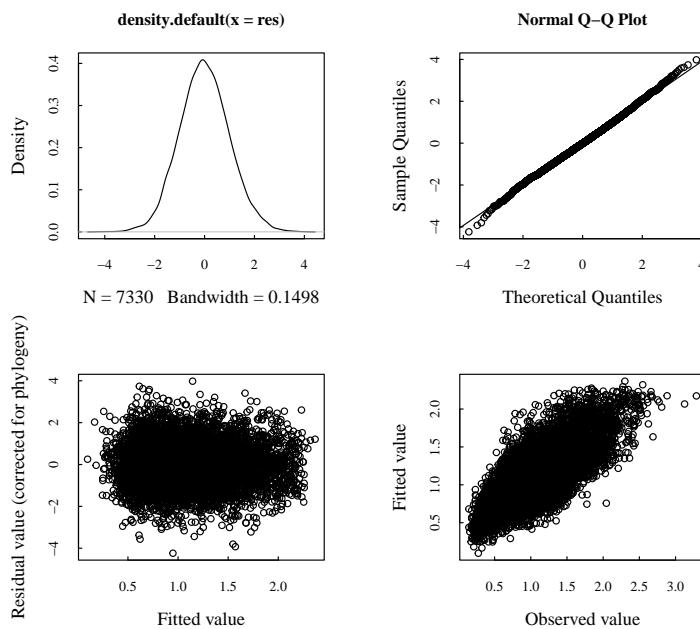


Figure S4.16: Diagnostic plots for the PGLS model fitted on reptiles, investigating associations between species-level ecological characteristics and climate-change sensitivity, excluding species whose range area was $\leq 100 \text{ km}^2$ (sample size: n=7,330).

S4.9.2 Effects for the PGLS models fitted on all species, against effects for the PGLS models fitted on species whose range area was $>100 \text{ km}^2$

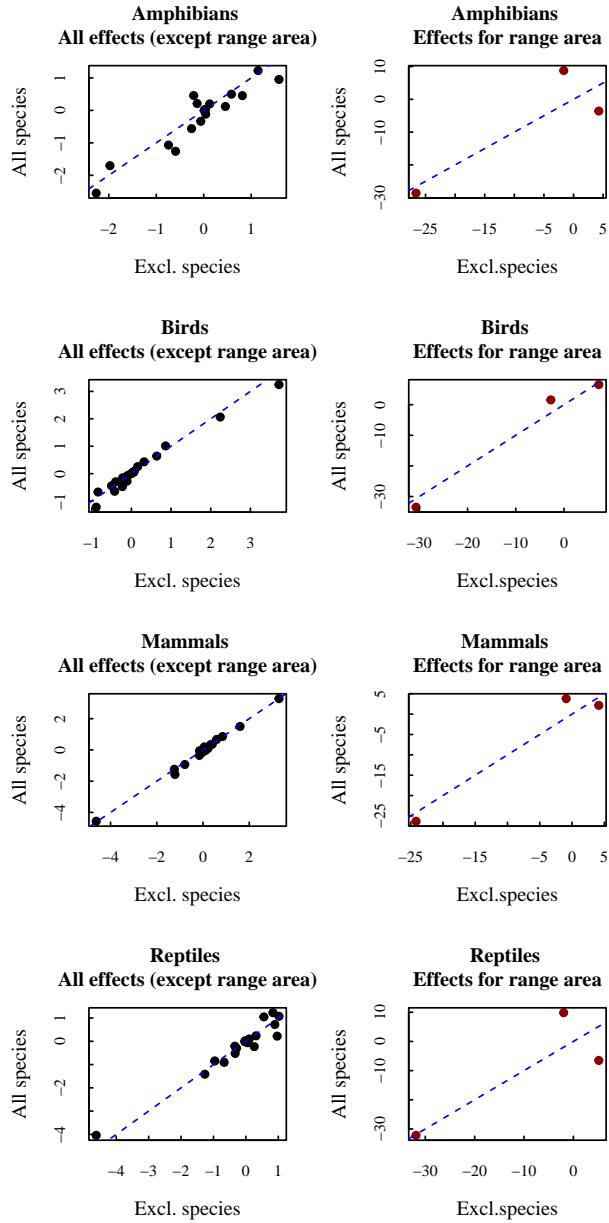


Figure S4.17: Effects for the PGLS models investigating associations between species-level ecological characteristics and climate-change sensitivity, either fitted on all species (y-axis), or fitted on the species whose range area was $>100 \text{ km}^2$ (x-axis). Overall, the estimates from both sets of models were congruent, except for those estimated for geographical range area (I show the effects for range area separately from the effects of other characteristics). Across all classes, the relationship between sensitivity and geographical range area was reversed between the two sets of models. I found that sensitivity was positively associated with geographical range area when including all species, likely because of the underestimation of climate-change sensitivity for the most narrow-ranging species when working with a resolution of 5 km^2 (see Figure S4.6). The dashed line is the identity line ($y=x$).

S4.10 Validations on complete trait data subsets

Table S4.18: Summary of the effects of the ecological characteristics (except for diet) on (a) species' responses to disturbed land uses ('within land-use type' effects) and (b) species climate-change sensitivity, for each class of terrestrial vertebrates, from the models fitted on empirical trait values (excluding all imputed values). The symbol  indicates where a characteristic has a significant negative effect on occurrence probability within a disturbed land-use type (within any of the land-use intensities), or where the characteristic renders species significantly more sensitive to climate change. A  indicates a significantly positive effect of a characteristic on occurrence probability in a land-use type (within any of the land-use intensities), or significantly lower sensitivity to climate change. For the land-use effects, I report 'within land-use type effects' here, that is, within a disturbed land use whether there were significant differences in occurrence probability among species with different trait values. These effects were derived from the interactive terms of the full models.

(a) "Within land-use type" effects of the species-level characteristics on occurrence probability - <=> more sensitive; + <=> less sensitive																Predictors				(b) Climate-change sensitivity: - <=> more sensitive + <=> less sensitive				
Secondary vegetation				Plantation forest				Agricultural				Urban												
																								
0	-	0	0	0	-	0	0	0	-	-	+	+	-	0	NA	More narrowly-distributed			-	-	-	(-)		
0	-	0	0	-	-	0	0	-	-	0	-	-	-	0	NA	Smaller habitat breadth		0	-	-	-	-		
-	-	0	0	0	-	0	0	-	-	-	+	0	-	0	NA	Natural habitat specialist			0	-	0	-		
0	+	+	0	+	+	(+)	+	0	+	+	0	0	0	0	NA	Non-nocturnal			0	0	0	0		
-	0	(+)	0	(-)	0	+	0	-	0	(+)	+	-	-	0	NA	Narrower diet breadth			0	0	0	0		
NA	(+)	+	NA	NA	+	+	NA	NA	-	0	NA	NA	+	0	NA	Smaller body mass			0	(+)	-	0		
NA	0	0	-	NA	-	(-)	0	NA	-	(-)	0	NA	0	-	NA	Smaller litter/clutch size			0	+	+	0		
NA	0	0	-	NA	(-)	0	0	NA	+	0	+	NA	-	0	NA	Shorter-lived			(+)	0	0	0		

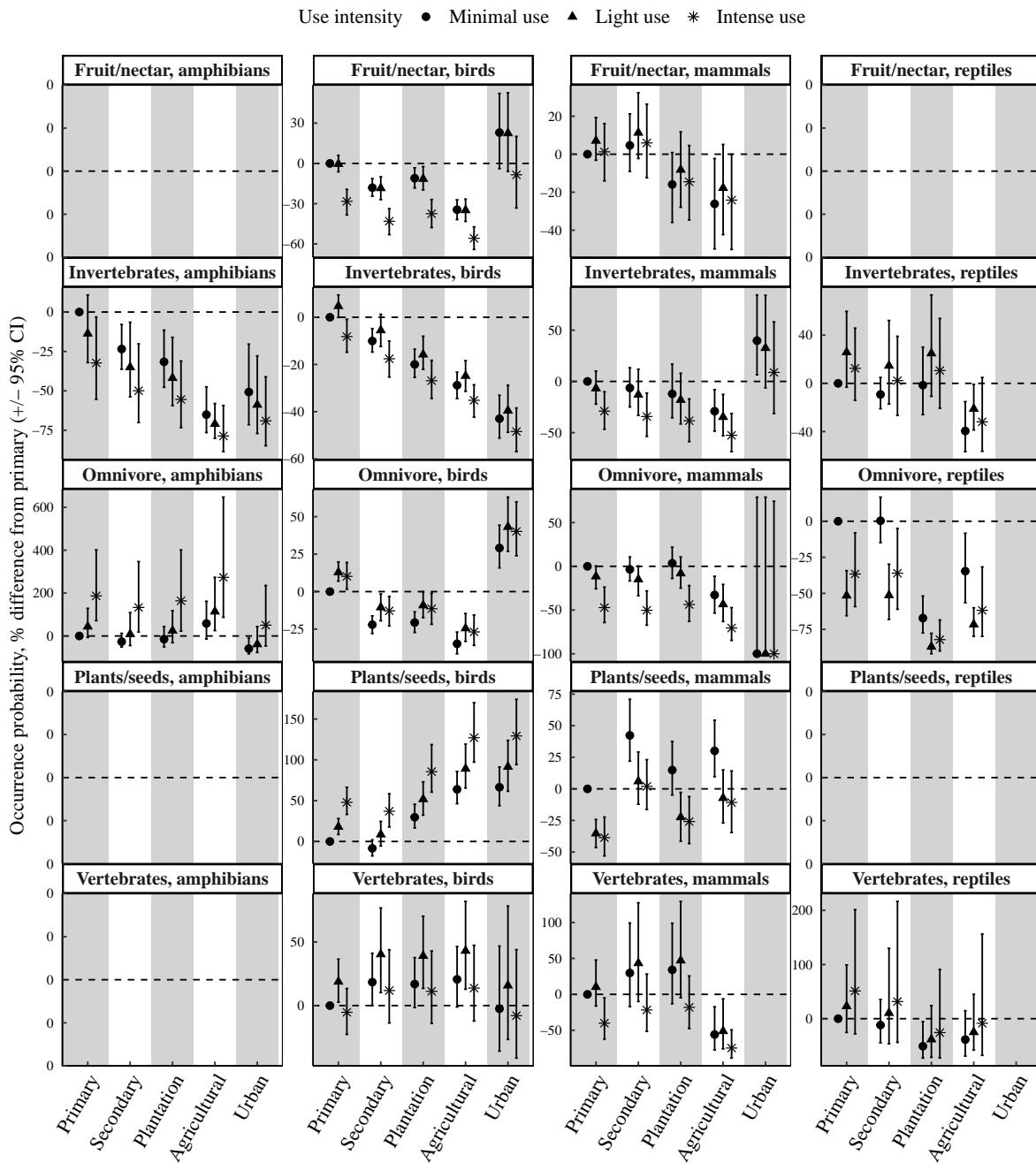


Figure S4.18: Predicted occurrence probability as a function of land use, land-use intensity, diet and their interactions in each class. The predictions were obtained from the partial models fitted in each class for diet, estimated using empirical trait data subsets (i.e., excluding imputed trait values). Empty plots are drawn where there were no data for a diet category in a given class (e.g., amphibian fruit/nectar eaters). Effects could not be estimated for urban reptiles, as well as for urban vertebrate, fruit/nectar and plant/seed eaters for mammals because there were no sampled species. The predictions are rescaled with reference to minimally-used primary vegetation. Primary: primary vegetation; Secondary: secondary vegetation; plantation: plantation forest; agricultural: cropland and pasture.

Appendix 4: Supporting information for Chapter 5

Table S5.1: Number of species for which RMR data was collected in each class & data sources, initial RMR coverage for PREDICTS species and phylogenetic signal in RMR.

Class	RMR data	Coverage for PREDICTS species	Phylogenetic signal (Pagel's λ , $\pm 95\%$ CI)
Amphibians	126 species from Stark et al. (2020)	16/379 species (4%)	0.89 (0.86-0.91)
Birds	719 species from McNab (2009) Fristoe et al. (2015) Londoño et al. (2015) Stark et al. (2020)	317/3129 species (10%)	0.97 (0.95-0.98)
Mammals	685 species from PanTHERIA (Jones et al., 2009) Fristoe et al. (2015) Stark et al. (2020)	148/556 species (27%)	0.99 (0.98-0.99)
Reptiles	173 species from Stark et al. (2020)	24/329 species (7.3%)	0.90 (0.86-0.92)

$$\begin{aligned} \log(\text{Abundance}) = & \text{LU} + \text{LUI} + \text{TG} + \log(\text{BM}) + \\ & \text{LU:LUI} + \text{LU:TG} + \text{LU:}\log(\text{BM}) + \text{LUI:TG} + \text{LUI:}\log(\text{BM}) + \text{TG:}\log(\text{BM}) + \\ & \text{LU:TG:}\log(\text{BM}) + \text{LUI:TG:}\log(\text{BM}) \end{aligned}$$

Figure S5.1: Formula for the abundance model, used to understand the role of shifts in the body mass of species on observed changes in tRMR (see Chapter 5, section 5.2.5, ‘Disentangling the effects of body mass and abundance on tRMR’). I fitted a model to explain changes in species abundance (given presence) by land use, land-use intensity, trophic group, body mass and their interactions. The model included all two-way interactions among these predictors. To account for potential differences in the slope of the relationship between abundance and body mass among the different trophic groups, I also included two three-way interactions in the model (among land use, trophic group and body mass; and among land-use intensity, trophic group and body mass). Random effects included study, site and species identity. LU: land use; LUI: land-use intensity; TG: trophic group; BM: body mass.

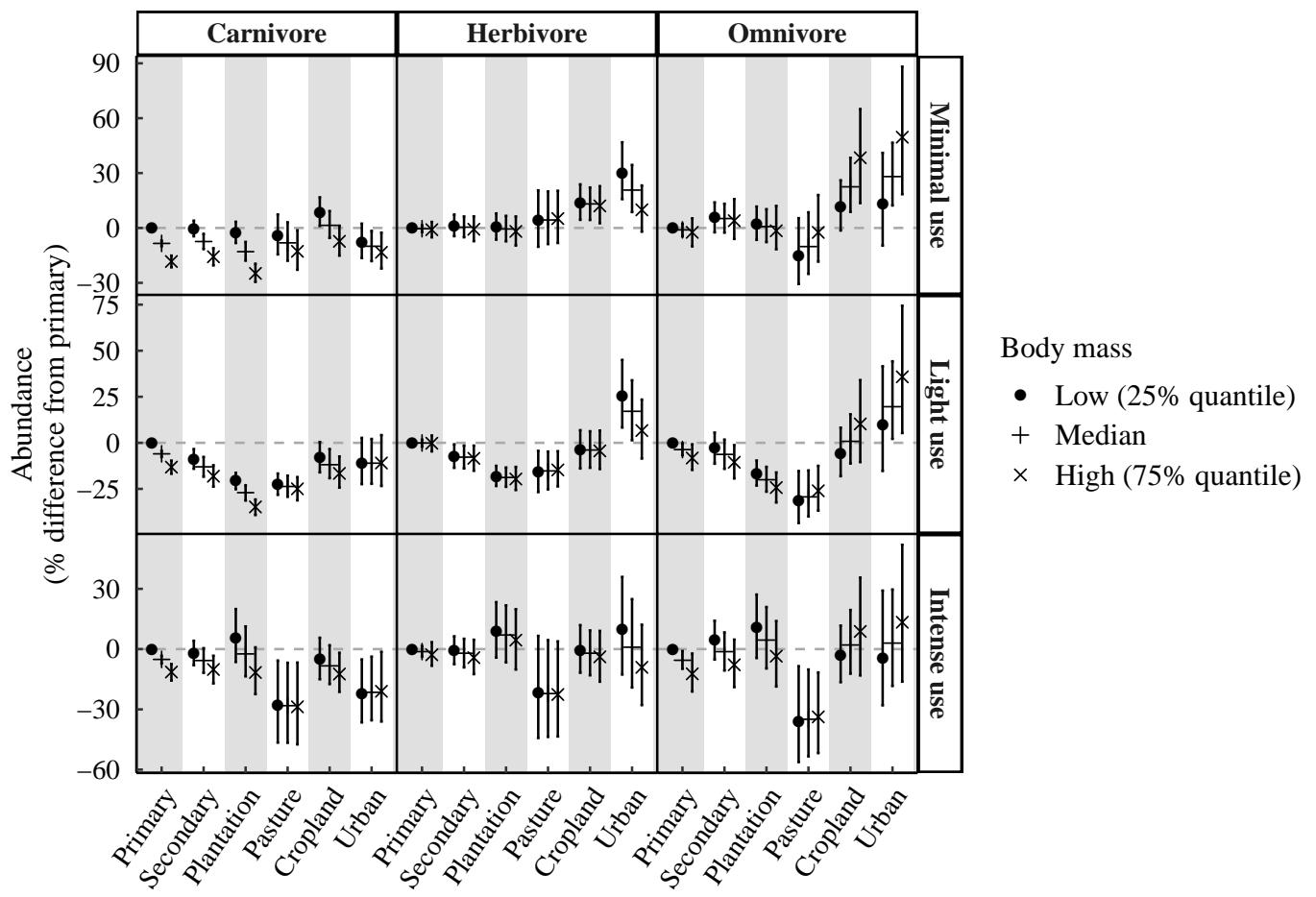


Figure S5.2: Effects of land use, land-use intensity, trophic group, body mass and their interactions on assemblage-level total abundance, estimated from the model specified in Figure S5.1. The predictions are rescaled with reference to minimally used primary vegetation, considered to be the undisturbed baseline. Primary: primary vegetation; secondary: secondary vegetation; plantation: plantation forest. For visualisation purposes, I plotted the predictions for three body mass levels (but body mass was considered as a continuous variable in the model).

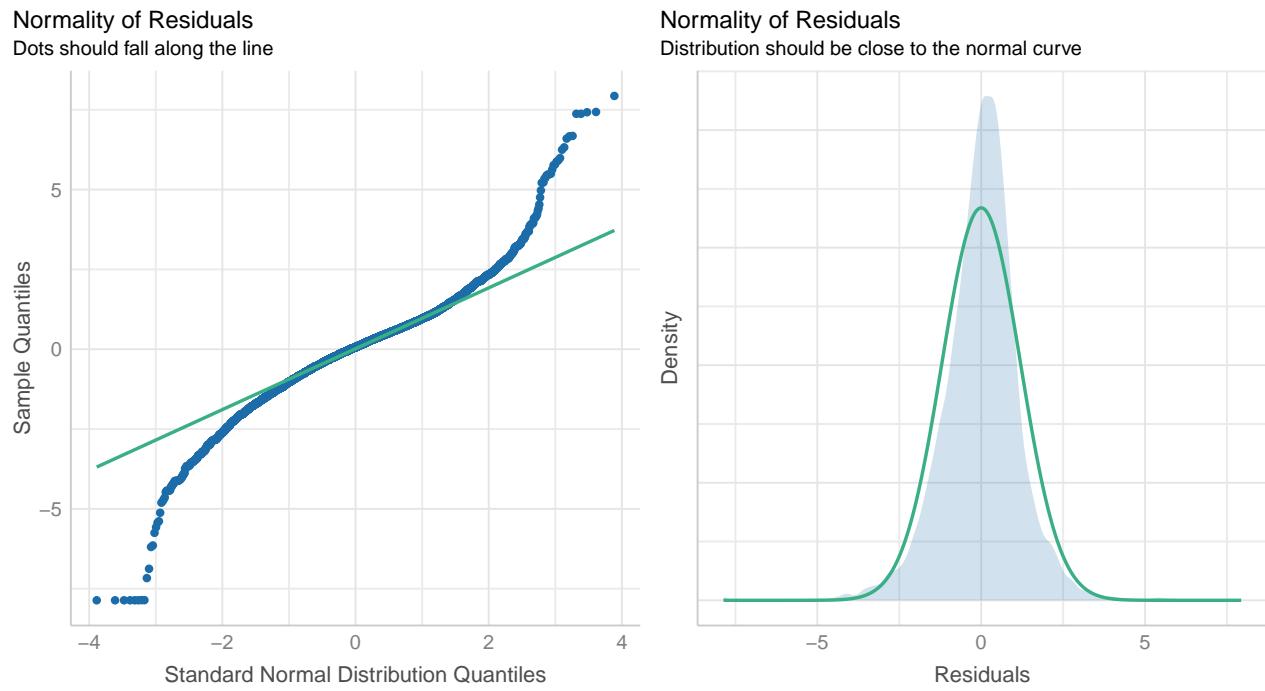
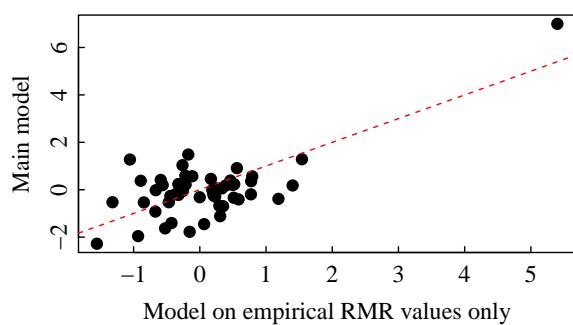


Figure S5.3: Diagnostic plots (qq-plot and residual distribution) for the linear mixed-effects model looking at the effects of land use, land-use intensity, trophic group and their interactions on assemblage-level total RMR (*model 1*). The diagnostic plots were obtained with the ‘performance’ R package (Lüdecke et al., 2021).

(a) Coefficient estimates



(b) Standard error estimates

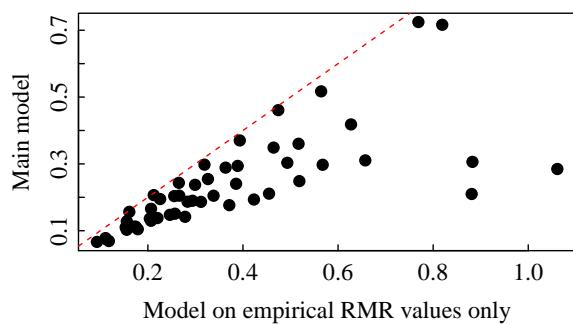


Figure S5.4: Estimates for the models looking at the effects of land use, land-use intensity, trophic group and their interactions on assemblage-level total RMR. I plotted the estimates from the model fitted on the empirical and imputed RMR values (*model 1*) on the y-axis, and the estimates from the model fitted on the empirical RMR values only on the x-axis.

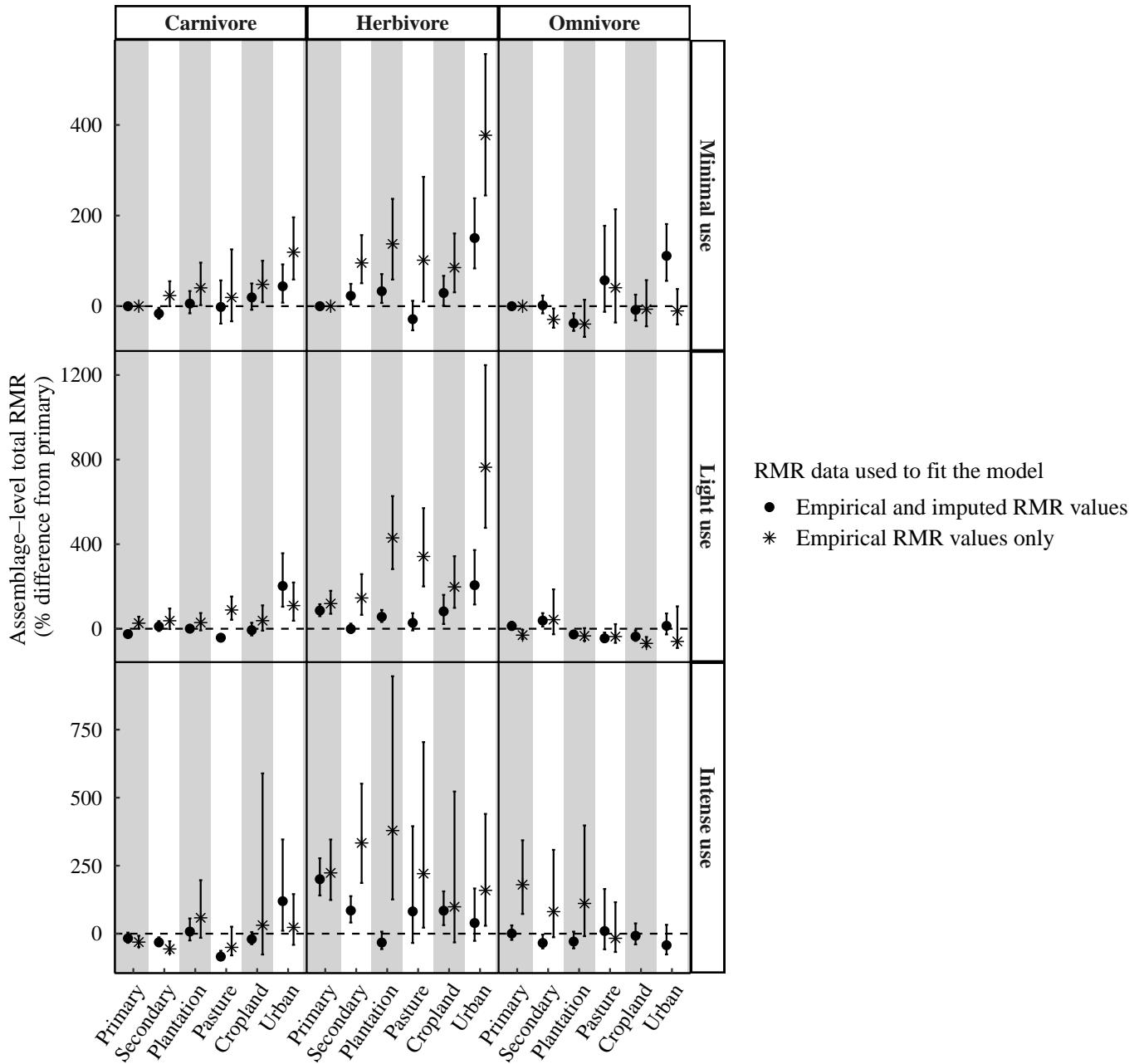


Figure S5.5: Effects of land use, land-use intensity, trophic level and their interactions on assemblage-level total RMR, estimated from the model fitted on the empirical and imputed RMR values (*model 1*) and from the model fitted on the empirical values only. The predictions are rescaled with reference to minimally used primary vegetation, considered to be the undisturbed baseline. Primary: primary vegetation; secondary: secondary vegetation; plantation: plantation forest.

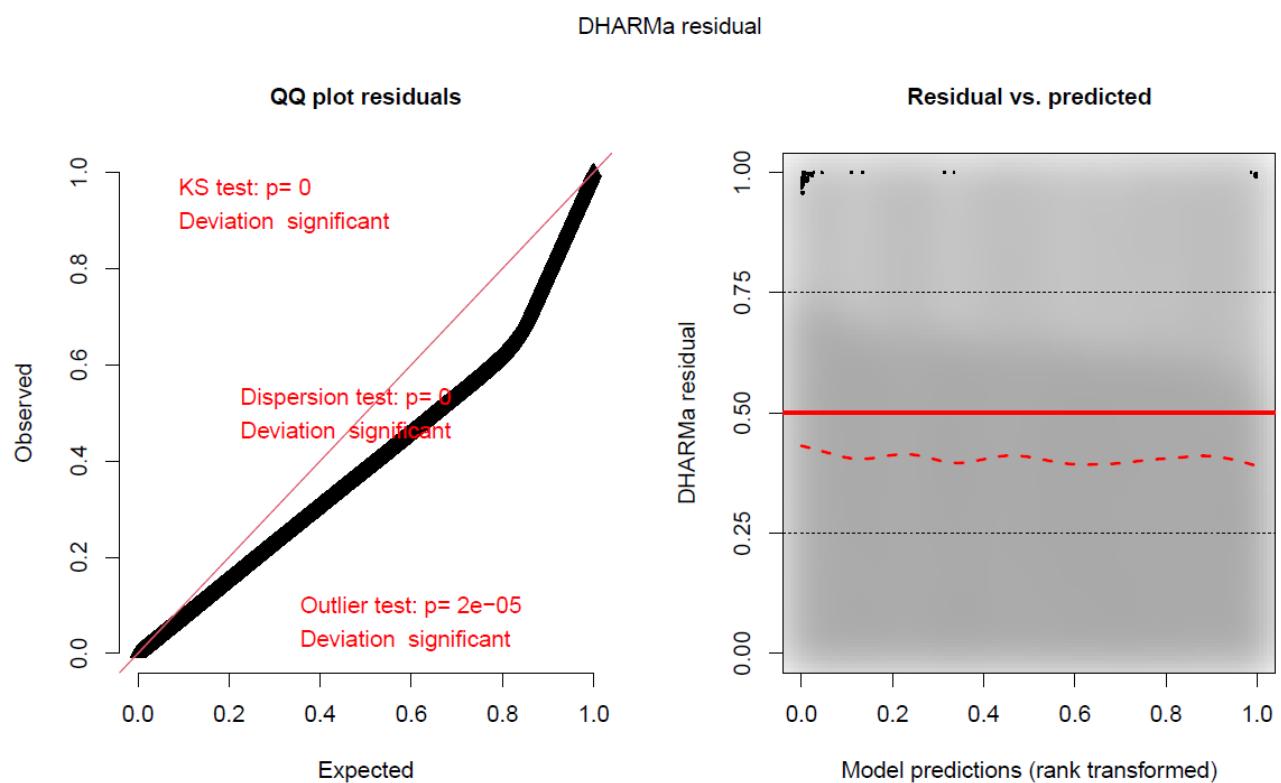


Figure S5.6: Diagnostic plots for the generalised mixed-effects model looking at the effects of land use, land-use intensity, trophic group, residual RMR and their interactions on species' probability of occurrence (*model 2*). The diagnostic plots were obtained with the 'DHARMA' R package (Hartig, 2021).

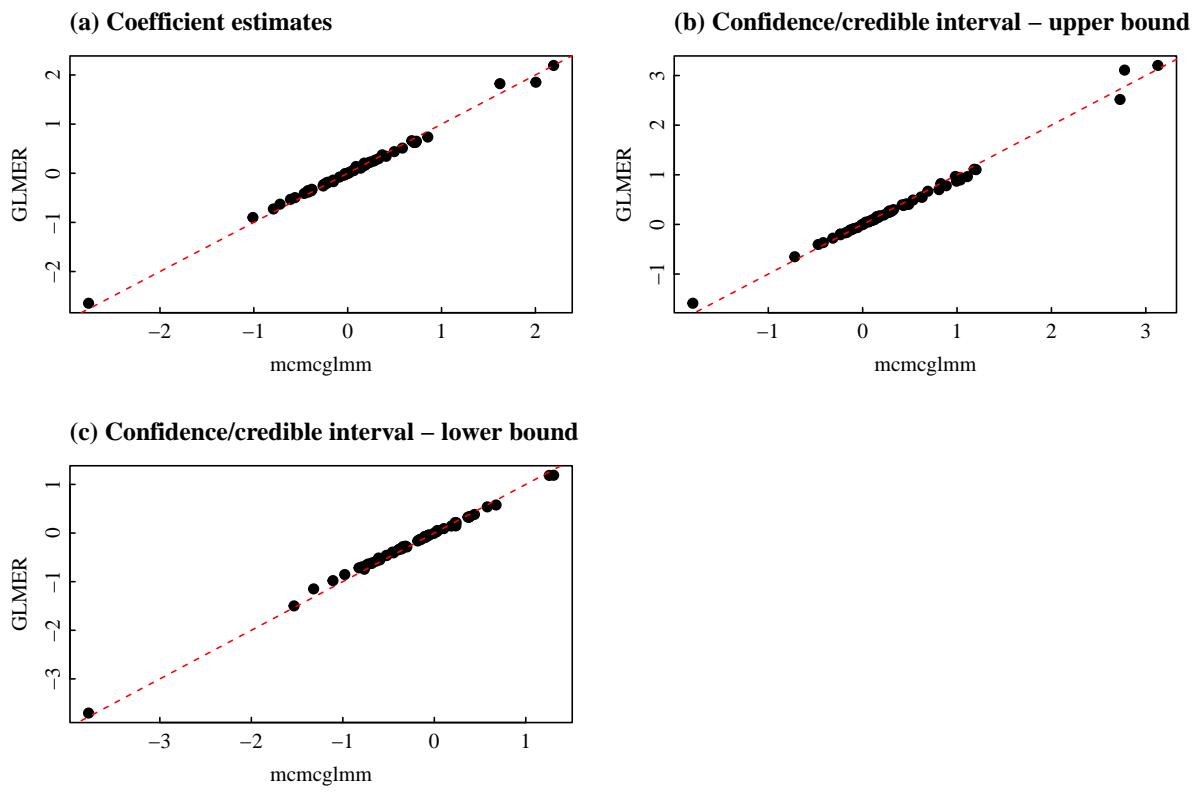
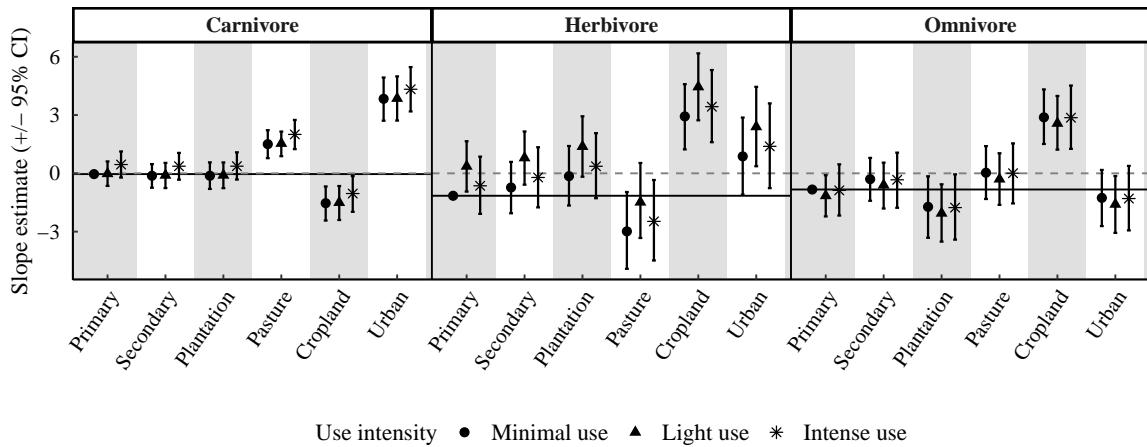


Figure S5.7: Model's coefficients from the occurrence model fitted using the 'lme4' package (Bates et al., 2015) against coefficients from the model fitted using a Bayesian framework with the 'MCMCglmm' package (Hadfield, 2010). The models were fitted to investigate the effects of land use, land-use intensity, trophic group and residual RMR on species occurrence probability (model 2).

(a) Slope of the relationships between occurrence probability (log-odds) and residual RMR



Use intensity ● Minimal use ▲ Light use * Intense use

(b) Predicted effects of residual RMR on occurrence probability (minimal use intensity)

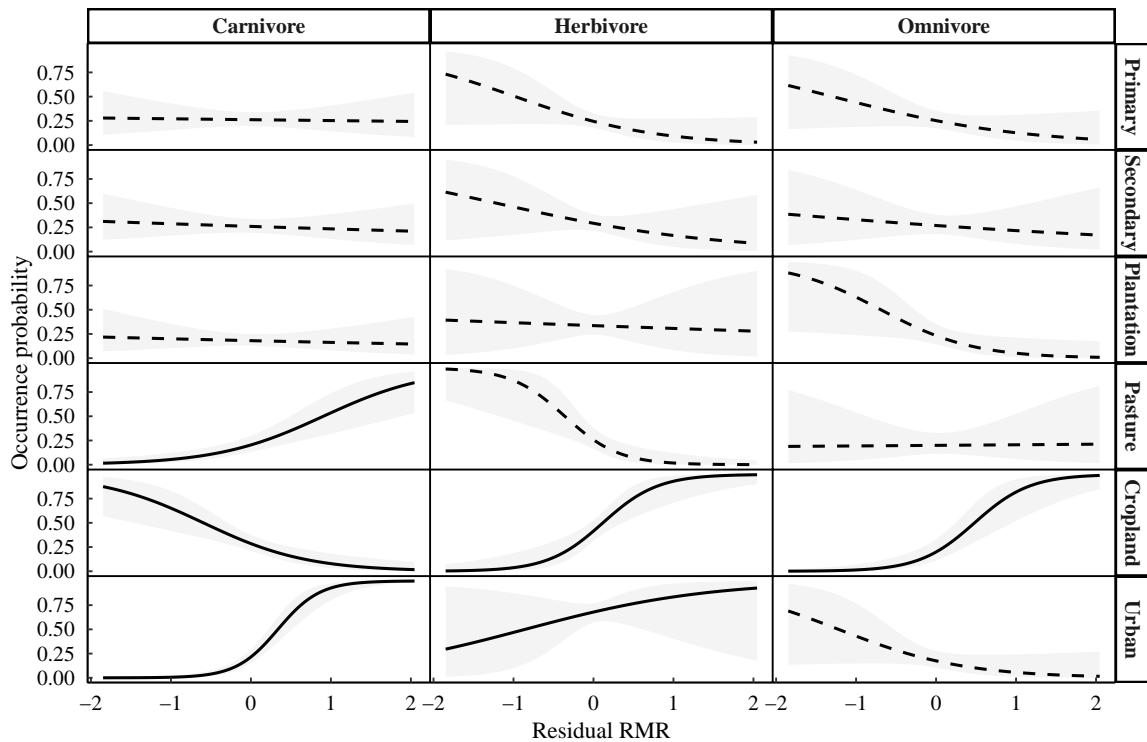


Figure S5.8: (a) Slope estimates for the relationship between residual RMR and occurrence probability in each land-use type and for the three levels of land-use intensity, from the model fitted using the empirical RMR values (i.e., *model 2*, excluding imputed RMR values). The black horizontal line indicates the slope for the reference level (primary vegetation) for minimal land-use intensity. The grey dashed line marks 0. Error bars are 95% confidence intervals. (b) Effect of residual RMR on species probability of occurrence within each trophic level and for each land use-type from the model fitted using the empirical RMR values (i.e., *model 2*, excluding imputed RMR values). I plotted the predictions for minimal land-use intensity only. Solid lines represent significant relationships. Primary: primary vegetation; secondary: secondary vegetation; plantation: plantation forest.

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