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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 | General introduction

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). 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).

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

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

1.1 Major drivers of global biodiversity change

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

1.1.1 Land-use change

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

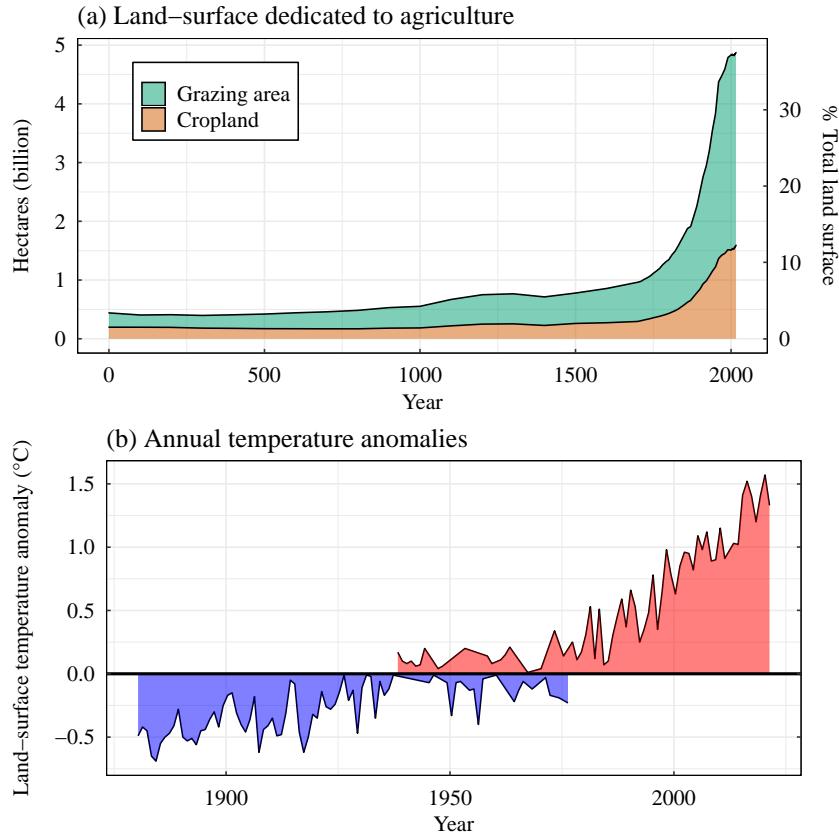


Figure 1.1: Characteristics of the ‘Great Acceleration’. (a) Land surface (and % land-surface) used for agricultural purposes between year 0 and 2016. Data from the HYDE database (Goldewijk et al., 2017), downloaded from <https://ourworldindata.org/land-use> (24/01/2022). (b) Annual land-surface temperature 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).

1.1.3 The future of biodiversity in the Anthropocene

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

1.2 Ecological importance of terrestrial vertebrates and current threats

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

Despite their cultural and ecological importance, terrestrial vertebrates are highly threatened by human activities. The latest Living Planet Report revealed that vertebrate populations have decreased by 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

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

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

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

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

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

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

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

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

1.3.3 Using physiological traits to understand land-use impacts on biodiversity and ecosystem functioning

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

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

1.3.4 Thesis aims

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

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

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

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

1.4 Detailed aims, hypotheses and outline of the following Chapters

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

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

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

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

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

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

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

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

Keywords

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

Abstract

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

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

2.1 Introduction

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

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

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

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

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

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

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

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

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

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

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

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

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

2.2 Methods

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

2.2.1 Trait data collection

Sources and taxonomic matching

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

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

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

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

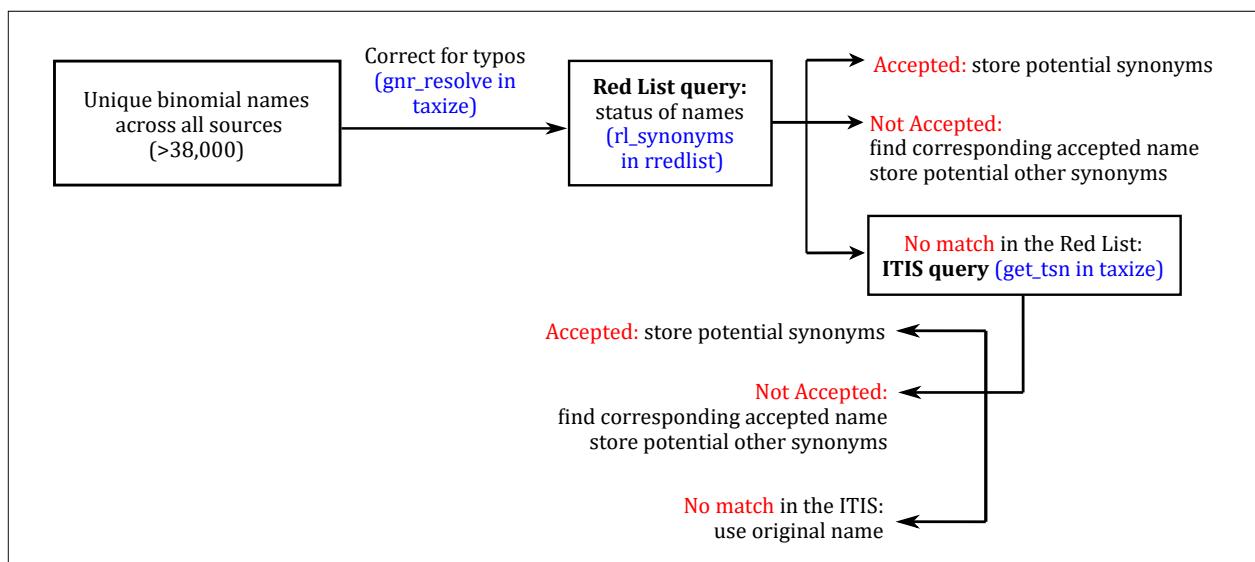


Figure 2.1: Procedure used to identify the accepted names of species. I extracted, where possible, the accepted names of species from either the IUCN Red List or the Integrated Taxonomic Information System (ITIS). Figure reproduced from Etard et al. (2020).

Compilation methods

For continuous traits, I took the median value within species when multiple estimates were available from different sources, after removal of any repeated values, which were assumed to represent estimates duplicated across secondary compilations and derived from the same underlying primary sources. Although intraspecific variation is increasingly being recognized to have important effects on ecological systems (Bolnick 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										✓

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

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

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

- **Body size**

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

- **Longevity**

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

- **Litter or clutch size**

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

- **Trophic level**

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

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

- **Activity time**

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

- **Habitat breadth**

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

- **Use of artificial habitats**

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

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

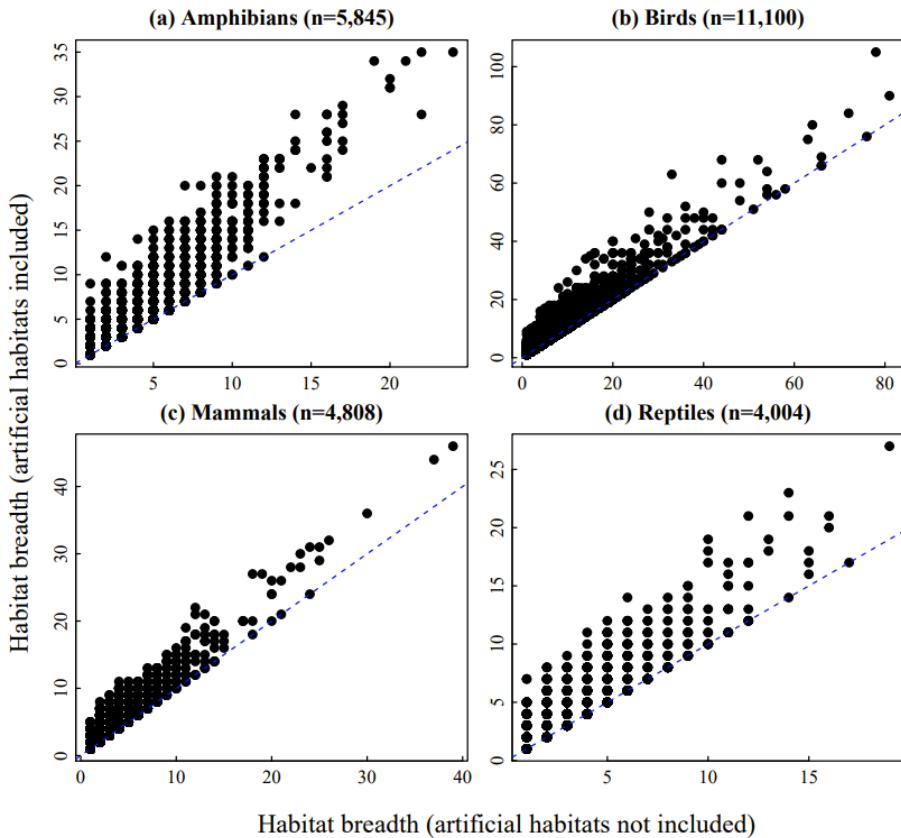


Figure 2.2: Number of natural and artificial habitats used by species against number of strictly natural habitats used by species. Pearson's correlation coefficients show a high positive correlation between these two metrics of habitat breadth in all terrestrial vertebrate classes: 0.92 for amphibians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

Phylogenies

I used class-specific phylogenetic trees downloaded on 13 April 2020. For mammals, I used ‘complete’ 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. For plotting purposes, I obtained consensus trees using the TreeAnnotator program of the BEAST software (Bouckaert et al., 2019).

Species distributions

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). For mammals and amphibians, species distribution maps were obtained from the IUCN Red List (IUCN

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

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

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

2.2.2 Investigating gaps and biases in trait data

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

Taxonomic biases

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

Phylogenetic biases

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

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

Spatial biases

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

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

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

other cases coverage was <55%, with very little information available for longevity-related traits.

Trait completeness (proportion of non-missing trait values for a species) reflected similar biases (Figure 2.3b). The distribution of trait completeness varied significantly among classes (pairwise Wilcoxon rank sum test: p-value<0.0001 in all cases). Distributions were highly left skewed in mammals and birds (skewness: -2 and -1.6). 84% of all mammalian species and 80% of avian species fell in the 80–100% completeness range. Moreover, the completeness distribution was moderately right skewed for reptiles (skewness: 0.4), and slightly right skewed for amphibians (skewness: 0.02). 56% of all reptiles and 57% of amphibians fell in the 0-50% completeness range.

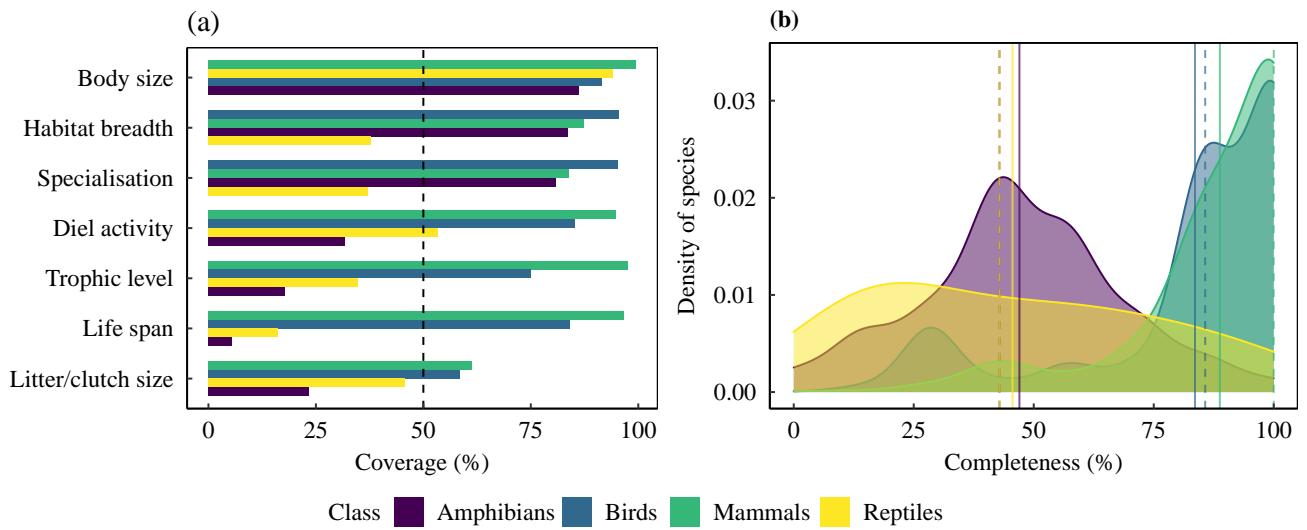


Figure 2.3: Trait coverage and completeness across species. (a) I defined coverage as the proportion of species for which an estimate is available for a given trait. The dashed line represents 50% coverage. (b) Trait completeness is the proportion of estimated traits for a species. Here, I show the distribution 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).*

2.3.2 Phylogenetic biases in trait completeness

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

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

It is important to underline that Figure 2.4 shows within-family median completeness, masking the considerable variation in species richness across families, hence masking potential important variation in completeness across species within families. For example, in the amphibian family *Allophrynidiae* (three recognized species), the within-family median completeness was 50%; but the dataset comprised two species of completeness 14% and 86%, respectively. I present similar plots to those in Figure 2.4 showing the within-family standard deviation in completeness in Appendix 1 (Figure S2.13). Within-family standard deviation tended to increase with within-family species richness (Appendix 1, Figure S2.14).

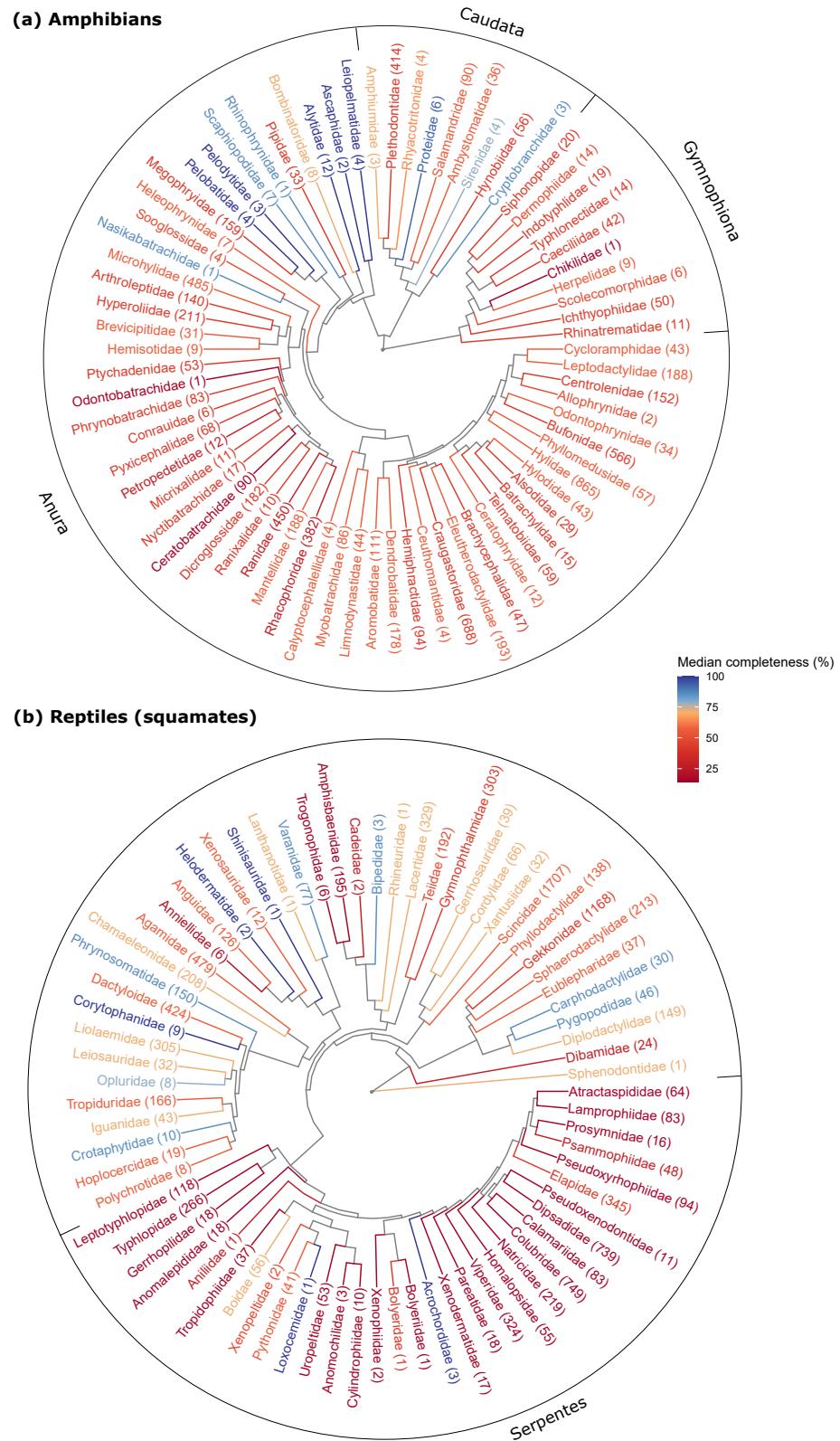


Figure 2.4: Within-family median trait completeness in herptiles. The number next to each family name represents the number of species included in the calculation of the median. *Figure reproduced from Etard et al. (2020).*

2.3.3 Spatial biases in trait completeness

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

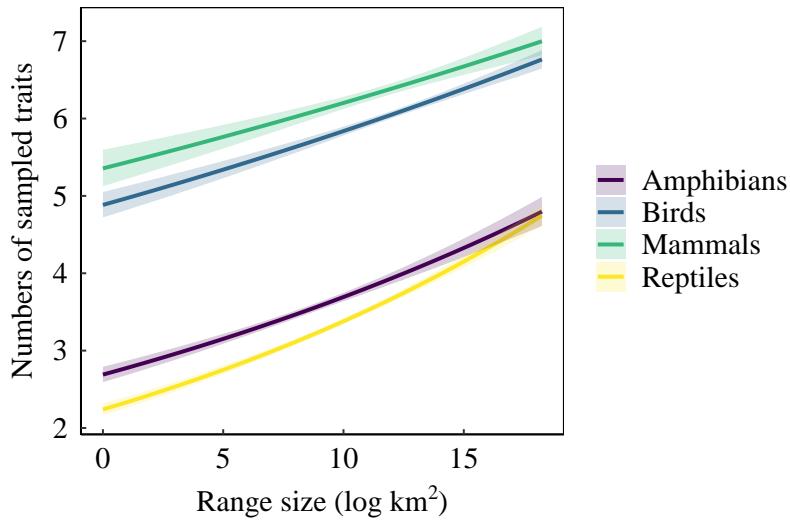
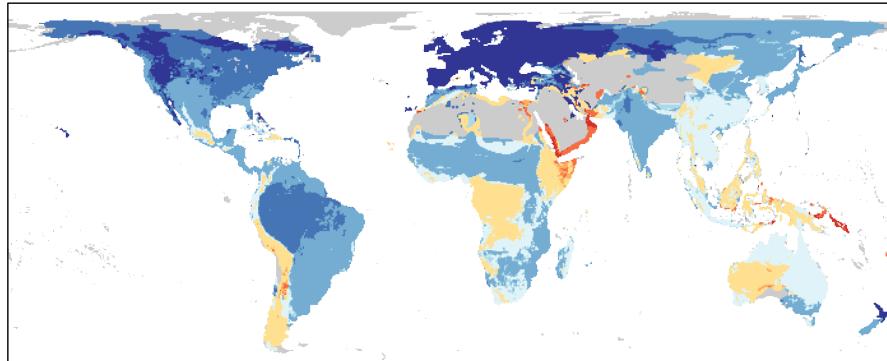


Figure 2.5: Relationship between number of sampled traits and geographical range size. The model was fitted using a Poisson error distribution. Class was added as a predictor interacting with range size. Rates of increase in number of sampled traits with range size were not significantly different for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

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

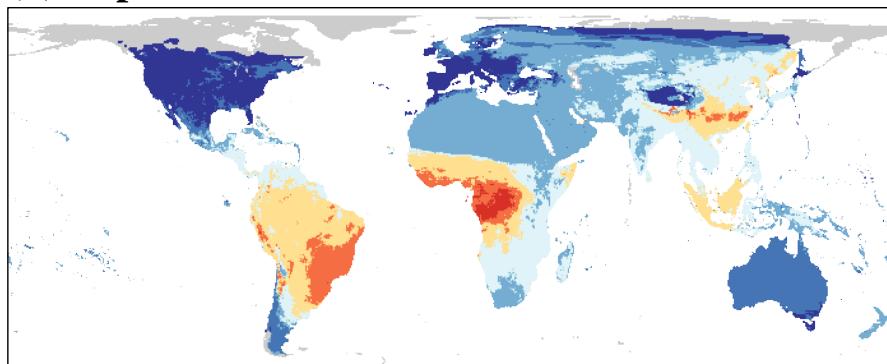


Figure 2.6: Spatial distribution of assemblage-level median trait completeness in herptiles. Similar maps for birds and mammals are shown in Appendix 1 (Figure S2.7). *Figure reproduced from Etard et al. (2020).*

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

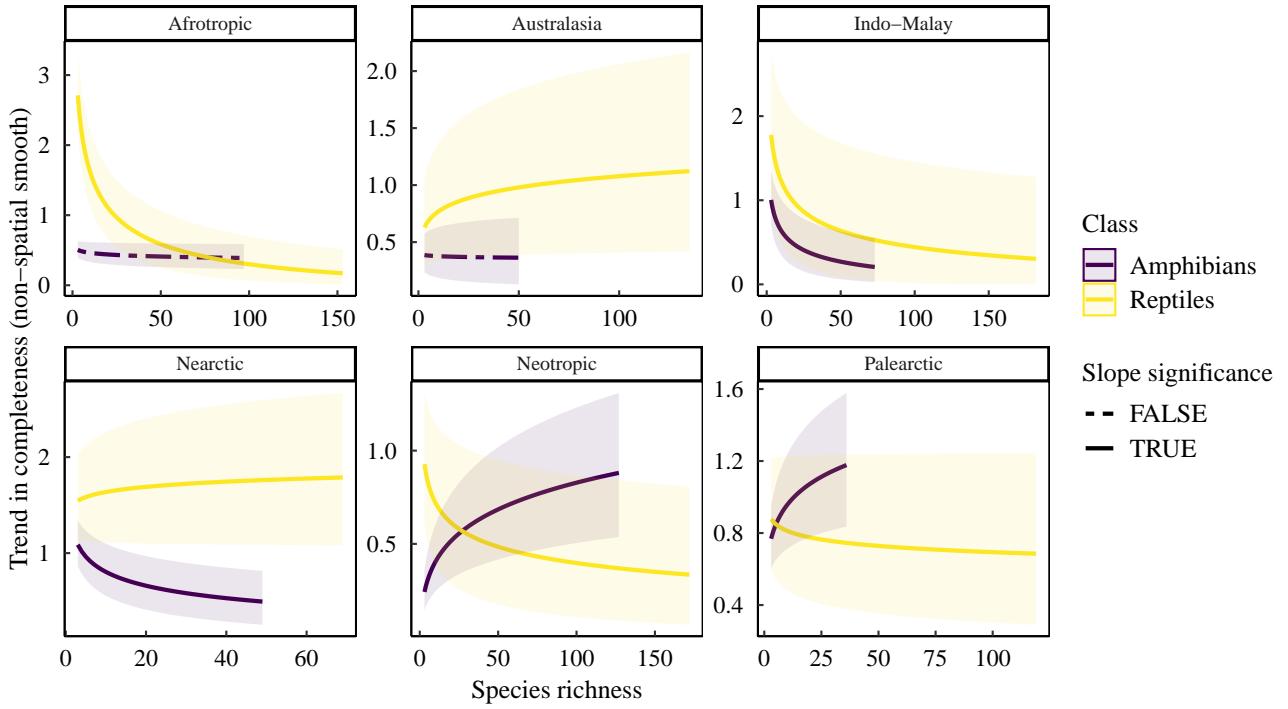


Figure 2.7: Spatial model trends for herptiles. The lines represent in-sample predictions (\pm standard error) for the trend components of the spatial models (trends after accounting for spatial autocorrelation). *Figure reproduced from Etard et al. (2020).*

2.4 Discussion

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

3 | Intensive human land uses negatively affect vertebrate functional diversity

Keywords

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

Abstract

Land-use change is the leading driver of global biodiversity loss, thus characterising its impacts on the functional structure of ecological communities is an urgent challenge. Using a database describing vertebrate assemblages in different land uses, I assess how the type and intensity of land use affect the functional diversity of vertebrates globally. I find that human land uses alter local functional structure by driving declines in functional diversity, with the strongest effects in the most disturbed land uses (intensely used urban sites, cropland and pastures), and among amphibians and birds. Both tropical and temperate areas experience important functional losses, which are only partially offset by functional gains. Tropical assemblages are more likely to show decreases in functional diversity that exceed those expected from species loss alone. These results indicate that land-use change non-randomly reshapes the functional structure of vertebrate assemblages, raising concerns about the continuation of ecological processes sustained by vertebrates.

3.1 Introduction

Anthropogenic activities are profoundly transforming global biodiversity. Although multiple pressures act in combination, land-use change currently poses the greatest threat to biodiversity (Maxwell et al., 2016; Newbold et al., 2015). However, not all species respond similarly to land-use change. Traits have been found 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

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

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

3.2 Methods

3.2.1 Vertebrate assemblages

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

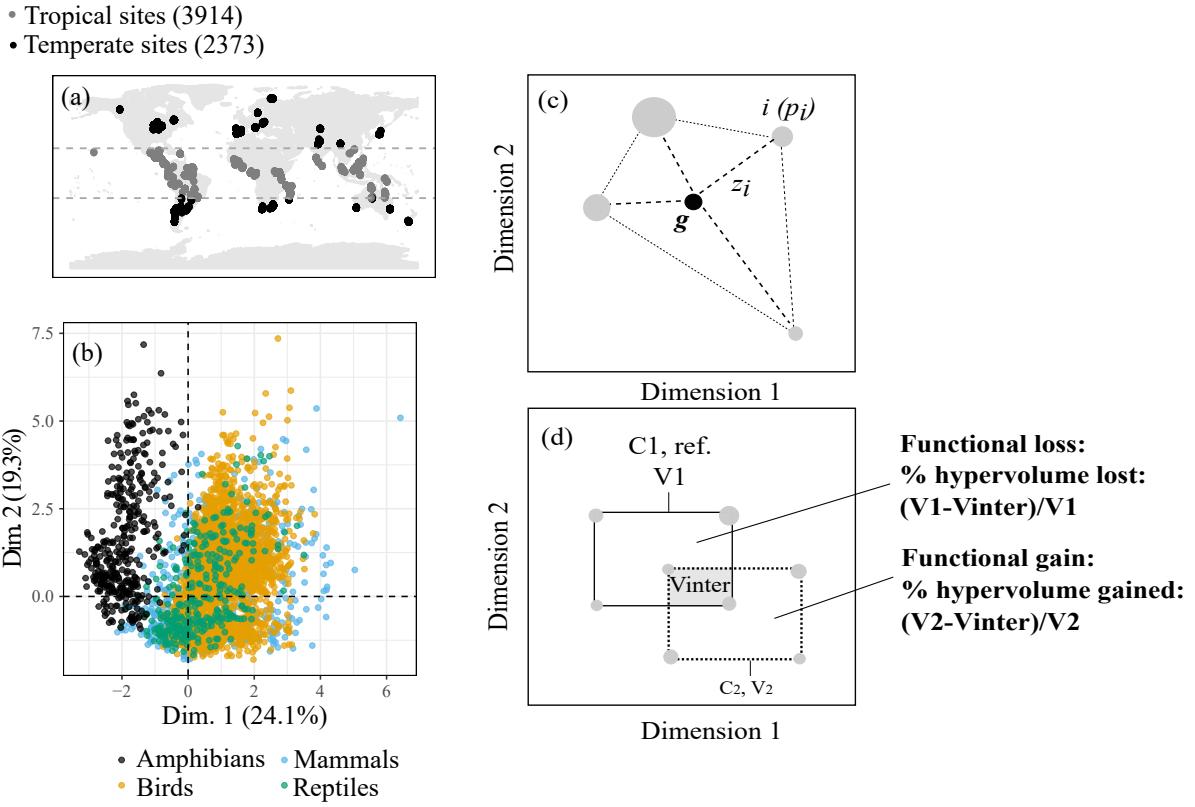


Figure 3.1: Overview of the study design and functional diversity metrics. I used occurrence data for vertebrate species from the PREDICTS database ((Hudson et al., 2014, 2017); 180 studies; 431,170 records; 4,339 species; 6,758 sampled sites). (a) shows the spatial distribution of sites I consider. 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).*

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

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

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

3.2.2 Functional traits and diversity metrics

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

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

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

(Model 1a)

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

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

(Model 1b)

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

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

(Model 2a)

For FDis, regional effects were dropped:

$$\begin{aligned} \arcsin(\sqrt{FDis}) \sim & \text{Land use} + \text{Land-use intensity} + \text{Class} + \text{Land use : Land-use intensity} + \text{Land use :} \\ & \text{Class} + \text{Land-use intensity : Class}. \end{aligned}$$

(Model 2b)

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

3.2.4 Investigating functional under-dispersion (Hypothesis 2)

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

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

(Model 3)

3.2.5 Functional loss and functional gain (Hypothesis 3)

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

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

(Model 4a)

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

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

(Model 4b)

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

$$\begin{aligned} \arcsin(\sqrt{\text{loss}}) \sim & \text{Land use} + \text{Land-use intensity} + \text{Class} + \text{Region} + \text{Land use :} \\ & \text{Land-use intensity} + \text{Land use : Class} + \text{Land use : Region} + \text{Land-use intensity : Class}. \end{aligned}$$

(Model 5a)

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

All data analyses were conducted using R version 3.5.1 (R Core Team, 2018). I made the code available 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>).

3.3 Results

3.3.1 Effects of land use on FRic and FDis

Across all vertebrates, land use and land-use intensity significantly affected FRic and FDis (Figure 3.2). FRic tended to decrease with increasing disturbance level and higher intensity of land use. For FRic, relative effects differed between regions (Figure 3.2a). Although declines were overall more important for disturbed tropical assemblages, significant declines were observed for the temperate assemblages (e.g., a 37% average decline in intensely used urban areas; a 49% decline in pastoral areas of high land-use intensity). Nevertheless, tropical assemblages typically showed more important reductions in FRic. For instance, declines averaged 63% for intensely used tropical cropland and 76% for urban areas. For FDis, relative effects were similar in both regions (Figure 3.2b). The most important average declines were observed for urban assemblages of intense use (20% decline), and for lightly- and intensely used cropland (by 15% and 26%). Note that confidence intervals around the estimated average declines were large in some cases, highlighting some heterogeneity in the responses.

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

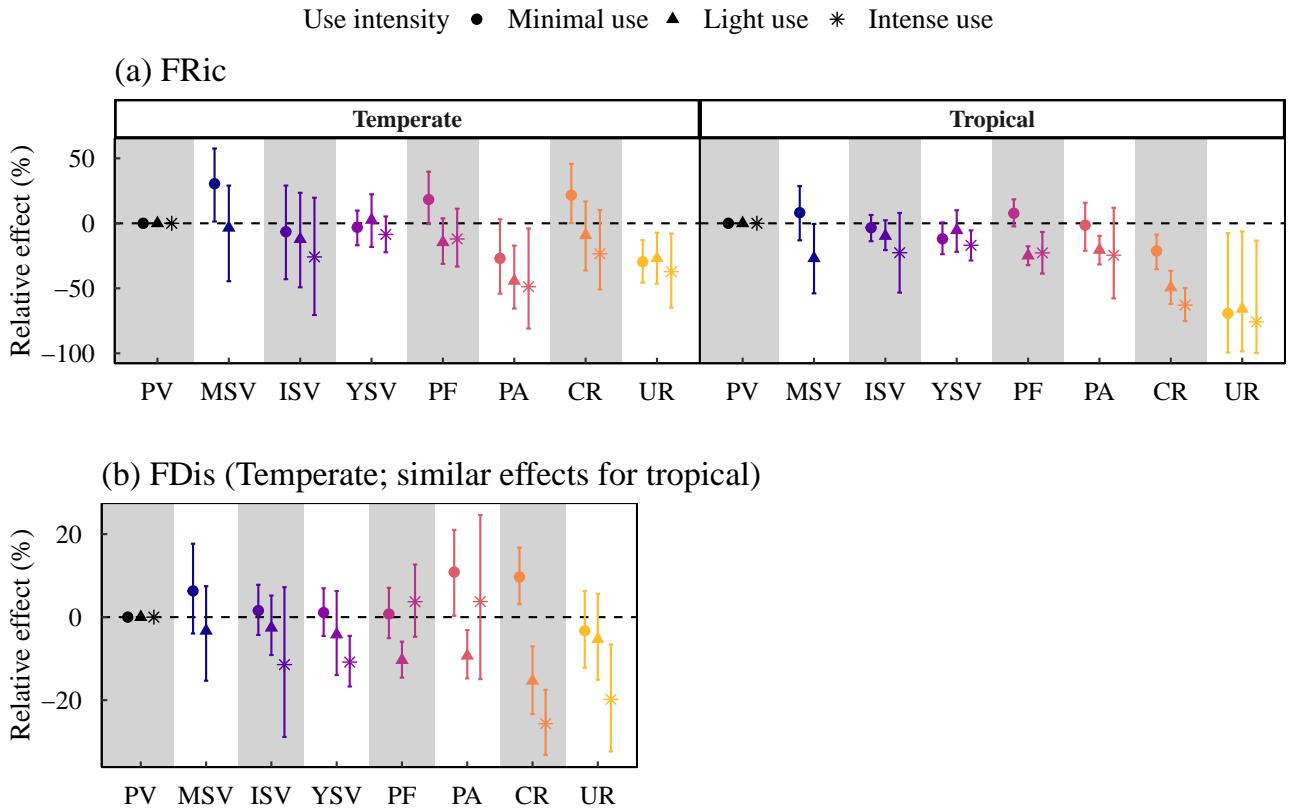


Figure 3.2: Effects of land use, land-use intensity and region on FRic (a) and on FDis (b) across all PREDICTS vertebrates. Effects were rescaled with reference to primary vegetation (PV) and are plotted as a % difference relative to PV within each land-use intensity. For FRic, the best-fitting model 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).*

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

Responses of FRic and FDis to land use and land-use intensity differed among taxonomic classes (Figure 3.3). Within-class effects for FDis were similar between regions. The most notable decreases were observed in lightly- and intensely used agricultural land uses in amphibians, birds and reptiles; and in intensely used urban land uses for birds and mammals. For FRic, the effects in tropical and temperate regions were qualitatively similar in three out of four classes (birds, mammals and reptiles), although effect sizes tended to be 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.

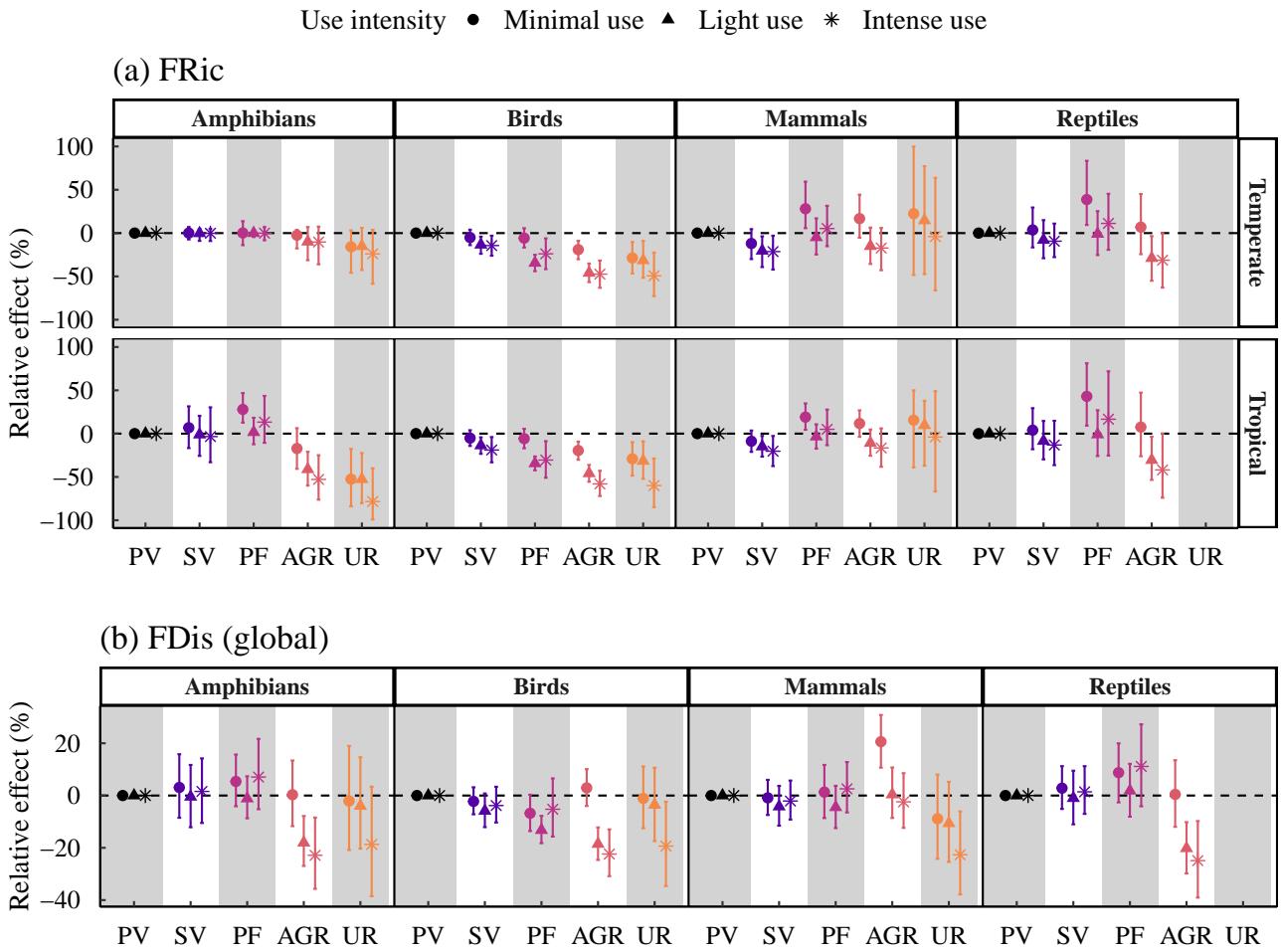


Figure 3.3: Effects of land use, land-use intensity, region and taxonomic class on FRic (a) and FDis (b). Effects were rescaled with reference to primary vegetation (PV) and are plotted as a % difference relative to PV within each land-use intensity. Error bars represent 95% confidence intervals. Effects 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

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

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

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

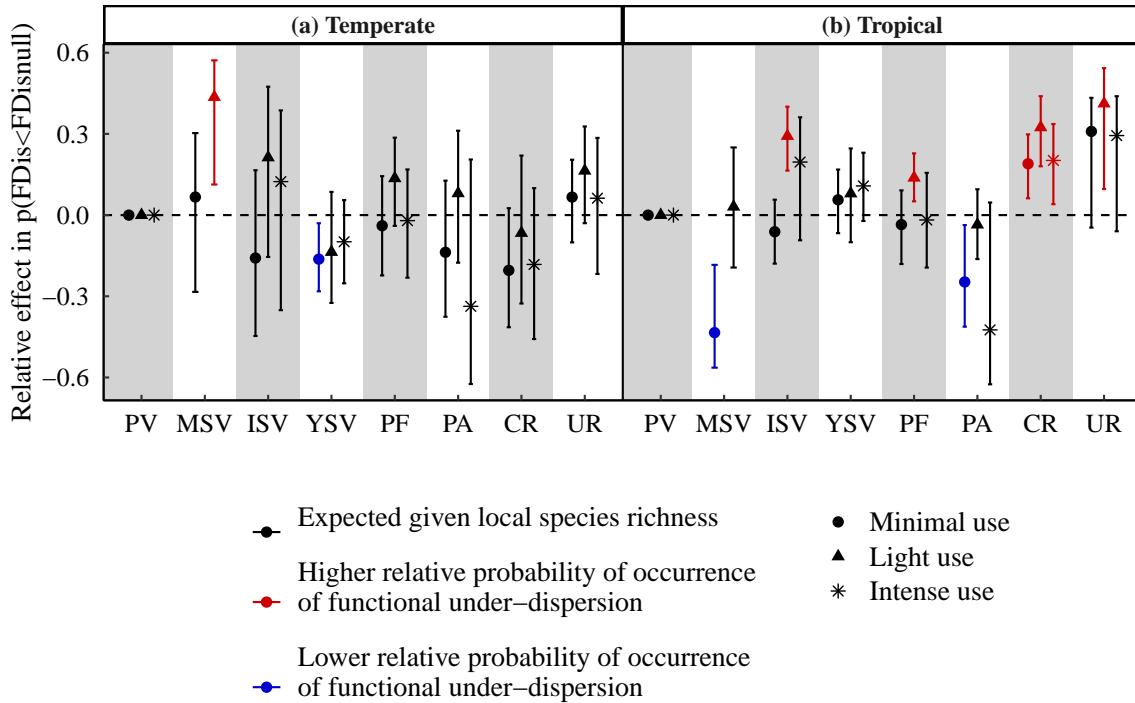


Figure 3.4: Effects of land use, land-use intensity and region on the probability of occurrence of functional under-dispersion. Error bars represent 95% confidence intervals. PV: primary vegetation; MSV, mature secondary vegetation; ISV, intermediate secondary vegetation; YSV, young secondary vegetation; 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).

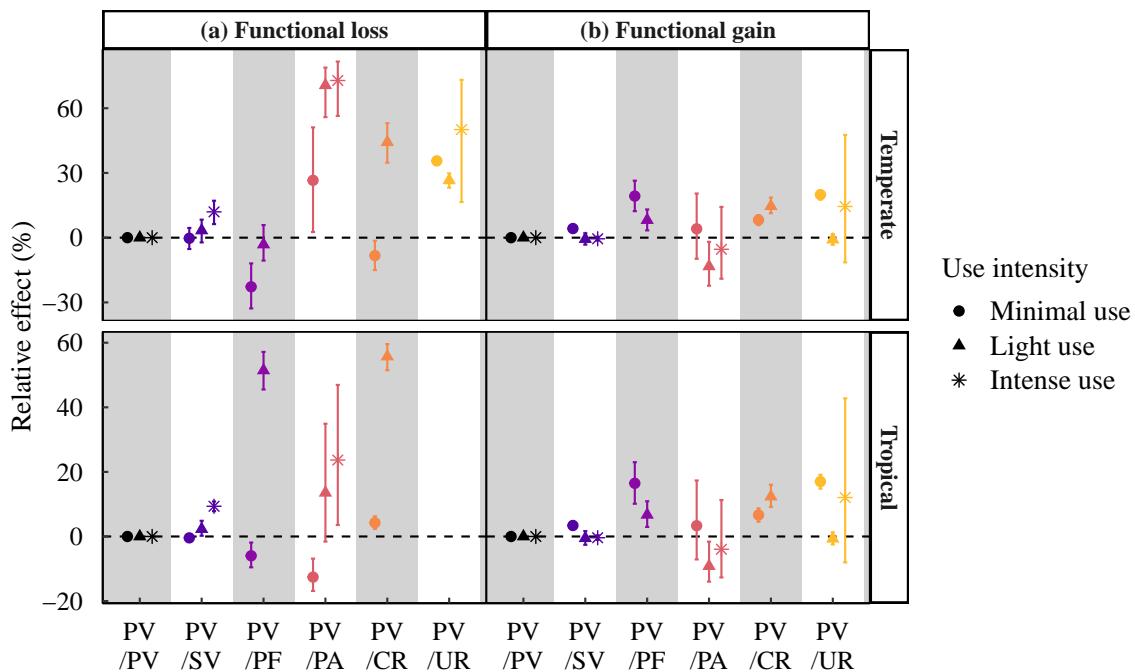


Figure 3.5: Effects of land use and land-use intensity on (a) functional loss and (b) functional gain across pairs of sites in temperate areas and tropical areas. PV: primary vegetation; SV, secondary vegetation; PF, plantation forest; PA, pasture; CR, cropland; UR, urban. Error bars represent 95% confidence 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).*

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

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

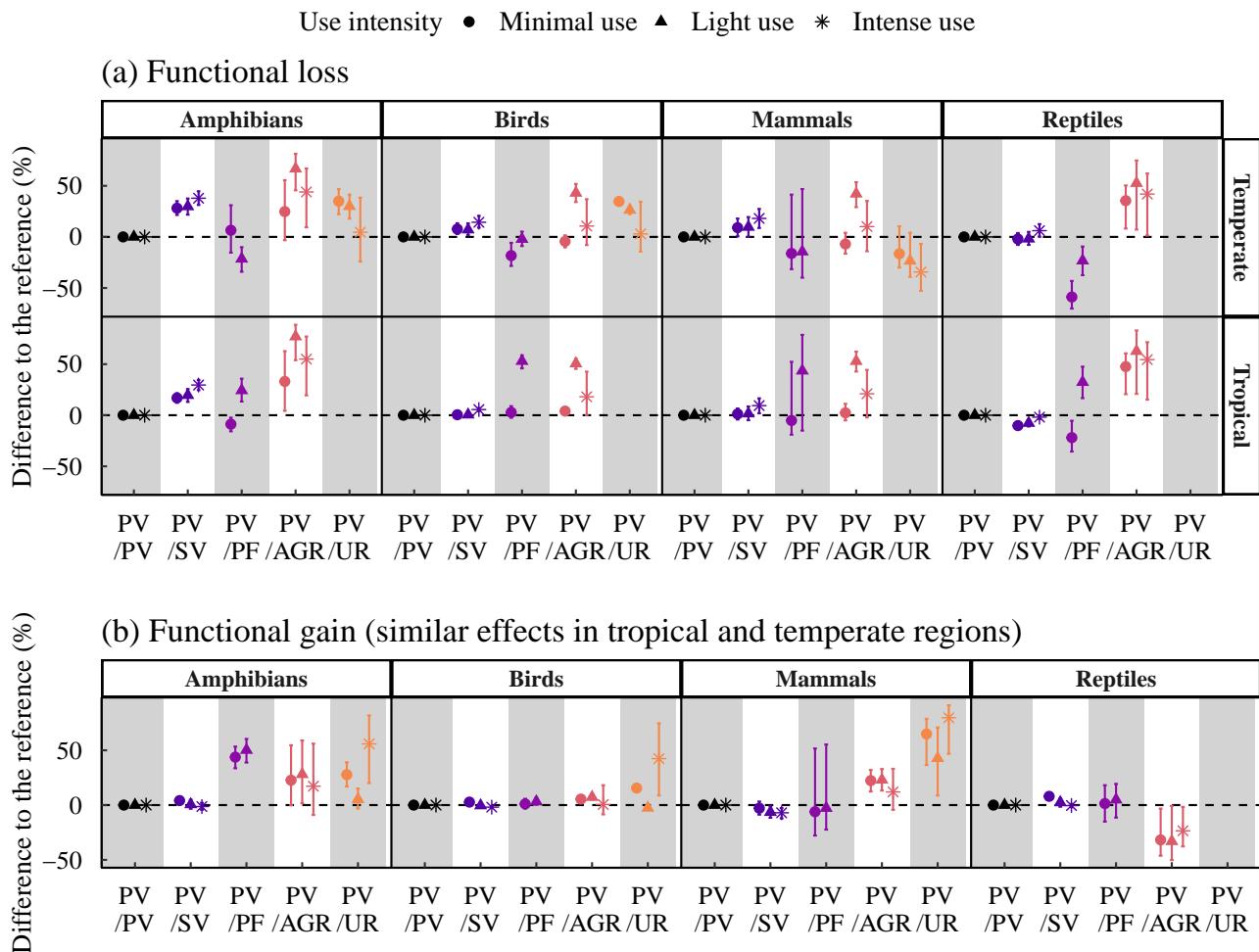


Figure 3.6: Effects of land use, land-use intensity, region and taxonomic class on functional loss (a) and functional gain (b) across pairs of sites. PV: primary vegetation; SV, secondary vegetation; PF, plantation forest; AGR, agricultural land uses (pasture and cropland); UR, urban. Error bars represent 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).*

3.4 Discussion

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

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

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

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

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

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

Keywords

Land use; land-use intensity; climate change; sensitivity; CENFA; dietary traits ; life-history traits; specialisation; geographical range area; terrestrial vertebrates.

Abstract

Land-use and climate change are two of the most important pressures on terrestrial biodiversity, however the factors that explain interspecific variation in responses to these pressures remain unclear. Although it is well established that extinction risk and some species' responses to human pressures relate to species traits, we lack large-scale comparative assessments across multiple clades linking traits to multiple human pressures. Here, I investigated whether a set of ecological characteristics that are commonly measured across terrestrial vertebrates (that is, ecological traits and geographical range area) are associated with (1) species' responses to different land-use types and (2) species' sensitivity to climate change. My aim was to test whether general-

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

4.1 Introduction

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

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

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

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

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

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

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

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

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

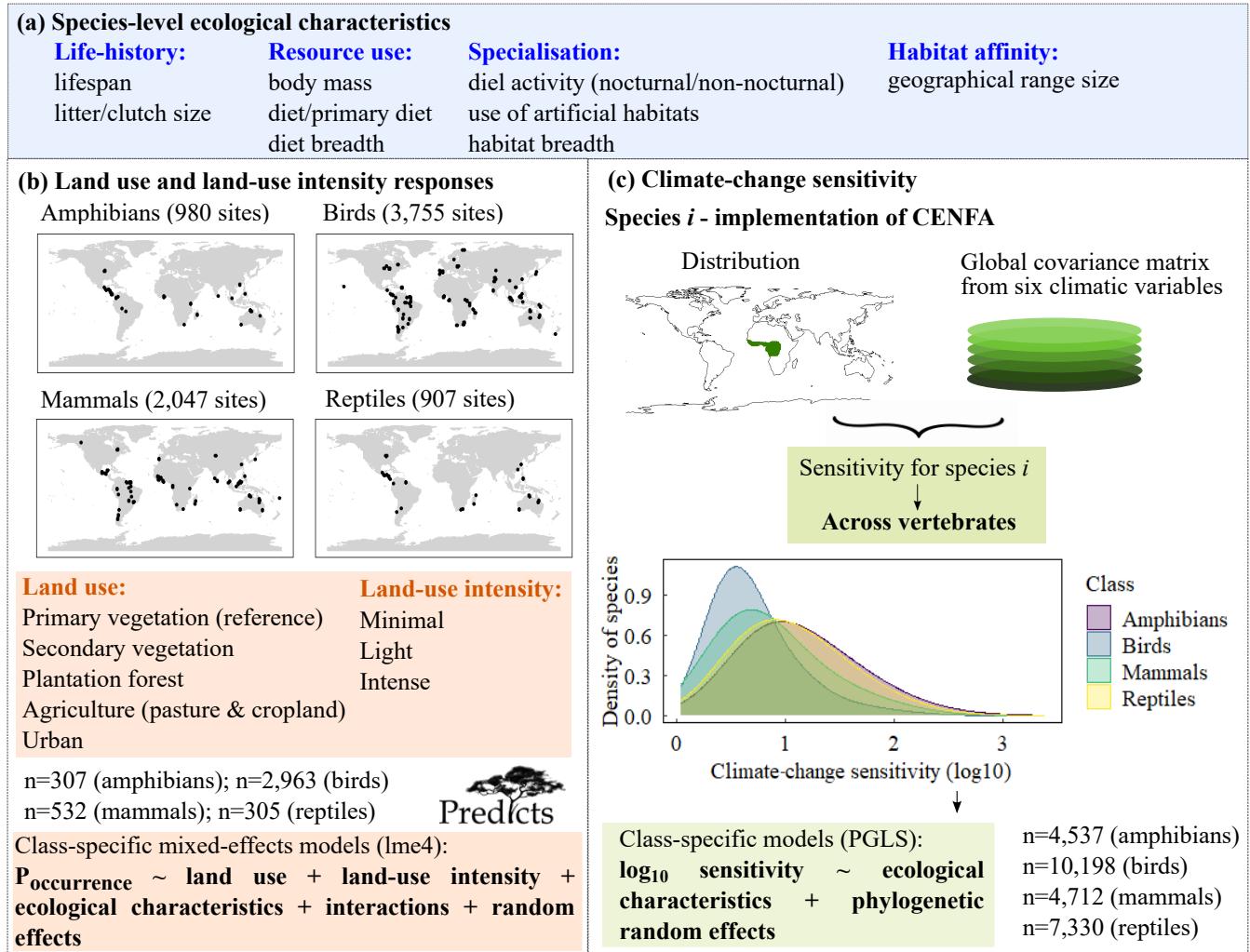


Figure 4.1: Framework of the study. (a) I collected ecological trait data and geographical range areas across terrestrial vertebrates (termed ‘ecological characteristics’). I then used two independent approaches to assess the influence of these characteristics on species’ responses to land-use and on 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.

4.2 Methods

4.2.1 Ecological characteristics (Figure 4.1a)

Traits

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

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

I standardised the diet data across the vertebrate classes, by grouping species in five different diet categories: vertebrate eaters; invertebrate eaters; plant/seed eaters; fruit/nectar eaters; and omnivores (for mammals and birds, species were classified as omnivores when all food items had a percent use $\leq 50\%$; and for amphibians and reptiles, when species were known to consume both plant and animal matter). I also calculated species diet breadth – the total number of recorded food items (in terms of presence/absence) known

to be consumed by a species. More information on the compilation of dietary information can be found in Appendix 3, S4.1: ‘Compiling diet information’.

Geographical range area

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 from Roll et al. (2017) for reptiles (all downloaded in April 2020). I excluded areas occupied during non-breeding seasons and areas falling outside species known elevational limits (following Chapter 2). The range maps were then converted to the raster format (‘raster’ package, version 3.5.15 Hijmans (2022)), and I estimated species geographical range areas using a resolution of 1 km² with Behrmann’s equal-area projection. Although range area cannot be considered a trait (which is a property measurable at the level of individual organisms), I included range area in the analyses because past work has shown that range area is an important correlate of species’ responses to land use (Newbold et al., 2018) and climate change (Thuiller et al., 2005). In addition, range area may correlate with other aspects of species’ ecology that I could not include directly in the analysis because of limited data availability, such as dispersal ability (Capurucho et al., 2020).

Phylogenies

I used information on species’ phylogenetic position in the imputations of missing trait values (see next section), and also to control for phylogenetic relationships in the models investigating effects of ecological characteristics on species’ estimated climate-change sensitivity. Class-specific 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 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.

4.2.2 Imputations of missing trait values

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

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

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

Vertebrate assemblage composition

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

Full models (all-predictor models)

Within each vertebrate class, I investigated whether interactions among the ecological characteristics, land 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:

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

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)).

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.

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 similar traits (I term such effects ‘among land-use type effects’, Figure 4.2a); or by comparing occurrence

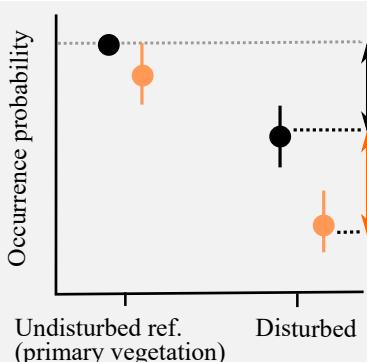
probability in a given land-use type relative to species with different traits (I term such effects ‘within land-use type effects’, Figure 4.2a).

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

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

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

(a) Assessing the effects of categorical ecological characteristics on land-use responses



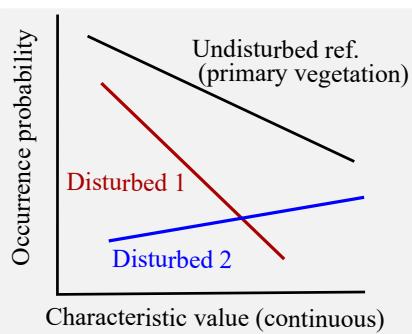
'Among land-use type' effects: main effect of given characteristic on occurrence probability, among land-use types

'Within land-use type' effects: interactive effect between land-use type and characteristic: difference in occurrence probability for two different values of the characteristic, within land-use types

Categorical characteristic:

- level 1
- level 2

(b) Assessing the effects of continuous ecological characteristics on land-use responses



Slope of the relationship between continuous characteristic & occurrence probability:

1: higher values of ecological characteristics associated with relatively **lower probability of occurrence** in disturbed relative to reference land-use type compared to lower values of ecological characteristics

2: lower values of ecological characteristics associated with relatively **lower probability of occurrence** in disturbed relative to reference land-use type compared to higher values of ecological characteristics

(Does not inform on absolute changes in occurrence probability among land-use types)

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.

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

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

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

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

Historical climate data

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

Estimating climate-change sensitivity from CENFA

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

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

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

Climate-change sensitivity models

I used phylogenetic least-square (PGLS) regressions, implemented in the 'caper' R package version 1.0.1 (Orme et al., 2018), to assess the effects of ecological characteristics on species estimated sensitivity to climate change, while controlling for phylogenetic relationships among species. I combined the ecological characteristics and the phylogenies using the 'comparative.data' function from the 'caper' package, and then built class-specific models to explain climate-change sensitivity with the ecological characteristics (Figure 4.1c). Before fitting the models, I checked for multicollinearity among the predictors using GVIF scores. Across all classes, the models included all the main effects of the ecological characteristics, except for amphibians, for which I dropped diet breadth (which was strongly collinear with diet; Tables S4.9-S4.13). For the continuous predictors, I fitted third-order polynomials to allow for non-linearity of the responses (I included third order polynomials for the climate-change sensitivity models but not for the land-use models because the PGLS model had a simpler structure than the land-use models, were less computationally intensive, and also because the number of estimated parameters was already high for the land-use models without allowing for third-order polynomials). As such, the general form of the PGLS models was:

$$\log_{10}(\text{climate-change sensitivity}) \sim \text{poly}(\log_{10}(\text{continuous ecological characteristics}), 3) + \\ \text{categorical ecological characteristics} + \text{phylogenetic random effects.}$$

Models' robustness

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

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

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

4.3 Results

4.3.1 Land-use responses

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

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

I would like to highlight that the ‘within land-use type’ effects summarised in Table 4.1a do not necessarily reflect occurrence patterns among land-use types. For example, in all classes, ‘among land-use type’ effects derived from partial models showed that occurrence probability in disturbed land uses was strongly negatively affected for natural habitat specialists, compared with primary vegetation levels Figure S4.7. On the other hand, in most classes and disturbed land uses, artificial habitat users either increased or showed no significant difference in occurrence probability. One exception was for reptiles, where the effect of habitat specialisation was mostly non-significant within land-use types (Table 4.1a), with both natural habitat specialists and artificial habitat users showing important declines in some disturbed land uses (e.g., intensely-used agricultural areas, Figure S4.7d). Similarly, the occurrence probability of both nocturnal and non-nocturnal species was negatively impacted in disturbed land uses compared with primary vegetation (Figure S4.8), such that land-use responses were not distinguishable between nocturnal and non-nocturnal 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 on (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				
																			More narrowly-distributed				
-	-	-	-	(-)	-	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	0	NA	Narrower diet breadth	NA	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	0	NA	Shorter-lived	(+)	-	0	-		

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

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

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

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

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

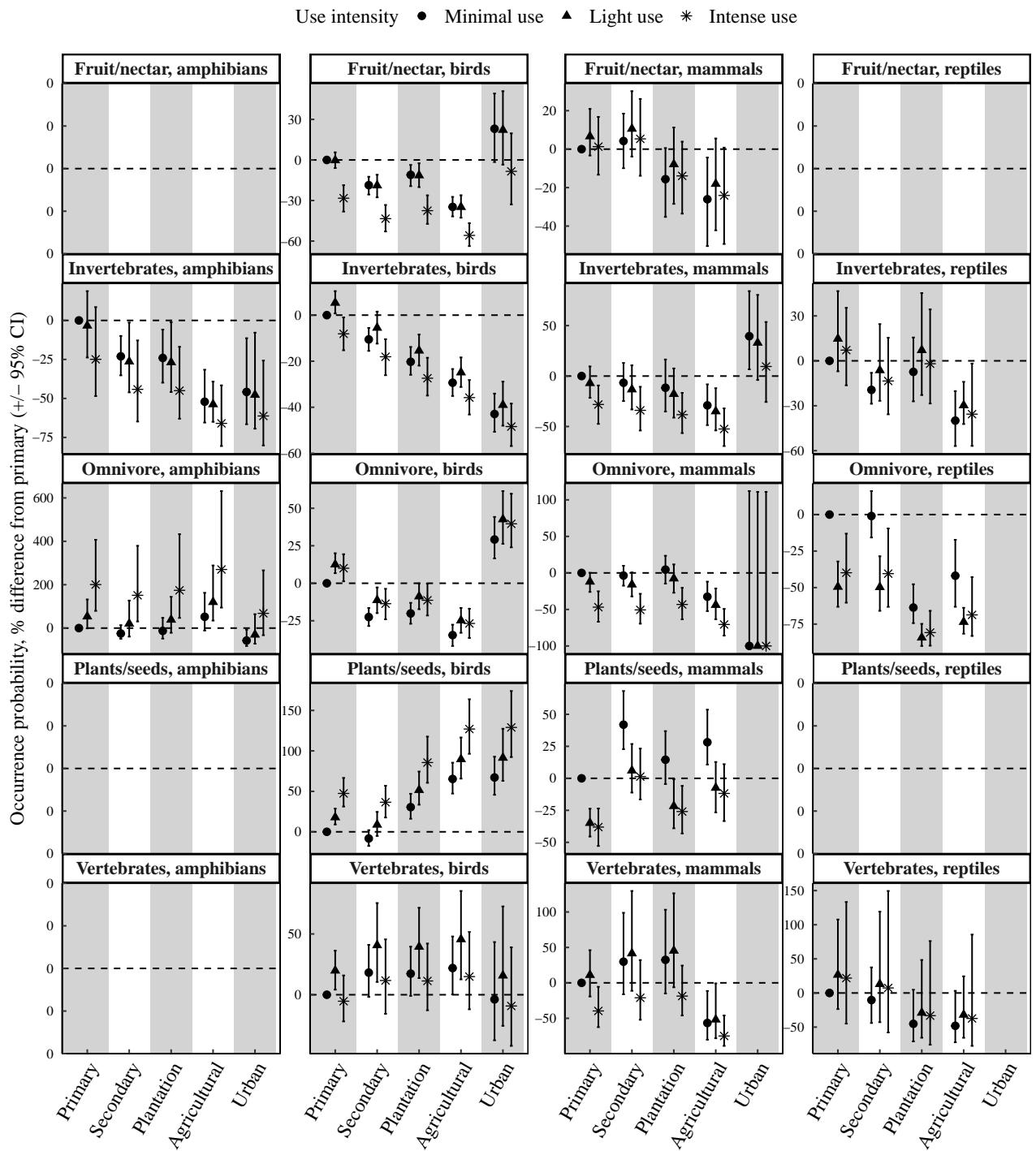


Figure 4.3: Predicted occurrence probability as a function of land use, land-use intensity, diet and their interactions, for each class of terrestrial vertebrates (median \pm 95% confidence interval; the predictions are rescaled with reference to minimally-used primary vegetation). The predictions were 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.

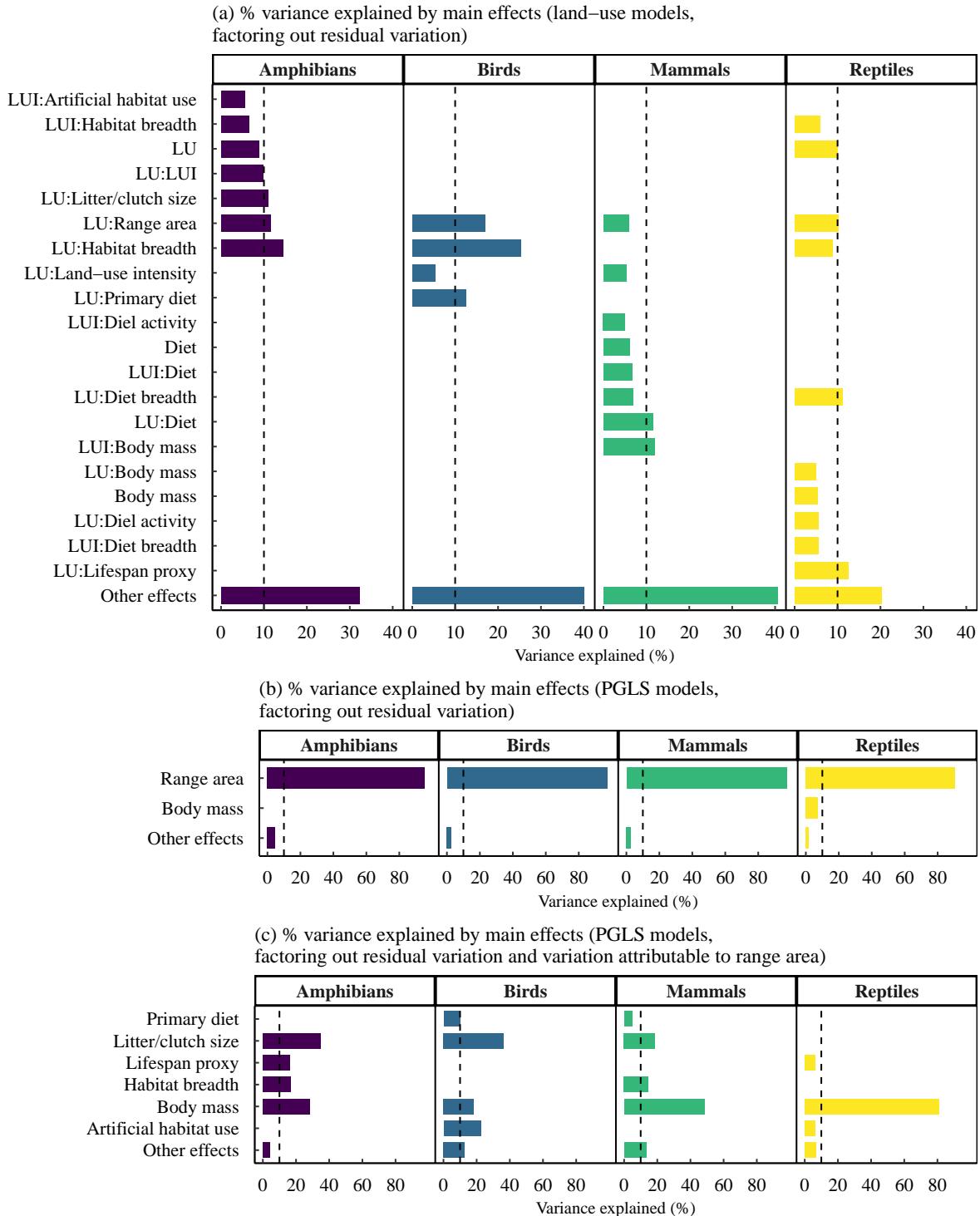


Figure 4.4: Proportion of the explained variance attributable to each of the main effects for (a) the mixed-effects models fitting the effects of land use, land-use intensity, and ecological characteristics on species occurrence probability (after factoring out residual variation); (b) for the phylogenetic 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.

4.3.2 Climate-change sensitivity

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

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

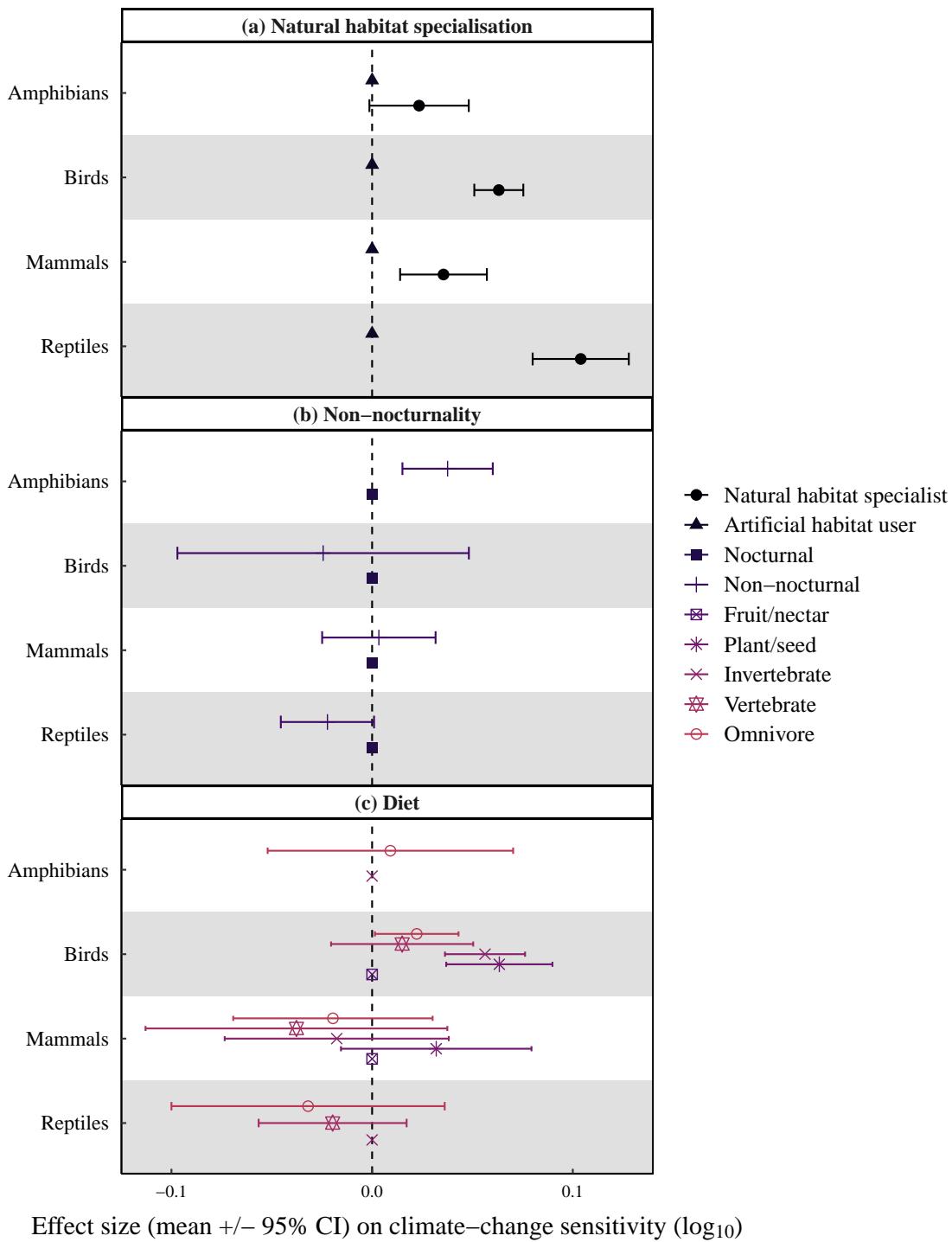


Figure 4.5: Estimated effects of the categorical traits on climate-change sensitivity, from the PGLS models fitted in each class (mean effect \pm 95% confidence interval). For each categorical trait, I show the effect size for all levels referring to the reference level (vertical dashed line). (a) For 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.

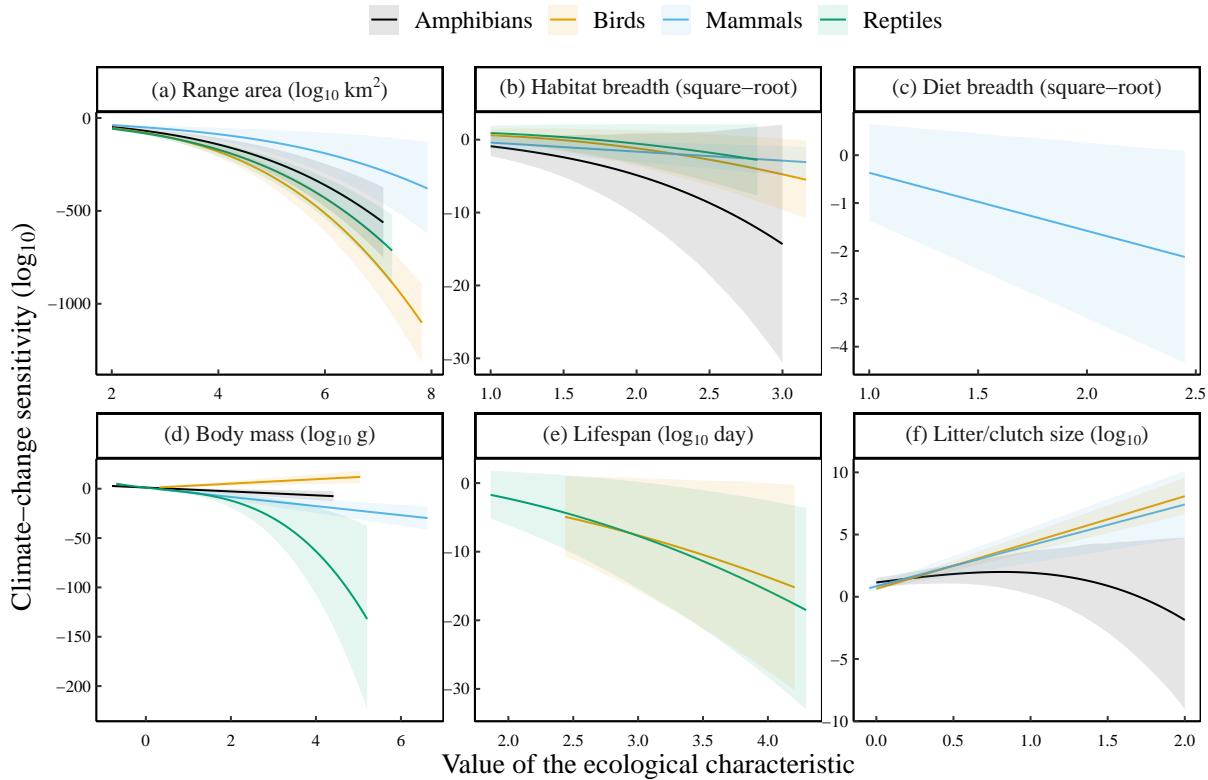


Figure 4.6: Effects of the continuous ecological characteristics on climate-change sensitivity, estimated from the PGLS models in each class. The lines represent the estimated relationships between climate-change sensitivity and ecological characteristics; the shaded areas are 95% confidence intervals.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

Robustness of the PGLS models

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

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

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 **
Birds	Diet	3	8.61E-04	2.87E-04	2.98E-01	8.27E-01
	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 **
Mammals	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
	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 ***
Reptiles	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 **
	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 ***

4.4 Discussion

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

This work further highlights the class-specific associations between most traits and likely responses to human-driven environmental changes, but again highlighting a non-random reshaping of vertebrate biodiversity 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). I would like to emphasize that this does not mean that life-history and dietary traits are unimportant for understanding species' responses, but it means that their effects and relative importance 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 is known about their potential effects at large scales and for different types of pressure. Thus, developments of my work could focus on the effects of trait interactions on species' sensitivity to climate change and land-use responses. I was also unable to consider intraspecific variation in this work. Intraspecific variation and the potential for acclimation and evolutionary adaptation are likely important determinants of species' ability to cope with human disturbance (Carlson et al., 2014; Rohr et al., 2018), but considering such effects at large scales is challenging because of the lack of available data.

Moreover, I investigated climate-change sensitivity and land-use responses separately, meaning that I did not consider the combined effects of these pressures. However, human pressures act in combination (Capdevila et al., 2022a; Harfoot et al., 2021; Segan et al., 2016), and a number of confounding factors and threats that I could not account for could possibly influence species' sensitivity. For example, larger species

might be more sensitive to warming than smaller species (Hantak et al., 2021; Merckx et al., 2018), but they could also be better able to persist in fragmented landscapes, such that habitat fragmentation and climate warming may have opposite effects on the responses of such species. Further, larger species might also be disproportionately exposed to other threats such as overexploitation and human-wildlife conflicts (Ripple et al., 2014, 2017). Interactions among traits, among types of pressure, and among traits and pressures should ideally be considered together to understand species' responses to human disturbances (Hantak et al., 2021). However, considering all these effects simultaneously may be challenging because of data-limitation issues, model complexity, and difficulty in assessing and disentangling individual and interactive effects. In addition, I would like to emphasize that my results, based on correlative assessments of the associations between ecological characteristics and species' sensitivity to climate change and species' land-use responses, do not allow to infer any causal links between traits and species' responses to global changes. Reinforcing our mechanistic understanding of how traits influence species' ability to cope with different disturbances may help understand opposite signatures of human impacts on vertebrate trait diversity. Further work could help elucidate the mechanistic links between species traits and responses to environmental change, perhaps supported by long-term population data and demographic models (Hernández-Yáñez et al., 2022).

To conclude, the results of this Chapter indicate that land-use and climate change are likely to impact terrestrial vertebrates non-randomly with respect to their ecological characteristics, which could have important consequences for ecosystem functioning (Duffy, 2003; Luck et al., 2012). For instance, I detected substantial declines in occurrence probability of certain dietary groups in disturbed land-use types, most notably invertebrate eaters and fruit/nectars eaters in all classes. I also found higher climate-change sensitivity for invertebrate- and plant/seed-eating birds. My findings thus highlight the potential risks from global changes for ecosystem processes and services sustained by those species, such as pest control, seed dispersal or pollination (Civantos et al., 2012; Fricke et al., 2022; González-Varo et al., 2013), highlighting the need to put into place 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,

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

5.1 Introduction

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

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

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

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

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

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

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

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

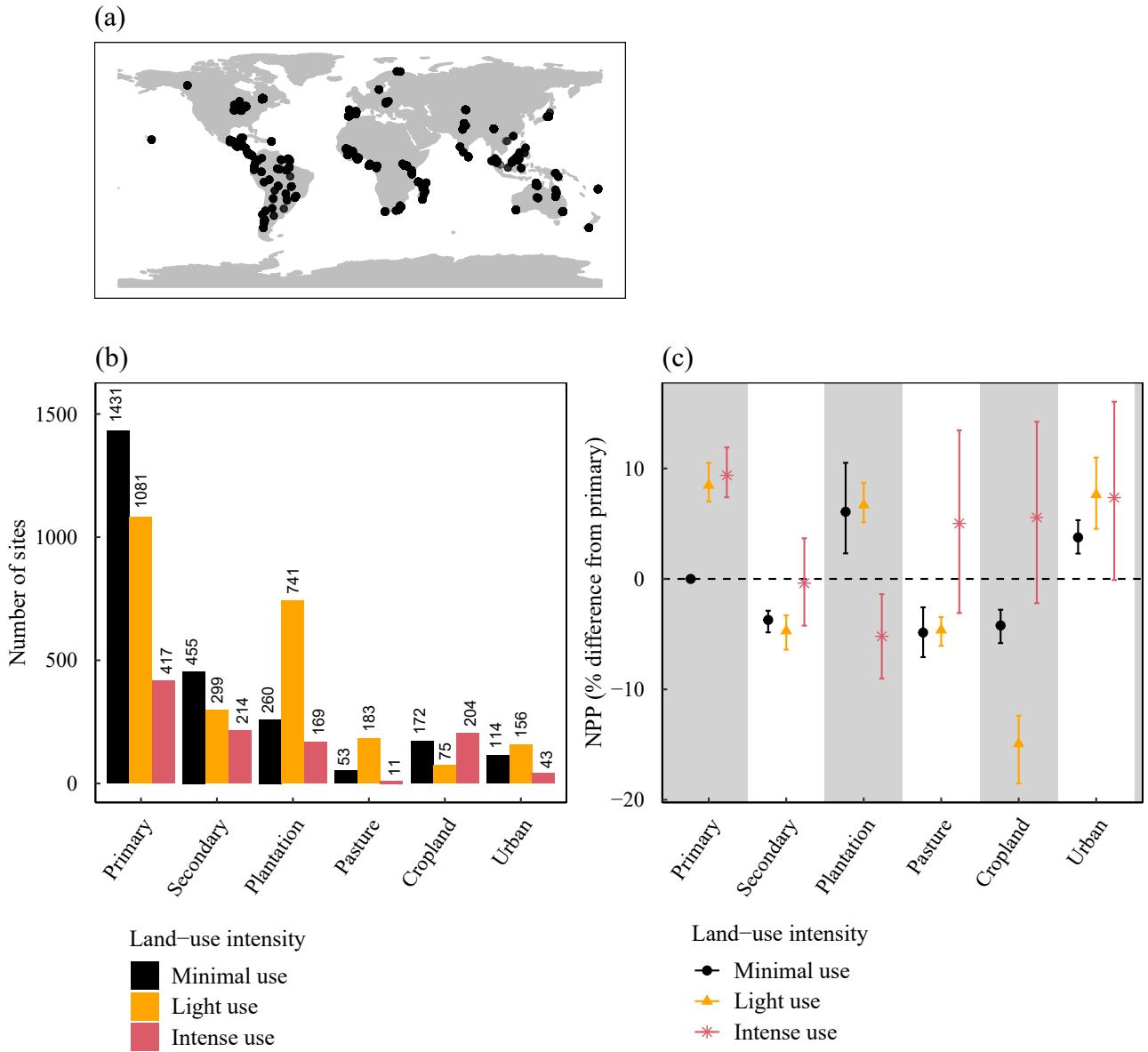
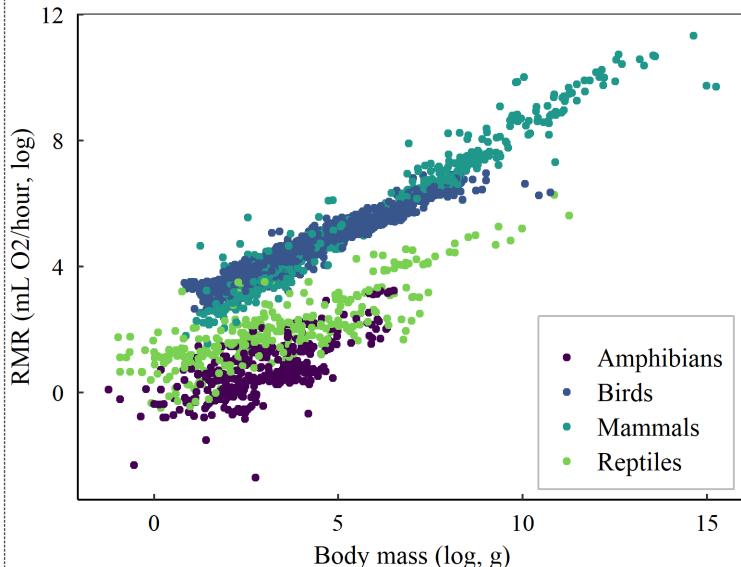


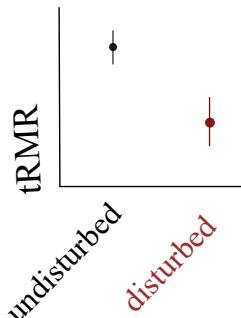
Figure 5.1: (a) Spatial distribution of the sampled sites from the PREDICTS database for terrestrial vertebrates (6,484 sites); (b) Number of sites in each land-use and land-use-intensity category; (c) Net primary productivity by land use and land-use intensity (derived from MODIS satellite imagery), 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.

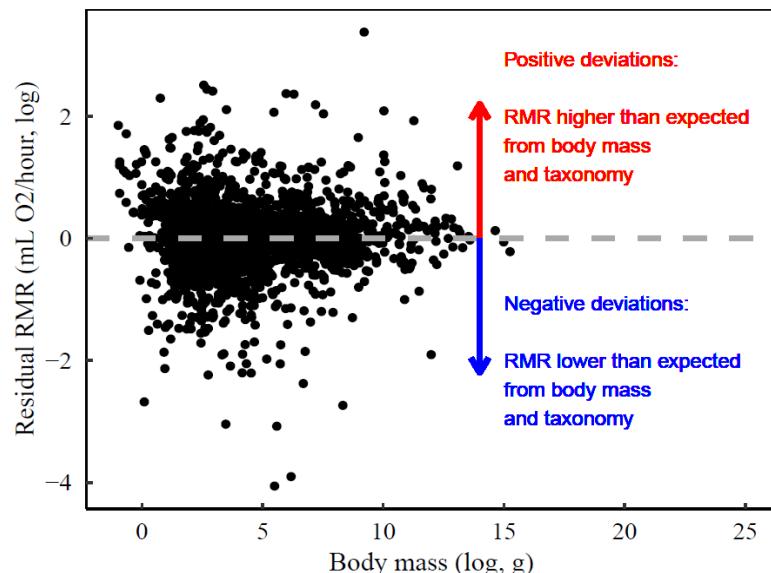
Assemblage level:
 $tRMR = \sum_i (RMR_i * a_i)$



Across assemblages - model 1:
 $\log(tRMR) \sim LU + LUI + TG + LU:LUI + LU:TG + LUI:TG + LU:LUI:TG + RE$

(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
 $\log(RMR) \sim \log(BM) + (1|Class/Order/Family)$



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:

$$\begin{aligned} P_{\text{occurrence}} \sim & LU + LUI + \text{resRMR} + TG + \\ & LU:LUI + LU:TG + LU:\text{resRMR} + \\ & LUI:TG + LUI:\text{resRMR} + TG:\text{resRMR} + \\ & LU:TG:\text{resRMR} + LUI:TG:\text{resRMR} + RE \end{aligned}$$

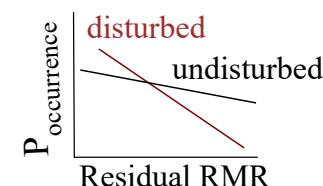


Figure 5.2: Framework for the predictions and models. I use resting metabolic rates (RMR) as a proxy for the amount of energy processed by vertebrate species. **(a)** I hypothesize that there is less energy overall that can be utilized by vertebrate species in disturbed land uses compared to undisturbed land uses. As such, I expect decreases in assemblage-level total metabolic rates ($tRMR$). $tRMR$ 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.

5.2 Methods

5.2.1 Vertebrate assemblage composition

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

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

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

The predictions of this Chapter rely on the assumption that resource types and abundance are modified in disturbed environments, with less energy available in disturbed compared to undisturbed land uses overall. To test this assumption, I used terrestrial net primary productivity (NPP) across land uses as a proxy for available energy. NPP quantifies the amount of atmospheric carbon fixed by plants and accumulated as biomass. NPP estimates were derived by Meghan Hayden, using imagery from the Moderate Resolution Imaging Spectroradiometer (MODIS) on board NASA's Terra satellite. NPP estimates were based on a yearly composite of measures made at 8-day intervals, captured at 500-m spatial resolution (Running and Zhao, 2015). Meghan Hayden obtained NPP for 4,062 of the PREDICTS sites used in the analysis (matching the sites to the NPP data using the sampling year available in PREDICTS). I fit a linear mixed-effects model ('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 (mLO_2/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).

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

5.2.4 Trophic group and body mass information

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

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

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

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

Model validation.

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

Disentangling the effects of body mass and abundance on tRMR.

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

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

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

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

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

Model validation.

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

5.3 Results

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

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

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

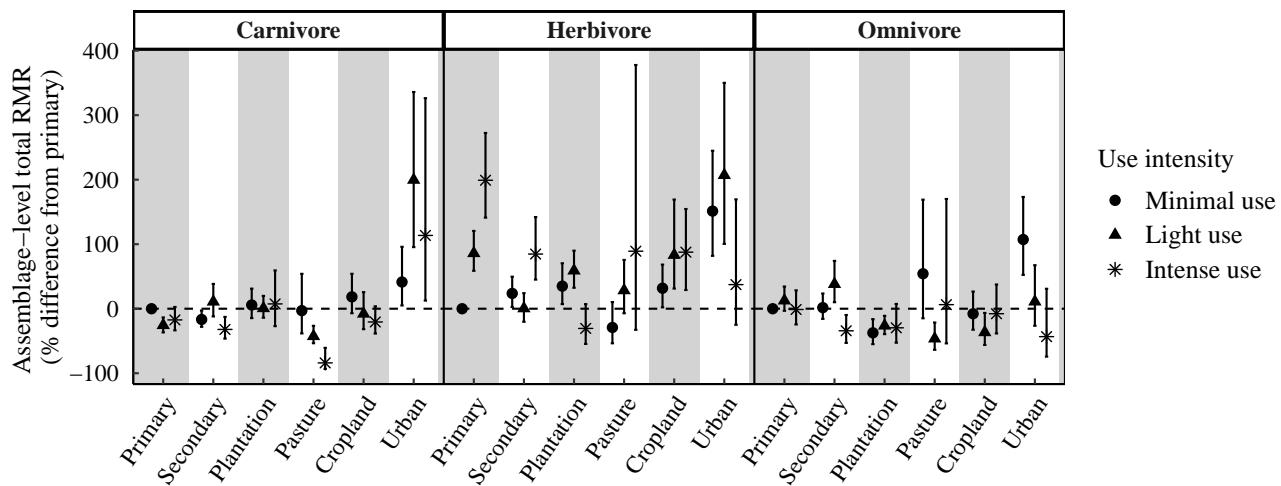
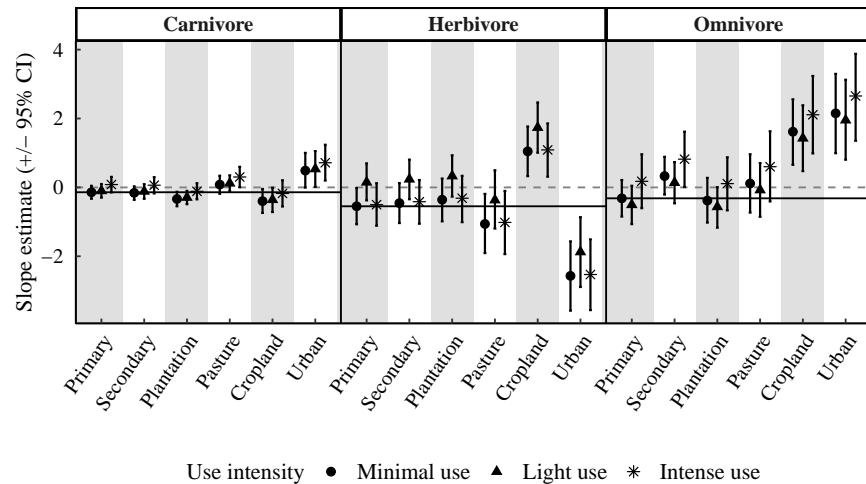


Figure 5.3: Effects of land use, land-use intensity and trophic group on assemblage-level total RMR (mean estimate $\pm 95\%$ confidence interval). Model predictions are rescaled with reference to minimally-used primary vegetation, considered to be the undisturbed baseline. Primary: primary vegetation;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

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

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

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



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

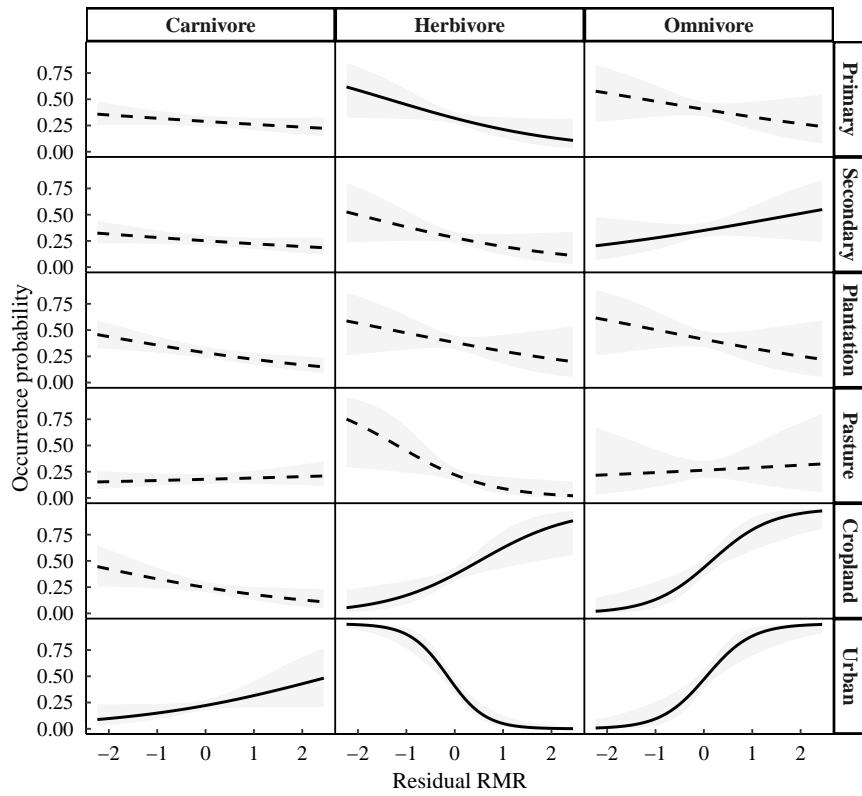


Figure 5.4: (a) Slope estimates for the relationship between residual RMR and occurrence probability in each land-use type and for the three levels of land-use intensity (mean estimate $\pm 95\%$ confidence interval). The black horizontal line indicates the slope for the reference level (primary vegetation) 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.

For minimally-used primary vegetation (reference), the model predicted negative effects of residual RMR on species occurrence probability in all trophic groups (but with a significant slope for herbivores only; Figure 5.4a). However, the directionality of this relationship was reversed in some disturbed land uses in all trophic groups (secondary vegetation, cropland and urban for omnivores; cropland for herbivores; urban for carnivores), with significant positive slopes, also significantly higher than those observed for primary vegetation (Figure 5.4a). The only exception was the opposite pattern for urban herbivores (Figure 5.4b), where residual RMR had a more negative effect on occurrence probability than in minimally-used primary vegetation.

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

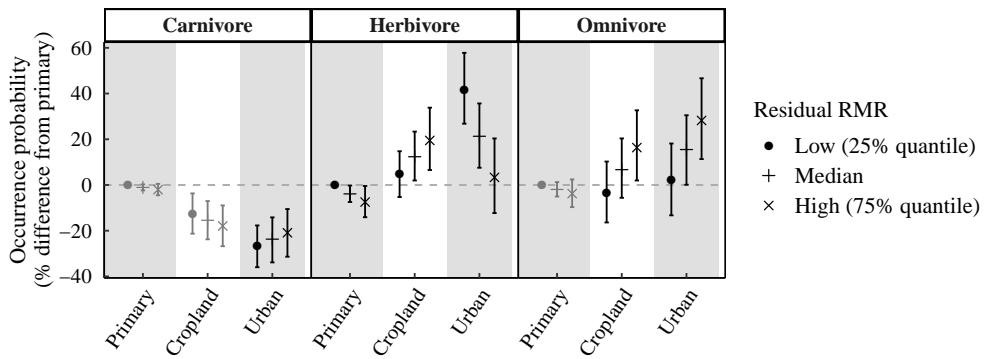


Figure 5.5: Predicted occurrence probabilities (mean effect $\pm 95\%$ confidence interval) in primary vegetation (primary) and for the most disturbed land uses where residual RMR was found to have a significant effect on occurrence probability. For visualisation purposes, I discretised residual RMR 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).

Finally, the model showed some degree of deviation from distributional assumptions (diagnostic plots, Appendix 4, Figure S5.6). Nevertheless, the model's coefficients were similar when estimated with a Bayesian framework, suggesting that the estimates were robust (Figure S5.7). The phylogenetic signal in the model residuals was weak and non-significant ($\lambda=0.004$, $P=0.24$). Re-fitting the model using the complete data subset (i.e., excluding imputed RMR estimates) showed that the conclusions are likely robust to

imputation uncertainty (Figure S5.8), with congruent results overall, although there were a few differences in the predictions between the two models – notably, for herbivores in urban land uses (Figure S5.8).

5.4 Discussion

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

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

been shown to affect food-web dynamics, with decreases in predation rates, loss of anti-predator abilities (Geffroy et al., 2020) and mesopredator release (Fischer et al., 2012). Thus, in urban areas, increases in anthropogenic food sources could provide support for a higher abundance of medium-sized species released from predation, increasing total energetic requirements.

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

At the species level, the results underline the role of energetic constraints on species' responses to land-use change. After controlling for the effects of body mass and taxonomy, I found that residual energetic expenditure was a significant predictor of species occurrence probability in disturbed land uses. Contrary to my expectations, in several disturbed land uses and in all trophic groups, species with higher residual energetic expenditure tended to have a higher occurrence probability than species with lower residual energetic expenditure. It could be that species with lower residual energetic requirements are less well equipped than species with higher residual energetic requirements at making use of the available food sources in disturbed land uses. Species in disturbed land uses may need to display higher levels of feeding innovation (Coogan et al., 2018), have larger brains (Sayol et al., 2020), or be bolder and more active to make use of the available resources. In mammals, past research has shown that larger brains are associated with larger residual energetic expenditure (Isler and Van Schaik, 2006). At the individual level, past research suggests that metabolic rates are linked to differences in behaviour, with bolder and more active individuals exhibiting higher metabolic rates than less active individuals, with consequences for food acquisition (Biro and Stamps, 2010). Although I am not aware of similar evidence at the species level, I propose that residual metabolic rates interact with species' ecological traits, behavioural traits and foraging strategy in influencing species' responses to land use. Among species with an adaptable diet, able to make use of the resources available in a disturbed landscape, those with higher residual metabolic rates could present a set of behavioural charac-

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

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

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

To conclude, the findings of this Chapter suggest important effects of land-use change on energetic fluxes, and thus potentially on ecosystem functioning. Further research is warranted as to the effects of these energetic patterns for ecosystem processes. Indeed, assemblage-level energy fluxes may serve as important

indicators of change for ecosystem processes, such as decomposition (Barnes et al., 2014). Understanding these impacts is particularly important given increasing land-use change and biodiversity loss across the globe.

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.

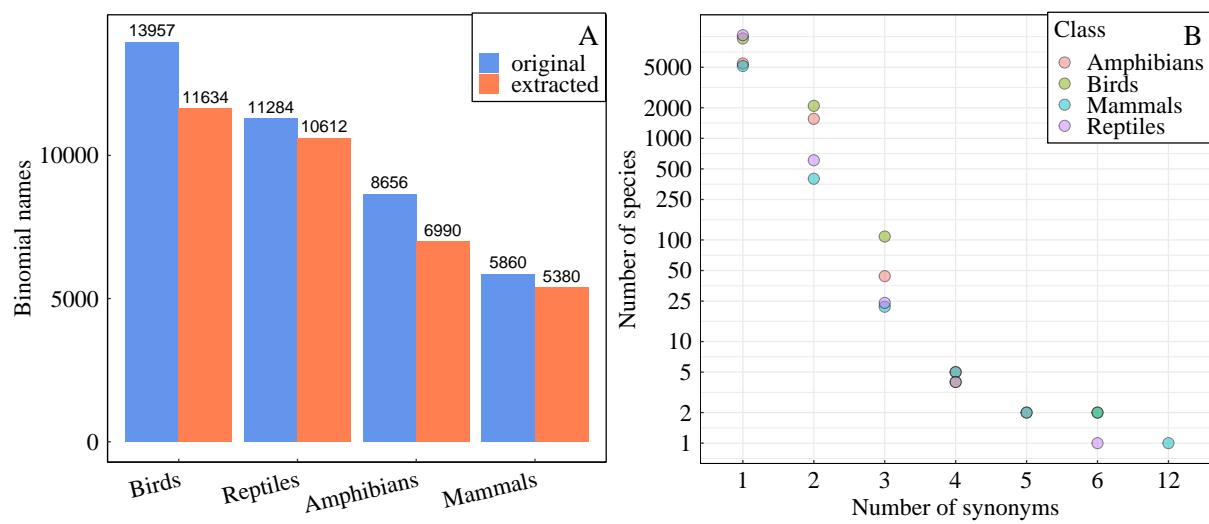


Figure S2.1: Difference in species number before and after taxonomic correction (A) and distribution of number of synonyms across datasets (B). (A) shows the number of species (binomial names) extracted from all sources (blue bars), and the number of uniquely identified accepted names (in red). Replacing 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

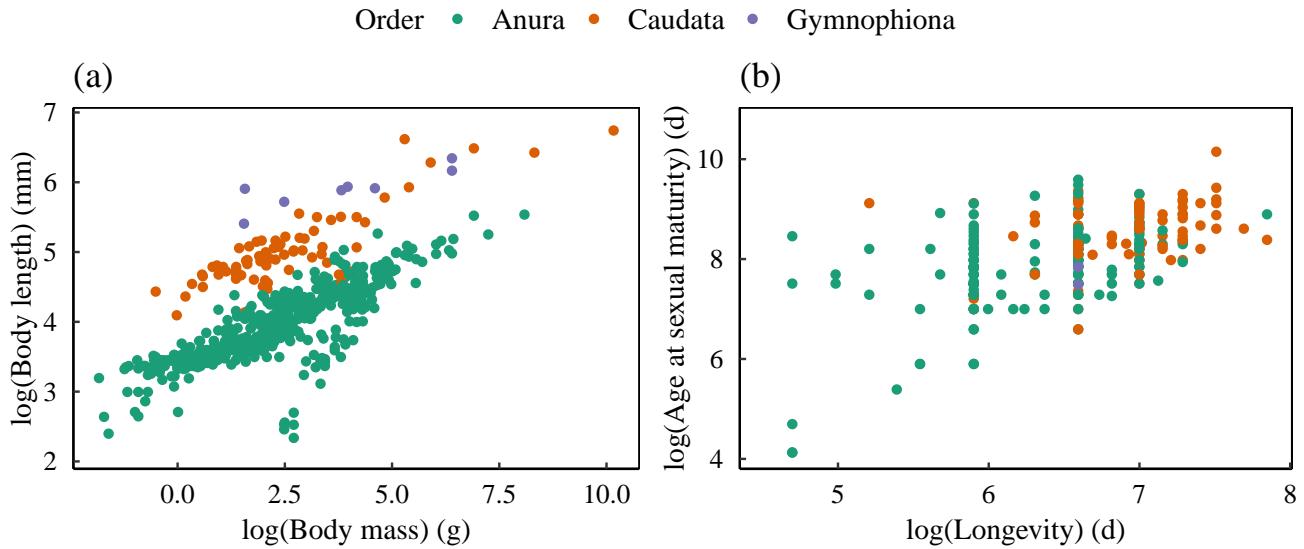


Figure S2.2: (a) Body mass versus body length and (b) longevity versus age at sexual maturity in amphibians. Pearson's correlation coefficient was 0.71 in (a) and 0.55 in (b) (taxonomic order was considered in these coefficients).

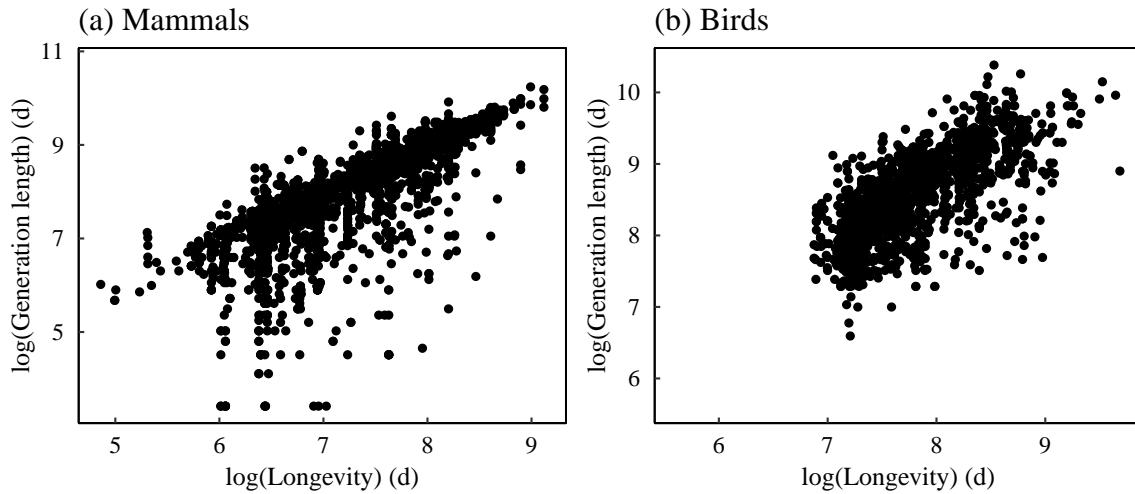


Figure S2.3: Generation length versus longevity data in (a) mammals and (b) birds. Pearson's correlation coefficient was 0.74 in (a) and 0.70 in (b).

S2.3 Cutting distribution maps by altitudinal limits

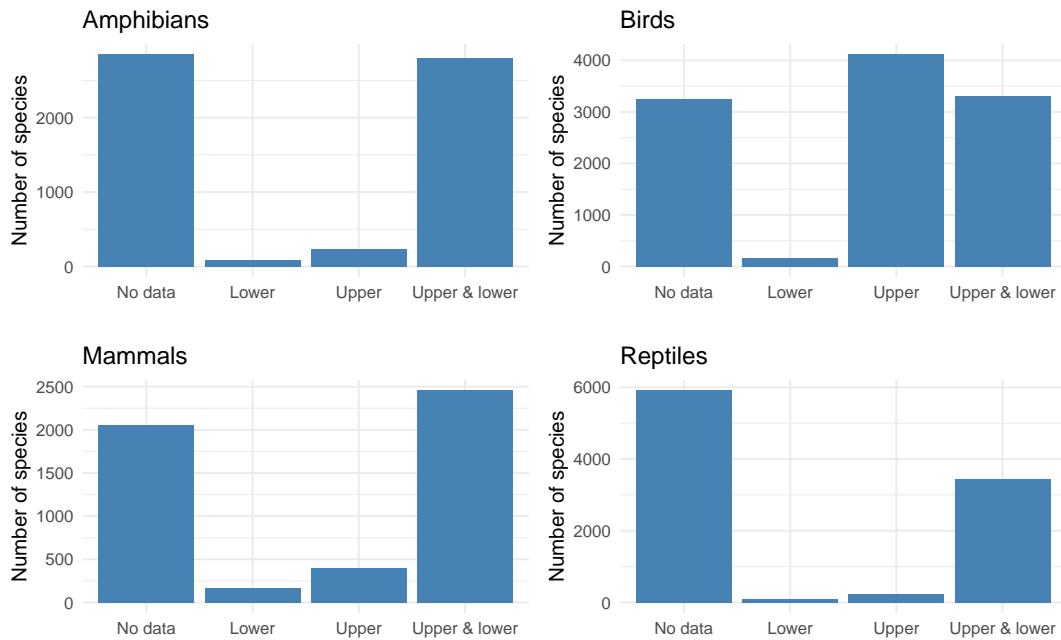


Figure S2.4: Availability of altitudinal limits across species. Upper and lower altitudinal limits were extracted from the IUCN Red List (IUCN, 2020).

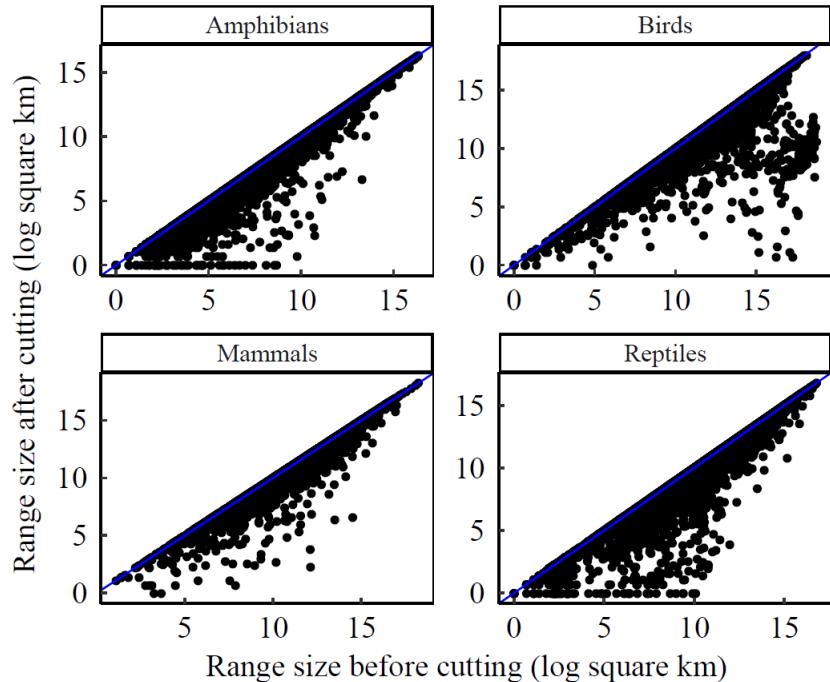


Figure S2.5: Range sizes before versus after cutting the range maps by altitudinal limits.

S2.4 Impact of taxonomic corrections on trait coverage

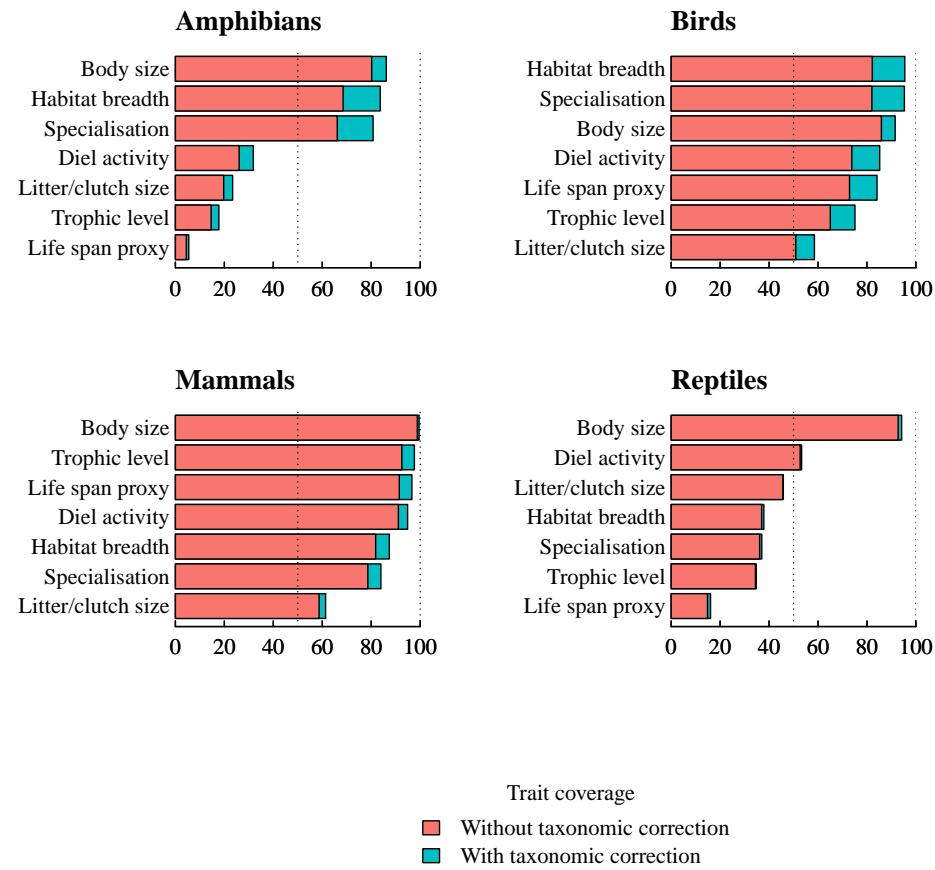
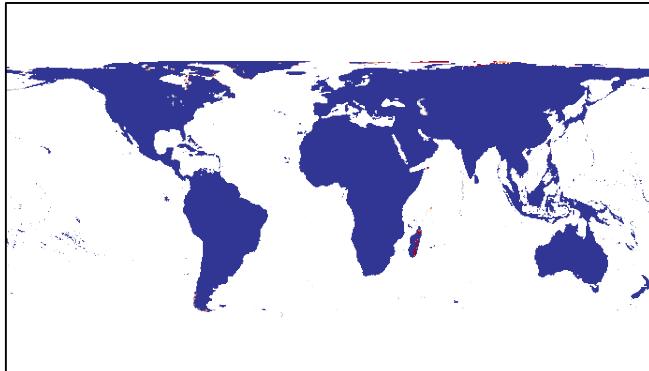


Figure S2.6: Trait coverage when no taxonomic correction is applied before matching sources by binomial names, versus when I applied the described procedure. The identification of synonymous names resulted in an increase in trait coverage in most cases.

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

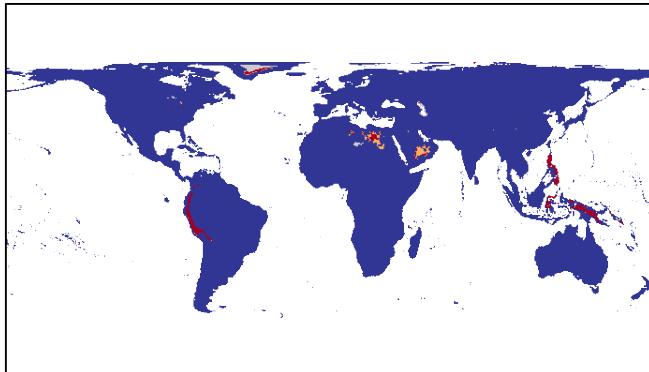
(a) Mammals



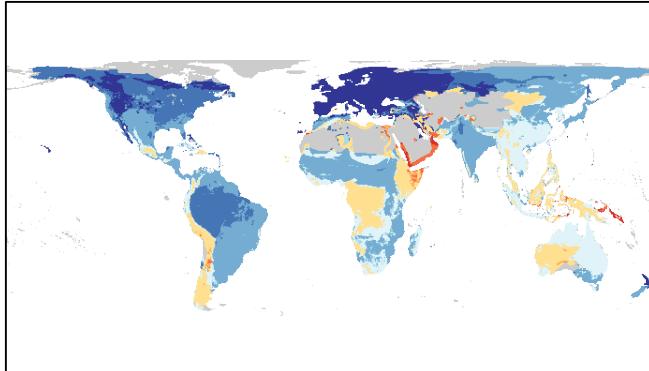
Median completeness
(birds and mammals):

- 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

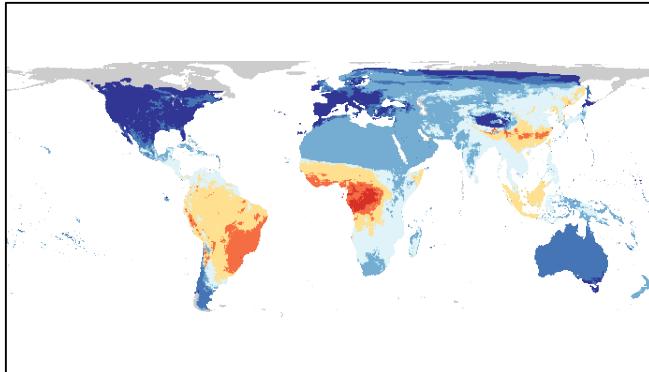
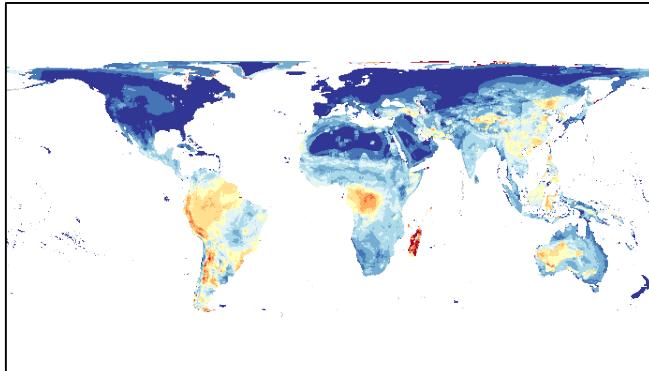


Figure S2.7: Spatial distribution of assemblage-level median trait completeness in each class. Note that the color breaks differ for mammals and birds and for herptiles.

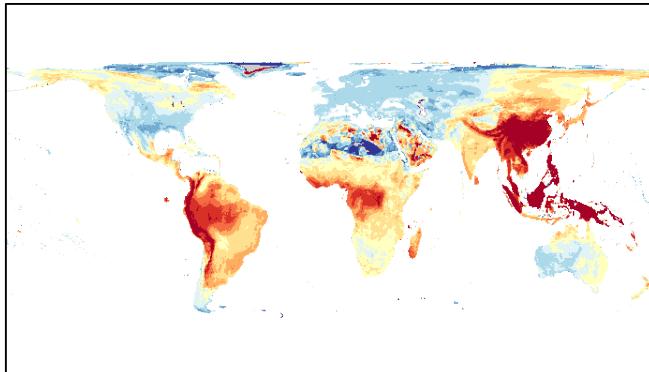
(a) Mammals



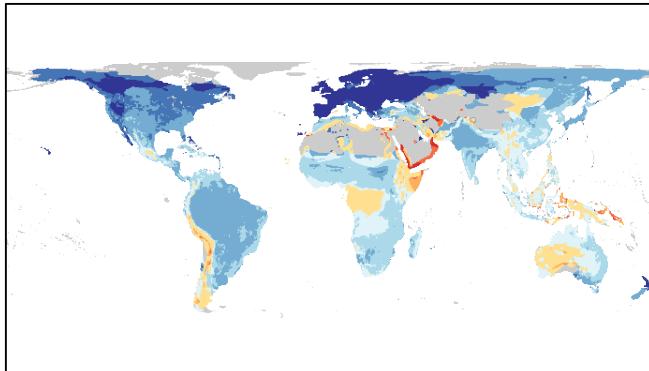
Mean completeness
(birds and mammals):

- 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

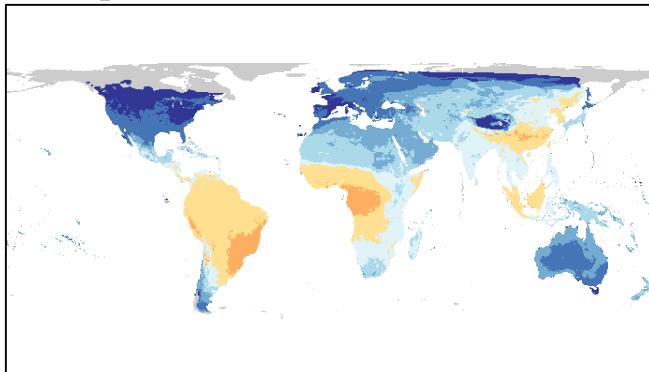
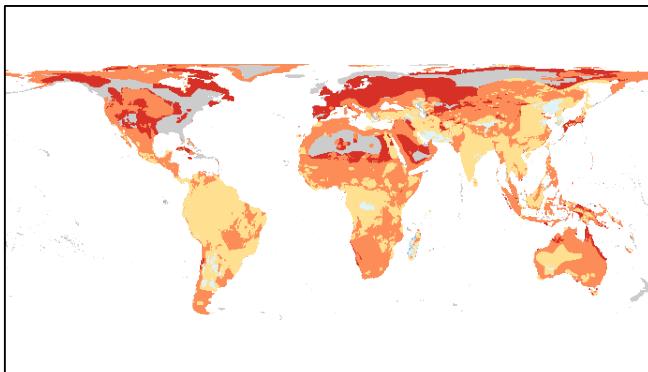


Figure S2.8: Spatial distribution of assemblage-level mean trait completeness in each class. Note that the color breaks differ for mammals and birds and for herptiles.

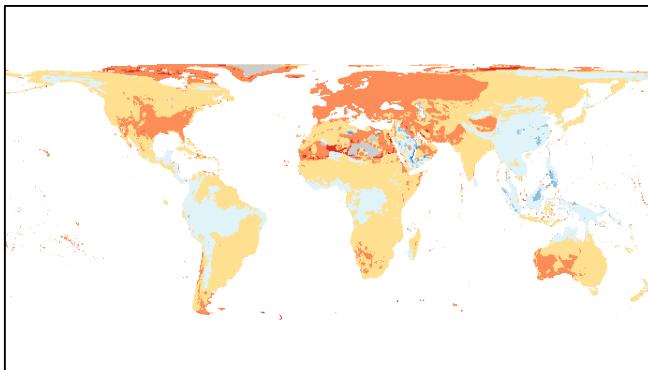
(a) Mammals



Standard deviation
of completeness
(birds and mammals):

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

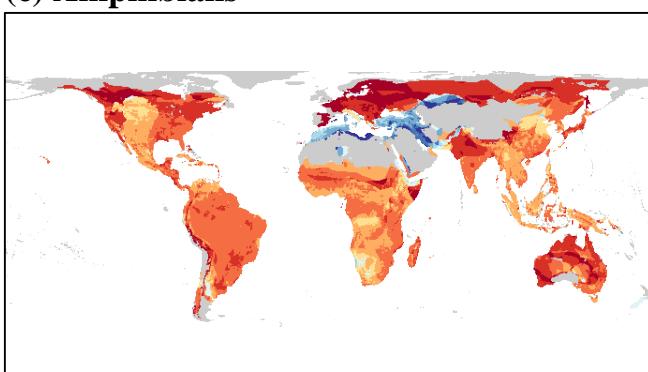
(b) Birds



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

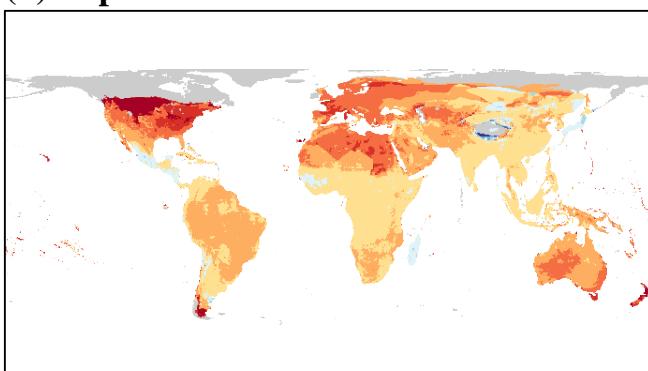


Figure S2.9: Spatial distribution of assemblage-level standard deviation of trait completeness in each class. Note that the color breaks differ for mammals and birds and for herptiles.

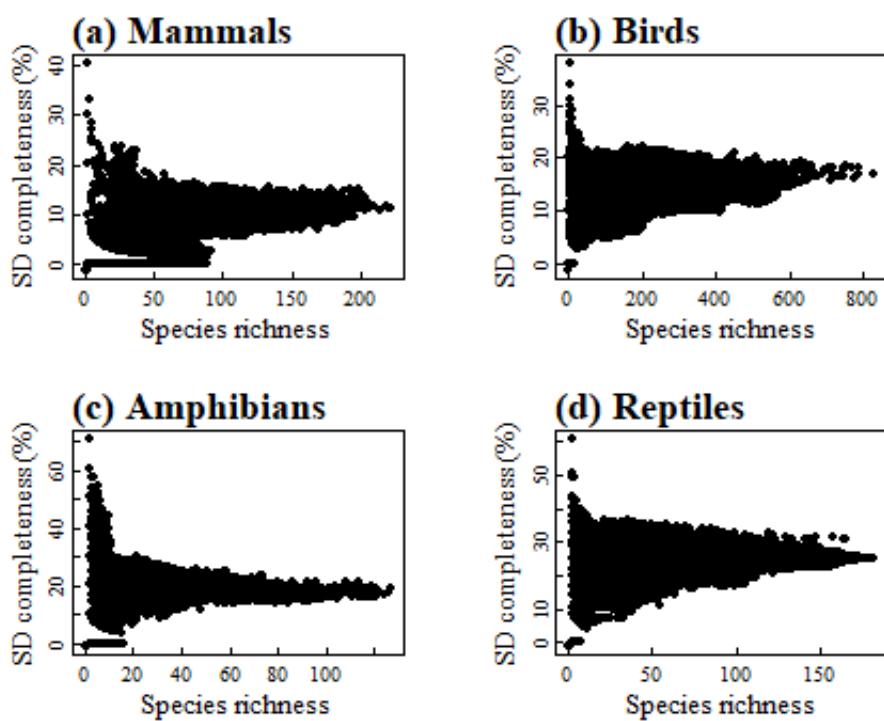


Figure S2.10: Assemblage-level species richness against standard deviation in trait completeness in each class.

S2.6 Phylogenetic patterns in trait completeness

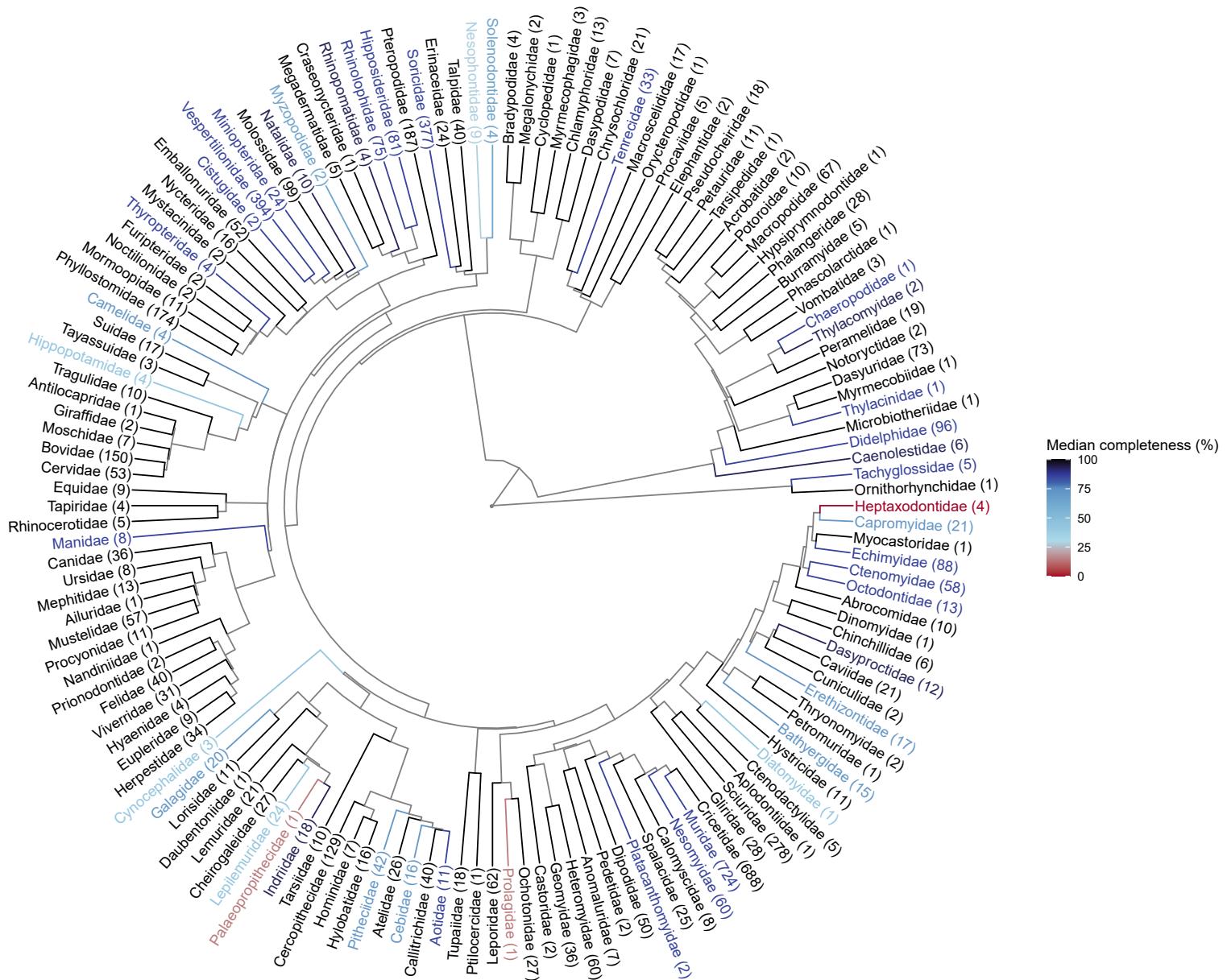


Figure S2.11: Within-family median trait completeness in mammals.

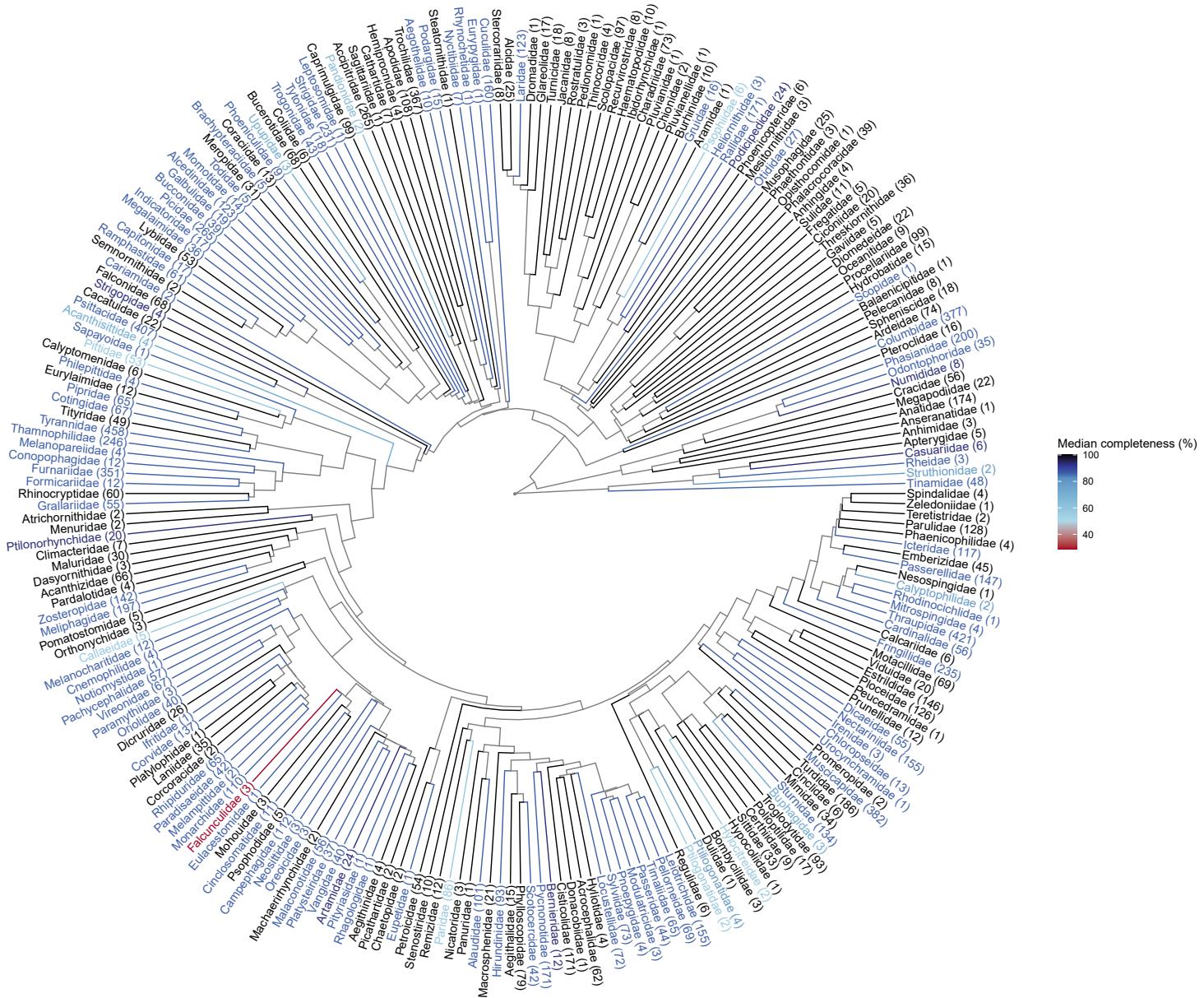


Figure S2.12: Within-family median trait completeness in birds.

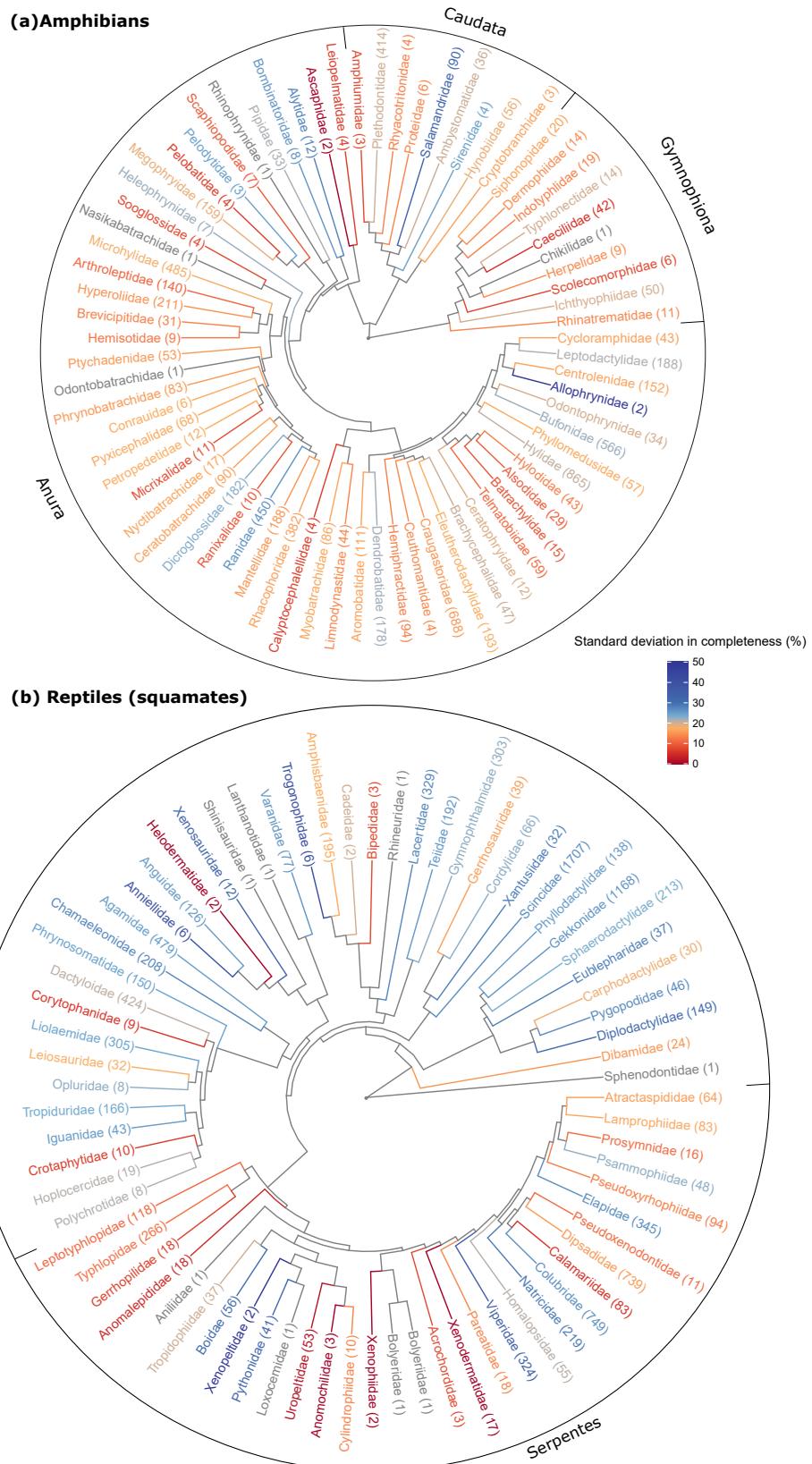


Figure S2.13: Within-family standard deviation in trait completeness (herptiles).

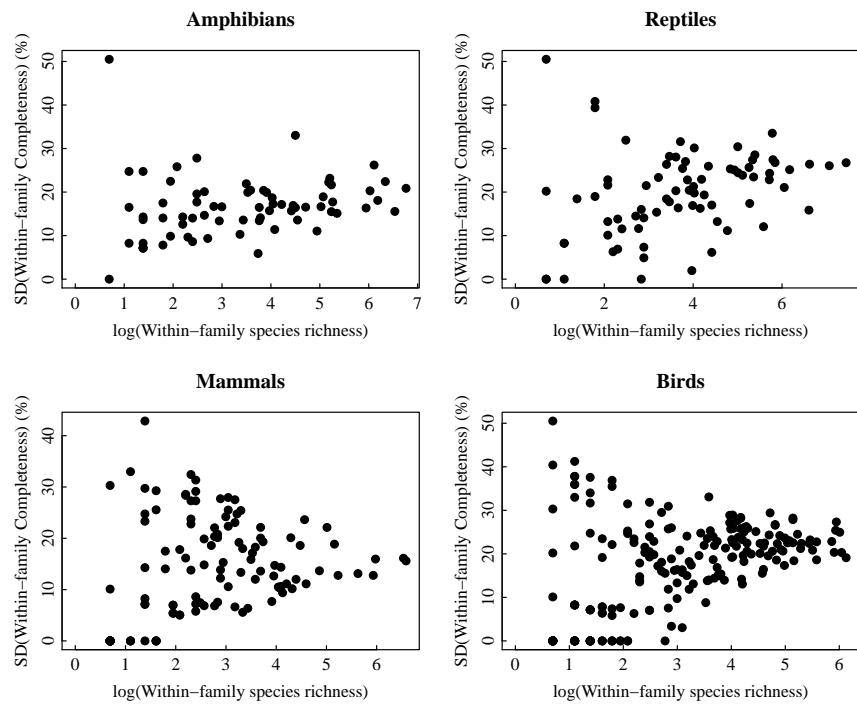


Figure S2.14: Within-family species richness against the within-family standard deviation of trait completeness.

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

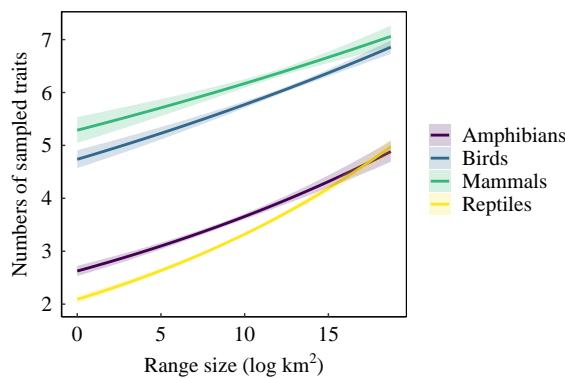


Figure S2.15: Relationship between number of sampled traits and geographical range size using distribution maps not cut by altitudinal limits. The model was fitted using a Poisson error distribution. Class was added as a predictor interacting with range size. Rates of increase were not significantly 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.

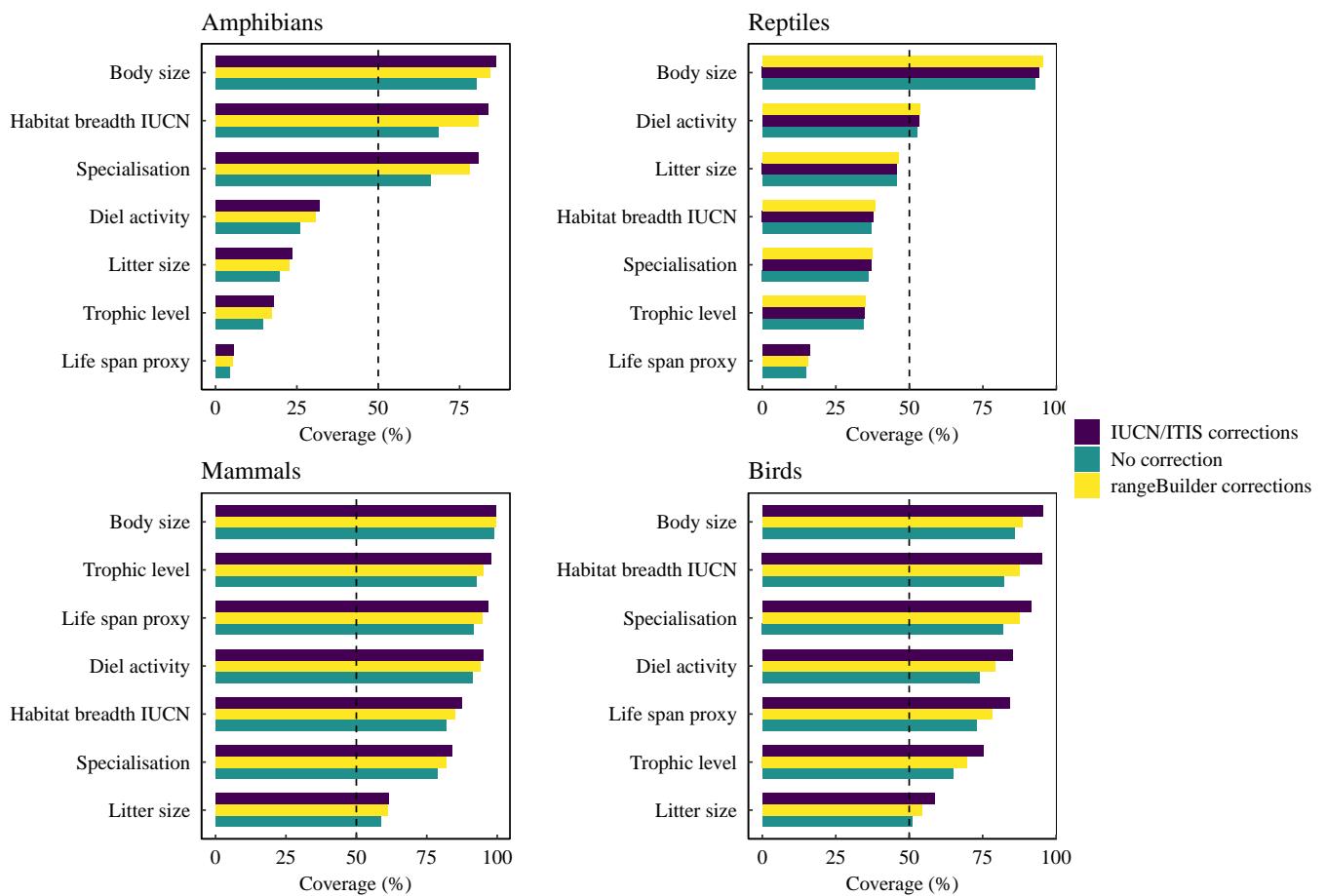


Figure S2.16: Comparison of trait coverage among datasets corrected for taxonomy in different ways: using the described procedure (purple bars); using datasets corrected for taxonomy with the ‘rangeBuilder’ package (yellow bars; Rabosky et al. (2016)); and using datasets uncorrected for taxonomy (green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

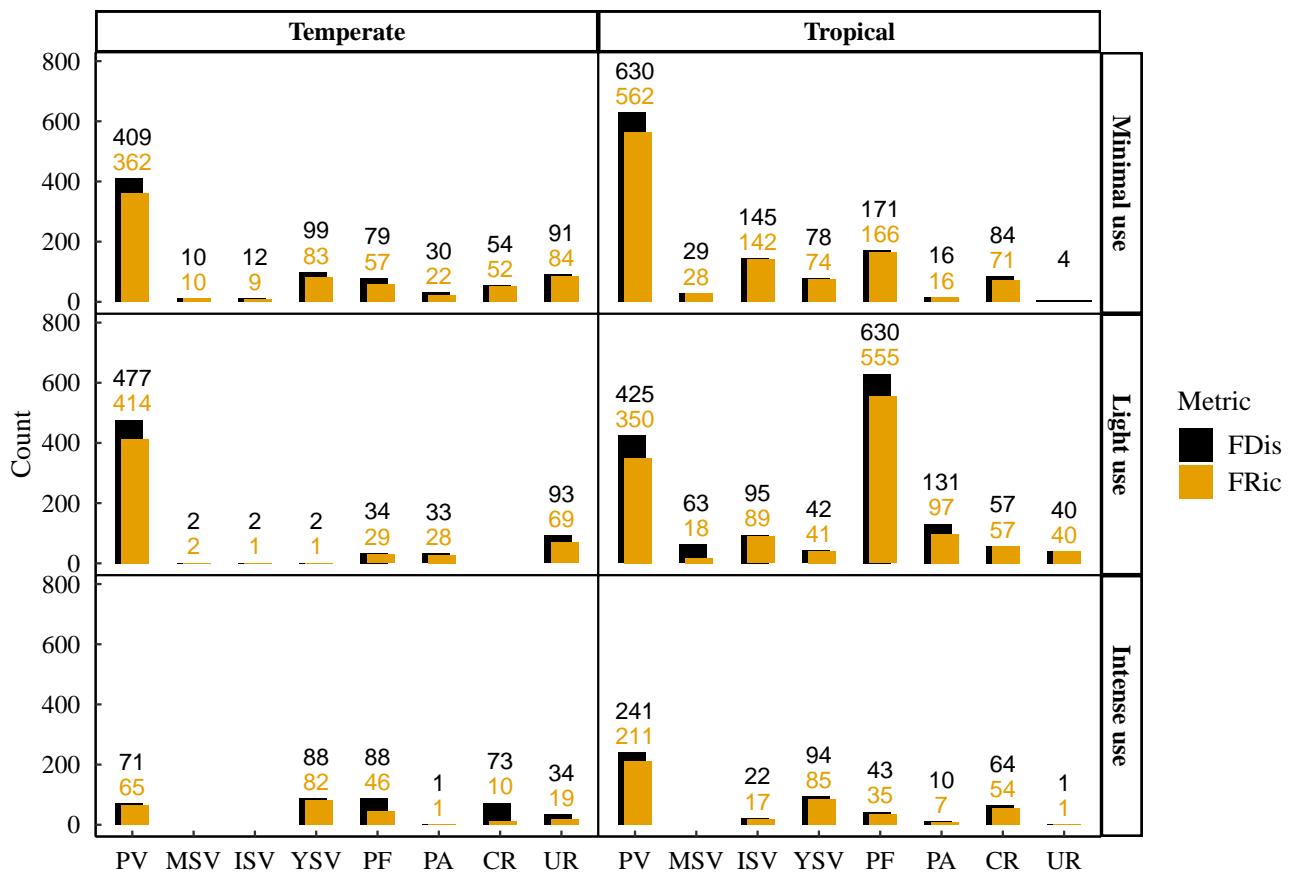


Figure S3.1: Number of sites in each land use and land-use intensity for which FRic and FDis were calculated, across all species. The number of sites for FRic can be smaller than the number of sites for FDis because FRic could not necessarily be computed for all assemblages in which FDis was estimated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

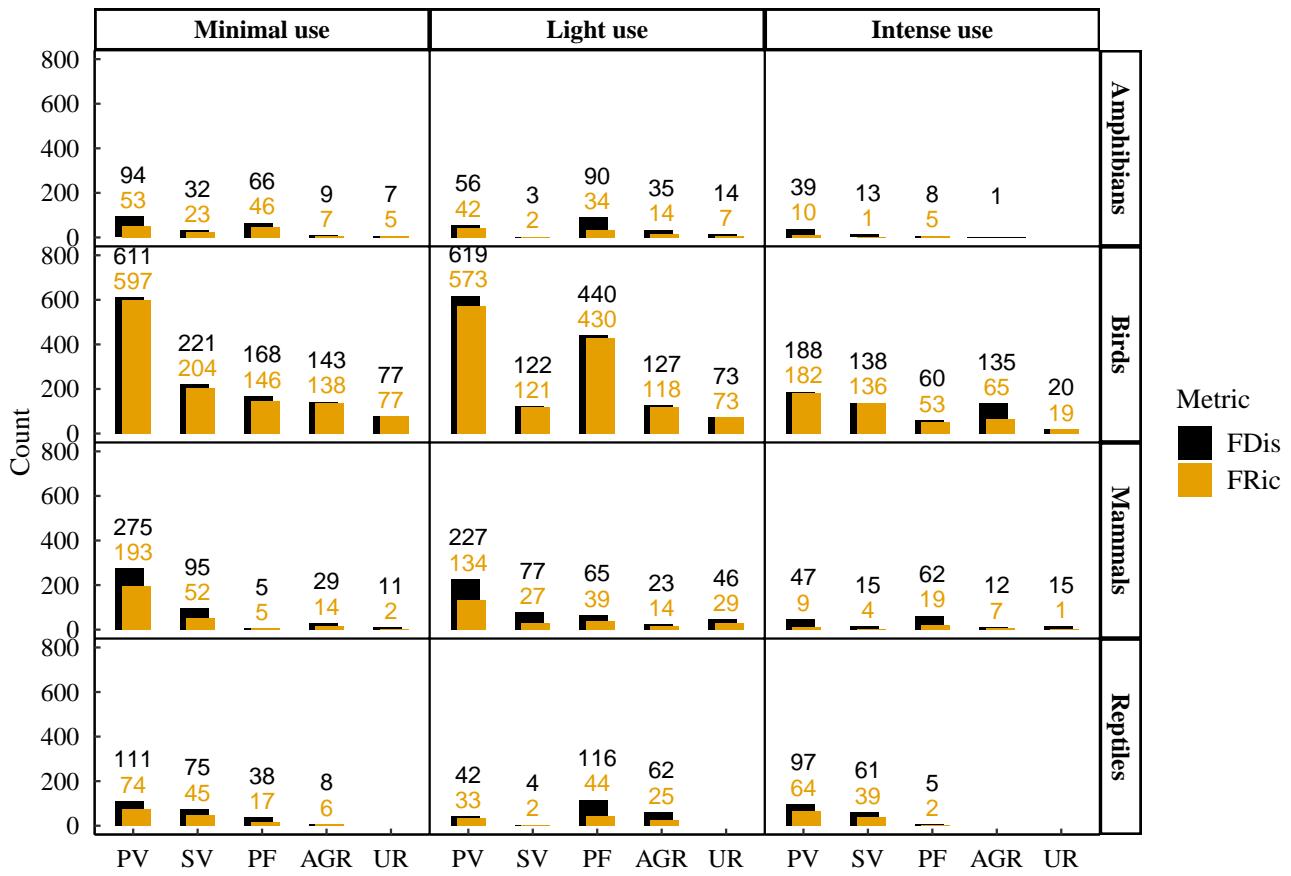


Figure S3.2: Number of sites in each land use, land-use intensity and for which FRic and FDis were calculated, within each class. The number of sites for FRic can be smaller than the number of sites for FDis because FRic could not necessarily be computed for all assemblages in which FDis was estimated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

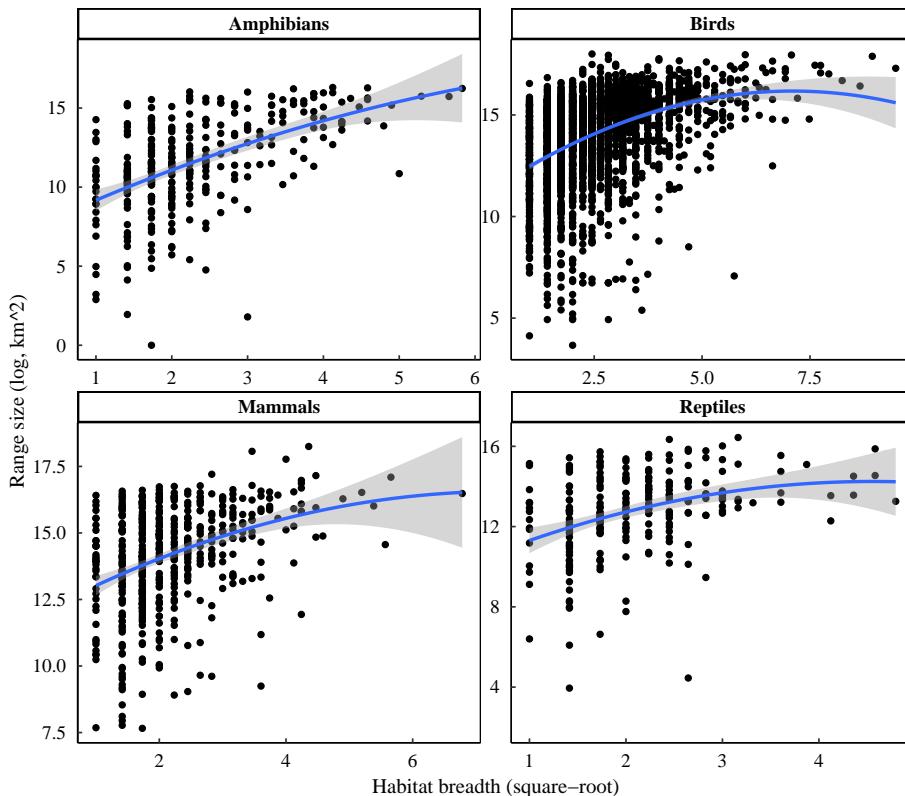


Figure S3.3: Relationship between habitat breadth and geographical range size across species in each class. The derivation of geographical range sizes is described in Chapter 2. The blue lines are the lines of best fit for the regression of geographical range size against habitat breadth in each class, 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.

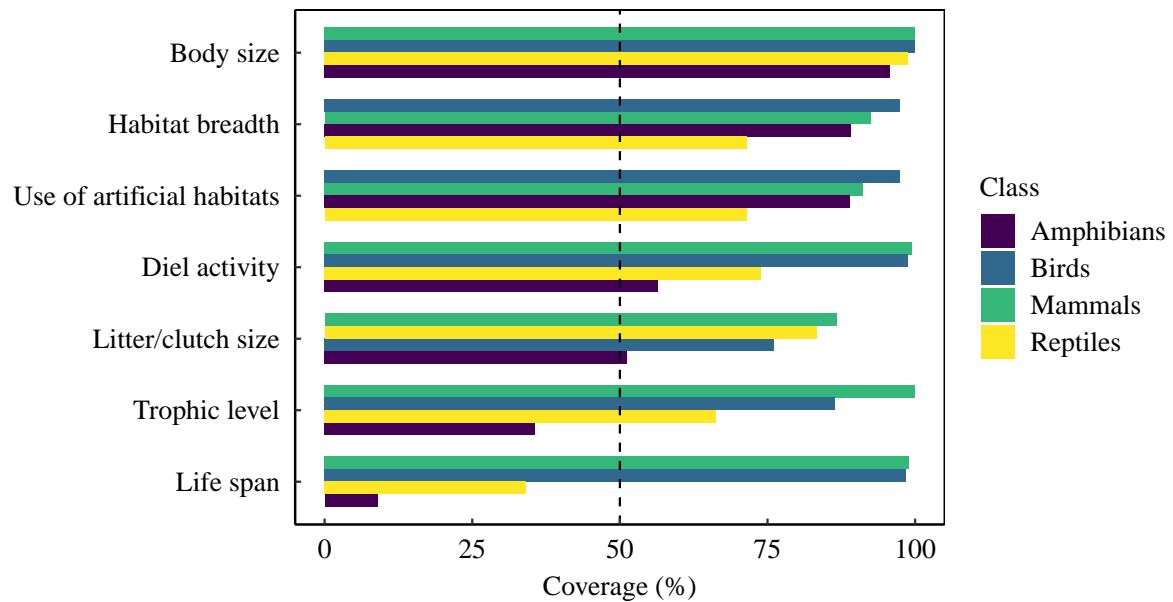


Figure S3.4: Trait coverage for the vertebrate species sampled in the PREDICTS database. For a given trait, coverage is calculated as the percentage of species for which an estimate was available.

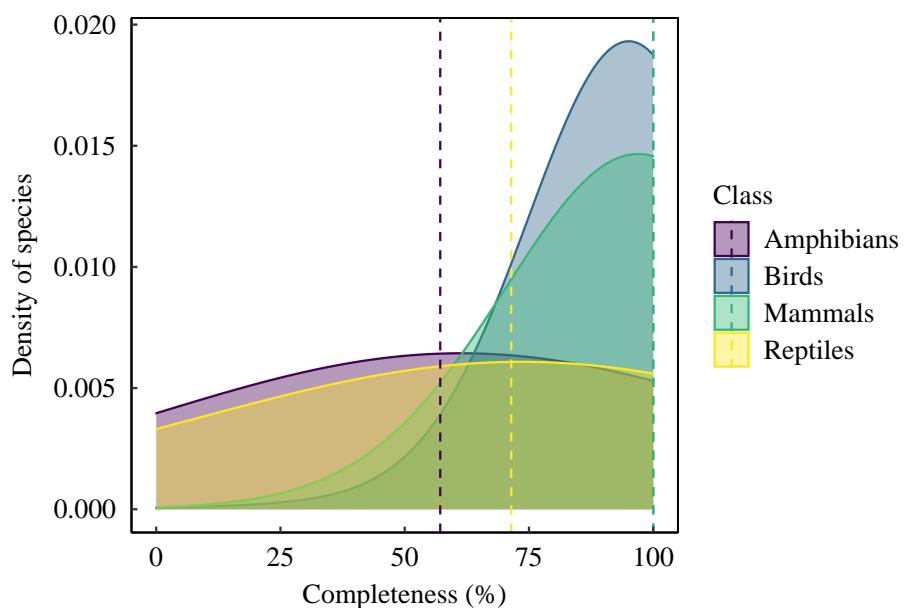


Figure S3.5: Distribution of trait completeness across the vertebrate species sampled in the PREDICTS database. For a given species, trait completeness is calculated as the proportion of traits for which an estimate was available. Dashed lines represent the median trait completeness.

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

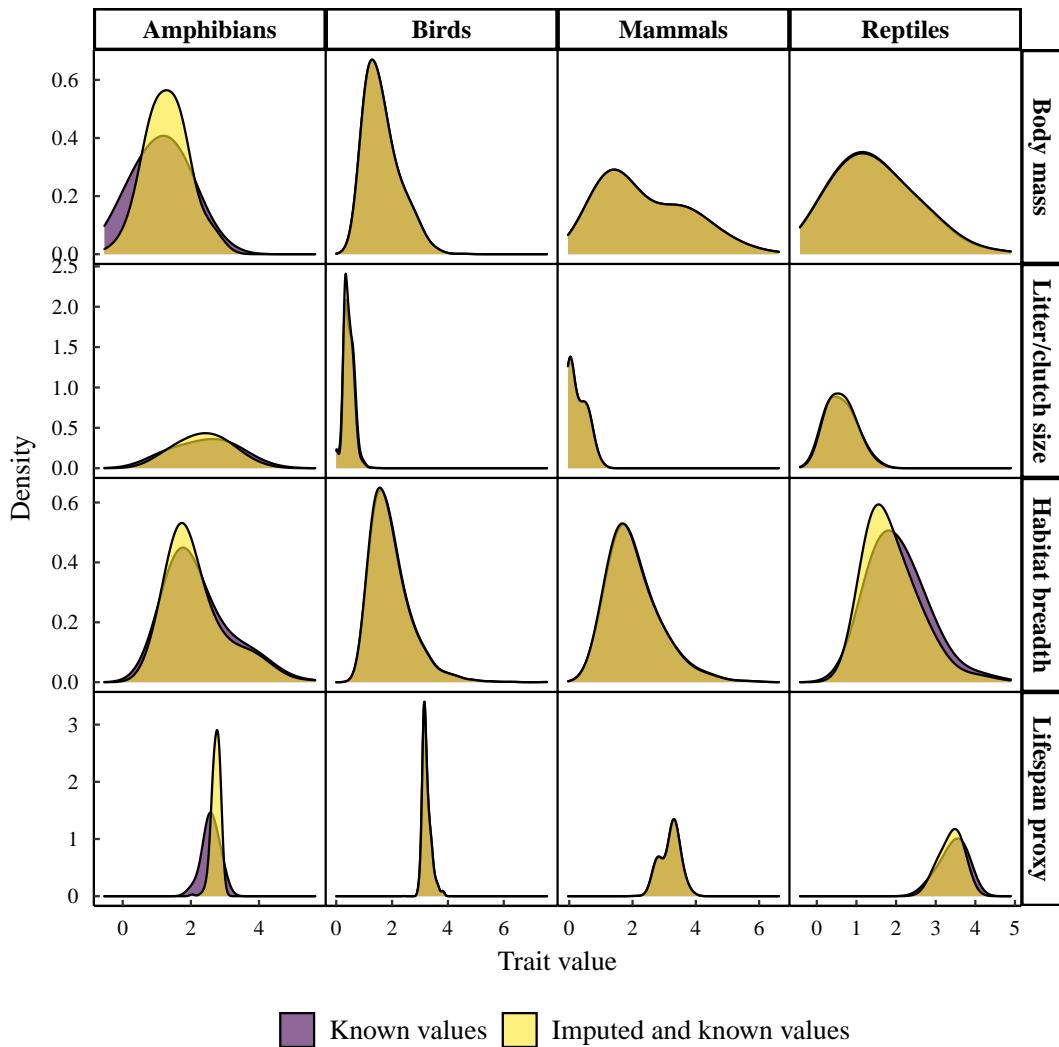


Figure S3.6: Distribution of continuous traits considered in the calculation of the functional diversity metrics (shown as density plots), before and after missing value imputations, in each class and for the species occurring in the PREDICTS database. All traits were log10-transformed, except habitat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

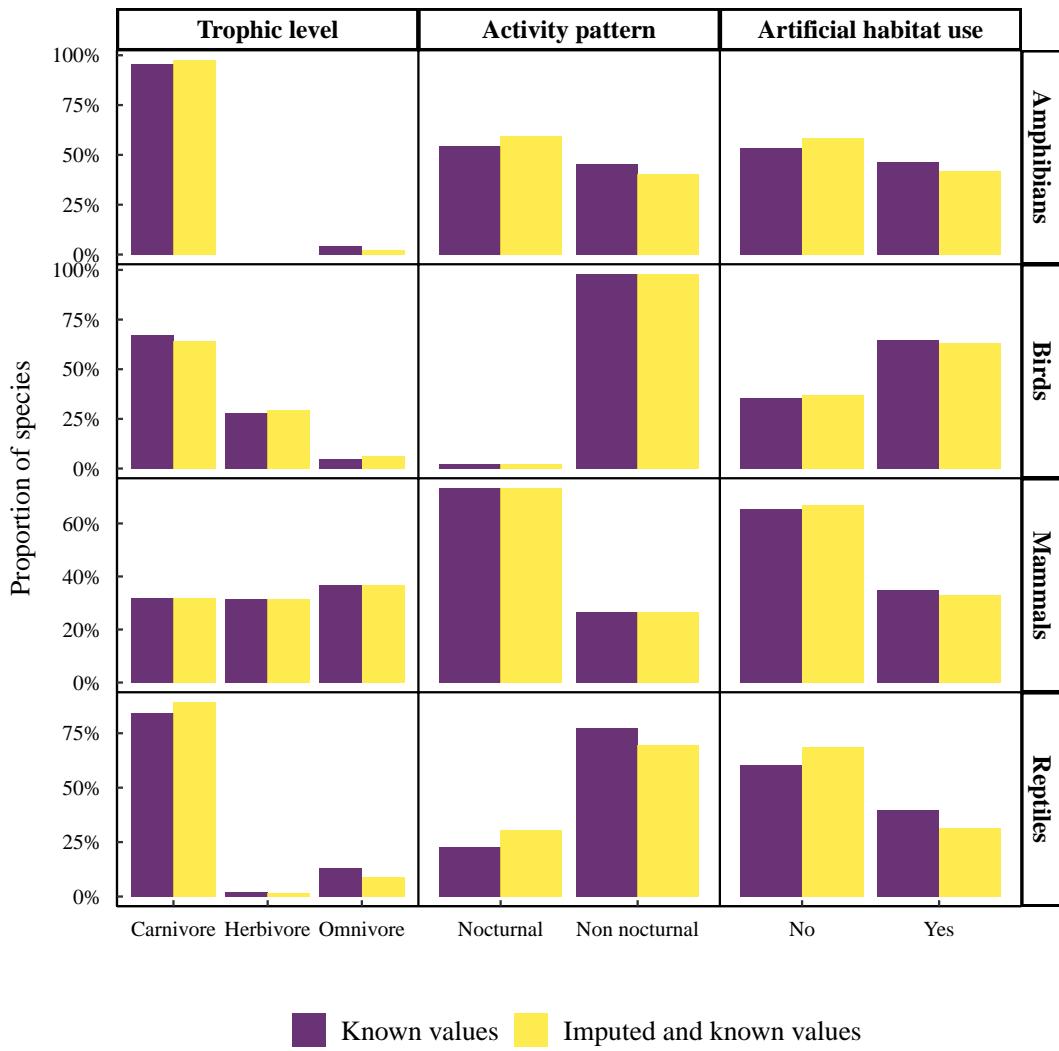


Figure S3.7: Frequency distribution for categorical traits considered in the calculation of the functional diversity metrics (shown as % of total species in each category) before and after missing value imputations, in each class, for the species occurring in the PREDICTS database.

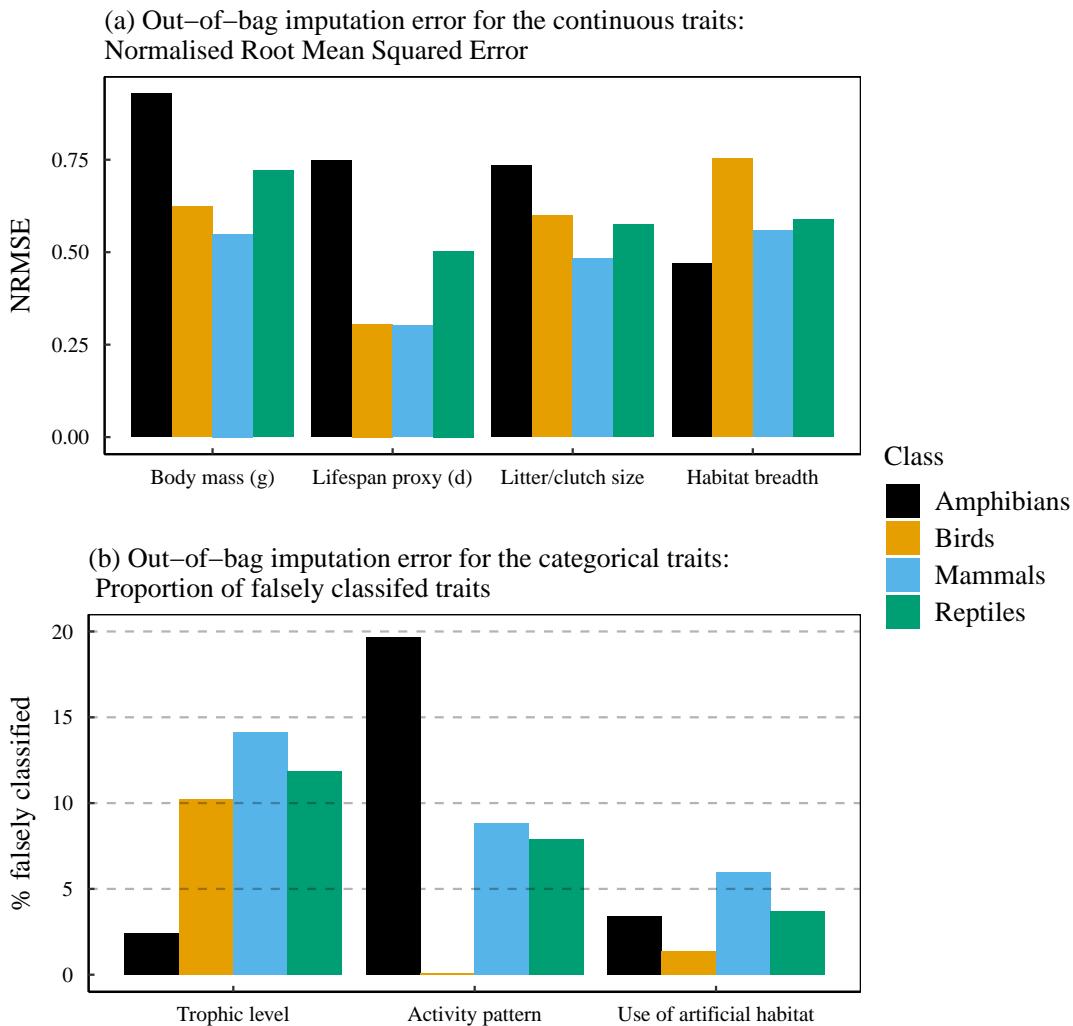


Figure S3.8: Out-of-bag imputation errors for the continuous traits (a) and categorical traits (b). For continuous traits, the Normalised Root Mean Squared Error (NRMSE) was obtained by dividing the Mean Squared Error (MSE) by the variance of the known trait distribution, then square-rooting the result. 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

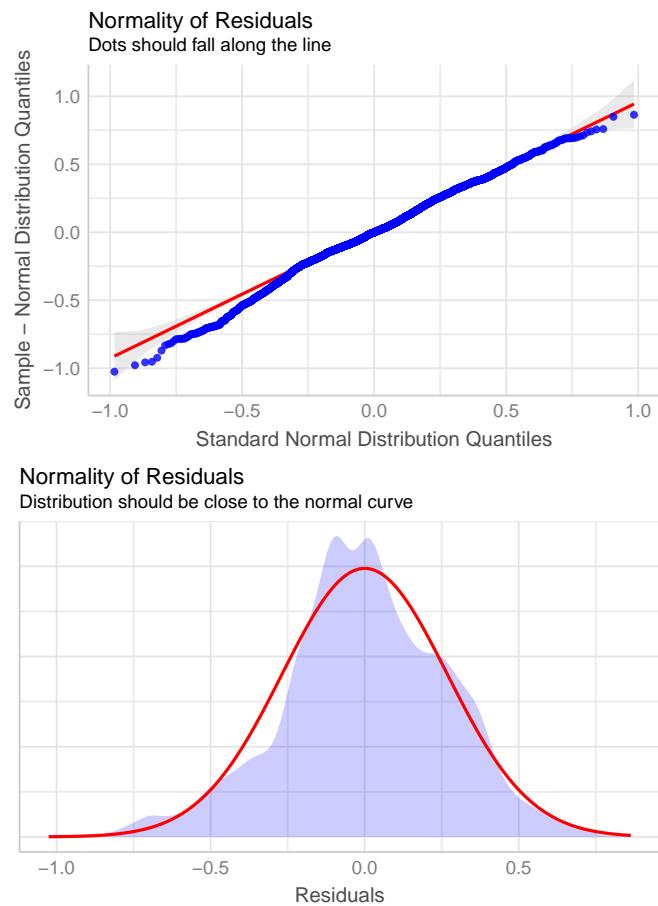


Figure S3.9: Diagnostic plots for Model 1a, obtained using the 'performance' R package (Lüdecke et al., 2021).

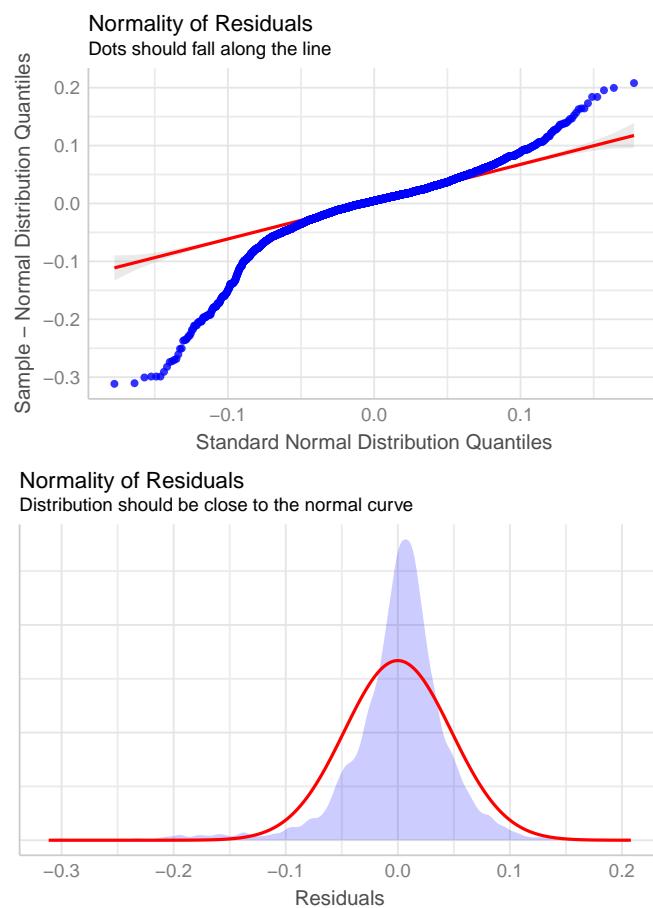


Figure S3.10: Diagnostic plots for Model 1b, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

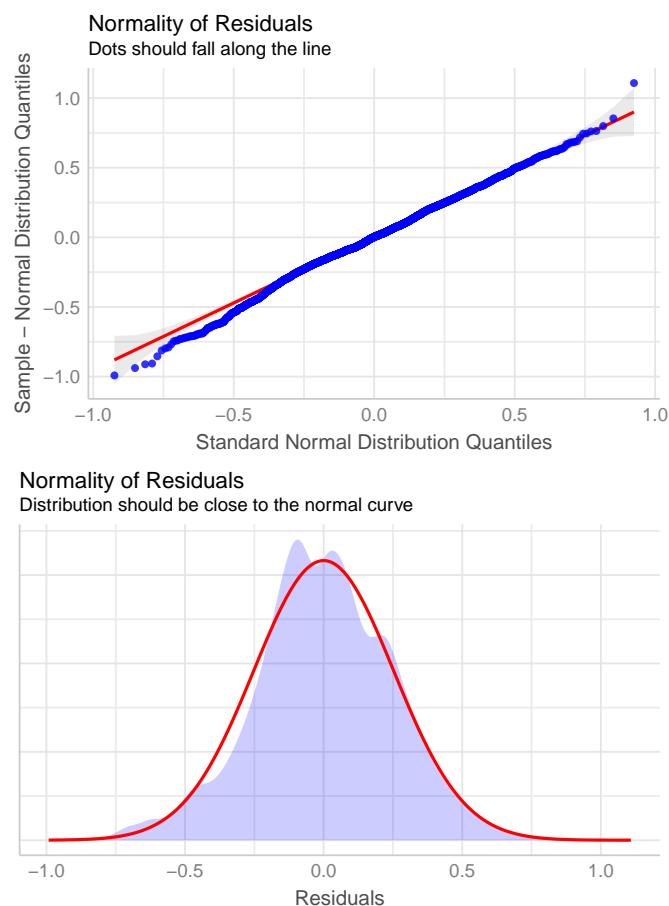


Figure S3.11: Diagnostic plots for Model 2a, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

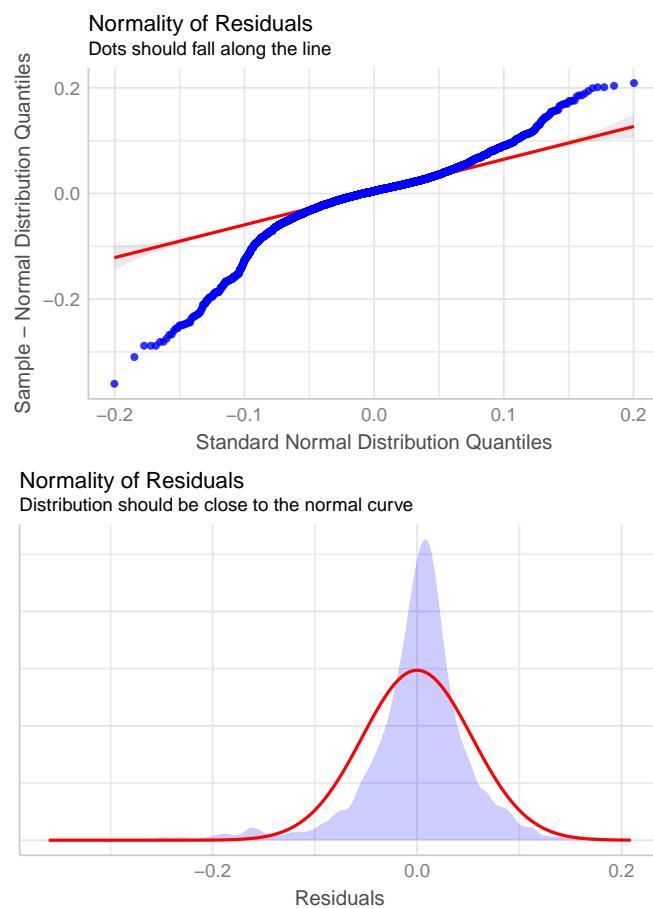


Figure S3.12: Diagnostic plots for Model 2b, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

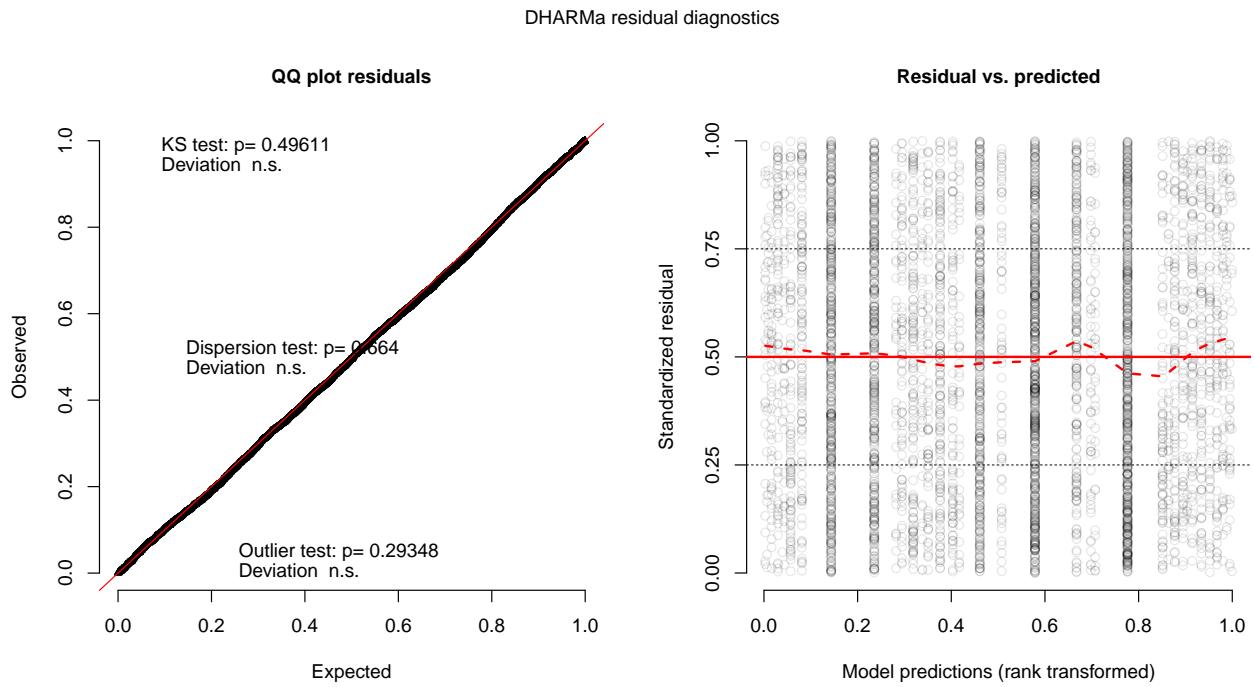


Figure S3.13: Diagnostic plots for Model 3, obtained using the ‘DHARMA’ R package (Hartig, 2021).

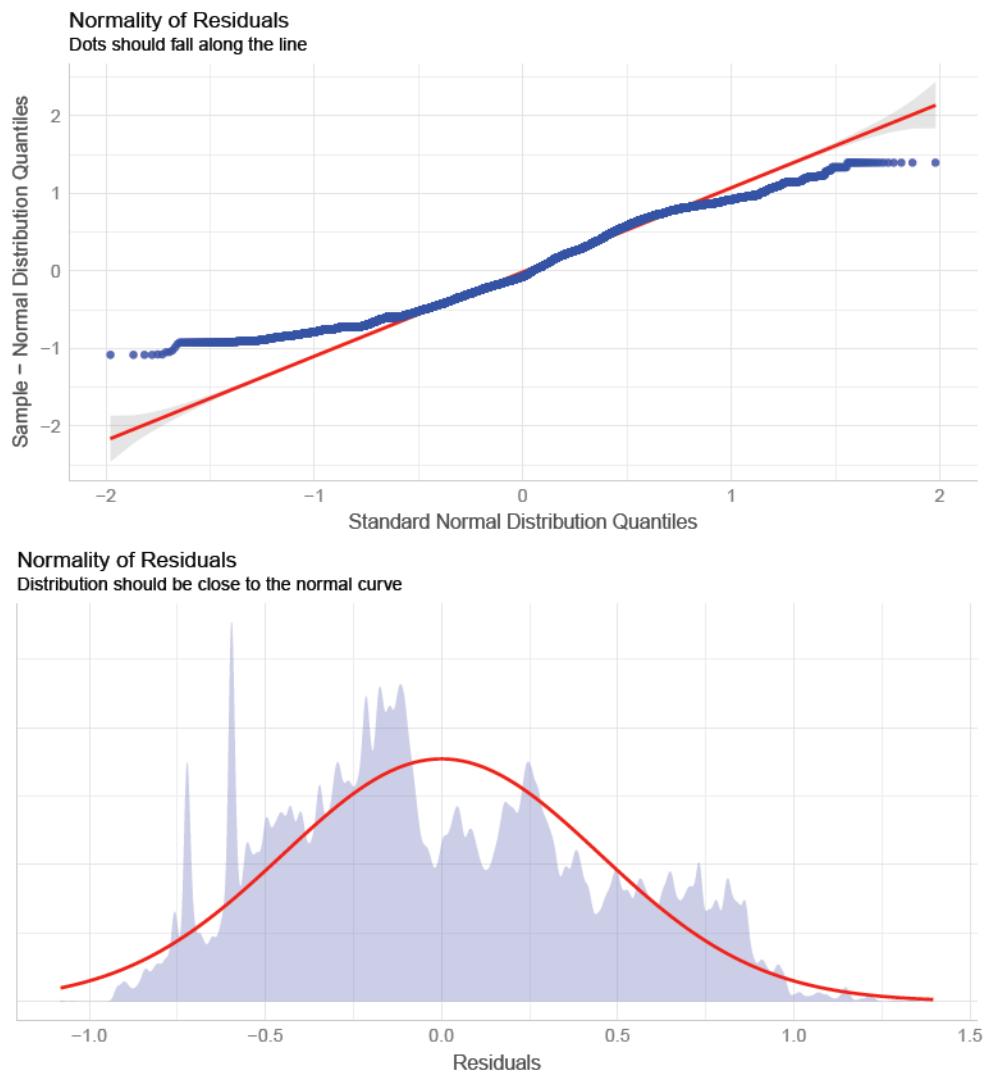


Figure S3.14: Diagnostic plots for Model 4a, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

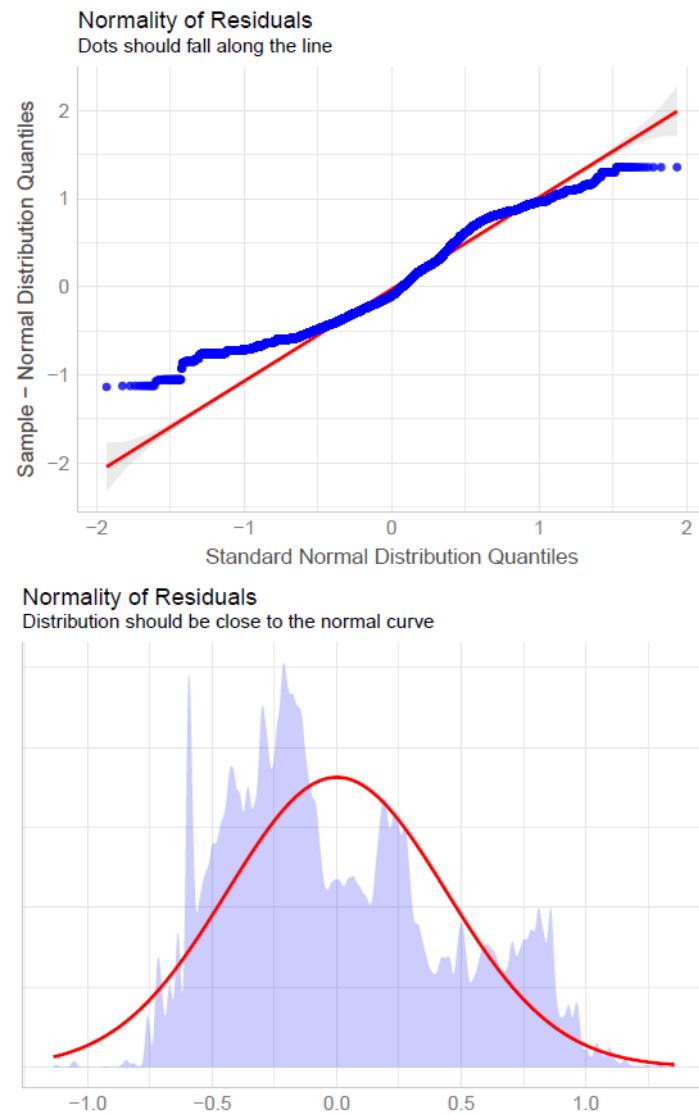


Figure S3.15: Diagnostic plots for Model 4b, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

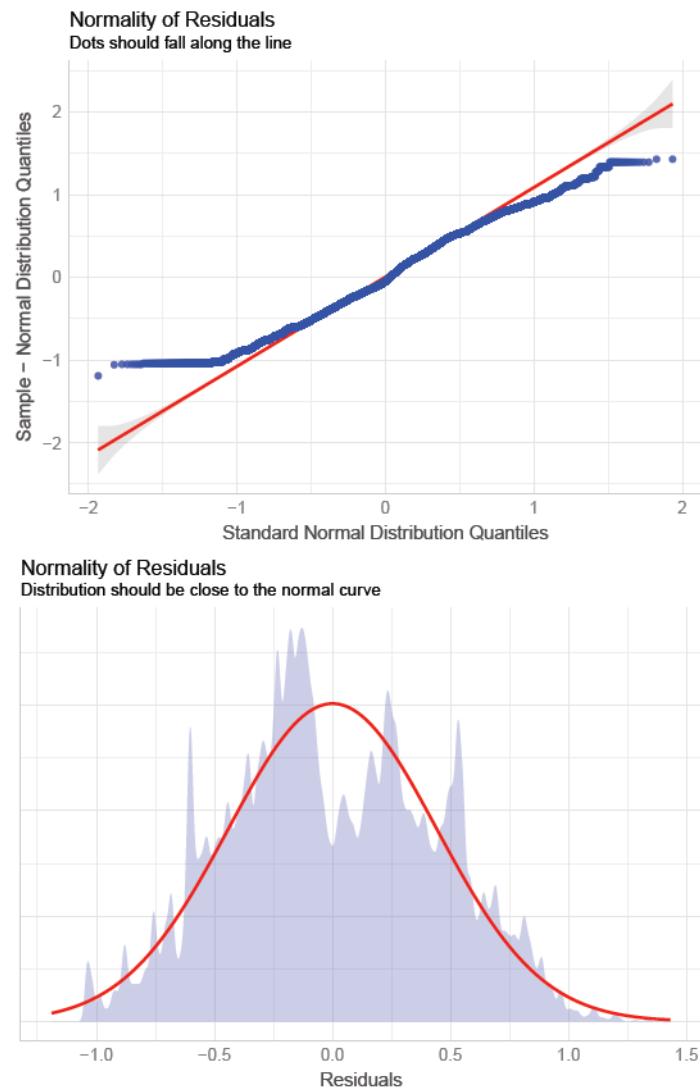


Figure S3.16: Diagnostic plots for Model 5a, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

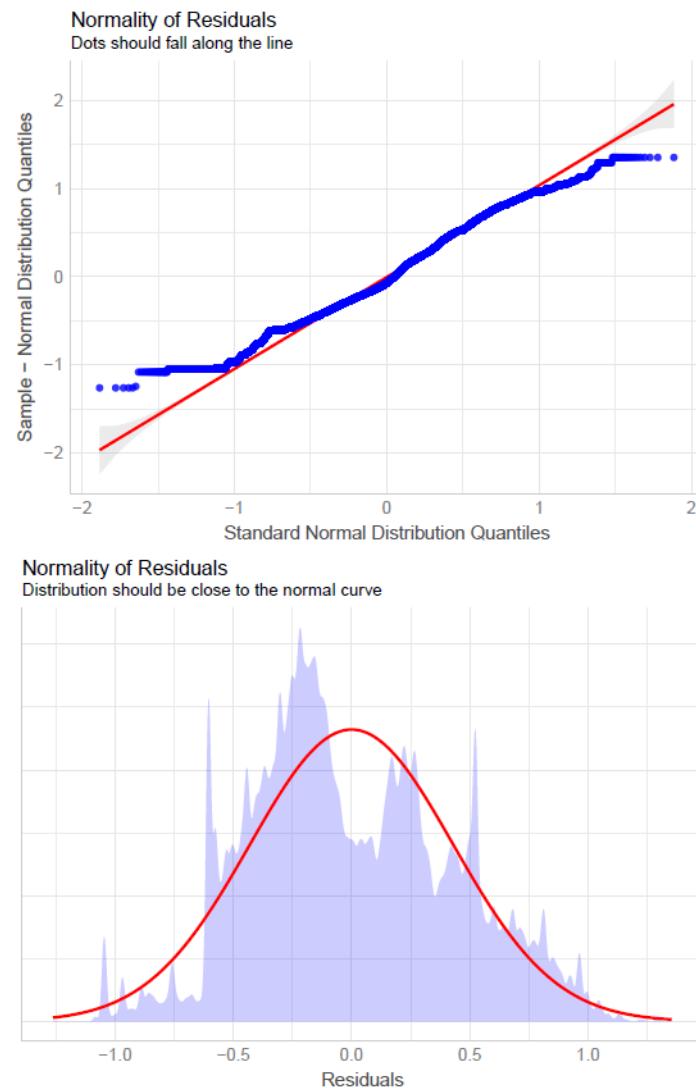


Figure S3.17: Diagnostic plots for Model 5b, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

S3.7 Model robustness

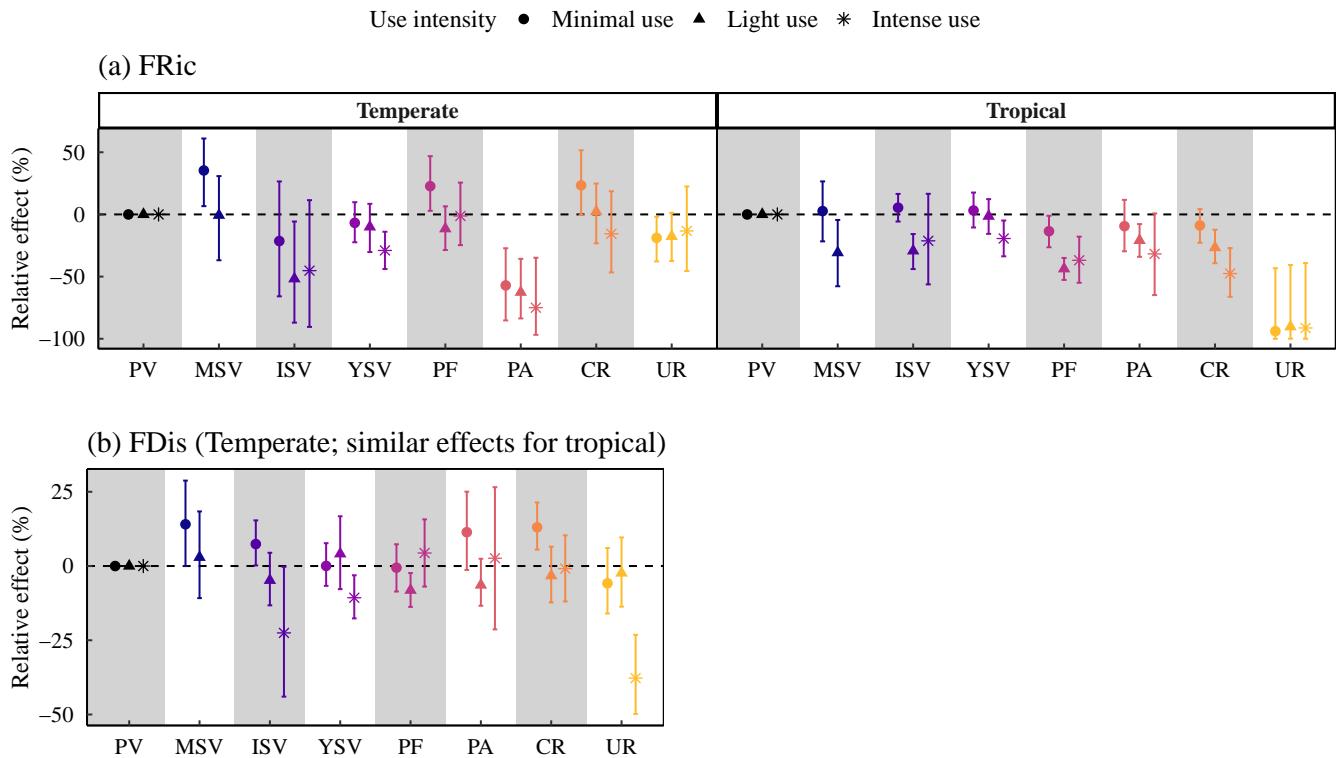


Figure S3.18: Effects of land use, land-use intensity and region on FRic (a) and FDis (b) across vertebrates, for the subset of species with complete trait data (i.e., excluding species with less than 100% trait completeness). Effects are plotted as a % difference relative to the reference land use (primary 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.

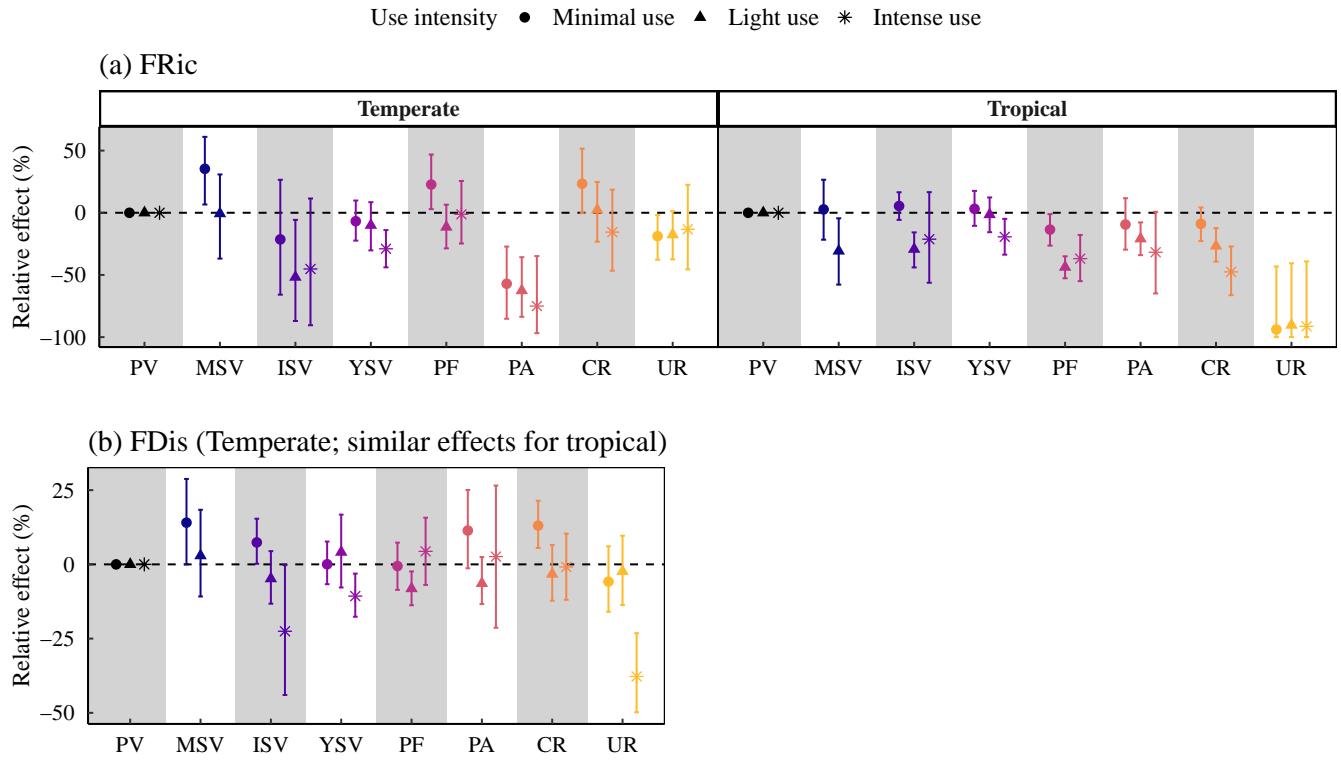


Figure S3.19: Effects of land use, land-use intensity and region on FRic (a) and FDis (b), for the subset of species with complete trait data (i.e., excluding species with less than 100% trait completeness), with geographical range size as an additional trait considered in the calculation of functional 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.

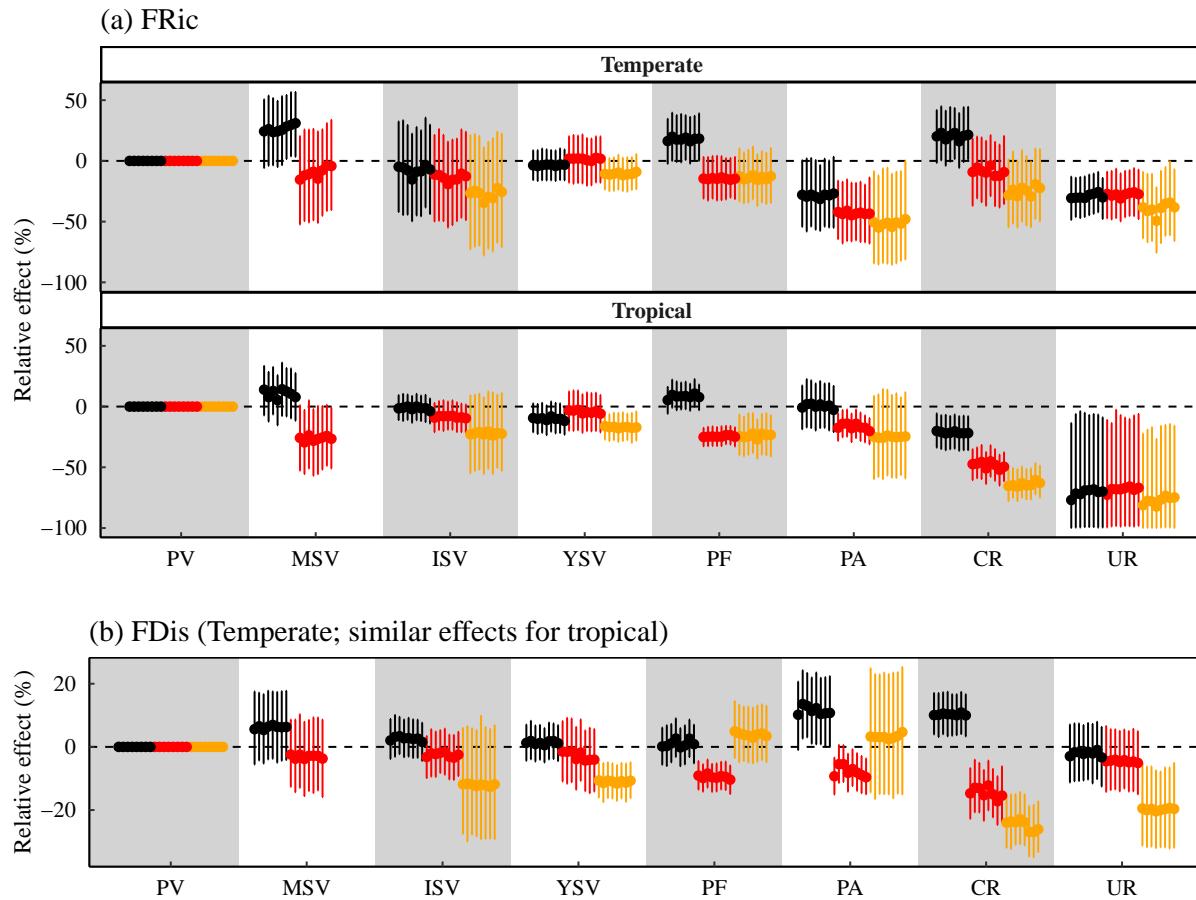


Figure S3.20: Effects of land use and land-use intensity on FRic (a) and FDis (b), obtained when calculating FRic and FDis with each set of imputed traits (eight in total). Effects are plotted as a % difference relative to the reference land use (primary vegetation, PV). For FRic, I fitted **Model 1a, 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.**

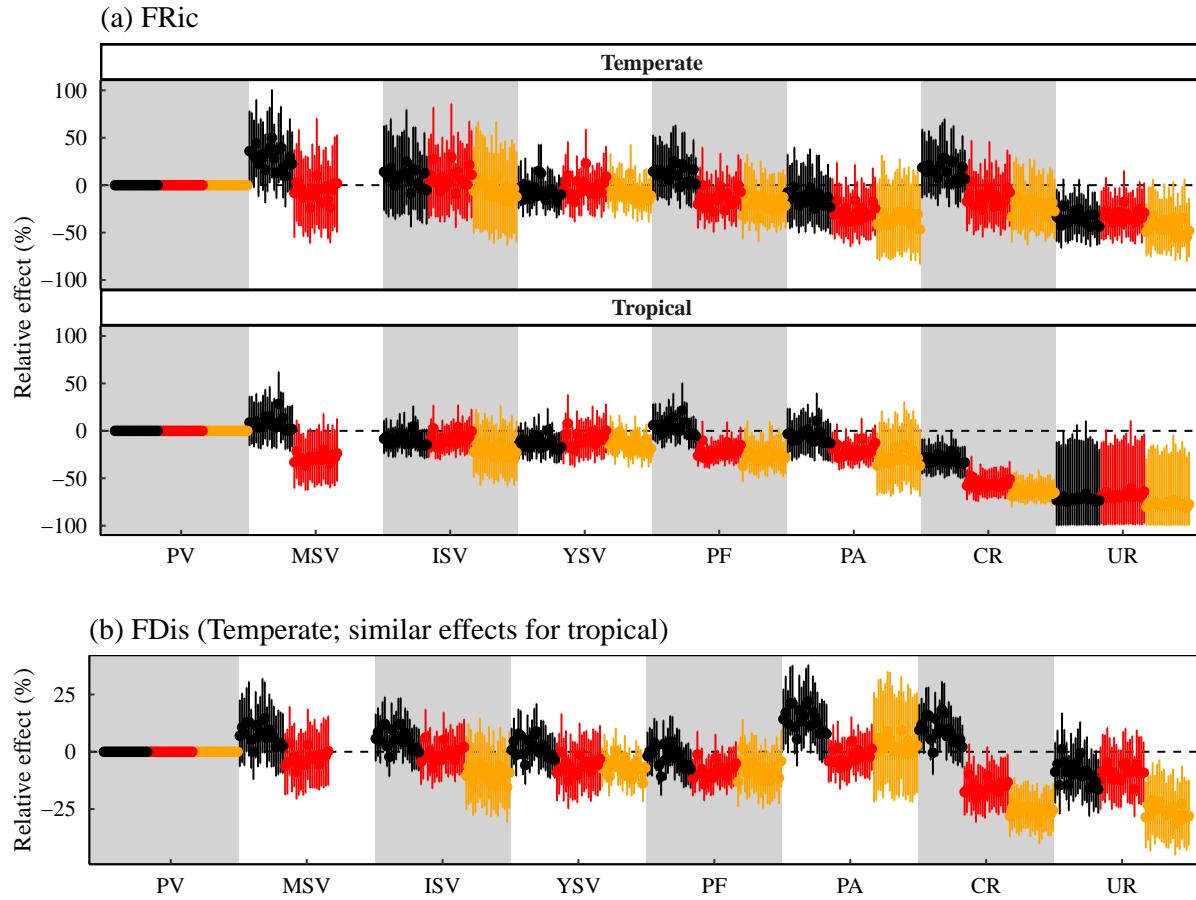


Figure S3.21: Effects of land use and land-use intensity on FRic (a) and FDis (b), obtained when re-sampling primary vegetation sites twenty independent times. I fixed the sample size for primary vegetation sites at 50. For FRic, we fitted **Model 1a**, which included the effects of land use, land-use 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.

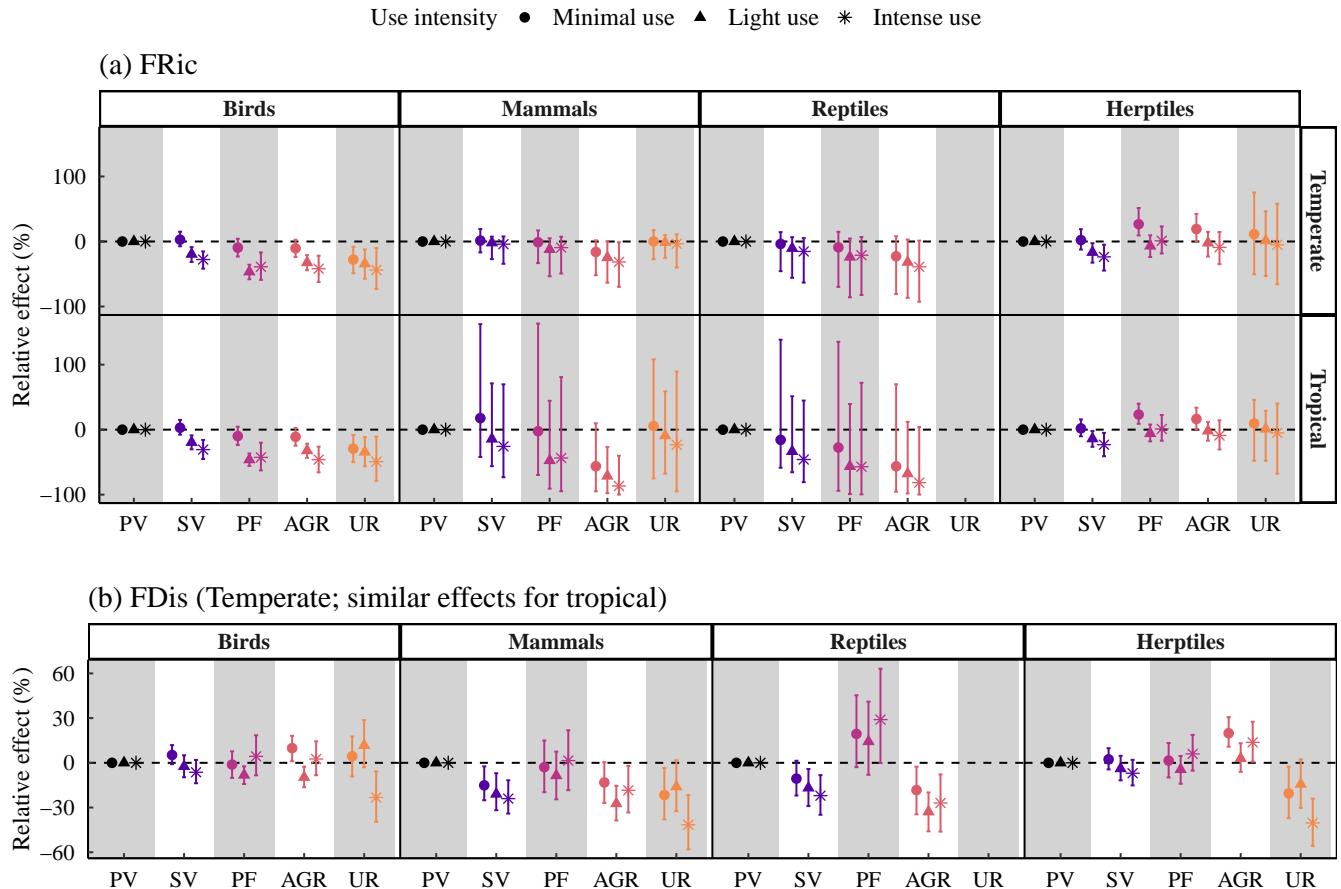
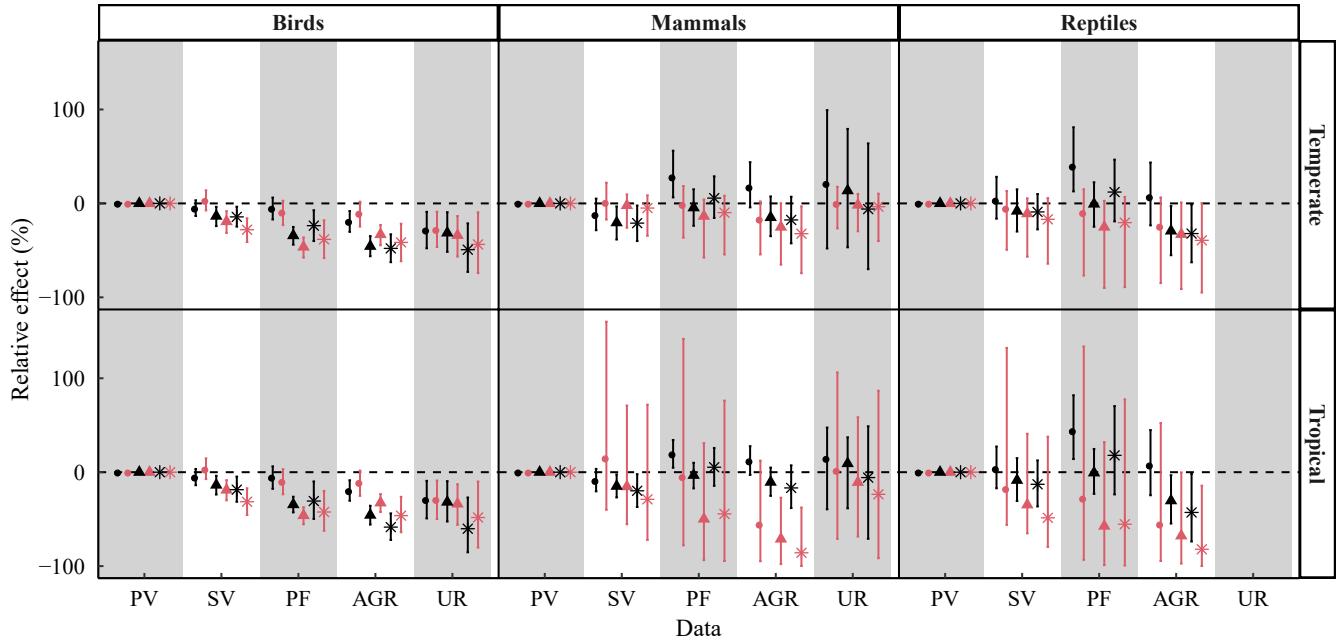


Figure S3.22: Effects of land use, land-use intensity and taxonomic class on FRic (a) and FDis (c), for the subset of species with complete trait data (i.e., excluding species with less than 100% trait completeness). Effects are plotted as a % difference relative to the reference land use (primary vegetation, 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

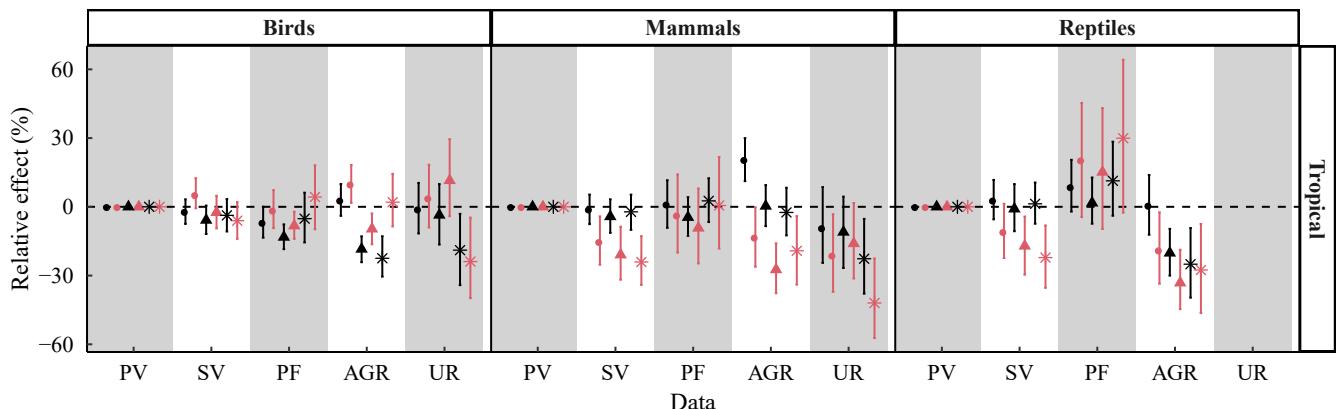
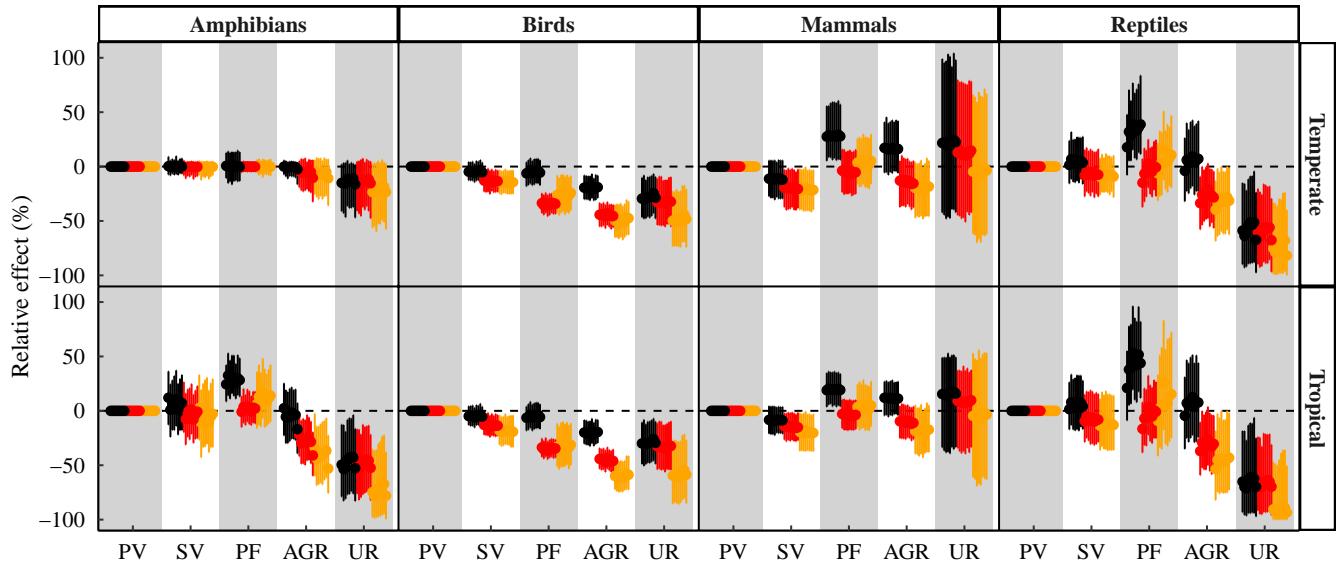


Figure S3.23: Effects of land use, region, land-use intensity and taxonomic class on FRic and FDis obtained with the imputed trait data (black points) or with the complete data subsets (red points). Effects are plotted as a % difference relative to the reference land use (primary vegetation, PV). For 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.

(a) FRic



(b) FDis (Temperate; similar effects for tropical)

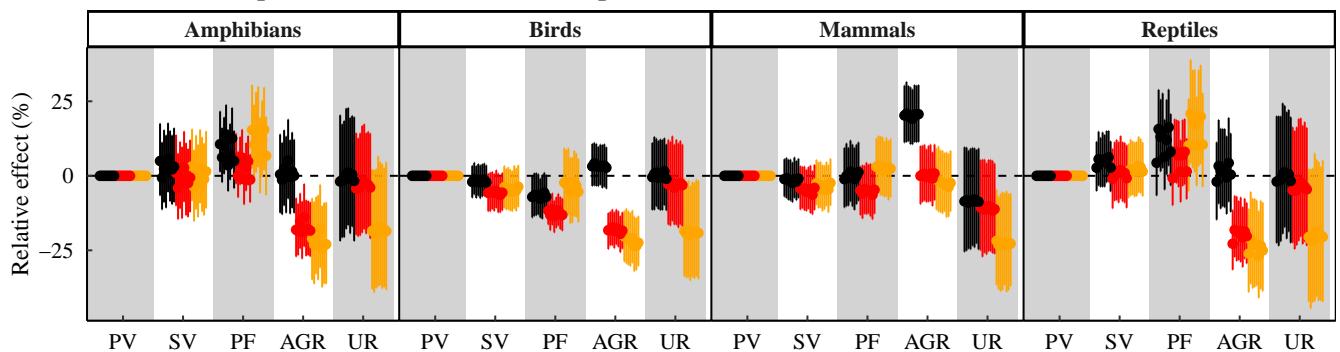


Figure S3.24: Effects of land use, region, land-use intensity and taxonomic class on FRic and FDis, obtained when calculating FRic and FDis with each set of imputed traits (eight in total). Effects are plotted as a % difference relative to the reference land use (primary vegetation, PV). For FRic, I 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.

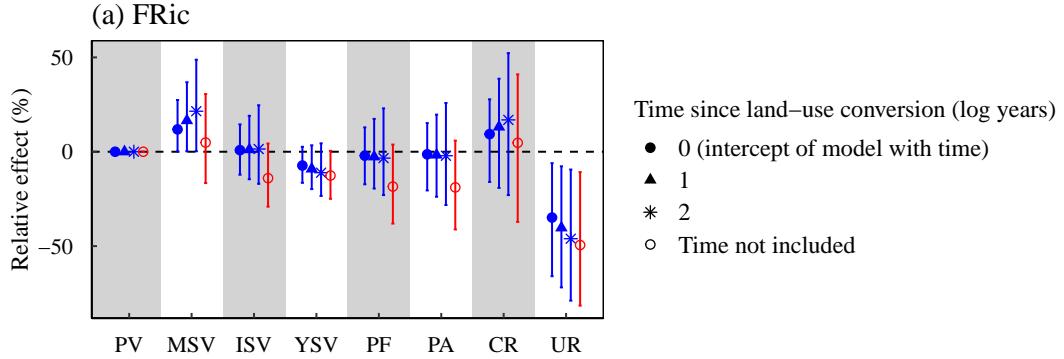


Figure S3.25: Effects of land use on FRic for the model that includes time since land-use conversion (blue points) versus the model that does not take time since land-use conversion into account (red points).

- 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 complied 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; and species consuming both vertebrates and invertebrates also classified as omnivores; and species consuming a plant or seed, fruit or nectar, 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 Etard et al. (2020)). 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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- Yap, C.H. & Jafaar, I. (2012). Feeding analysis of *Hylarana cf. labialis*, *Leptobrachium hendricksoni*, and *Occidozyga laevis* (Amphibia: Anura) from a lowland dipterocarp forest in Kedah, Malaysia. *Herpetological Review*, 43(1).
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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

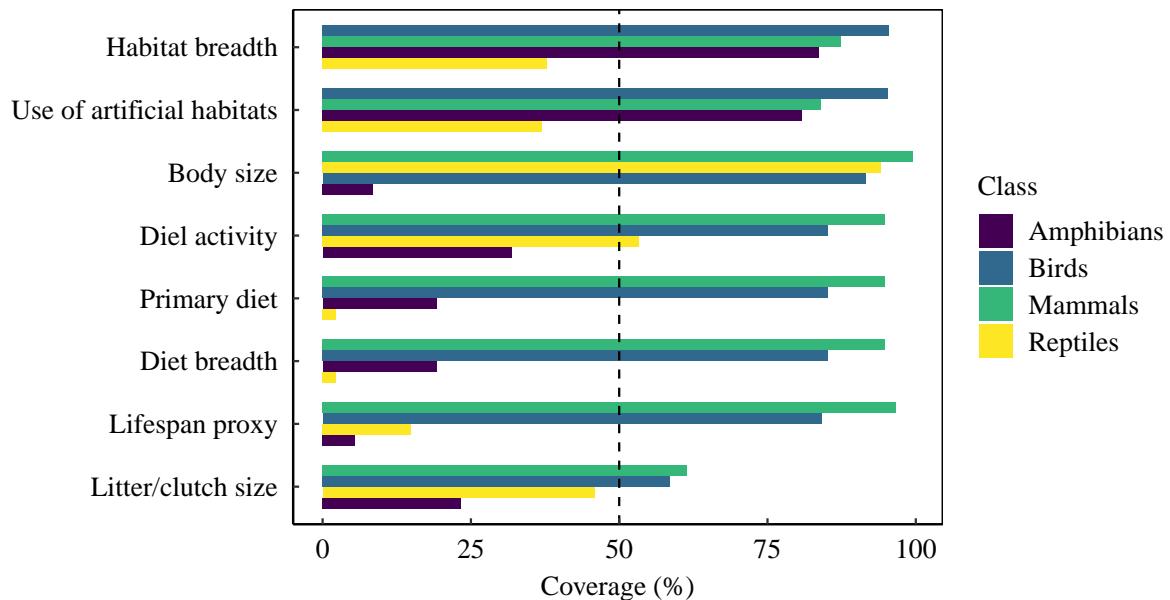


Figure S4.1: Trait coverage, including coverage for diet information, calculated as the proportion of species for which trait values are not missing. The dashed line represents 50% coverage.

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 which was 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

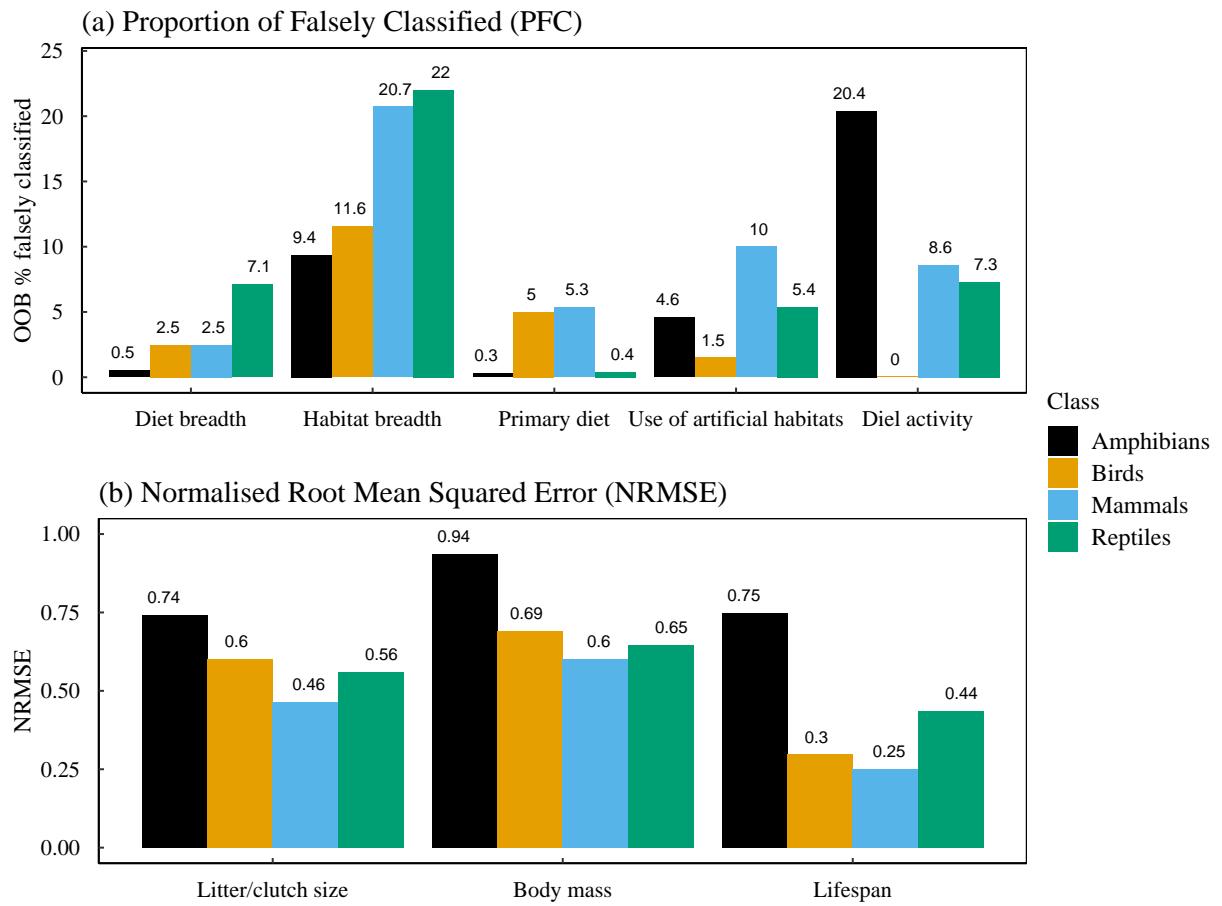


Figure S4.2: Out-of-bag estimation of imputation errors for the traits included in the analyses. (a) For the categorical traits, I show the proportion of falsely classified traits ('PFC', out-of-bag estimates); (b) For the continuous traits, I calculate the normalised root-mean-squared error (NRMSE), 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.

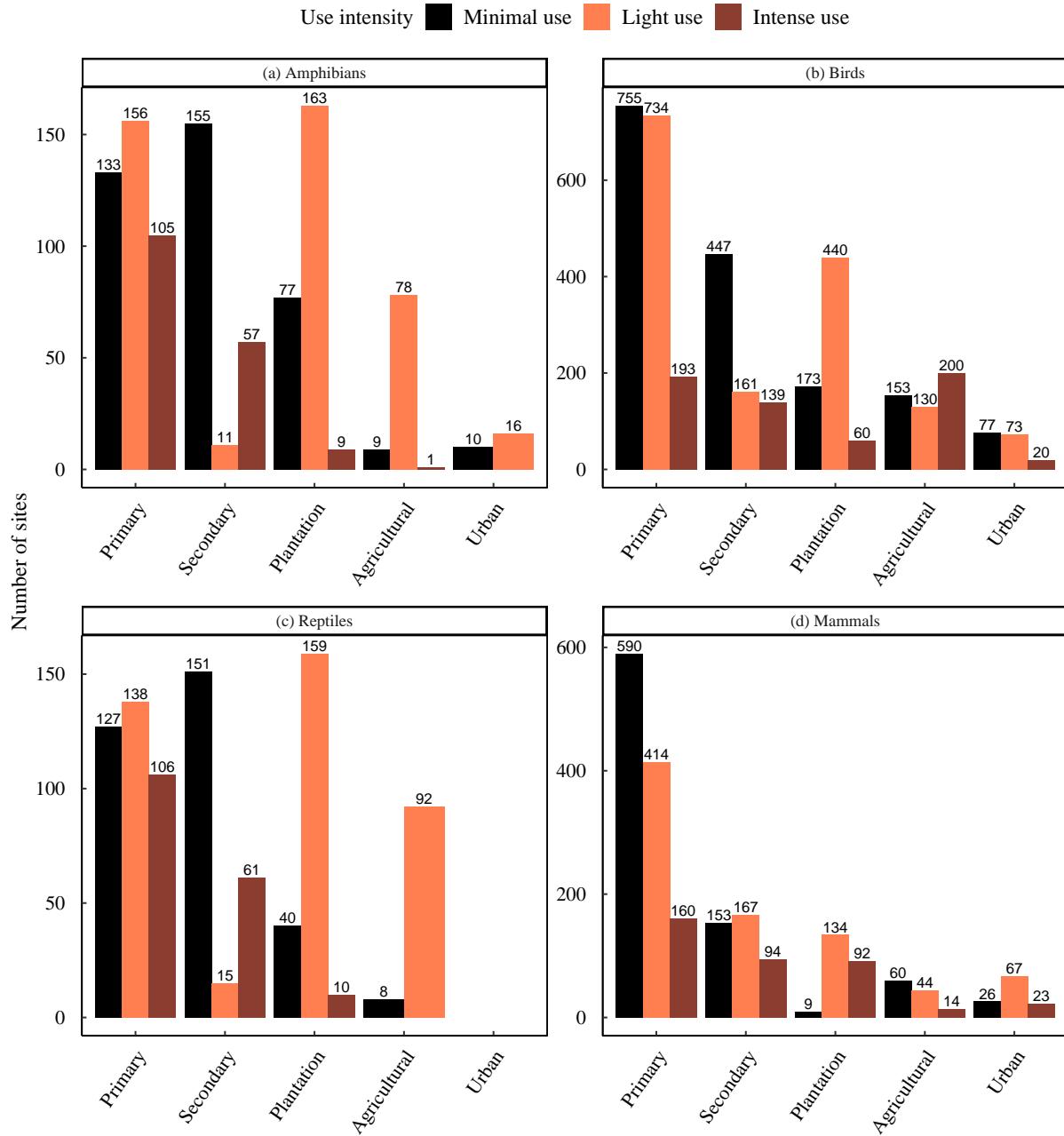


Figure S4.3: Sample sizes (number of PREDICTS sites) for the different land-use types, in each class.

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 (sqrt)	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

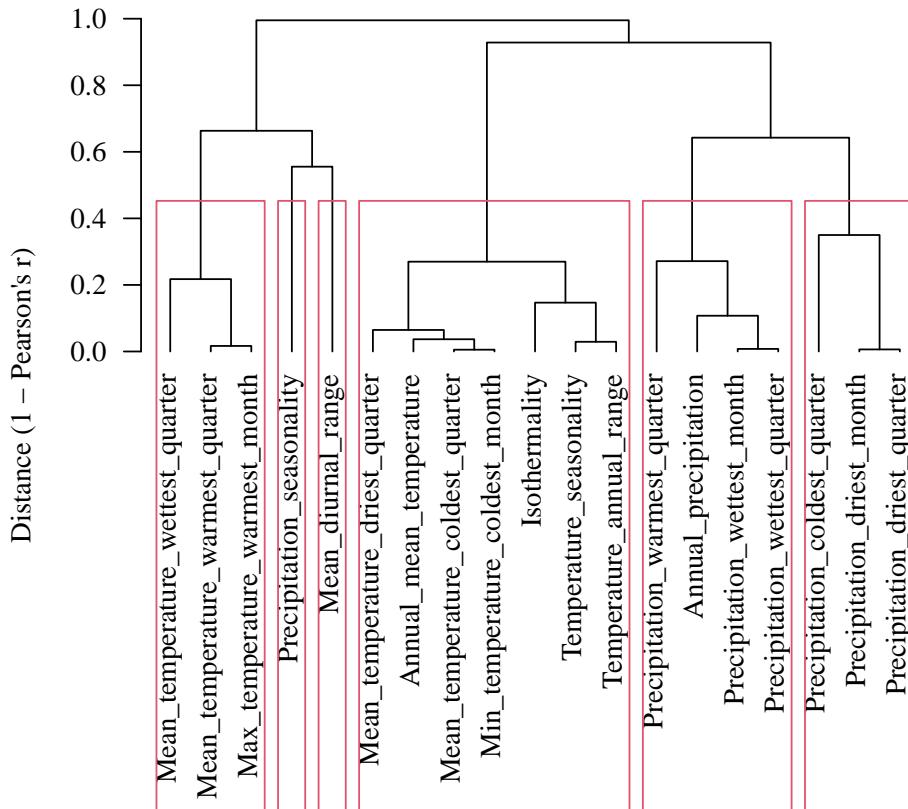


Figure S4.4: Groups of intercorrelated climatic variables using a cutoff of 0.65 for Pearson's correlation coefficient, obtained using the ‘removeCollinearity’ R function (‘virtualspecies’ package, Leroy et al. (2015)). Variables figuring in the same red boxes were correlated with Pearson's correlation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

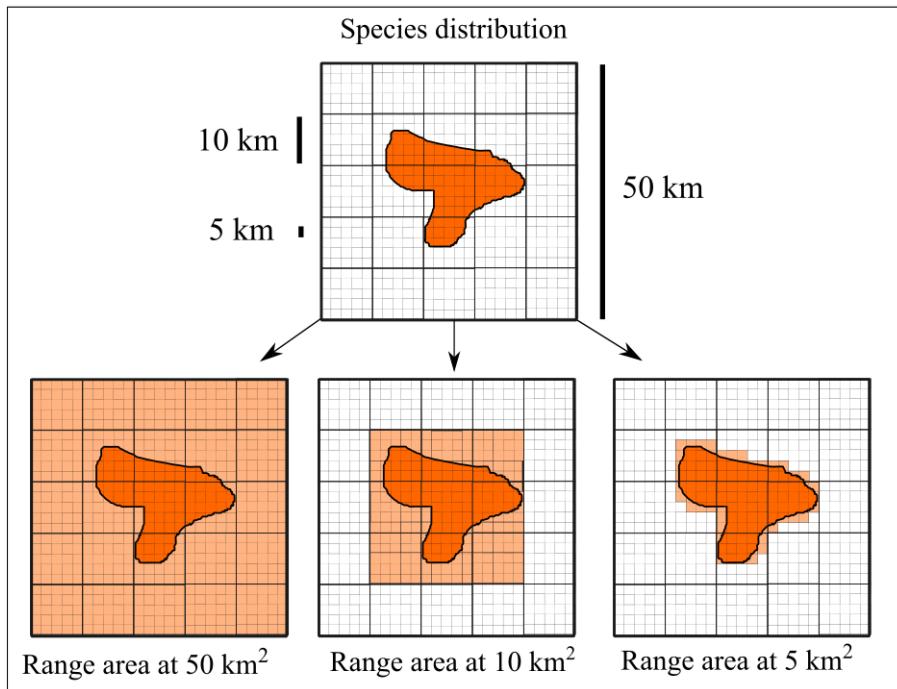


Figure S4.5: Possible impact of resolution on estimated geographical range area. I represent a virtual distribution for a species (orange shape). The species distribution is more accurately captured at finer resolutions (e.g., 5 km^2) than at coarser resolutions (e.g., 10 km^2 or 50 km^2). A possible 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.

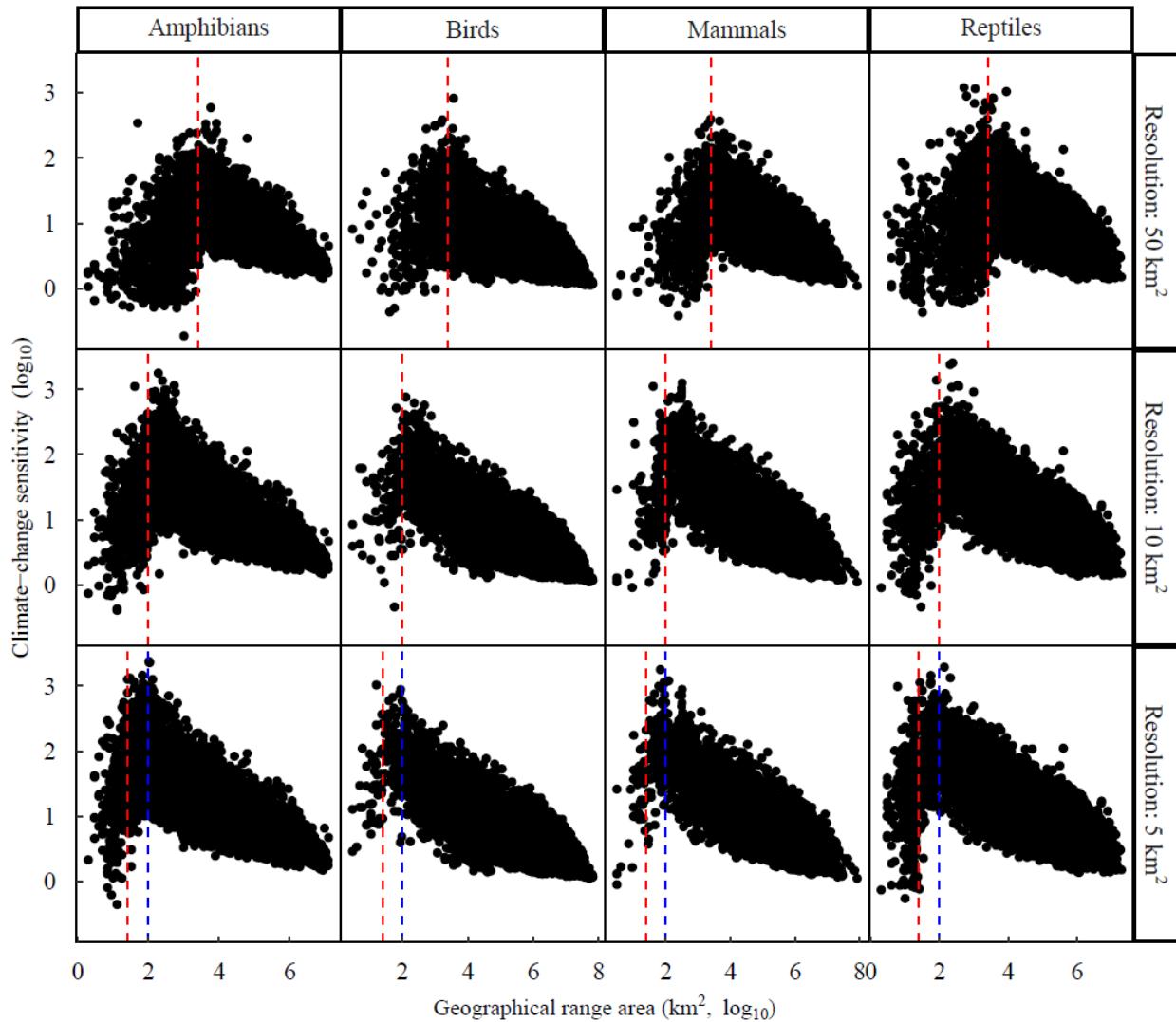


Figure S4.6: Estimated climate-change sensitivity estimations at three different resolutions (50 km², 10 km² and 5 km²) against geographical range area (estimated at 1 km²). With the red dashed lines, I highlight the range areas that correspond to the surface area of one grid cell (i.e., 2,500 km², 100 km² and 25 km² respectively). Climate-change sensitivity was estimated using the CENFA framework (Rinnan and Lawler, 2019). I chose to work at a resolution of 5 km² 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 km².

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

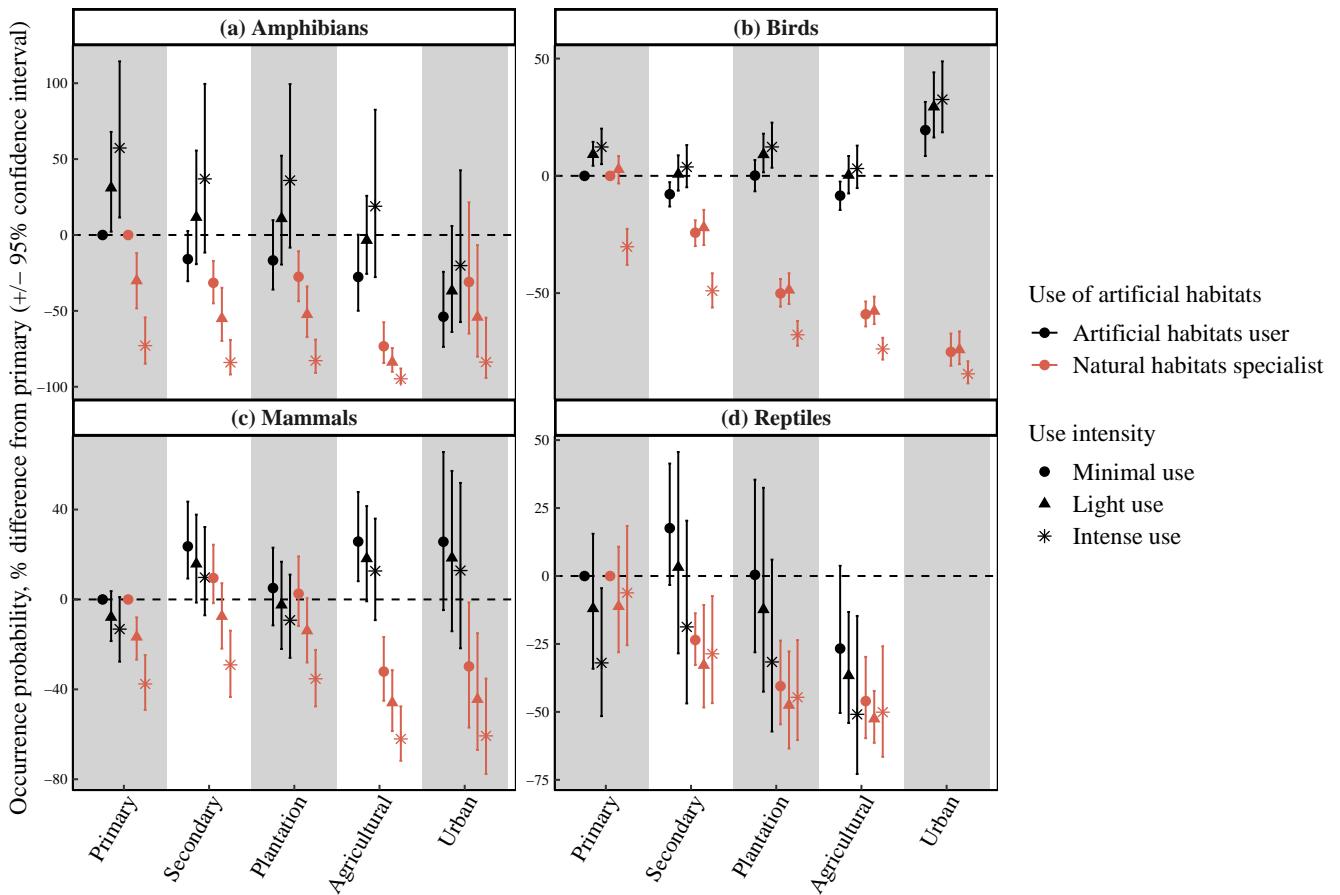


Figure S4.7: Predicted occurrence probability as a function of land use, land-use intensity, artificial habitat use and their interactions, for each class of terrestrial vertebrates (median $\pm 95\%$ confidence interval; the predictions are rescaled with reference to minimally-used primary vegetation). 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.

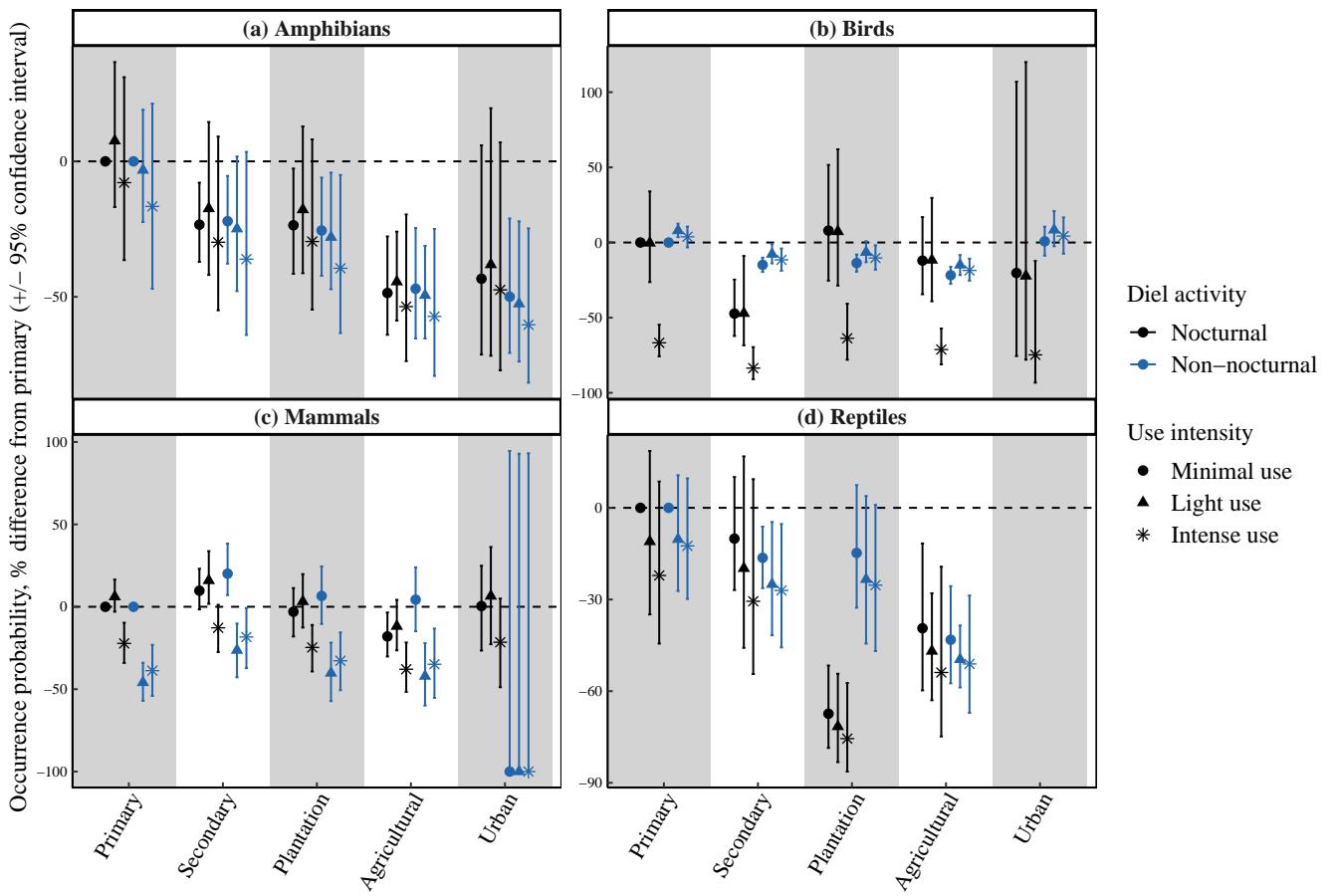


Figure S4.8: Predicted occurrence probability as a function of land use, land-use intensity, diel activity and their interactions, for each class of terrestrial vertebrates (median $\pm 95\%$ confidence interval; the predictions are rescaled with reference to minimally-used primary vegetation). The predictions 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

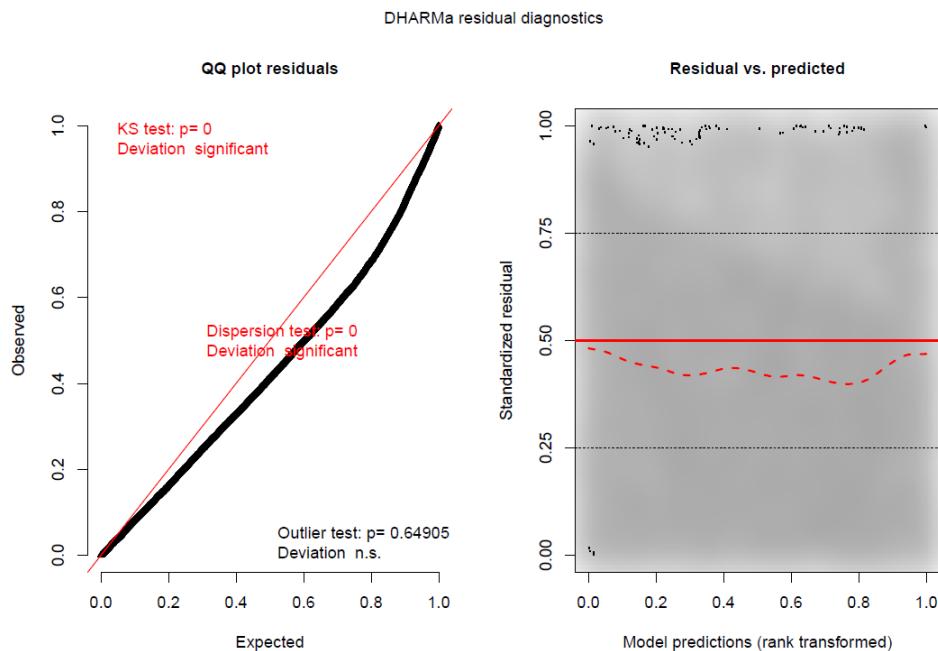


Figure S4.9: Diagnostic plots for the mixed-effects model fitted on amphibians, looking at the effects of land use, land-use intensity and the species-level ecological characteristics on species occurrence probability (full model). The diagnostic plots were obtained from the ‘DHARMA’ R package (Hartig,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

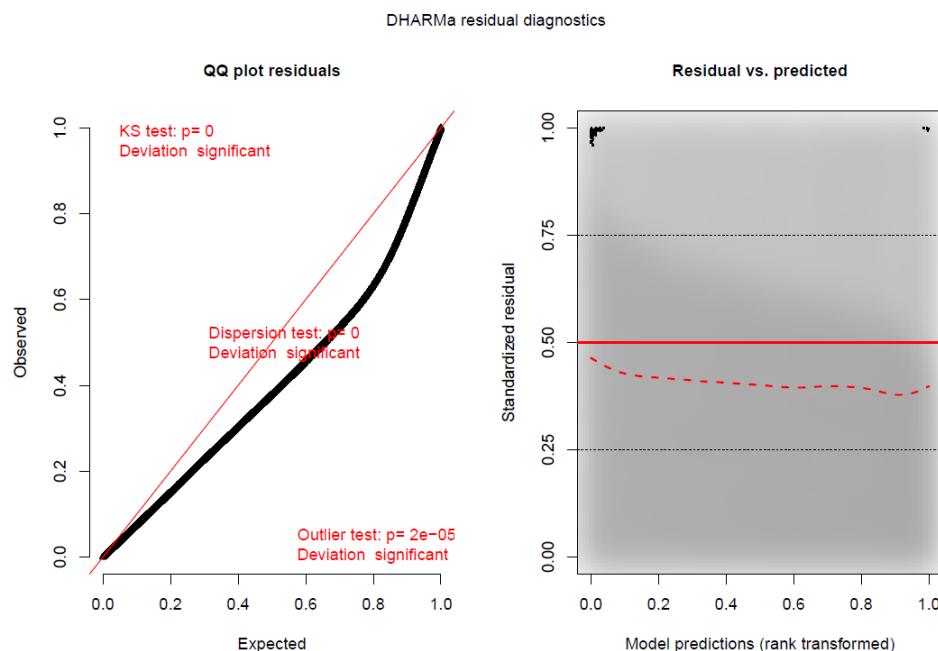


Figure S4.10: Diagnostic plots for the mixed-effects model fitted on birds, looking at the effects of land use, land-use intensity and the species-level ecological characteristics on species occurrence probability (full model). The diagnostic plots were obtained from the ‘DHARMA’ R package (Hartig, 2021).

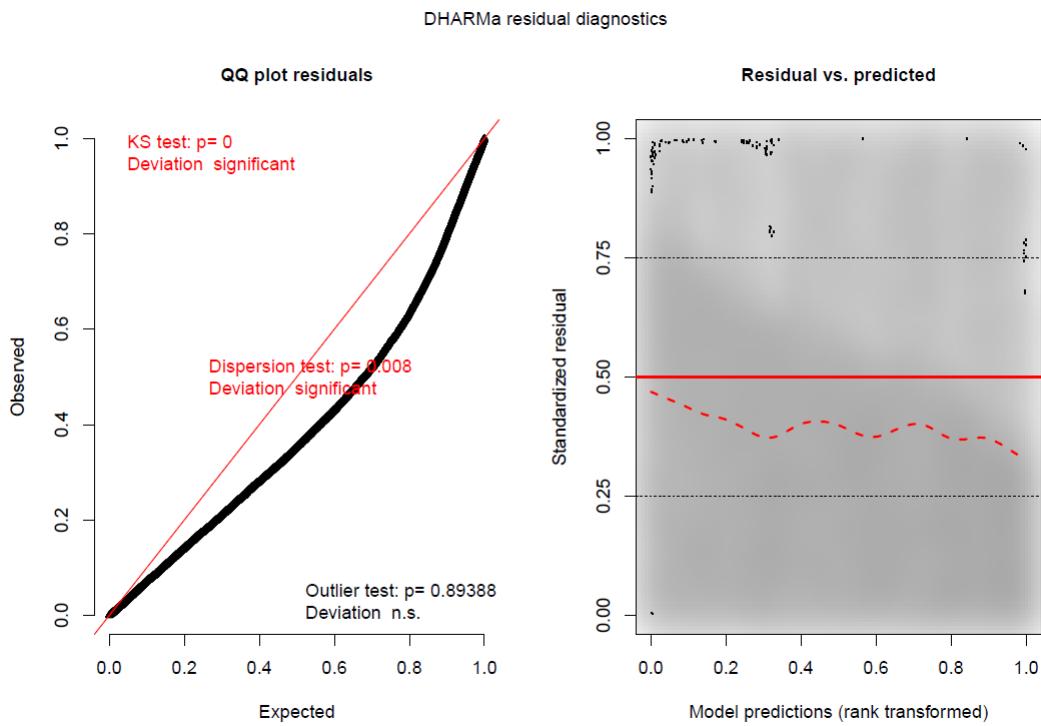


Figure S4.11: Diagnostic plots for the mixed-effects model fitted on mammals, looking at the effects of land use, land-use intensity and the species-level ecological characteristics on species occurrence probability (full model). The diagnostic plots were obtained from the ‘DHARMA’ R package (Hartig,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

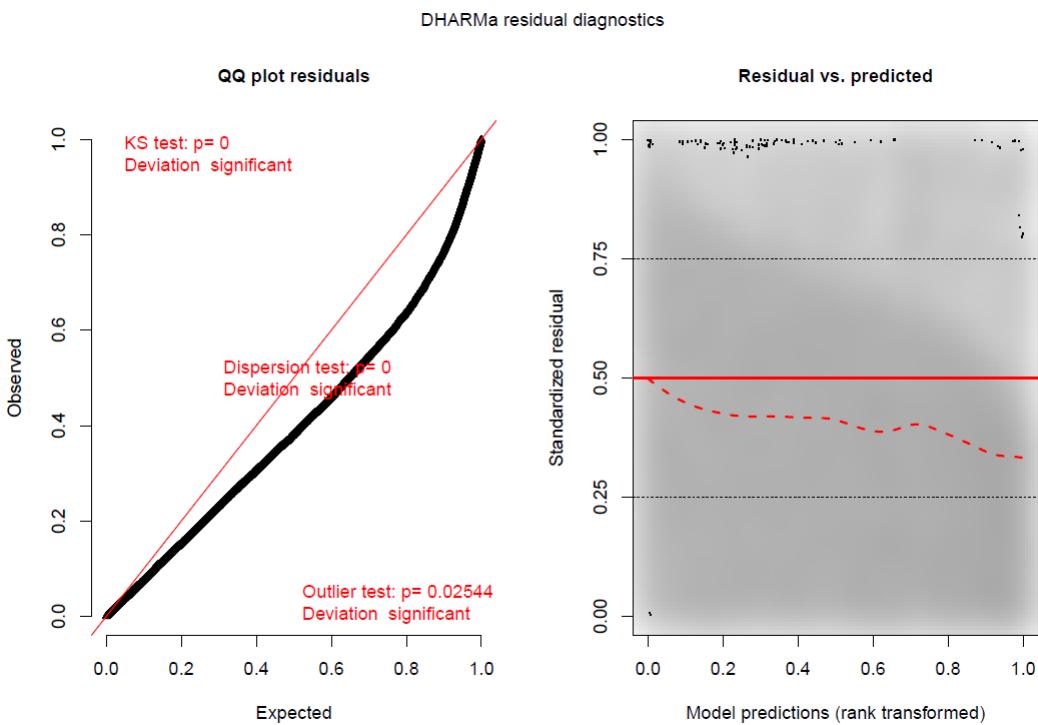


Figure S4.12: Diagnostic plots for the mixed-effects model fitted on reptiles, looking at the effects of land use, land-use intensity and the species-level ecological characteristics on species occurrence probability (full model). The diagnostic plots were obtained from the 'DHARMA' R package (Hartig,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

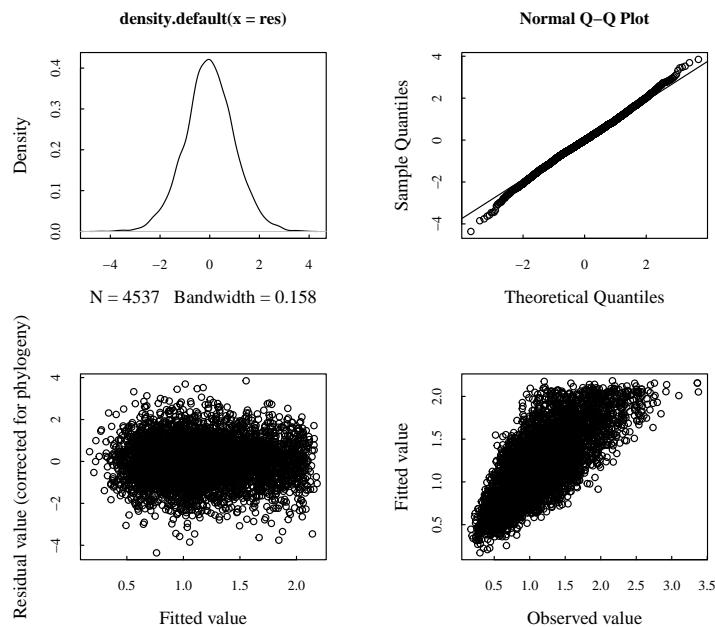


Figure S4.13: Diagnostic plots for the PGLS model fitted on amphibians, investigating associations between species-level ecological characteristics and climate-change sensitivity, excluding species whose range area was $\leq 100 \text{ km}^2$ (sample size: n=4,537).

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

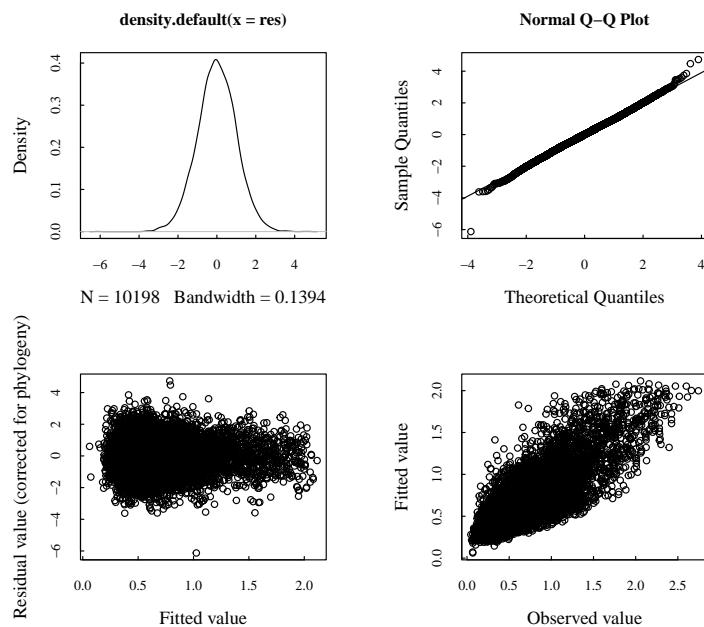


Figure S4.14: Diagnostic plots for the PGLS model fitted on birds, investigating associations between species-level ecological characteristics and climate-change sensitivity, excluding species whose range area was $\leq 100 \text{ km}^2$ (sample size: n=10,198).

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

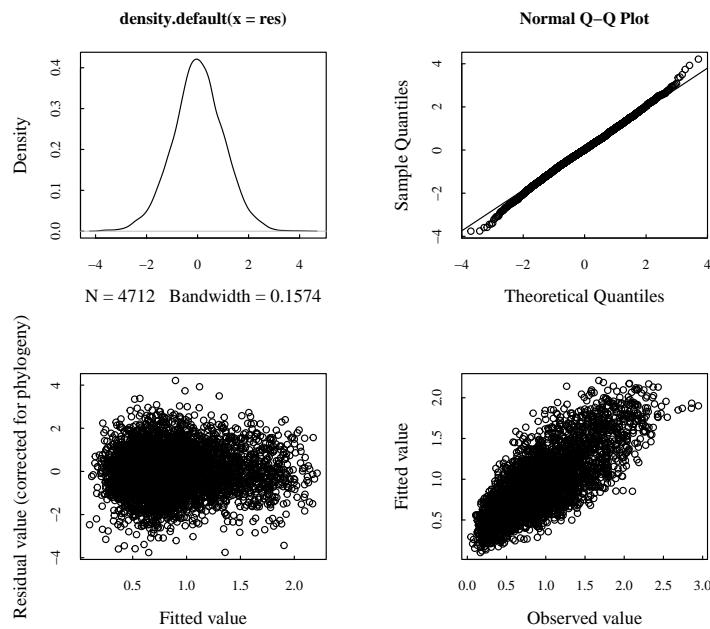


Figure S4.15: Diagnostic plots for the PGLS model fitted on mammals, investigating associations between species-level ecological characteristics and climate-change sensitivity, excluding species whose range area was $\leq 100 \text{ km}^2$ (sample size: n=4,712).

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

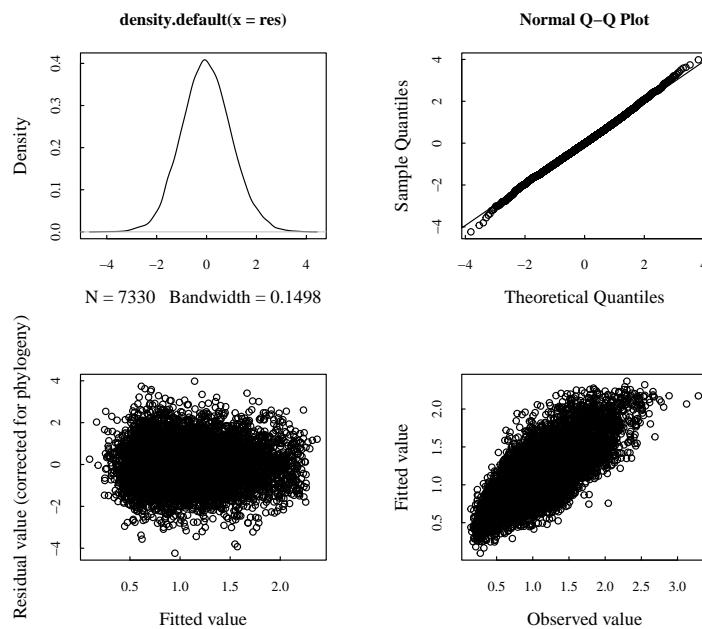


Figure S4.16: Diagnostic plots for the PGLS model fitted on reptiles, investigating associations between species-level ecological characteristics and climate-change sensitivity, excluding species whose range area was $\leq 100 \text{ km}^2$ (sample size: n=7,330).

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 $>100 \text{ km}^2$

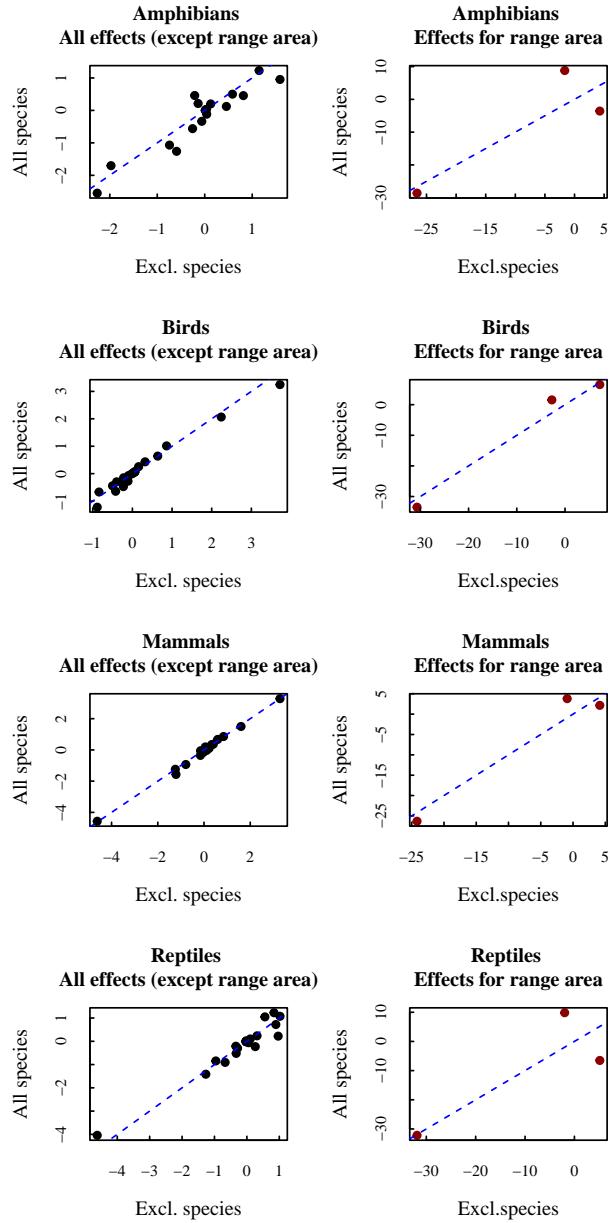


Figure S4.17: Effects for the PGLS models investigating associations between species-level ecological characteristics and climate-change sensitivity, either fitted on all species (y-axis), or fitted on the species whose range area was $>100 \text{ km}^2$ (x-axis). Overall, the estimates from both sets 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							
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	NA	Natural habitat specialist							
0	+	+	0	+	(+)	+	0	+	+	+	0	0	0	0	NA	Non-nocturnal							
-	0	(+)	0	(-)	0	+	0	-	0	(+)	+	-	-	0	NA	Narrower diet breadth							
NA	(+)	+	NA	NA	+	+	NA	NA	-	0	NA	NA	+	0	NA	Smaller body mass							
NA	0	0	-	NA	-	(-)	0	NA	-	(-)	0	NA	0	-	NA	Smaller litter/clutch size							
NA	0	0	-	NA	(-)	0	0	NA	+	0	+	NA	-	0	NA	Shorter-lived							

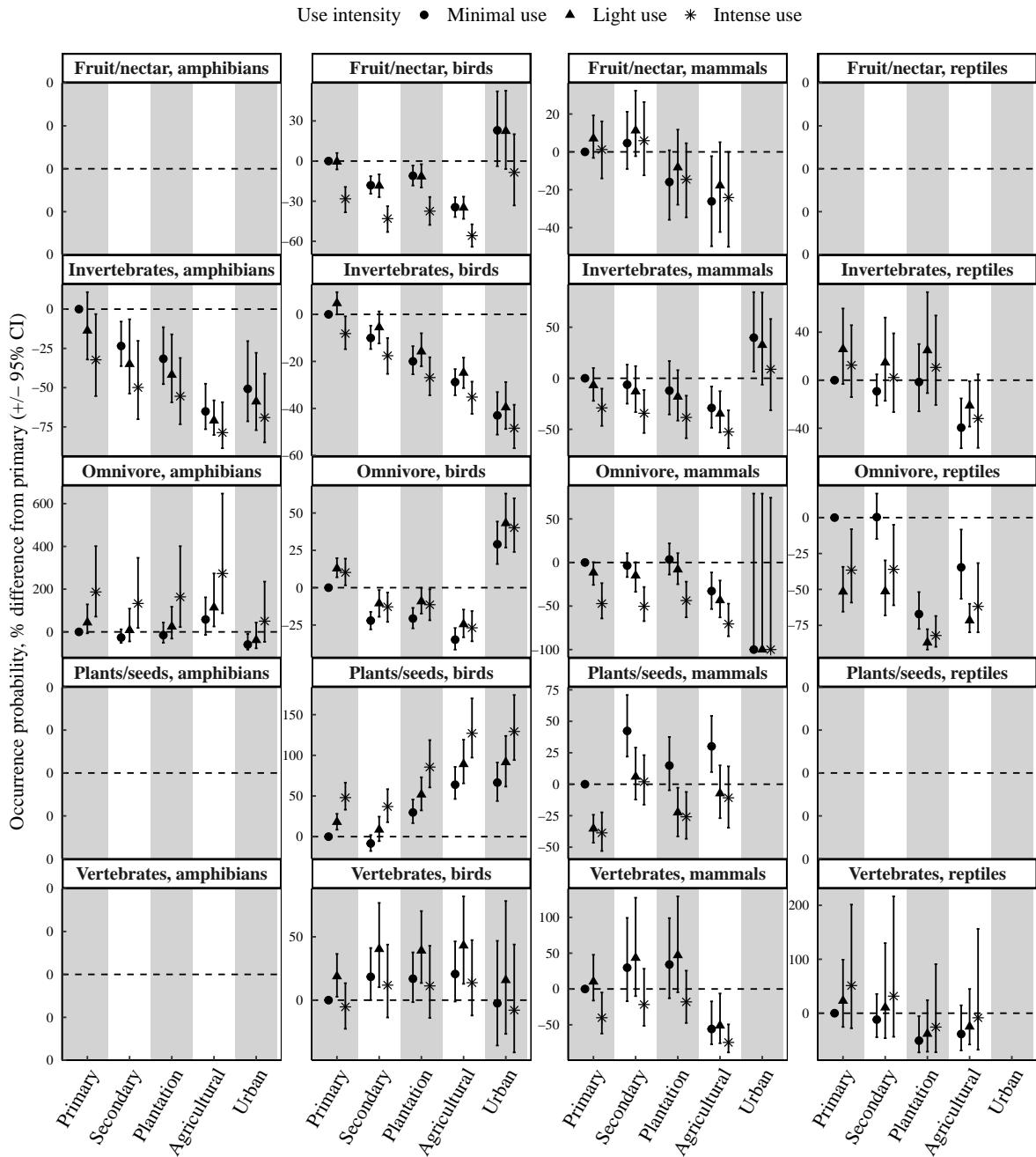


Figure S4.18: Predicted occurrence probability as a function of land use, land-use intensity, diet and their interactions in each class. The predictions were obtained from the partial models fitted in each class for diet, estimated using empirical trait data subsets (i.e., excluding imputed trait values). 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)

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

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.

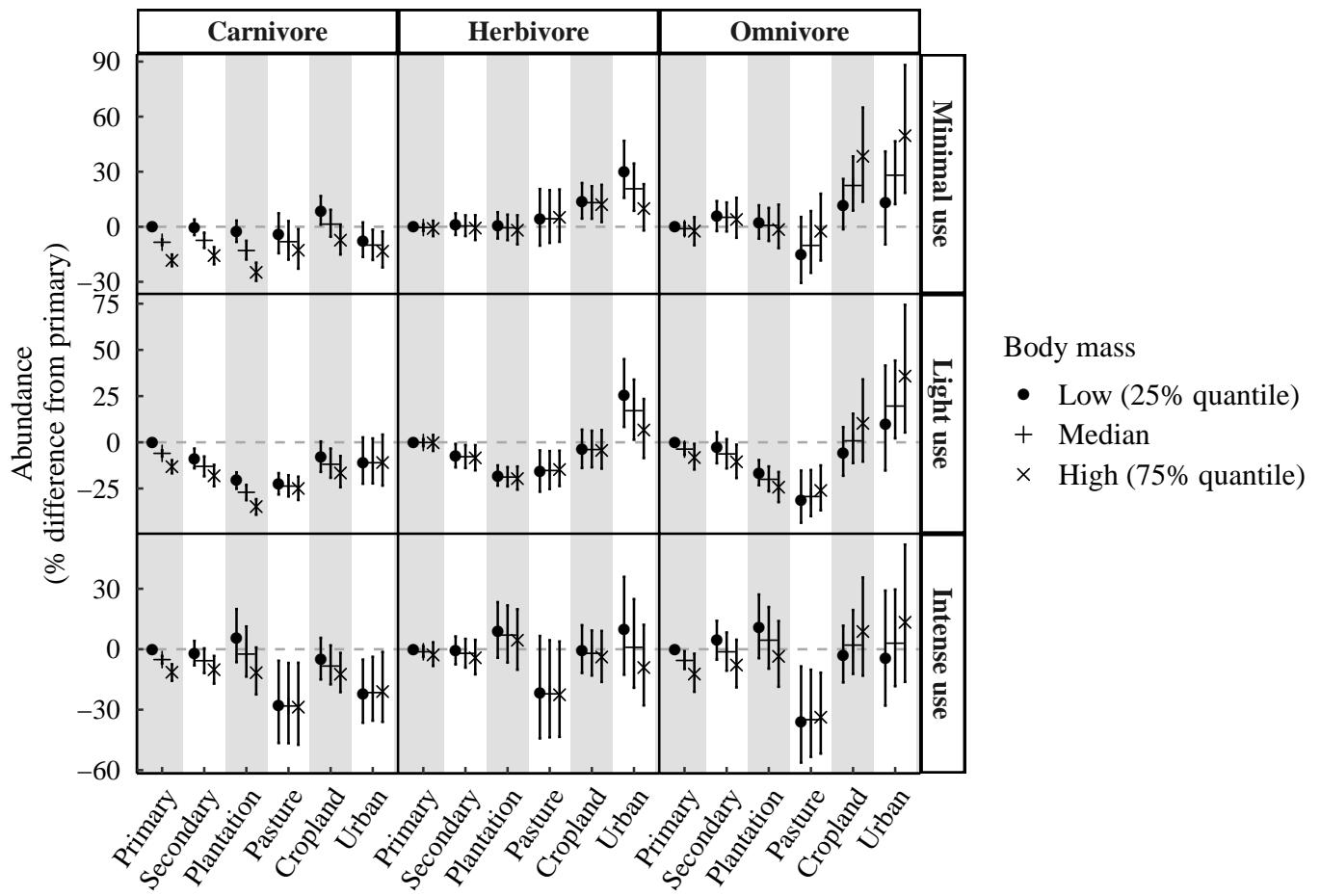


Figure S5.2: Effects of land use, land-use intensity, trophic group, body mass and their interactions on assemblage-level total abundance, estimated from the model specified in Figure S5.1. The predictions are rescaled with reference to minimally used primary vegetation, considered to be the undisturbed 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).

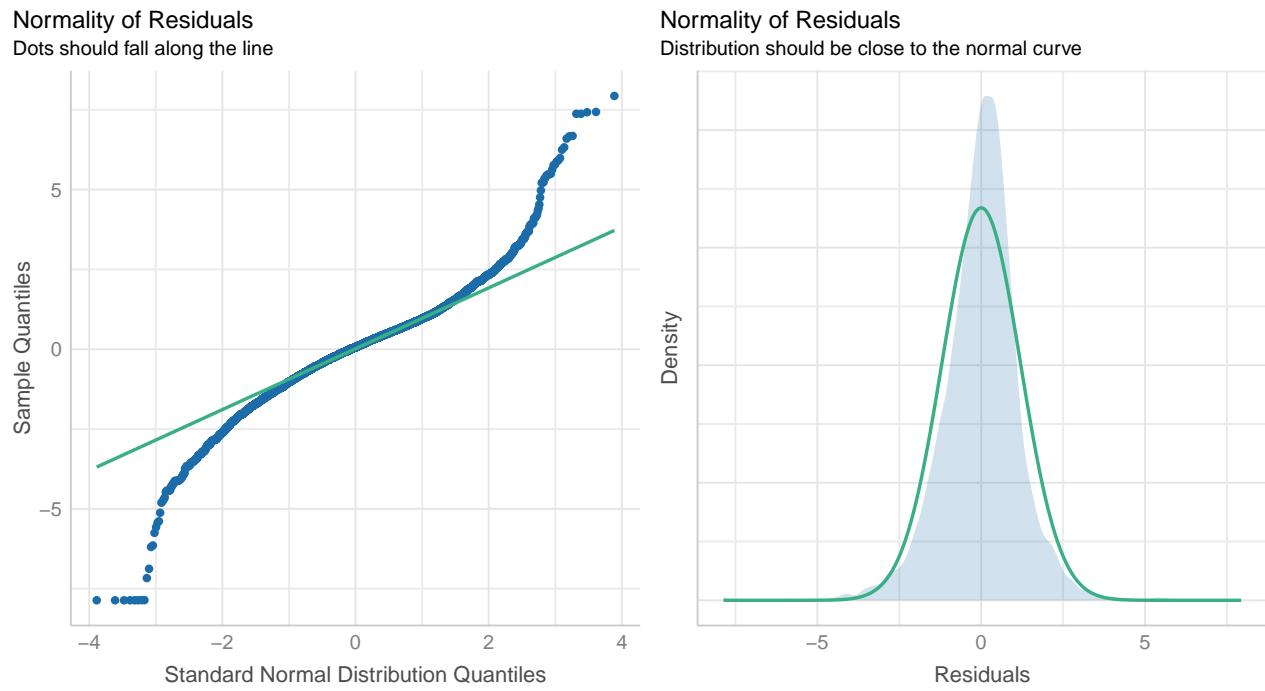
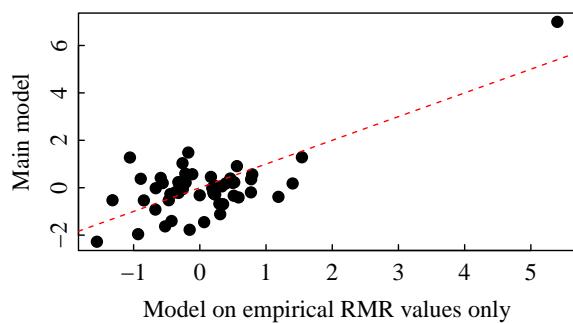


Figure S5.3: Diagnostic plots (qq-plot and residual distribution) for the linear mixed-effects model looking at the effects of land use, land-use intensity, trophic group and their interactions on assemblage-level total RMR. The diagnostic plots were obtained with the ‘performance’ R package (Lüdecke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

(a) Coefficient estimates



(b) Standard error estimates

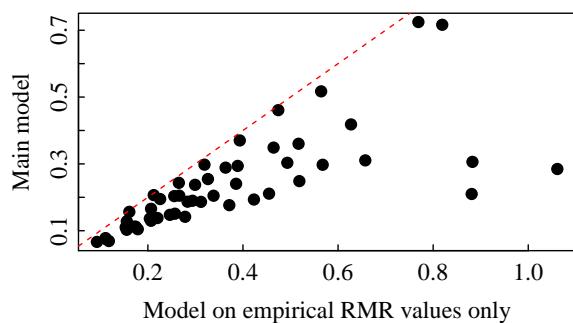


Figure S5.4: Estimates for the models looking at the effects of land use, land-use intensity, trophic group and their interactions on assemblage-level total RMR. I plotted the estimates from the model fitted on the empirical and imputed RMR values (presented in the main text) on the y-axis, and the estimates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

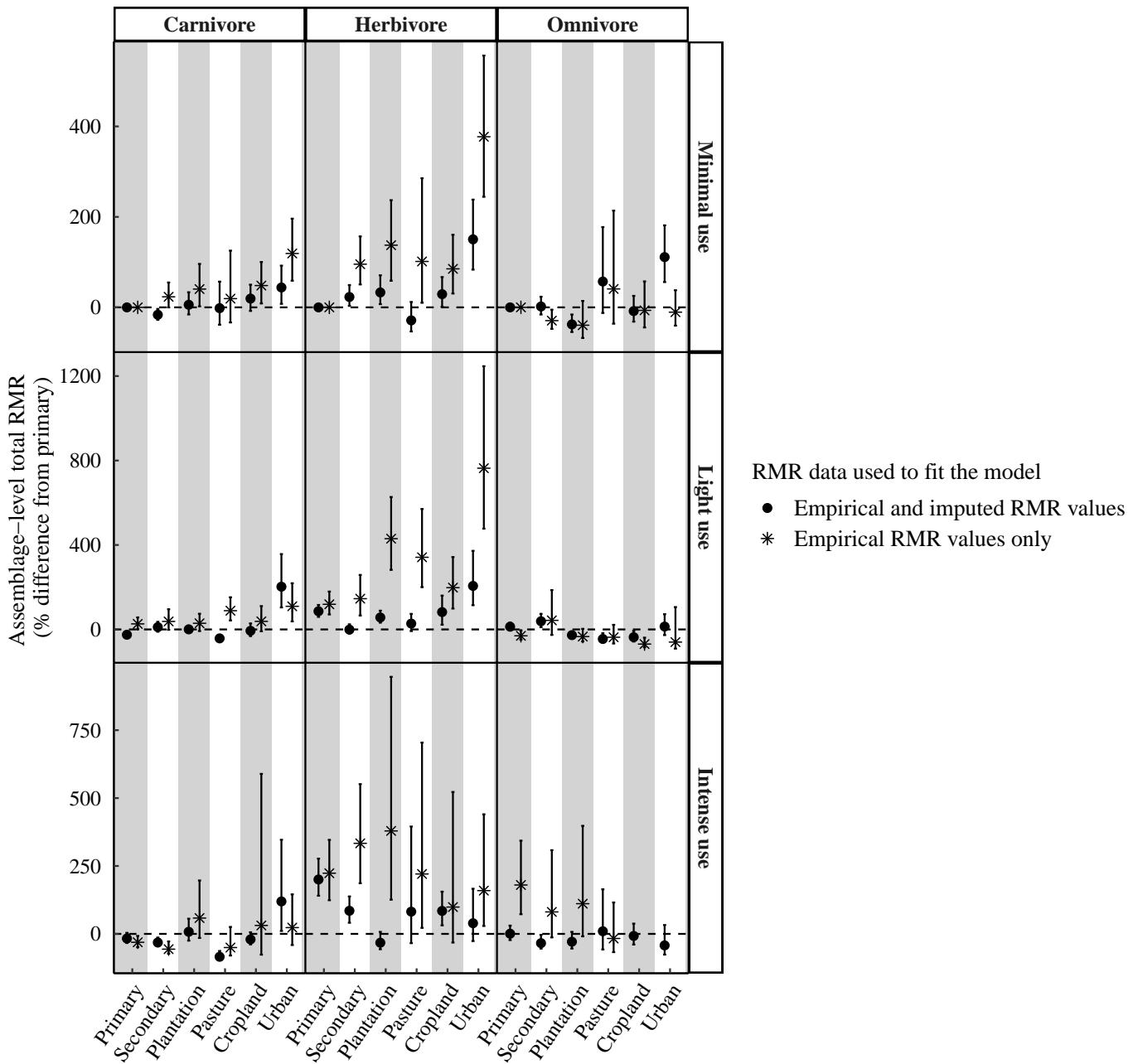


Figure S5.5: Effects of land use, land-use intensity, trophic level and their interactions on assemblage-level total RMR, estimated from the model fitted on the empirical and imputed RMR values (presented in the main text) and from the model fitted on the empirical values only. The predictions are rescaled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

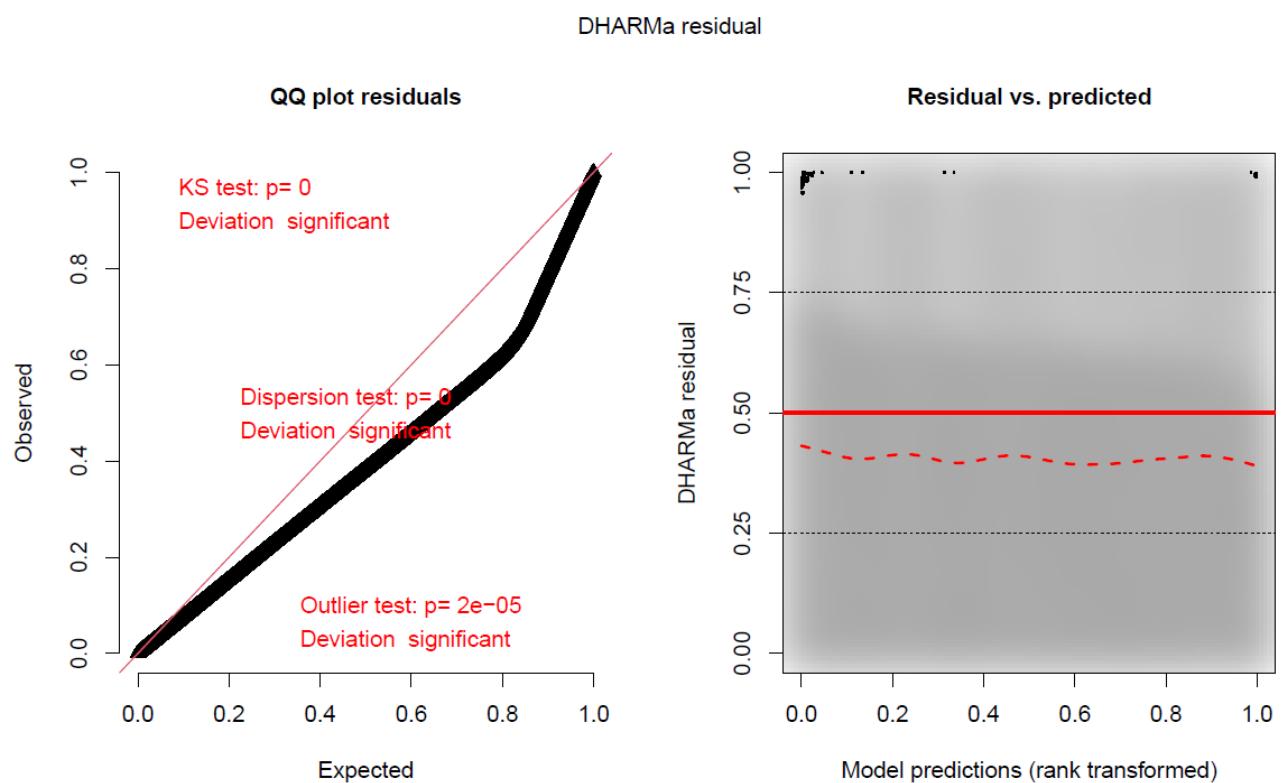


Figure S5.6: Diagnostic plots for the generalised mixed-effects model looking at the effects of land use, land-use intensity, trophic group, residual RMR and their interactions on species' probability of occurrence. The diagnostic plots were obtained with the 'DHARMA' R package (Hartig, 2021).

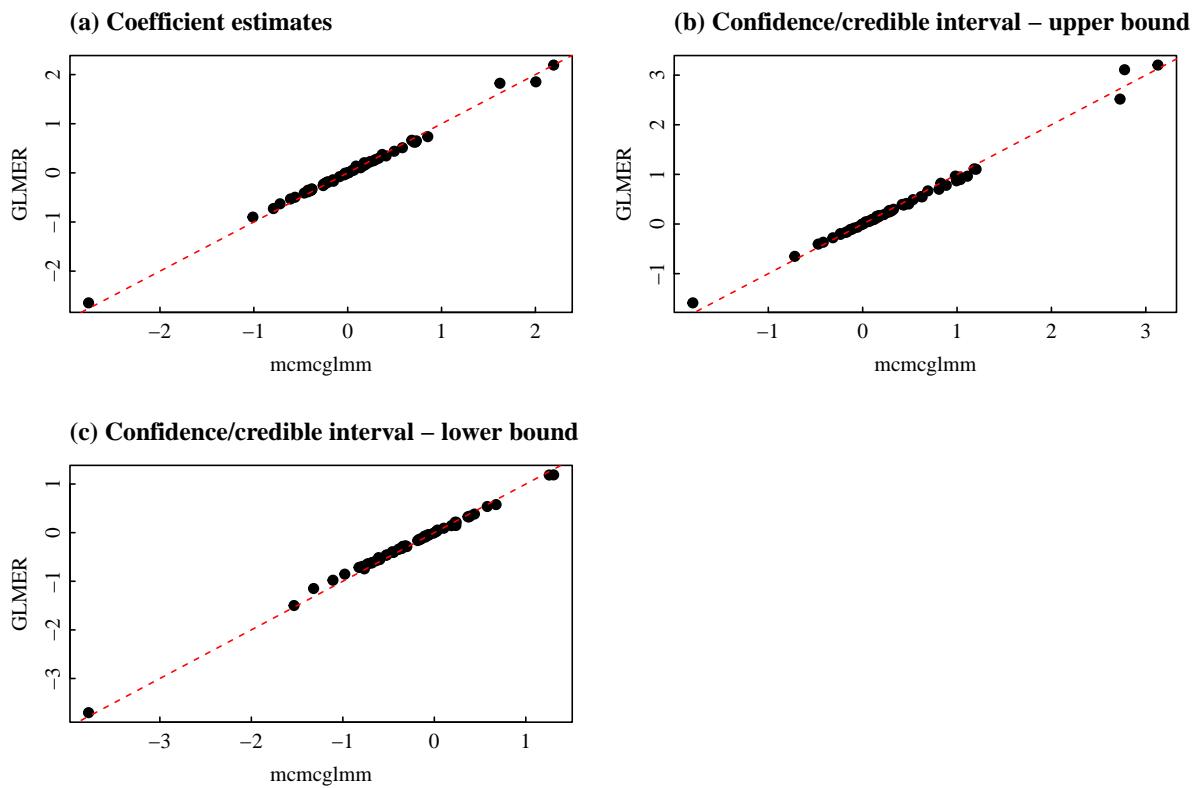
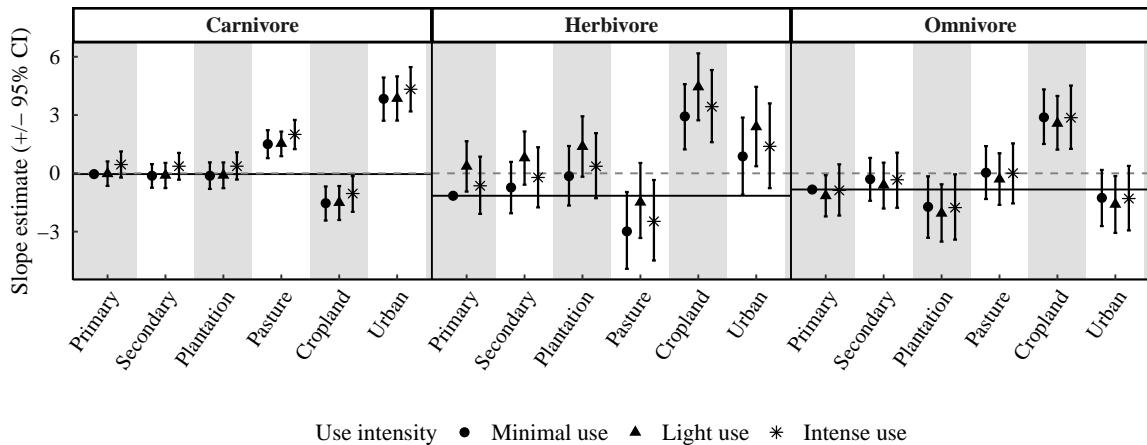


Figure S5.7: Model's coefficients from the occurrence model fitted using the 'lme4' package (Bates et al., 2015) against coefficients from the model fitted using a Bayesian framework with the 'MCMCglmm' package (Hadfield, 2010). The models were fitted to investigate the effects of land use, land-use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

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



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

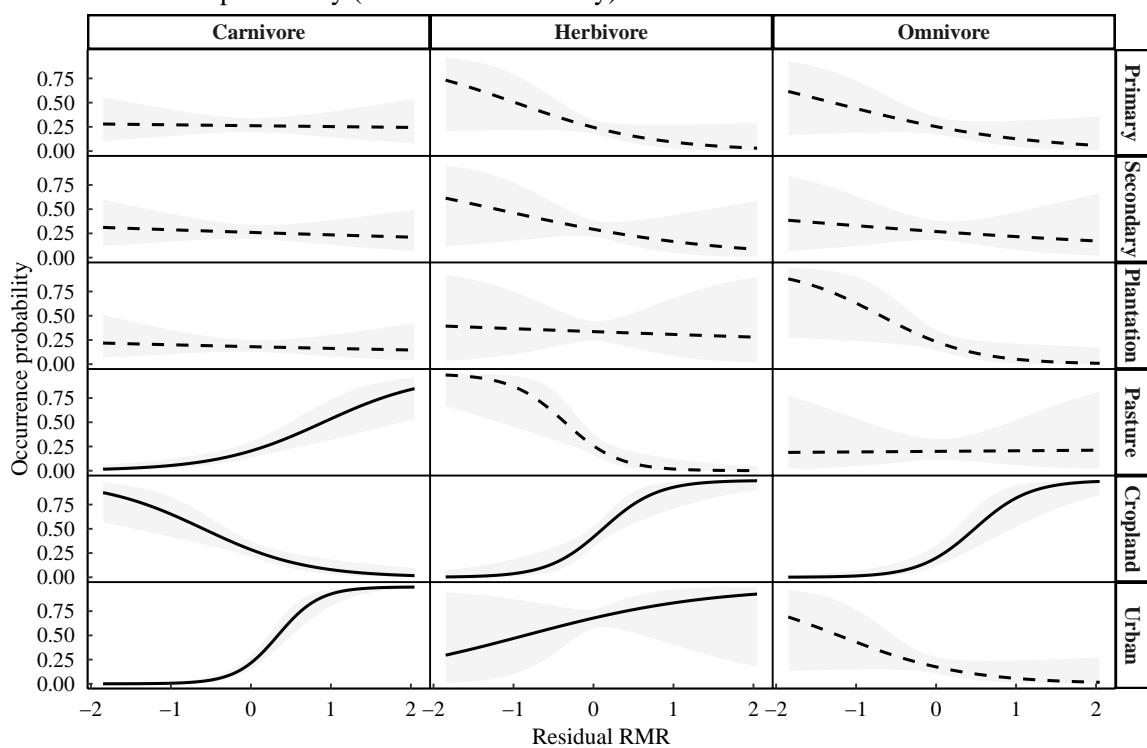


Figure S5.8: (a) Slope estimates for the relationship between residual RMR and occurrence probability in each land-use type and for the three levels of land-use intensity, from the model fitted using the empirical RMR values (i.e., excluding imputed RMR values). The black horizontal line indicates the 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. 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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