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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.

A handwritten signature in black ink, appearing to read "Adrienne Etard".

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First and foremost, huge thanks to my primary supervisor, Tim Newbold, whose guidance has been pivotal to the completion of this PhD journey. I am extremely grateful to Tim for enabling, trusting and encouraging me throughout, for the countless opportunities, for his availability and optimism.

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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 attributes and intrinsic characteristics (traits), 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 on 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 researchers in the field (e.g., Capdevila et al. (2022), *preprint*) 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, notably at the annual meeting of the British Ecological Society (BES) (in 2019, 2020 and 2021), at the annual meeting of the BES Macroecology Special Interest Group (in 2019), and at the International Biogeography Society early-career conference (in 2021). I will additionally present my work at the International Biogeography Society conference (June 2022, 10th Biennial meeting), and at the BES Macroecology conference (July 2022). 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 explain 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 MSc 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. I plan to submit this Chapter as a research article to a scientific journal.

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 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 to a scientific journal.

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

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

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

26 **2.1 Introduction**

27 Species traits are fundamental to ecological and evolutionary research. Comparative studies regularly use
28 trait data across organisms to understand evolutionary processes and species coexistence (Escudero and
29 Valladares, 2016; Zamudio et al., 2016), to investigate global patterns of life forms and functions (Díaz et
30 al., 2016), or to assess species' vulnerability to environmental changes (Böhm et al., 2016; Pacifici et al.,
31 2015; Pearson et al., 2014). Because traits influence species' ability to cope with environmental changes
32 (Newbold et al., 2013) and underpin species' contributions to ecosystem processes (Lavorel and Garnier,
33 2002; Violle et al., 2007; Wong et al., 2018), they play an increasingly important role in functional and
34 conservation ecology.

35 Past and recent efforts to collate and release trait data in the public domain have facilitated the develop-
36 ment of trait-based research. For instance, a global trait database has been published for plants (Kattge et al.,
37 2011). As of May 2020, data from this database had been used in 297 publications since its release (Ac-
38 tivity report, 18/06/2020, <https://www.try-db.org/TryWeb/Home.php>). Such databases hence
39 constitute invaluable research tools and have the potential to greatly advance the field.

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

48 Nevertheless, despite the importance of vertebrate species in global research outputs, there is no single
49 source for vertebrate ecological traits. Consequently, researchers wishing to conduct comparative studies
50 across vertebrate groups may have to collate trait data from a range of sources (such as in Cooke et al.
51 (2019a,b) or in González-Suárez et al. (2018)), a time-consuming prerequisite which may be a limiting
52 step of the research process. Indeed, collating data from heterogeneously-formatted sources presents many

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

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

69 A major issue with incomplete, biased data is the introduction of bias in subsequent analyses. Assessing
70 the amount of missing data as well as the so-called ‘missingness mechanism’ – whether missing data are
71 missing at random, as opposed to there being systematic biases in the way missing values are distributed, see
72 Baraldi and Enders (2010) – is an important prerequisite. Indeed, there exist diverse techniques to deal with
73 data missingness. The simplest one consists of retaining complete cases only by filtering out missing values
74 (case deletion, see Nakagawa and Freckleton (2008)). Nevertheless, case deletion may lead to biased param-
75 eter estimates and erroneous conclusions when values are not missing at random (González-Suárez et al.,
76 2012). Therefore, it is critical to determine the most appropriate way to deal with data incompleteness. For
77 instance, previous studies using terrestrial vertebrate trait data have employed multiple imputation techniques
78 to fill in the gaps (Cooke et al., 2019a; González-Suárez et al., 2012). Yet, imputation techniques could be
79 sensitive to non-randomness in trait data. Phylogenetic biases (where some clades are under-sampled com-
80 pared to other clades) could notably impact the performance of several imputation approaches. It is thus
81 vital to characterise the gaps in trait data prior to any analysis. However, there has been no study to date
82 investigating global patterns in the availability of trait data across terrestrial vertebrates.

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

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

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

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

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

108 Finally, I investigate phylogenetic biases in the trait data. I assess whether particular clades have received
109 more attention than others by looking for patterns in the distribution of trait completeness across the terminal
110 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.

111 2.2 Methods

112 I produced class-specific trait datasets that were made available on figshare (DOI: 10.6084/m9.figshare.
113 10075421). Data compilation and all analyses were conducted with R version 3.5.1 (R Core Team, 2018).
114 Distribution maps were processed using both R and the ‘ArcPy’ package available in ArcGIS v.10.6 (ESRI,
115 2011) (implemented in Python 2.7; van Rossum, G. (1995)).

116 2.2.1 Trait data collection

117 Sources and taxonomic matching

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

128 Briefly, the procedure consisted of extracting synonyms from the IUCN (IUCN, 2020) or from the In-
129 tegrated Taxonomic Information System (ITIS; <https://www.itis.gov/>), using the ‘rredlist’ (Cham-
130 berlain, 2018) and ‘taxize’ (Chamberlain and Szöcs, 2013) R packages. One accepted name was assigned to
131 each synonym. I produced a "Synonym" dataset that I have also made available. I then normalized taxonomy

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

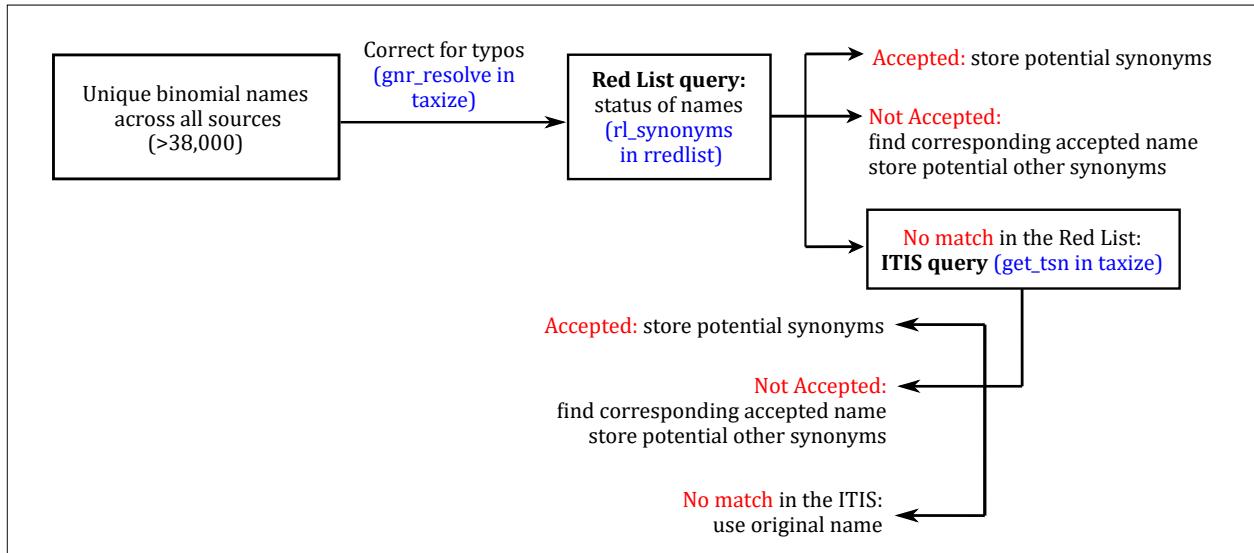


Figure 2.1: Procedure used to identify the accepted names of species. I extracted, where possible, the accepted names of species from either the IUCN Red List or the Integrated Taxonomic Information System (ITIS). Figure reproduced from Etard et al. (2020).

142 Compilation methods

143 For continuous traits, I took the median value within species when multiple estimates were available from
 144 different sources, after removal of any repeated values, which were assumed to represent estimates duplicated
 145 across secondary compilations and derived from the same underlying primary sources. Although intraspe-
 146 cific variation is increasingly being recognized to have important effects on ecological systems (Bolnick
 147 et al., 2011; Des Roches et al., 2018; González-Suárez and Revilla, 2012; Siefert et al., 2015), it was not
 148 feasible to obtain measures of intraspecific variability from all sources; therefore, estimates were provided

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										✓

¹⁴⁹ as a single measure for each species. For some species and some traits, measures were provided separately
¹⁵⁰ for females and males. In such cases, I first obtained the mean of these two measures.

¹⁵¹ Across sources, there were multiple traits related to each of body size and life span. For instance, body
¹⁵² mass and/or body length information could be provided. Different proxies were also available for life span,
¹⁵³ such as the age at sexual maturity or generation length. In such cases, I focused on the trait presenting the

154 highest coverage.

155 • **Body size**

156 Adult body mass estimates were compiled for mammals, birds and reptiles. Body length information
157 was compiled for amphibians, because the coverage for body length was higher than that for body
158 mass. Body mass and body length are known to scale allometrically, although the allometric rela-
159 tionship differs across amphibian clades (Santini et al., 2018). In the amphibian dataset, Pearson’s
160 correlation coefficient between log(Body mass) and log(Body length) was 0.71 (data points shown in
161 Appendix 1, S2.2, Figure S2.2).

162 • **Longevity**

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

171 • **Litter or clutch size**

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

176 • **Trophic level**

177 In all classes, species were described as omnivores, carnivores or herbivores. For reptiles and mam-
178 mals, this information was compiled directly from the sources. For amphibians and birds, trophic
179 levels were not provided. For these two classes, I inferred trophic levels from dietary information
180 (Table 2.1). For birds, I used the primary diet (based on food items recorded as composing $\geq 50\%$
181 of the diet of a species). Diet for amphibians was described without respect to the percentage use of
182 food items; simply as a binary record of whether or not food items were used. In both cases, species
183 recorded to only consume plant-based resources (seeds, nectar, fruit or other plant material) were

184 classified as herbivores. Species consuming only animal resources (invertebrates or vertebrates) were
185 classified as carnivores. Species consuming a mixture of plant and animal resources were classified as
186 omnivores.

187 • **Activity time**

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

194 • **Habitat breadth**

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

202 • **Use of artificial habitats**

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

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

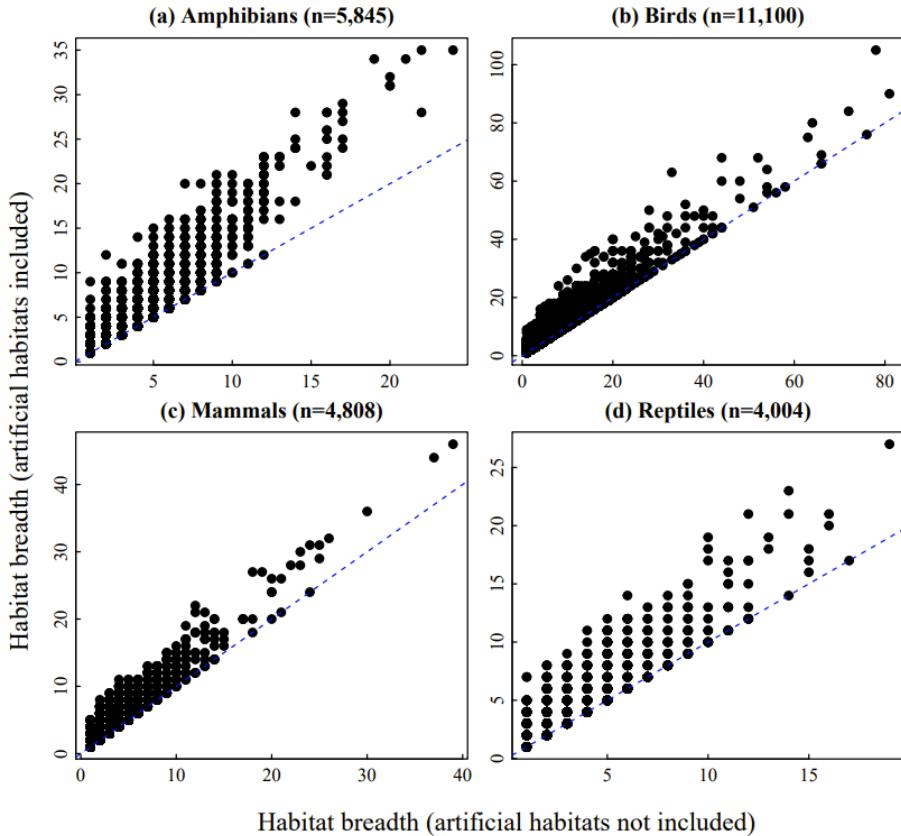


Figure 2.2: Number of natural and artificial habitats used by a species against number of strictly natural habitats used by a species. Pearson's correlation coefficients show a high positive correlation between these two metrics of habitat breadth in all terrestrial vertebrate classes: 0.92 for amphibians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

210 Phylogenies

211 I used class-specific phylogenetic trees downloaded on 13 April 2020. For mammals, I used ‘complete’
 212 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.
 213
 214 For plotting purposes, I obtained consensus trees using the TreeAnnotator program of the BEAST software
 215
 216 (Bouckaert et al., 2019).

218 Species distributions

219 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).
 220
 221 For mammals and amphibians, species distribution maps were obtained from the IUCN Red List (IUCN

222 (2020), downloaded 13 April 2020); for birds, they were obtained from BirdLife International (<http://datazone.birdlife.org/species/requestdis>, downloaded 17 April 2020).

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

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

232 **2.2.2 Investigating gaps and biases in trait data**

233 I used trait coverage and completeness to investigate taxonomic, phylogenetic and spatial biases in the trait
234 data. Table 2.2 summarizes the sample sizes (number of species) in each of the following analyses. Note
235 that species for which completeness was 0% were included in all analyses (for more details, see Figure 2.3).
236 Also note that I did not filter out species identified as extinct or extinct in the wild, because they represented
237 a small proportion of the datasets (0.48% for amphibians, 1.4% for both birds and mammals, and 0.50% for
238 reptiles) and also because I could not exclude such species systematically, because it is likely that I did not
239 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

240 **Taxonomic biases**

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

244 **Phylogenetic biases**

245 Initially, to assess whether more closely related species were more likely to be similar in trait completeness,
246 I estimated the phylogenetic signal in completeness with Pagel's λ (Pagel, 1999) in each class. I used a boot-
247 strapping approach, calculating λ for each of 50 trees randomly sampled in each class (using the 'phylosig'
248 function of the 'phytools' R package; Revell, 2012). I then estimated the mean and 95% confidence intervals
249 (95% CIs) of λ . Sample sizes for computing λ (number of species represented in both the phylogenies and
250 trait datasets) are shown in Table 2.2.

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

254 **Spatial biases**

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

260
$$N_{traits} \sim \log(\text{Range size}) * \text{Class}.$$

261 Second, I mapped assemblage-level median completeness. Assemblages were characterized at the pixel level
262 at 50 km² resolution. I determined pixel-level composition and richness by stacking species geographical
263 distributions. I then calculated median completeness across species in each pixel. I show the resulting
264 maps for herptiles in the main text, and for mammals and birds in Appendix 1 (S2.5, Figure S2.7; median
265 completeness was very high across most pixels for mammals and birds). In addition, I provide maps of
266 assemblage-level mean completeness and standard deviation for all classes in Appendix 1 (S2.5; Figures
267 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.

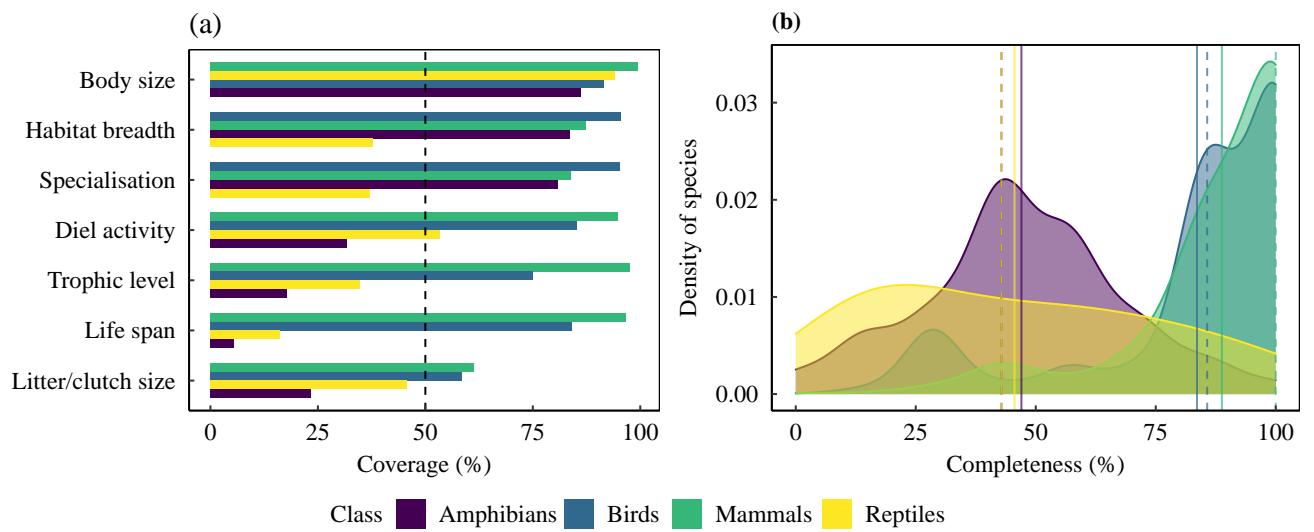


Figure 2.3: Trait coverage and completeness across species. (a) I defined coverage as the proportion of species for which an estimate is available for a given trait. The dashed line represents 50% coverage. (b) Trait completeness is the proportion of estimated traits for a species. Here, I show the distribution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

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

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

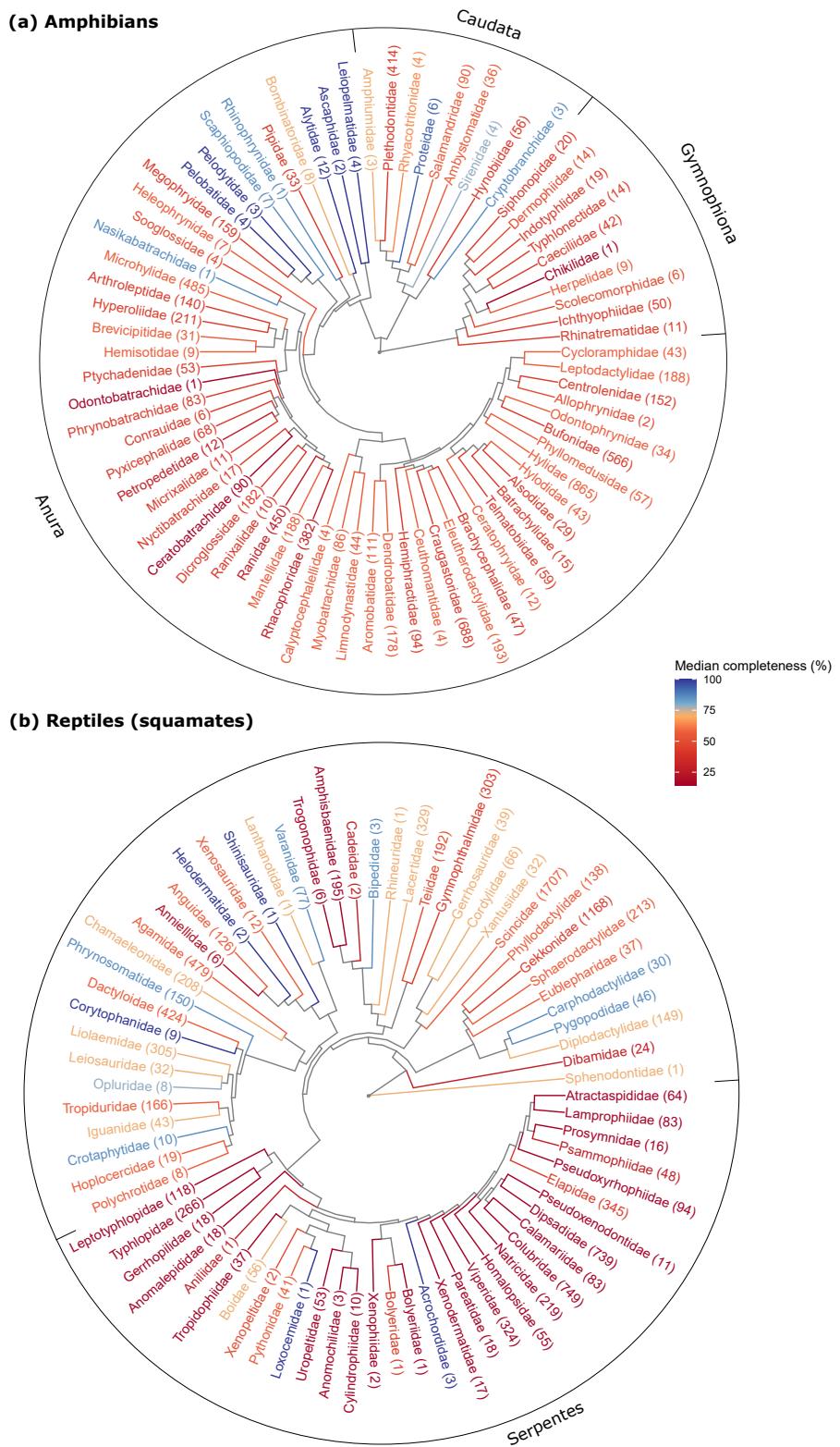


Figure 2.4: Within-family median trait completeness in herptiles. The number next to each family name represents the number of species included in the calculation of the median. *Figure reproduced from Etard et al. (2020).*

330 **2.3.3 Spatial biases in trait completeness**

331 Range size was significantly correlated with the number of sampled traits. Larger range sizes were associated
332 with a higher number of sampled traits (i.e., with higher completeness; Figure 2.5; Appendix 1, S2.7, Table
333 S2.1). Similar results were obtained when using distribution maps not cut by elevational limits (Appendix 1,
334 S2.7, Table S2.2; Figure S2.15). The rate of increase was steepest for reptiles, then for amphibians, then for
335 birds and mammals (slope estimates for birds and mammals were not significantly different from each other;
336 Appendix 1, Table S2.1).

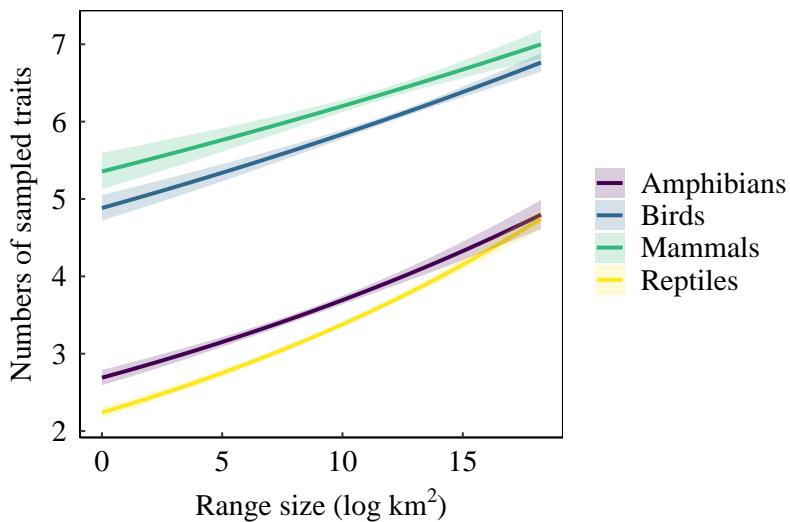
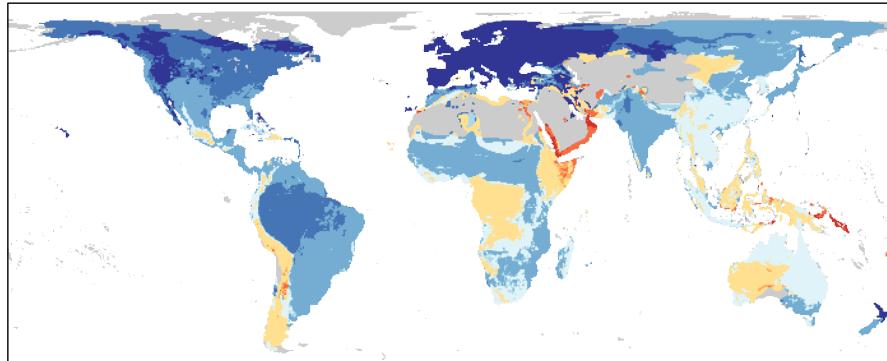


Figure 2.5: Relationship between number of sampled traits and geographical range size. Models were fitted using a Poisson error distribution. Class was added as a predictor interacting with range size. Rates of increase in number of sampled traits with range size were not significantly different for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

337 There were marked spatial variations in median trait completeness in herptiles (Figure 2.6). North Amer-
338 ica and Europe were well sampled for both amphibians and reptiles. Moreover, Southeast Asia and the Congo
339 basin were on average less well sampled. In other regions, contrasting patterns emerged between amphibians
340 and reptiles. For instance, median completeness was poorer for amphibians than for reptiles in Australia,
341 but opposite patterns were observed in South America. As in the phylogenetic analyses, assemblage-level
342 median completeness could mask potential important variation in completeness within species of a given
343 assemblage. Assemblage-level mean and standard deviation maps are shown in Appendix 1 (S2.5, Figures
344 S2.8 and S2.9). There was a trend for increasing standard deviation with increasing species richness, with a
345 larger spread in standard deviation at lower species richness (Appendix 1, section S2.5, 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

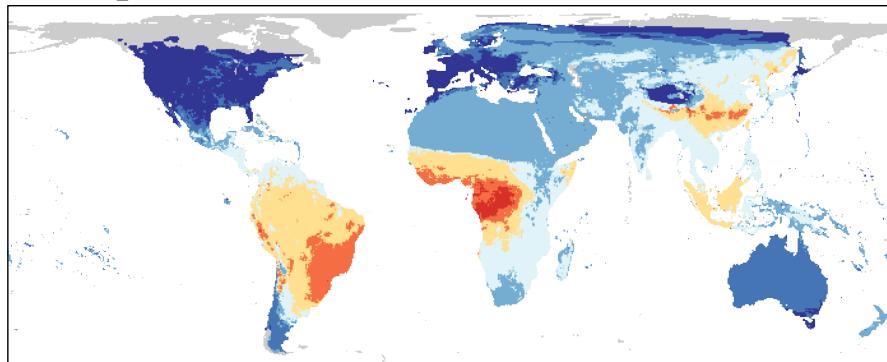


Figure 2.6: Spatial distribution of assemblage-level median trait completeness in herptiles. Similar maps for birds and mammals are shown in Appendix 1 (S2.5, Figure S2.7). *Figure reproduced from Etard et al. (2020).*

346 Spatial models showed that species richness explained median trait completeness in herptiles in most
347 realms (Figure 2.7; Appendix 1, S2.8, Tables S2.3 and S2.4); including spatial lags improved the models
348 (amphibians: $\rho = 0.92$, p-value < 0.0001; reptiles: $\rho = 0.91$, p-value < 0.0001). For reptiles, completeness
349 was negatively correlated with species richness in the most species-rich realms (Afrotropics, Indo-Malayan
350 and Neotropics) and in the Palaearctic; the relationship was steepest in the Afrotropics and shallowest in the
351 Palaearctic. In the Australasian and Nearctic realms, completeness tended to increase with species richness.
352 For amphibians, negative relationships were observed in the Indo-Malay and Nearctic realms, whereas pos-
353 itive trends were observed in the Neotropics and the Palaearctic. The opposite trends between reptiles and
354 amphibians observed in the Australasian and Neotropical realms reflected patterns observed on the maps.
355 The Indo-Malayan was the only realm where median completeness tended to decrease with species richness
356 for both reptiles and amphibians.

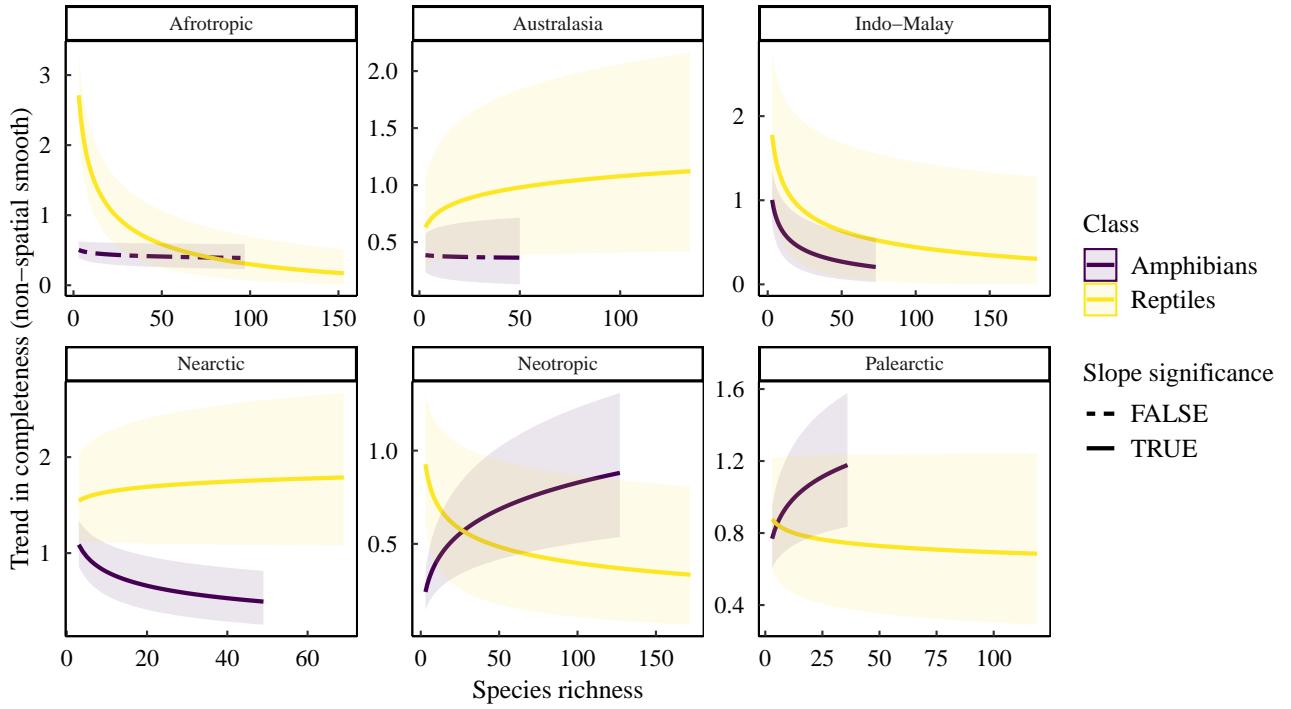


Figure 2.7: Spatial model trends for herptiles. The lines represent in-sample predictions (\pm standard error) for the trend components of the spatial models (trends after accounting for spatial autocorrelation). *Figure reproduced from Etard et al. (2020).*

357 2.4 Discussion

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

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

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

377 I believe that the results presented here are robust to taxonomic uncertainty, although taxonomic match-
378 ing might potentially be improved further using class-specific sources, such as the Reptile Database or Am-
379 phibiaWeb, for identification of synonyms (but see Appendix 1, S2.9, Figure S2.16). I have made two
380 versions of the data compilations available, one in which my own corrections were applied and one using the
381 original binomial names of the sources, meaning that users are free to use their own taxonomic backbones
382 and identify synonyms within the compilations. I believe that taxonomic matching is a recurring issue when
383 working across thousands of species. Taxonomic synonymy artefactually inflates the numbers of identified
384 species, potentially lowering trait coverage (whereas clumping subspecies together can have the opposite
385 effect). Tackling this problem is difficult (Isaac et al., 2004; Jones et al., 2012), notably because there is no
386 global curated database recording the status of species names, and also because of the nature of taxonomy
387 and the debates around the species concept (May, 2011). Nevertheless, taxonomic uncertainty can have
388 important consequences. For instance, Cardoso et al. (2017) showed that inaccuracies and errors in species
389 checklists contributed to the overestimation of plant diversity in the Amazon (but see Freeman and Pennell
390 (2021): the relative underdescription of species in tropical areas compared to temperate areas –‘taxonomic
391 debt’, also referred to as ‘latitudinal taxonomic gradient’ by the authors– may lead to the underestimation of
392 species richness at low latitudes).

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

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

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

422 Ecosystem processes sustained by animals might be harder to quantify and might be influenced by a
423 combination of traits. The traits compiled in this work are likely to have a role in diverse processes. Never-
424 theless, there was one important omission, in that I did not compile species diet in this chapter, potentially the
425 most straightforward trait to link with diverse processes, such as grazing, pollination, scavenging and seed
426 dispersal. From a practical perspective, I chose traits that had been estimated at least for some of the species
427 in each class, and that were readily available. Diet was excluded because although estimates were available
428 for amphibians, birds and mammals, there was no readily available database for reptilian diet. Movement or
429 dispersal abilities were also excluded because information was not readily available for any class. Although
430 I expect that species diet and dispersal abilities would present similar sampling biases to the ones presented
431 in this work, the addition of such traits to the compilation would represent a valuable contribution and would
432 notably facilitate studies looking at the functional roles of reptiles.

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

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

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

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

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

468 (10%–80%) in a complete trait dataset of carnivorans and measured imputation performance in different
469 scenarios. Given that phylogenetic non-randomness in missing trait values can impact imputation accuracy,
470 Penone et al. (2014) removed values in three different ways (completely at random; with a phylogenetic
471 bias; and with a body mass bias). Out of the four techniques, missForest and PhyloPars performed best when
472 species phylogenetic position was included as a predictor of missing trait values. Such imputations appeared
473 to be robust even when trait coverage was as low as 40%, which might be relevant for many reptilian and
474 amphibian traits. The performance was not significantly affected by phylogenetic non-randomness of the
475 data. Hence, missForest and PhyloPars appear to be well suited when traits are phylogenetically conserved,
476 because they allow species phylogenetic position to be included as a predictor of missing trait values. The
477 study by Penone et al. (2014) highlights that there are robust imputation techniques allowing to deal with
478 incomplete trait data where biases might otherwise be problematic. Nevertheless, it is important to highlight
479 that some imputation techniques, such as single or mean imputation, can be problematic because they do
480 not allow an estimation of uncertainty and suffer from a lack of accuracy (Nakagawa and Freckleton, 2008);
481 indeed, imputation techniques sometimes perform no better than case deletion. More work should be con-
482 ducted to assess imputation performance in various contexts (see Johnson 2021), and the datasets compiled
483 in this chapter might provide an opportunity for such studies.

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

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

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

⁴⁹⁸ **fect vertebrate functional diversity**

⁴⁹⁹ **Keywords**

⁵⁰⁰ Land use; land-use intensity; terrestrial vertebrates; functional diversity; traits.

⁵⁰¹ **Abstract**

⁵⁰² Land-use change is the leading driver of global biodiversity loss, thus characterising its impacts on the func-
⁵⁰³ tional structure of ecological communities is an urgent challenge. Using a database describing vertebrate
⁵⁰⁴ assemblages in different land uses, I assess how the type and intensity of land use affect the functional di-
⁵⁰⁵ versity of vertebrates globally. I find that human land uses alter local functional structure by driving declines
⁵⁰⁶ in functional diversity, with the strongest effects in the most disturbed land uses (intensely used urban sites,
⁵⁰⁷ cropland and pastures), and among amphibians and birds. Both tropical and temperate areas experience im-
⁵⁰⁸ portant functional losses, which are only partially offset by functional gains. Tropical assemblages are more
⁵⁰⁹ likely to show decreases in functional diversity that exceed those expected from species loss alone. These re-
⁵¹⁰ sults indicate that land-use change non-randomly reshapes the functional structure of vertebrate assemblages,
⁵¹¹ raising concerns about the continuation of ecological processes sustained by vertebrates.

⁵¹² **3.1 Introduction**

⁵¹³ Anthropogenic activities are profoundly transforming global biodiversity. Although multiple pressures act
⁵¹⁴ in combination, land-use change currently poses the greatest threat to biodiversity (Maxwell et al., 2016;
⁵¹⁵ Newbold et al., 2015). However, not all species respond similarly to land-use change. Traits have been found
⁵¹⁶ to explain species' sensitivity to land-use change in diverse groups (Newbold et al., 2013; Nowakowski et

517 al., 2017; Quesnelle et al., 2014; Todd et al., 2017). Previous work has also shown that land-use change
518 leads to non-random modification of assemblage trait composition (or functional diversity) (Chapman et al.,
519 2018; Colin et al., 2018; Flynn et al., 2009; La Sorte et al., 2018; Newbold et al., 2013; Tinoco et al., 2018).
520 Since it is widely acknowledged that biodiversity, and in particular trait diversity, may promote ecosystem
521 functioning and stability, modification to the trait composition of assemblages could have far-reaching and
522 adverse impacts on ecological processes (Hooper et al., 2012; Magioli et al., 2021; Oliver et al., 2015; Tilman
523 and Downing, 1994).

524 Terrestrial vertebrates support many processes, ranging from pollination (Ratto et al., 2018), to seed
525 dispersal to the regulation of lower trophic levels (Barber et al., 2010; Letnic et al., 2012; Salo et al., 2010;
526 Zhang et al., 2018a). However, we lack a global understanding of how the functional diversity of entire
527 vertebrate assemblages responds to changes in land use. Most previous studies have been conducted at
528 regional or local scales (Davison et al., 2021), but these may not be representative of global patterns. Indeed,
529 recent global syntheses have highlighted how biodiversity responses can differ substantially between regions
530 and across latitudes, with higher sensitivity reported for the tropics (Matuoka et al., 2020; Millard et al.,
531 2021; Newbold et al., 2020b). Another key issue is the taxonomic coverage of past work. Few studies
532 investigating effects of land use on functional diversity have considered several vertebrate classes together,
533 and comparative studies remain rare. Thus, how land-use change affects the functional diversity of local
534 vertebrate assemblages at global scales, and the potential geographical and taxonomic variation in the effects,
535 still largely remains to be explored.

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

545 To this end, I combine (1) the trait data across terrestrial vertebrates collected in Chapter 2 (also published
546 in Etard et al. (2020)), with (2) global records of species occurrence in eight land-use types of differing
547 intensity of use (the PREDICTS database: Hudson et al. (2014, 2017), Figure 3.1, Appendix 2: Table S3.1).
548 The PREDICTS database is currently the most comprehensive database of sampled species occurrence,

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

- 553 1. I expect decreases in functional diversity in human land uses compared to primary vegetation, caused
554 by contractions of occupied trait space. I expect such effects to be more pronounced where land is
555 used more intensively by humans. This hypothesis builds upon evidence that species with certain
556 traits are more sensitive to land-use disturbance (Newbold et al., 2013), meaning that disturbed land
557 uses will retain only disturbance-tolerant species, more functionally similar to one another. Given the
558 reported higher sensitivity of tropical assemblages to land-use disturbance, I predict that such effects
559 are stronger in the tropics.
- 560 2. I hypothesise that decreases in functional diversity in disturbed land uses exceed decreases expected
561 by chance, given local species loss. Thus, I expect disturbed land uses to promote functional under-
562 dispersion. Functional under-dispersion occurs when species within an assemblage are more similar,
563 in term of their traits, than expected by chance (Cadotte and Tucker, 2017; Wong et al., 2018) – or,
564 in other words, when functional dispersion is lower than expected given local species richness. I
565 predict that under-dispersion is more likely to occur in the highly disturbed sites, in both temperate
566 and tropical areas. This hypothesis is based on the idea that species are being removed non-randomly
567 from sensitive areas of the trait space, and increasingly so with higher disturbance level.
- 568 3. Finally, I expect decreases in functional diversity in human land uses to be driven by high functional
569 loss, whereby species are being removed from previously occupied areas of the trait space; I expect
570 no functional gain. This hypothesis is based on the idea that the functional trait space in undisturbed
571 land uses represents all of the possible regional trait combinations and that species with functional
572 attributes rendering them unable to persist in altered conditions will be filtered out (Cornwell et al.,
573 2006).

574 3.2 Methods

575 3.2.1 Vertebrate assemblages

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

- Tropical sites (3914)
- Temperate sites (2373)

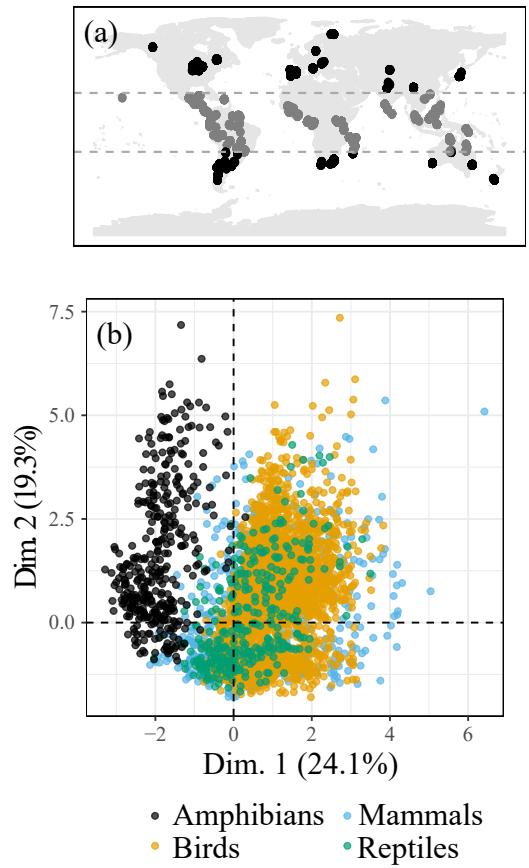


Figure 3.1: Overview of the study design and functional metrics. I used occurrence data for vertebrate species from the PREDICTS database ((Hudson et al., 2014, 2017); 180 studies; 431,170 records; 4,339 species; 6,758 sampled sites). (a) shows the spatial distribution of sites I consider. I combine occurrence data with trait data compiled in Chapter 2 to calculate functional 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, \mathbf{g} Laliberte 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. (2021).*

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

583 Land uses in PREDICTS were assigned to the following categories, based on the descriptions of the

584 habitat given by the original collectors of the data: primary vegetation (considered to be the undisturbed ref-
585 erence); secondary vegetation; plantation forest; pasture; cropland; urban (considered human, or disturbed;
586 Appendix 2, Table S3.1; Hudson et al., 2014, 2017). Secondary vegetation is further divided into three cat-
587 egories: mature, intermediate and young, depending on the stage of recovery of the vegetation. Land-use
588 intensity is reported as minimal, light or intense, according to criteria that depended on the land-use type in
589 question (e.g., crop diversity, degree of mechanisation and chemical inputs in cropland, or bushmeat harvest-
590 ing and selective logging in primary vegetation; Hudson et al., 2014). I excluded sites for which the land use
591 could not be characterised or for which the stage of recovery of secondary vegetation was unclear. As the
592 PREDICTS database is a collection of independent studies, the design of this study was not balanced: the
593 sample size varied across land uses (Appendix 2, Figures S3.1, S3.2), and across taxonomic groups (3103
594 species of birds; 531 mammals; 379 amphibians; 326 reptiles).

595 3.2.2 Functional traits and diversity indices

596 Trait choice is a critical step when calculating functional diversity metrics, which are highly sensitive to trait
597 selection (Mouillot et al., 2021). However, trait selection trades off with data availability. Here, a constraint
598 was to use similar traits across the different classes. I thus used the seven traits compiled in Chapter 2
599 across terrestrial vertebrates. Most of these traits were available for at least 50% of the species in each
600 class (except trophic level in amphibians and lifespan in herptiles; Appendix 2, Figure S3.4). In addition, I
601 chose these traits as they were ecologically relevant, thus I broadened the biological definition of traits (i.e.,
602 a characteristic measurable at the level of an individual) to include measures of habitat breadth and habitat
603 specialisation (still theoretically measurable at the level of an individual). The final set constituted seven traits
604 that influence species responses to environmental change: body mass, trophic level, lifespan, litter/clutch
605 size, diel activity, habitat breadth and use of artificial habitats. These traits related to life-history, habitat
606 specialisation and use of geographical space (e.g., habitat breadth is a significant predictor of geographical
607 range size in all classes; Appendix 2, Figure S3.3). Here, I did not consider estimations of dispersal abilities
608 or home range size as these were available for a small fraction of the species (<3%, Alex Smith and M.
609 Green, 2005; Paradis et al., 1998; Sutherland et al., 2000; Whitmee and Orme, 2013), neither did I include
610 geographical range size which is measured across many individuals, and hence cannot be considered a trait.
611 As in Chapter 2, I did not consider intraspecific trait variation, thus assuming no effect of the environment
612 on trait values.

613 Trait coverage was variable among classes and traits, with important gaps for reptiles and amphibians
614 (Appendix 2, Figures S3.4, S3.5; Chapter 2; Etard et al. (2020)). I imputed missing trait values using random

615 forest algorithms ('missForest' package: Stekhoven and Bühlmann (2012), Stekhoven (2016)), including
616 traits, taxonomic order and phylogenetic eigenvectors as predictors (Debastiani et al., 2021; Penone et al.,
617 2014). To further assess the sensitivity of the results to imputation (see next section), I imputed missing
618 trait values eight times, thereby obtaining eight sets of imputed traits. I randomly selected one imputed trait
619 set for the calculation of functional metrics. Imputations of missing trait values & imputation performance
620 are detailed in Appendix 2, sections S3.2 and S3.4 (and see Figures S3.6-S3.8). Post-imputation, continuous
621 traits were log10-transformed (except habitat breadth which was square-rooted) and z-scored (standardised to
622 unit variance and zero mean). In addition, I also assessed whether the results were robust to imputation error
623 using a subset of the PREDICTS data considering only species for which I had complete trait information
624 (see next section).

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

633 3.2.3 Effects of land use and land-use intensity on FRic and FDis (Hypothesis 1)

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

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

648 $\text{arcsin}(\sqrt{\text{FRic}}) \sim \text{Land use} + \text{Land-use intensity} + \text{Region} + \text{Land use : Land-use intensity} + \text{Land use : Region}$

649

650 (Model 1a)

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

653 $\text{arcsin}(\sqrt{\text{FDis}}) \sim \text{Land use} + \text{Land-use intensity} + \text{Region} + \text{Land use : Land-use intensity}$.

654 (Model 1b)

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

660 $\text{arcsin}(\sqrt{\text{FRic}}) \sim \text{Land use} + \text{Land-use intensity} + \text{Region} + \text{Class} + \text{Land use : Land-use intensity} + \text{Land use : Class} + \text{Land-use intensity : Region} + \text{Class : Region}$

661

662 (Model 2a)

663 For FDis, regional effects were dropped:

664 $\text{arcsin}(\sqrt{\text{FDis}}) \sim \text{Land use} + \text{Land-use intensity} + \text{Class} + \text{Land use : Land-use intensity} + \text{Land use : Class} + \text{Land-use intensity : Class}$

665

666 (Model 2b)

667 To assess whether the results were robust to imputation error, I used a subset of the PREDICTS data
668 considering only species for which there were complete trait information (6,212 sites; 442 mammals; 1,975
669 birds; 78 reptiles; 9 amphibians), and I fitted models again to this data subset. I did not have enough complete
670 trait data among amphibians to be able to consider this class separately, so I first considered amphibians and
671 reptiles together (herptiles), and reptiles only. In addition, I complemented this validation with a sensitivity
672 analysis to variation in imputed values. I calculated FDis and FRic using each of the eight imputed trait
673 datasets and fitted the previous models to each set. I then qualitatively evaluated the congruence of the
674 estimates from the different models. Finally, because there tended to be more sites sampled in primary

675 vegetation than in other land uses (Appendix 2, Figures S3.1, S3.1), I ran additional sensitivity tests to assess
676 whether the results were robust to resampling primary vegetation sites to a number equal to 50 (a sample
677 size close to the median number of sites sampled in land uses other than primary vegetation in both regions
678 (median = 37 for the temperate subset and 57 for the tropical subset, Appendix 2, Figure S3.1)).

679 **3.2.4 Investigating functional under-dispersion (Hypothesis 2)**

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

$$690 P_{\text{under-dispersion}} \sim \text{Land use} + \text{Land-use intensity} + \text{Region} + \text{Land use : Land-use intensity} + \text{Land use : Region}$$

692 (Model 3)

693 **3.2.5 Functional loss and functional gain (Hypothesis 3)**

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

703 $\arcsin(\sqrt{\text{loss}}) \sim \text{Land use} + \text{Land-use intensity} + \text{Region} + \text{Land use : Land-use intensity} + \text{Land use : Region}$.

705 (Model 4a)

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

707 $\arcsin(\sqrt{\text{gain}}) \sim \text{Land use} + \text{Land-use intensity} + \text{Region} + \text{Land use : Land-use intensity}$.

708 (Model 4b)

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

710 $\arcsin(\sqrt{\text{loss}}) \sim \text{Land use} + \text{Land-use intensity} + \text{Class} + \text{Region} + \text{Land use : Land-use intensity} + \text{Land use : Class} + \text{Land use : Region} + \text{Land-use intensity : Class}$.

712 (Model 5a)

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

715 All data analyses were conducted using R version 3.5.1 (R Core Team, 2018). I made the code available
716 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>).

719 3.3 Results

720 3.3.1 Effects of land use on FRic and FDis

721 Across all vertebrates, land use and land-use intensity significantly affected FRic and FDis (Figure 3.2).
722 FRic tended to decrease with increasing disturbance level and higher intensity of land use. For FRic, relative
723 effects differed between regions (Figure 3.2a). Although declines were overall more important for disturbed
724 tropical assemblages, significant declines were observed for the temperate assemblages (e.g., a 37% average
725 decline in intensely used urban areas; a 49% decline in pastoral areas of high land-use intensity). Never-
726 theless, tropical assemblages typically showed more important reductions in FRic. For instance, declines
727 averaged 63% for intensely used tropical cropland and 76% for urban areas. For FDis, relative effects were
728 similar in both regions (Figure 3.2b). The most important average declines were observed for urban assem-
729 blages of intense use (20% decline), and for lightly- and intensely used cropland (by 15% and 26%). Note

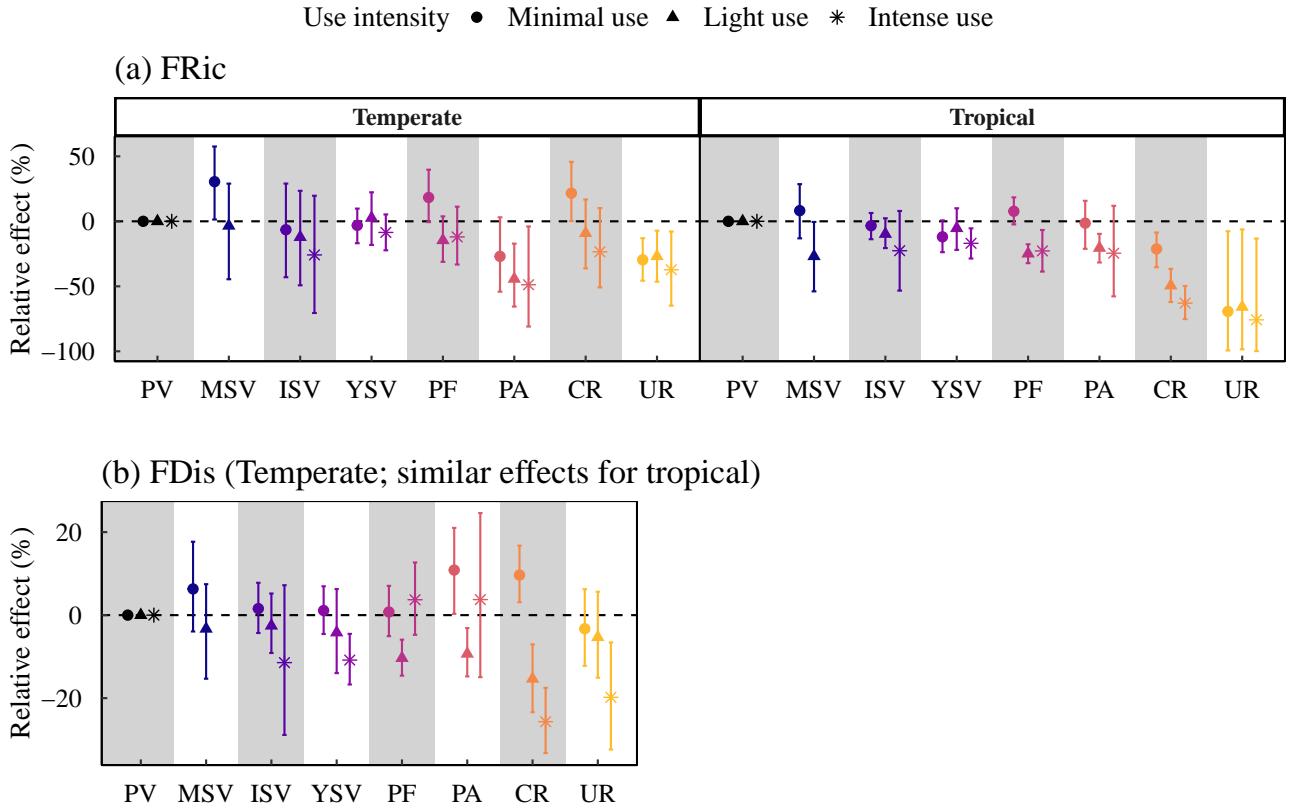


Figure 3.2: Effects of land use, land-use intensity and region on FRic (a) and on FDis (b) across all PREDICTS vertebrates. Effects were rescaled with reference to primary vegetation (PV) and are plotted as a % difference relative to PV within each land-use intensity. For FRic, the best-fitting model 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. (2021).*

730 that confidence intervals around the estimated average declines were large in some cases, highlighting some
 731 heterogeneity in the responses.

732 Fitting the same models to the subset of species with complete trait data, I detected important declines in
 733 functional diversity in a number of land uses, showing that the conclusions are robust to trait imputation un-
 734 certainty (for example, FRic declined on average by 75% in intensely used temperate pastoral assemblages;
 735 by 48% for intensely used tropical cropland; and FDis declined by an average 37% in intensely used tropical
 736 urban assemblages; Appendix 2, Figure S3.18). Furthermore, using the subset of species with complete trait
 737 data, I found that the results were not sensitive to the inclusion of geographical range size as an additional
 738 trait (Appendix 2, Figure S3.19). Finally, the results were not sensitive to variation across imputed trait val-
 739 ues (Appendix 2, Figure S3.20) and were also robust to resampling in primary-vegetation sites (Appendix 2,
 740 Figure S3.21).

741 Responses of FRic and FDis to land use and land-use intensity differed among taxonomic classes (Figure
742 3.3). Within-class effects for FDis were similar between regions. The most notable decreases were observed
743 in lightly- and intensely used agricultural land uses in amphibians, birds and reptiles; and in intensely used
744 urban land uses for birds and mammals. For FRic, the effects in tropical and temperate regions were qualitatively
745 similar in three out of four classes (birds, mammals and reptiles), although effect sizes tended to be
746 bigger for tropical assemblages. Birds and reptiles showed reductions in disturbed land uses in both tropical
747 and temperate regions, whereas I detected few significant effects for mammals. For birds, the most important
748 average decline, of 50%, was observed in intensely used tropical urban land uses, while for reptiles I detected
749 significant decreases in lightly- and intensely used agricultural sites (but I could not estimate effects for urban
750 land uses due to the small sample size). Finally, the effects differed between tropical and temperate regions
751 for amphibians, with no significant effects detected across temperate assemblages, but important reductions
752 across tropical agricultural and urban assemblages.

753 Fitting similar models only for species with complete trait data showed that these patterns are unlikely
754 to be affected by imputation uncertainty for birds; for mammals and reptiles, the main results could even be
755 conservative (Appendix 2, Figures S3.22, S3.23). Indeed, although confidence intervals around the estimates
756 were large, I typically observed larger decreases in functional diversity when using the complete data subset,
757 including an 86% decline in FRic for mammals in intensely used tropical agricultural areas. The results were
758 also unaffected by variation across replicate sets of imputed trait values (Appendix 2, Figure S3.24).

759 **3.3.2 Changes in the probability of occurrence of functional under-dispersion**

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

766 **3.3.3 Functional loss and gain**

767 Across and within vertebrate classes, I detected high levels of functional loss, exceeding the natural turnover
768 between primary-vegetation sites, both in temperate and tropical regions. Across vertebrates (Figure 3.5a),
769 functional loss was notably high in temperate pastures (+27% above reference for minimal use; +73% for
770 intense use), temperate urban sites (+27% for light use; +50% for intense use; effects for tropical urban sites

Use intensity • Minimal use ▲ Light use * Intense use

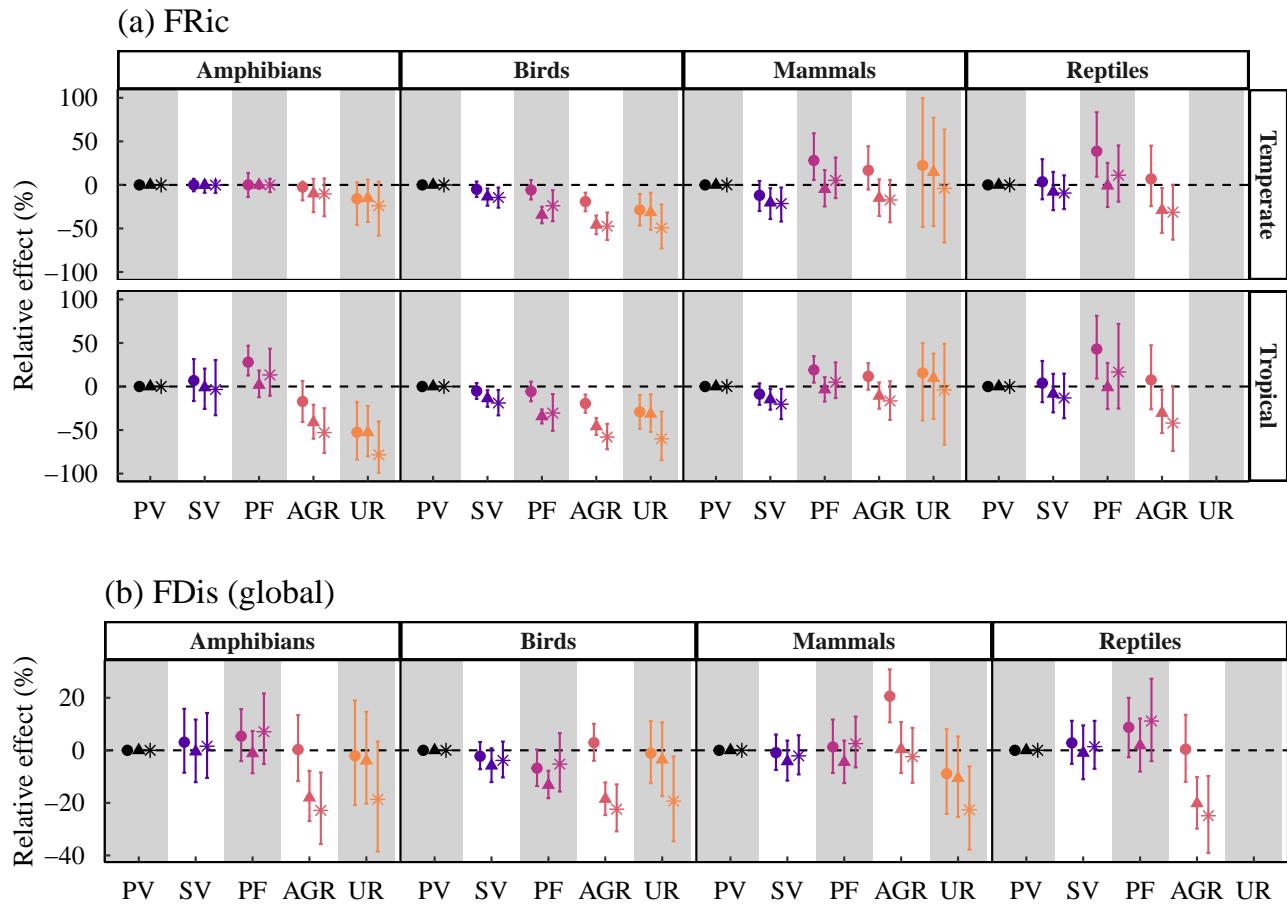


Figure 3.3: Effects of land use, land-use intensity, region and taxonomic class on FRic (a) and FDis (b). Effects were rescaled with reference to primary vegetation (PV) and are plotted as a % difference relative to PV within each land-use intensity. Error bars represent 95% confidence intervals. Effects 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. (2021).*

771 could not be estimated), temperate and tropical cropland (+44% and +56% respectively for light use; effects
 772 for intense use could not be estimated). Important levels of functional loss were also observed in tropical
 773 plantation forest of light use intensity (+51%; effects for the intense use could not be estimated). High
 774 levels of functional loss were also observed within each class (Figure 3.6a) (although not all effects could
 775 be estimated because of limited sample sizes, Appendix 2, Table S3.5). The highest losses were observed
 776 in agricultural areas for amphibians and reptiles, with important losses also observed in temperate urban
 777 areas for both birds and amphibians (+35% for minimal use; effects for tropical urban areas could not be
 778 estimated).

779 Across vertebrates (Figure 3.5b), average functional gain (average proportion of novel trait space in the

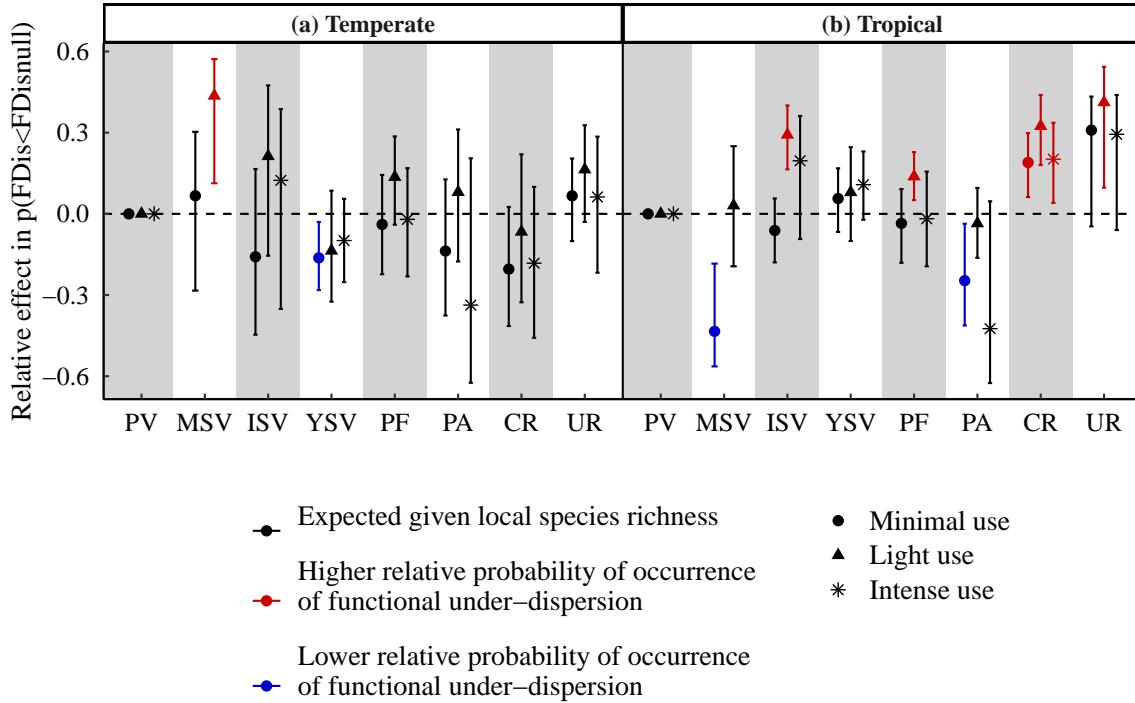


Figure 3.4: Effects of land use, land-use intensity and region on the probability of occurrence of functional under-dispersion. Error bars represent 95% confidence intervals. PV: primary vegetation; MSV, mature secondary vegetation; ISV, intermediate secondary vegetation; YSV, young secondary vegetation; 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. (2021).*

disturbed assemblage) was moderate and on average did not exceed 20% in any disturbed land uses. 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)).

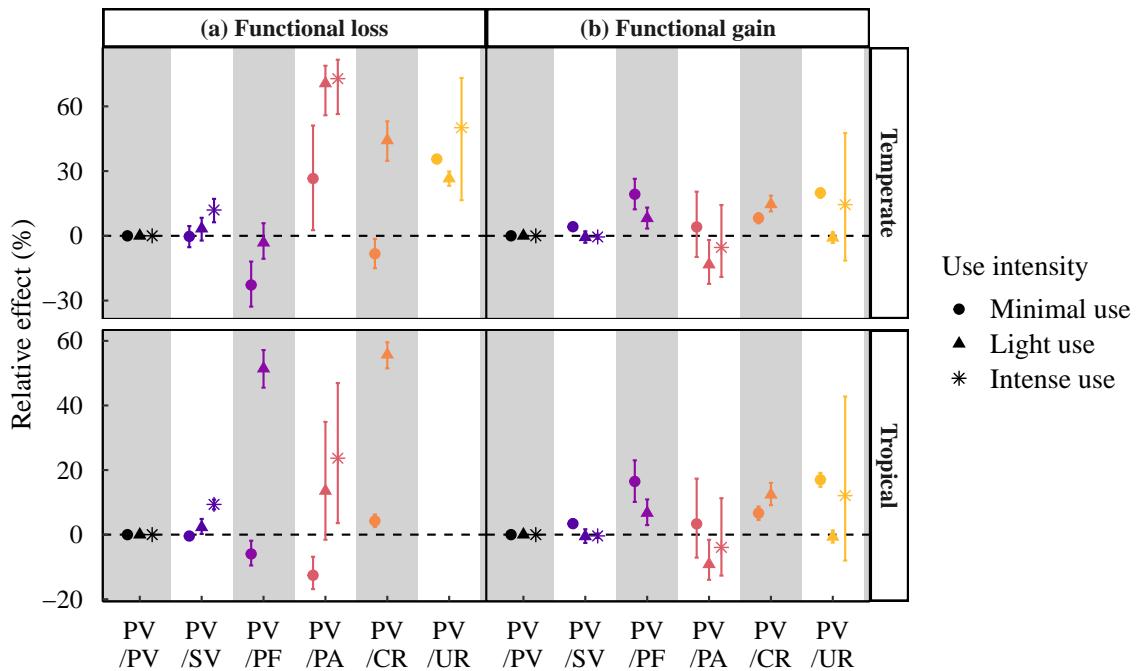


Figure 3.5: Effects of land use and land-use intensity on (a) functional loss and (b) functional gain across pairs of sites in temperate areas and tropical areas. PV: primary vegetation; SV, secondary vegetation; PF, plantation forest; PA, pasture; CR, cropland; UR, urban. Error bars represent 95% confidence 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. (2021).*

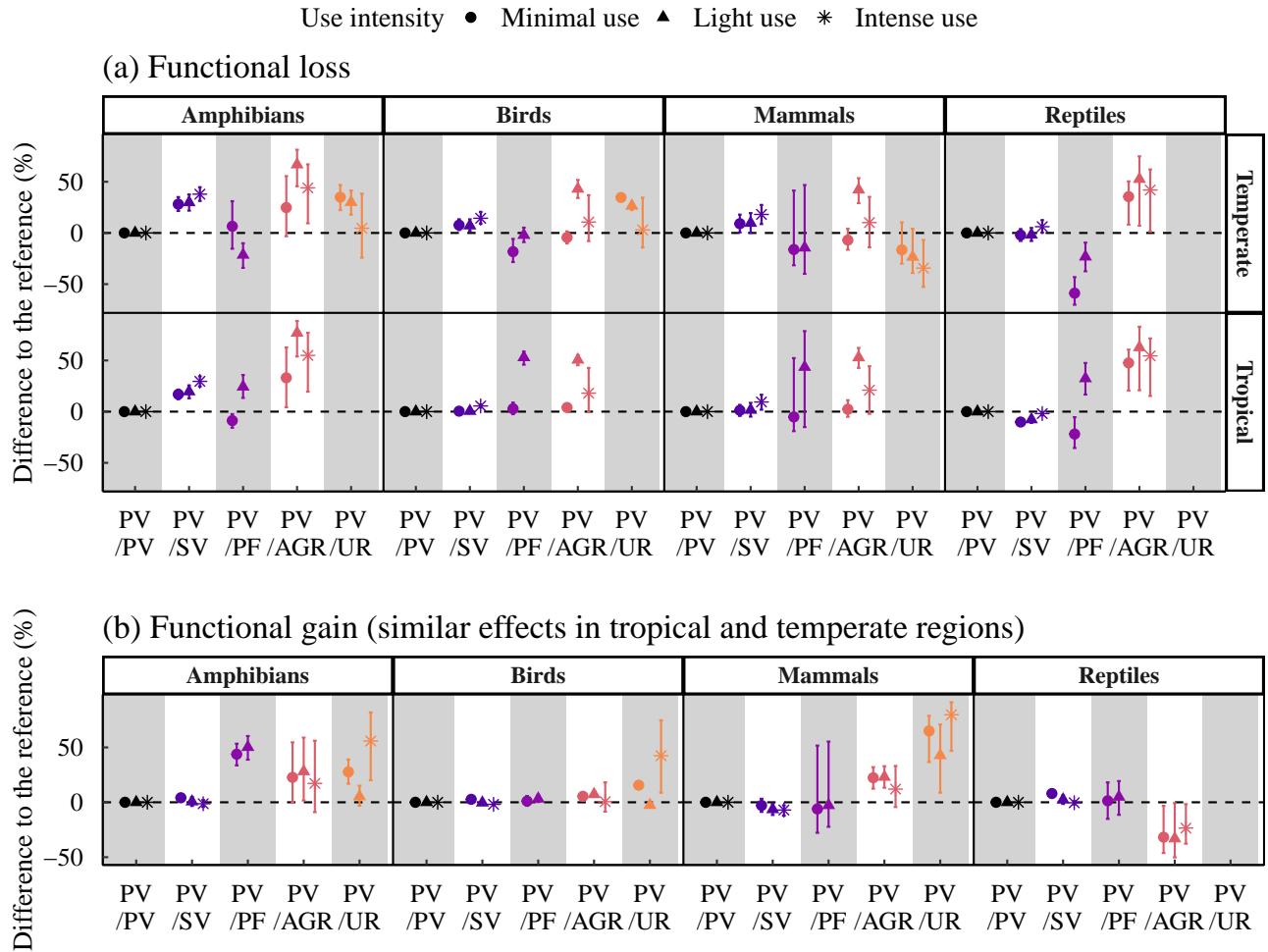


Figure 3.6: Effects of land use, land-use intensity, region and taxonomic class on functional loss and functional gain across pairs of sites. PV: primary vegetation; SV, secondary vegetation; PF, plantation forest; AGR, agricultural land uses (pasture and cropland); UR, urban. Error bars represent 95% 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. (2021).*

788 **3.4 Discussion**

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

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

809 Overall, the negative effects of land use on functional richness tended to be more pronounced in the
810 tropics. This is congruent with past studies that have found tropical biodiversity to be disproportionately
811 sensitive to human pressures (Martins and Pereira, 2017; Newbold et al., 2020b). There are a number of
812 potential explanations for this. First, it could be that a long history of intense land-use disturbance at large
813 scales in many temperate regions (e.g. Western Europe; Stephens et al. (2019)) means that biodiversity is
814 now less sensitive to new disturbances, because the most sensitive species have been filtered out (Balmford,
815 1996; Krauss et al., 2010; Le Provost et al., 2020; Munteanu et al., 2020). Species unable to cope with such
816 disturbances may have gone extinct in the past, while the remaining species would be more disturbance-
817 tolerant (Betts et al., 2019). Tropical regions, historically less disturbed at large scales, would then contain
818 a higher proportion 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 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 I have information on time since land-use conversion [see Appendix 2, section S3.8]).

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 func-

883 tional richness in at least three out of four vertebrate classes (amphibians, birds, and reptiles), in accordance
884 with past studies focusing on each of these groups (Gallmetzer and Schulze, 2015; Marcacci et al., 2021;
885 Riemann et al., 2017; Sol et al., 2020). Although overall mammalian functional richness was less affected,
886 high levels of functional gain suggest that the functional composition of mammalian assemblages is heavily
887 modified in disturbed land uses.

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

895 **4 | Geographical range area, habitat breadth**

896 **and specialisation on natural habitats**

897 **explain land-use responses and climate-**

898 **change sensitivity more consistently than**

899 **life-history and dietary traits in terres-**

900 **trial vertebrates**

901 **Keywords**

902 **Abstract**

903 **4.1 Introduction**

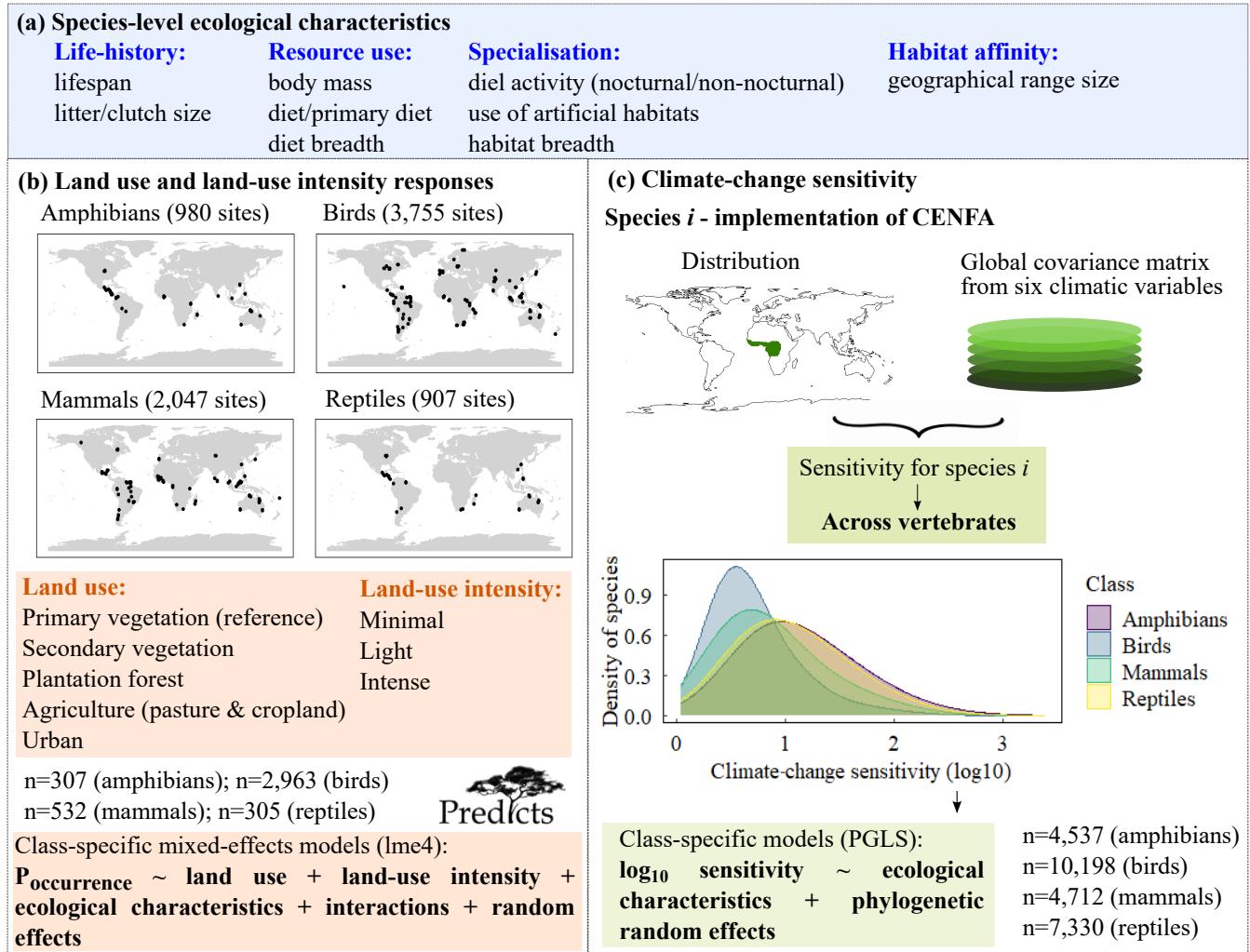
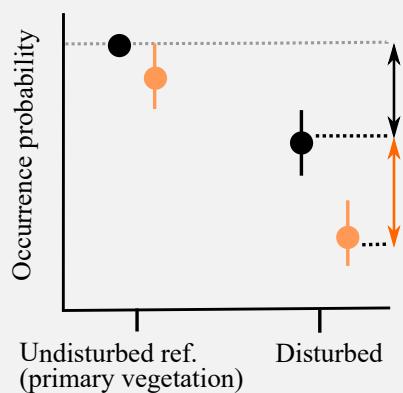


Figure 4.1: Framework of the study. (a) I collected ecological trait data and geographical range areas across terrestrial vertebrates (termed ‘ecological characteristics’). I then used two independent approaches to assess the influence of these characteristics on species responses to land-use and on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

904 **4.2 Methods**

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



"Among land-use types" effects:

Main effect of given characteristic on occurrence probability, **among land-use types**

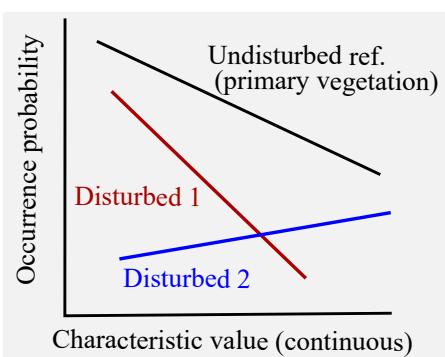
"Within land-use type" effects:

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: more negative in disturbed than in reference land-use type: more negative effects of characteristic on occurrence probability than in reference land-use type

2: more positive in disturbed than in reference land-use type: more positive effects of characteristic on occurrence probability than in reference land-use type

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

Figure 4.2

905 **4.3 Results**

906 **4.4 Discussion**

907 **5 | Energetic constraints and trophic group**

908 **explain species persistence in disturbed**

909 **land uses**

910 **Keywords**

911 Land use; land-use intensity; metabolic rates; energetic constraints; energetic requirements; terrestrial verte-
912 brates; trophic group; occurrence.

913 **Abstract**

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

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

935 **5.1 Introduction**

936 Land-use change is currently the strongest driver of global biodiversity declines (Maxwell et al., 2016;
937 Newbold et al., 2015), with major and long-lasting impacts on the structure and functioning of ecological
938 communities (Bregman et al., 2016; Fukasawa and Akasaka, 2019; Magioli et al., 2021; Marcacci et al.,
939 2021). With land-use change likely to continue to intensify (Stehfest et al., 2019), it is vital to put into
940 place conservation and mitigation measures to minimise future losses of biodiversity and negative impacts
941 on ecosystem functioning. To this end, pressing questions remain as to what renders species able or unable
942 to cope with human disturbance, and how losses of sensitive species might influence ecosystem functioning
943 (Dirzo et al., 2014; Young et al., 2016).

944 Land-use change acts as an environmental filter affecting species persistence (Edwards et al., 2021;
945 Evans et al., 2018). Past studies have shown that sensitivity to land-use change is distributed unevenly across
946 the tree of life (Nowakowski et al., 2018), and across behavioural (Lowry et al., 2013; Samia et al., 2015)
947 and ecological strategies (De Palma et al., 2015; Møller, 2009; Newbold et al., 2013). For instance, long-
948 lived and large forest specialist birds respond more negatively to land-use change than generalist species
949 (Newbold et al., 2013). In addition, human land uses impose energetic constraints on species, by modifying
950 the amount and type of available resources (Inger et al., 2016; Zuñiga-Palacios et al., 2021). Consequently,
951 land-use change brings about modifications in dietary and foraging strategies (Møller, 2009; Ramesh et al.,
952 2017; Sévèque et al., 2020), which can have cascading effects on local trophic structure (e.g., mesopredator
953 release; Crooks and Soule (2010)). The impacts of land-use change on biodiversity also depend on land-
954 use intensity (Davison et al., 2021; Newbold et al., 2015), that is, the magnitude of human disturbance in
955 a given land-use type, which can vary importantly according to local practices and management (Dullinger
956 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 our 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, we 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.

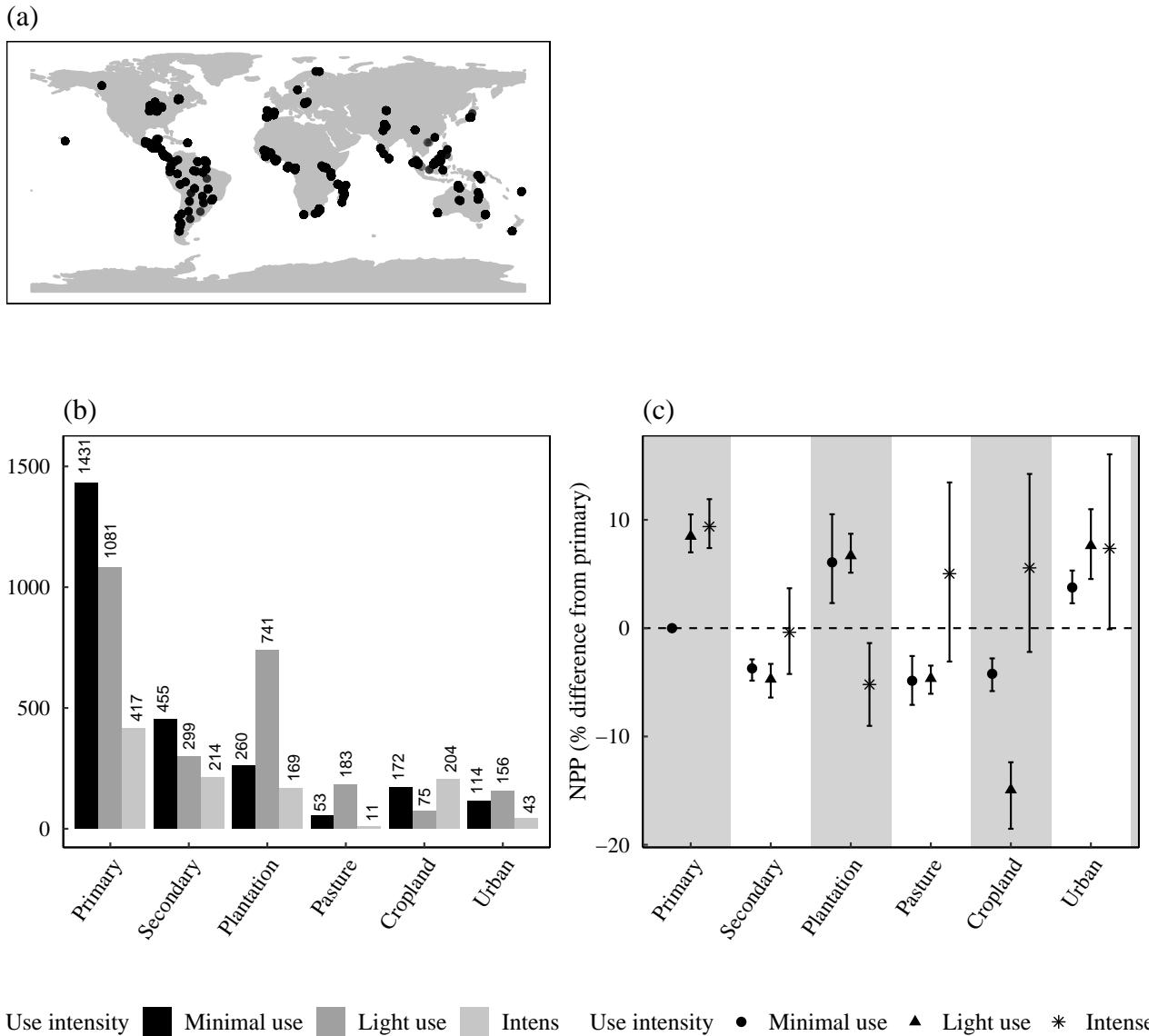
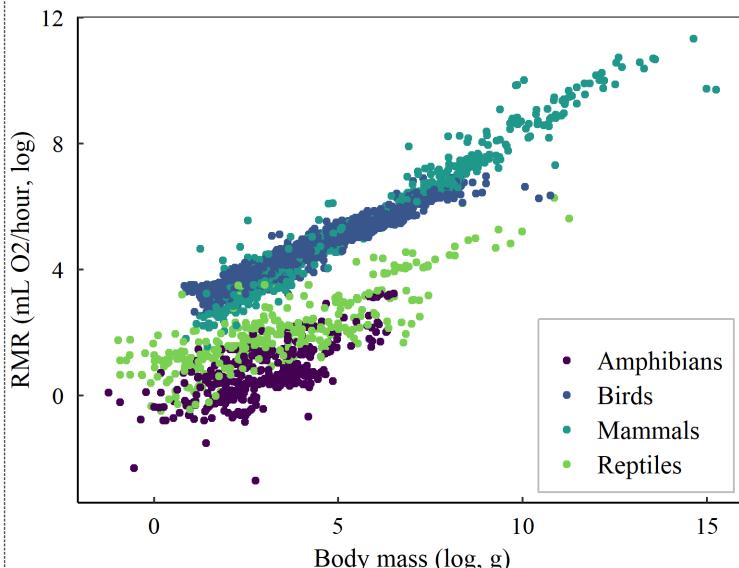


Figure 5.1: (a) **Spatial distribution of the sampled sites** from the PREDICTS database for terrestrial vertebrates (6,484 sites); (b) **Number of sites in each land-use and land-use-intensity category**; (c) **Net primary productivity by land use and land-use intensity** (derived from MODIS satellite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

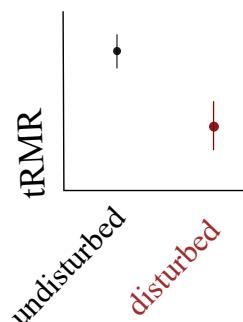
(a) Assemblage-level: there is less energy available to utilize by vertebrate assemblages in disturbed land uses than in undisturbed land uses.



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

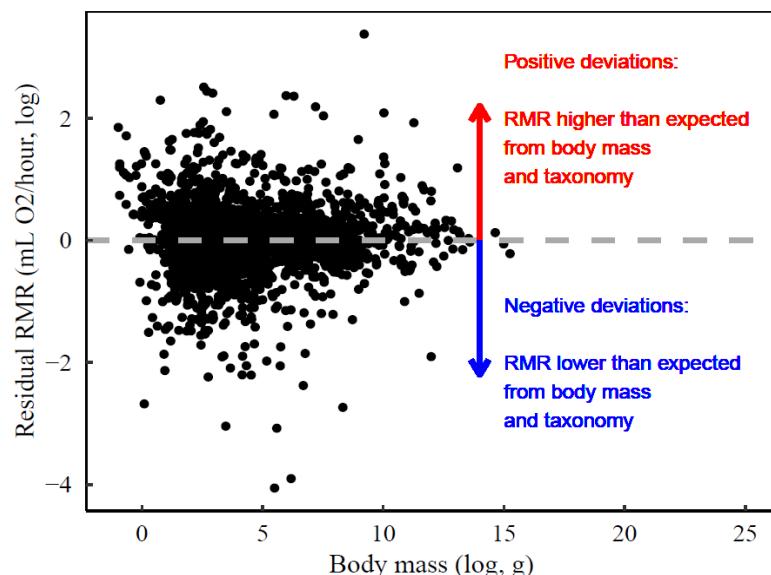
$$\text{Assemblage level: } tRMR = \sum_i (RMR_i * a_i)$$

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



(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:

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

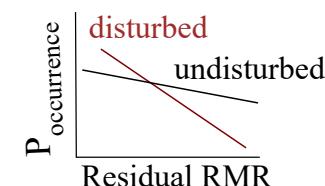


Figure 5.2: Framework for the predictions and models. I use resting metabolic rates (RMR) as a proxy for the amount of energy processed by vertebrate species. (a) I hypothesize that there is less energy overall that can be utilized by vertebrate species in disturbed land uses compared to undisturbed 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 taxonomic position, 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.

1013 **5.2 Methods**

1014 **5.2.1 Vertebrate assemblage composition**

1015 I obtained vertebrate assemblage composition in different land uses from the PREDICTS database (Hudson
1016 et al., 2014, 2017). The PREDICTS database is a large collection of published studies that measure bio-
1017 diversity across different land uses and is one of the most comprehensive global databases of its type. In
1018 each PREDICTS study, species occurrence and often abundance were recorded across different sites. Each
1019 site was assigned to one of the following land-use types: primary vegetation (natural, undisturbed vegeta-
1020 tion), secondary vegetation (recovering after complete destruction of primary vegetation), plantation forest
1021 (woody crops), pasture (areas grazed by livestock), cropland (herbaceous crops) and urban (built-up areas).
1022 The land-use categories were assigned based on habitat descriptions from the original studies (Hudson et al.,
1023 2014), sometimes in consultation with the original study authors. Each site was also classified in terms of
1024 land-use intensity as either minimal, light or intense. The land-use-intensity assignment was also made on
1025 the basis of the habitat description in the original studies, and depended on criteria specific to each land use
1026 (such as degree of mechanisation, yield or chemical inputs for cropland; or the amount of green space in
1027 urban areas; Hudson et al. (2014)).

1028 I subset the PREDICTS database for studies that sampled terrestrial vertebrates, and for which both land
1029 use and land-use intensity had been characterised. I thus obtained 181 studies for 4,238 species sampled
1030 across 6,484 sites (Figure 5.1a). Sample sizes varied across land uses and land-use intensities (Figure 5.1b).

1031 **5.2.2 Energy availability by land-use type and land-use intensity**

1032 The predictions of this Chapter rely on the assumption that resource types and abundance are modified in dis-
1033 turbed environments, with less energy available in disturbed compared to undisturbed land uses overall. To
1034 test this assumption, I used terrestrial net primary productivity (NPP) across land uses as a proxy for available
1035 energy. NPP quantifies the amount of atmospheric carbon fixed by plants and accumulated as biomass. NPP
1036 estimates were derived using imagery from the Moderate Resolution Imaging Spectroradiometer (MODIS)
1037 on board NASA's Terra satellite. NPP estimates were based on a yearly composite of measures made at
1038 8-day intervals, captured at 500-m spatial resolution (Running and Zhao, 2015). I obtained NPP for 4,062
1039 of the PREDICTS sites used in the analysis (matching the sites to the NPP data using the sampling year
1040 available in PREDICTS). I fit a linear mixed-effects model ('lme4' package, version 1.1-23, Bates et al.
1041 (2015)) explaining site-level NPP by land use and land-use intensity, with a random intercept accounting for

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

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

As a proxy for species-level energetic expenditure, I used estimates of the minimum amount of energy required for organismal maintenance, i.e., basal metabolic rates (BMR) for endotherms, and resting metabolic rates (RMR) for ectotherms. From the literature, I obtained estimates of BMR for 719 species of birds and 685 mammals, and estimates of RMR for 126 amphibians and 173 reptiles (Appendix 4, Table S5.1). For endotherms, BMR are measured when species are in their thermoneutral zone, that is, when there is little to no energy expenditure allocated to thermoregulation. Thus, BMR estimates were derived from lab studies that mostly measured oxygen consumption of the organisms at rest under controlled conditions and in the thermoneutral zone of the species. For an ectotherm, there is no ‘basal’ metabolic rate, as body temperature mainly depends on environmental temperature. Their metabolic rates follow a hump-shaped relationship with environmental temperature, highest at an optimal temperature which corresponds to a performance peak.

To be able to compare endotherms’ BMR with ectotherms’ RMR, Stark et al. (2020) used the metabolic rates that correspond to a performance peak for both groups (i.e., BMR in the thermoneutral zone for endotherms, and metabolic rates at optimal temperature for ectotherms). Thus, I used the data compiled in Stark et al. (2020) for ectotherms, and from the sources specified in Table S5.1 for endotherms. The units for BMR and RMR were standardized to mL of dioxygen consumed per hour (mLO₂/h). As in Stark et al. (2020), I henceforth refer to both basal and resting metabolic rates as RMR.

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

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 (see 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 level, 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 level 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 addi-

1103 tion, because it is well established that resting metabolic rates are influenced by temperature (Clarke and
1104 Fraser, 2004), I checked whether including annual mean temperature in the model affected the conclusions.
1105 Annual mean temperature at each PREDICTS site was estimated from WorldClim version 2.1 (Fick and
1106 Hijmans, 2017), using a 2.5 arc-minute resolution. Adding annual mean temperature did not improve model
1107 fit (likelihood-ratio test: $P=0.113$), thus I did not consider its effects any further.

1108 **Model validation.**

1109 To ensure that imputation uncertainty did not affect the conclusions, I refitted model 1 using the subset of
1110 species ($n = 426$) from PREDICTS for which there were empirical RMR information (i.e., excluding imputed
1111 RMR values).

1112 **Disentangling the effects of body mass and abundance on tRMR.**

1113 Since RMR correlates strongly with body mass, changes in tRMR are likely to be driven in part by changes
1114 in the size-spectrum of ecological assemblages. I fitted an additional model to explain changes in species'
1115 abundance (given presence) by land use, land-use intensity, trophic group, body mass and their interactions,
1116 to understand the role of shifts in the body mass of species on observed changes in tRMR (Appendix 4,
1117 Figure S5.1).

1118 **5.2.6 Effects of land use, land-use intensity, trophic group and residual RMR on species
1119 occurrence probability (prediction 2; Figure 5.2b)**

1120 To control for the effects of body mass and taxonomy on RMR, I used the residual variation in RMR after
1121 accounting for these variables, from a linear mixed-effects model fitting \log_e -RMR as a function of \log_e -
1122 body mass with nested random taxonomic effects (1|Class/Order/Family; Figure 5.2). Hence, I used a metric
1123 that describes how much more energy (positive deviations) or less energy (negative deviations) than expected
1124 from body mass and taxonomic position a species spends for organismal maintenance. Similar approaches
1125 have been used in previous papers (Furness and Speakman, 2008; Naya et al., 2013). As detailed earlier, I
1126 expect species with lower residual RMR to do better in disturbed land uses than species with higher residual
1127 RMR (prediction 2; Figure 5.2b) because, given any body mass, investing less energy in maintenance could
1128 contribute to persistence in a context of resource scarcity.

1129 To test the second prediction, I fitted a binomial mixed-effects model explaining species occurrence
1130 with land use, land-use intensity, trophic group and residual RMR. I started with a complete model that
1131 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 our 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, we 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).

1160 The model residuals were appropriately distributed (see diagnostic plots in Appendix 4, Figure S5.3).
 1161 Investigating the sensitivity of our results to imputation uncertainty showed that our results and conclusions
 1162 were robust to the removal of all imputed estimates of RMR (the correlation coefficient was 0.72 between the
 1163 two sets of model coefficients; Figure S5.4). Comparing model predictions showed that effects were mostly
 1164 congruent, although there were some differences (Figure S5.5). In particular, for herbivores, effect sizes
 1165 tended to be bigger for the model fitted on empirical data compared with the model that included imputed
 1166 data. Thus, our main results appear to be conservative if anything. The model fitted on empirical data had
 1167 larger standard errors, likely due to the reduction in sample size.

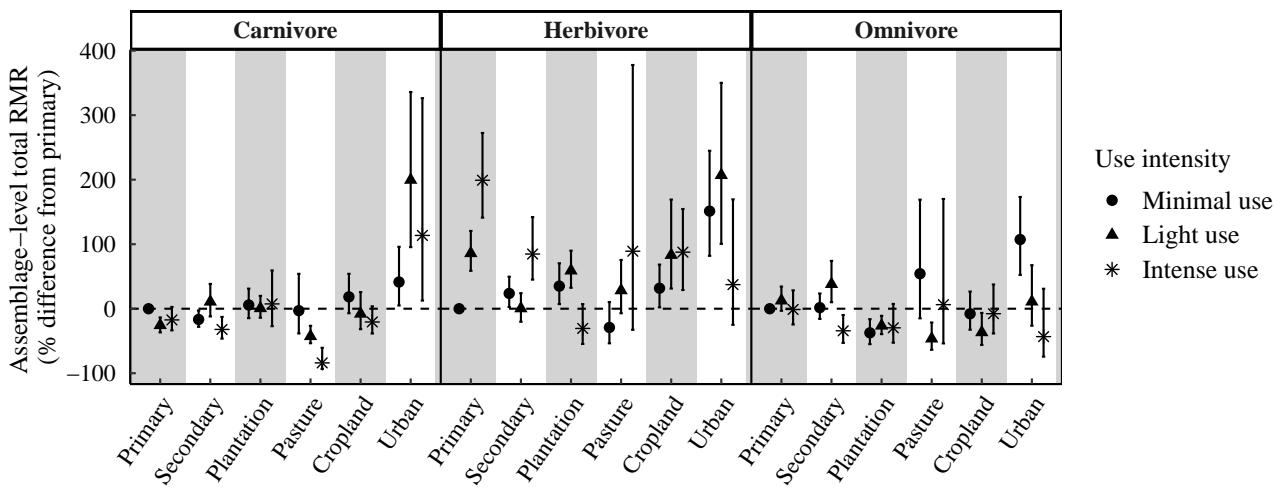
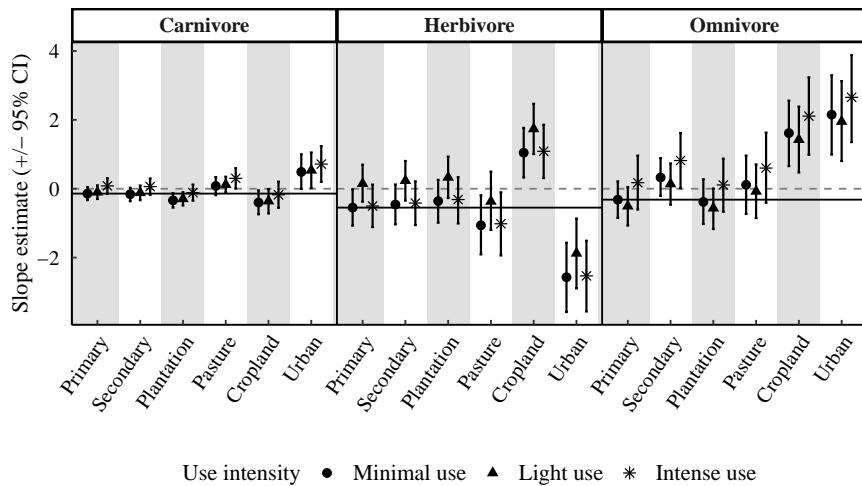


Figure 5.3: Effects of land use, land-use intensity and trophic group on assemblage-level total RMR. Model predictions are rescaled with reference to minimally-used primary vegetation, considered to be the undisturbed baseline. Primary: primary vegetation; secondary: secondary vegetation; plantation: plantation forest.

1168 5.3.2 Effects of land use, land-use intensity, trophic group and residual RMR on species' 1169 occurrence probability

1170 Species' occurrence probability was significantly affected by land use, land-use intensity, trophic level, resid-
 1171 ual RMR and their interactions (Figures 5.4, 5.5). Contrary to our expectations, species with higher residual
 1172 RMR (relative to their body mass and taxonomic position) tended to do better than species with lower resid-
 1173 ual RMR in a number of disturbed land uses. Overall, land-use type was more important for determining the
 1174 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)

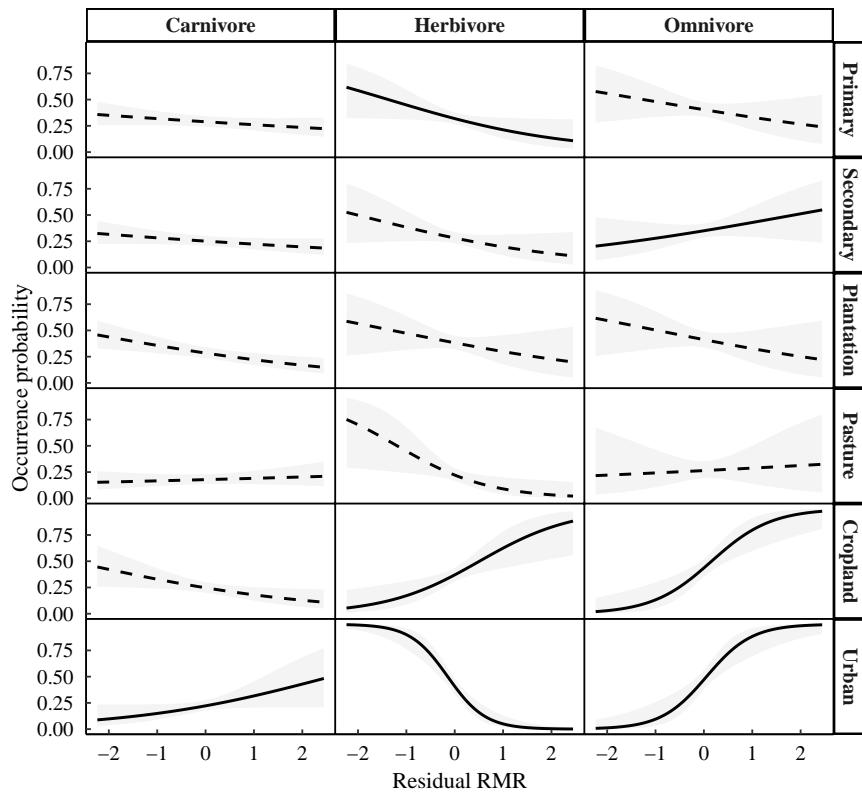


Figure 5.4: (a) Slope estimates for the relationship between residual RMR and occurrence probability in each land-use type and for the three levels of land-use intensity. The black horizontal line indicates the slope for the reference level (primary vegetation) for minimal land-use intensity. The grey 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.

For minimally-used primary vegetation (reference), the model predicted negative effects of residual RMR on species occurrence probability in all trophic levels (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.

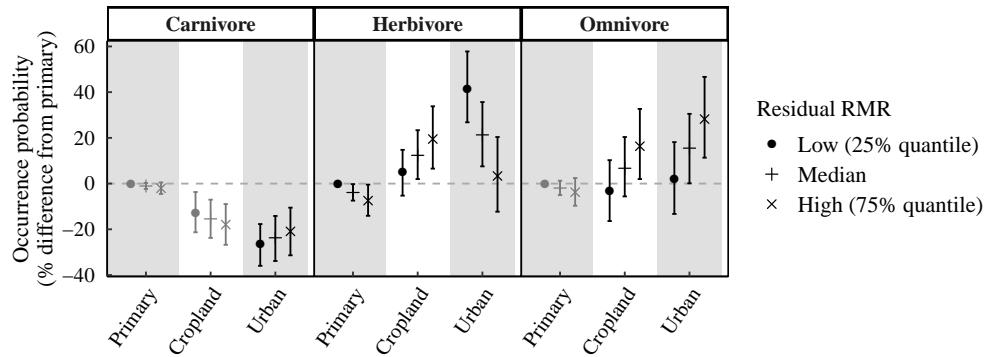


Figure 5.5: Predicted occurrence probabilities (+/- 95% confidence interval) in primary vegetation (primary) and for the most disturbed land uses where residual RMR was found to have a significant effect on occurrence probability. For visualisation purposes, I discretised residual RMR in three levels.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

1194 5.4 Discussion

1195 The results of this Chapter provide insights into the relationship between land-use change and energetic
1196 requirements at two levels of organisation (at the assemblage level and the species level), and contradict
1197 both my initial predictions. I found that total energetic requirements did not show systematic decreases in
1198 disturbed land uses. On the contrary, there were strong increases in all trophic groups, most notably in urban
1199 land uses. Further, in all trophic groups, species with higher energetic expenditure (than expected from body
1200 mass and taxonomy) tended to be better in some of the most disturbed land uses (that is, cropland and urban)
1201 than species with lower energetic expenditure (than expected from body mass and taxonomy).

1202 At the assemblage level, the results first highlight the effects of land-use change on vertebrate com-
1203 munity metabolism. Contrary to my expectations, I found differing effects of land use on total energetic
1204 requirements among trophic groups, reflecting changes in the size-spectrum of ecological assemblages (i.e.,
1205 changes in the distribution of abundance along the body mass gradient). On the one hand, decreases in total
1206 energetic requirements, such as observed for carnivores in intensely used pastures, are likely due to overall
1207 reductions in local abundance (with carnivorous species in pastures perceived as a threat to livestock; Eeden
1208 et al., 2018; or because of increased competition for fewer resources). On the other hand, increases in total
1209 energetic requirements could reflect higher levels of resource intake in some disturbed land-use types. On the
1210 basis of net primary productivity, I hypothesized that there would be fewer resources available in disturbed
1211 areas. However, it could be that the carrying capacity of some disturbed land-use types actually increases
1212 for some trophic groups compared to that of primary vegetation, because of the presence of novel or more
1213 abundant food sources. For instance, in urban areas, both wildlife feeding and the presence of anthropogenic
1214 food sources, such as human refusal or pet food, could lead to an increase in resource availability all year-
1215 round for species with a non-specialised diet that are able to exploit such food sources (Fischer et al., 2012).
1216 Past research on urban carnivores has shown that some species have adapted to urban environments by ex-
1217 ploiting anthropogenic food sources, and also benefit from physical protection (with some human structures
1218 providing shelter) and from reduced occurrence of natural enemies (Bateman and Fleming, 2012). Herbi-
1219 vores and omnivores could also benefit from increased resources in urban areas, notably where the urban
1220 matrix includes semi-natural habitats, which is congruent with observed increases in occurrence probability
1221 in minimally used urban areas for these trophic groups. Further, anthropogenic ‘bottom-up food forcing’ has
1222 been shown to affect food-web dynamics, with decreases in predation rates, loss of anti-predator abilities
1223 (Geffroy et al., 2020) and mesopredator release (Fischer et al., 2012). Thus, in urban areas, increases in
1224 anthropogenic food sources could provide support for a higher abundance of medium-sized species released

1225 from predation, increasing total energetic requirements.

1226 I hypothesized that resource availability would be the main driver behind changes in energetic require-
1227 ments. However, resource availability likely interacts with other factors to explain the patterns. In particular,
1228 past work has shown that brain size is an important predictor of species ability to cope with disturbance,
1229 notably in urban settings (Sayol et al., 2020). Since brain size scales allometrically with body mass, it is
1230 possible that I observe increases in total energetic requirements where having larger brains is advantageous
1231 for resource acquisition, and in turn where resources are both exploitable and abundant enough to sustain
1232 the larger energetic expenditures associated with bigger brain sizes. In addition, body size, which explains
1233 an important proportion of the interspecific variation in mobility, likely interacts with characteristics of the
1234 landscape (such as fragmentation) to predict species survival in disturbed land uses (Merckx et al., 2018).
1235 Hence, the patterns I observe in this Chapter could emerge from interactions and trade-offs among resource
1236 availability, diet, body size and human management of the landscape.

1237 At the species level, the results underline the role of energetic constraints on species responses to land-
1238 use change. After controlling for the effects of body mass and taxonomy, I found that residual energetic
1239 expenditure was a significant predictor of species occurrence probability in disturbed land uses. Contrary
1240 to my expectations, in several disturbed land uses and in all trophic groups, species with higher residual ener-
1241 getic expenditure tended to have a higher occurrence probability than species with lower residual ener-
1242 getic expenditure. It could be that species with lower residual energetic requirements are less well equipped
1243 than species with higher residual energetic requirements at making use of the available food sources in dis-
1244 turbed land uses. Species in disturbed land uses may need to display higher levels of feeding innovation
1245 (Coogan et al., 2018), have larger brains (Sayol et al., 2020), or be bolder and more active to make use of
1246 the available resources. In mammals, past research has shown that larger brains are associated with larger
1247 residual energetic expenditure (Isler and Van Schaik, 2006). At the individual level, past research suggests
1248 that metabolic rates are linked to differences in behaviour, with bolder and more active individuals exhibiting
1249 higher metabolic rates than less active individuals, with consequences for food acquisition (Biro and Stamps,
1250 2010). Although I am not aware of similar evidence at the species level, I propose that residual metabolic
1251 rates interact with species' ecological traits, behavioural traits and foraging strategy in influencing species'
1252 responses to land use. Among species with an adaptable diet, able to make use of the resources available in
1253 a disturbed landscape, those with higher residual metabolic rates could present a set of behavioural charac-
1254 teristics that render them better at acquiring the available resources, hence more able to cope with land-use
1255 disturbance. This could be the case for urban carnivores and omnivores, as well as herbivores in cropland.
1256 Thus, it is possible that disturbed land uses favour species with higher residual resting metabolic rates be-

cause 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 (Robert 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 downregulate 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.

1289 **6 | General discussion**

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Appendices

Appendix 1: Supporting information for Chapter 2

S2.1 Taxonomic corrections

Across the different sources, 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. We 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, we 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 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). We started by generating a list of all names featuring in any of the sources. These ‘original’ names were corrected for typos (using ‘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 ITIS. When species were not found in 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 Red List or in 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. We 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 we 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 S2.1). The species presenting the highest number of synonyms was the East African mole rat (*Tachyoryctes splendens*), for which we 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 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 Red List or the ITIS contained enough information. Taxonomy may be further improved by using class-specific sources in an automated procedure.

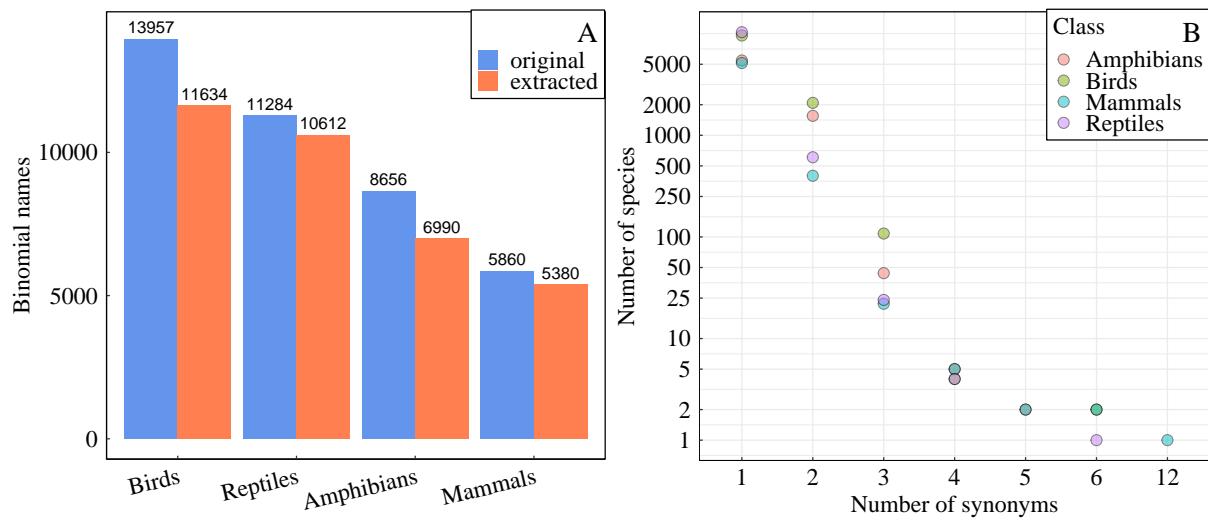


Figure S2.1: Difference in species number before and after taxonomic correction (A) and distribution of number of synonyms across datasets (B). (A) shows the number of species (binomial names) extracted from all sources (blue bars), and the number of uniquely identified accepted names (in red). Replacing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

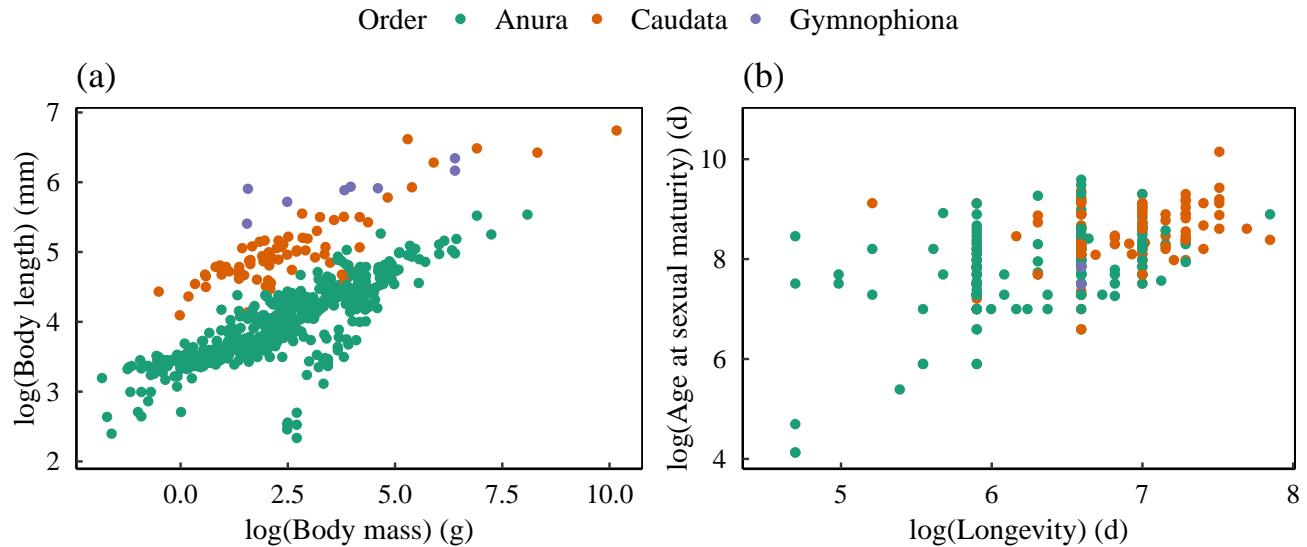


Figure S2.2: (a) Body mass versus body length and (b) longevity versus age at sexual maturity in amphibians. The Pearson's correlation coefficient was 0.71 in (a) and 0.55 in (b) (order was not included in these coefficients).

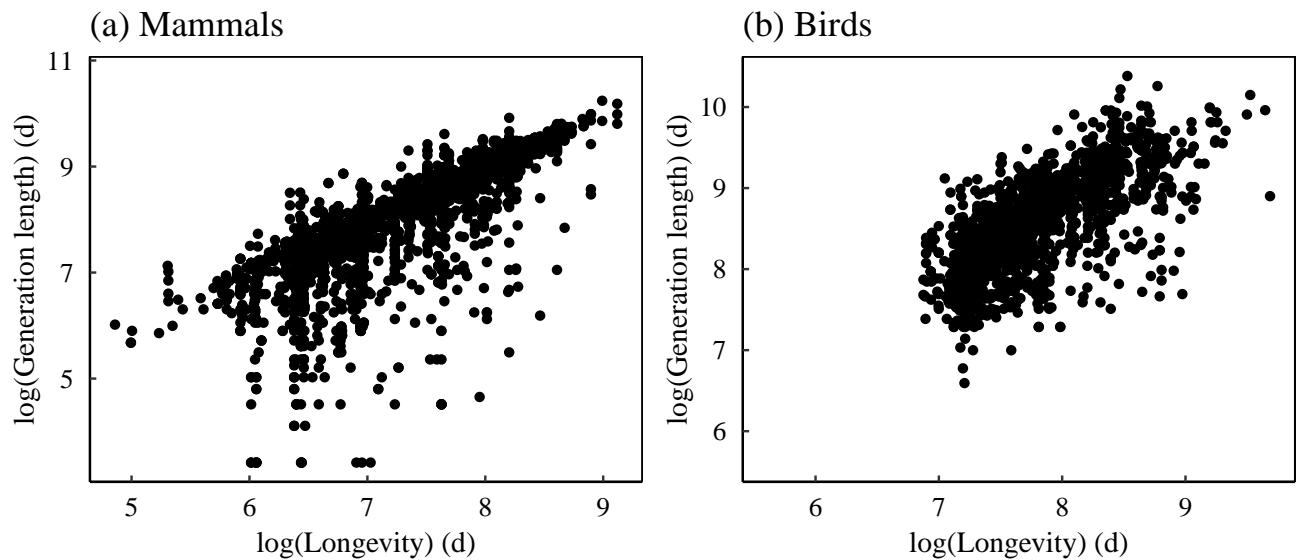


Figure S2.3: Generation length versus longevity data in mammals and birds. The Pearson's correlation coefficient was 0.74 in (a) and 0.70 in (b).

S2.3 Cutting distribution maps by altitudinal limits

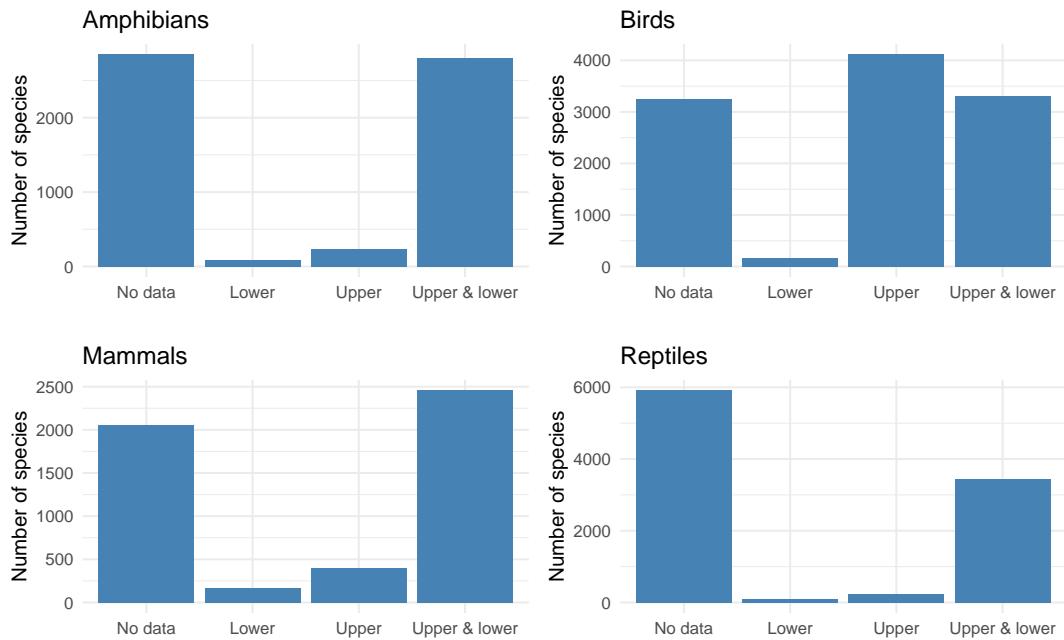


Figure S2.4: Availability of altitudinal limits across species. Upper and lower altitudinal limits were extracted from the IUCN Red List.

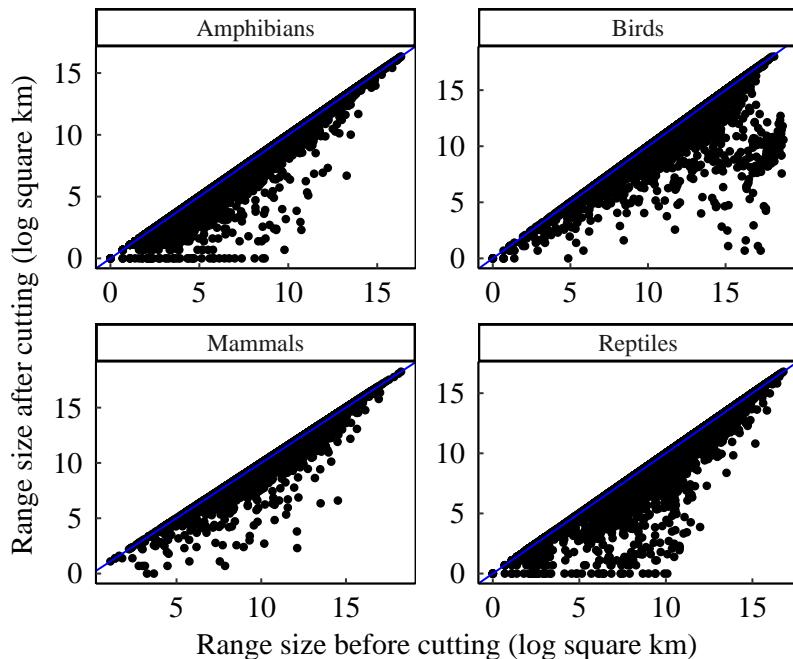


Figure S2.5: Range sizes before versus after cutting by altitudinal limits.

S2.4 Impact of taxonomic corrections on trait coverage

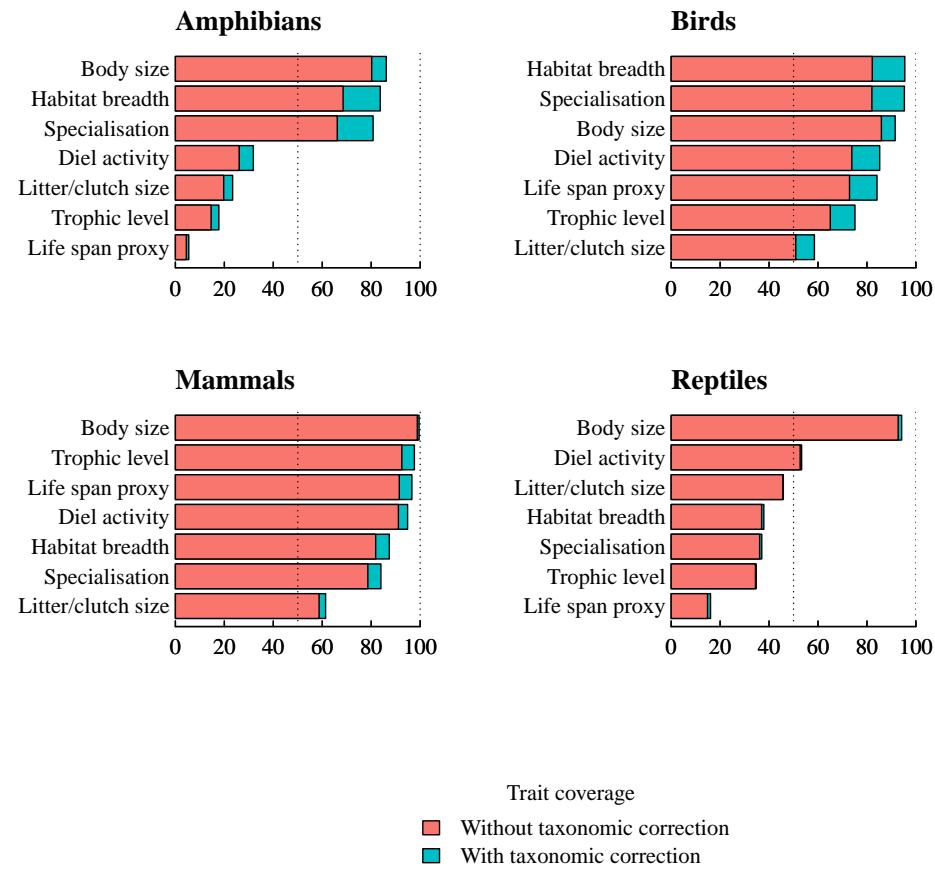
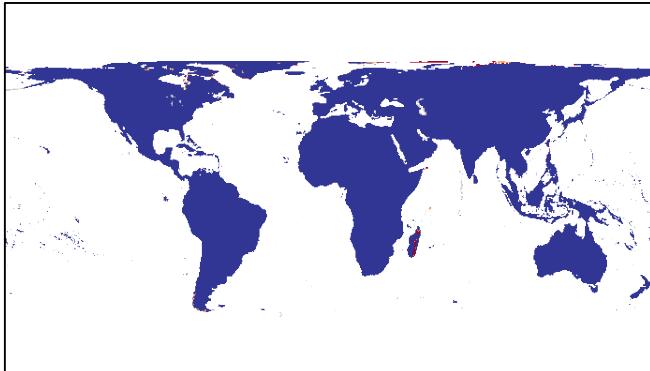


Figure S2.6: Trait coverage when no taxonomic correction is applied before matching sources by binomial names, versus when we applied the described procedure. Identification of synonyms allowed to increase trait coverage in most cases.

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

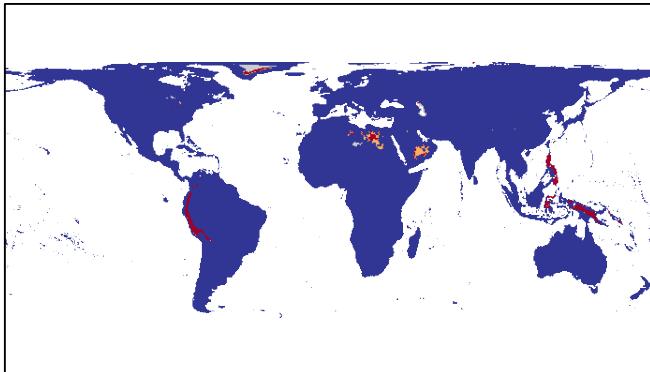
(a) Mammals



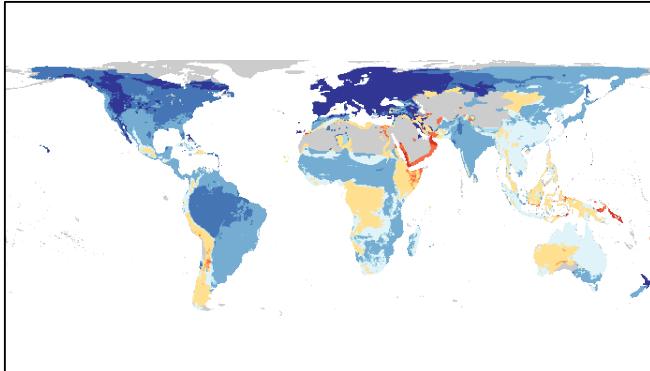
Median completeness
(birds and mammals):

- 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

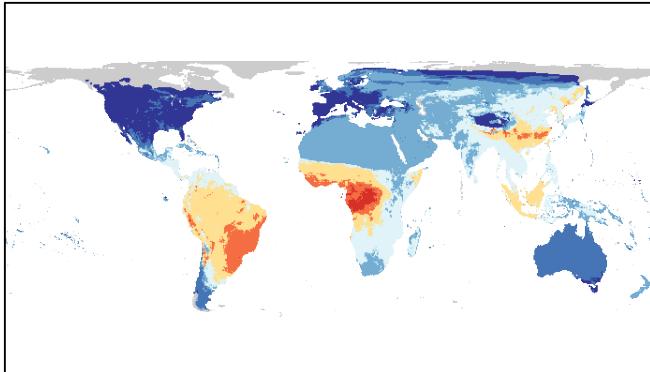
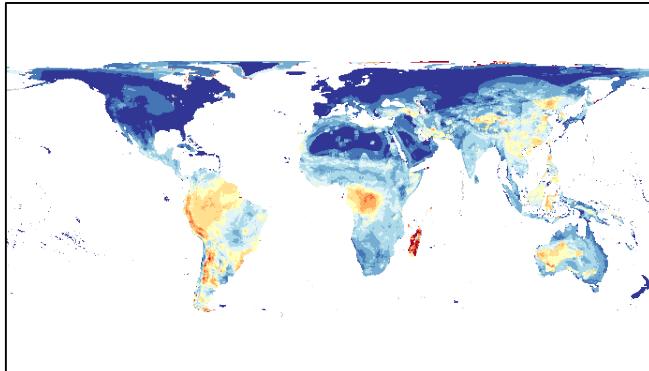


Figure S2.7: Spatial distribution of assemblage-level median trait completeness in each class. Note that the color breaks differ for mammals and birds and for herptiles.

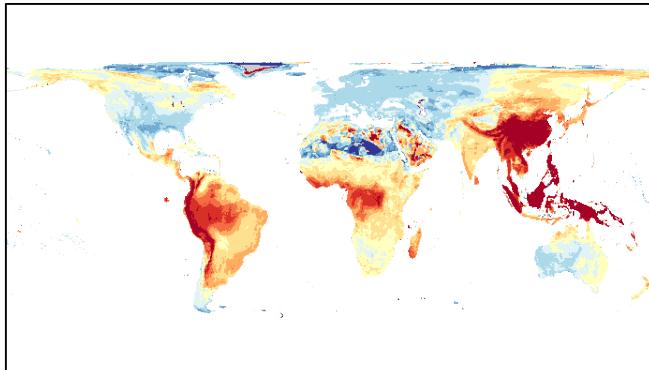
(a) Mammals



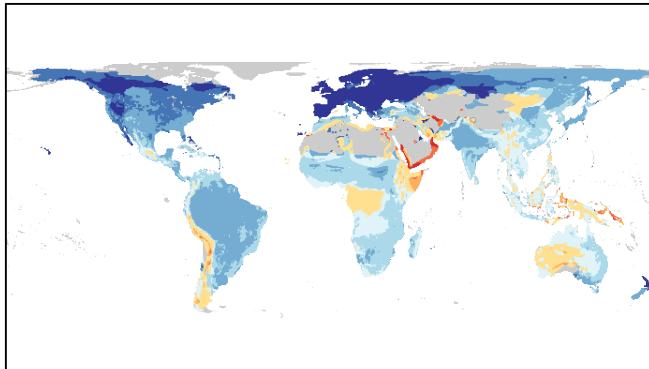
Mean completeness
(birds and mammals):

- 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

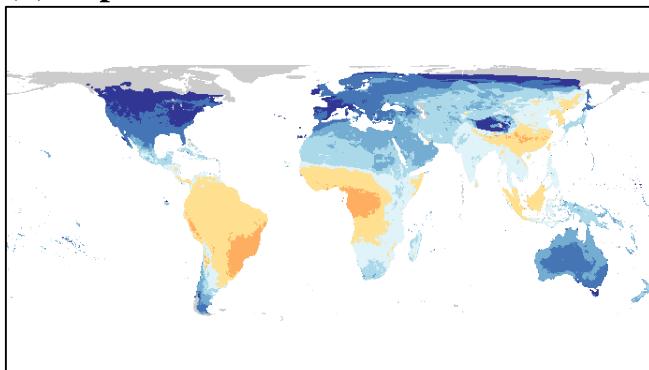
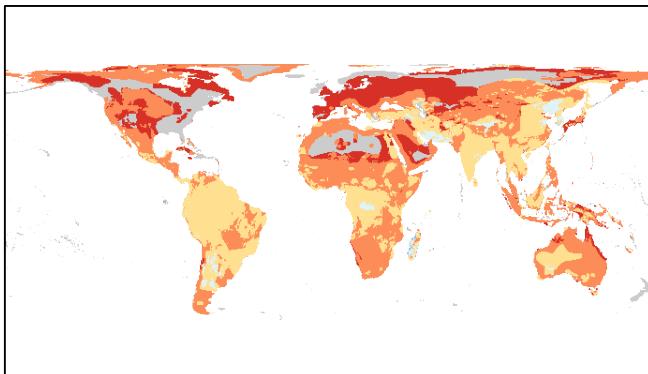


Figure S2.8: Spatial distribution of assemblage-level mean trait completeness in each class. Note that the color breaks differ for mammals and birds and for herptiles.

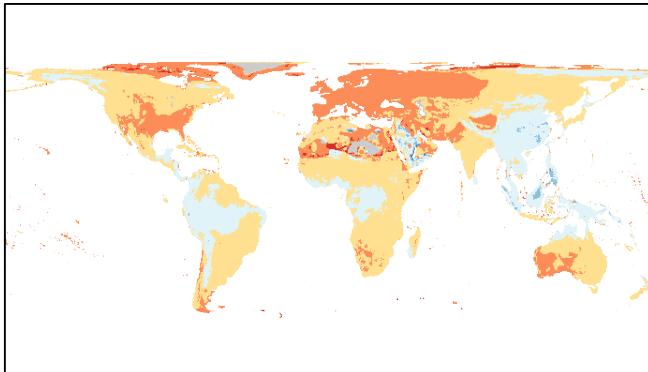
(a) Mammals



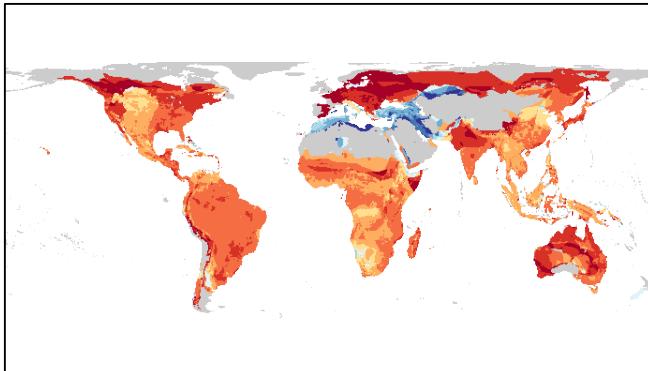
Standard deviation
of completeness
(birds and mammals):

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

(b) Birds



(c) Amphibians



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%

(d) Reptiles

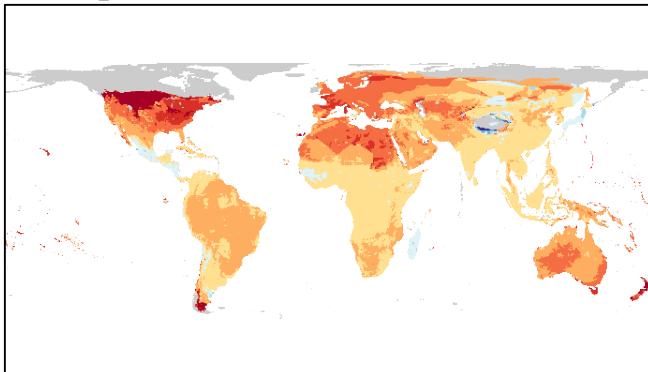


Figure S2.9: Spatial distribution of assemblage-level standard deviation of trait completeness in each class. Note that the color breaks differ for mammals and birds and for herptiles.

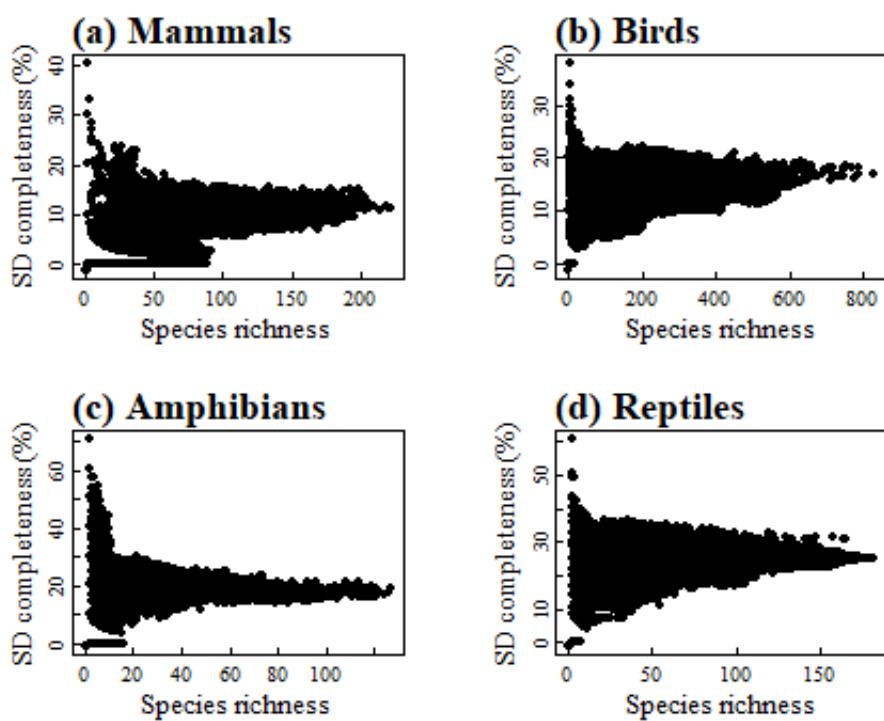


Figure S2.10: Assemblage-level species richness against standard deviation in completeness in each class.

S2.6 Phylogenetic patterns in trait completeness

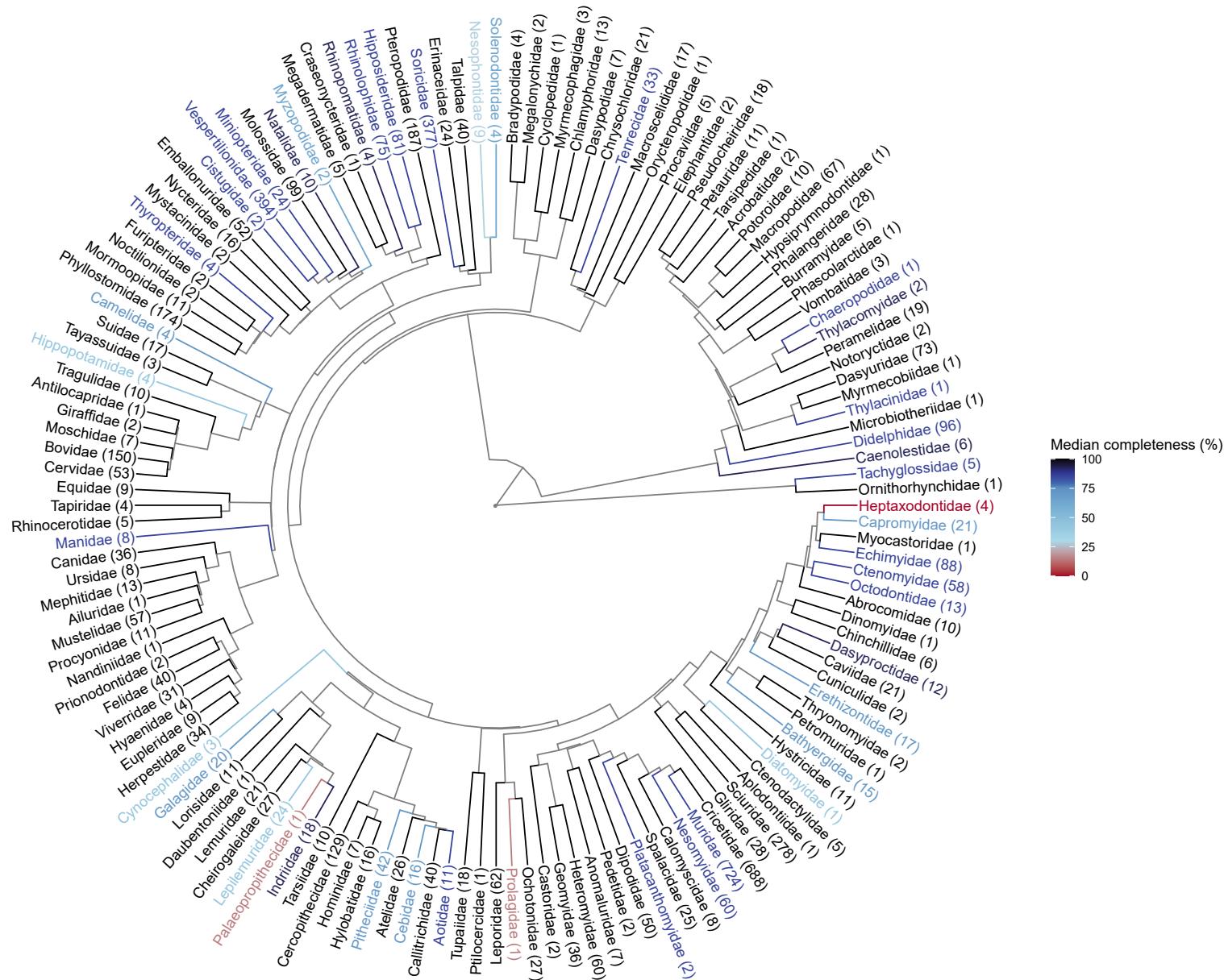


Figure S2.11: Within-family median trait completeness in mammals.

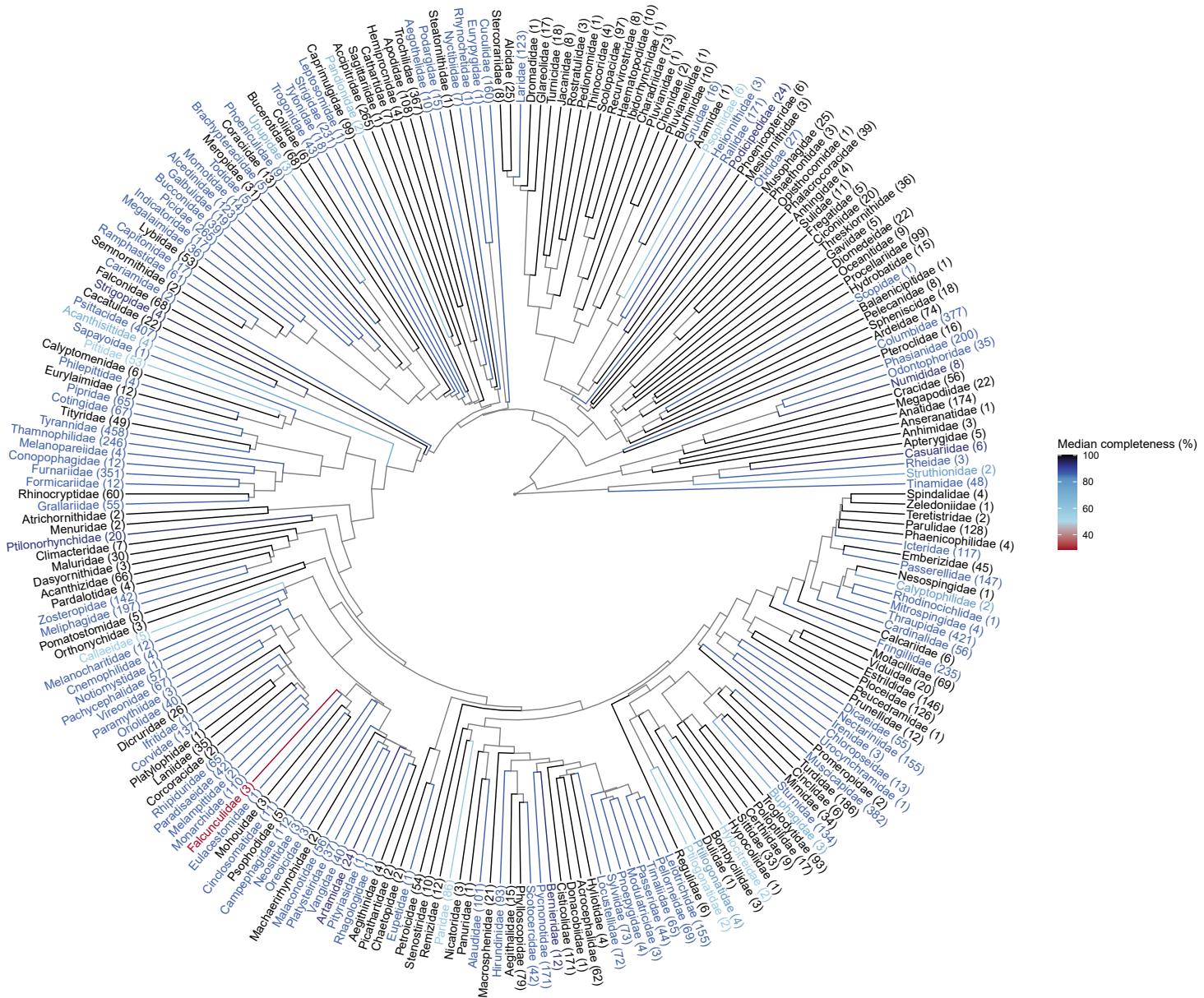


Figure S2.12: Within-family median trait completeness in birds.

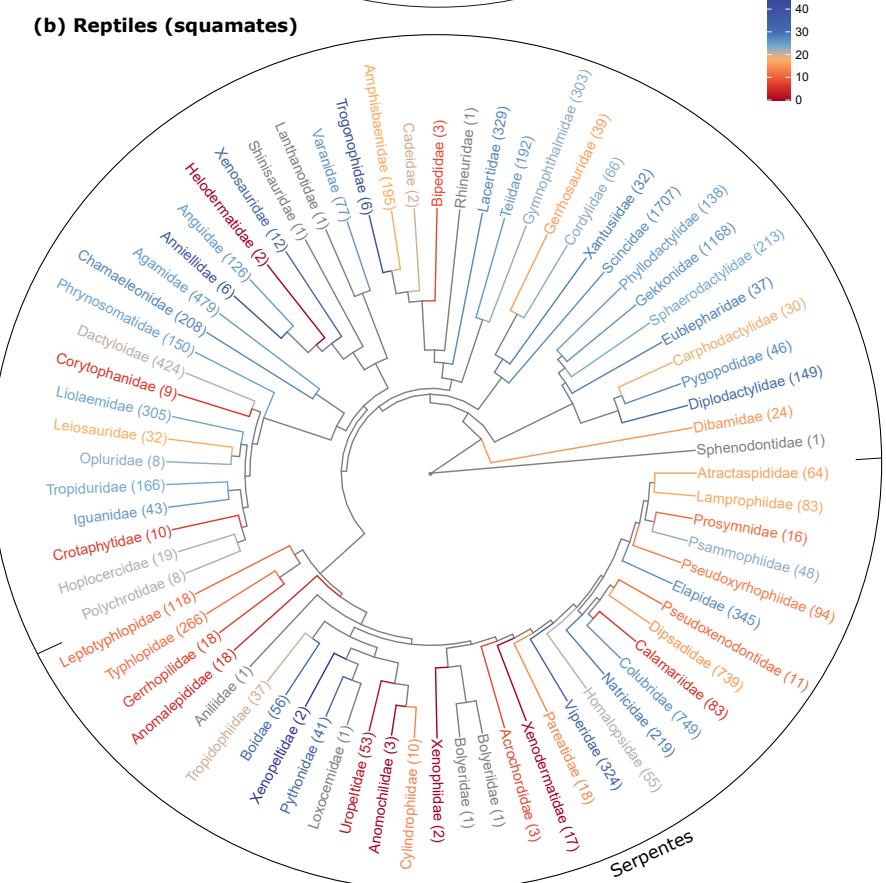
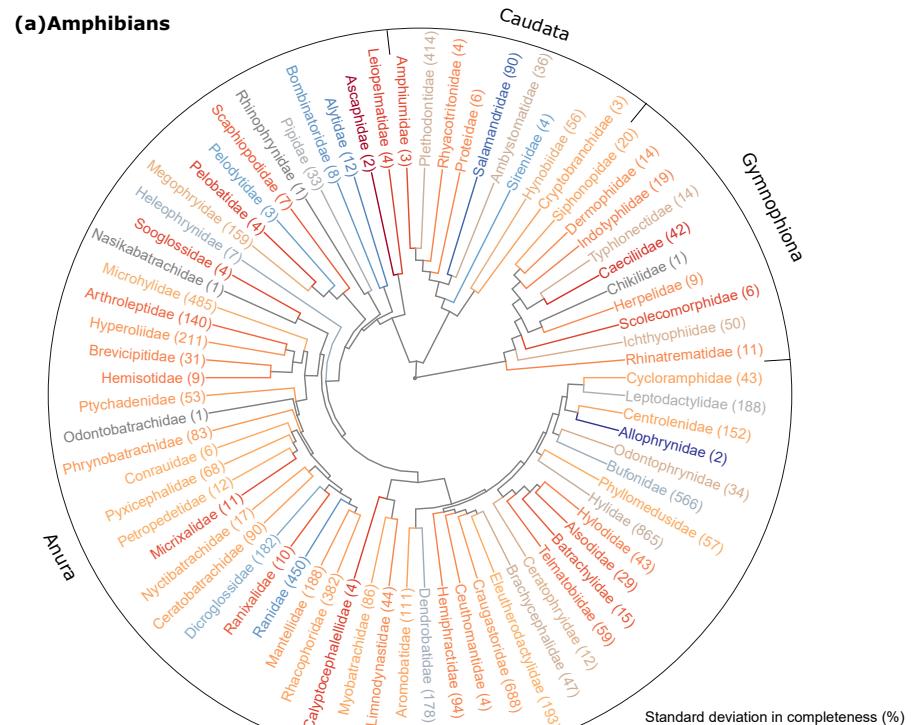


Figure S2.13: Within-family standard deviation in completeness (herptiles).

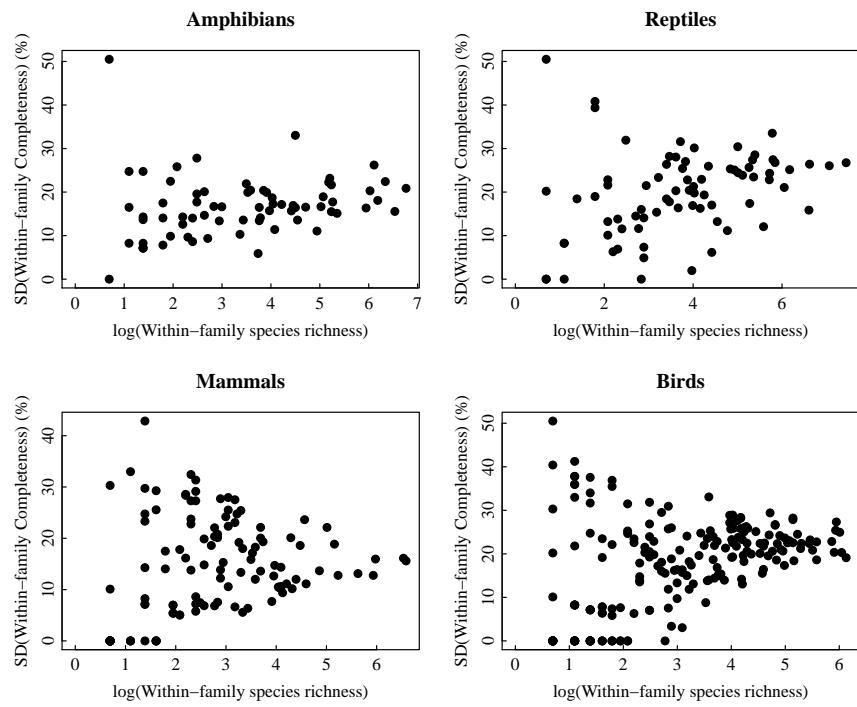


Figure S2.14: Within-family species richness against the within-family standard deviation of completeness.

S2.7 Model coefficients for Range size against Number of sampled traits (Poisson model).

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 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 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

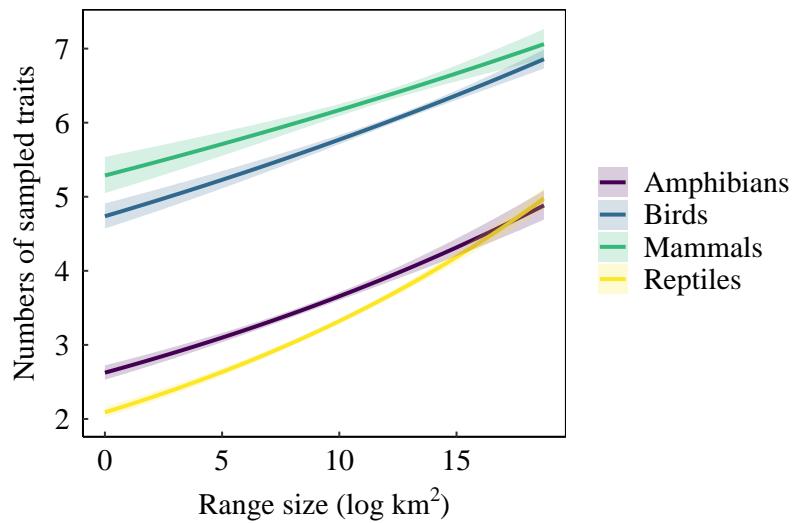


Figure S2.15: Relationship between number of sampled traits and geographical range size using distribution maps not cut by altitudinal limits. Models were fitted using a Poisson error distribution. Class was added as a predictor interacting with range size. Rates of increase were not significantly different for mammals and birds, but differed for reptiles and amphibians, with steeper rates of increase for reptiles overall. Cutting range maps by altitudinal limits had little effects on the results (see Figure 2.5 in Main text).

S2.8 Spatial models 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, we briefly explore the robustness of our work to taxonomic uncertainty by comparing trait coverage obtained with our procedure for taxonomic matching against trait coverage obtained when extracting synonyms from class-specific sources, which could contain more information, notably for herptiles. We aligned taxonomy again using the ‘rangeBuilder’ R package (Rabosky et al., 2016), which allows the extraction of accepted names from class-specific sources. Overall, our results are robust to the use of different taxonomic backbones; the main conclusions are likely to be unaffected by taxonomic uncertainty.

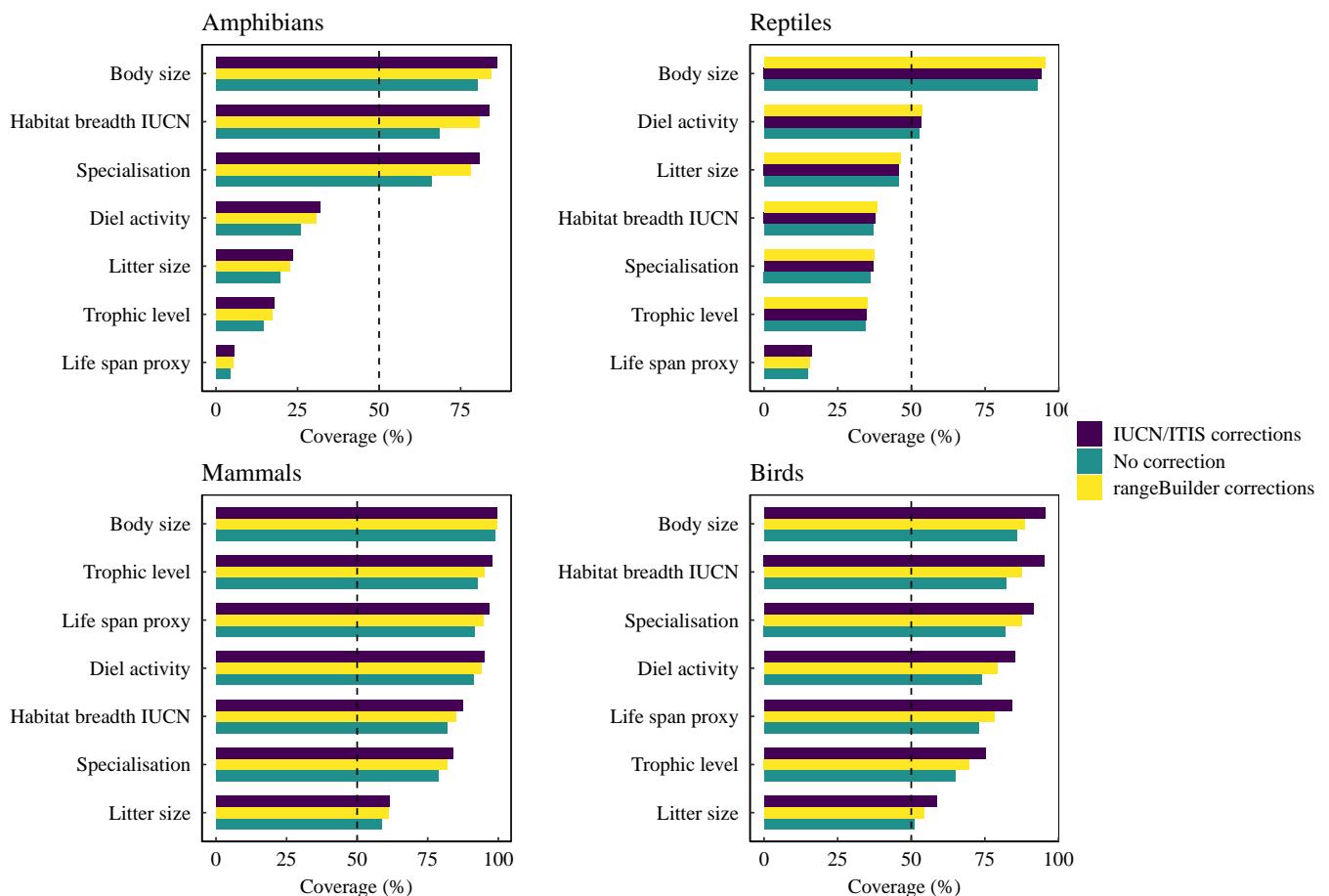


Figure S2.16: Comparison of trait coverage among datasets corrected for taxonomy in different ways: using the described procedure (purple bars), datasets corrected using the ‘rangeBuilder’ package (extraction of synonyms from class-specific sources, yellow bars; Rabosky et al. (2016)) and datasets where no taxonomic correction was applied when matching sources (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.

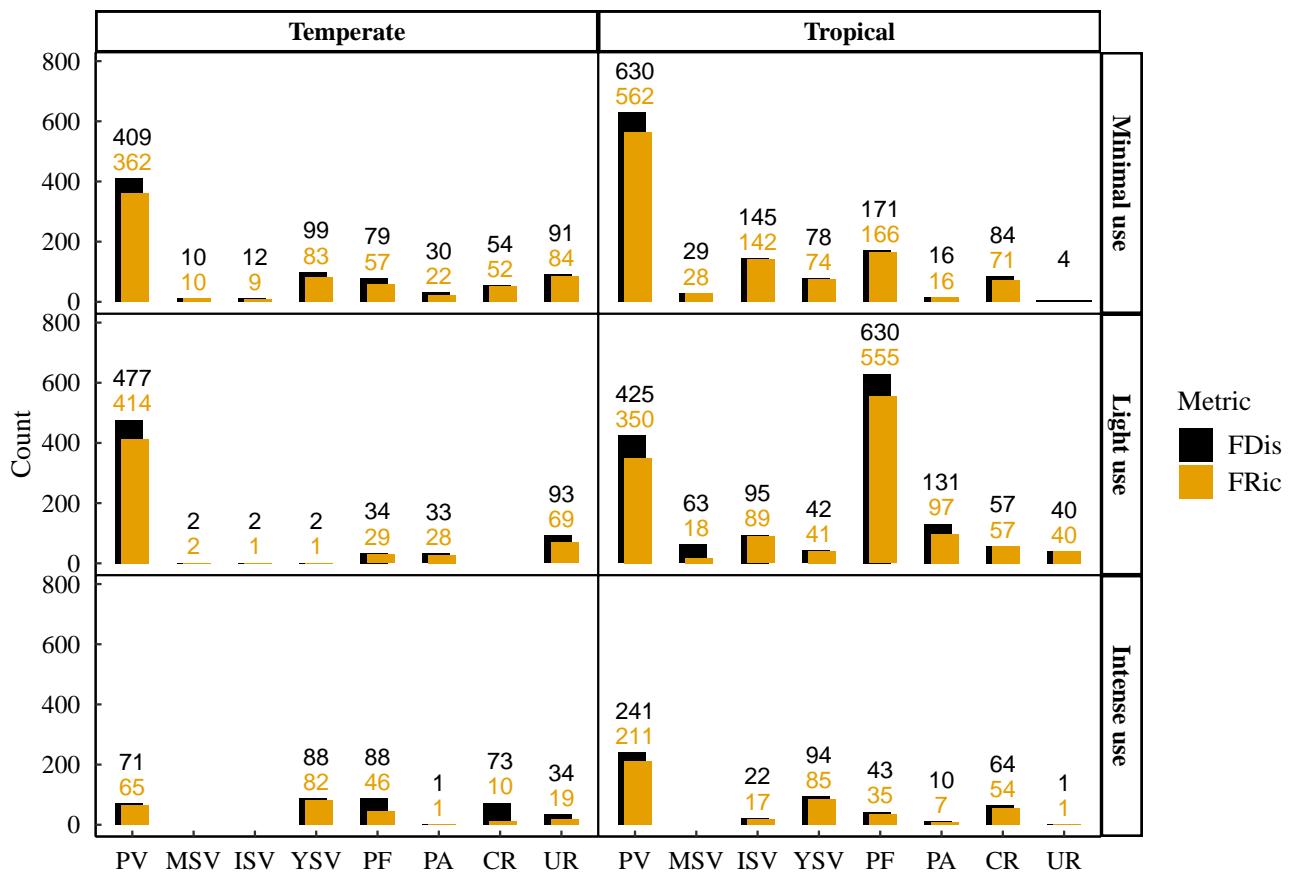


Figure S3.1: Number of sites in each land use and land-use intensity for which FRic and FDis were calculated, across all species. The number of sites for FRic can be smaller than the number of sites for FDis because FRic could not necessarily be computed for all assemblages in which FDis was estimated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

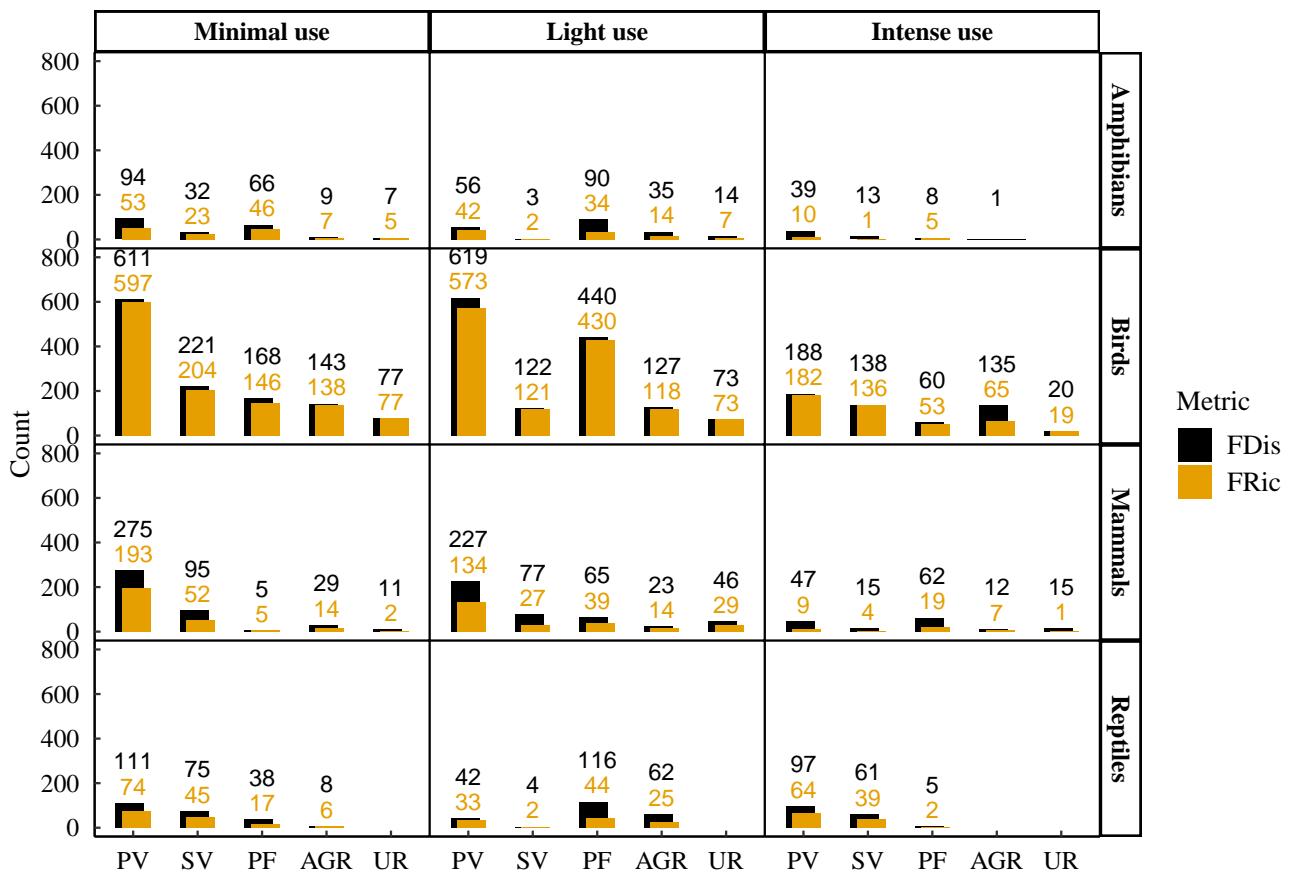


Figure S3.2: Number of sites in each land use, land-use intensity and for which FRic and FDis were calculated, within each class. The number of sites for FRic can be smaller than the number of sites for FDis because FRic could not necessarily be computed for all assemblages in which FDis was estimated (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 (and published in Etard et al. (2020)). 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).

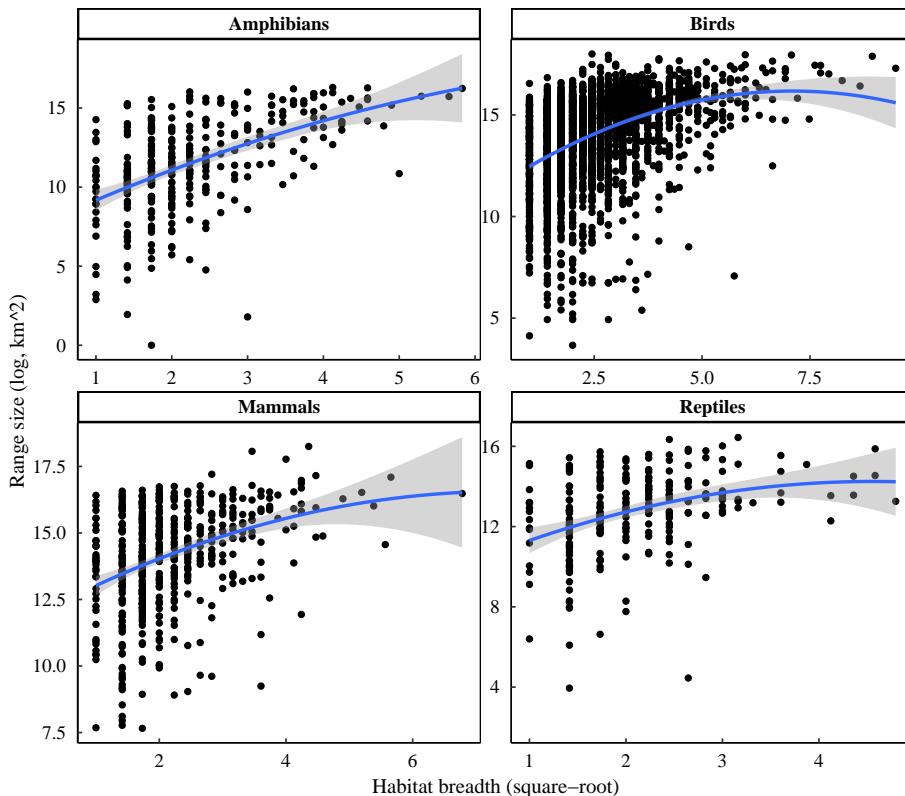


Figure S3.3: Relationship between habitat breadth and geographical range size across species in each class. The derivation of geographical range sizes is described in Chapter 2.

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; Etard et al., 2020; 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 our 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.

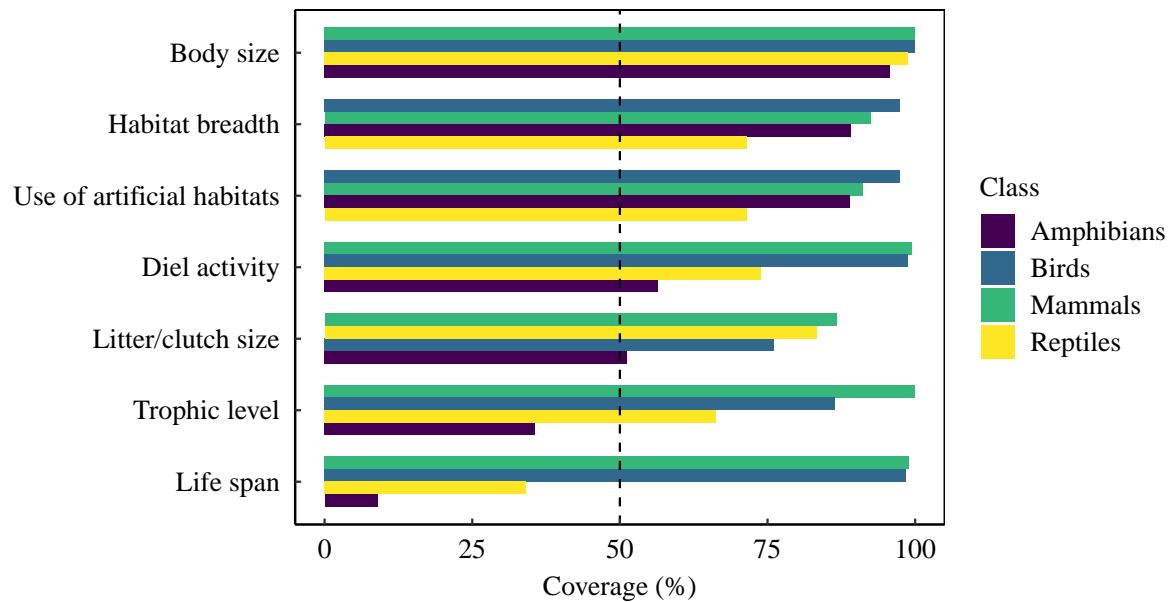


Figure S3.4: Trait coverage for the vertebrate species sampled in the PREDICTS database. For a given trait, coverage is calculated as the percentage of species for which an estimate was available.

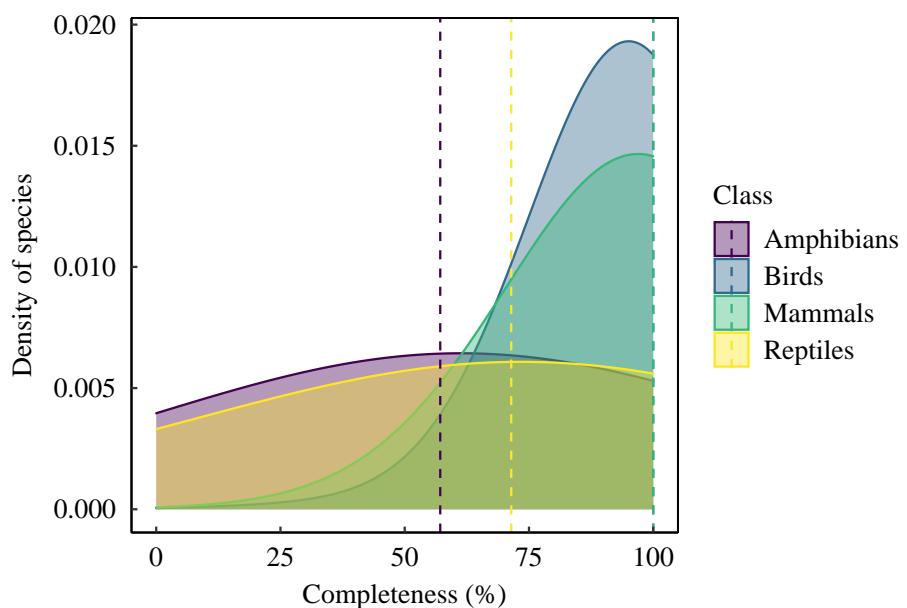


Figure S3.5: Distribution of trait completeness across the vertebrate species sampled in the PREDICTS database. For a given species, trait completeness is calculated as the proportion of traits for which an estimate was available. Dashed lines represent the median trait completeness.

S3.2.1 Choice of imputation technique

There exist several imputation techniques (Debastiani et al., 2021; Etard et al., 2020; Johnson et al., 2021; Penone et al., 2014), such as K-nearest neighbour (Troyanskaya et al., 2001), multivariate imputation by chained equations (Buuren and Oudshoorn, 2007), random forest algorithms (implementable in R with ‘missForest’; 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 trait data. For continuous traits, I used Pagel’s λ (Pagel, 1999), and for categorical traits I used Borges’ δ (Borges et al., 2018). Strong phylogenetic signal 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 (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 hence assessed whether the degree of multicollinearity among categorical and continuous traits was not problematically high. To that 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). Multicollinearity across 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 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

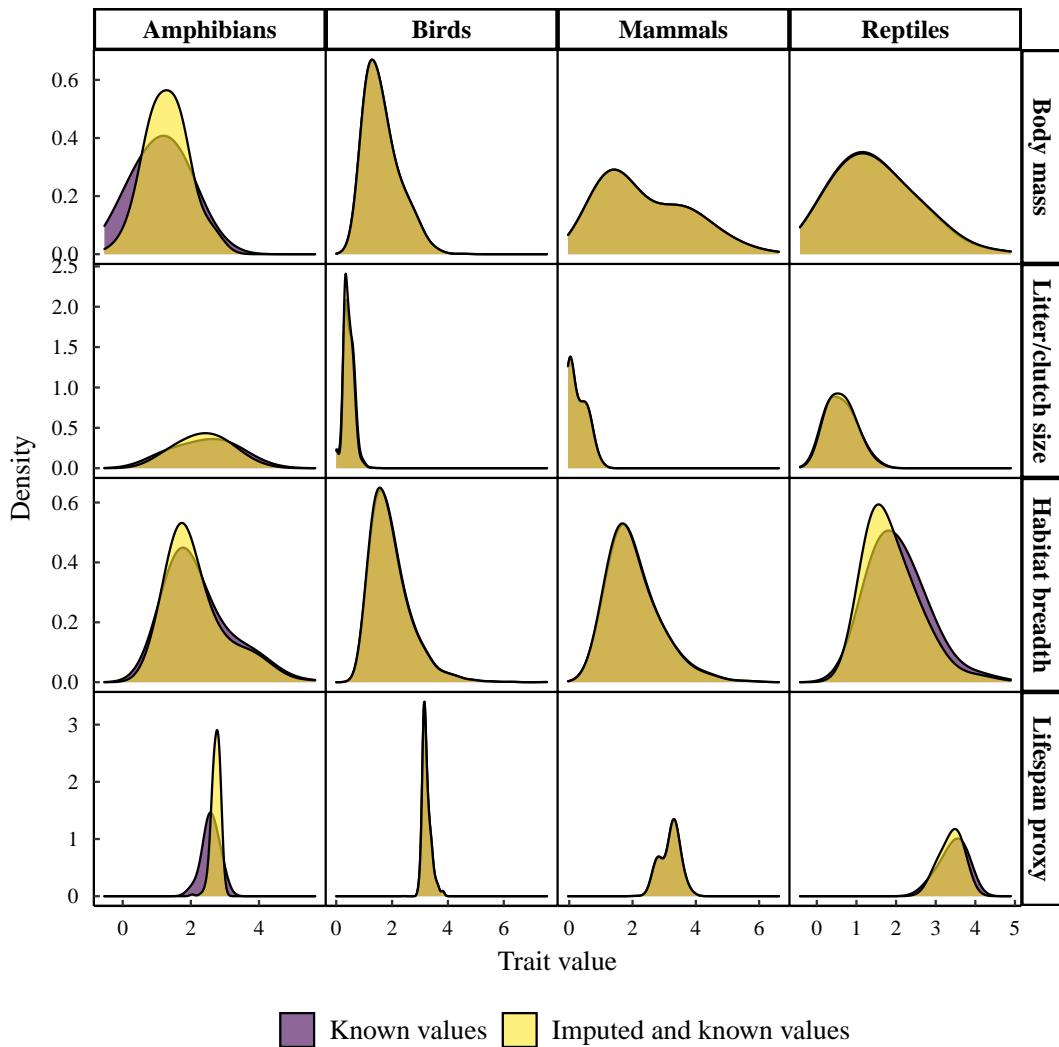


Figure S3.6: Distribution of continuous traits considered in the calculation of the functional diversity metrics (shown as density plots), before and after missing value imputations, in each class and for the species occurring in the PREDICTS database. All traits were log₁₀-transformed except Habitat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

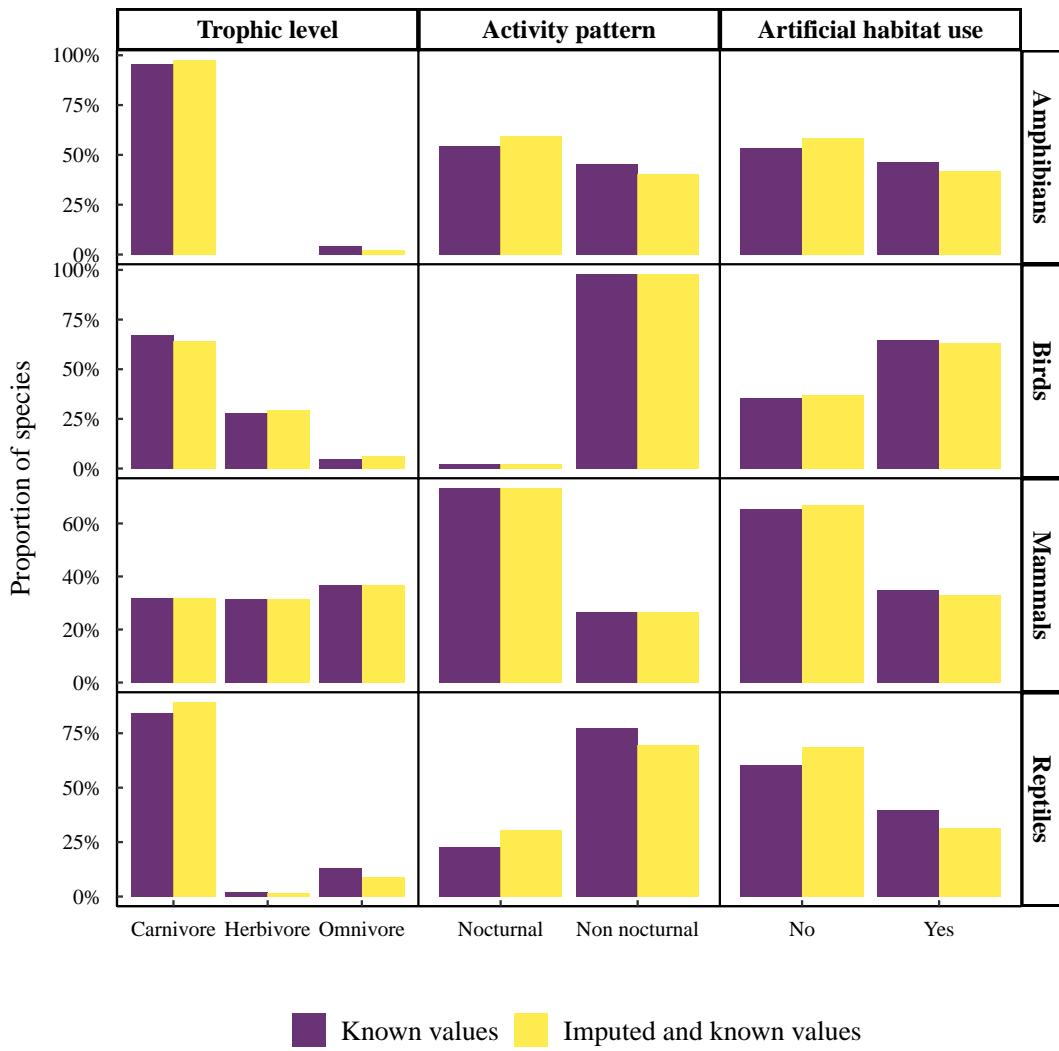


Figure S3.7: Frequency distribution for categorical traits considered in the calculation of the functional diversity metrics (shown as % of total species in each category) before and after missing value imputations, in each class, for the species occurring in the PREDICTS database.

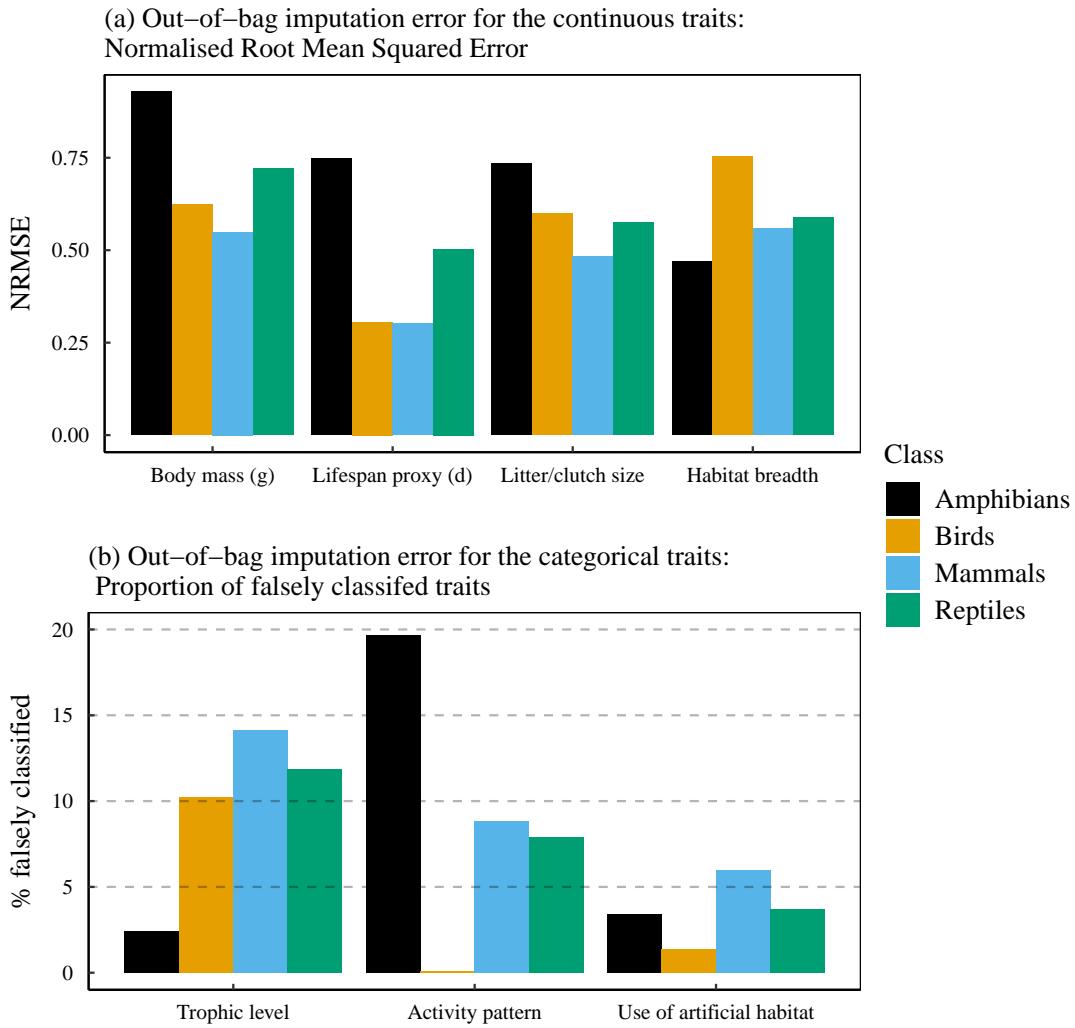


Figure S3.8: Out-of-bag imputation errors for the continuous traits (a) and categorical traits (b). For continuous traits, the Normalised Root Mean Squared Error (NRMSE) was obtained by dividing the Mean Squared Error (MSE) by the variance of the known trait distribution, then square-rooting the result.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

Within classes, I used 18 tropical studies and 1 temperate study for amphibians; 38 and 21 for birds (respectively); 28 and 9 for mammals; and 11 and 7 for reptiles. As sample sizes differed among pairs of land uses and use 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 was first subsetted to the species occurring in a given pair of sites (see Chapter 3, Methods, ‘Functional traits and diversity indices’). 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 volume 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

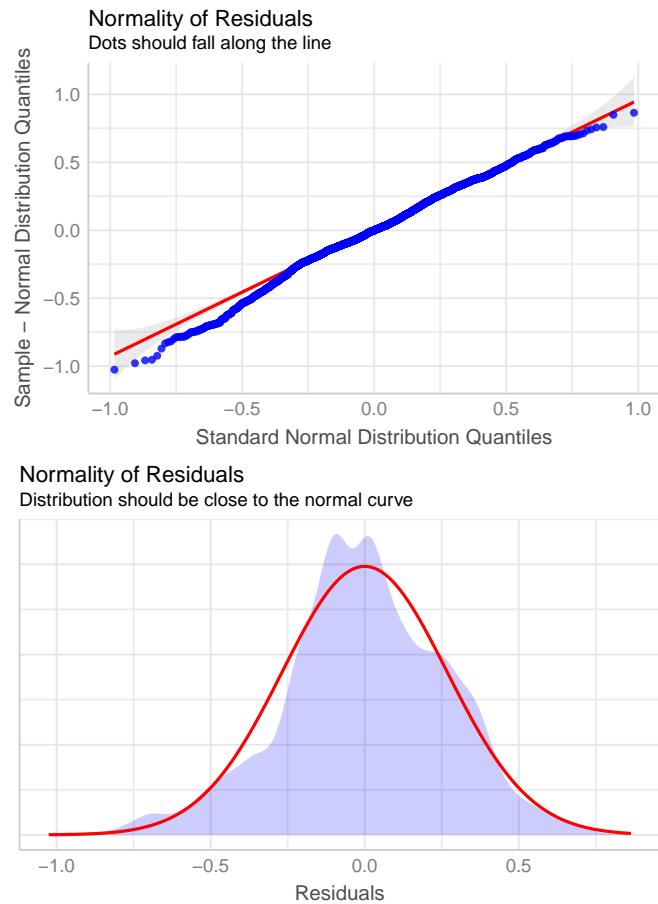


Figure S3.9: Diagnostic plots for Model 1a, obtained using the 'performance' R package (Lüdecke et al., 2021).

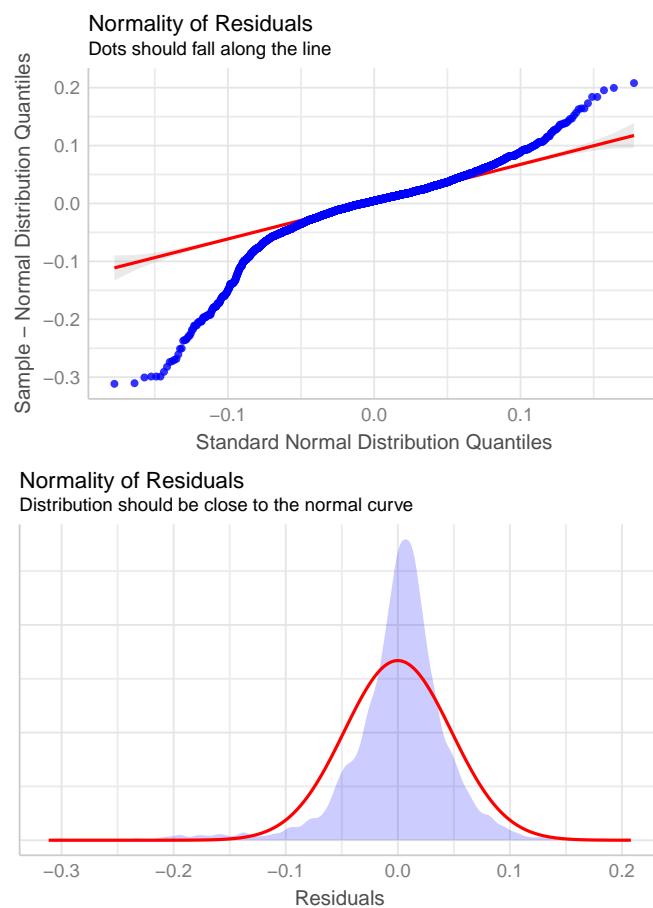


Figure S3.10: Diagnostic plots for **Model 1b**, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

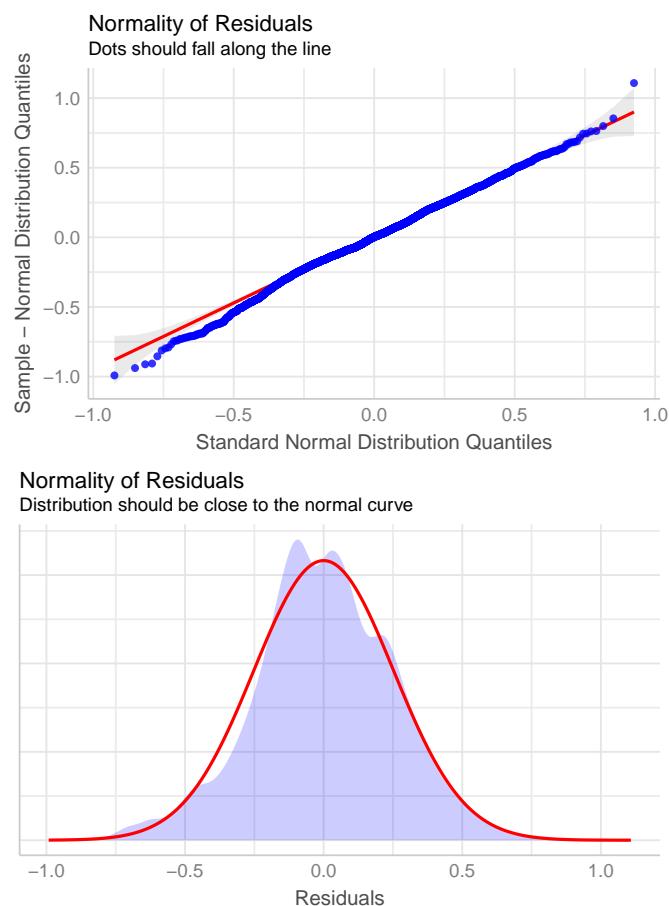


Figure S3.11: Diagnostic plots for Model 2a, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

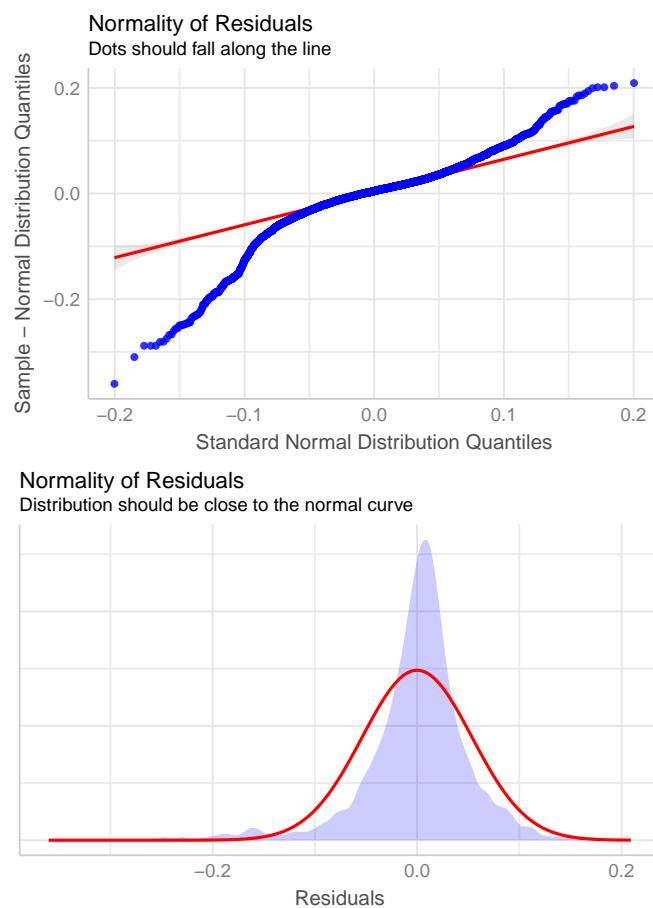


Figure S3.12: Diagnostic plots for Model 2b, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

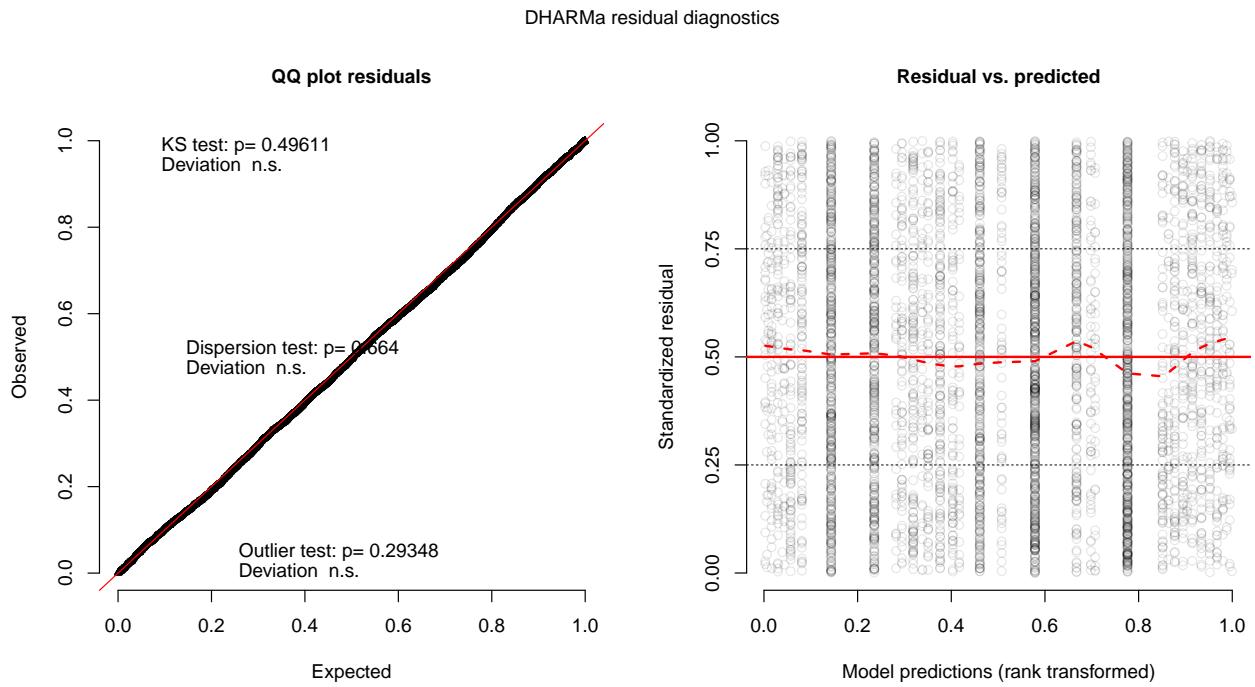


Figure S3.13: Diagnostic plots for Model 3, obtained using the ‘DHARMA’ R package (Hartig, 2021).

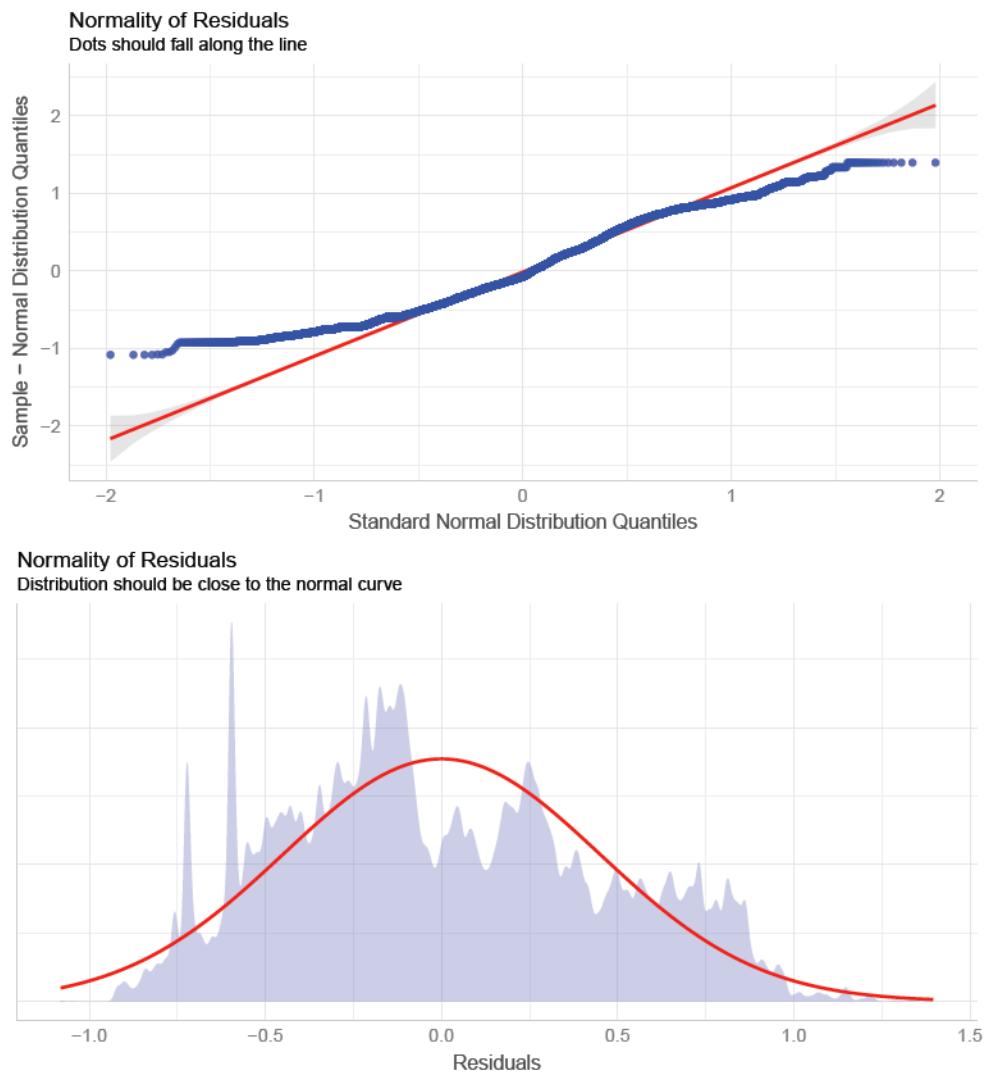


Figure S3.14: Diagnostic plots for Model 4a, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

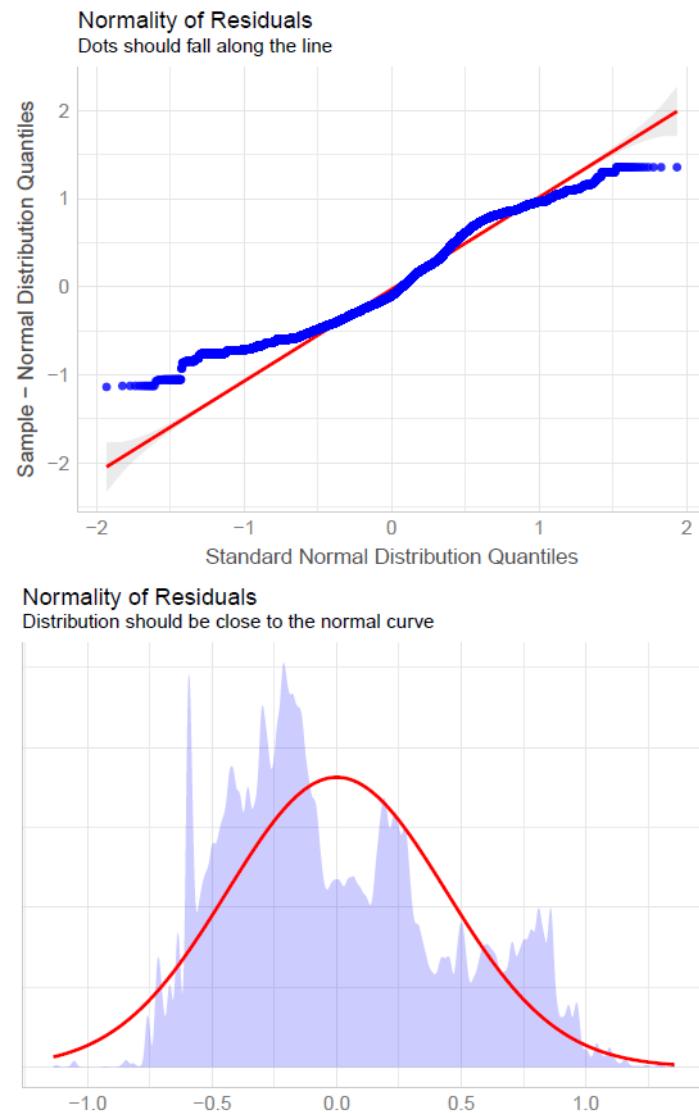


Figure S3.15: Diagnostic plots for Model 4b, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

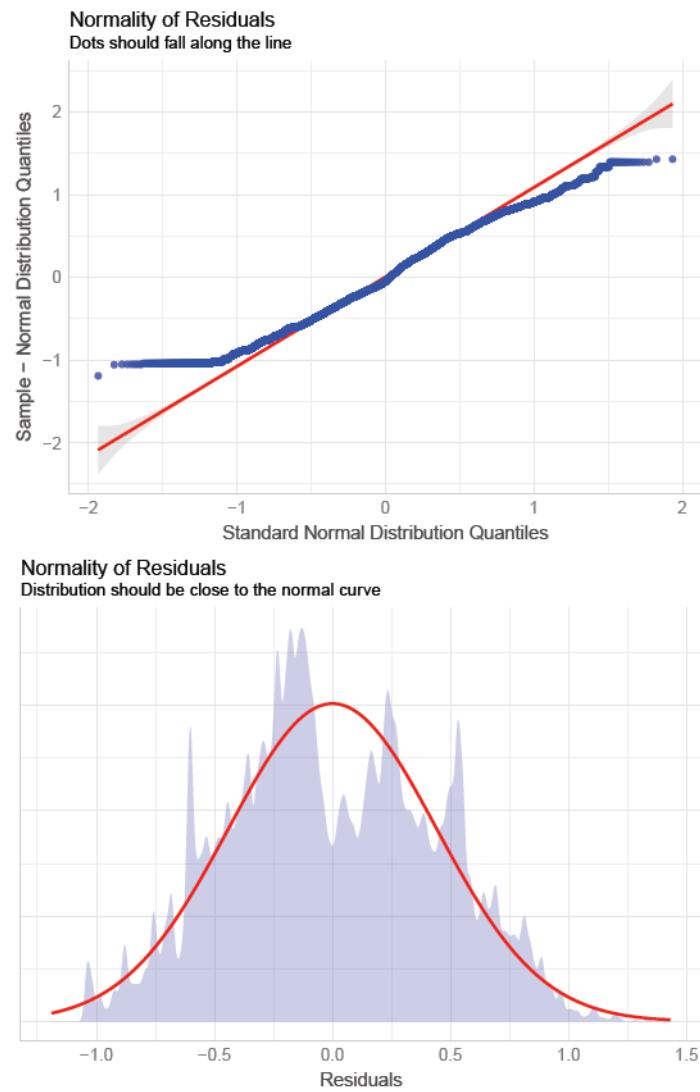


Figure S3.16: Diagnostic plots for Model 5a, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

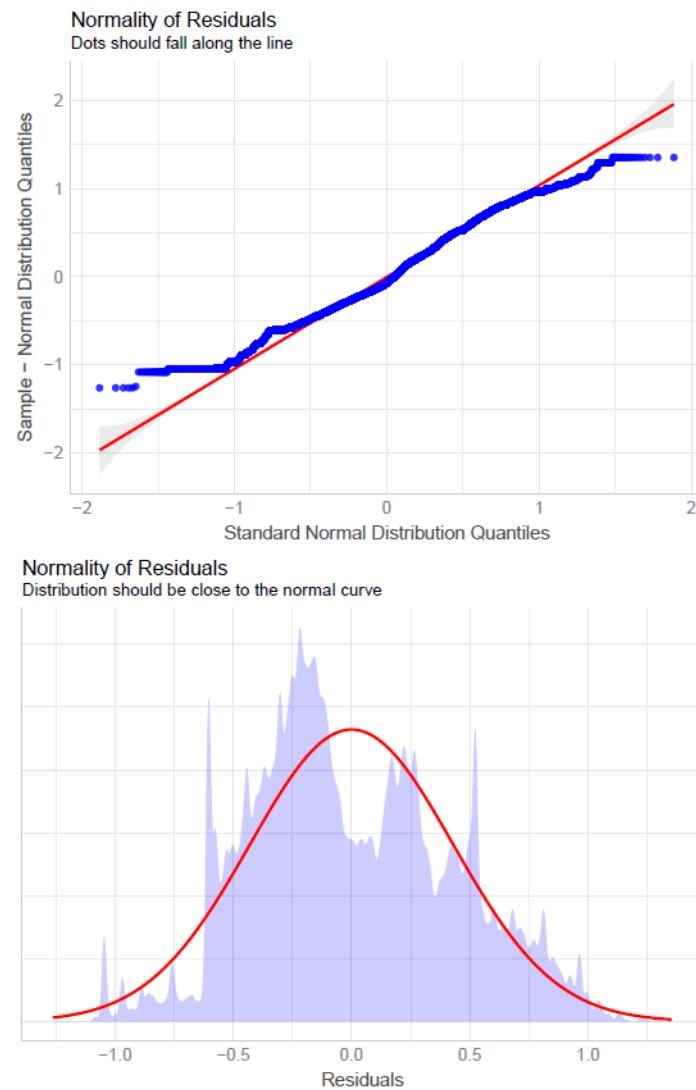


Figure S3.17: Diagnostic plots for Model 5b, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

S3.7 Model robustness

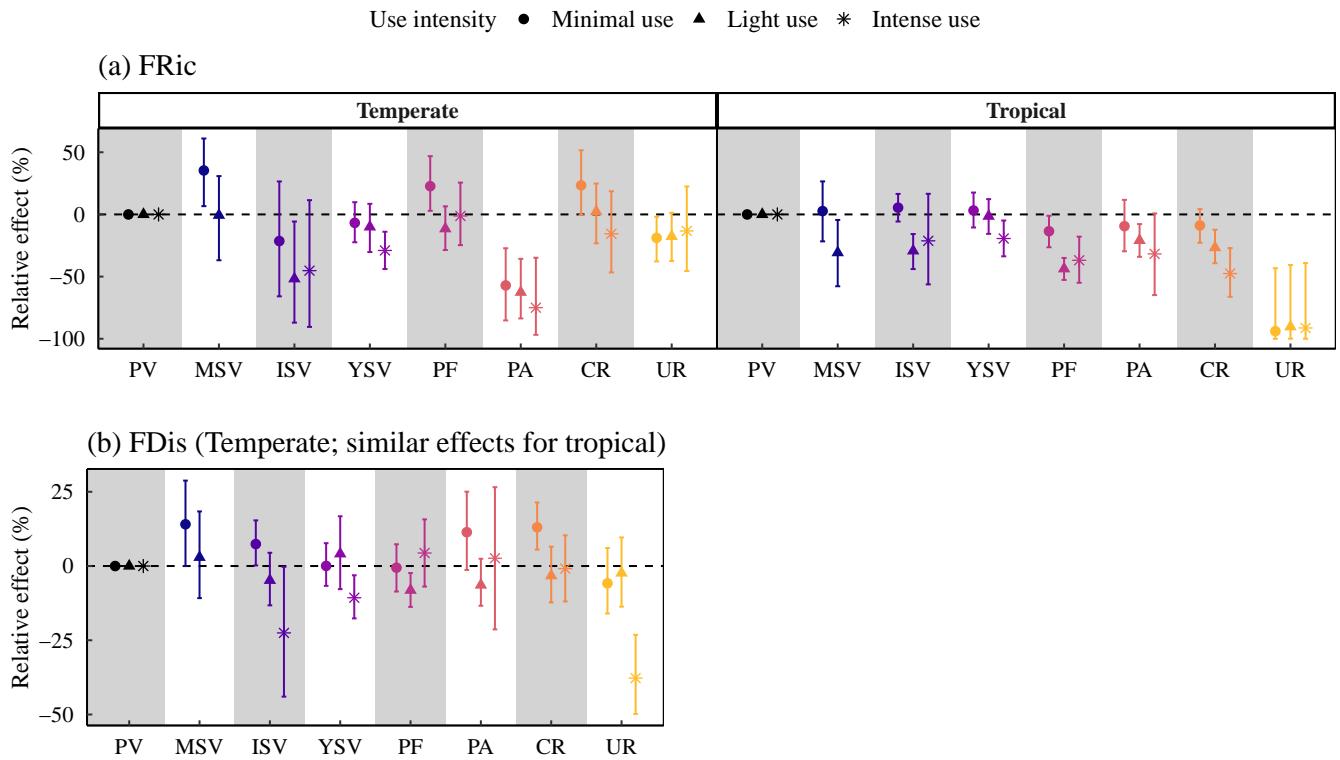


Figure S3.18: Effects of land use, land-use intensity and region on FRic (a) and FDis (b) across vertebrates, for the subset of species with complete trait data (i.e., excluding species with less than 100% trait completeness). Effects are plotted as a % difference relative to the reference land use (primary vegetation, PV). For FRic, I fitted Model 1a (see main text, Chapter 3), 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.

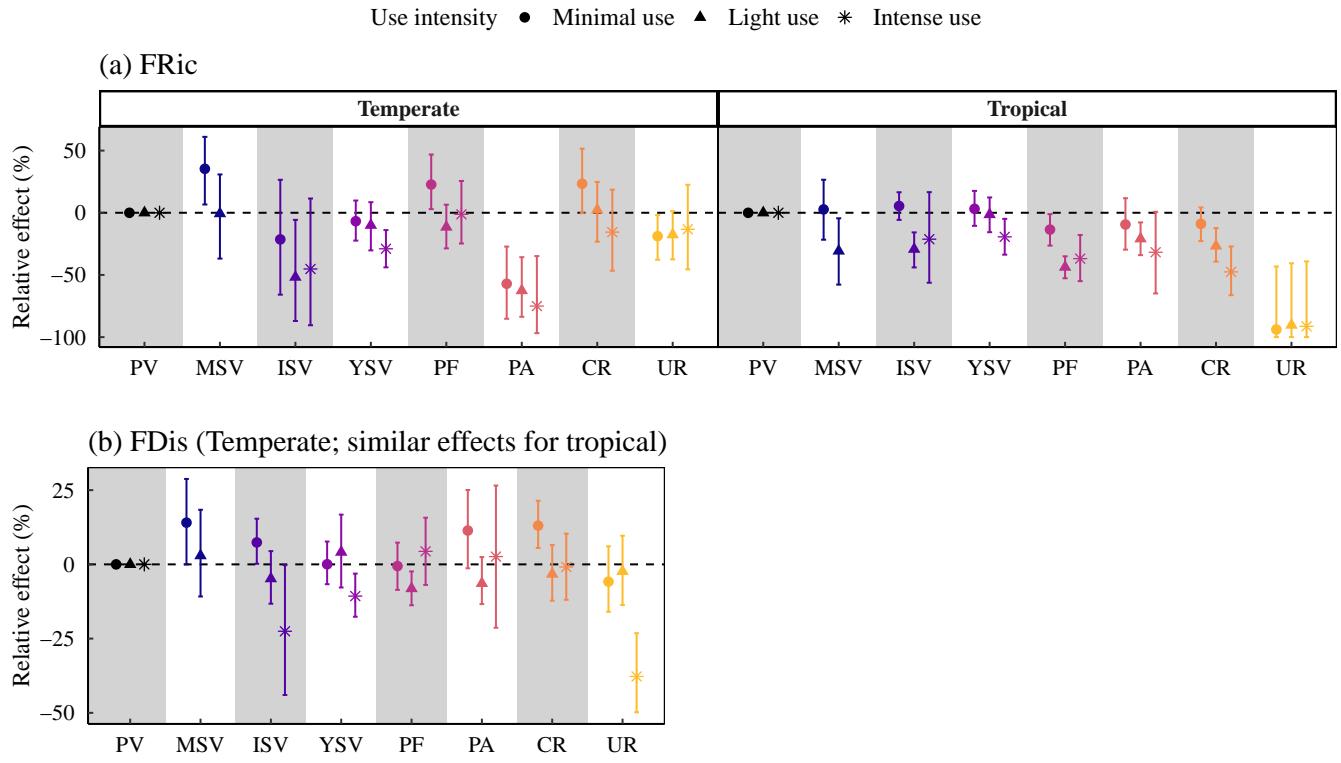


Figure S3.19: Effects of land use, land-use intensity and region on FRic (a) and FDis (b), for the subset of species with complete trait data (i.e., excluding species with less than 100% trait completeness), with geographical range size as an additional trait considered in the calculation of functional diversity metrics. Effects are plotted as a % difference relative to the reference land use (primary vegetation, PV). For FRic, I fitted Model 1a (see main text, Chapter 3), 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.

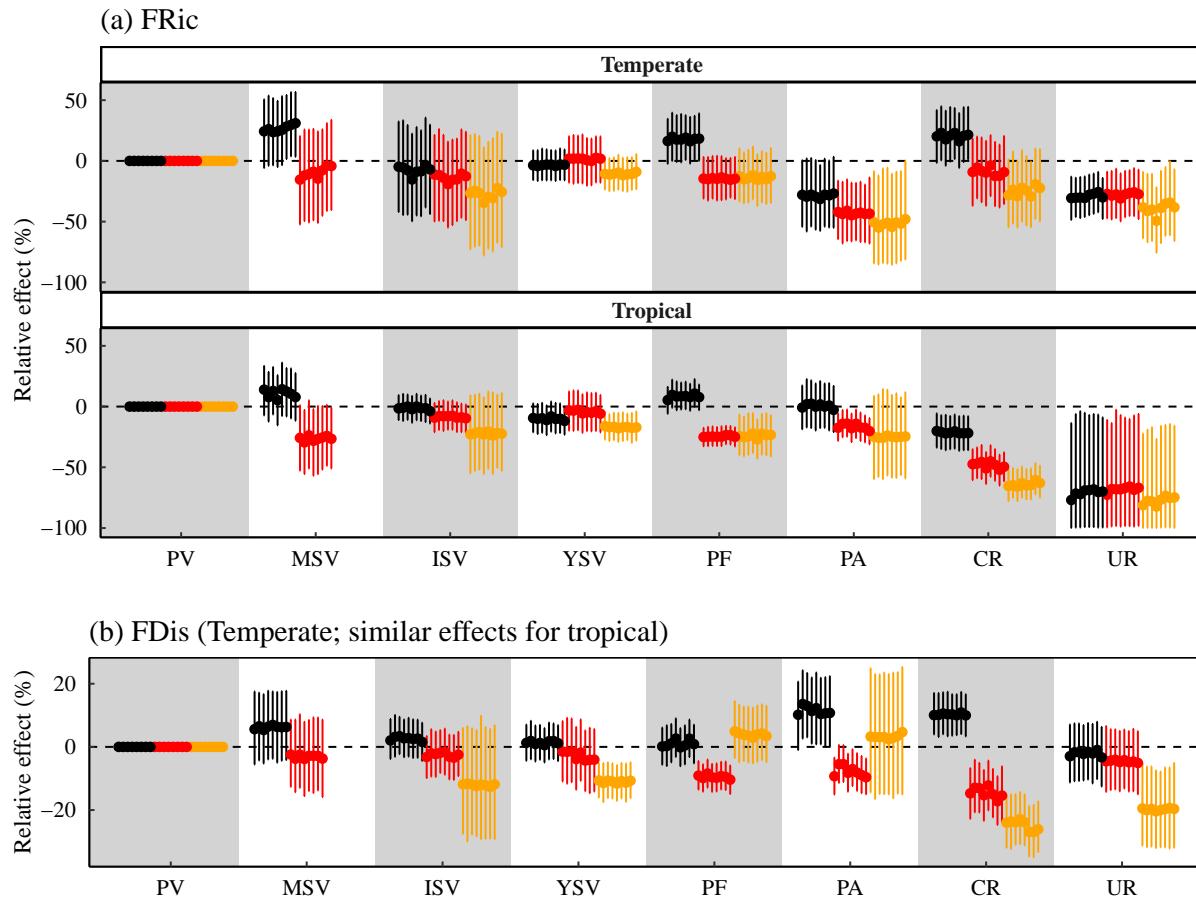


Figure S3.20: Effects of land use and land-use intensity on FRic (a) and FDis (b), obtained when calculating FRic and FDis with each set of imputed traits (eight in total). Effects are plotted as a % difference relative to the reference land use (primary vegetation, PV). For FRic, I fitted Model 1a (see main text, Chapter 3), 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.

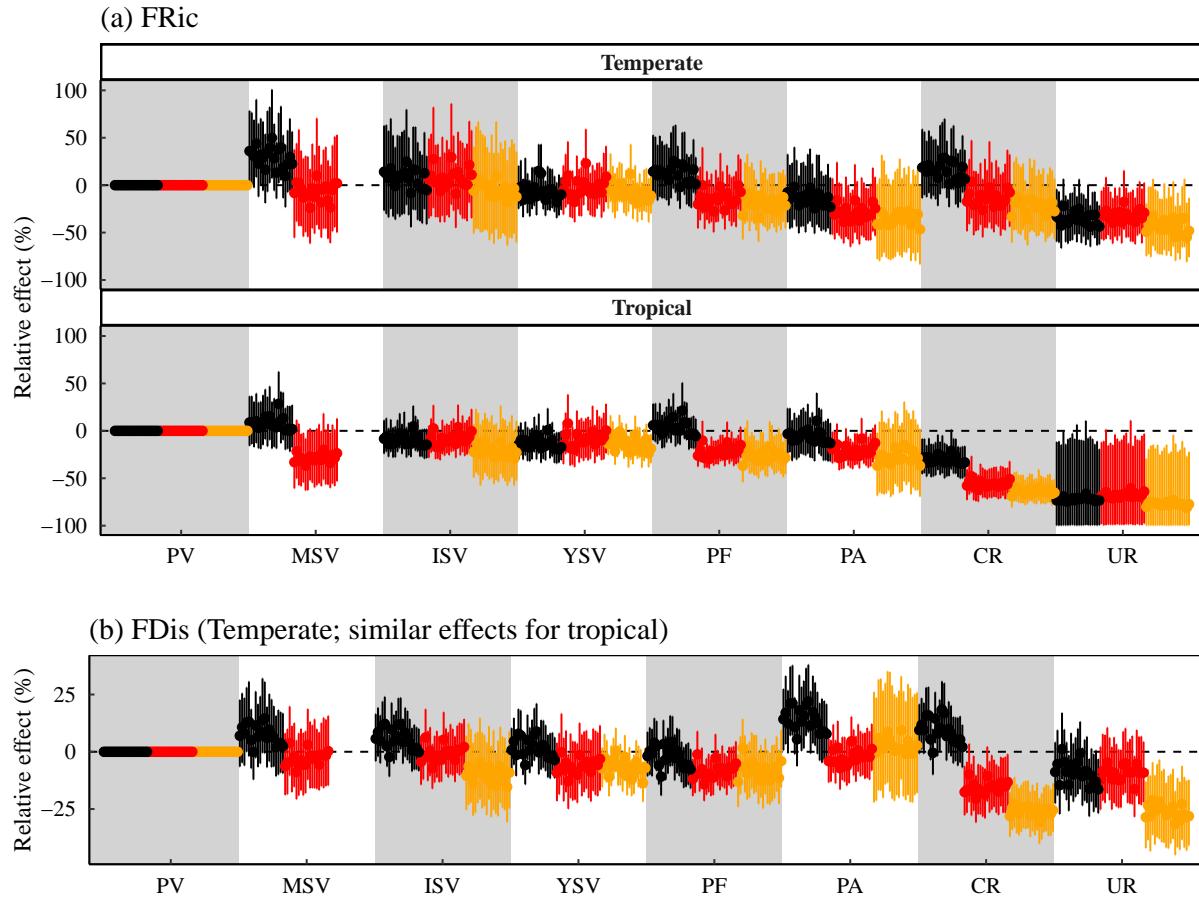


Figure S3.21: Effects of land use and land-use intensity on FRic (a) and FDis (b), obtained when re-sampling primary vegetation sites twenty independent times. I fixed the sample size for primary vegetation sites at 50. For FRic, we fitted Model 1a (see main text, Chapter 3), which included the effects 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.

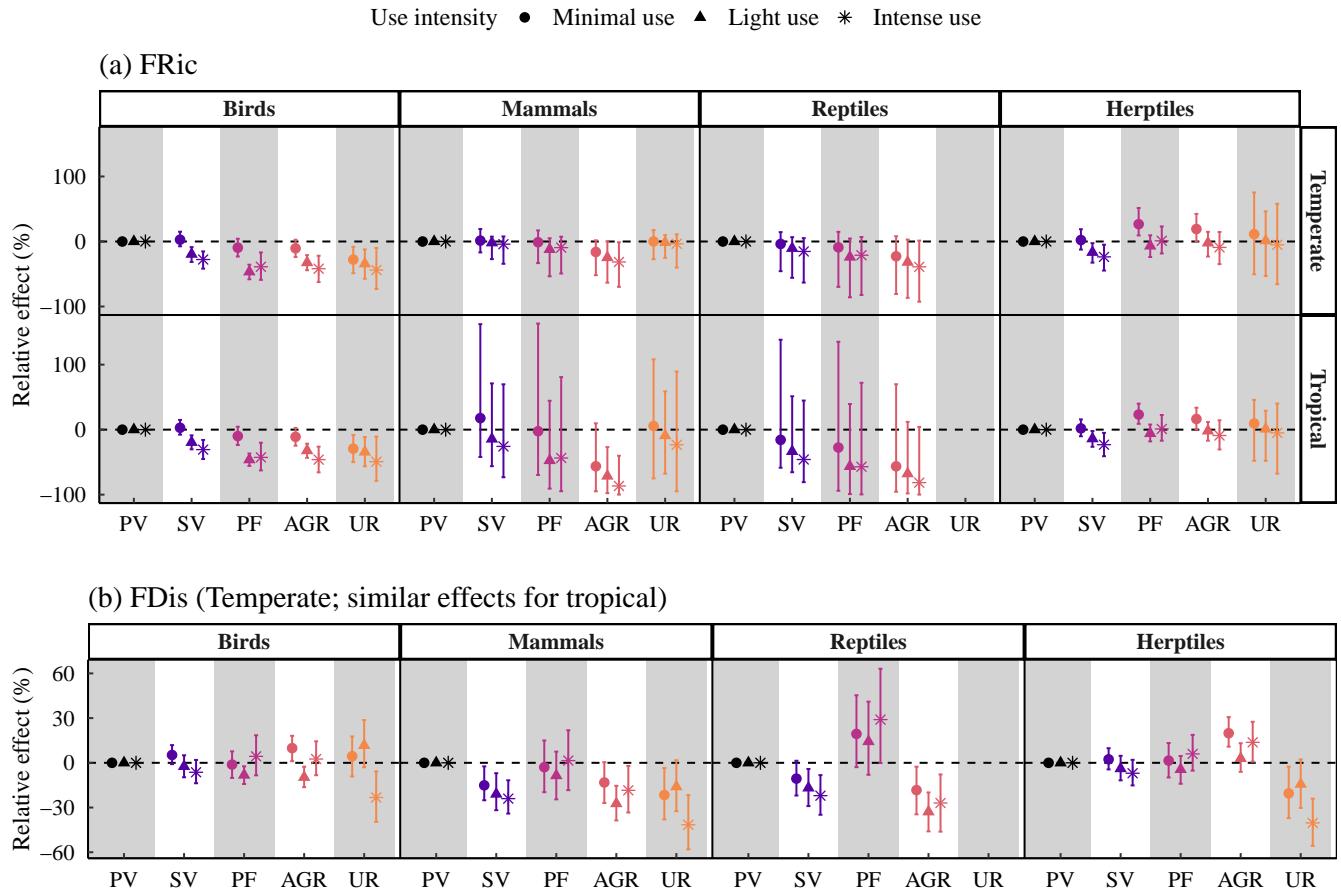
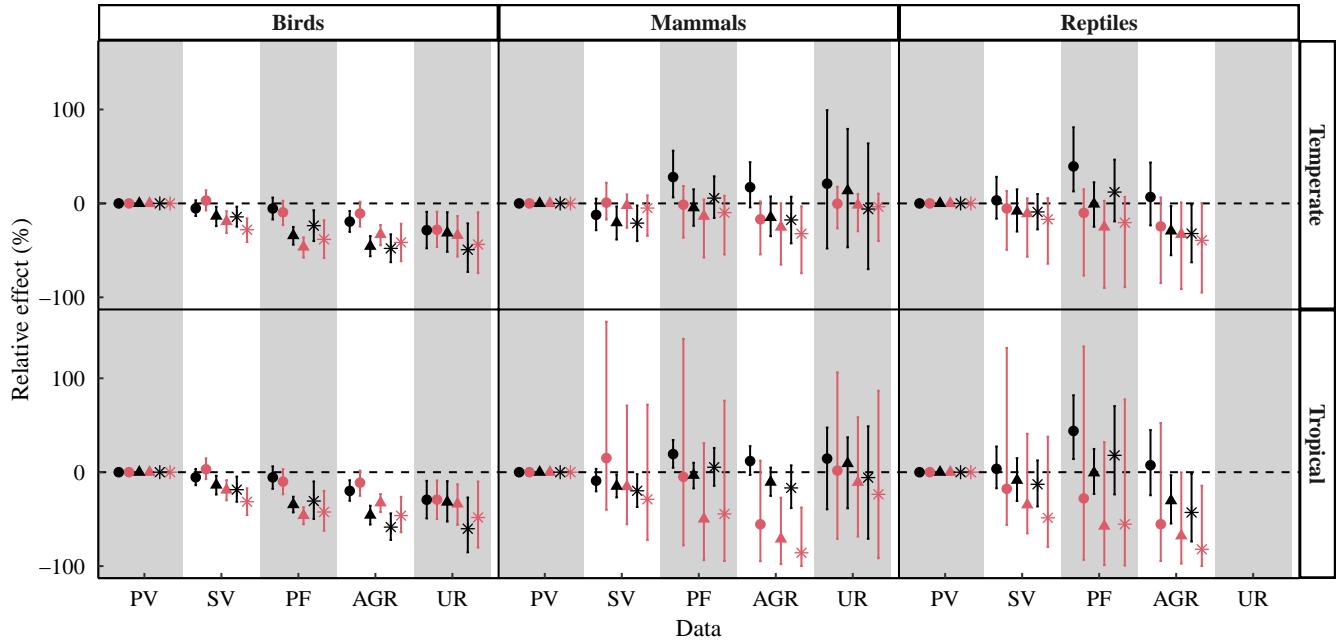


Figure S3.22: Effects of land use, land-use intensity and taxonomic class on FRic (a) and FDis (c), for the subset of species with complete trait data (i.e., excluding species with less than 100% trait completeness). Effects are plotted as a % difference relative to the reference land use (primary vegetation,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



(a) FDis

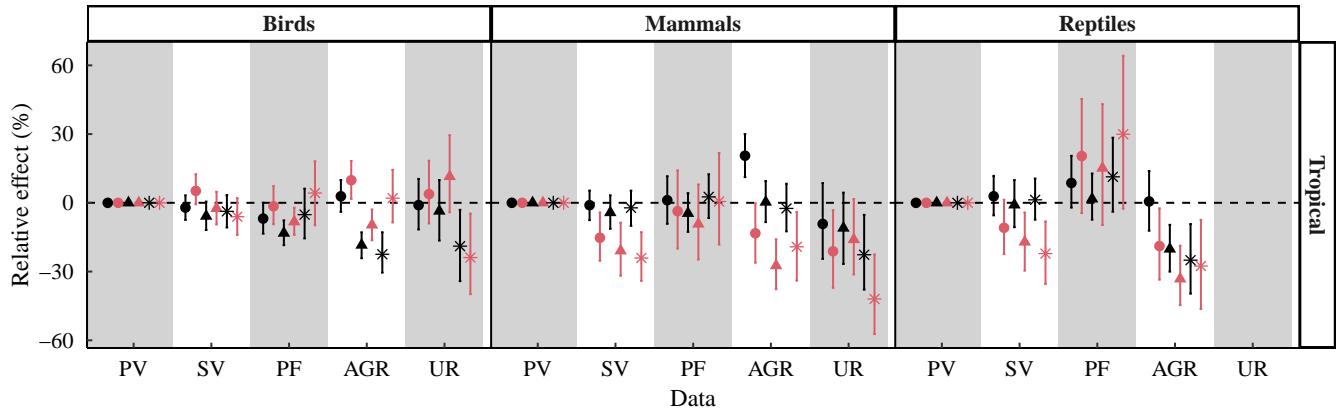
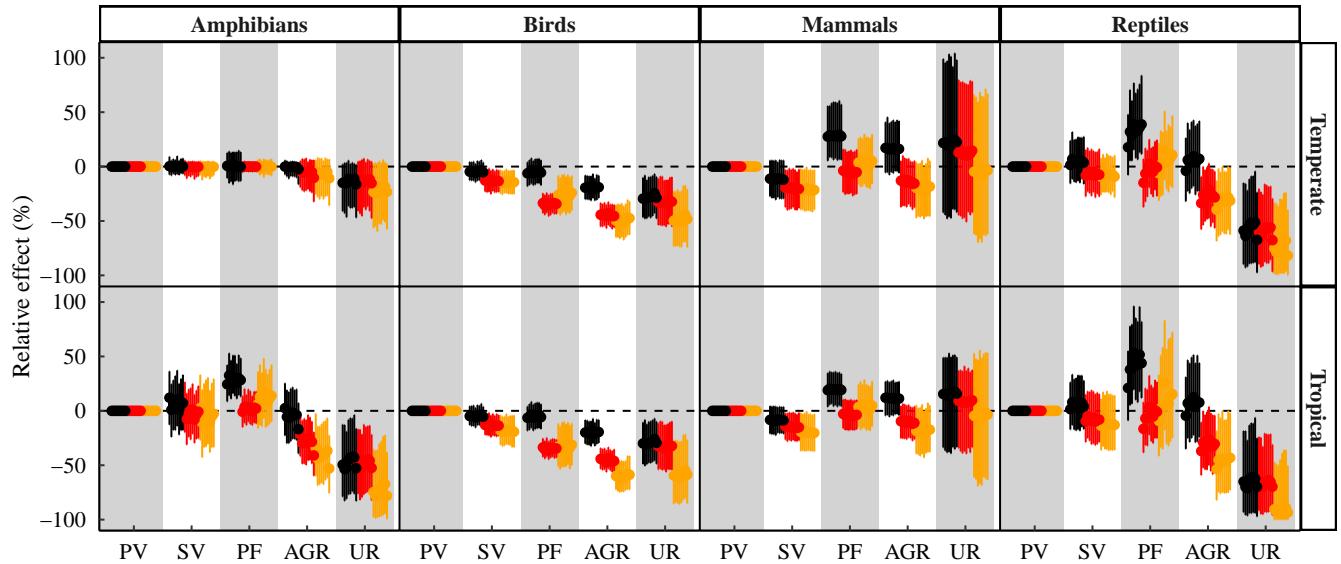


Figure S3.23: Effects of land use, region, land-use intensity and taxonomic class on FRic and FDis obtained with the imputed trait data (black points) or with the complete data subsets (red points). Effects are plotted as a % difference relative to the reference land use (primary vegetation, PV). For FRic, I fitted Model 2a (see main text, Chapter 3), 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)

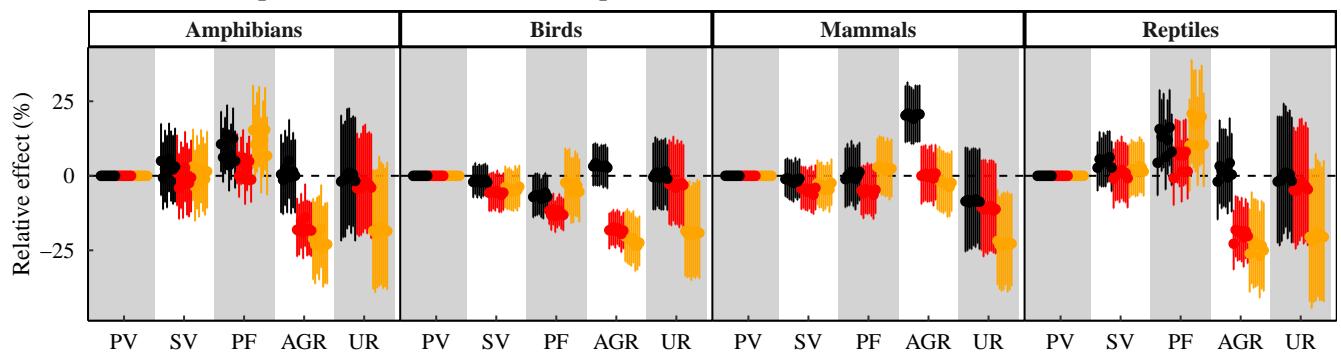


Figure S3.24: Effects of land use, region, land-use intensity and taxonomic class on FRic and FDis, obtained when calculating FRic and FDis with each set of imputed traits (eight in total). Effects are plotted as a % difference relative to the reference land use (primary vegetation, PV). For FRic, I fitted Model 2a (see main text, Chapter 3), 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 includes 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) show that time since conversion has a significant negative effect on FRic, but the relationship between FRic and time since land-use conversion is similar in different land uses (as there are no interactions between land use and time since conversion, such that the slopes are similar in different land uses, and so the rate at which FRic decreases with time is similar in different land uses). The intercept is 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 uses.

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
log_Years	-0.094	0.021	-4.566

I then compare this model's predictions with a simpler model that does not account for time since land-use conversion ($\text{FRic} \sim \text{Land use}$). The predictions (Fig. S3.25) show that including time since land-use conversion does not bias the results, as I find a similar significant effect with both models in

urban land uses, and elsewhere the effects are congruent. Thus, given this data subset, I argue that the results are robust to the inclusion of time since land-use conversion.

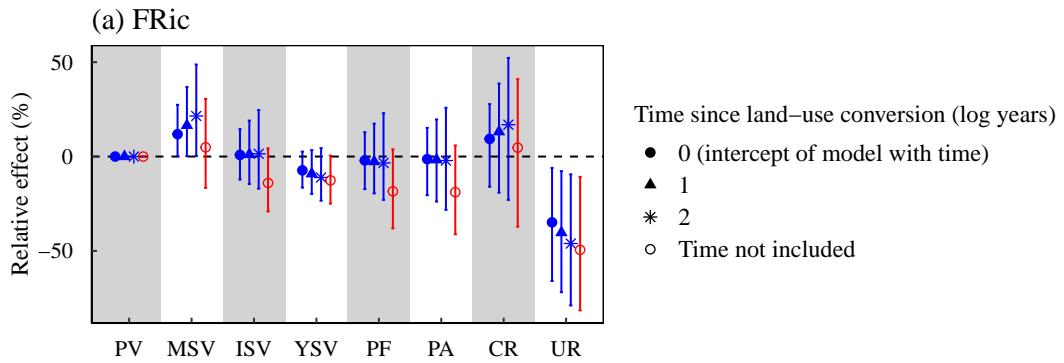


Figure S3.25: Effects of land use on FRic for the model that includes time since land-use conversion (blue points) versus the model that does not take time since land-use conversion into account (red points).

- For FDis, the best-fitting model includes 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 didn't consider land-use intensity in the starting model because of sample size issues). Nevertheless, the main effect of time since land-use conversion is not significant (Table S3.7), and the relationship between time since land-use conversion and FDis is not significant in most 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
log_Years	-0.004	0.004	-1.186
Mature secondary vegetation:log_Years	-0.005	0.015	-0.335
Intermediate secondary vegetation:log_Years	0.011	0.016	0.650
Young secondary vegetation:log_Years	-0.008	0.007	-1.170
Plantation forest:log_Years	-0.023	0.007	-3.077
Pasture:log_Years	0.010	0.015	0.688
Cropland:log_Years	0.007	0.012	0.620
Urban:log_Years	-0.016	0.022	-0.714

Appendix 3: Supporting information for Chapter 4

Appendix 4: Supporting information for Chapter 5

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

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

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

Figure S5.1: Formula for the abundance model, used to understand the role of shifts in the body mass of species on observed changes in tRMR (see main text, ‘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.

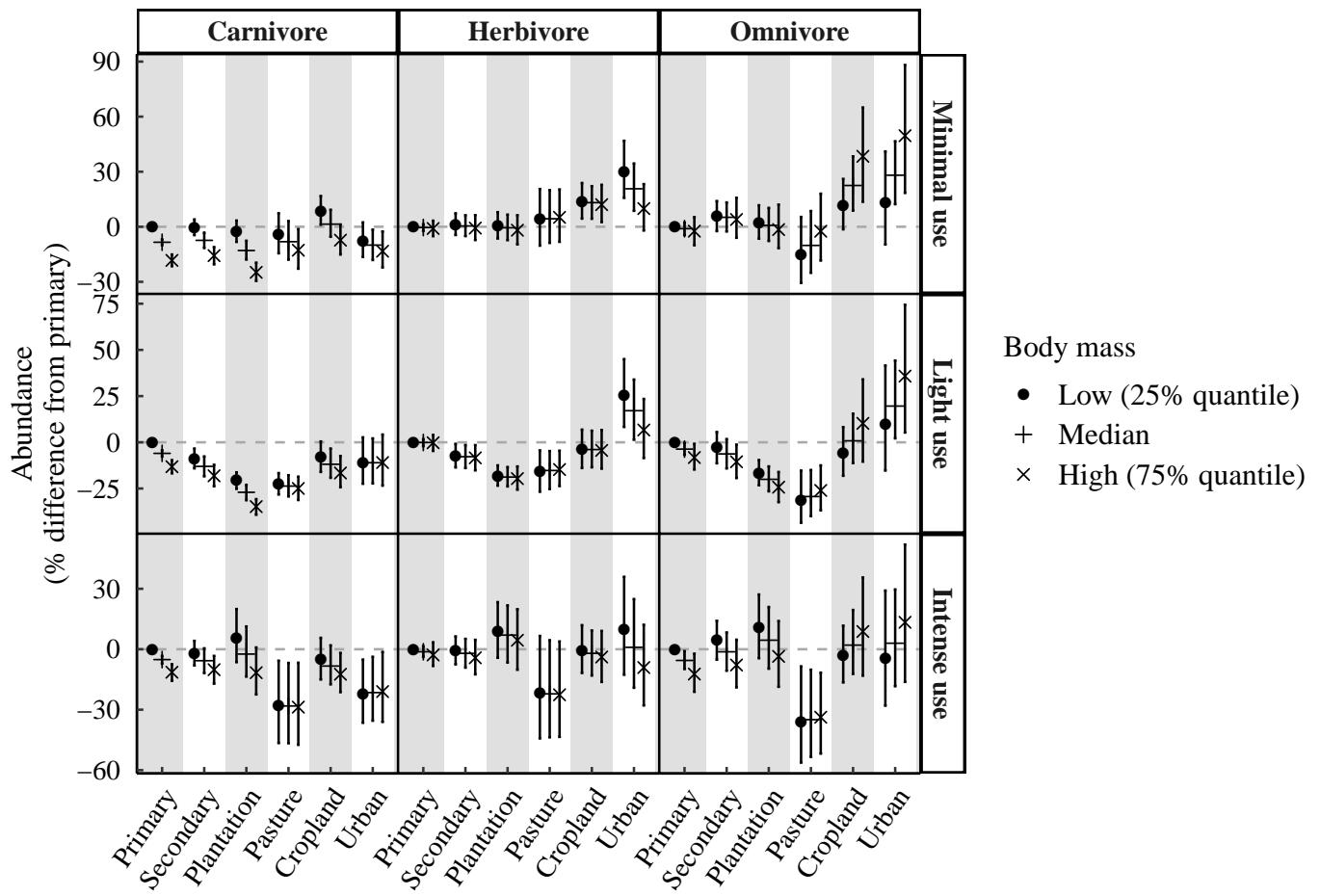


Figure S5.2: Effects of land use, land-use intensity, trophic group, body mass and their interactions on assemblage-level total abundance, estimated from the model specified in Fig. S1. The predictions are rescaled with reference to minimally used primary vegetation, considered to be the undisturbed 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).

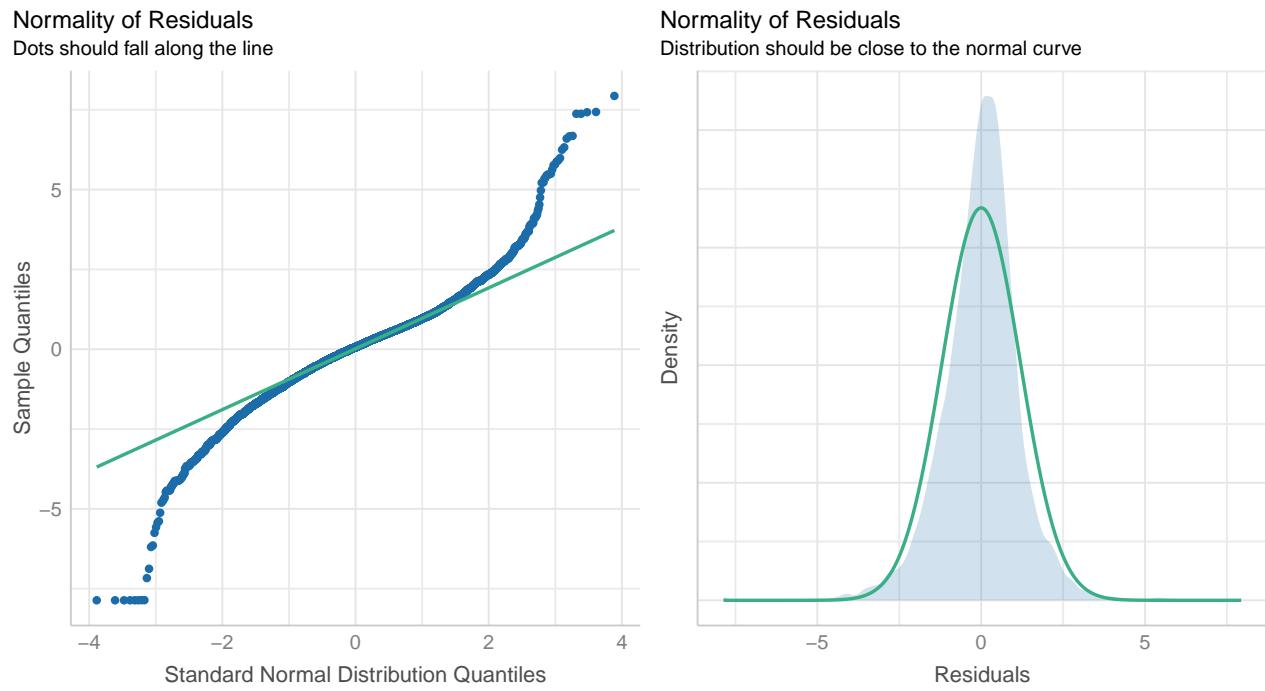
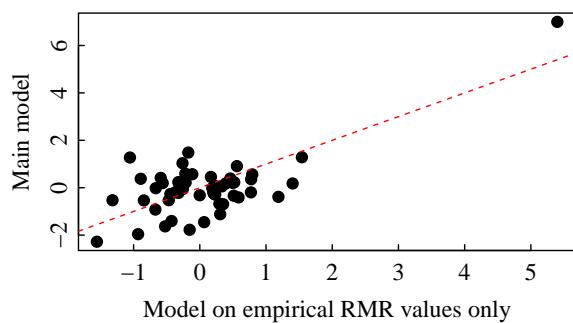


Figure S5.3: Diagnostic plots (qq-plot and residual distribution) for the linear mixed-effects model looking at the effects of land use, land-use intensity, trophic group and their interactions on assemblage-level total RMR. The diagnostic plots were obtained with the 'performance' R package (Lüdecke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

(a) Coefficient estimates



(b) Standard error estimates

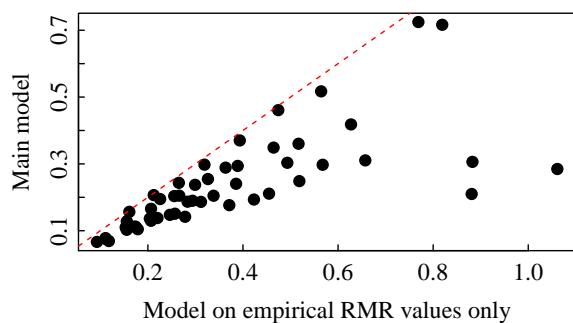


Figure S5.4: Estimates for the models looking at the effects of land use, land-use intensity, trophic group and their interactions on assemblage-level total RMR. I plotted the estimates from the model fitted on the empirical and imputed RMR values (presented in the main text) on the y-axis, and the estimates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

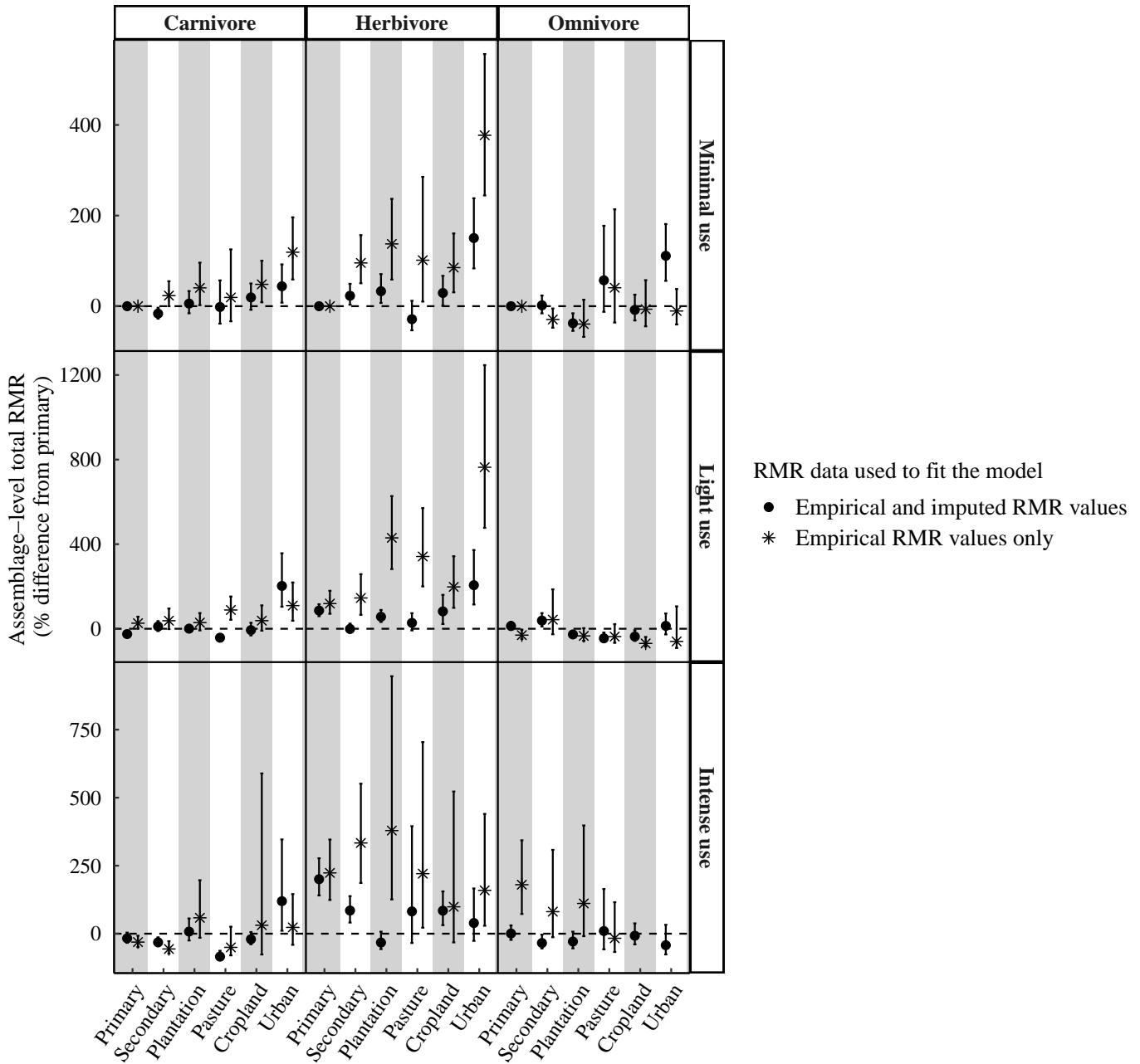


Figure S5.5: Effects of land use, land-use intensity, trophic level and their interactions on assemblage-level total RMR, estimated from the model fitted on the empirical and imputed RMR values (presented in the main text) and from the model fitted on the empirical values only. The predictions are rescaled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

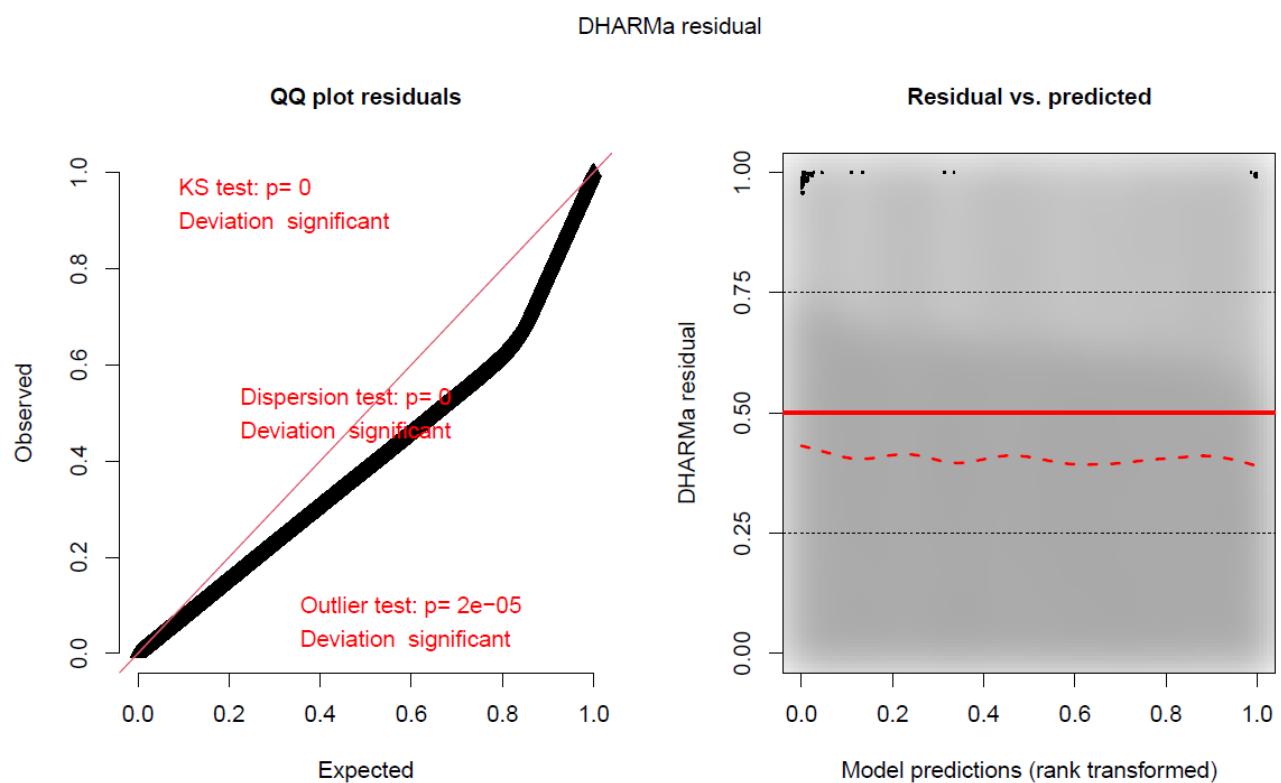


Figure S5.6: Diagnostic plots for the generalised mixed-effects model looking at the effects of land use, land-use intensity, trophic group, residual RMR and their interactions on species' probability of occurrence. The diagnostic plots were obtained with the 'DHARMA' R package (Hartig, 2021).

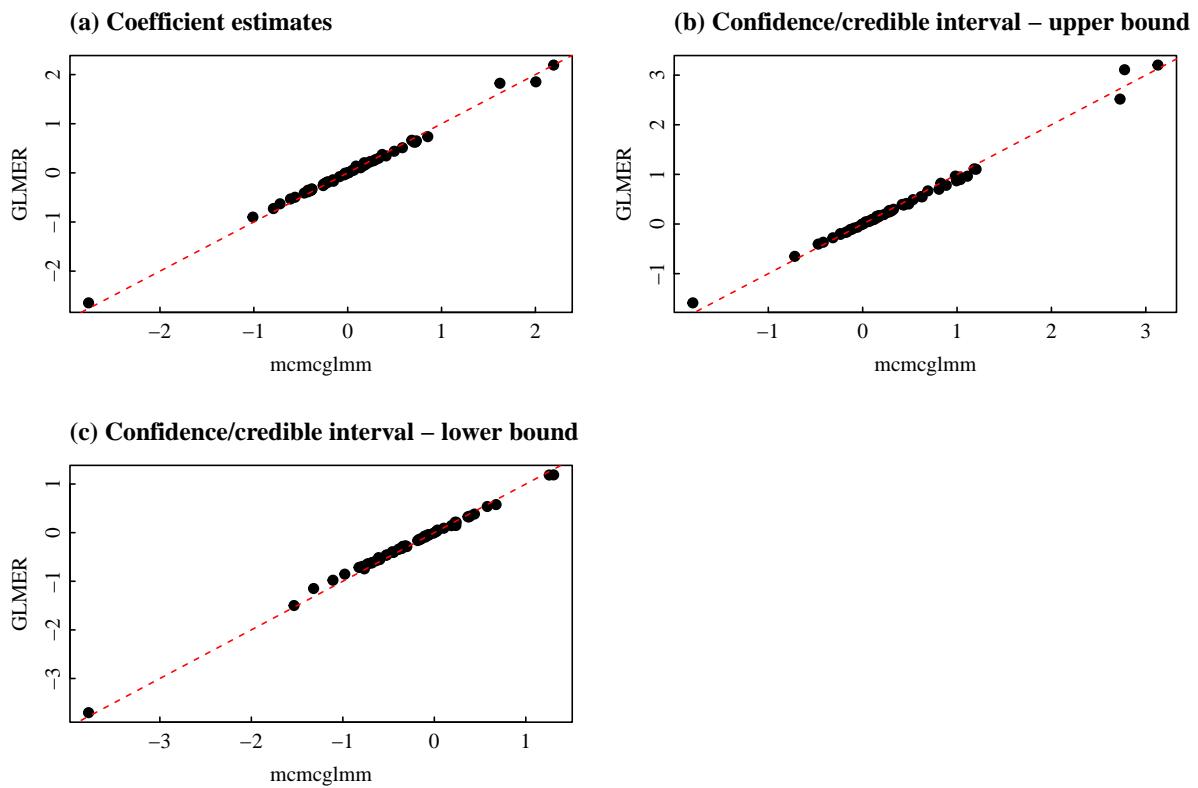
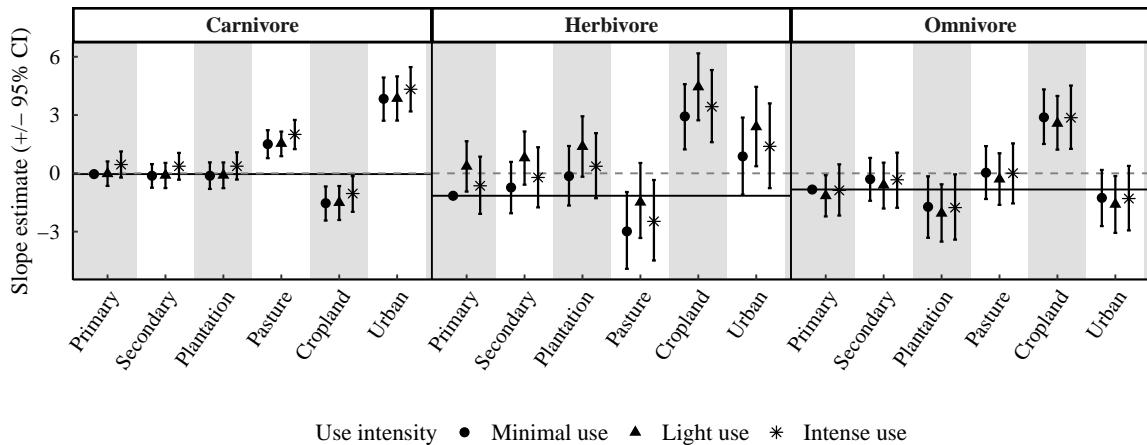


Figure S5.7: Model's coefficients from the occurrence model fitted using the 'lme4' package (Bates et al., 2015) against coefficients from the model fitted using a Bayesian framework with the 'MCMCglmm' package (Hadfield, 2010). The models were fitted to investigate the effects of land use, land-use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

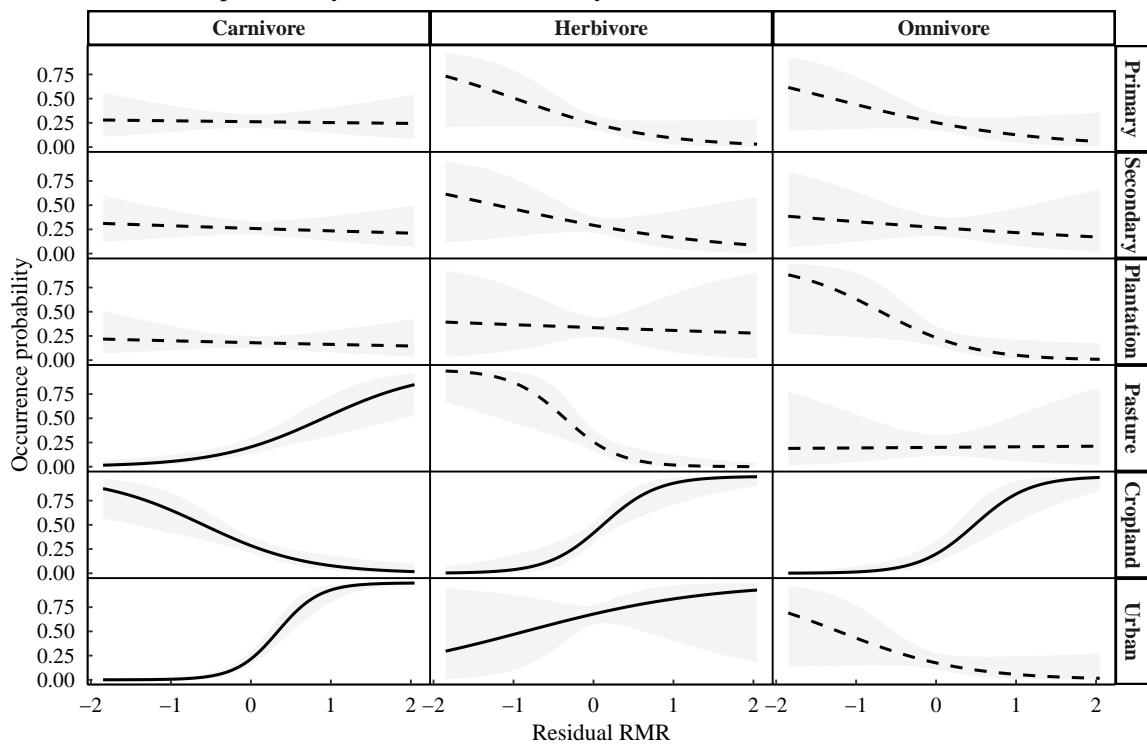


Figure S5.8: (a) Slope estimates for the relationship between residual RMR and occurrence probability in each land-use type and for the three levels of land-use intensity, from the model fitted using the empirical RMR values (i.e., excluding imputed RMR values). The black horizontal line indicates the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