



University College London  
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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.

# **Acknowledgements**

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

# **Thesis outline of contents, authorship and collaborations**

## **Chapter 1: General introduction**

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

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

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

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

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

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

In this Chapter, I assess whether ecological traits as well as geographical range area are associated with species' land-use responses and species' estimated climate-change sensitivity, comparatively among terrestrial vertebrate classes. Rhiannon Osborne-Tonner contributed to this Chapter by collecting data on amphibian and reptile diet during her 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-level energetic requirements, and I assess whether species' energetic requirements influence species persistence in disturbed land uses. To this end, I use physiological data, compiling species resting metabolic rates (used as a proxy for energetic requirements) from the literature. Meghan Hayden and Laura Dee of the University of Colorado, Boulder, as well as Tim Newbold, contributed to the elaboration of the research questions for this Chapter. Meghan Hayden further contributed to this Chapter by retrieving information on net primary productivity for PREDICTS sites, using data from MODIS satellite imagery. All collaborators also provided feedback on the work and participated in writing the manuscript. This Chapter was submitted to a scientific journal and underwent a round of peer-review. I am preparing this Chapter for resubmission 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](https://github.com/AdrienneEtard/PhD_thesis_code).

This document was compiled with L<sup>A</sup>T<sub>E</sub>X; 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](https://figshare.com/articles/dataset/Global_gaps_in_terrestrial_vertebrate_trait_data/10075421).

# Contents

|   |           |
|---|-----------|
| <b>List of Tables</b>   | <b>13</b> |
| <b>List of Figures</b>  | <b>15</b> |
| <b>1 General introduction</b>   | <b>20</b> |
| 1.1 Major drivers of global biodiversity change . . . . .   | 21        |
| 1.1.1 Land-use change . . . . .   | 21        |
| 1.1.2 Climate change . . . . .  | 22        |
| 1.1.3 The future of biodiversity in the Anthropocene . . . . .  | 24        |
| 1.2 Ecological importance of terrestrial vertebrates and current threats . . . . .                                  | 24        |
| 1.3 Using trait-based approaches to understand global biodiversity change . . . . .                                 | 25        |
| 1.3.1 Traits as common currencies across species . . . . .  | 25        |
| 1.3.2 Using ecological traits to assess which species are at most risk from human-driven changes . . . . .          | 26        |
| 1.3.3 Using physiological traits to understand land-use impacts on biodiversity and ecosystem functioning . . . . . | 27        |
| 1.3.4 Thesis aims . . . . .   | 27        |
| 1.4 Detailed aims, hypotheses and outline of the following Chapters . . . . .                                       | 28        |
| <b>2 Global gaps and biases in trait data for terrestrial vertebrates</b>   | <b>32</b> |
| 2.1 Introduction . . . . .  | 33        |
| 2.2 Methods . . . . .   | 36        |
| 2.2.1 Trait data collection . . . . .   | 36        |
| 2.2.2 Investigating gaps and biases in trait data . . . . .   | 42        |
| 2.3 Results . . . . .   | 44        |
| 2.3.1 Taxonomic biases in trait information . . . . .   | 44        |

|          |  |           |
|----------|--|-----------|
| 2.3.2    | Phylogenetic biases in trait completeness . . . . .  | 45        |
| 2.3.3    | Spatial biases in trait completeness . . . . .   | 48        |
| 2.4      | Discussion . . . . .   | 50        |
| <b>3</b> | <b>Intensive human land uses negatively affect vertebrate functional diversity</b>   | <b>55</b> |
| 3.1      | Introduction . . . . .   | 55        |
| 3.2      | Methods . . . . .  | 57        |
| 3.2.1    | Vertebrate assemblages . . . . .   | 57        |
| 3.2.2    | Functional traits and diversity metrics . . . . .  | 59        |
| 3.2.3    | Effects of land use and land-use intensity on FRic and FDis (Hypothesis 1) . . . . .   | 60        |
| 3.2.4    | Investigating functional under-dispersion (Hypothesis 2) . . . . .   | 62        |
| 3.2.5    | Functional loss and functional gain (Hypothesis 3) . . . . .   | 62        |
| 3.3      | Results . . . . .  | 63        |
| 3.3.1    | Effects of land use on FRic and FDis . . . . .   | 63        |
| 3.3.2    | Changes in the probability of occurrence of functional under-dispersion . . . . .  | 66        |
| 3.3.3    | Functional loss and gain . . . . .   | 67        |
| 3.4      | Discussion . . . . .   | 69        |
| <b>4</b> | <b>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</b> | <b>73</b> |
| 4.1      | Introduction . . . . .   | 73        |
| 4.2      | Methods . . . . .  | 75        |
| 4.3      | Results . . . . .  | 75        |
| 4.4      | Discussion . . . . .   | 82        |
| <b>5</b> | <b>Energetic constraints and trophic group explain species persistence in disturbed land uses</b>  | <b>83</b> |
| 5.1      | Introduction . . . . .   | 84        |
| 5.2      | Methods . . . . .  | 89        |
| 5.2.1    | Vertebrate assemblage composition . . . . .  | 89        |
| 5.2.2    | Energy availability by land-use type and land-use intensity . . . . .  | 89        |
| 5.2.3    | Resting Metabolic Rates (RMR) & imputations of missing RMR values . . . . .  | 90        |
| 5.2.4    | Trophic group and body mass information . . . . .  | 91        |

|   |   |            |
|---|---|------------|
| 5.2.5   | Effects of land use, land-use intensity and trophic group on assemblage-level total RMR (prediction 1; Figure 5.2a) . . . . .                   | 91         |
| 5.2.6   | Effects of land use, land-use intensity, trophic group and residual RMR on species occurrence probability (prediction 2; Figure 5.2b) . . . . . | 92         |
| 5.3   | Results . . . . .   | 93         |
| 5.3.1   | Effects of land use, land-use intensity and trophic group on assemblage-level total RMR . . . . .   | 93         |
| 5.3.2   | Effects of land use, land-use intensity, trophic group and residual RMR on species' occurrence probability . . . . .                            | 94         |
| 5.4   | Discussion . . . . .  | 97         |
| <b>6</b>  | <b>General discussion</b>   | <b>100</b> |
| <b>Bibliography</b>                                     |   | <b>101</b> |
| <b>Appendices</b>                                       |   | <b>124</b> |
| <b>Appendix 1: Supporting information for Chapter 2</b> |   | <b>125</b> |
| S2.1  | Taxonomic corrections . . . . .   | 125        |
| S2.2  | Additional information for trait compilation . . . . .  | 128        |
| S2.3  | Cutting distribution maps by altitudinal limits . . . . .   | 129        |
| S2.4  | Impact of taxonomic corrections on trait coverage . . . . .   | 130        |
| S2.5  | Assemblage-level median, mean and standard deviation of trait completeness (maps) . . .   | 131        |
| S2.6  | Phylogenetic patterns in trait completeness . . . . .   | 136        |
| S2.7  | Poisson model summaries . . . . .   | 141        |
| S2.8  | Spatial model summaries . . . . .   | 142        |
| S2.9  | Trait coverage and taxonomic matching . . . . .   | 143        |
| <b>Appendix 2: Supporting information for Chapter 3</b> |   | <b>143</b> |
| S3.1  | Land-use categories in PREDICTS and sample sizes . . . . .  | 144        |
| S3.2  | Trait data & imputation of missing trait values . . . . .   | 147        |
| S3.2.1  | Choice of imputation technique . . . . .  | 149        |
| S3.2.2  | Phylogenetic signal in traits . . . . .   | 149        |
| S3.2.3  | Implementation of missForest imputations . . . . .  | 150        |

|  |   |            |
|--|---|------------|
| S3.3                                   | Degree of multicollinearity among traits . . . . .          | 151        |
| S3.4                                   | Imputation performance . . . . .                            | 152        |
| S3.5                                   | Functional loss and functional gain . . . . .               | 155        |
| S3.6                                   | Diagnostic plots . . . . .                                  | 158        |
| S3.7                                   | Model robustness . . . . .                                  | 167        |
| S3.8                                   | Model robustness – time since land-use conversion . . . . . | 174        |
| <b>Appendix 3:</b>                     | <b>Supporting information for Chapter 4</b>                 | <b>175</b> |
| <b>Appendix 4:</b>                     | <b>Supporting information for Chapter 5</b>                 | <b>177</b> |
| <b>Bibliography for the Appendices</b> |   | <b>186</b> |

# List of Tables

|  |            |
|--|------------|
| <b>Chapter 2</b>   | <b>32</b>  |
| 2.1    Data sources for each trait . . . . .   | 38         |
| 2.2    Number of species for each analysis . . . . .   | 42         |
| <b>Chapter 4</b>   | <b>73</b>  |
| 4.1    Summary of the effects of the ecological characteristics (except for primary diet) on species responses to disturbed land uses ('within land-use type' effects) and on species climate-change sensitivity, for each Class of terrestrial vertebrates. . . . . | 76         |
| 4.2    ANOVA summaries for the PGLS models investigating the effects of the species-level ecological characteristics on species climate-change sensitivity. . . . .  | 81         |
| <b>Appendix 1</b>  | <b>125</b> |
| S2.1    Coefficients of the model investigating whether species range size explained the number of sampled traits . . . . .  | 141        |
| 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 . . . . .  | 141        |
| S2.3    Spatial model summary for amphibians . . . . .   | 142        |
| S2.4    Spatial model summary for reptiles . . . . .   | 142        |
| <b>Appendix 2</b>  | <b>143</b> |
| S3.1    Land-use categories in the PREDICTS database . . . . .   | 144        |
| S3.2    Phylogenetic signal in continuous and categorical traits . . . . .   | 150        |
| S3.3    Variance inflation factors across considered (imputed) traits . . . . .  | 151        |
| S3.4    Sample sizes (number of pairs of sites) for the calculation of functional loss and functional gain across all species . . . . .  | 156        |

|      |   |     |
|------|---|-----|
| S3.5 | Sample sizes (number of pairs of sites) for the calculation of functional loss and functional gain within each class . . . . .  | 157 |
| 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 | 174 |

**Appendix 3** **175**

|      |  |     |
|------|--|-----|
| 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 | 176 |
|------|--|-----|

**Appendix 4** **177**

|      |   |     |
|------|---|-----|
| 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 . . . . . | 178 |
|------|---|-----|

# List of Figures

|                             |  |           |
|-----------------------------|--|-----------|
| 1.1                         | Characteristics of the ‘Great Acceleration’ . . . . .  | 23        |
| <b>General introduction</b> |  | <b>31</b> |
| <b>Chapter 2</b>            |  | <b>32</b> |
| 2.1                         | Procedure used to identify the accepted names of species . . . . .   | 37        |
| 2.2                         | Number of natural and artificial habitats used by species against number of strictly natural habitats used by species . . . . .                                | 41        |
| 2.3                         | Trait coverage and completeness across species . . . . .   | 45        |
| 2.4                         | Within-family median trait completeness in herptiles . . . . .   | 47        |
| 2.5                         | Relationship between number of sampled traits and geographical range size . . . . .  | 48        |
| 2.6                         | Spatial distribution of assemblage-level median trait completeness in herptiles . . . . .  | 49        |
| 2.7                         | Spatial model trends for herptiles . . . . .   | 50        |
| <b>Chapter 3</b>            |  | <b>55</b> |
| 3.1                         | Overview of the study design and functional diversity metrics . . . . .  | 58        |
| 3.2                         | Effects of land use, land-use intensity and region on FRic (a) and on FDis (b) across all PREDICTS vertebrates. . . . .  | 64        |
| 3.3                         | Effects of land use, land-use intensity, region and taxonomic class on FRic (a) and FDis (b). . . . .  | 65        |
| 3.4                         | Effects of land use, land-use intensity and region on the probability of occurrence of functional under-dispersion. . . . .                                    | 66        |
| 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. . . . . | 67        |
| 3.6                         | Effects of land use, land-use intensity, region and taxonomic class on functional loss and functional gain across pairs of sites. . . . .                      | 68        |

|   |            |
|---|------------|
| <b>Chapter 4</b>  | <b>73</b>  |
| 4.1 Framework of the study . . . . .  | 74         |
| 4.2 Assessing the effects of ecological characteristics on species land-use responses: methodology for (a) categorical characteristics and (b) continuous characteristics. . . . .      | 75         |
| 4.3 Predicted occurrence probability as a function of land use, land-use intensity, diet and their interactions, for each class of terrestrial vertebrates. . . . .                     | 77         |
| 4.4 Proportion of the explained variance attributable to each of the main effects in the land-use and climate-change sensitivity models . . . . .                                       | 78         |
| 4.5 Effects of the categorical traits on climate-change sensitivity, estimated from the PGLS models in each class. . . . .  | 79         |
| 4.6 Effects of the continuous ecological characteristics on climate-change sensitivity, estimated from the PGLS models in each class. . . . .   | 80         |
| <b>Chapter 5</b>  | <b>83</b>  |
| 5.1 Map of PREDICTS sites, sample sizes and NPP by land use and land-use intensity . . . . .  | 87         |
| 5.2 Framework for the predictions and models . . . . .  | 88         |
| 5.3 Effects of land use, land-use intensity and trophic group on assemblage-level total RMR. .  | 94         |
| 5.4 Slope estimates and predictions for the relationship between occurrence probability and residual RMR . . . . .  | 95         |
| 5.5 Predicted occurrence probabilities in primary vegetation and for the most disturbed land uses where residual RMR was found to have a significant effect on occurrence probability . | 96         |
| <b>Appendix 1</b>   | <b>125</b> |
| S2.1 Difference in species number before and after taxonomic correction (A) and distribution of number of synonyms across datasets (B) . . . . .  | 127        |
| S2.2 (a) Body mass versus body length and (b) longevity versus age at sexual maturity in amphibians . . . . .   | 128        |
| S2.3 Generation length versus longevity data in mammals and birds . . . . .   | 128        |
| S2.4 Availability of altitudinal limits across species . . . . .  | 129        |
| S2.5 Range sizes before versus after cutting by altitudinal limits . . . . .  | 129        |
| S2.6 Trait coverage when no taxonomic correction is applied before matching sources by binomial names, versus when I applied the described procedure . . . . .                          | 130        |

|       |  |     |
|-------|--|-----|
| S2.7  | Spatial distribution of assemblage-level median trait completeness in each class . . . . .   | 132 |
| S2.8  | Spatial distribution of assemblage-level mean trait completeness in each class . . . . .   | 133 |
| S2.9  | Spatial distribution of assemblage-level standard deviation of trait completeness in each class . . . . .                                  | 134 |
| S2.10 | Assemblage-level species richness against standard deviation in trait completeness in each class . . . . .                                 | 135 |
| S2.11 | Within-family median trait completeness in mammals . . . . .   | 137 |
| S2.12 | Within-family median trait completeness in birds . . . . .   | 138 |
| S2.13 | Within-family standard deviation in trait completeness (herptiles) . . . . .   | 139 |
| S2.14 | Within-family species richness against the within-family standard deviation of trait completeness . . . . .                                | 140 |
| S2.15 | Relationships between number of sampled traits and geographical range size using distribution maps not cut by altitudinal limits . . . . . | 141 |
| S2.16 | Comparison of trait coverage among datasets corrected for taxonomy in different ways . .   | 143 |

## **Appendix 2** **143**

|       |   |     |
|-------|---|-----|
| S3.1  | Number of sites in each land use and land-use intensity for which FRic and FDis were calculated, across all species . . . . . | 145 |
| S3.2  | Number of sites in each land use, land-use intensity and for which FRic and FDis were calculated, within each class . . . . . | 146 |
| S3.3  | Relationship between habitat breadth and geographical range size across species in each class                                 | 147 |
| S3.4  | Trait coverage for the vertebrate species sampled in the PREDICTS database . . . . .  | 148 |
| S3.5  | Distribution of trait completeness across the vertebrate species sampled in the PREDICTS database . . . . .                   | 148 |
| S3.6  | Distribution of continuous traits considered in the calculation of the functional diversity metrics . . . . .                 | 152 |
| S3.7  | Frequency distribution for categorical traits considered in the calculation of the functional diversity metrics . . . . .     | 153 |
| S3.8  | Out-of-bag imputation errors for the continuous traits (a) and categorical traits (b) . . . . .                               | 154 |
| S3.9  | Diagnostic plots for Model 1a . . . . .   | 158 |
| S3.10 | Diagnostic plots for Model 1b . . . . .   | 159 |
| S3.11 | Diagnostic plots for Model 2a . . . . .   | 160 |
| S3.12 | Diagnostic plots for Model 2b . . . . .   | 161 |

|                   |   |            |
|-------------------|---|------------|
| S3.13             | Diagnostic plots for Model 3 . . . . .  | 162        |
| S3.14             | Diagnostic plots for Model 4a . . . . .   | 163        |
| S3.15             | Diagnostic plots for Model 4b . . . . .   | 164        |
| S3.16             | Diagnostic plots for Model 5a . . . . .   | 165        |
| S3.17             | Diagnostic plots for Model 5b . . . . .   | 166        |
| 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 . . . . .  | 167        |
| 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, with geographical range size as an additional trait . . . . .              | 168        |
| 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 . . . . .  | 169        |
| S3.21             | Effects of land use and land-use intensity on FRic (a) and FDis (b), obtained when resampling primary vegetation sites twenty independent times . . . . .   | 170        |
| 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 . . . . .  | 171        |
| 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) . . . . .           | 172        |
| 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 . . . . .                                     | 173        |
| 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) . . . . . | 175        |
| <b>Appendix 3</b> |   | <b>175</b> |
| <b>Appendix 4</b> |   | <b>177</b> |
| 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 . . . . .  | 178        |
| S5.2              | Effects of land use, land-use intensity, trophic group, body mass and their interactions on assemblage-level total abundance . . . . .  | 179        |
| S5.3              | Diagnostic plots 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 . . . . .                    | 180        |

|      |   |     |
|------|---|-----|
| 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 . . . . .   | 181 |
| S5.5 | Effects of land use, land-use intensity, trophic level and their interactions on assemblage-level total RMR: empirical versus imputed . . . . .   | 182 |
| 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 . . . . . | 183 |
| S5.7 | Model's coefficients from the occurrence model fitted using the 'lme4' package against coefficients from the model fitted using the 'MCMCglmm' package . . . . .  | 184 |
| S5.8 | Slope estimates and predictions for the relationship between occurrence probability and residual RMR for the model fitted on empirical RMR values only . . . . .  | 185 |

# <sup>1</sup> 1 | General introduction

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

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

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

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

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

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

### 45 **1.1.1 Land-use change**

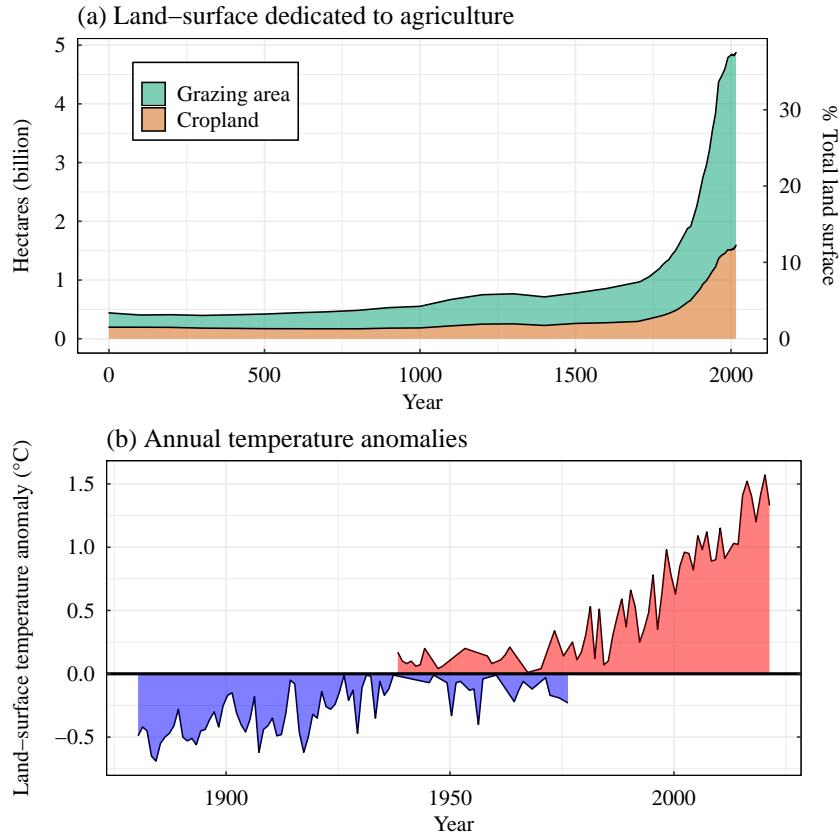
46 Land cover describes the physical aspect and composition of the land surface from dominant biotic and abi-  
47 otic features, typically classifying the Earth's surface into determined sets of natural and artificial ensembles;  
48 land cover can notably be characterised with satellite imagery (Wulder et al., 2018). Land use, however, de-  
49 scribes the human intent behind a particular land cover (Lambin et al., 2001). Land-use change thus refers  
50 to the process by which humans transform the landscape to achieve socio-economic needs. Land-use change  
51 includes transitions from natural to anthropogenic landscapes, as exemplified by agricultural-driven defor-  
52 estation in tropical areas (Jayathilake et al., 2021). It also describes transitions between different forms of  
53 human-dominated land uses, such as the expansion of urban areas over agricultural lands (Ustaoglu and  
54 Williams, 2017). Land-use change can also describe transitions from anthropogenic land uses to natural

55 habitats, for example with the restoration of human-degraded landscapes (Banks-Leite et al., 2020). Al-  
56 though humans have been modifying terrestrial ecosystems for millennia – between 75% and 95% of the  
57 total land surface could have been altered by human activities at some point in history (Ellis et al., 2013,  
58 2021) – it is only during the past three centuries that the terrestrial surface made the transition from mostly  
59 wild to mostly human-dominated (Ellis et al., 2010). The most important driver behind this transition has  
60 been agricultural expansion, with major increases in cropland and grazing areas from the mid-18<sup>th</sup> century  
61 onward (Figure 1.1a). In recent decades, the expansion of grazing areas and animal feed crops, fuelled by  
62 the rising demand for animal products, has been identified as the most important driver of land-use change  
63 (Alexander et al., 2015).

64 The effects of land-use change on biodiversity have been characterised at local, regional and global  
65 scales – although global-scale studies represent a small proportion of the published research (Davison et  
66 al., 2021). Overall, land-use change has a negative impact on species richness and abundance (Newbold  
67 et al., 2015). For example, habitat loss and fragmentation due to agricultural expansion is a major driver  
68 of biodiversity declines (Foley et al., 2005). Urban areas, which have been expanding at faster rates than  
69 urban populations themselves (Seto et al., 2010), can have a considerable negative impact on biodiversity  
70 and ecosystem services, despite currently representing a small proportion of the terrestrial surface (about  
71 1%; Goldewijk et al. (2017)). In particular, the expansion of impervious surfaces, which characterizes urban  
72 development, has been linked to a reduction in species richness (Souza et al., 2019; Yan et al., 2019) and to  
73 increases in environmental risks (e.g., due to flooding, Hou et al. (2022); or to heat-island effects). Another  
74 important aspect of land-use change for biodiversity outcomes and ecosystem service delivery is the level of  
75 intensity at which the land is used to fulfil its purpose. For instance, management practices in agricultural  
76 areas are a major determinant of local biodiversity and related ecosystem services such as pollination and  
77 pest control (Foley et al., 2005; Kehoe et al., 2015; Millard et al., 2021). In urban areas, introducing and  
78 managing green spaces can lead to positive biodiversity outcomes (Aronson et al., 2017; Ives et al., 2016),  
79 and can also help mitigate flooding risks and heat islands (Livesley et al., 2016). Yet, land-use intensity  
80 has not been explicitly considered by a majority of past studies investigating impacts of land-use change on  
81 biodiversity (Davison et al., 2021; Dullinger et al., 2021), despite its likely importance.

## 82 1.1.2 Climate change

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



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

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

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

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

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

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

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

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

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

## 1.3 Using trait-based approaches to understand global biodiversity change

### 1.3.1 Traits as common currencies across species

Despite the global average declines reported for vertebrate populations, not all species respond similarly to environmental changes (Dornelas et al., 2019; Leung et al., 2020): while some species are impacted negatively, others benefit from global environmental changes (Newbold et al., 2018; Thomas, 2013). One of the reasons why species differ in their ability to cope with disturbances is that species present different intrinsic characteristics, or traits. Although the formal definition of a trait can vary depending on studies, in this thesis I consider traits to be characteristics that are measurable at an organismal level, comparable across different species, and that likely influence organismal fitness and performance (this is also the definition adopted in McGill et al. (2006)). The idea that species traits mediate species' responses to environmental change was formalised in the 'response-effect' framework, developed in the field of plant ecology (Lavorel and Garnier, 2002), where traits that influence species responses to environmental change were termed 'response traits' (and those that underpin ecological processes were termed 'effect traits'). One of the appeals of trait-based approaches is that individual species are no longer the fundamental unit of biodiversity investigations. Rather, traits become the focus and act as 'common currencies' across species, which is of particular interest for conservation when long-term population data are lacking. If species' responses to human threats consistently relate to certain traits, it may be possible to generalise patterns, and estimate the responses of species for which population data are not available (Verberk et al., 2013).

157 **1.3.2 Using ecological traits to assess which species are at most risk from human-driven  
158 changes**

159 Vertebrate ecological traits (which I define here as traits relating to the life-history, diet, morphology, and  
160 habitat use of species) have been used to explain species' responses to global changes. Past studies have  
161 notably investigated whether species extinction risk is associated with species traits, in order to understand  
162 which types of species are likely to be at more risk of extinction (Chichorro et al., 2019; Lebreton, 2011;  
163 Ripple et al., 2017), which is of high interest for conservation, but often lacks a consideration of specific  
164 threats (González-Suárez et al., 2013).

165 Other studies have focused on the influence of traits on species' responses to particular human threats.  
166 For example, a number of correlative trait-based approaches have been used to understand whether traits  
167 are associated with species' responses to climate change (with studies focusing on explaining interspecific  
168 variation in past or projected range shifts with traits (Di Marco et al., 2021; Mccain and King, 2014; Pacifici  
169 et al., 2017; Schloss et al., 2012a); with range-filling approaches, that is, looking at whether traits explain  
170 differences between the realised and potentially suitable climatic niche of species (Estrada et al., 2018); or  
171 with demographic approaches (Capdevila et al., 2022; Spooner et al., 2018)). Ecological traits have also  
172 been used in a predictive fashion, notably with frameworks aiming to assess species' vulnerability to climate  
173 change (Foden et al., 2013; Pacifici et al., 2015), assuming that given traits confer higher sensitivity to  
174 climate change.

175 In addition, past studies have investigated whether traits are associated with species' responses to habitat  
176 disturbance. For example, Newbold et al. (2013) investigated whether traits explained interspecific varia-  
177 tion in land-use responses in pantropical birds; Quesnelle et al. (2014) assessed whether traits influenced  
178 responses to habitat loss in wetland vertebrates; and Nowakowski et al. (2017) investigated effects of am-  
179 phibian traits on sensitivity to habitat modification.

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

186 Finally, although trait-based approaches using ecological traits have been widely employed to understand  
187 the effects of human-driven changes on vertebrate species, past studies have mostly been conducted at local

188 to regional scales (Davison et al., 2021), and have tended to focus on given taxa within vertebrates classes  
189 (Hevia et al., 2017). Thus, global comparative assessments of the relationships between ecological traits and  
190 species' responses to human pressures across terrestrial vertebrates are lacking.

191 **1.3.3 Using physiological traits to understand land-use impacts on biodiversity and ecosys-  
192 tem functioning**

193 Physiological traits are typically measured to capture aspects of species' metabolism, performance or bio-  
194 chemistry. Recent decades have seen advances in large-scale studies linking physiological traits to macroe-  
195 cological patterns of species existence across levels of organisation (Chown et al., 2004; Robert Burger et al.,  
196 2021), as exemplified by the development of the 'metabolic theory of ecology' (Brown et al., 2004; Gillooly  
197 et al., 2001). In particular, metabolic rates reflect the amount of energy used at the organismal level (I define  
198 metabolic rates here as the rates at which an organism processes available energy, which is often measured  
199 in the lab by estimating the amount of consumed O<sub>2</sub> by a whole organism over a period of time). As energy  
200 is a fundamental currency across all living organisms, metabolic rates can be employed comparatively across  
201 species to investigate interspecific variation in energetic expenditure. Thus, past studies have focused on  
202 understanding both intraspecific variation in metabolic rates (Auer et al., 2017; Burton et al., 2011) as well  
203 as interspecific variation (such as variation in metabolic rates with temperature, Clarke and Fraser (2004); or  
204 variation in metabolic rates with longevity – e.g., testing the 'pace of life' theory, Stark et al. (2020)).

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

215 **1.3.4 Thesis aims**

216 As exposed above, studies investigating relationships between ecological traits and environmental change  
217 have mostly been conducted at local to regional scale (Davison et al., 2021; Hevia et al., 2017), and have

218 mostly focused on single vertebrate classes or sub-taxa within particular classes. Thus, although response  
219 traits to land-use and climate change have been identified in various vertebrate taxa, whether the effects of  
220 such traits can be generalised geographically and taxonomically remains largely uncertain, emphasising the  
221 need for global comparative assessments of the relationships between traits and species' responses to human  
222 threats.

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

230 Throughout my thesis, assemblage-level and species-level responses to land use and land-use intensity  
231 are assessed using a 'space-for-time' approach (De Palma et al., 2018). To this end, I use one of the most  
232 comprehensive databases recording species occurrence and abundance in different land uses (the PREDICTS  
233 database, Hudson et al. (2014, 2017)). I estimate sensitivity to climate change from properties of species'  
234 climatic niche space, and thus it is important to emphasize that this does not allow a consideration of species'  
235 *responses* to climate change. Indeed, it is difficult to capture the responses of many species to climate change,  
236 given that capturing climate-change responses requires to disentangle the effects of climate change from that  
237 of other drivers of change over the considered time period (which can be complex; MacLean and Beissinger  
238 (2017)), and also requires to gather data on the occurrence or abundance of species over several decades  
239 (which may be particularly challenging when working at large taxonomic scales).

## 240 **1.4 Detailed aims, hypotheses and outline of the following Chapters**

241 The overarching aims of my thesis are to investigate whether species traits are associated with species' land-  
242 use responses and species' estimated climate-change sensitivity in terrestrial vertebrates, and to highlight  
243 some of the consequences of global changes for ecosystem processes sustained by terrestrial vertebrates.  
244 One of the obstacles that has hindered the application of trait-based approaches at large scales in animal  
245 taxa is the lack of a centralised repository for readily available trait data, as emphasized by the recent calls  
246 to compile and release trait data for animals (Junker et al., 2022; Kissling et al., 2018). Thus, collecting  
247 trait data and investigating the current availability of the data for terrestrial vertebrates is an important and

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

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

Chapter 3 highlights the effects of land-use change on the functional composition of vertebrate assemblages, but does not allow an assessment of the effects of particular traits on species' land-use responses, as multidimensional interspecific trait variation is summarised into single indices of functional diversity. Chapter 4 aims at assessing such effects, by investigating whether species traits are associated species' land-use responses and species' climate-change sensitivity. In addition to the traits considered in Chapter 3, Chapter 4 includes dietary traits and species geographical range area. Although geographical range area is not a trait *per se*, it has been shown to influence species' responses to land-use and climate change (Newbold et al., 2018; Thuiller et al., 2005), and it is likely an important determinant of climate-change sensitivity

estimated from species' climatic niche space, so I include it in this Chapter to account for its potential effects. Thus, in Chapter 4, I enhance the trait data compiled in Chapter 2 with dietary traits and geographical range area, which together with the traits previously collected I term 'ecological characteristics'. I investigate whether these ecological characteristics are associated with species' land-use responses on the one hand and with species' estimated climate-change sensitivity on the other hand, comparatively among the terrestrial vertebrate classes. To the best of my knowledge, Chapter 4 constitutes the first global comparative assessment, across terrestrial vertebrate classes, of associations between species' ecological characteristics and both land-use responses and estimated climate-change sensitivity.

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

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

<sup>312</sup> knowledge for understanding species- and community-level responses to human pressures.

313 **2 | Global gaps and biases in trait data for**  
314 **terrestrial vertebrates**

315 **Keywords**

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

317 **Abstract**

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

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

## 337 **2.1 Introduction**

338 Species traits are fundamental to ecological and evolutionary research. Comparative studies regularly use  
339 trait data across organisms to understand evolutionary processes and species coexistence (Escudero and  
340 Valladares, 2016; Zamudio et al., 2016), to investigate global patterns of life forms and functions (Díaz et  
341 al., 2016), or to assess species' vulnerability to environmental changes (Böhm et al., 2016; Pacifici et al.,  
342 2015; Pearson et al., 2014). Because traits influence species' ability to cope with environmental changes  
343 (Newbold et al., 2013) and underpin species' contributions to ecosystem processes (Lavorel and Garnier,  
344 2002; Violle et al., 2007; Wong et al., 2018), they play an increasingly important role in functional and  
345 conservation ecology.

346 Past and recent efforts to collate and release trait data in the public domain have facilitated the develop-  
347 ment of trait-based research. For instance, a global trait database has been published for plants (Kattge et al.,  
348 2011). As of May 2020, data from this database had been used in 297 publications since its release (Ac-  
349 tivity report, 18/06/2020, <https://www.try-db.org/TryWeb/Home.php>). Such databases hence  
350 constitute invaluable research tools and have the potential to greatly advance the field.

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

359 Nevertheless, despite the importance of vertebrate species in global research outputs, there is no single  
360 source for vertebrate ecological traits. Consequently, researchers wishing to conduct comparative studies  
361 across vertebrate groups may have to collate trait data from a range of sources (such as in Cooke et al.  
362 (2019a,b) or in González-Suárez et al. (2018)), a time-consuming prerequisite which may be a limiting  
363 step of the research process. Indeed, collating data from heterogeneously-formatted sources presents many

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

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

380 A major issue with incomplete, biased data is the introduction of bias in subsequent analyses. Assessing  
381 the amount of missing data as well as the so-called ‘missingness mechanism’ – whether missing data are  
382 missing at random, as opposed to there being systematic biases in the way missing values are distributed, see  
383 Baraldi and Enders (2010) – is an important prerequisite. Indeed, there exist diverse techniques to deal with  
384 data missingness. The simplest one consists of retaining complete cases only by filtering out missing values  
385 (case deletion, see Nakagawa and Freckleton (2008)). Nevertheless, case deletion may lead to biased param-  
386 eter estimates and erroneous conclusions when values are not missing at random (González-Suárez et al.,  
387 2012). Therefore, it is critical to determine the most appropriate way to deal with data incompleteness. For  
388 instance, previous studies using terrestrial vertebrate trait data have employed multiple imputation techniques  
389 to fill in the gaps (Cooke et al., 2019a; González-Suárez et al., 2012). Yet, imputation techniques could be  
390 sensitive to non-randomness in trait data. Phylogenetic biases (where some clades are under-sampled com-  
391 pared to other clades) could notably impact the performance of several imputation approaches. It is thus  
392 vital to characterise the gaps in trait data prior to any analysis. However, there has been no study to date  
393 investigating global patterns in the availability of trait data across terrestrial vertebrates.

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

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

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

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

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

419 Finally, I investigate phylogenetic biases in the trait data. I assess whether particular clades have received  
420 more attention than others by looking for patterns in the distribution of trait completeness across the terminal  
421 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.

## **422 2.2 Methods**

423 I produced class-specific trait datasets that were made available on figshare ([https://figshare.com/articles/dataset/Global\\_gaps\\_in\\_terrestrial\\_vertebrate\\_trait\\_data/10075421/](https://figshare.com/articles/dataset/Global_gaps_in_terrestrial_vertebrate_trait_data/10075421/))  
424 2). Data compilation and all analyses were conducted with R version 3.5.1 (R Core Team, 2018). Distribu-  
425 tion maps were processed using both R and the ‘ArcPy’ package available in ArcGIS v.10.6 (ESRI, 2011)  
426 (implemented in Python 2.7; van Rossum, G. (1995)).

### **428 2.2.1 Trait data collection**

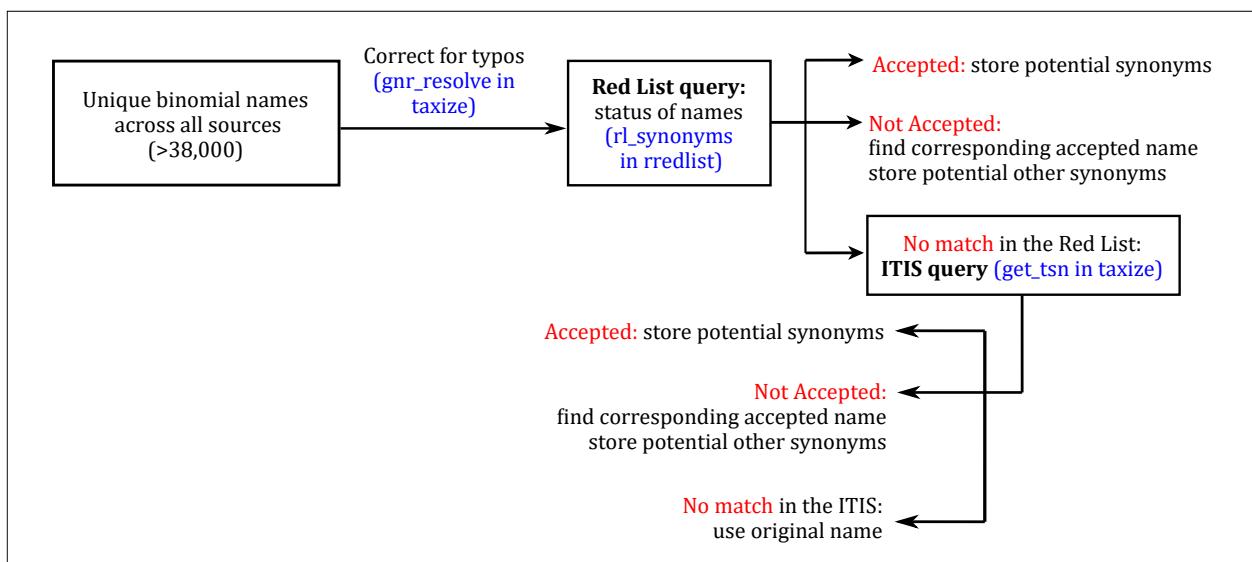
#### **429 Sources and taxonomic matching**

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

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

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

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



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

#### 454 Compilation methods

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

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

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

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

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

467

- **Body size**

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

474

- **Longevity**

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

483

- **Litter or clutch size**

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

488

- **Trophic level**

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

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

499 **• Activity time**

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

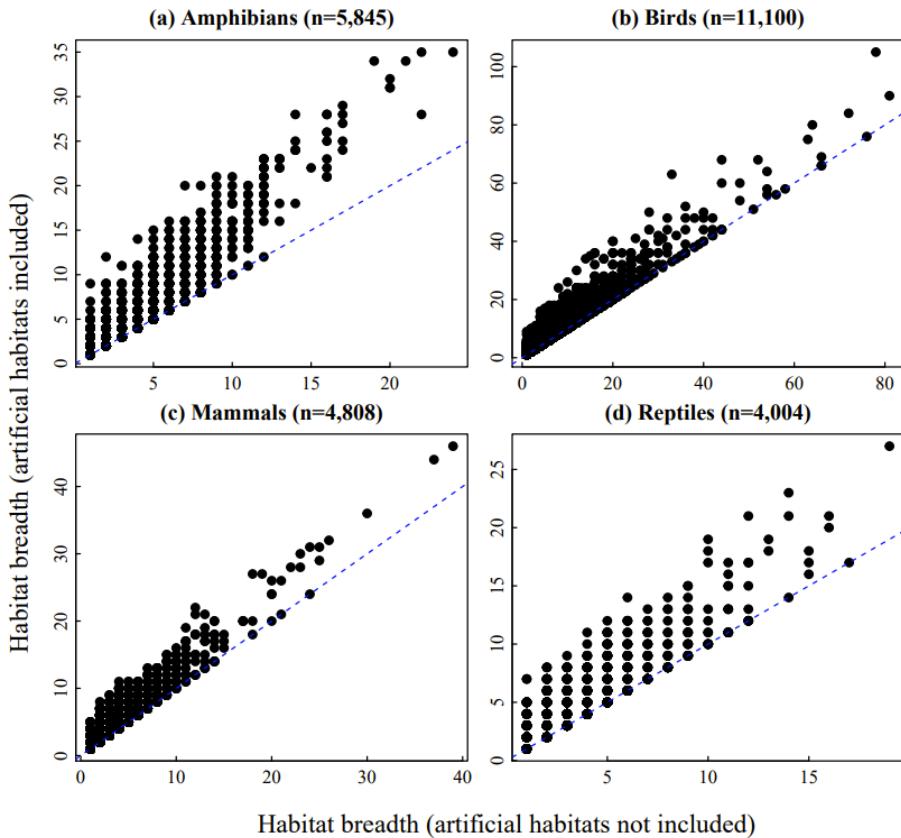
506 **• Habitat breadth**

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

514 **• Use of artificial habitats**

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

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



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

## 522 Phylogenies

523 I used class-specific phylogenetic trees downloaded on 13 April 2020. For mammals, I used ‘complete’  
 524 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.  
 525  
 526 For plotting purposes, I obtained consensus trees using the TreeAnnotator program of the BEAST software  
 527 (Bouckaert et al., 2019).

## 530 Species distributions

531 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).  
 532  
 533 For mammals and amphibians, species distribution maps were obtained from the IUCN Red List (IUCN

534 (2020), downloaded 13 April 2020); for birds, they were obtained from BirdLife International (<http://datazone.birdlife.org/species/requestdis>, downloaded 17 April 2020).

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

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

544 **2.2.2 Investigating gaps and biases in trait data**

545 I used trait coverage and completeness to investigate taxonomic, phylogenetic and spatial biases in the trait  
546 data. Table 2.2 summarizes the sample sizes (number of species) in each of the following analyses. Note  
547 that species for which completeness was 0% were included in all analyses (for more details, see Figure 2.3).  
548 Also note that I did not filter out species identified as extinct or extinct in the wild, because they represented  
549 a small proportion of the datasets (0.48% for amphibians, 1.4% for both birds and mammals, and 0.50% for  
550 reptiles) and also because I could not exclude such species systematically, because it is likely that I did not  
551 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              |

552 **Taxonomic biases**

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

557 **Phylogenetic biases**

558 Initially, to assess whether more closely related species were more likely to be similar in trait completeness,  
559 I estimated the phylogenetic signal in completeness with Pagel’s  $\lambda$  (Pagel, 1999) in each class. I used a boot-  
560 strapping approach, calculating  $\lambda$  for each of 50 trees randomly sampled in each class (using the ‘phylosig’  
561 function of the ‘phytools’ R package; Revell, 2012). I then estimated the mean and 95% confidence intervals  
562 (95% CIs) of  $\lambda$ . Sample sizes for computing  $\lambda$  (number of species represented in both the phylogenies and  
563 trait datasets) are shown in Table 2.2.

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

567 **Spatial biases**

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

$$573 N_{traits} \sim \log(\text{Range size}) * \text{Class.}$$

574 Second, I mapped assemblage-level median completeness. Assemblages were characterized at the pixel level  
575 at 50 km<sup>2</sup> resolution. I determined pixel-level composition and richness by stacking species geographical  
576 distributions. I then calculated median completeness across species in each pixel. I show the resulting maps  
577 for herptiles in the main text, and for mammals and birds in Appendix 1 (Figure S2.7; median completeness  
578 was very high across most pixels for mammals and birds). In addition, I provide maps of assemblage-  
579 level mean completeness and standard deviation for all classes in Appendix 1 (Figures S2.8 and S2.9 show  
580 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,  $\rho$ , associated with an n-by-n matrix of spatial weights,  $W$ . The final model was:

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

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

## 2.3 Results

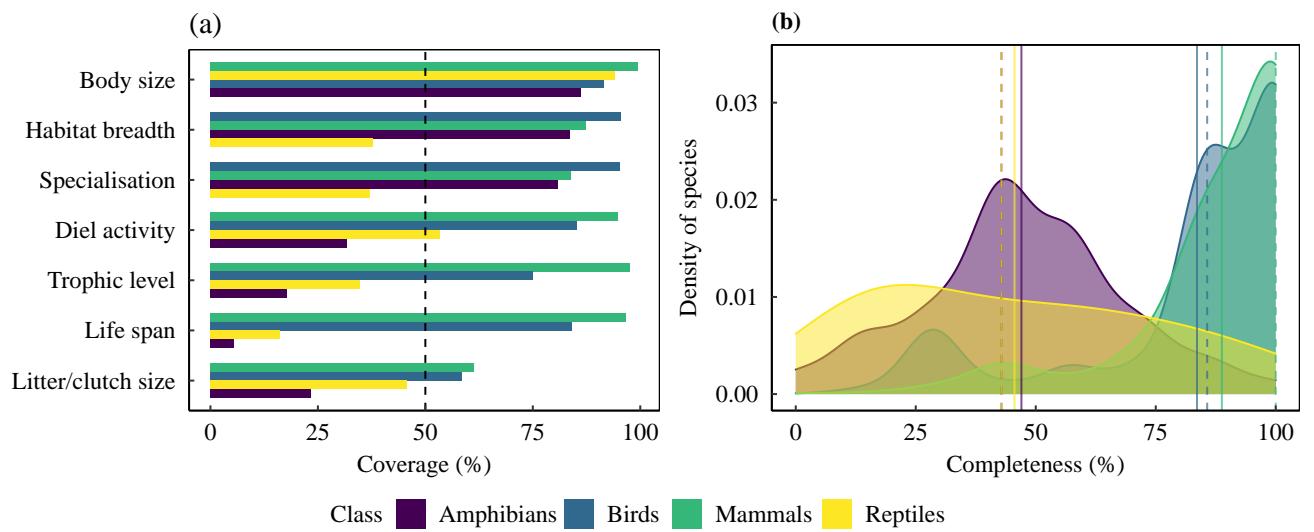
### 2.3.1 Taxonomic biases in trait information

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

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

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

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



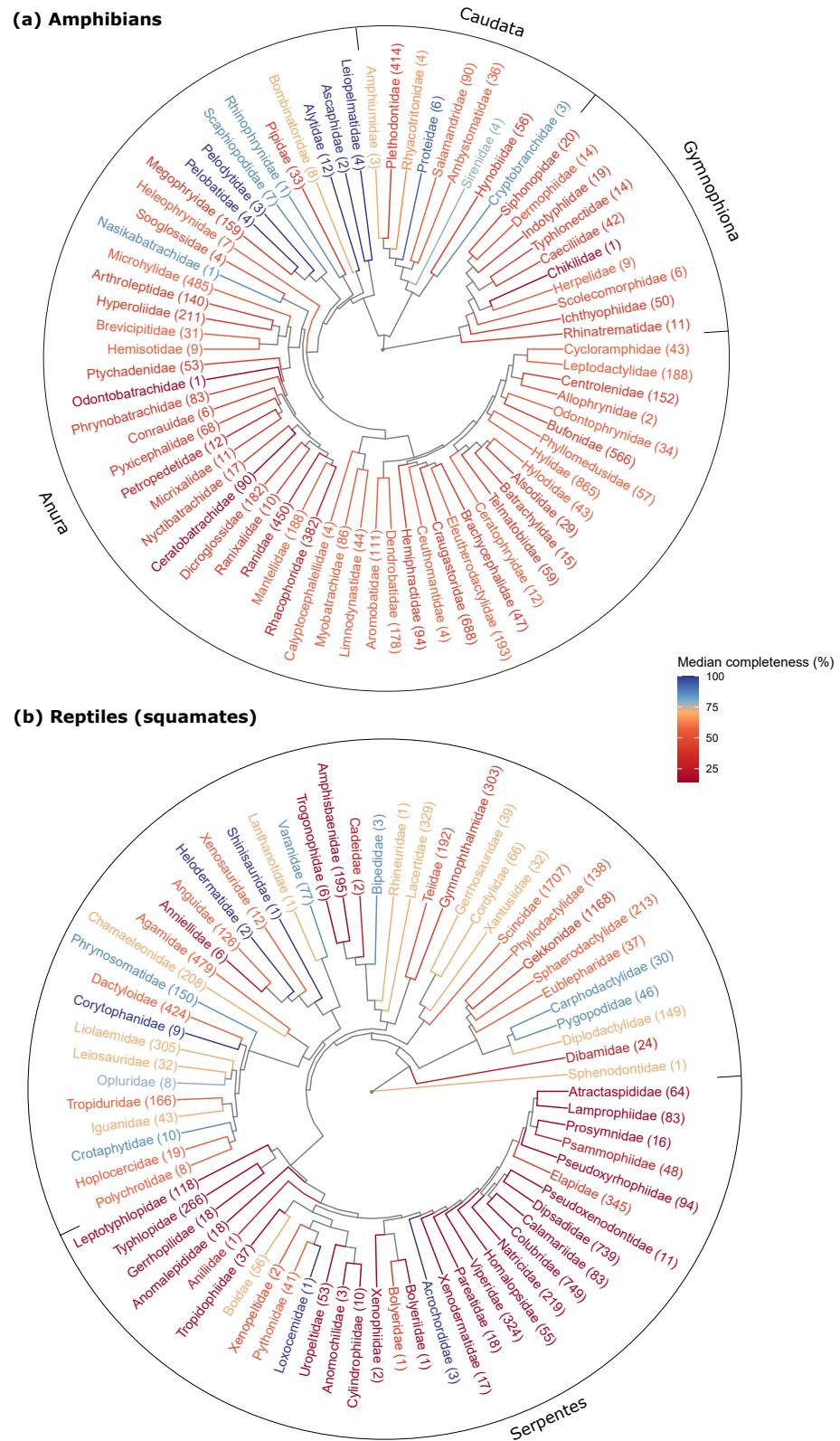
**Figure 2.3: Trait coverage and completeness across species.** (a) I defined coverage as the proportion of species for which an estimate is available for a given trait. The dashed line represents 50% coverage. (b) Trait completeness is the proportion of estimated traits for a species. Here, I show the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

### 2.3.2 Phylogenetic biases in trait completeness

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

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

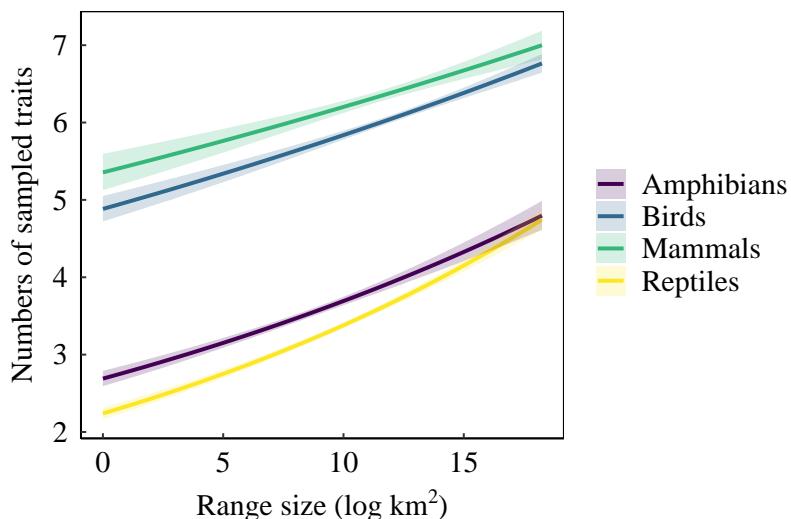
636 It is important to underline that Figure 2.4 shows within-family median completeness, masking the con-  
637 siderable variation in species richness across families, hence masking potential important variation in com-  
638 pleteness across species within families. For example, in the amphibian family *Allophrynididae* (three recog-  
639 nized species), the within-family median completeness was 50%; but the dataset comprised two species of  
640 completeness 14% and 86%, respectively. I present similar plots to those in Figure 2.4 showing the within-  
641 family standard deviation in completeness in Appendix 1 (Figure S2.13). Within-family standard deviation  
642 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).*

### 643 2.3.3 Spatial biases in trait completeness

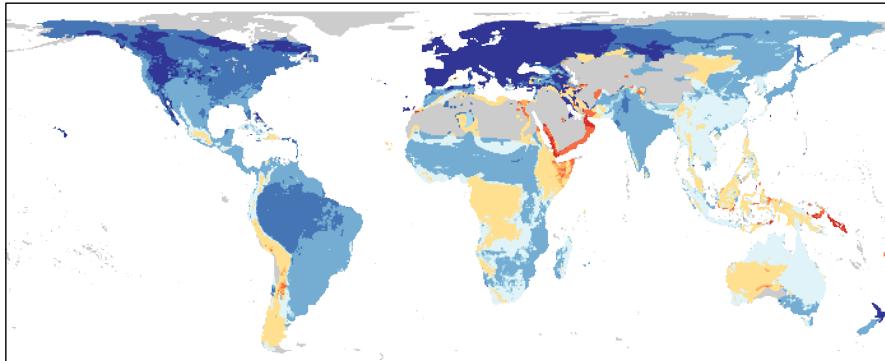
644 Range size was significantly correlated with the number of sampled traits. Larger range sizes were associated  
645 with a higher number of sampled traits (i.e., with higher completeness; Figure 2.5; Appendix 1, Table S2.1).  
646 Similar results were obtained when using distribution maps not cut by elevational limits (Appendix 1, Table  
647 S2.2; Figure S2.15). The rate of increase was steepest for reptiles, then for amphibians, then for birds and  
648 mammals (slope estimates for birds and mammals were not significantly different from each other; Appendix  
649 1, Table S2.1).



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

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

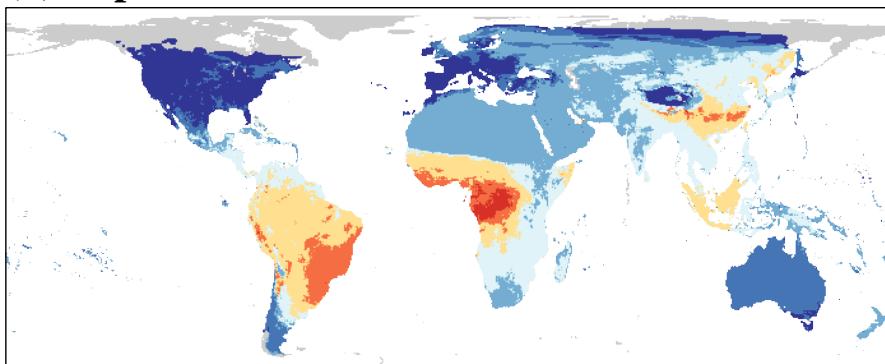
### (a) Amphibians



Median completeness:

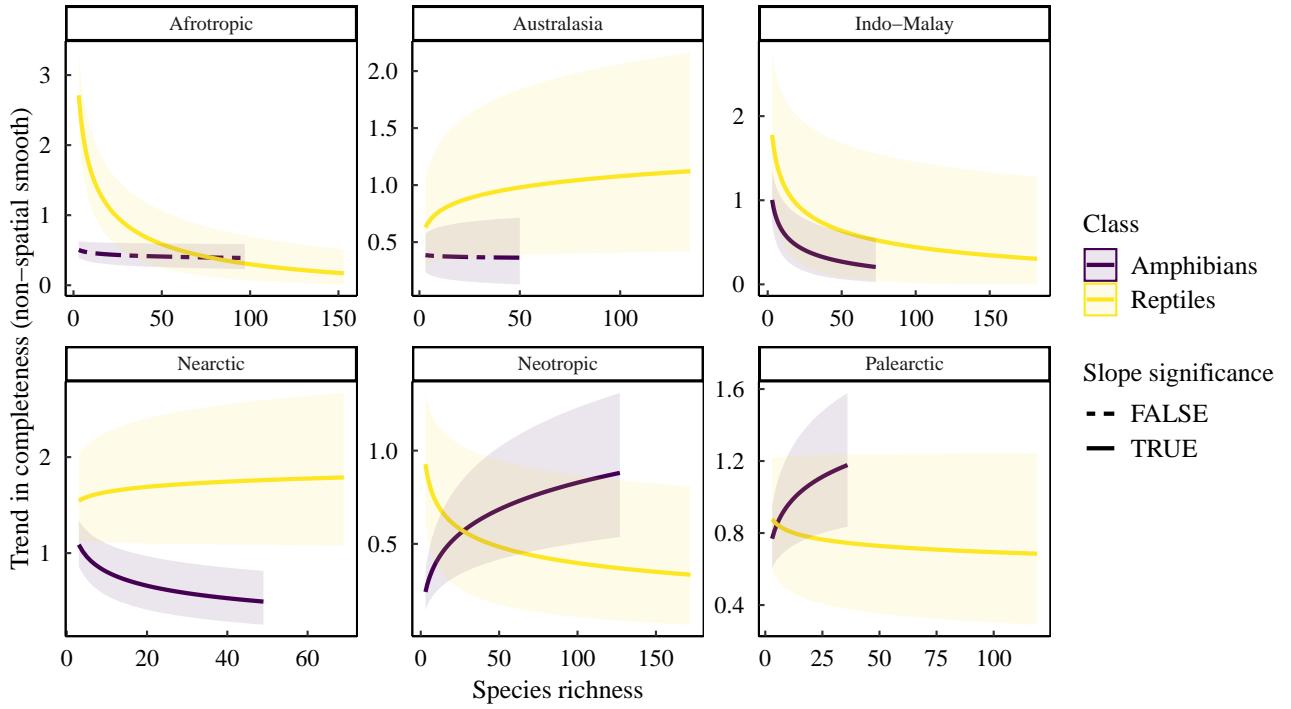
|           |
|-----------|
| NA        |
| 0 – 10%   |
| 10 – 20%  |
| 20 – 30%  |
| 30 – 40%  |
| 40 – 50%  |
| 50 – 60%  |
| 60 – 70%  |
| 70 – 80%  |
| 80 – 90%  |
| 90 – 100% |

### (b) Reptiles



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

659 Spatial models showed that species richness explained median trait completeness in herptiles in most  
660 realms (Figure 2.7; Appendix 1, Tables S2.3 and S2.4); including spatial lags improved the models (am-  
661 phibians:  $\rho = 0.92$ , p-value < 0.0001; reptiles:  $\rho = 0.91$ , p-value < 0.0001). For reptiles, completeness was  
662 negatively correlated with species richness in the most species-rich realms (Afrotropics, Indo-Malayan and  
663 Neotropics) and in the Palaearctic; the relationship was steepest in the Afrotropics and shallowest in the  
664 Palaearctic. In the Australasian and Nearctic realms, completeness tended to increase with species richness.  
665 For amphibians, negative relationships were observed in the Indo-Malay and Nearctic realms, whereas pos-  
666 itive trends were observed in the Neotropics and the Palaearctic. The opposite trends between reptiles and  
667 amphibians observed in the Australasian and Neotropical realms reflected patterns observed on the maps.  
668 The Indo-Malayan was the only realm where median completeness tended to decrease with species richness  
669 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).*

## 670 2.4 Discussion

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

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

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

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

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

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

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

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

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

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

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

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

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

781 (10%–80%) in a complete trait dataset of carnivorans and measured imputation performance in different  
782 scenarios. Given that phylogenetic non-randomness in missing trait values can impact imputation accuracy,  
783 Penone et al. (2014) removed values in three different ways (completely at random; with a phylogenetic  
784 bias; and with a body mass bias). Out of the four techniques, missForest and PhyloPars performed best when  
785 species phylogenetic position was included as a predictor of missing trait values. Such imputations appeared  
786 to be robust even when trait coverage was as low as 40%, which might be relevant for many reptilian and  
787 amphibian traits. The performance was not significantly affected by phylogenetic non-randomness of the  
788 data. Hence, missForest and PhyloPars appear to be well suited when traits are phylogenetically conserved,  
789 because they allow species phylogenetic position to be included as a predictor of missing trait values. The  
790 study by Penone et al. (2014) highlights that there are robust imputation techniques allowing to deal with  
791 incomplete trait data where biases might otherwise be problematic. Nevertheless, it is important to highlight  
792 that some imputation techniques, such as single or mean imputation, can be problematic because they do  
793 not allow an estimation of uncertainty and suffer from a lack of accuracy (Nakagawa and Freckleton, 2008);  
794 indeed, imputation techniques sometimes perform no better than case deletion. More work should be con-  
795 ducted to assess imputation performance in various contexts (e.g., Johnson et al. (2021)), and the datasets  
796 compiled in this Chapter might provide an opportunity for such studies.

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

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

810 **3 | Intensive human land uses negatively af-**

811 **fect vertebrate functional diversity**

812 **Keywords**

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

814 **Abstract**

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

825 **3.1 Introduction**

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

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

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

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

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

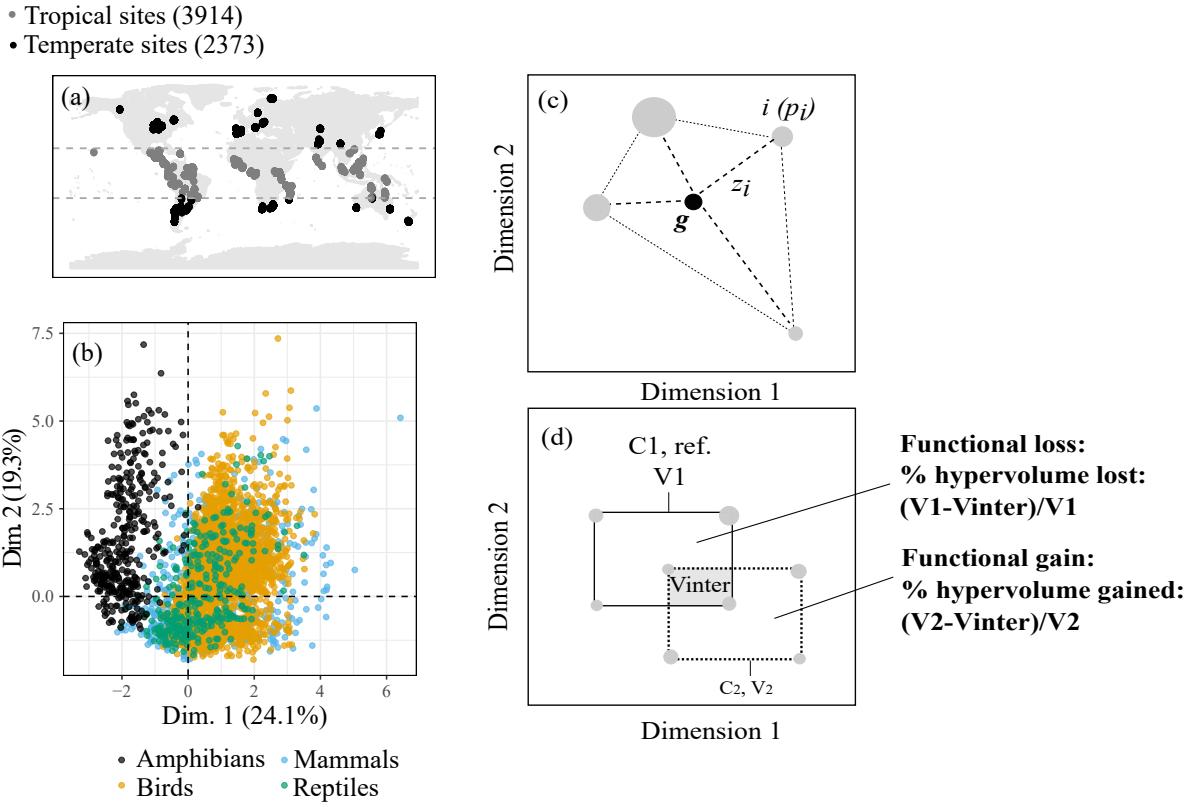
862 abundance, across multiple land uses of different land-use intensity. Using the PREDICTS database allows  
863 me to contrast biodiversity metrics among intact land uses (primary-vegetation sites, considered to be the  
864 undisturbed reference condition), and all other human land-use types. Specifically,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

- 866 1. I expect decreases in functional diversity in human land uses compared to primary vegetation, caused  
867 by contractions of occupied trait space. I expect such effects to be more pronounced where land is  
868 used more intensively by humans. This hypothesis builds upon evidence that species with certain  
869 traits are more sensitive to land-use disturbance (Newbold et al., 2013), meaning that disturbed land  
870 uses will retain only disturbance-tolerant species, more functionally similar to one another. Given the  
871 reported higher sensitivity of tropical assemblages to land-use disturbance, I predict that such effects  
872 are stronger in the tropics.
- 873 2. I hypothesise that decreases in functional diversity in disturbed land uses exceed decreases expected  
874 by chance, given local species loss. Thus, I expect disturbed land uses to promote functional under-  
875 dispersion. Functional under-dispersion occurs when species within an assemblage are more similar,  
876 in term of their traits, than expected by chance (Cadotte and Tucker, 2017; Wong et al., 2018) – or,  
877 in other words, when functional dispersion is lower than expected given local species richness. I  
878 predict that under-dispersion is more likely to occur in the highly disturbed sites, in both temperate  
879 and tropical areas. This hypothesis is based on the idea that species are being removed non-randomly  
880 from sensitive areas of the trait space, and increasingly so with higher disturbance level.
- 881 3. Finally, I expect decreases in functional diversity in human land uses to be driven by high functional  
882 loss, whereby species are being removed from previously occupied areas of the trait space; I expect  
883 no functional gain. This hypothesis is based on the idea that the functional trait space in undisturbed  
884 land uses represents all of the possible regional trait combinations and that species with functional  
885 attributes rendering them unable to persist in altered conditions will be filtered out (Cornwell et al.,  
886 2006).

## 887 3.2 Methods

### 888 3.2.1 Vertebrate assemblages

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



**Figure 3.1: Overview of the study design and functional diversity metrics.** I used occurrence data for vertebrate species from the PREDICTS database ((Hudson et al., 2014, 2017); 180 studies; 431,170 records; 4,339 species; 6,758 sampled sites). (a) shows the spatial distribution of sites I consider. I combine occurrence data with trait data compiled in Chapter 2 to calculate functional diversity metrics. (b) is a representation of the trait data in two dimensions, plotted across PREDICTS vertebrates. Traits that contributed most to dimension 1 were lifespan (29%) and litter/clutch size (22%), while traits that contributed most to dimension 2 were habitat breadth (47%) and use of artificial habitats (35%). (c) and (d) present the conceptual framework for the calculation of the functional diversity metrics: local measures (c) and pairwise metrics (d). (c) Given a trait space, functional richness is calculated as the hypervolume occupied by the minimum convex hull encompassing all species (Villéger et al., 2008). Functional dispersion is calculated as the mean distance of the species to the centroid,  $g$  (Laliberté and Legendre, 2010). (d) I compute functional loss as the proportion of hypervolume lost from the reference assemblage, and I define functional gain as the proportion of hypervolume of the disturbed assemblage that was gained (proportion of novel trait space in the disturbed assemblage). *Figure reproduced from Etard et al. (2021).*

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

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

900 egories: mature, intermediate and young, depending on the stage of recovery of the vegetation. Land-use  
901 intensity is reported as minimal, light or intense, according to criteria that depended on the land-use type in  
902 question (e.g., crop diversity, degree of mechanisation and chemical inputs in cropland, or bushmeat harvest-  
903 ing and selective logging in primary vegetation; Hudson et al., 2014). I excluded sites for which the land use  
904 could not be characterised or for which the stage of recovery of secondary vegetation was unclear. As the  
905 PREDICTS database is a collection of independent studies, the design of this study was not balanced: the  
906 sample size varied across land uses (Appendix 2, Figures S3.1, S3.2), and across taxonomic groups (3103  
907 species of birds; 531 mammals; 379 amphibians; 326 reptiles).

### 908 **3.2.2 Functional traits and diversity metrics**

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

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

times, thereby obtaining eight sets of imputed traits. I randomly selected one imputed trait set for the calculation of functional metrics. Imputations of missing trait values & imputation performance are detailed in Appendix 2, sections S3.2 and S3.4 (and see Figures S3.6-S3.8). Post-imputation, continuous traits were log<sub>10</sub>-transformed (except habitat breadth which was square-rooted) and z-scored (standardised to unit variance and zero mean). In addition, I assessed whether the results were robust to imputation error using a subset of the PREDICTS data considering only species for which I had complete trait information (see next section).

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

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

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

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

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

## Region.

(Model 1a)

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

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

(Model 1b)

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

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

Land-use intensity + Land use : Class + Land-use intensity : Region + Class : Region.

(Model 2a)

976 For FDis, regional effects were dropped:

977  $\text{arcsin}(\sqrt{\text{FDIs}}) \sim \text{Land use} + \text{Land-use intensity} + \text{Class} + \text{Land use : Land-use intensity} + \text{Land use :}$   
 978  $\text{Class} + \text{Land-use intensity : Class}.$

(Model 2b)

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

992 **3.2.4 Investigating functional under-dispersion (Hypothesis 2)**

993 To assess whether effects of land use and land-use intensity on FDis differed from what would be expected  
994 by chance given changes in local species richness, I generated null expectations of FDis at each site. I  
995 randomised assemblage composition 500 times, drawing species from the corresponding study's species  
996 pool while maintaining local species richness. For each site, I thus obtained a null distribution for FDis.  
997 Then, I tested whether FDis differed from null expectations using Wilcoxon signed-rank tests. I created  
998 a binary variable which was assigned 1 if FDis was significantly lower than null expectations at a given  
999 site (significant under-dispersion), and 0 otherwise. I investigated how land use, land-use intensity, region  
1000 and taxonomic class affected the probability of occurrence of under-dispersion using a generalised linear  
1001 mixed-effects model with a binomial distribution of errors. The best-fitting model did not retain any effect  
1002 of taxonomic class:

1003  $P_{\text{under-dispersion}} \sim \text{Land use} + \text{Land-use intensity} + \text{Region} + \text{Land use : Land-use intensity} + \text{Land use : Region}$ .

1005 (Model 3)

1006 **3.2.5 Functional loss and functional gain (Hypothesis 3)**

1007 I calculated the proportion of trait space that was lost in disturbed land uses compared to reference land uses  
1008 (functional loss) and the proportion of trait space that was gained in disturbed land uses (functional gain)  
1009 (Figure 3.1c), across and within taxonomic classes. I selected studies where at least one site was sampled in  
1010 primary vegetation. I then made within study pairwise comparisons between reference assemblages, sampled  
1011 in primary vegetation, and disturbed assemblages. In addition, I considered all comparisons between pairs  
1012 of primary-vegetation sites, to create reference pairs. I then investigated how land use, land-use intensity  
1013 and region affected functional loss and gain across and within taxonomic classes using linear mixed-effects  
1014 models, controlling for study identity in the random effects. Across vertebrates, the best-fitting model for  
1015 functional loss was:

1016  $\text{arcsin}(\sqrt{\text{loss}}) \sim \text{Land use} + \text{Land-use intensity} + \text{Region} + \text{Land use : Land-use intensity} + \text{Land use : Region}$ .

1018 (Model 4a)

1019 For functional gain, one interaction term (land use with region) was dropped:

1020  $\arcsin(\sqrt{\text{gain}}) \sim \text{Land use} + \text{Land-use intensity} + \text{Region} + \text{Land use : Land-use intensity}$ .

(Model 4b)

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

1023  $\arcsin(\sqrt{\text{loss}}) \sim \text{Land use} + \text{Land-use intensity} + \text{Class} + \text{Region} + \text{Land use} :$

1024 Land-use intensity + Land use : Class + Land use : Region + Land-use intensity : Class.

(Model 5a)

1026 For functional gain (Model 5b), the fitted effects were the same as those of Model 2b. More details about  
1027 the calculation of functional loss and gain can be found in Appendix S3.5.

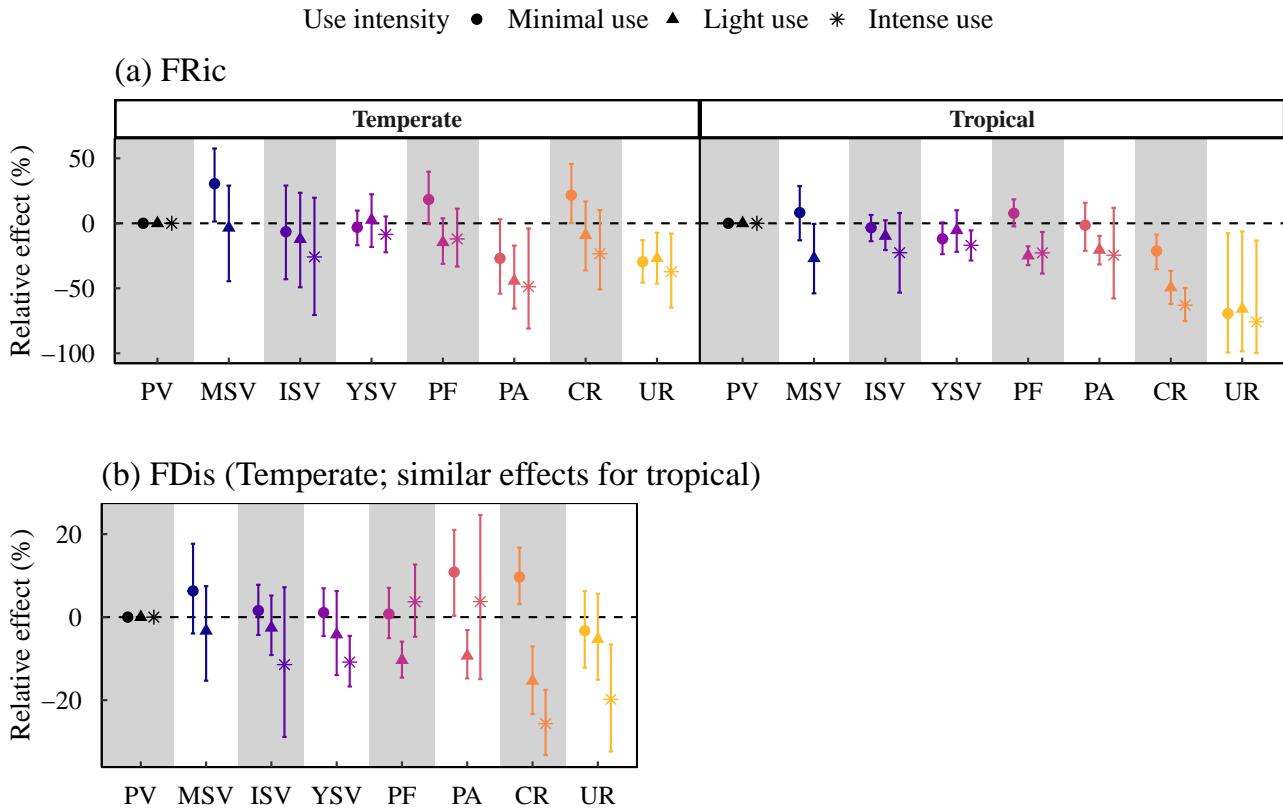
1028 All data analyses were conducted using R version 3.5.1 (R Core Team, 2018). I made the code available  
1029 on figshare (DOIs: <https://doi.org/10.6084/m9.figshare.14161883> and <https://doi.org/10.6084/m9.figshare.15163926>), as well as the main result datasets (<https://doi.org/10.6084/m9.figshare.15163971>).

1032 3.3 Results

### 1033 3.3.1 Effects of land use on FRic and FDis

1034 Across all vertebrates, land use and land-use intensity significantly affected FRic and FDis (Figure 3.2).  
1035 FRic tended to decrease with increasing disturbance level and higher intensity of land use. For FRic, relative  
1036 effects differed between regions (Figure 3.2a). Although declines were overall more important for disturbed  
1037 tropical assemblages, significant declines were observed for the temperate assemblages (e.g., a 37% average  
1038 decline in intensely used urban areas; a 49% decline in pastoral areas of high land-use intensity). Never-  
1039 theless, tropical assemblages typically showed more important reductions in FRic. For instance, declines  
1040 averaged 63% for intensely used tropical cropland and 76% for urban areas. For FDis, relative effects were  
1041 similar in both regions (Figure 3.2b). The most important average declines were observed for urban assem-  
1042 blages of intense use (20% decline), and for lightly- and intensely used cropland (by 15% and 26%). Note  
1043 that confidence intervals around the estimated average declines were large in some cases, highlighting some  
1044 heterogeneity in the responses.

1045 Fitting the same models to the subset of species with complete trait data, I detected important declines in  
1046 functional diversity in a number of land uses, showing that the conclusions are robust to trait imputation un-  
1047 certainty (for example, FRic declined on average by 75% in intensely used temperate pastoral assemblages;  
1048 by 48% for intensely used tropical cropland; and FDis declined by an average 37% in intensely used tropical

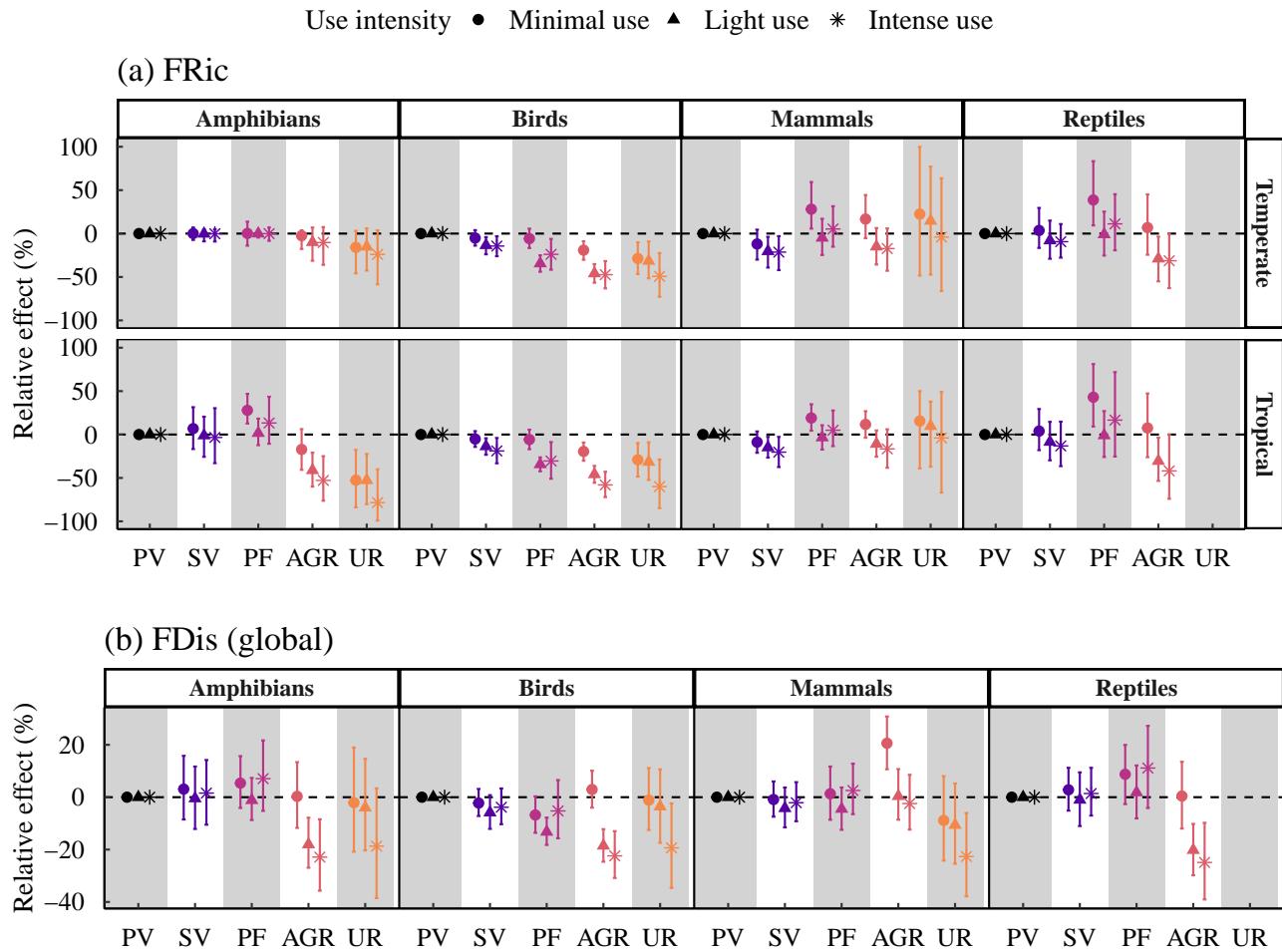


**Figure 3.2: Effects of land use, land-use intensity and region on FRic (a) and on FDis (b) across all PREDICTS vertebrates.** Effects were rescaled with reference to primary vegetation (PV) and are plotted as a % difference relative to PV within each land-use intensity. For FRic, the best-fitting model included interactions between land use and region, while these interactions were dropped for FDis, explaining the similar relative effects in both regions. Error bars represent 95% confidence intervals. MSV: mature secondary vegetation; ISV, intermediate secondary vegetation; YSV, young secondary vegetation; PF, plantation forest; PA, pasture; CR, cropland; UR, urban. Effects for intense use in MSV could not be estimated as there were not enough sampled sites. *Figure reproduced from Etard et al. (2021).*

1049 urban assemblages; Appendix 2, Figure S3.18). Furthermore, using the subset of species with complete trait  
 1050 data, I found that the results were not sensitive to the inclusion of geographical range size as an additional  
 1051 trait (Appendix 2, Figure S3.19). Finally, the results were not sensitive to variation across imputed trait val-  
 1052 ues (Appendix 2, Figure S3.20) and were also robust to resampling in primary-vegetation sites (Appendix 2,  
 1053 Figure S3.21).

1054 Responses of FRic and FDis to land use and land-use intensity differed among taxonomic classes (Figure  
 1055 3.3). Within-class effects for FDis were similar between regions. The most notable decreases were observed  
 1056 in lightly- and intensely used agricultural land uses in amphibians, birds and reptiles; and in intensely used  
 1057 urban land uses for birds and mammals. For FRic, the effects in tropical and temperate regions were qual-  
 1058 itatively similar in three out of four classes (birds, mammals and reptiles), although effect sizes tended to be  
 1059 bigger for tropical assemblages. Birds and reptiles showed reductions in disturbed land uses in both tropical

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



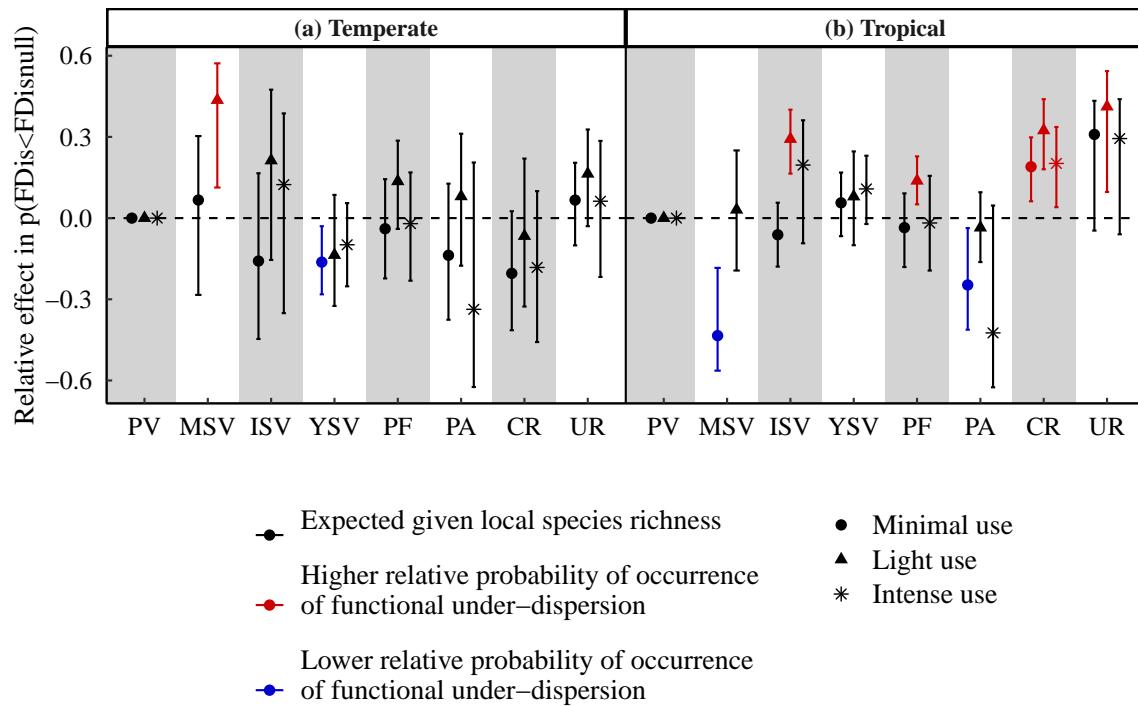
**Figure 3.3: Effects of land use, land-use intensity, region and taxonomic class on FRic (a) and FDis (b).** Effects were rescaled with reference to primary vegetation (PV) and are plotted as a % difference relative to PV within each land-use intensity. Error bars represent 95% confidence intervals. Effects for FRic were estimated from Model 2a, and from Model 2b for FDis. SV, secondary vegetation; PF, plantation forest; AGR, agricultural land uses (pasture and cropland); UR, urban. Effects for reptiles in urban land uses could not be estimated as there were not enough sampled sites. *Figure reproduced from Etard et al. (2021).*

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

1069 were large, I typically observed larger decreases in functional diversity when using the complete data subset,  
 1070 including an 86% decline in FRic for mammals in intensely used tropical agricultural areas. The results were  
 1071 also unaffected by variation across replicate sets of imputed trait values (Appendix 2, Figure S3.24).

### 1072 3.3.2 Changes in the probability of occurrence of functional under-dispersion

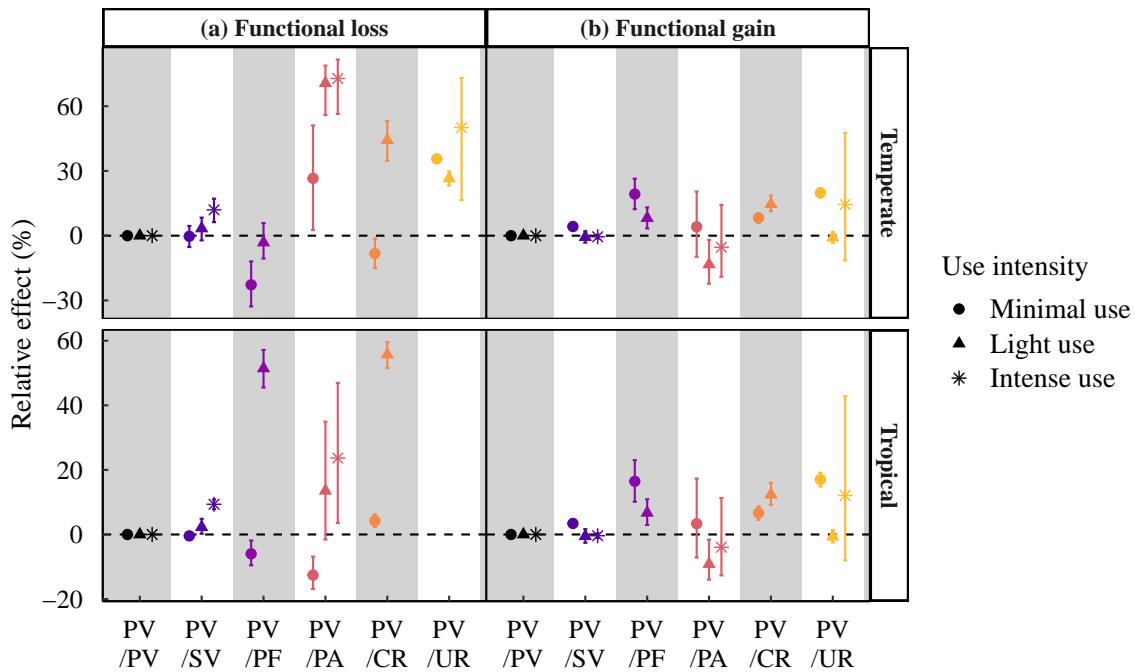
1073 Land use, land-use intensity and region significantly affected the probability of occurrence of functional  
 1074 under-dispersion across vertebrates. Functional under-dispersion was more likely to occur in tropical crop-  
 1075 land of all land-use intensities (Figure 3.4b), as well as in some of the lightly-used land uses (notably urban  
 1076 and plantation forest). Contrary to my expectations, and with the exception of tropical cropland, functional  
 1077 under-dispersion was not more likely to occur in intensely-used land uses. For minimally-used sites, changes  
 1078 in FDis were mostly consistent with that expected given changes in species richness.



**Figure 3.4: Effects of land use, land-use intensity and region on the probability of occurrence of functional under-dispersion.** Error bars represent 95% confidence intervals. PV: primary vegetation; MSV, mature secondary vegetation; ISV, intermediate secondary vegetation; YSV, young secondary vegetation; PF, plantation forest; PA, pasture; CR, cropland; UR, urban. Effects are rescaled and represent the average difference in the probability of occurrence of functional under-dispersion between the reference (PV, probability of functional under-dispersion set at 0 within each land-use intensity) and the disturbed land uses. *Figure reproduced from Etard et al. (2021).*

### 1079 3.3.3 Functional loss and gain

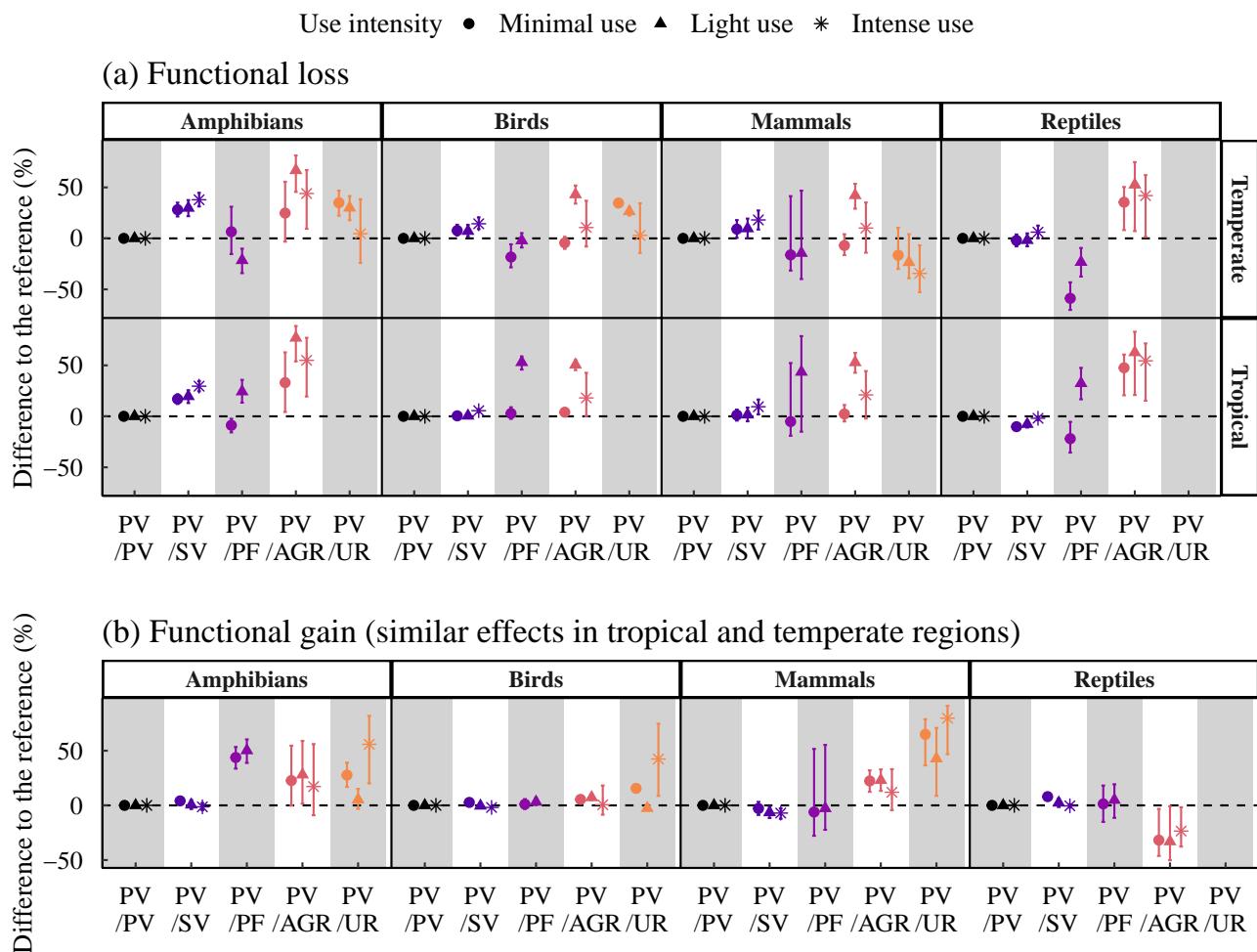
1080 Across and within vertebrate classes, I detected high levels of functional loss, exceeding the natural turnover  
 1081 between primary-vegetation sites, both in temperate and tropical regions. Across vertebrates (Figure 3.5a),  
 1082 functional loss was notably high in temperate pastures (+27% above reference for minimal use; +73% for  
 1083 intense use), temperate urban sites (+27% for light use; +50% for intense use; effects for tropical urban sites  
 1084 could not be estimated), temperate and tropical cropland (+44% and +56% respectively for light use; effects  
 1085 for intense use could not be estimated). Important levels of functional loss were also observed in tropical  
 1086 plantation forest of light use intensity (+51%; effects for the intense use could not be estimated). High  
 1087 levels of functional loss were also observed within each class (Figure 3.6a) (although not all effects could  
 1088 be estimated because of limited sample sizes, Appendix 2, Table S3.5). The highest losses were observed  
 1089 in agricultural areas for amphibians and reptiles, with important losses also observed in temperate urban  
 1090 areas for both birds and amphibians (+35% for minimal use; effects for tropical urban areas could not be  
 1091 estimated).



**Figure 3.5: Effects of land use and land-use intensity on (a) functional loss and (b) functional gain across pairs of sites in temperate areas and tropical areas.** PV: primary vegetation; SV, secondary vegetation; PF, plantation forest; PA, pasture; CR, cropland; UR, urban. Error bars represent 95% confidence intervals. Effects are rescaled and represent the average difference in functional loss and gain between the reference pairs (PV/PV, with loss and gain set at 0% within each land-use intensity), and pairs of primary vegetation with disturbed land uses. Negative effects mean that, on average, levels of functional loss (or gain) were lower than functional loss (or gain) observed between pairs of primary-vegetation sites, and not that there were absolute ‘negative losses’ or ‘negative gains’. *Figure reproduced from Etard et al. (2021).*

1092 Across vertebrates (Figure 3.5b), average functional gain (average proportion of novel trait space in the  
 1093 disturbed assemblage) was moderate and on average did not exceed 20% in any disturbed land uses. Patterns  
 1094 of functional gain were similar in both regions. The highest functional gains were observed for minimally-  
 1095 used urban sites and plantation forest (range: +16% to +20%). On the other hand, important levels of  
 1096 functional gain were observed in some classes (Figure 3.6b), with the highest functional gain for mammals  
 1097 (+80% in intensely used urban sites).

1098 Diagnostic plots (qq-plots and residual distributions) for the models are shown in Appendix 2, Figures  
 1099 S3.9–S3.17. Overall, the model residuals were appropriately distributed (but with some leptokurtic residual  
 1100 distributions, to which mixed-effect models are generally robust (Schielzeth et al., 2020)).



**Figure 3.6: Effects of land use, land-use intensity, region and taxonomic class on functional loss 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).*

1101 **3.4 Discussion**

1102 Here, I showed that the functional diversity of vertebrate assemblages is negatively impacted in human land  
1103 uses, particularly in the most intensely used land types. The results of this Chapter extend previous studies  
1104 that have been more taxonomically or geographically restricted (Flynn et al., 2009; Matuoka et al., 2020).  
1105 Matuoka et al. (2020) found that the functional diversity of tropical bird assemblages was negatively affected  
1106 by human disturbance, a pattern that did not appear in temperate assemblages. Yet, I found that functional  
1107 diversity was negatively affected in both tropical and temperate, with important functional losses in all four  
1108 vertebrate classes.

1109 Using multiple metrics allowed me to explore different facets of functional diversity. For instance, func-  
1110 tional gain could locally offset functional loss in some disturbed land uses. This could indicate that despite  
1111 no apparent negative effect on FRic, some disturbed land uses (e.g. lightly-used temperate cropland) could  
1112 experience important functional loss, and highlights the importance of using a variety of indicators. This  
1113 mechanism could be at play in mammalian assemblages, for which important levels of functional gain were  
1114 observed in agricultural and urban sites. Further, functional gain in disturbed land uses could indicate that  
1115 disturbances facilitate the introduction of functionally novel species, falling into previously unoccupied parts  
1116 of the trait space. This may be because non-native species are more likely to become established in disturbed  
1117 assemblages. Previous work has shown that land-use disturbance facilitates biological invasions in island  
1118 ecosystems (Jesse et al., 2018; Sanchez-Ortiz et al., 2019), but to my knowledge, this has not been tested  
1119 specifically across continental areas for invasive vertebrates (but see Pyšek et al. (2010)). It is also pos-  
1120 sible that disturbed areas harbour synanthropic species that do not occur in primary vegetation, leading to  
1121 substantial functional gain.

1122 Overall, the negative effects of land use on functional richness tended to be more pronounced in the  
1123 tropics. This is congruent with past studies that have found tropical biodiversity to be disproportionately  
1124 sensitive to human pressures (Martins and Pereira, 2017; Newbold et al., 2020b). There are a number of  
1125 potential explanations for this. First, it could be that a long history of intense land-use disturbance at large  
1126 scales in many temperate regions (e.g. Western Europe; Stephens et al. (2019)) means that biodiversity is  
1127 now less sensitive to new disturbances, because the most sensitive species have been filtered out (Balmford,  
1128 1996; Krauss et al., 2010; Le Provost et al., 2020; Munteanu et al., 2020). Species unable to cope with such  
1129 disturbances may have gone extinct in the past, while the remaining species would be more disturbance-  
1130 tolerant (Betts et al., 2019). Tropical regions, historically less disturbed at large scales, would then contain  
1131 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., 2012b; 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-

1196 tional richness in at least three out of four vertebrate classes (amphibians, birds, and reptiles), in accordance  
1197 with past studies focusing on each of these groups (Gallmetzer and Schulze, 2015; Marcacci et al., 2021;  
1198 Riemann et al., 2017; Sol et al., 2020). Although overall mammalian functional richness was less affected,  
1199 high levels of functional gain suggest that the functional composition of mammalian assemblages is heavily  
1200 modified in disturbed land uses.

1201 To conclude, the results of this third chapter highlight the negative impacts of human land uses on mul-  
1202 tiple dimensions of functional diversity, within and across terrestrial vertebrate classes, at a global scale.  
1203 In many disturbed sites, decreases in functional diversity exceed changes expected from species loss alone,  
1204 showing that human activities non-randomly reshape ecological assemblages. By intensifying functional  
1205 loss and promoting functional under-dispersion, land-use change could have deleterious effects on ecosys-  
1206 tem functioning, highlighting the necessity of putting into place effective conservation measures in the face  
1207 of anthropogenic change.

1208 **4 | Geographical range area, habitat breadth**

1209 **and specialisation on natural habitats**

1210 **explain land-use responses and climate-**

1211 **change sensitivity more consistently than**

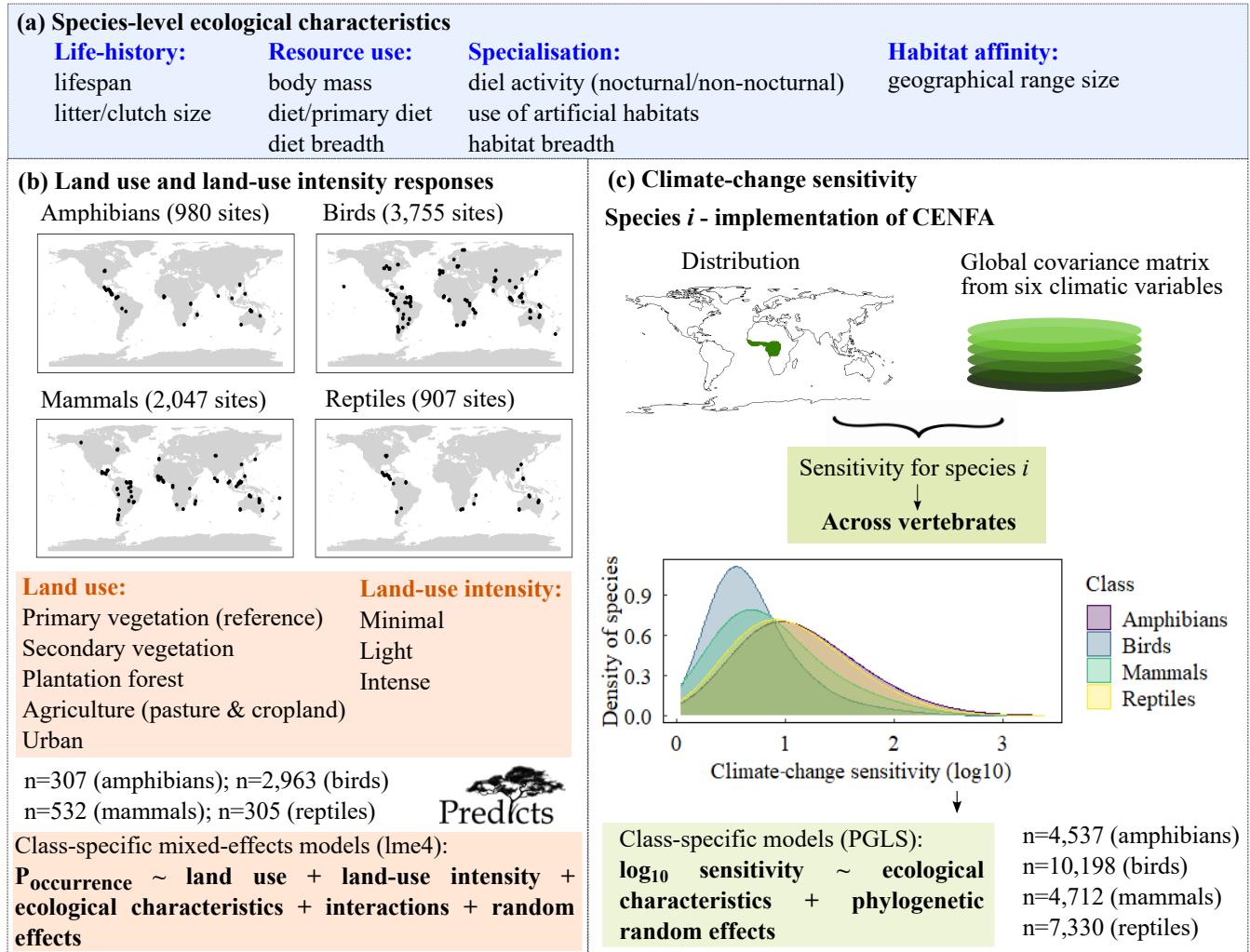
1212 **life-history and dietary traits in terres-**

1213 **trial vertebrates**

1214 **Keywords**

1215 **Abstract**

1216 **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.

## 1217 4.2 Methods

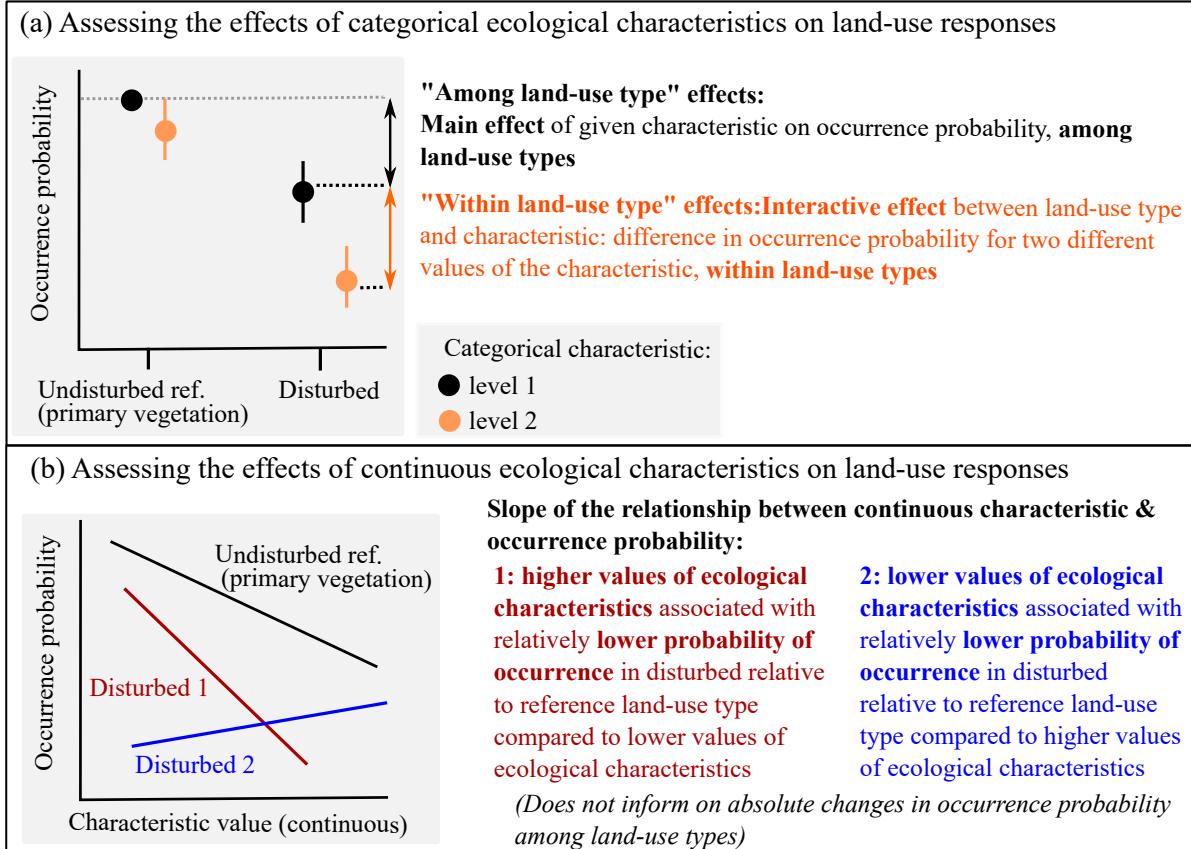
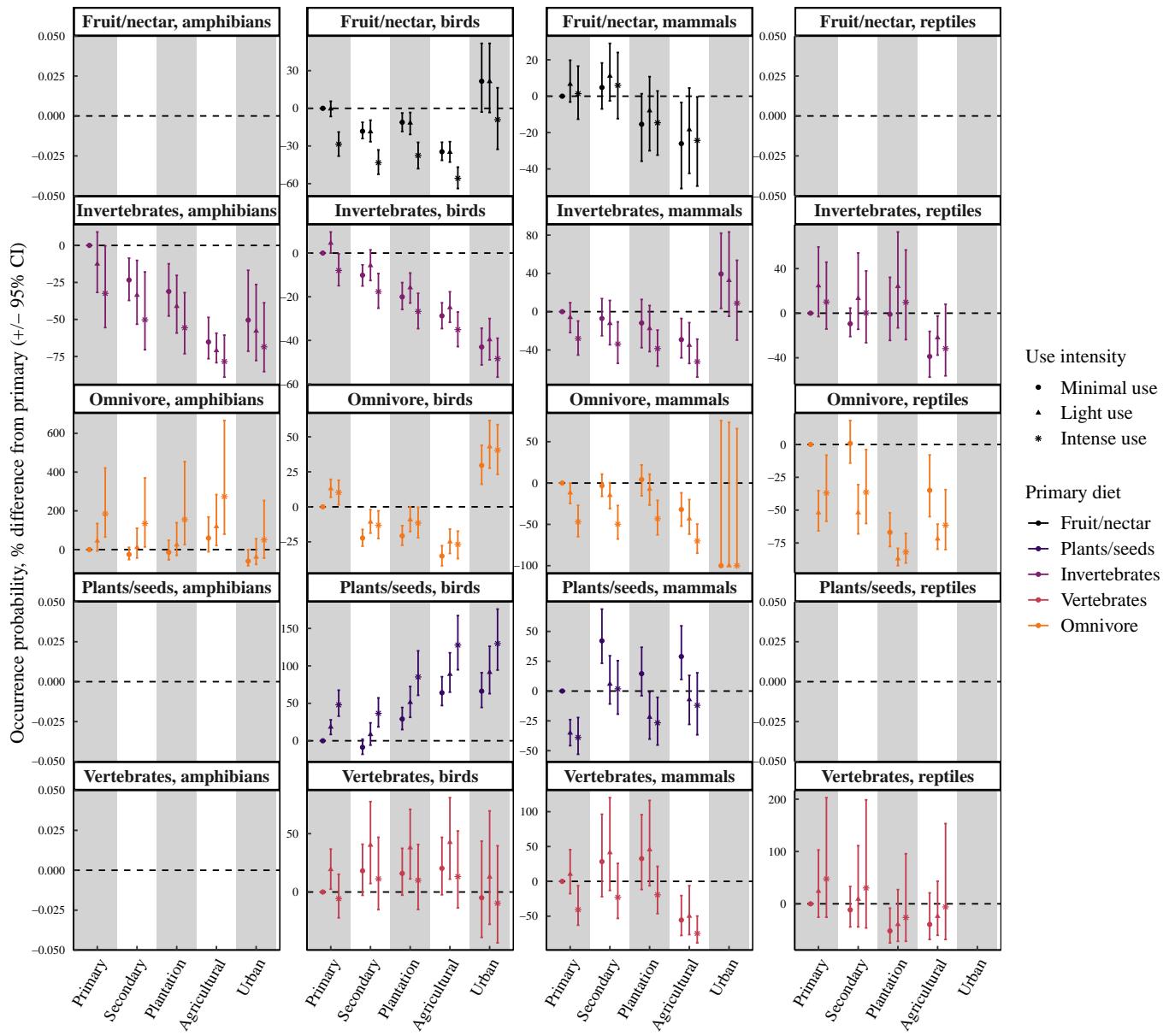


Figure 4.2: Assessing the effects of ecological characteristics on species land-use responses: methodology for (a) categorical characteristics and (b) continuous characteristics. (a) For all categorical characteristics, except diet, I look at ‘within land-use type’ effects, asking whether there are significant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

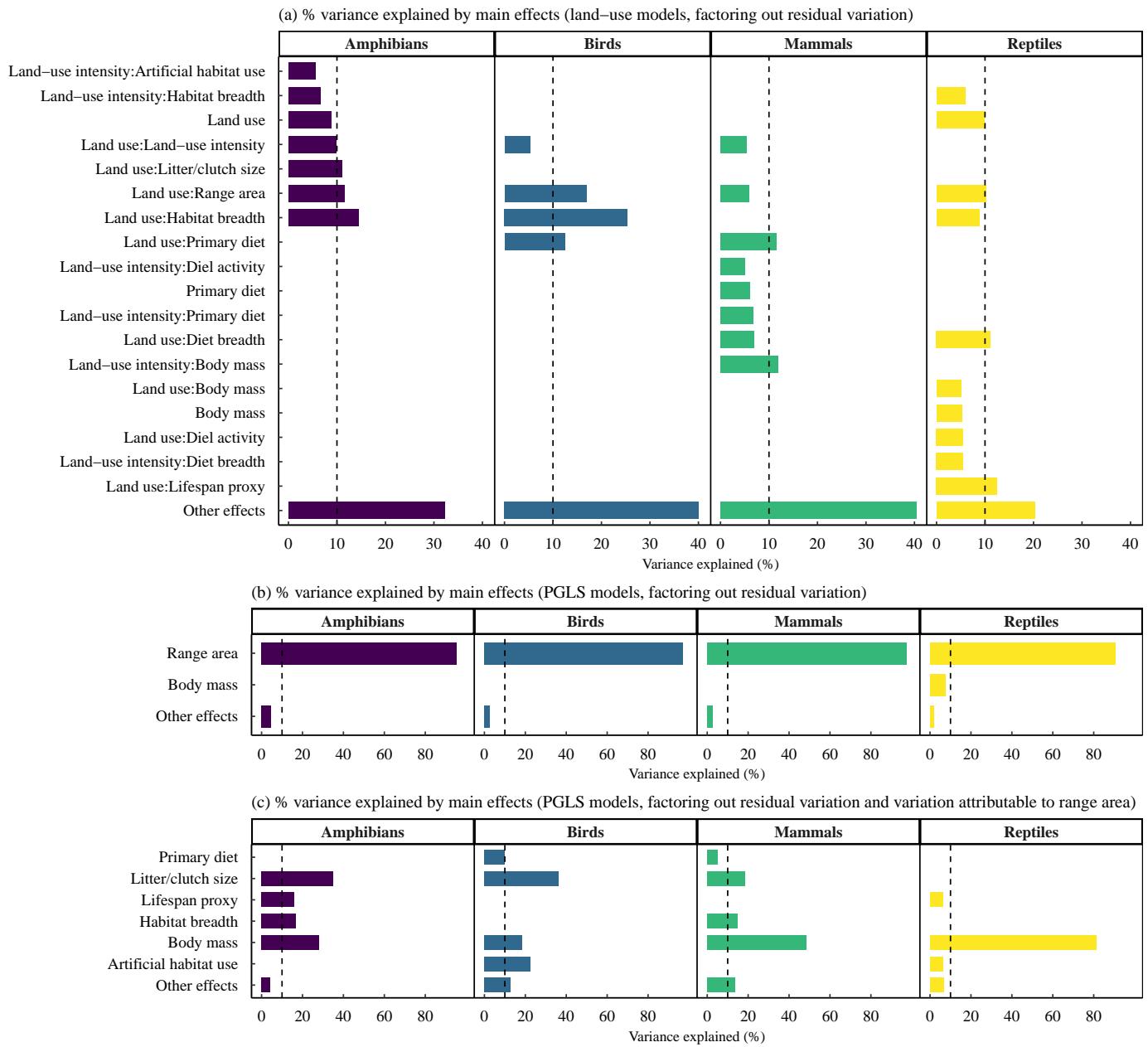
## 1218 4.3 Results

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

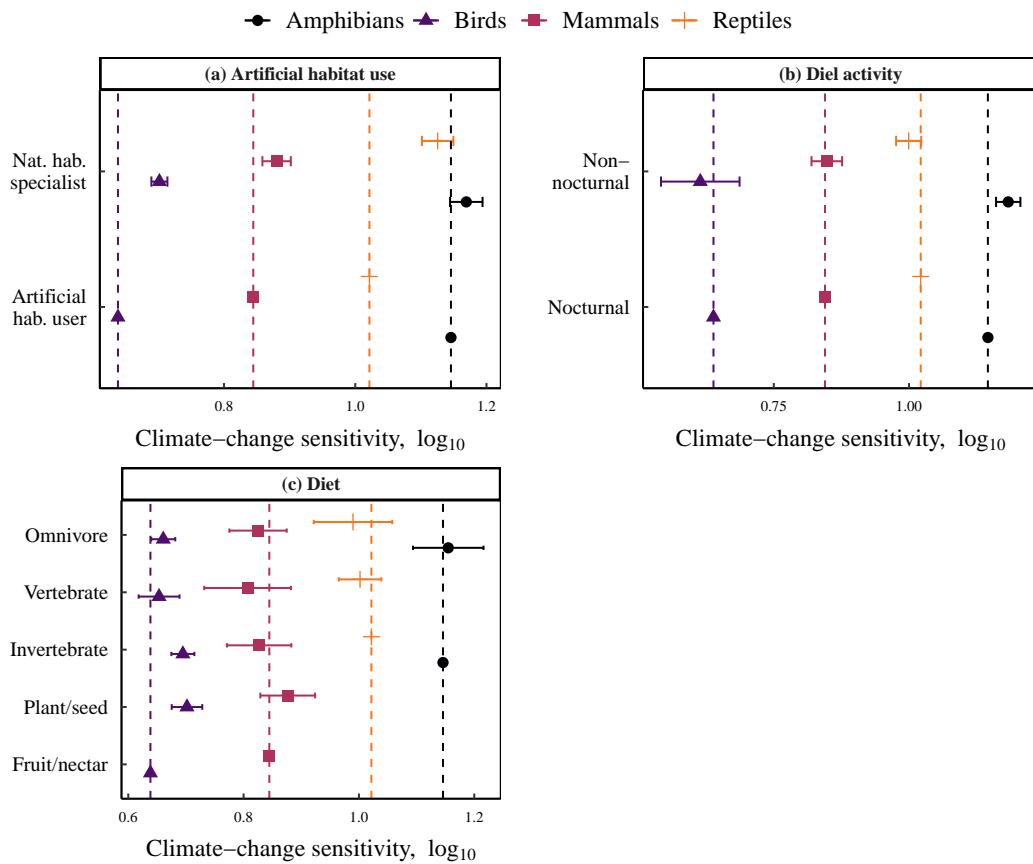
| (a) "Within land-use type" effects of the species-level characteristics on occurrence probability<br>- <=> more sensitive; + <=> less sensitive |   |                   |     |     |              |   |   |       |   |     |            |   |   |   |   | Predictors                 |  |  |  | (b) Climate-change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



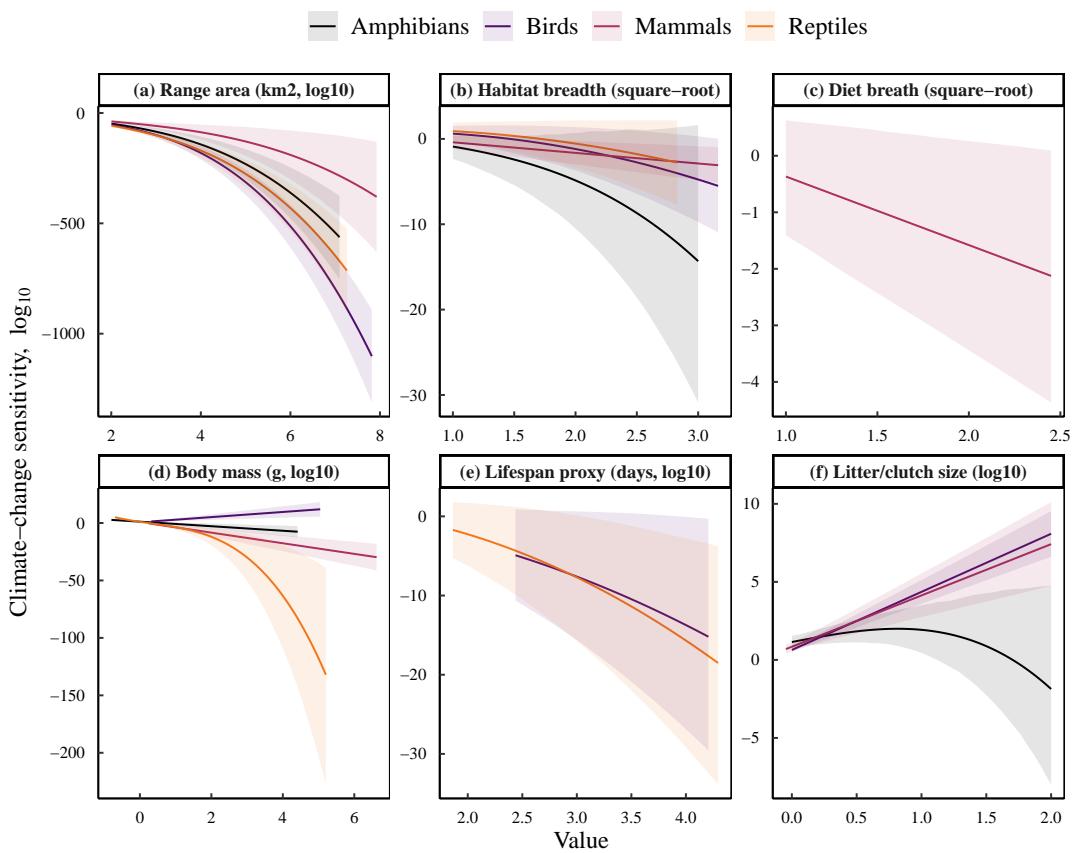
**Figure 4.3: Predicted occurrence probability as a function of land use, land-use intensity, diet and their interactions, for each class of terrestrial vertebrates.** The predictions were obtained from the partial models fitted for each class considering only the diet trait. Empty plots are drawn where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



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



**Figure 4.5: Effects of the categorical traits on climate-change sensitivity, estimated from the PGLS models in each class.** For artificial habitat use (a), the reference level is “artificial habitat user”; for diel activity, the reference level is “nocturnal”; for diet, the reference level for mammals and birds is “fruit/nectar eaters”, but “invertebrate eaters” for amphibians and reptiles.



**Figure 4.6: Effects of the continuous ecological characteristics on climate-change sensitivity, estimated from the PGLS models in each class.** We plotted the estimated relationships only when they were found to be significant.

**Table 4.2: ANOVA summaries for the PGLS models investigating the effects of the species-level ecological characteristics on species climate-change sensitivity.**

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

1219 **4.4 Discussion**

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

## **Keywords**

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

## **Abstract**

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

1240 significant increases for urban areas in all trophic groups, highlighting that disturbed areas may not be as  
1241 energy-poor as I initially assumed. Second, I found a positive effect of metabolic rates (after controlling  
1242 for body mass and taxonomy) on species probability of occurrence across all trophic groups for at least one  
1243 of the most disturbed land uses I considered (pasture, cropland and urban). Species for which there are  
1244 exploitable resources in disturbed environments may benefit from having larger energetic expenditure: they  
1245 may display a set of characteristics rendering them more able to cope with disturbances and more able to  
1246 acquire available resources, such as higher activity levels or bigger brain sizes. The findings of this Chapter  
1247 highlight that land-use change has substantial impacts on vertebrate community metabolism.

## 1248 5.1 Introduction

1249 Land-use change is currently the strongest driver of global biodiversity declines (Maxwell et al., 2016;  
1250 Newbold et al., 2015), with major and long-lasting impacts on the structure and functioning of ecological  
1251 communities (Bregman et al., 2016; Fukasawa and Akasaka, 2019; Magioli et al., 2021; Marcacci et al.,  
1252 2021). With land-use change likely to continue to intensify (Stehfest et al., 2019), it is vital to put into  
1253 place conservation and mitigation measures to minimise future losses of biodiversity and negative impacts  
1254 on ecosystem functioning. To this end, pressing questions remain as to what renders species able or unable  
1255 to cope with human disturbance, and how losses of sensitive species might influence ecosystem functioning  
1256 (Dirzo et al., 2014; Young et al., 2016).

1257 Land-use change acts as an environmental filter affecting species persistence (Edwards et al., 2021;  
1258 Evans et al., 2018). Past studies have shown that sensitivity to land-use change is distributed unevenly across  
1259 the tree of life (Nowakowski et al., 2018), and across behavioural (Lowry et al., 2013; Samia et al., 2015)  
1260 and ecological strategies (De Palma et al., 2015; Møller, 2009; Newbold et al., 2013). For instance, long-  
1261 lived and large forest specialist birds respond more negatively to land-use change than generalist species  
1262 (Newbold et al., 2013). In addition, human land uses impose energetic constraints on species, by modifying  
1263 the amount and type of available resources (Inger et al., 2016; Zuñiga-Palacios et al., 2021). Consequently,  
1264 land-use change brings about modifications in dietary and foraging strategies (Møller, 2009; Ramesh et al.,  
1265 2017; Sévèque et al., 2020), which can have cascading effects on local trophic structure (e.g., mesopredator  
1266 release; Crooks and Soulé (2010)). The impacts of land-use change on biodiversity also depend on land-  
1267 use intensity (Davison et al., 2021; Newbold et al., 2015), that is, the magnitude of human disturbance in  
1268 a given land-use type, which can vary importantly according to local practices and management (Dullinger  
1269 et al., 2021). In particular, land-use intensity affects the types and availability of resources (by homogenising

1270 resources for example), which in turn may affect biodiversity patterns (Weiner et al., 2011).

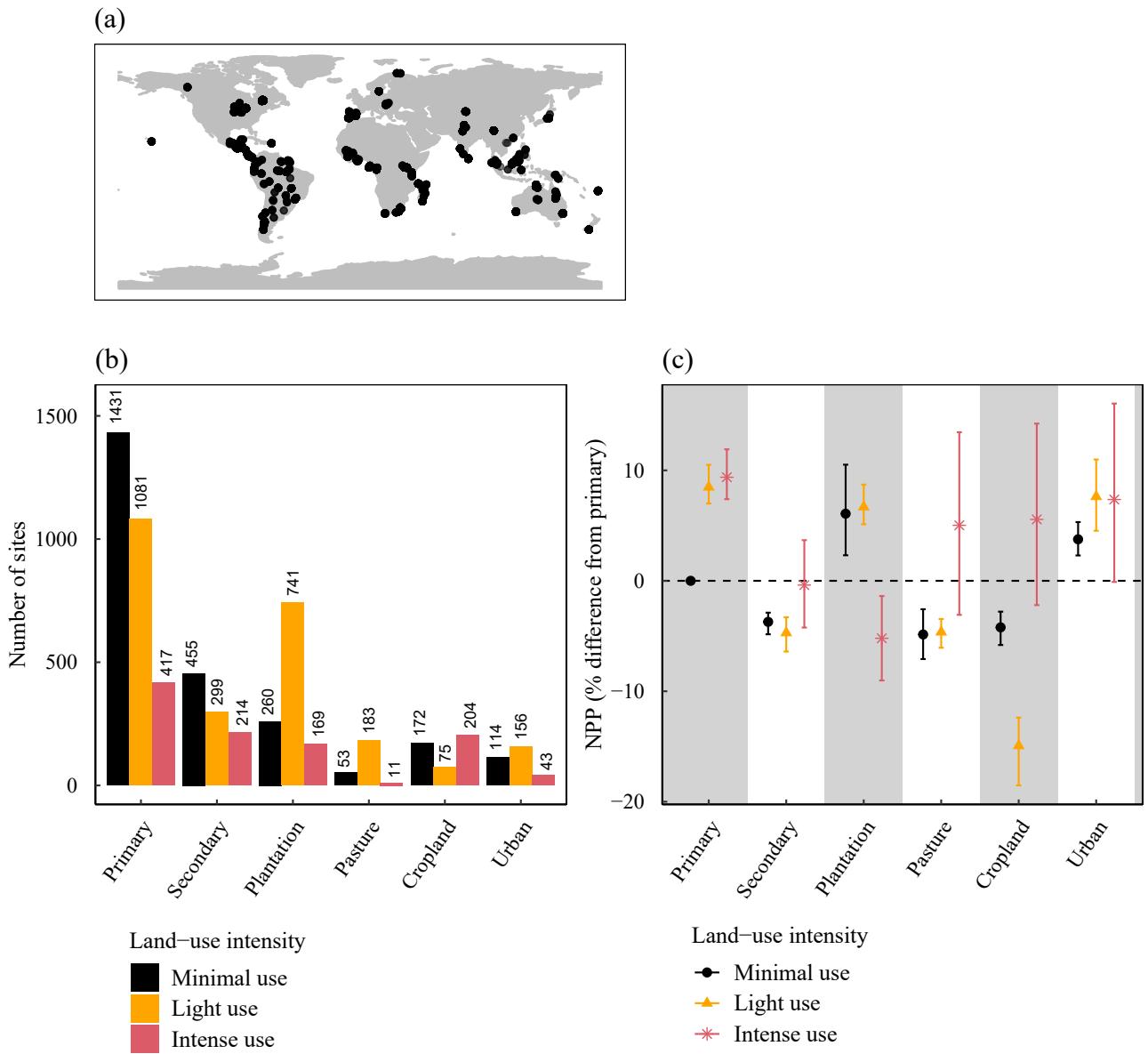
1271 Energetic requirements are likely to be important predictors of species' ability to cope with a disturbed  
1272 environment where resource availability and resource types are strongly impacted (Auer et al., 2020). Past  
1273 research has shown that metabolic rates (the amount of energy required for organismal maintenance and  
1274 for other processes such as growth and reproduction) are heritable and subject to selection, for instance  
1275 with species in energy-rich environments having evolved faster metabolic rates than species in less energy-  
1276 rich environments (Mueller and Diamond, 2001). However, metabolic rates have received less attention  
1277 than other life-history traits in studies aiming to understand different species' responses to land-use change.  
1278 Body mass, known to explain much of the variation in metabolic rates (Bushuev et al., 2018; Hudson et  
1279 al., 2013; White and Seymour, 2003), has been considered in past studies examining effects of land-use  
1280 disturbance on assemblage composition (Hevia et al., 2017). Since metabolic rates correlate positively with  
1281 body mass, the effects of land-use change on local energetic requirements have been indirectly assessed  
1282 through investigations of changes in body mass composition along land-use gradients (Newbold et al., 2020a;  
1283 Tinoco et al., 2018). However, to the best of our knowledge, no study has yet directly reported the effects of  
1284 land-use change on assemblage-level energetic requirements.

1285 Thus, the first objective of this Chapter is to investigate how land-use change impacts assemblage-level  
1286 energetic requirements in terrestrial vertebrates. To this end, I use metabolic rates as a proxy for maintenance  
1287 energetic requirements at the species level. I predict that, at the assemblage level, total energetic requirements  
1288 in disturbed land uses are lower than in undisturbed land uses. This prediction relies on the assumption that  
1289 there is less energy available overall in disturbed land uses than in undisturbed land uses (Figure 5.1c), with  
1290 disturbed land uses being characterised by human appropriation of net primary productivity (Krausmann et  
1291 al., 2013). Because species' ability to exploit particular resources and meet energetic demands also depends  
1292 on food types and diet (McNab, 1986; Mendoza and Araújo, 2019), I test whether this prediction holds  
1293 true within trophic groups (i.e., within herbivores, omnivores, and carnivores). Here, I consider energetic  
1294 requirements at the assemblage level, not controlling for species body mass, to obtain estimates of total  
1295 energy expenditure in different land-use types (Figure 5.2a). Thus, any changes in assemblage-level energetic  
1296 requirements could be ultimately driven by shifts in the size-spectrum of local assemblages.

1297 Body mass explains much of the variation in metabolic rates, but species with similar body masses still  
1298 display important variation in metabolic rates (Mueller and Diamond, 2001). Some of this variation can  
1299 be explained by taxonomic position (which also accounts for differences in thermoregulatory strategy be-  
1300 tween endotherms and ectotherms). However, there remains substantial interspecific variation in metabolic  
1301 rates even after accounting for body mass and taxonomic affiliation (Mueller and Diamond, 2001; White

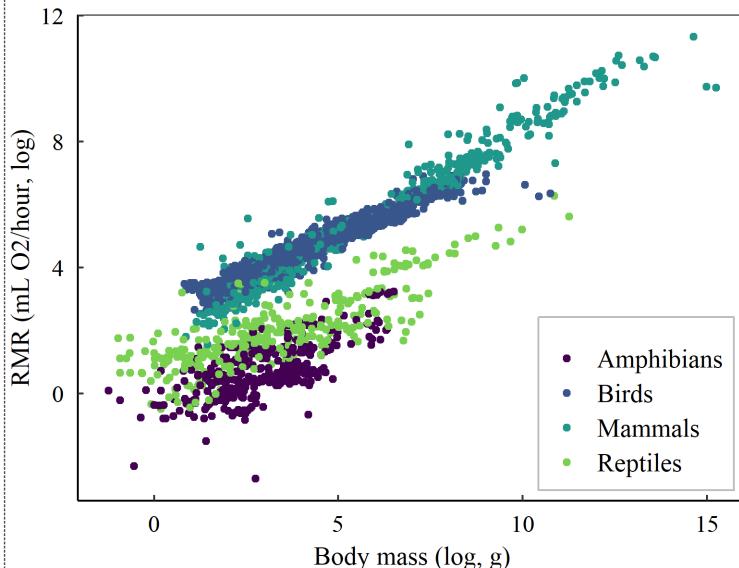
1302 and Kearney, 2013). Food availability and food type might explain this residual variation in metabolic rates  
1303 among species (Mueller and Diamond, 2001). Species that evolved in areas with abundant resources assim-  
1304 ilate and burn calories at high rates, regardless of their body mass – while species that evolved with limiting  
1305 resources could process resources at lower rates, irrespectively of their body mass (Mueller and Diamond,  
1306 2001). Building upon this idea and the ‘allocation’ principle (i.e., the trade-offs in resource allocation; Auer  
1307 et al. (2020)), species with lower energetic expenditure (than expected from body mass and taxonomy) may  
1308 be able to cope with food scarcity better than those with larger energy expenditure (than expected from body  
1309 mass and taxonomy). Indeed, regardless of their body mass, such species should need fewer resources to  
1310 meet energetic demands (Clarke and Fraser, 2004). Thus, as land-use disturbance modifies the types and  
1311 abundance of resources, we expect species energetic requirements –after removing the effects of body mass  
1312 and taxonomic position– to influence responses to land-use change. Yet, whether energetic constraints ex-  
1313 plain species responses to land-use change in terrestrial vertebrates has not been investigated before (Hevia et  
1314 al., 2017). Thus, the second objective of this Chapter is to characterise the influence of energetic constraints  
1315 on species occurrence probability in disturbed land uses, compared to undisturbed land uses. I approximate  
1316 energetic constraints at the species level from residual variation in metabolic rates, that is, the variation not  
1317 explained by body mass or taxonomy. I predict that species with negative deviations (lower rates than ex-  
1318 pected from body mass and taxonomy) are more likely to persist in disturbed land uses than species with  
1319 positive deviations (higher rates than expected from body mass and taxonomy; Figure 5.2b). Given that  
1320 trophic group can influence resource acquisition and species ability to assimilate various types of food, I  
1321 investigate whether this prediction is consistent among trophic groups.

1322 To test both predictions, I use a space-for-time substitution approach, obtaining vertebrate assemblage  
1323 composition data from the PREDICTS database (Hudson et al., 2014, 2017). I combine this database with  
1324 trophic-group information (characterising species as either omnivores, herbivores, or carnivores), and with  
1325 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.

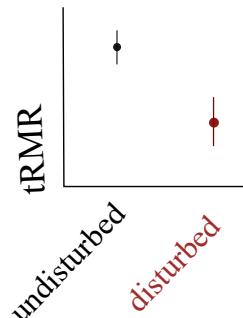
**(a) Assemblage-level:** there is less energy available to utilize by vertebrate assemblages in disturbed land uses than in undisturbed land uses.



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

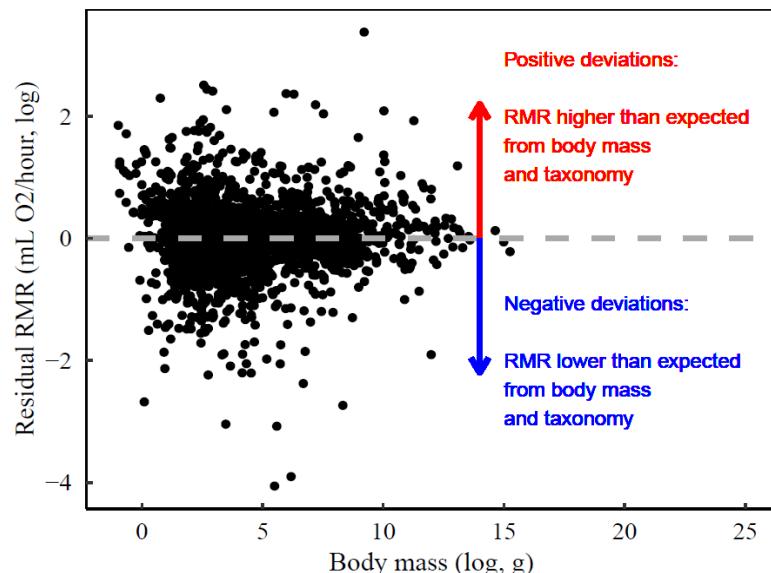
$$\text{Assemblage level: } tRMR = \sum_i (RMR_i * a_i)$$

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



**(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).

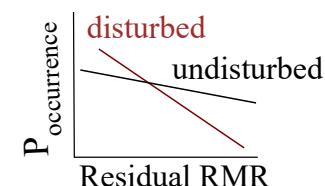
$$\text{residuals of } \log(RMR) \sim \log(BM) + (1|\text{Class/Order/Family})$$



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

Across species - model 2:

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



**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.

1326 **5.2 Methods**

1327 **5.2.1 Vertebrate assemblage composition**

1328 I obtained vertebrate assemblage composition in different land uses from the PREDICTS database (Hudson  
1329 et al., 2014, 2017). The PREDICTS database is a large collection of published studies that measure bio-  
1330 diversity across different land uses and is one of the most comprehensive global databases of its type. In  
1331 each PREDICTS study, species occurrence and often abundance were recorded across different sites. Each  
1332 site was assigned to one of the following land-use types: primary vegetation (natural, undisturbed vegeta-  
1333 tion), secondary vegetation (recovering after complete destruction of primary vegetation), plantation forest  
1334 (woody crops), pasture (areas grazed by livestock), cropland (herbaceous crops) and urban (built-up areas).  
1335 The land-use categories were assigned based on habitat descriptions from the original studies (Hudson et al.,  
1336 2014), sometimes in consultation with the original study authors. Each site was also classified in terms of  
1337 land-use intensity as either minimal, light or intense. The land-use-intensity assignment was also made on  
1338 the basis of the habitat description in the original studies, and depended on criteria specific to each land use  
1339 (such as degree of mechanisation, yield or chemical inputs for cropland; or the amount of green space in  
1340 urban areas; Hudson et al. (2014)).

1341 I subset the PREDICTS database for studies that sampled terrestrial vertebrates, and for which both land  
1342 use and land-use intensity had been characterised. I thus obtained 181 studies for 4,238 species sampled  
1343 across 6,484 sites (Figure 5.1a). Sample sizes varied across land uses and land-use intensities (Figure 5.1b).

1344 **5.2.2 Energy availability by land-use type and land-use intensity**

1345 The predictions of this Chapter rely on the assumption that resource types and abundance are modified in dis-  
1346 turbed environments, with less energy available in disturbed compared to undisturbed land uses overall. To  
1347 test this assumption, I used terrestrial net primary productivity (NPP) across land uses as a proxy for available  
1348 energy. NPP quantifies the amount of atmospheric carbon fixed by plants and accumulated as biomass. NPP  
1349 estimates were derived using imagery from the Moderate Resolution Imaging Spectroradiometer (MODIS)  
1350 on board NASA's Terra satellite. NPP estimates were based on a yearly composite of measures made at  
1351 8-day intervals, captured at 500-m spatial resolution (Running and Zhao, 2015). I obtained NPP for 4,062  
1352 of the PREDICTS sites used in the analysis (matching the sites to the NPP data using the sampling year  
1353 available in PREDICTS). I fit a linear mixed-effects model ('lme4' package, version 1.1-23, Bates et al.  
1354 (2015)) explaining site-level NPP by land use and land-use intensity, with a random intercept accounting for

1355 study identity, to control for differences in experimental design across studies. Model predictions showed  
1356 that NPP decreased significantly in several land uses (e.g., pasture and cropland) compared with the primary  
1357 vegetation reference level, although the strength and in some cases direction of the difference varied among  
1358 land-use and land-use intensity combinations (e.g., increases in urban land uses; Figure 5.1c).

### 1359 **5.2.3 Resting Metabolic Rates (RMR) & imputations of missing RMR values**

1360 As a proxy for species-level energetic expenditure, I used estimates of the minimum amount of energy re-  
1361 quired for organismal maintenance, i.e., basal metabolic rates (BMR) for endotherms, and resting metabolic  
1362 rates (RMR) for ectotherms. From the literature, I obtained estimates of BMR for 719 species of birds and  
1363 685 mammals, and estimates of RMR for 126 amphibians and 173 reptiles (Appendix 4, Table S5.1). For  
1364 endotherms, BMR are measured when species are in their thermoneutral zone, that is, when there is little to  
1365 no energy expenditure allocated to thermoregulation. Thus, BMR estimates were derived from lab studies  
1366 that mostly measured oxygen consumption of the organisms at rest under controlled conditions and in the  
1367 thermoneutral zone of the species. For an ectotherm, there is no ‘basal’ metabolic rate, as body tempera-  
1368 ture mainly depends on environmental temperature. Their metabolic rates follow a hump-shaped relationship  
1369 with environmental temperature, highest at an optimal temperature which corresponds to a performance peak.  
1370 To be able to compare endotherms’ BMR with ectotherms’ RMR, Stark et al. (2020) used the metabolic rates  
1371 that correspond to a performance peak for both groups (i.e., BMR in the thermoneutral zone for endotherms,  
1372 and metabolic rates at optimal temperature for ectotherms). Thus, I used the data compiled in Stark et al.  
1373 (2020) for ectotherms, and from the sources specified in Table S5.1 for endotherms. The units for BMR  
1374 and RMR were standardized to mL of dioxygen consumed per hour (mLO<sub>2</sub>/h). As in Stark et al. (2020), I  
1375 henceforth refer to both basal and resting metabolic rates as RMR.

1376 For the species occurring in PREDICTS, initial data coverage for RMR was poor (Table S5.1), necessi-  
1377 tating imputation of missing values. To do so, I first measured the phylogenetic signal in BMR and RMR  
1378 ( $\log_e$ -transformed), using Pagel’s  $\lambda$  (Pagel, 1999), to assess whether metabolic rates were sufficiently phylo-  
1379 genetically conserved to be estimated from species phylogenetic position. I obtained class-specific phyloge-  
1380 netic trees from Jetz et al. (2012) for birds, from Faurby et al. (2018, 2020) for mammals, from (Tonini et al.,  
1381 2016) for reptiles (squamates), and from Jetz and Pyron (2018) for amphibians (all downloaded in April  
1382 2020). For each class, I randomly sampled 100 trees. To account for phylogenetic uncertainty, I calculated  
1383 Pagel’s  $\lambda$  for each sampled tree and reported the median value, as well as the 2.5th and 97.5th percentiles  
1384 (Table S5.1).

1385 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-

1416 tion, because it is well established that resting metabolic rates are influenced by temperature (Clarke and  
1417 Fraser, 2004), I checked whether including annual mean temperature in the model affected the conclusions.  
1418 Annual mean temperature at each PREDICTS site was estimated from WorldClim version 2.1 (Fick and  
1419 Hijmans, 2017), using a 2.5 arc-minute resolution. Adding annual mean temperature did not improve model  
1420 fit (likelihood-ratio test:  $P=0.113$ ), thus I did not consider its effects any further.

1421 **Model validation.**

1422 To ensure that imputation uncertainty did not affect the conclusions, I refitted model 1 using the subset of  
1423 species ( $n = 426$ ) from PREDICTS for which there were empirical RMR information (i.e., excluding imputed  
1424 RMR values).

1425 **Disentangling the effects of body mass and abundance on tRMR.**

1426 Since RMR correlates strongly with body mass, changes in tRMR are likely to be driven in part by changes  
1427 in the size-spectrum of ecological assemblages. I fitted an additional model to explain changes in species'  
1428 abundance (given presence) by land use, land-use intensity, trophic group, body mass and their interactions,  
1429 to understand the role of shifts in the body mass of species on observed changes in tRMR (Appendix 4,  
1430 Figure S5.1).

1431 **5.2.6 Effects of land use, land-use intensity, trophic group and residual RMR on species  
1432 occurrence probability (prediction 2; Figure 5.2b)**

1433 To control for the effects of body mass and taxonomy on RMR, I used the residual variation in RMR after  
1434 accounting for these variables, from a linear mixed-effects model fitting  $\log_e$ -RMR as a function of  $\log_e$ -  
1435 body mass with nested random taxonomic effects (1|Class/Order/Family; Figure 5.2). Hence, I used a metric  
1436 that describes how much more energy (positive deviations) or less energy (negative deviations) than expected  
1437 from body mass and taxonomic position a species spends for organismal maintenance. Similar approaches  
1438 have been used in previous papers (Furness and Speakman, 2008; Naya et al., 2013). As detailed earlier, I  
1439 expect species with lower residual RMR to do better in disturbed land uses than species with higher residual  
1440 RMR (prediction 2; Figure 5.2b) because, given any body mass, investing less energy in maintenance could  
1441 contribute to persistence in a context of resource scarcity.

1442 To test the second prediction, I fitted a binomial mixed-effects model explaining species occurrence  
1443 with land use, land-use intensity, trophic group and residual RMR. I started with a complete model that  
1444 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.

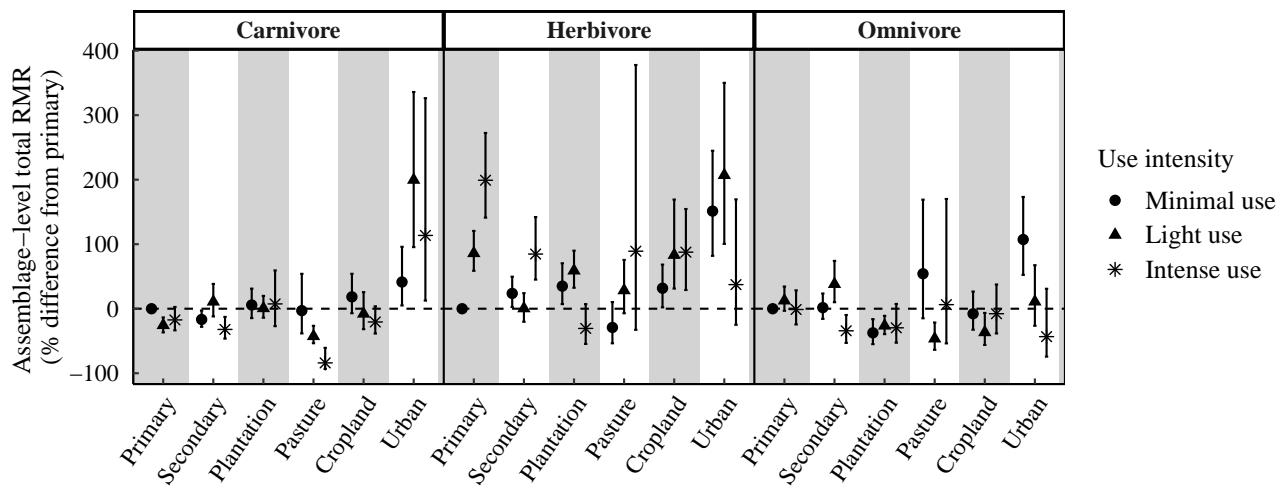
I checked the phylogenetic signal in the model residuals using Pagel's  $\lambda$  (Pagel, 1999). Non-significant phylogenetic signal in the residuals would indicate that fitting species identity in the model's random effects was sufficient to account for residual phylogenetic variation in RMR. Further, 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).

1473 The model residuals were appropriately distributed (see diagnostic plots in Appendix 4, Figure S5.3).  
 1474 Investigating the sensitivity of our results to imputation uncertainty showed that our results and conclusions  
 1475 were robust to the removal of all imputed estimates of RMR (the correlation coefficient was 0.72 between the  
 1476 two sets of model coefficients; Figure S5.4). Comparing model predictions showed that effects were mostly  
 1477 congruent, although there were some differences (Figure S5.5). In particular, for herbivores, effect sizes  
 1478 tended to be bigger for the model fitted on empirical data compared with the model that included imputed  
 1479 data. Thus, our main results appear to be conservative if anything. The model fitted on empirical data had  
 1480 larger standard errors, likely due to the reduction in sample size.

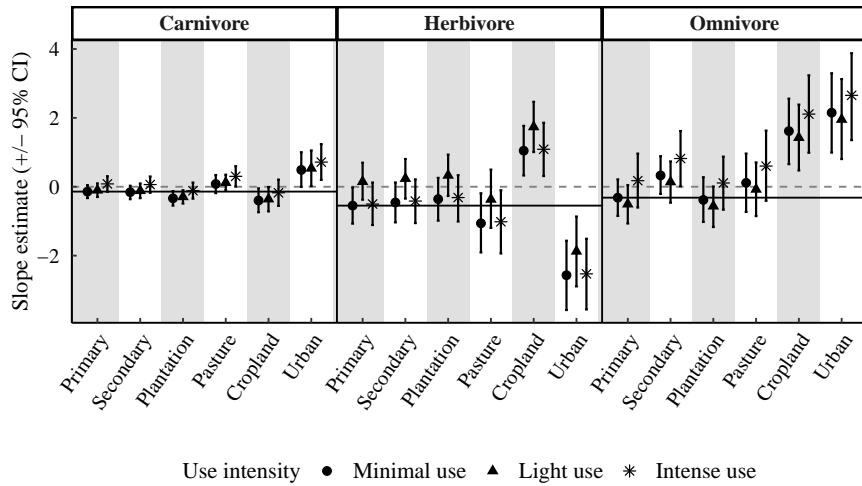


**Figure 5.3: Effects of land use, land-use intensity and trophic group on assemblage-level total RMR.** Model predictions are rescaled with reference to minimally-used primary vegetation, considered to be the undisturbed baseline. Primary: primary vegetation; secondary: secondary vegetation; plantation: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

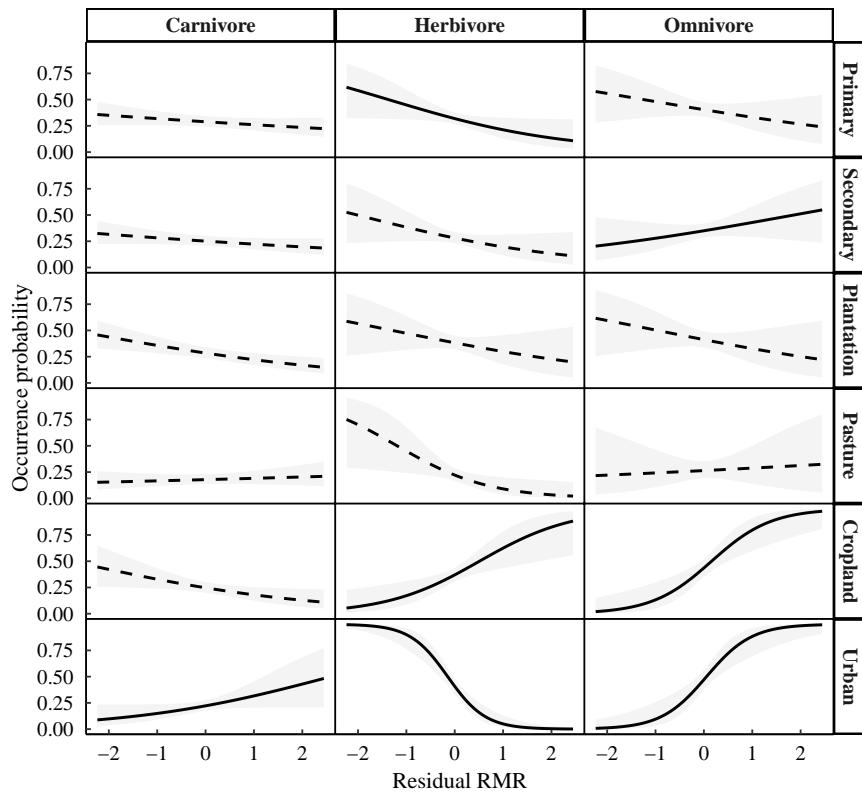
1481 **5.3.2 Effects of land use, land-use intensity, trophic group and residual RMR on species'**  
 1482 **occurrence probability**

1483 Species' occurrence probability was significantly affected by land use, land-use intensity, trophic level, resid-  
 1484 ual RMR and their interactions (Figures 5.4, 5.5). Contrary to our expectations, species with higher residual  
 1485 RMR (relative to their body mass and taxonomic position) tended to do better than species with lower resid-  
 1486 ual RMR in a number of disturbed land uses. Overall, land-use type was more important for determining the  
 1487 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



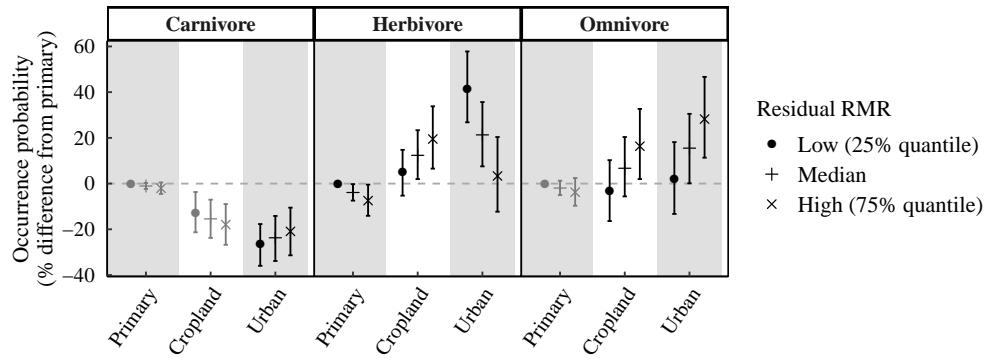
(b) Predicted effects of residual RMR on occurrence probability (minimal use intensity)



**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.

1488 For minimally-used primary vegetation (reference), the model predicted negative effects of residual RMR  
 1489 on species occurrence probability in all trophic levels (but with a significant slope for herbivores only; Figure  
 1490 5.4a). However, the directionality of this relationship was reversed in some disturbed land uses in all trophic  
 1491 groups (secondary vegetation, cropland and urban for omnivores; cropland for herbivores; urban for carni-  
 1492 vores), with significant positive slopes, also significantly higher than those observed for primary vegetation  
 1493 (Figure 5.4a). The only exception was the opposite pattern for urban herbivores (Figure 5.4b), where residual  
 1494 RMR had a more negative effect on occurrence probability than in minimally-used primary vegetation.

1495 I would like to emphasize that positive effects of residual RMR on occurrence probability in some of the  
 1496 most disturbed land uses (e.g., urban for carnivores) do not mean that there were absolute increases in species  
 1497 occurrence probability in disturbed land uses compared to primary vegetation (and vice-versa). I illustrate  
 1498 this point in Figure 5.5. For carnivores with a median value for residual RMR, occurrence probability was  
 1499 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).

1500 Finally, the model showed some degree of deviation from distributional assumptions (diagnostic plots,  
 1501 Appendix 4, Figure S5.6). Nevertheless, the model's coefficients were similar when estimated with a  
 1502 Bayesian framework, suggesting that the estimates were robust (Figure S5.7). The phylogenetic signal in  
 1503 the model residuals was weak and non-significant ( $\lambda=0.004$ ,  $P=0.24$ ). Re-fitting the model using the com-  
 1504 plete data subset (i.e., excluding imputed RMR estimates) showed that our conclusions are likely robust to  
 1505 imputation uncertainty (Figure S5.8), with congruent results overall, although there were a few differences  
 1506 in the predictions between the two models – notably, for herbivores in urban land uses (Figure S5.8).

1507 **5.4 Discussion**

1508 The results of this Chapter provide insights into the relationship between land-use change and energetic  
1509 requirements at two levels of organisation (at the assemblage level and the species level), and contradict  
1510 both my initial predictions. I found that total energetic requirements did not show systematic decreases in  
1511 disturbed land uses. On the contrary, there were strong increases in all trophic groups, most notably in urban  
1512 land uses. Further, in all trophic groups, species with higher energetic expenditure (than expected from body  
1513 mass and taxonomy) tended to do better in some of the most disturbed land uses (that is, cropland and urban)  
1514 than species with lower energetic expenditure (than expected from body mass and taxonomy).

1515 At the assemblage level, the results first highlight the effects of land-use change on vertebrate com-  
1516 munity metabolism. Contrary to my expectations, I found differing effects of land use on total energetic  
1517 requirements among trophic groups, reflecting changes in the size-spectrum of ecological assemblages (i.e.,  
1518 changes in the distribution of abundance along the body-mass gradient). On the one hand, decreases in total  
1519 energetic requirements, such as observed for carnivores in intensely used pastures, are likely due to overall  
1520 reductions in local abundance (with carnivorous species in pastures perceived as a threat to livestock; Eeden  
1521 et al., 2018; or because of increased competition for fewer resources). On the other hand, increases in total  
1522 energetic requirements could reflect higher levels of resource intake in some disturbed land-use types. On the  
1523 basis of net primary productivity, I hypothesized that there would be fewer resources available in disturbed  
1524 areas. However, it could be that the carrying capacity of some disturbed land-use types actually increases  
1525 for some trophic groups compared to that of primary vegetation, because of the presence of novel or more  
1526 abundant food sources. For instance, in urban areas, both wildlife feeding and the presence of anthropogenic  
1527 food sources, such as human refusal or pet food, could lead to an increase in resource availability all year-  
1528 round for species with a non-specialised diet that are able to exploit such food sources (Fischer et al., 2012).  
1529 Past research on urban carnivores has shown that some species have adapted to urban environments by ex-  
1530 ploiting anthropogenic food sources, and also benefit from physical protection (with some human structures  
1531 providing shelter) and from reduced occurrence of natural enemies (Bateman and Fleming, 2012). Herbi-  
1532 vores and omnivores could also benefit from increased resources in urban areas, notably where the urban  
1533 matrix includes semi-natural habitats, which is congruent with observed increases in occurrence probability  
1534 in minimally used urban areas for these trophic groups. Further, anthropogenic ‘bottom-up food forcing’ has  
1535 been shown to affect food-web dynamics, with decreases in predation rates, loss of anti-predator abilities  
1536 (Geffroy et al., 2020) and mesopredator release (Fischer et al., 2012). Thus, in urban areas, increases in  
1537 anthropogenic food sources could provide support for a higher abundance of medium-sized species released

1538 from predation, increasing total energetic requirements.

1539 I hypothesized that resource availability would be the main driver behind changes in energetic require-  
1540 ments. However, resource availability likely interacts with other factors to explain the patterns. In particular,  
1541 past work has shown that brain size is an important predictor of species ability to cope with disturbance,  
1542 notably in urban settings (Sayol et al., 2020). Since brain size scales allometrically with body mass, it is  
1543 possible that I observe increases in total energetic requirements where having larger brains is advantageous  
1544 for resource acquisition, and in turn where resources are both exploitable and abundant enough to sustain  
1545 the larger energetic expenditures associated with bigger brain sizes. In addition, body size, which explains  
1546 an important proportion of the interspecific variation in mobility, likely interacts with characteristics of the  
1547 landscape (such as fragmentation) to predict species survival in disturbed land uses (Merckx et al., 2018).  
1548 Hence, the patterns I observe in this Chapter could emerge from interactions and trade-offs among resource  
1549 availability, diet, body size and human management of the landscape.

1550 At the species level, the results underline the role of energetic constraints on species responses to land-  
1551 use change. After controlling for the effects of body mass and taxonomy, I found that residual energetic  
1552 expenditure was a significant predictor of species occurrence probability in disturbed land uses. Contrary  
1553 to my expectations, in several disturbed land uses and in all trophic groups, species with higher residual ener-  
1554 getic expenditure tended to have a higher occurrence probability than species with lower residual ener-  
1555 getic expenditure. It could be that species with lower residual energetic requirements are less well equipped  
1556 than species with higher residual energetic requirements at making use of the available food sources in dis-  
1557 turbed land uses. Species in disturbed land uses may need to display higher levels of feeding innovation  
1558 (Coogan et al., 2018), have larger brains (Sayol et al., 2020), or be bolder and more active to make use of  
1559 the available resources. In mammals, past research has shown that larger brains are associated with larger  
1560 residual energetic expenditure (Isler and Van Schaik, 2006). At the individual level, past research suggests  
1561 that metabolic rates are linked to differences in behaviour, with bolder and more active individuals exhibiting  
1562 higher metabolic rates than less active individuals, with consequences for food acquisition (Biro and Stamps,  
1563 2010). Although I am not aware of similar evidence at the species level, I propose that residual metabolic  
1564 rates interact with species' ecological traits, behavioural traits and foraging strategy in influencing species'  
1565 responses to land use. Among species with an adaptable diet, able to make use of the resources available in  
1566 a disturbed landscape, those with higher residual metabolic rates could present a set of behavioural charac-  
1567 teristics that render them better at acquiring the available resources, hence more able to cope with land-use  
1568 disturbance. This could be the case for urban carnivores and omnivores, as well as herbivores in cropland.  
1569 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, Zhang2018a showed that, subjected to food restrictions, the Chinese bulbul (*Pycnonotus sinensis*) was able to lower its basal metabolic rate not only passively through body and organ mass reductions, but also by modifying enzymatic activity and metabolism in the muscles and liver. Other studies have also found that bird nestlings down-regulate energetic costs allocated to maintenance when exposed to food shortage (Brzék and Konarzewski, 2001; Moe et al., 2004), or to disturbances such as urban noise (Brischoux et al., 2017). Intraspecific variation in energetic expenditure could affect individual responses to land-use change, which in turn could affect species' ability to adapt to human pressures. However, the lack of spatially explicit estimates of metabolic rates precluded its consideration in this Chapter.

To conclude, the findings of this Chapter suggest important effects of land-use change on energetic fluxes, and thus potentially on ecosystem functioning. Further research is warranted as to the effects of these energetic patterns for ecosystem processes. Indeed, assemblage-level energy fluxes may serve as important indicators of change for ecosystem processes, such as decomposition (Barnes et al., 2014). Understanding these impacts is particularly important given increasing land-use change and biodiversity loss across the globe.

1602 **6 | General discussion**

1603 **Bibliography**

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# **Appendices**

# **Appendix 1: Supporting information for Chapter 2**

## **S2.1 Taxonomic corrections**

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

### **Automated procedure and outputs**

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

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

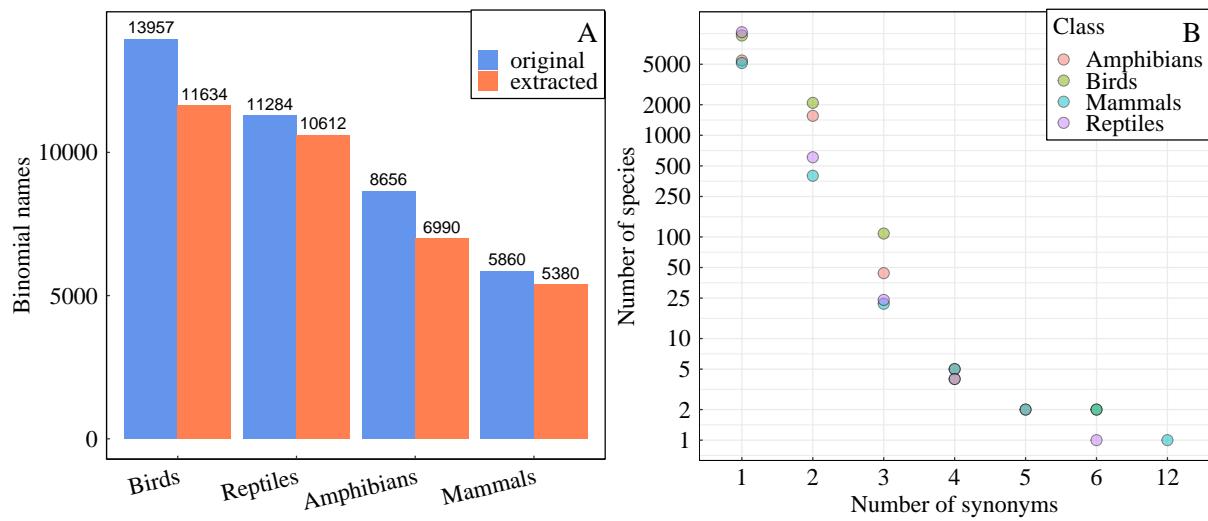
IUCN Red List or from the ITIS, using the ‘rredlist’ (Chamberlain, 2018) and ‘taxize’ (Chamberlain and Szöcs, 2013) R packages; and (2) identify the status of each name (accepted or not accepted). I started by generating a list of all names featuring in any of the sources. These ‘original’ names were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

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

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

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

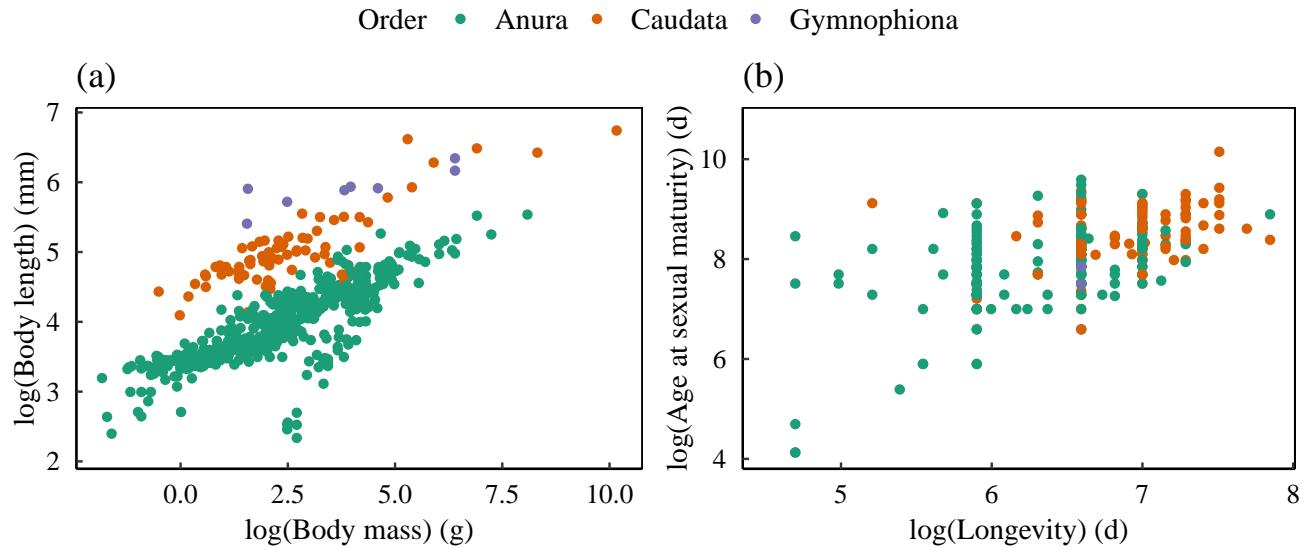
The automated procedure was not perfect, and taxonomic errors are likely to have persisted in the trait datasets. The IUCN Red List and the ITIS were not comprehensive taxonomic sources, and for clades with high degrees of synonymy in names, such as reptiles or amphibians, neither the IUCN Red List or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



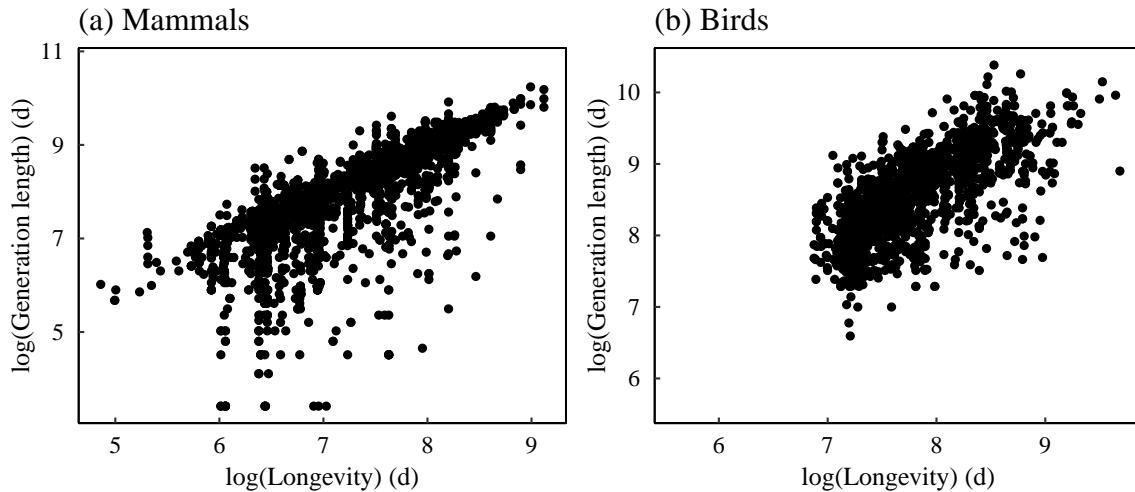
**Figure S2.1: Difference in species number before and after taxonomic correction (A) and distribution of number of synonyms across datasets (B).** (A) shows the number of species (binomial names) extracted from all sources (blue bars), and the number of uniquely identified accepted names (in red). Replacing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

## S2.2 Additional information for trait compilation

### Correlations among closely related traits

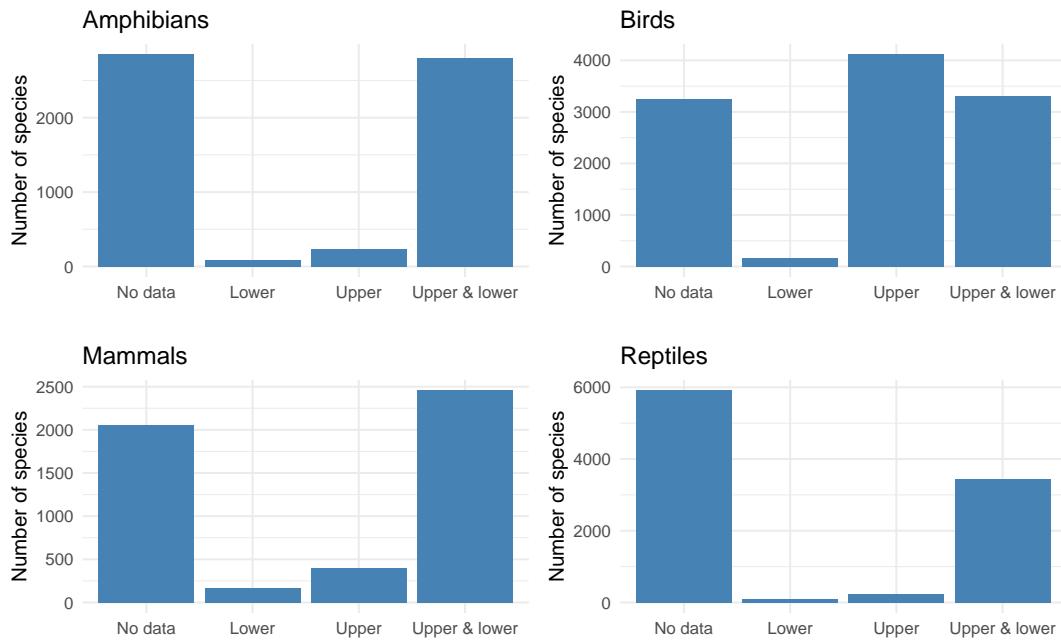


**Figure S2.2:** (a) Body mass versus body length and (b) longevity versus age at sexual maturity in amphibians. Pearson's correlation coefficient was 0.71 in (a) and 0.55 in (b) (taxonomic order was considered in these coefficients).

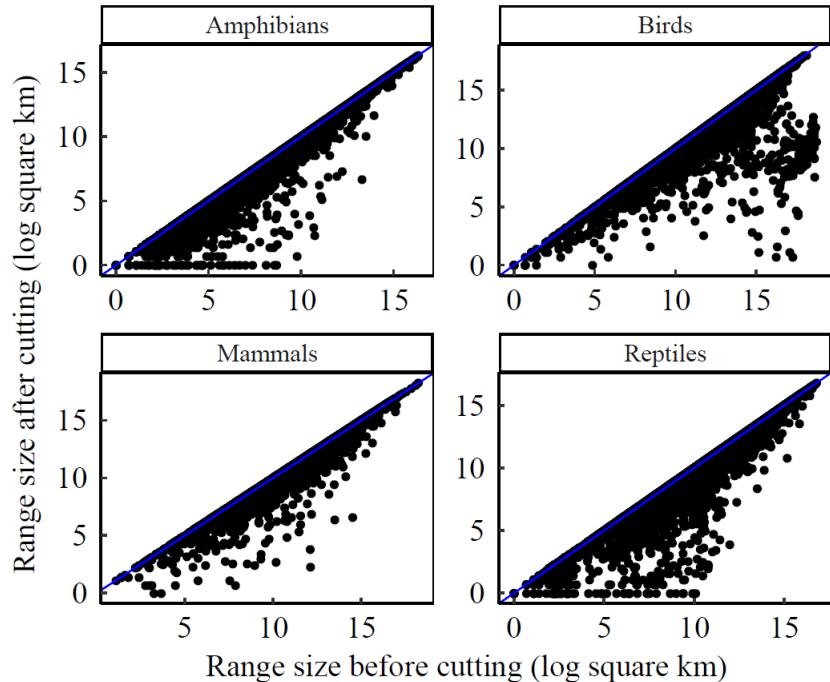


**Figure S2.3:** Generation length versus longevity data in (a) mammals and (b) birds. Pearson's correlation coefficient was 0.74 in (a) and 0.70 in (b).

### S2.3 Cutting distribution maps by altitudinal limits

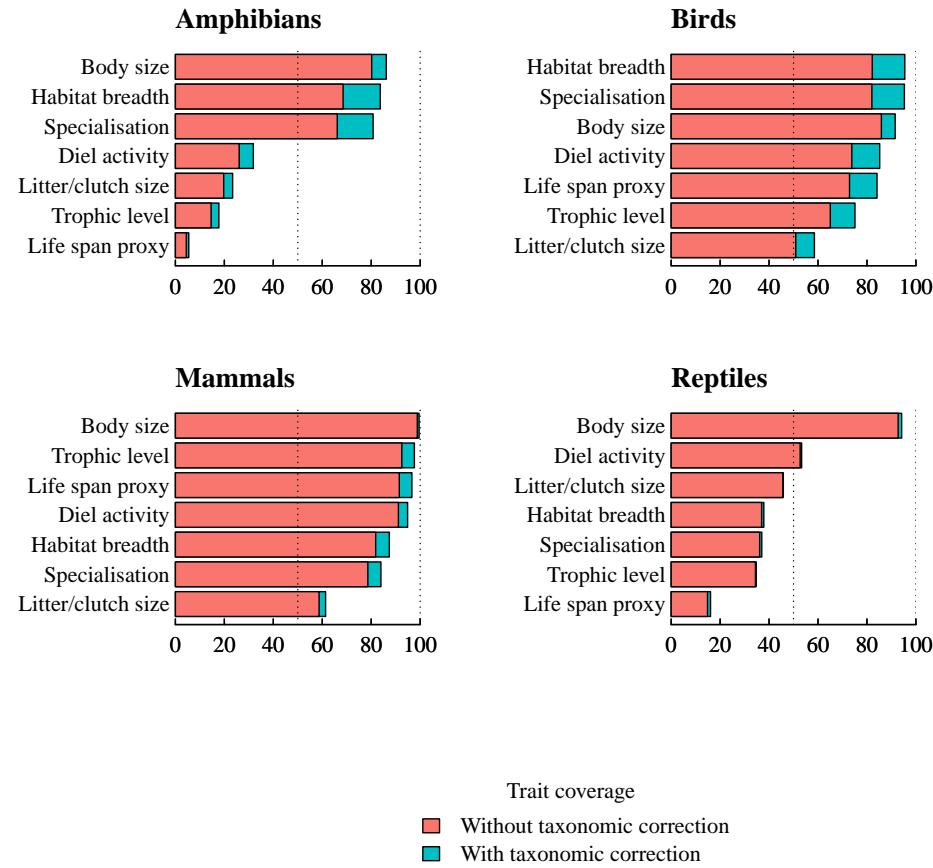


**Figure S2.4: Availability of altitudinal limits across species.** Upper and lower altitudinal limits were extracted from the IUCN Red List (IUCN, 2020).



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

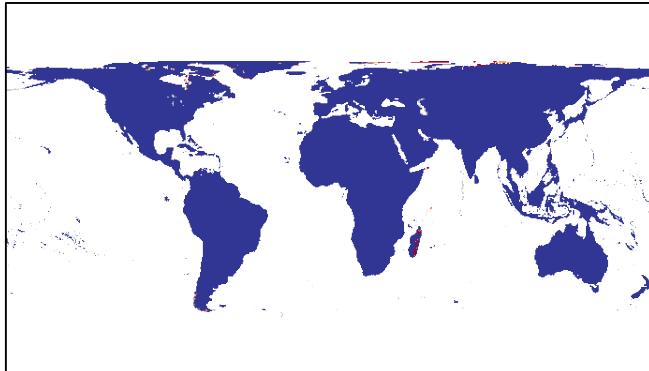
## S2.4 Impact of taxonomic corrections on trait coverage



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

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

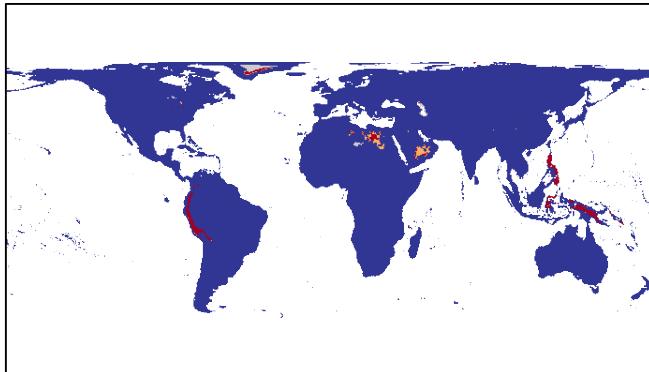
**(a) Mammals**



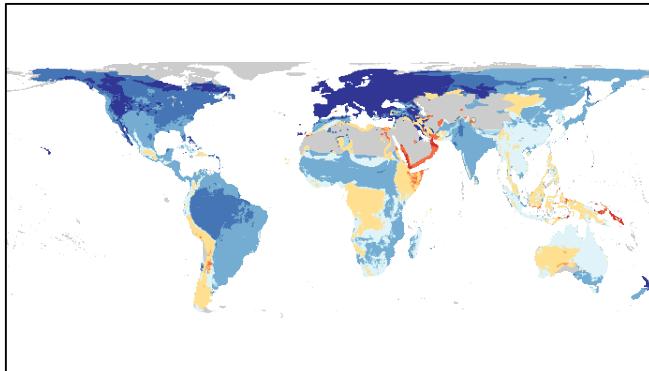
Median completeness  
(birds and mammals):

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

**(b) Birds**



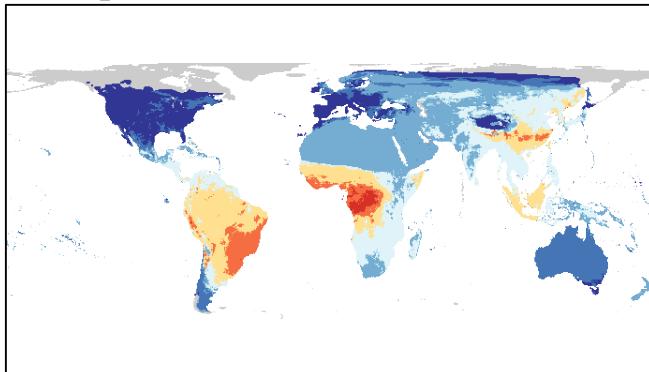
**(c) Amphibians**



Median completeness  
(herptiles):

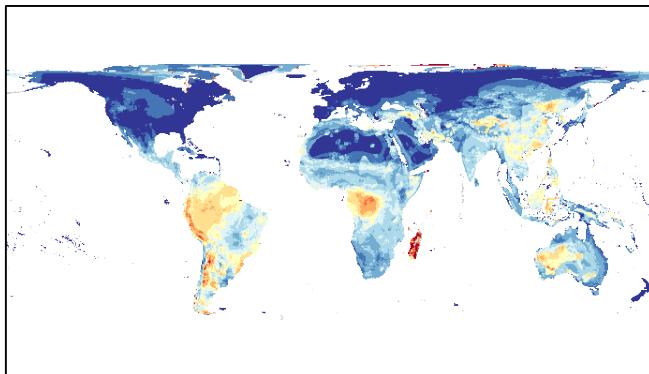
- NA
- 0 – 10%
- 10 – 20%
- 20 – 30%
- 30 – 40%
- 40 – 50%
- 50 – 60%
- 60 – 70%
- 70 – 80%
- 80 – 90%
- 90 – 100%

**(d) Reptiles**



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

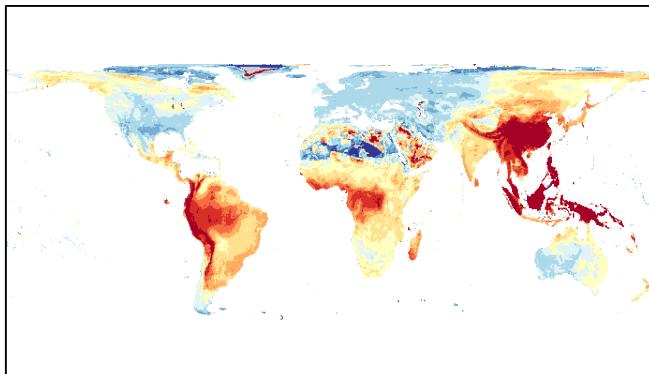
**(a) Mammals**



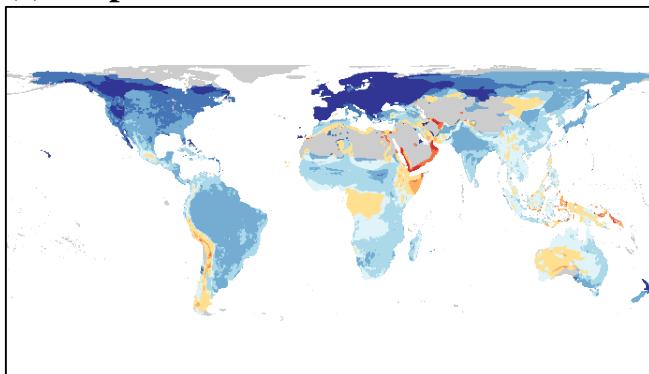
Mean completeness  
(birds and mammals):

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

**(b) Birds**



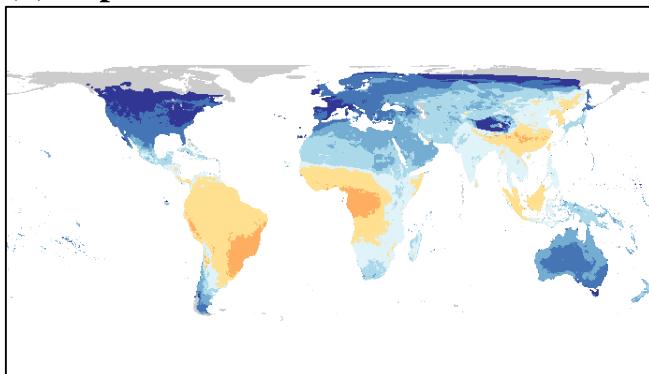
**(c) Amphibians**



Mean completeness  
(herptiles):

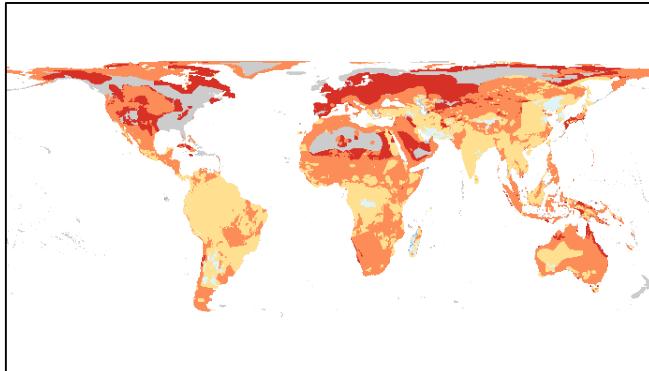
- NA
- 0 – 10%
- 10 – 20%
- 20 – 30%
- 30 – 40%
- 40 – 50%
- 50 – 60%
- 60 – 70%
- 70 – 80%
- 80 – 90%
- 90 – 100%

**(d) Reptiles**



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

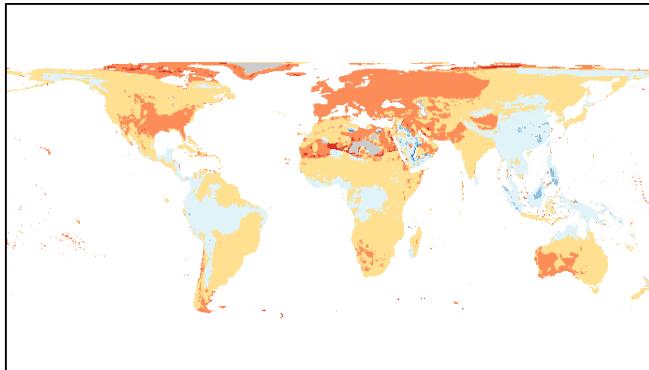
**(a) Mammals**



Standard deviation  
of completeness  
(birds and mammals):

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

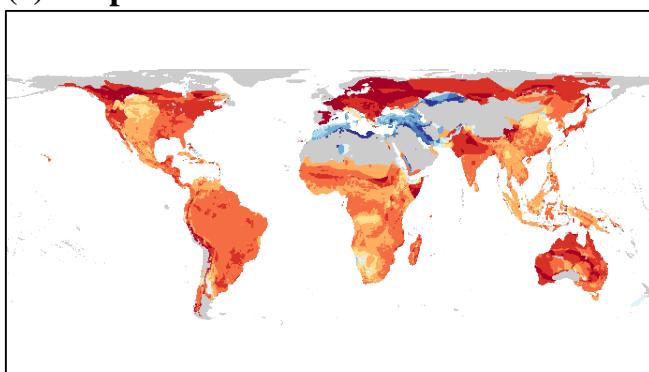
**(b) Birds**



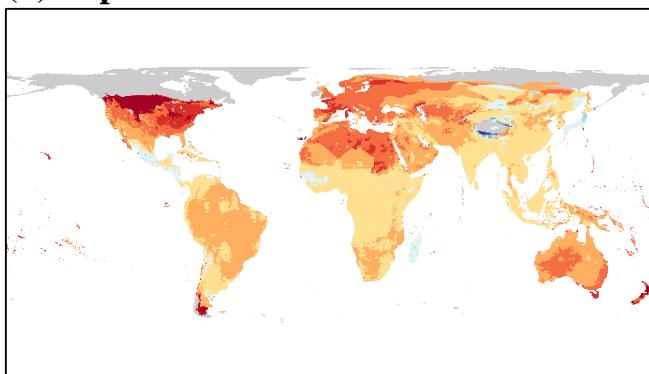
Standard deviation  
of completeness  
(herptiles):

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

**(c) Amphibians**



**(d) Reptiles**



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

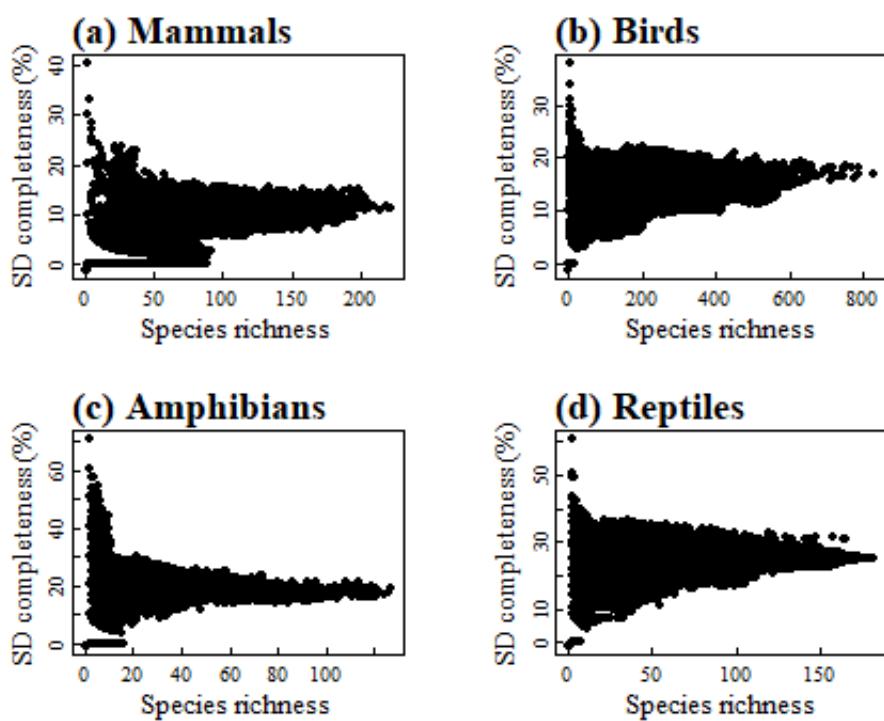
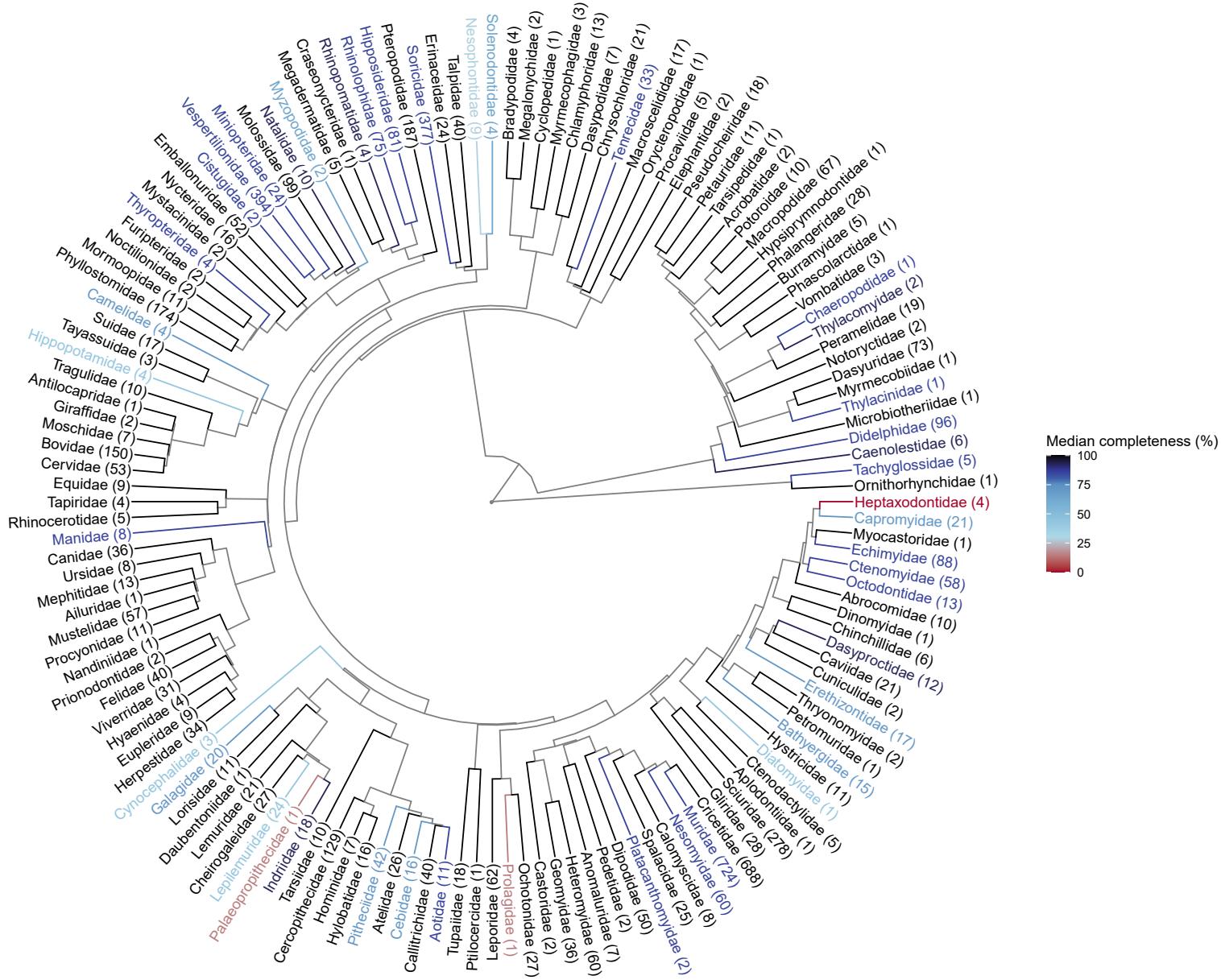
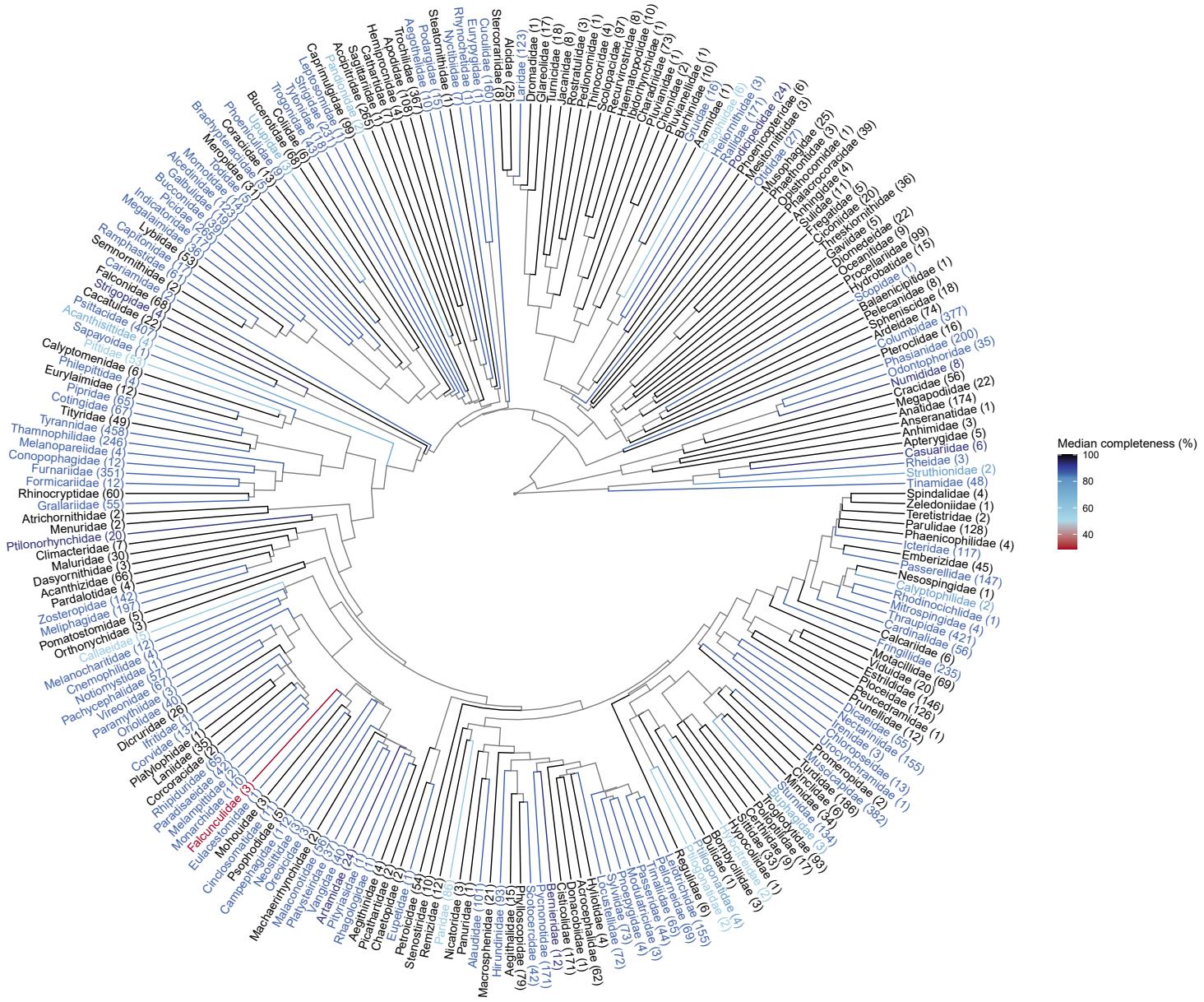


Figure S2.10: Assemblage-level species richness against standard deviation in trait completeness in each class.

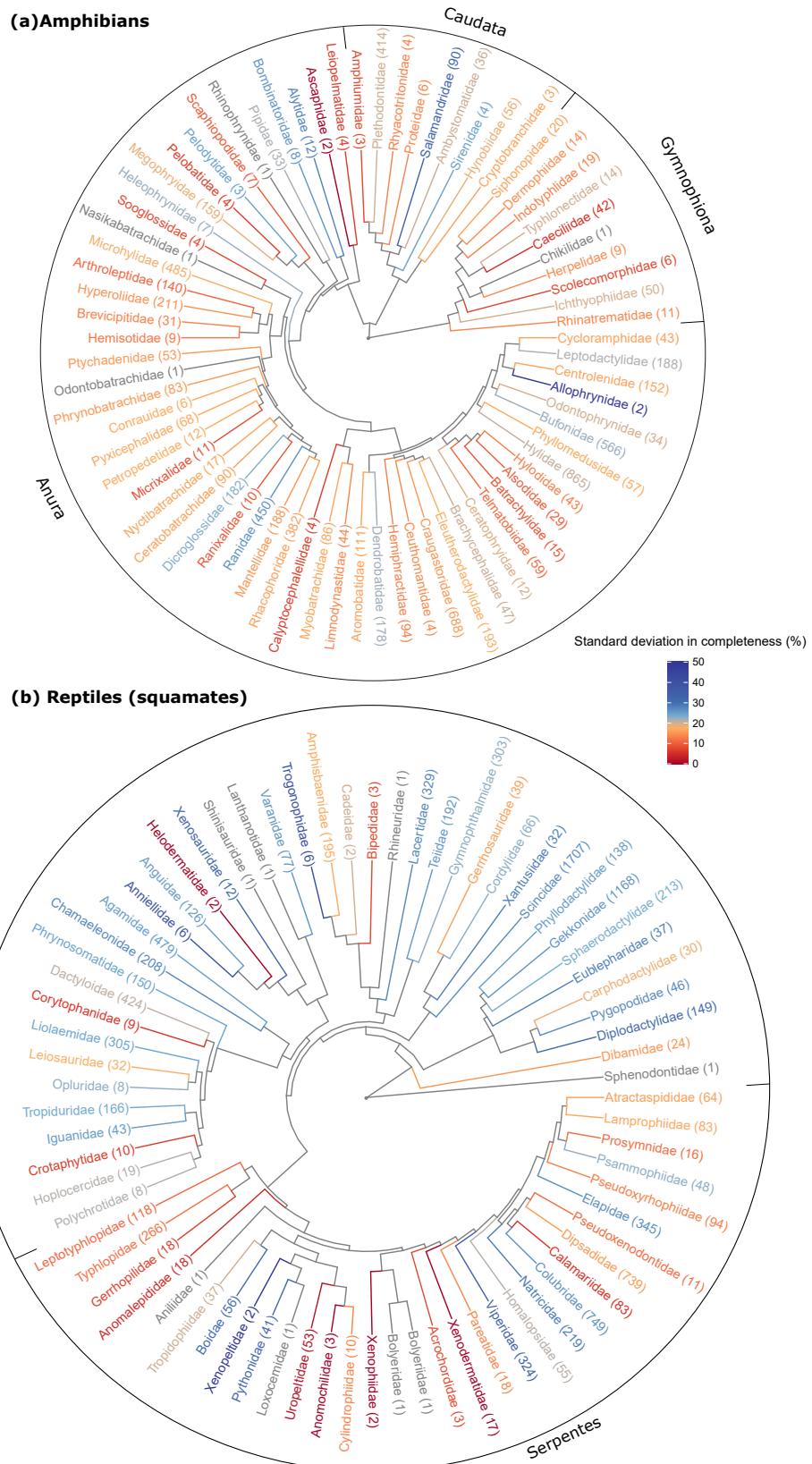
## **S2.6 Phylogenetic patterns in trait completeness**



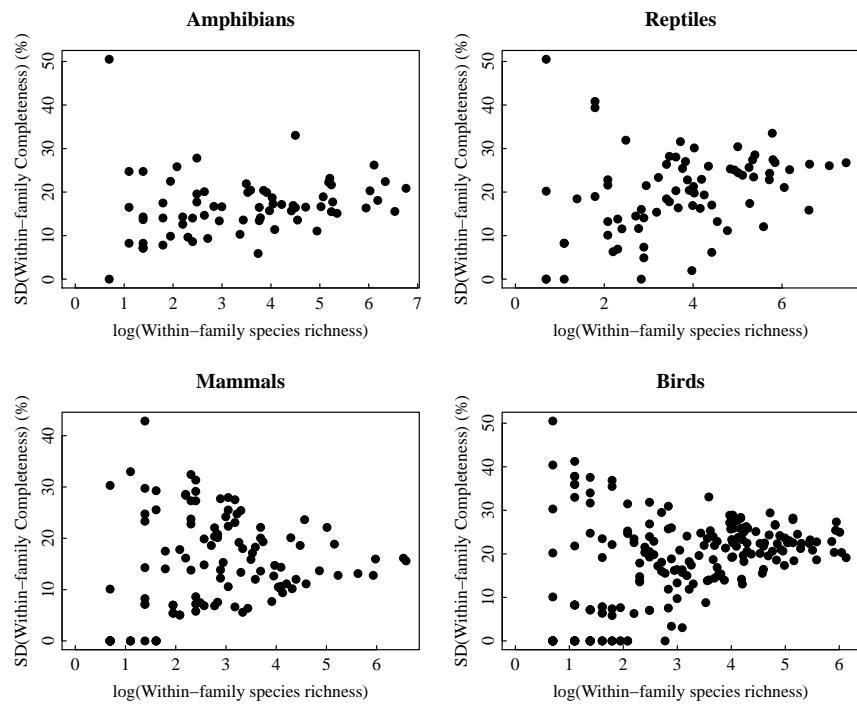
**Figure S2.11: Within-family median trait completeness in mammals.**



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



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



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

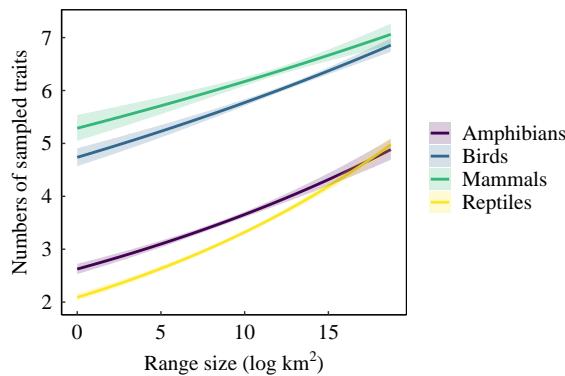
## S2.7 Poisson model summaries

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

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

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

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



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

## S2.8 Spatial model summaries

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

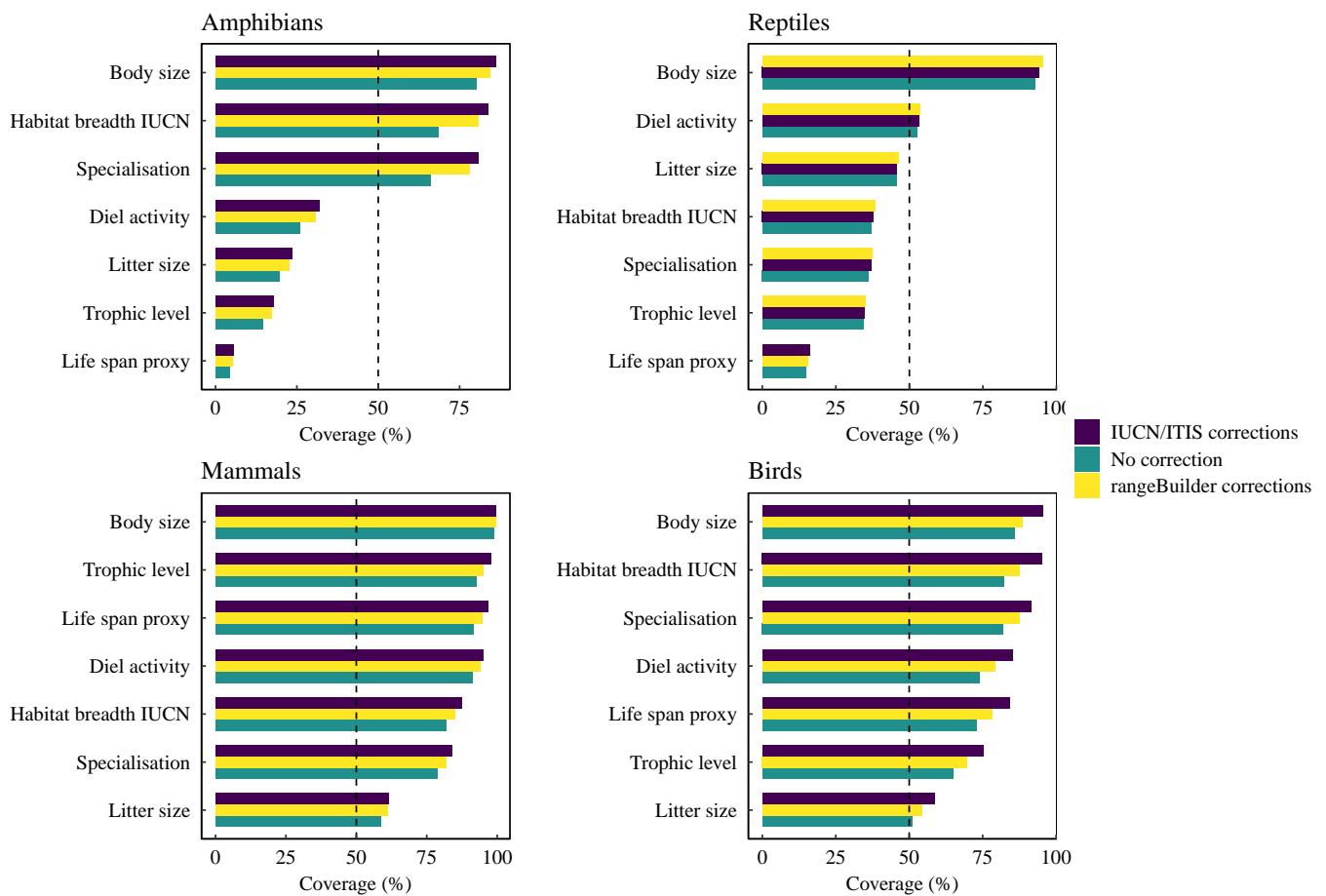
|                                   | Estimate | Std. Error | z value | Pr(> z ) |
|-----------------------------------|----------|------------|---------|----------|
| Intercept - Realm: Afrotropic     | 0.0738   | 0.0064     | 11.4908 | 0        |
| log(Species richness)             | -0.0025  | 0.0017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

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

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

## S2.9 Trait coverage and taxonomic matching

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



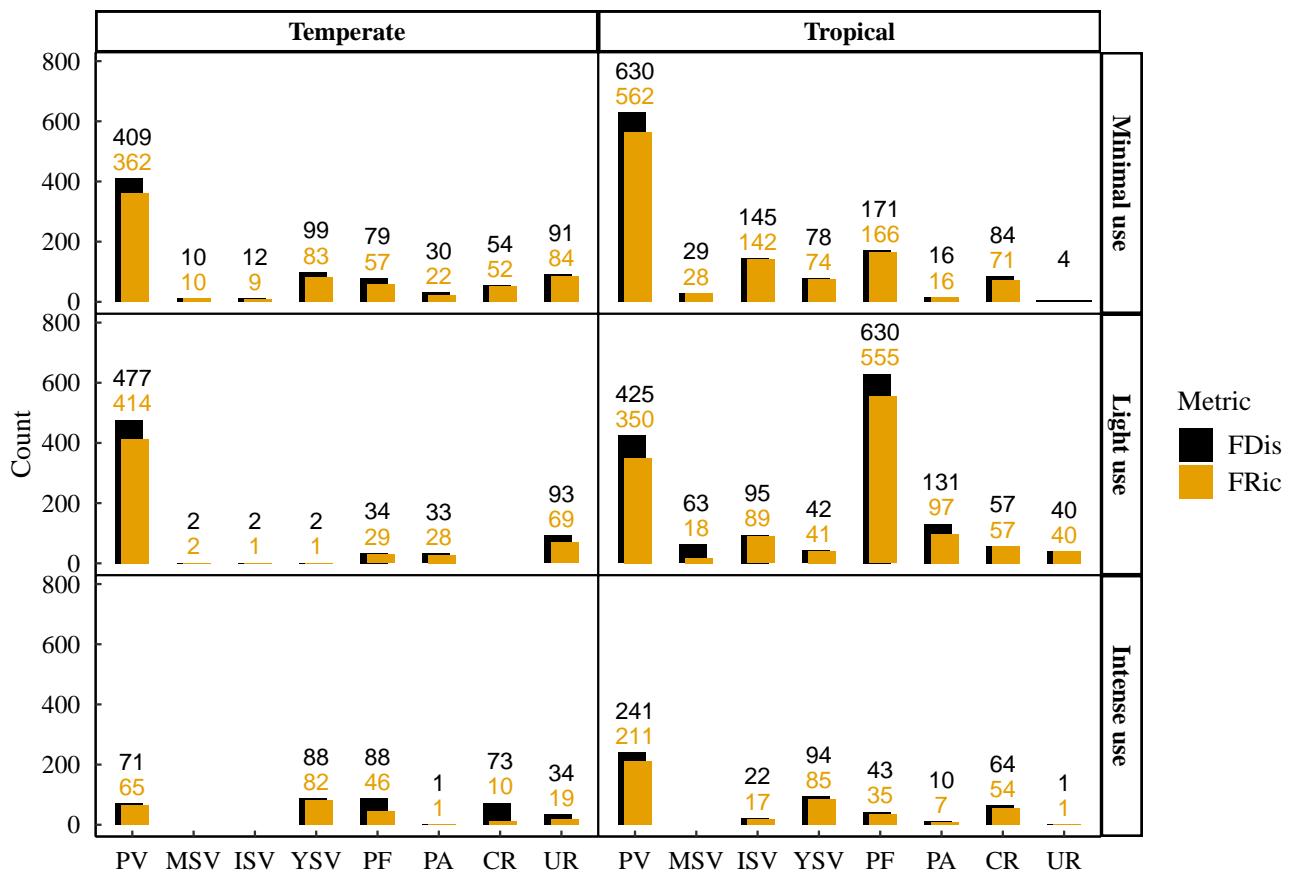
**Figure S2.16: Comparison of trait coverage among datasets corrected for taxonomy in different ways:** using the described procedure (purple bars); using datasets corrected for taxonomy with the ‘rangeBuilder’ package (yellow bars; Rabosky et al. (2016)); and using datasets uncorrected for taxonomy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

# Appendix 2: Supporting information for Chapter 3

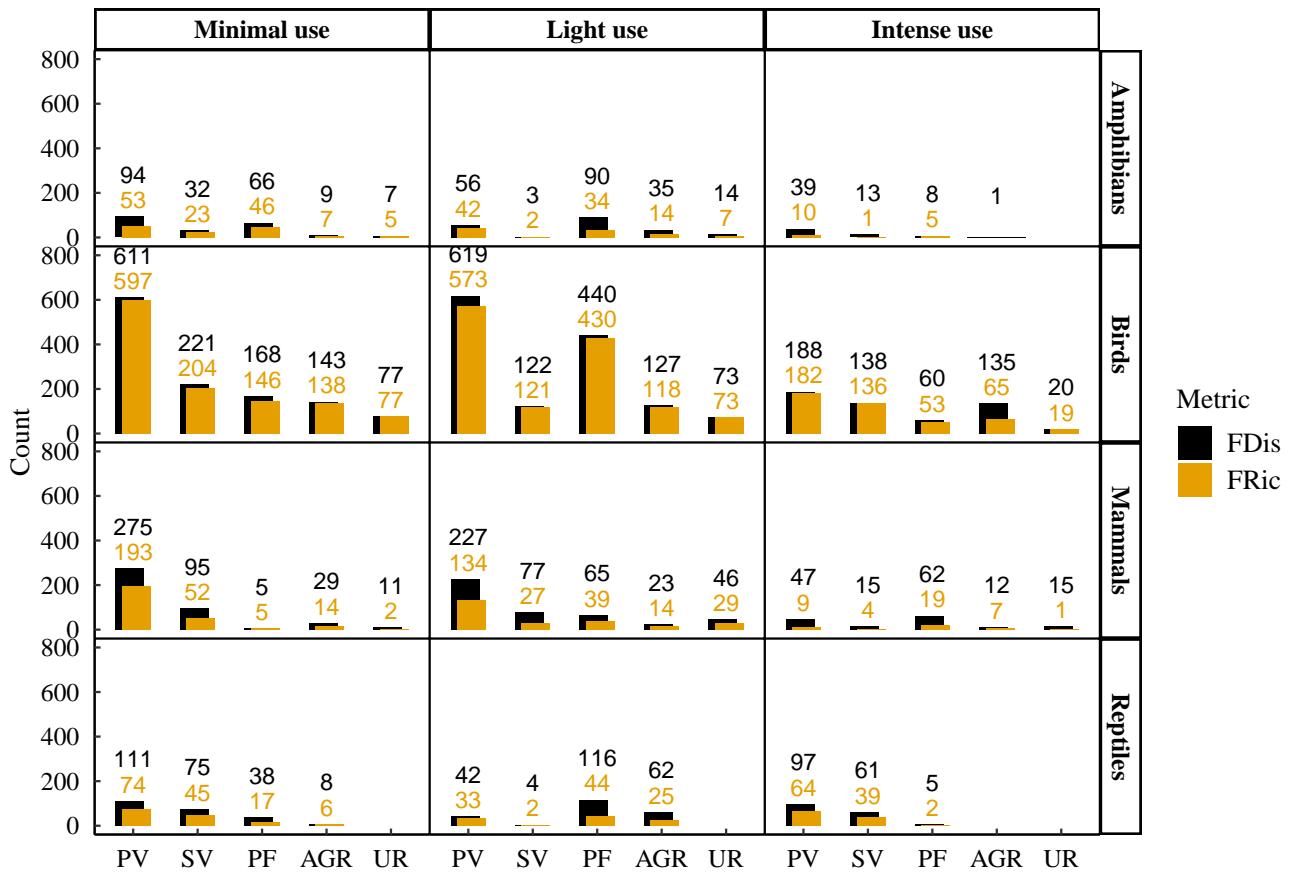
## S3.1 Land-use categories in PREDICTS and sample sizes

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

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



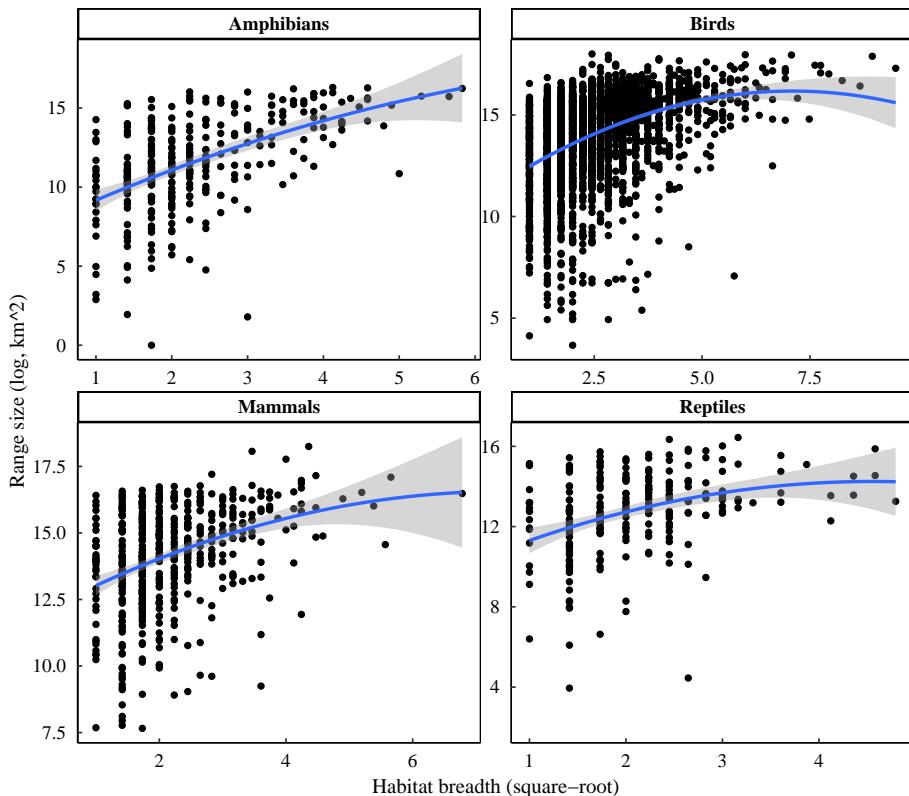
**Figure S3.1: Number of sites in each land use and land-use intensity for which FRic and FDis were calculated, across all species.** The number of sites for FRic can be smaller than the number of sites for FDis because FRic could not necessarily be computed for all assemblages in which FDis was estimated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



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

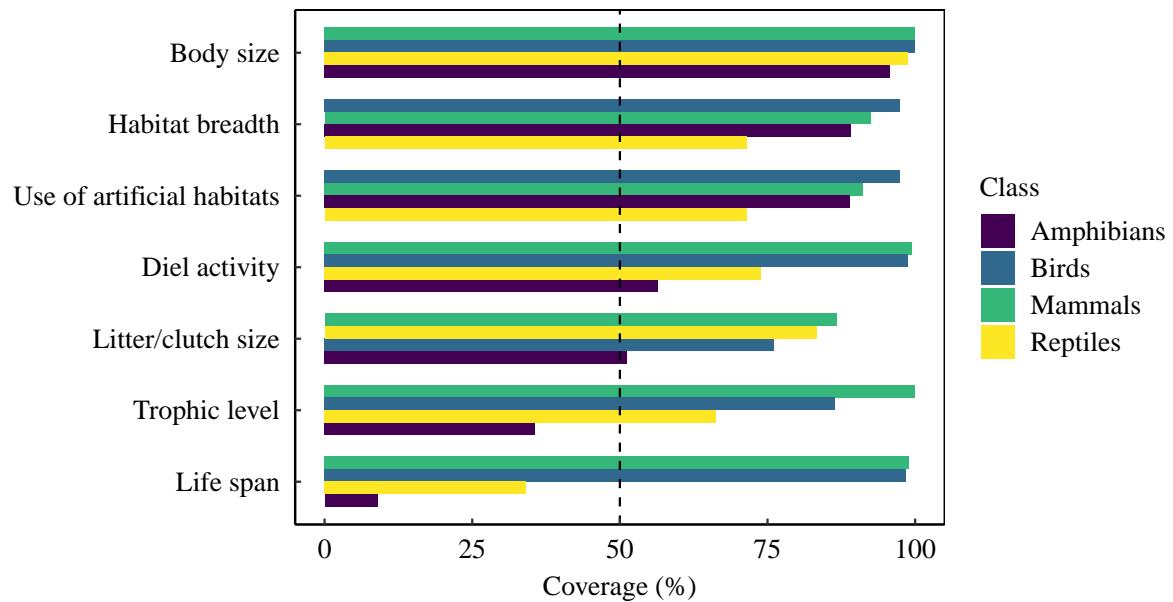
## S3.2 Trait data & imputation of missing trait values

I used the compilation of trait data across terrestrial vertebrates from Chapter 2 (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).

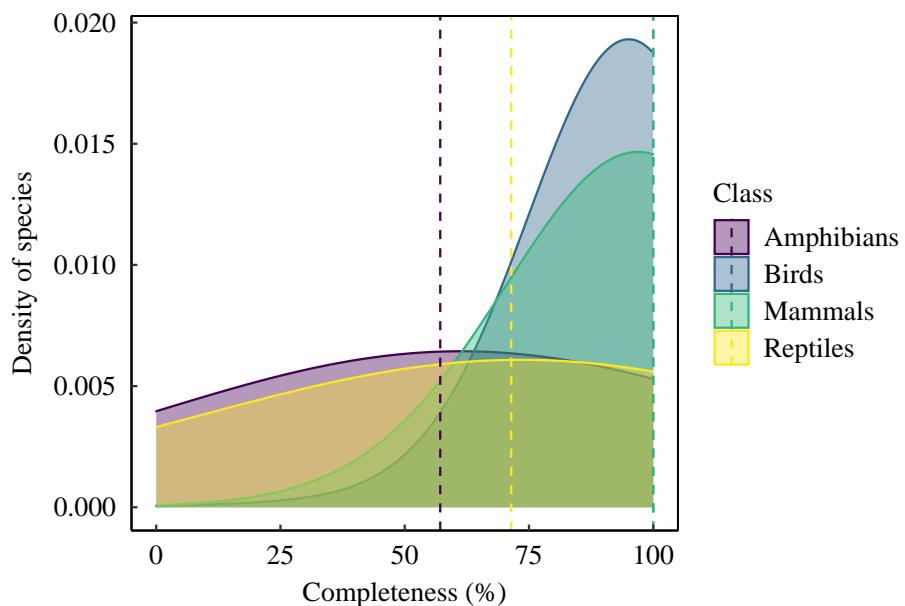


**Figure S3.3: Relationship between habitat breadth and geographical range size across species in each class.** The derivation of geographical range sizes is described in Chapter 2.

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  $\lambda$  (Pagel, 1999), and for categorical traits I used Borges’  $\delta$  (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  $\lambda$  to improve normality. Pagel’s  $\lambda$  was estimated using the ‘phylosig’ function of the ‘phytools’ package (Revell, 2012), and Borges’  $\delta$  was assessed using code provided by Borges et al. (2018), available at : [https://github.com/mrborges23/delta\\_statistic](https://github.com/mrborges23/delta_statistic). To test for the significance of  $\delta$ , I generated null distributions of  $\delta$  for each categorical trait by randomising trait vectors 50 times, and calculating  $\delta$  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  $\lambda$  – 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  $\lambda$ ; and a significant difference from the simulated null distribution of  $\delta$  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 $\lambda$ |       |       |       |       |       |       |       | Borges' $\delta$ |       |      |
|-------------------|-------------------|-------|-------|-------|-------|-------|-------|-------|------------------|-------|------|
|                   | BM                | BL    | GL    | MA    | ML    | L     | LCS   | HB    | TL               | DA    | UA   |
| <b>Amphibians</b> | 0.98*             | 0.94* | NA    | 0.85* | 0.82* | NA    | 0.93* | 0.99* | 18*              | 3.4*  | 4.5* |
| <b>Birds</b>      | 0.99*             | NA    | 0.97* | NA    | NA    | NA    | 0.95* | 0.60* | 13*              | 32e3* | 1.8* |
| <b>Mammals</b>    | 0.99*             | NA    | 0.97  | NA    | NA    | NA    | 0.99  | 0.71  | 26*              | 17*   | 1.3* |
| <b>Reptiles</b>   | 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.

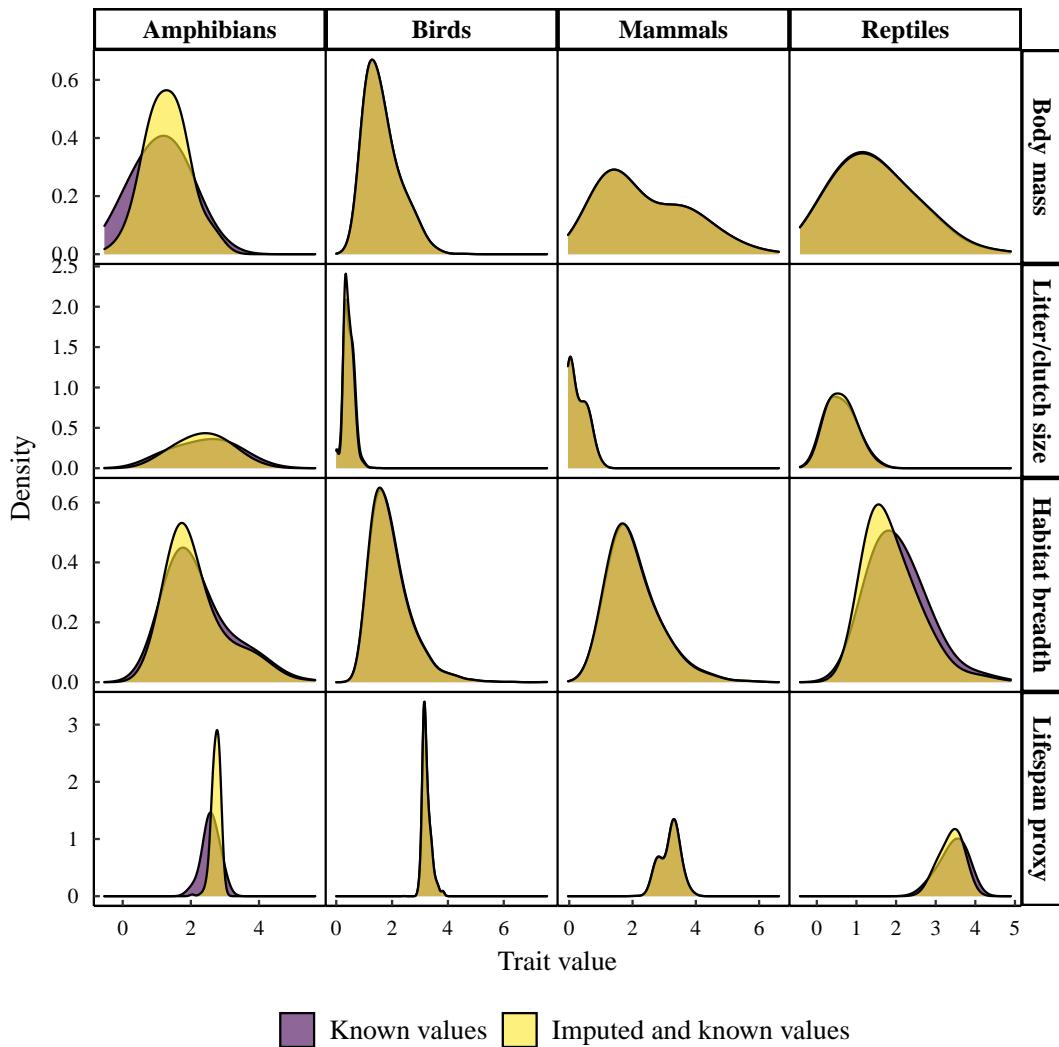
### S3.3 Degree of multicollinearity among traits

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.

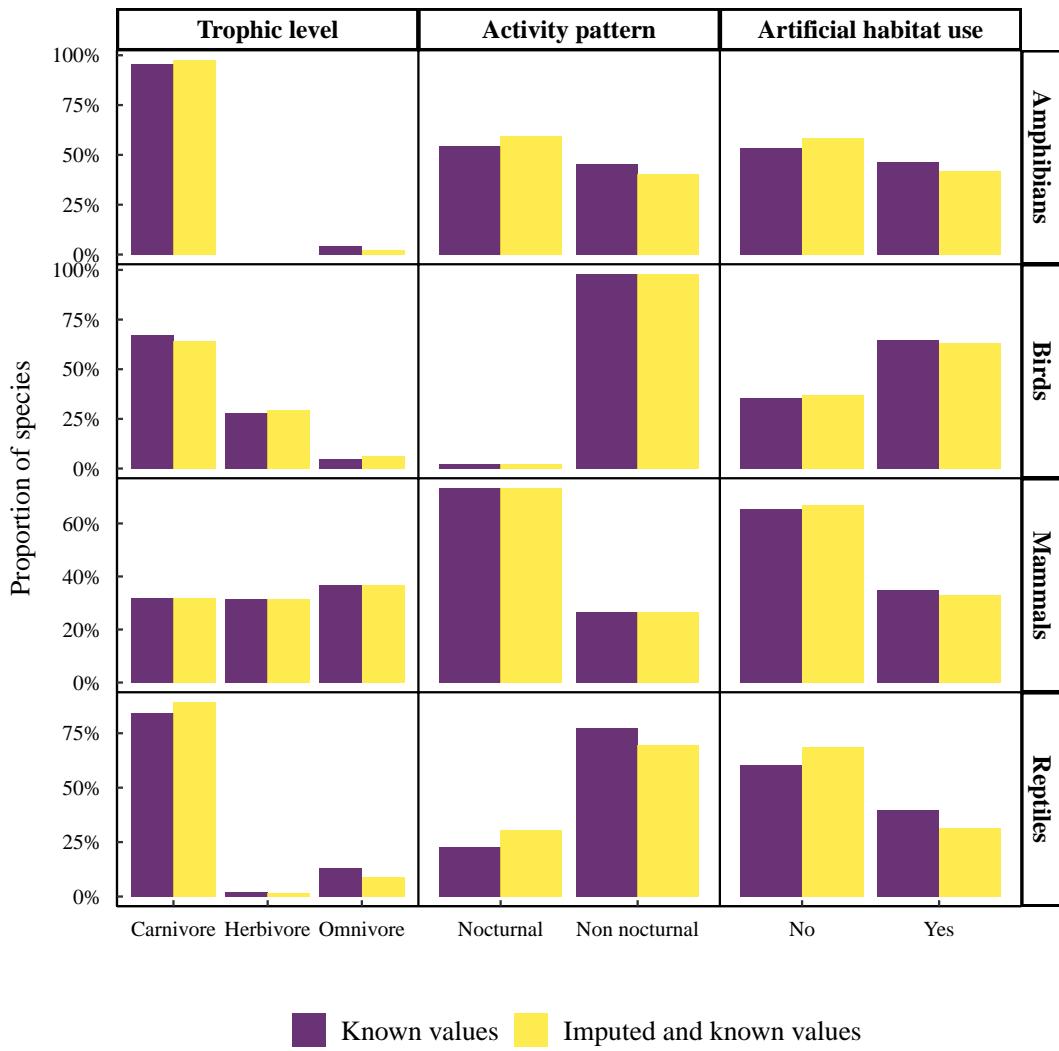
**Table S3.3: Variance inflation factors across considered (imputed) traits.**

| 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  |

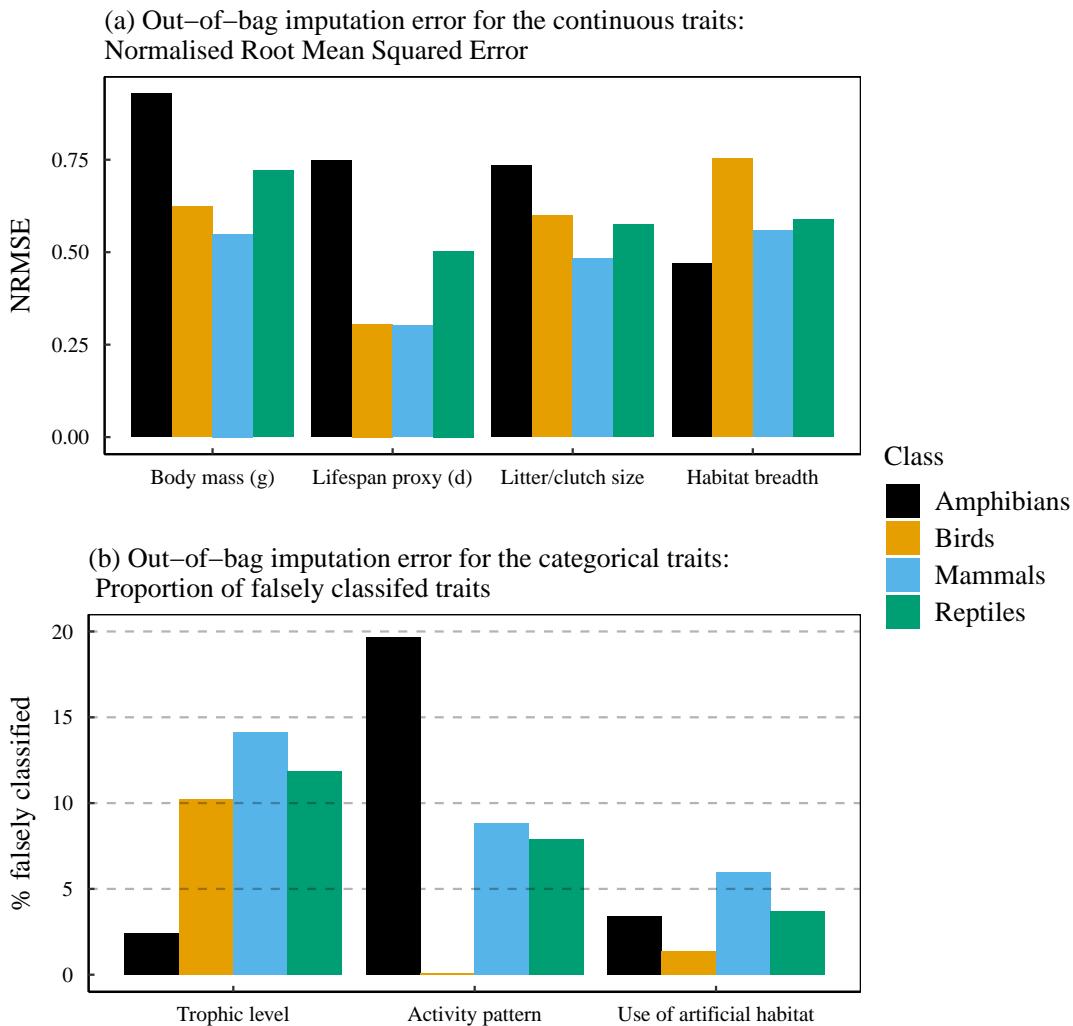
## S3.4 Imputation performance



**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 log<sub>10</sub>-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.

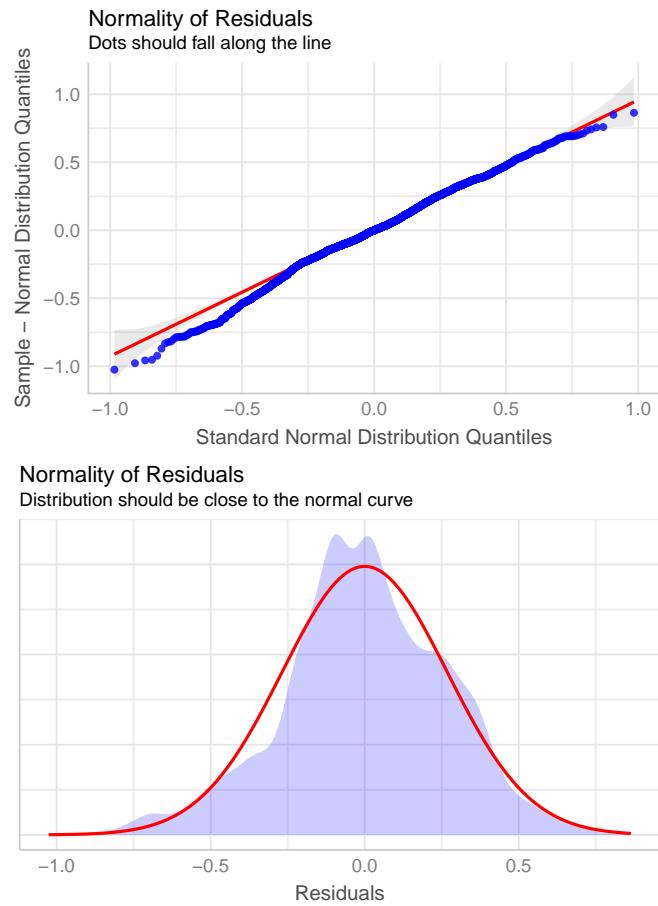
**Table S3.4: Sample sizes (number of pairs of sites) for the calculation of functional loss and functional gain across all species.**

| 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 | –           | –         | –           |

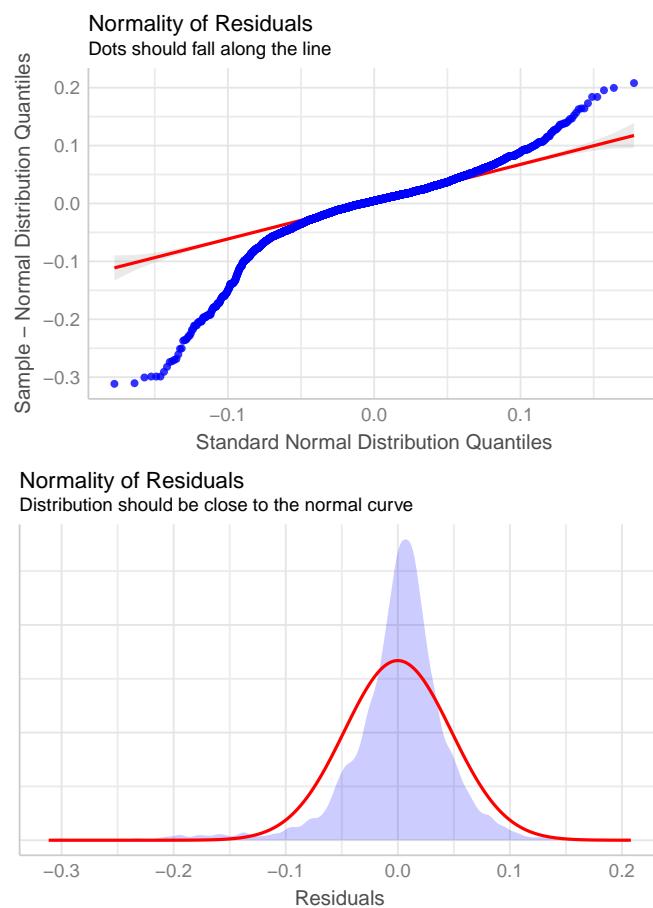
**Table S3.5: Sample sizes (number of pairs of sites) for the calculation of functional loss and functional gain within each class.**

| 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       | –           |

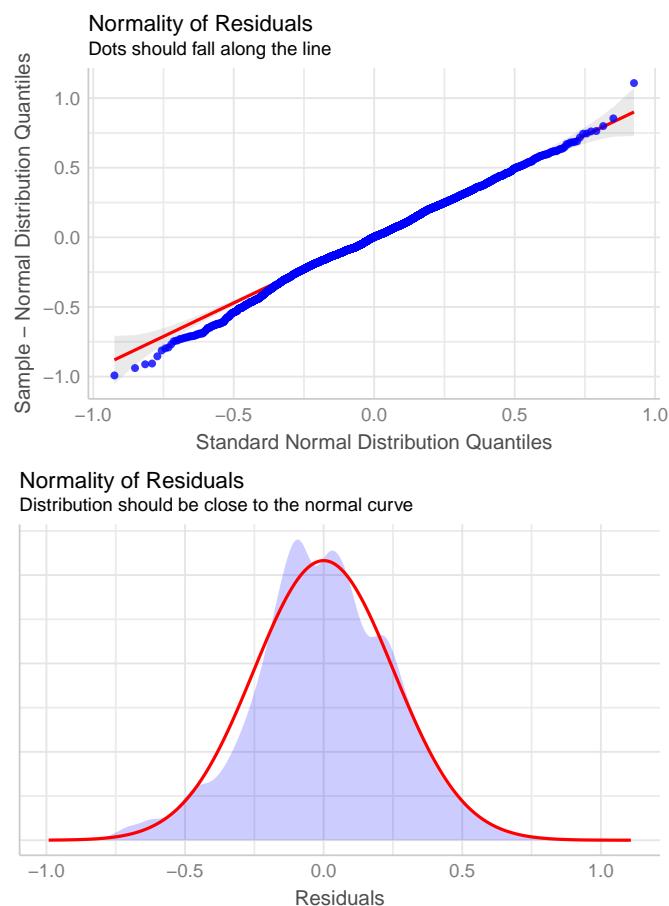
## S3.6 Diagnostic plots



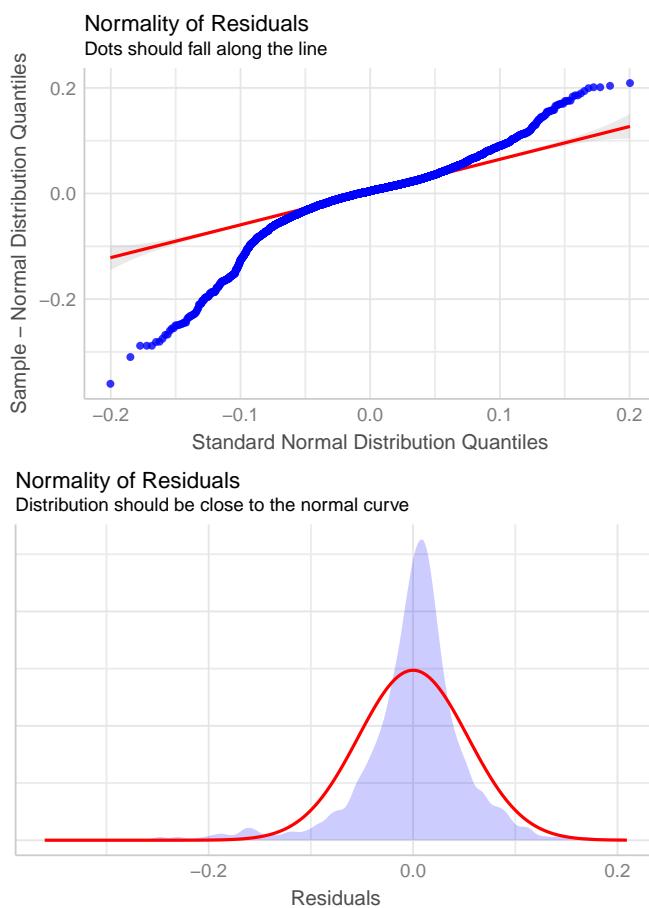
**Figure S3.9:** Diagnostic plots for Model 1a, obtained using the 'performance' R package (Lüdecke et al., 2021).



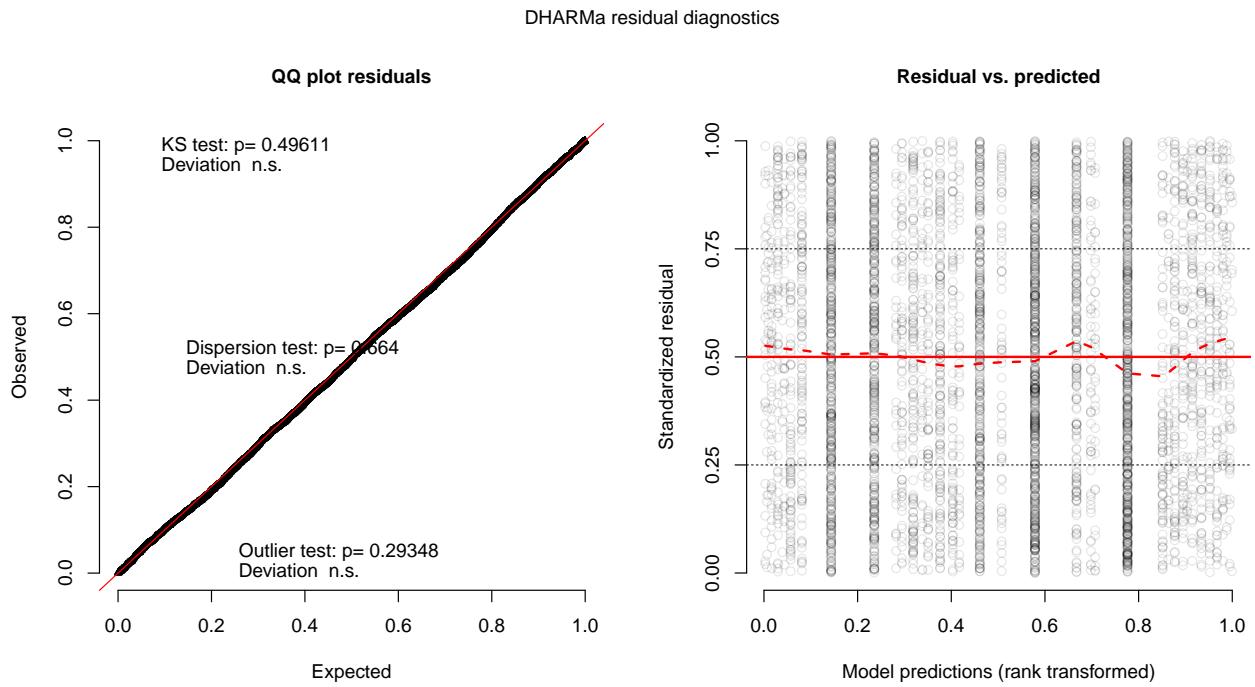
**Figure S3.10:** Diagnostic plots for **Model 1b**, obtained using the ‘performance’ R package (Lüdecke et al., 2021).



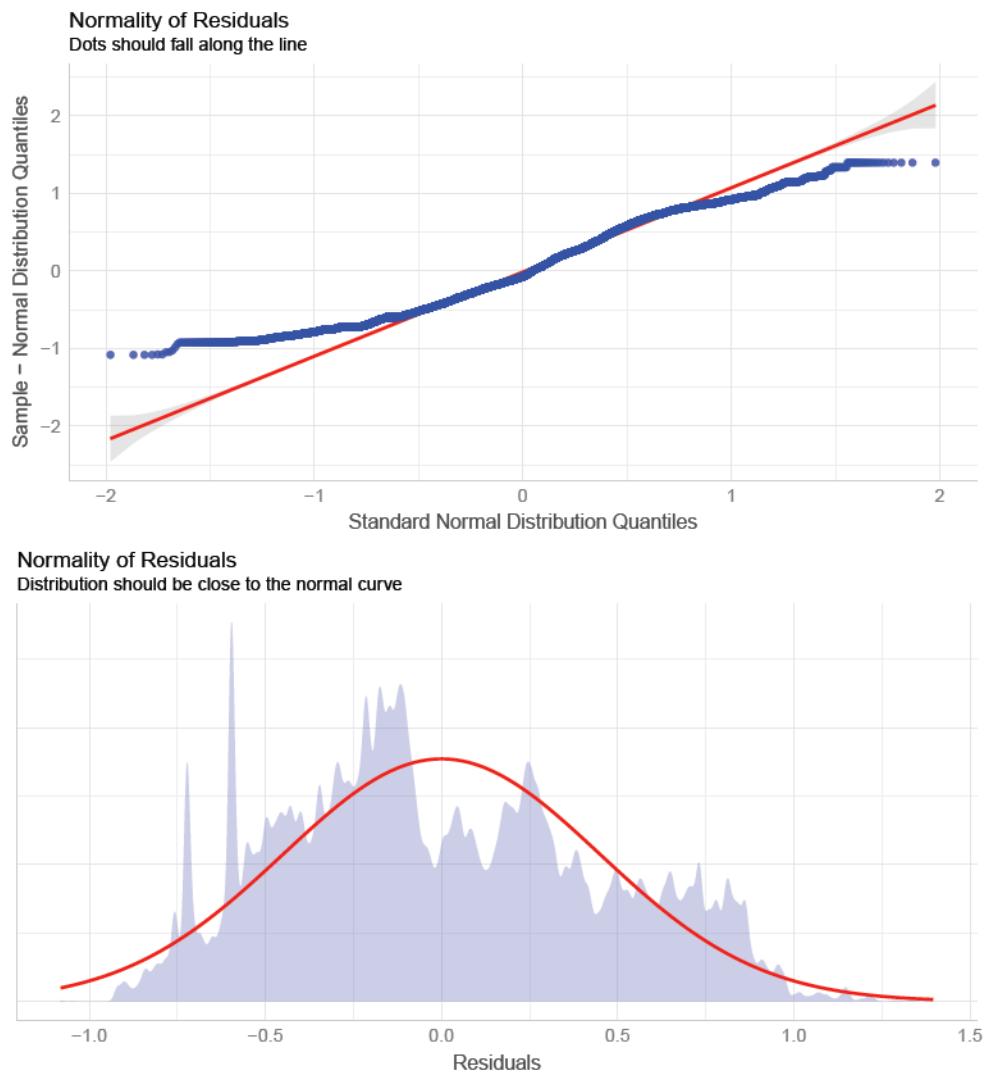
**Figure S3.11:** Diagnostic plots for Model 2a, obtained using the ‘performance’ R package (Lüdecke et al., 2021).



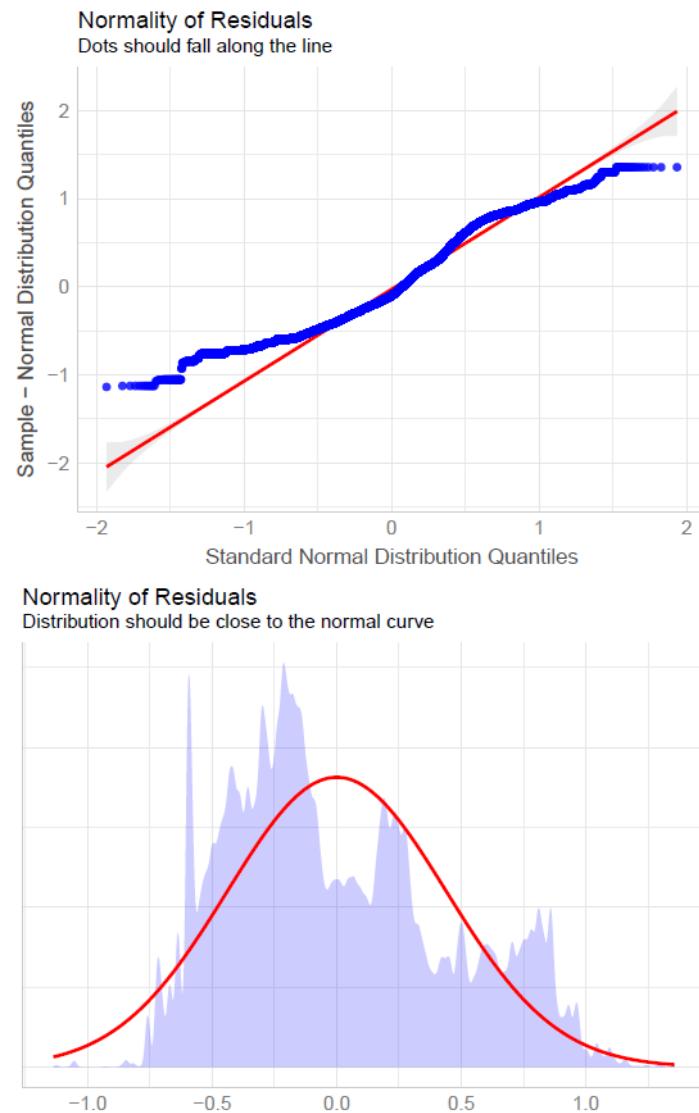
**Figure S3.12:** Diagnostic plots for Model 2b, obtained using the ‘performance’ R package (Lüdecke et al., 2021).



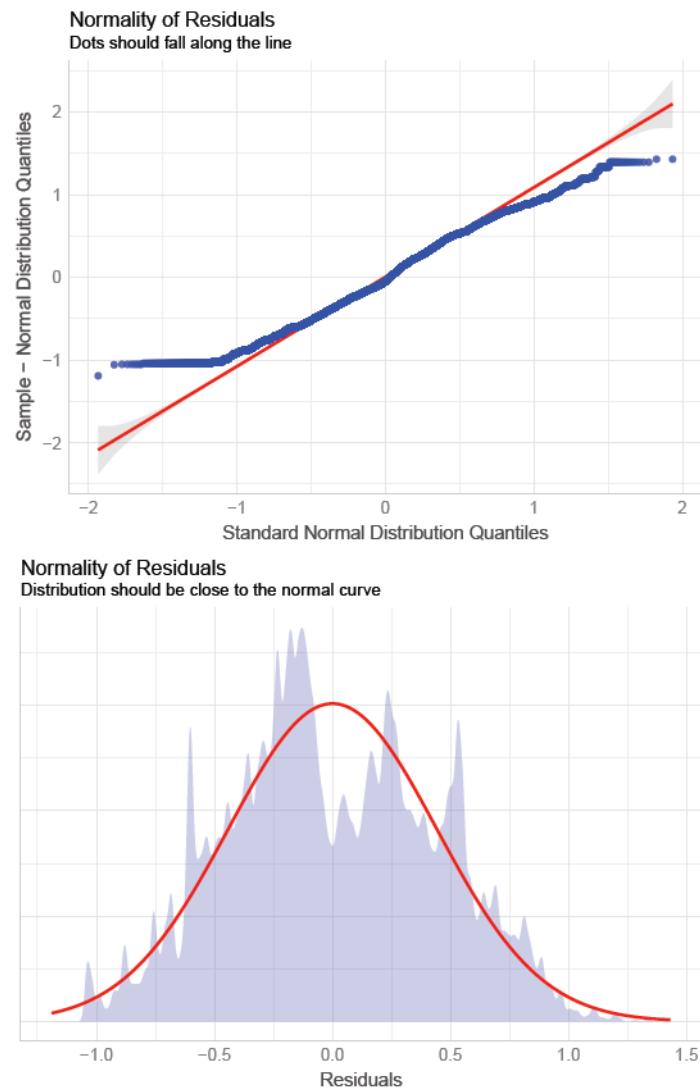
**Figure S3.13: Diagnostic plots for Model 3**, obtained using the ‘DHARMA’ R package (Hartig, 2021).



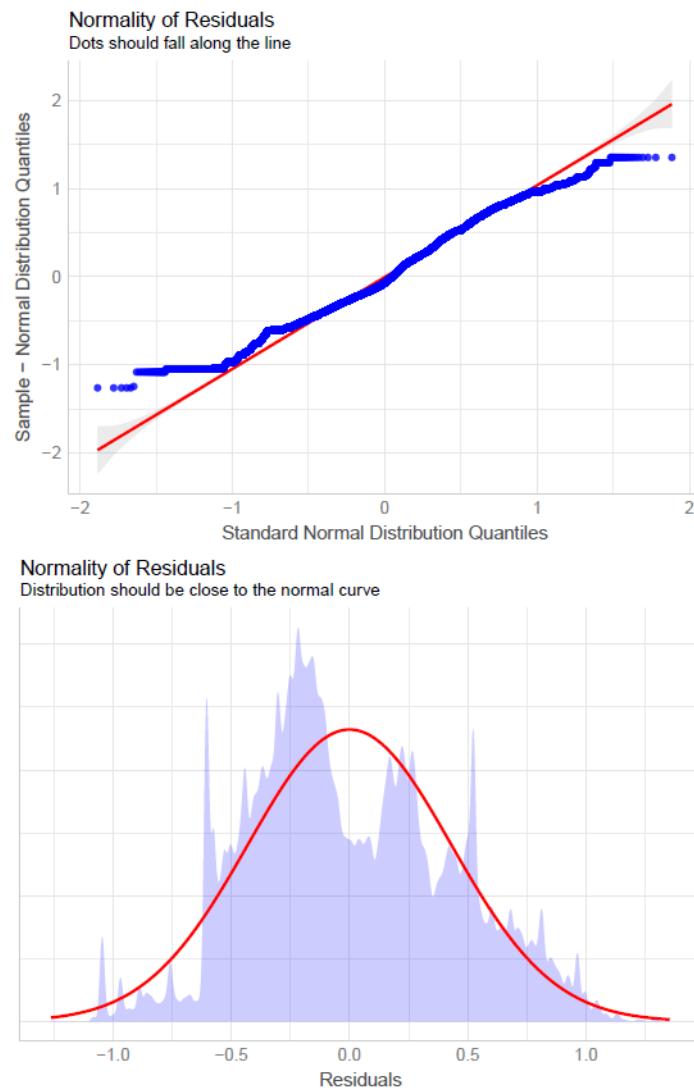
**Figure S3.14:** Diagnostic plots for Model 4a, obtained using the ‘performance’ R package (Lüdecke et al., 2021).



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

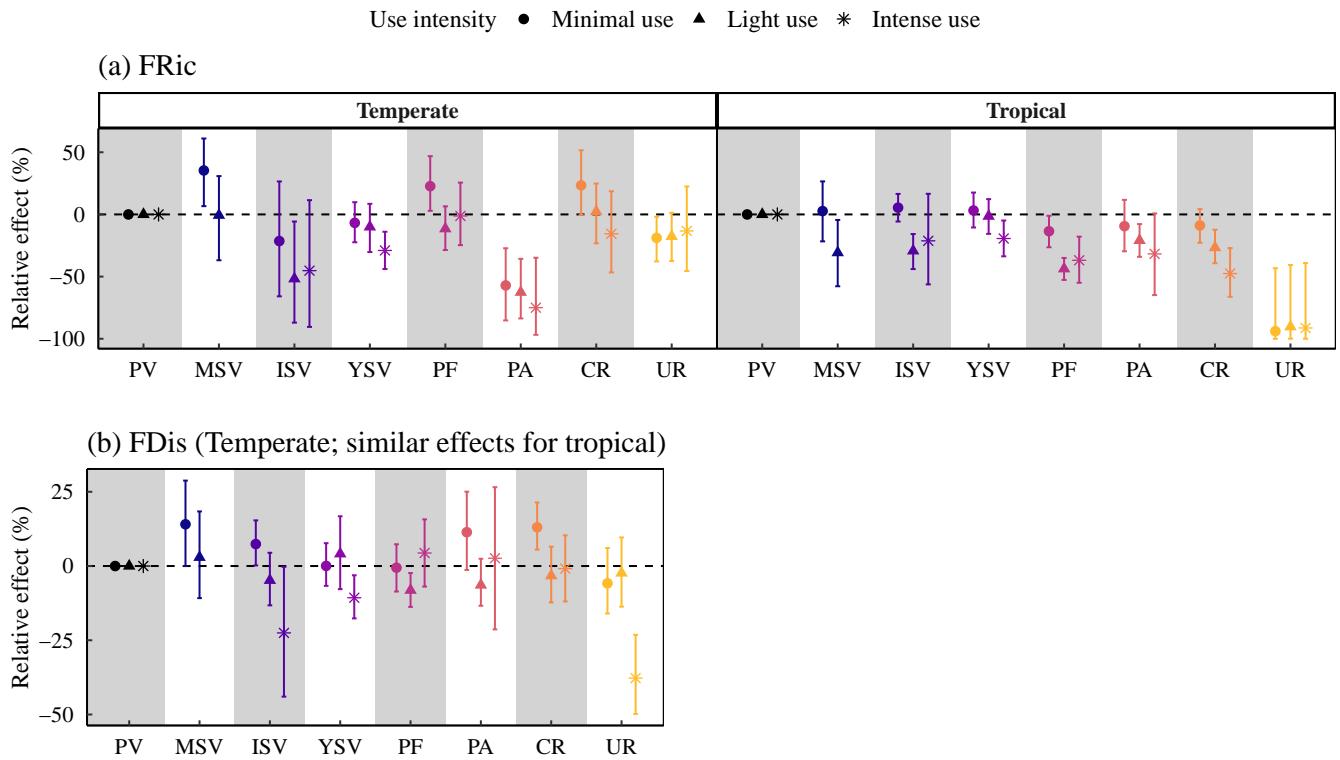


**Figure S3.16:** Diagnostic plots for Model 5a, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

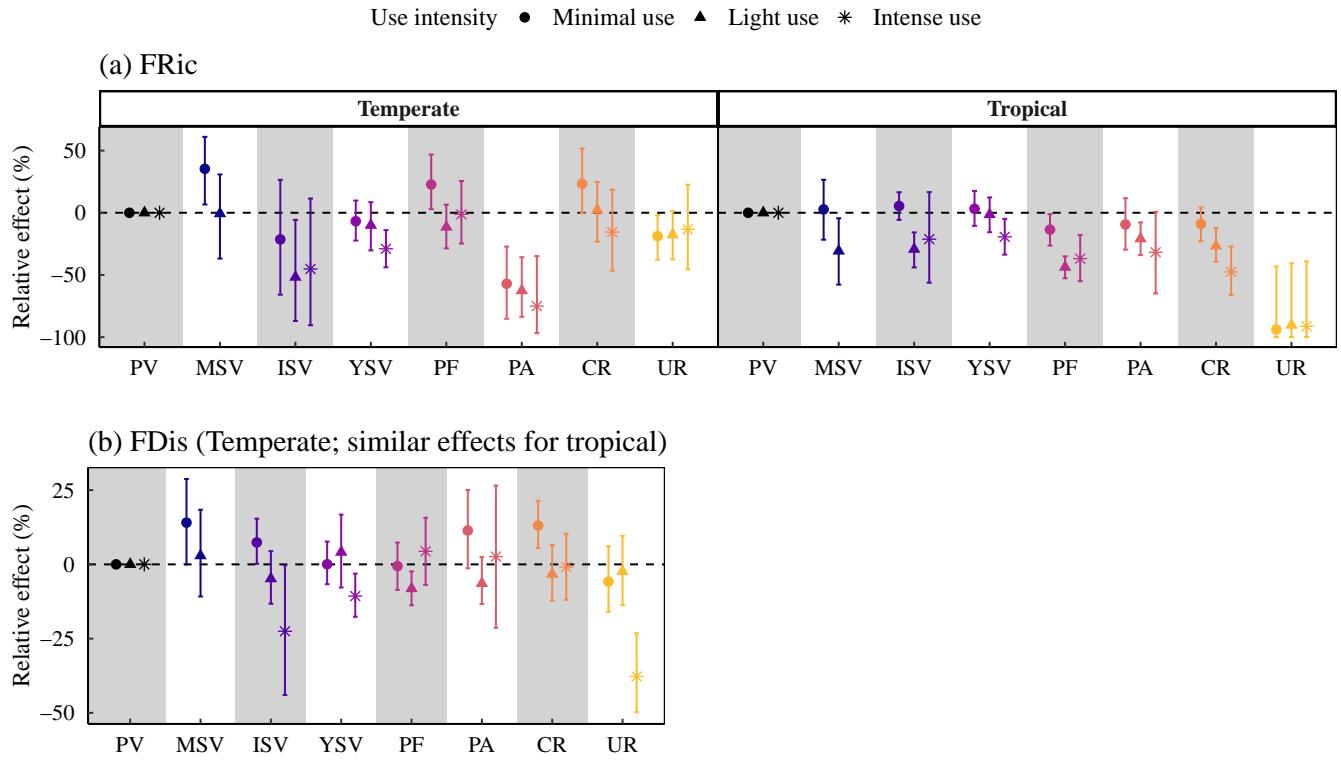


**Figure S3.17: Diagnostic plots for Model 5b**, obtained using the ‘performance’ R package (Lüdecke et al., 2021).

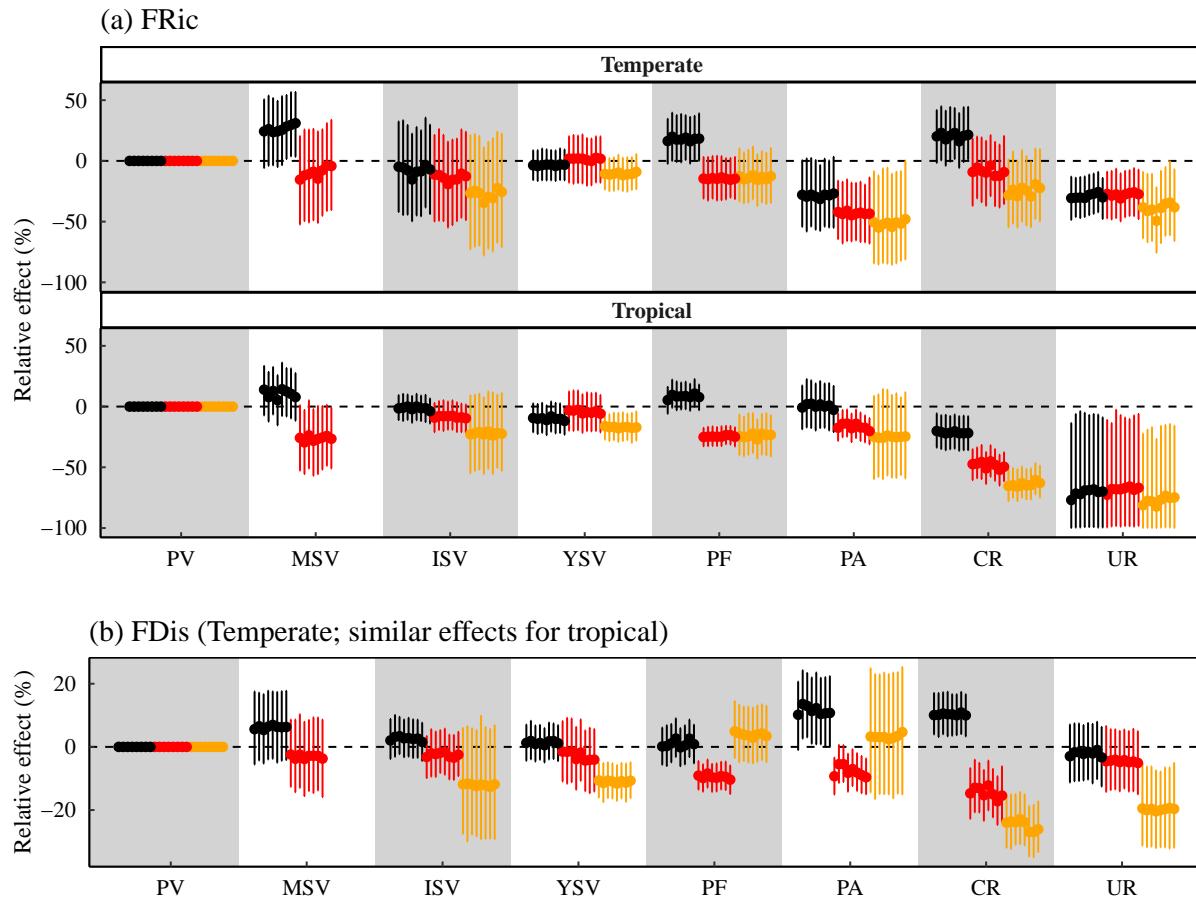
### S3.7 Model robustness



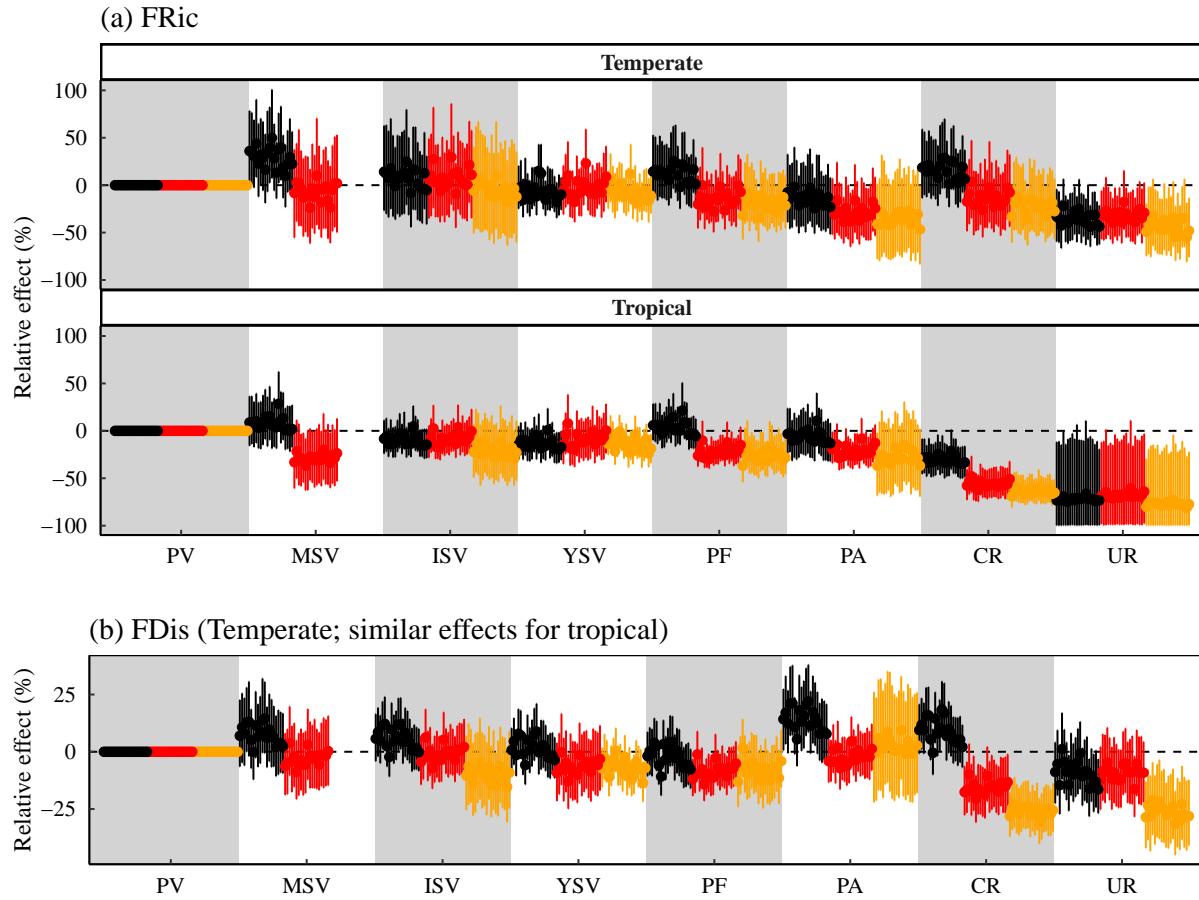
**Figure S3.18: Effects of land use, land-use intensity and region on FRic (a) and FDis (b) across vertebrates, for the subset of species with complete trait data (i.e., excluding species with less than 100% trait completeness).** Effects are plotted as a % difference relative to the reference land use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



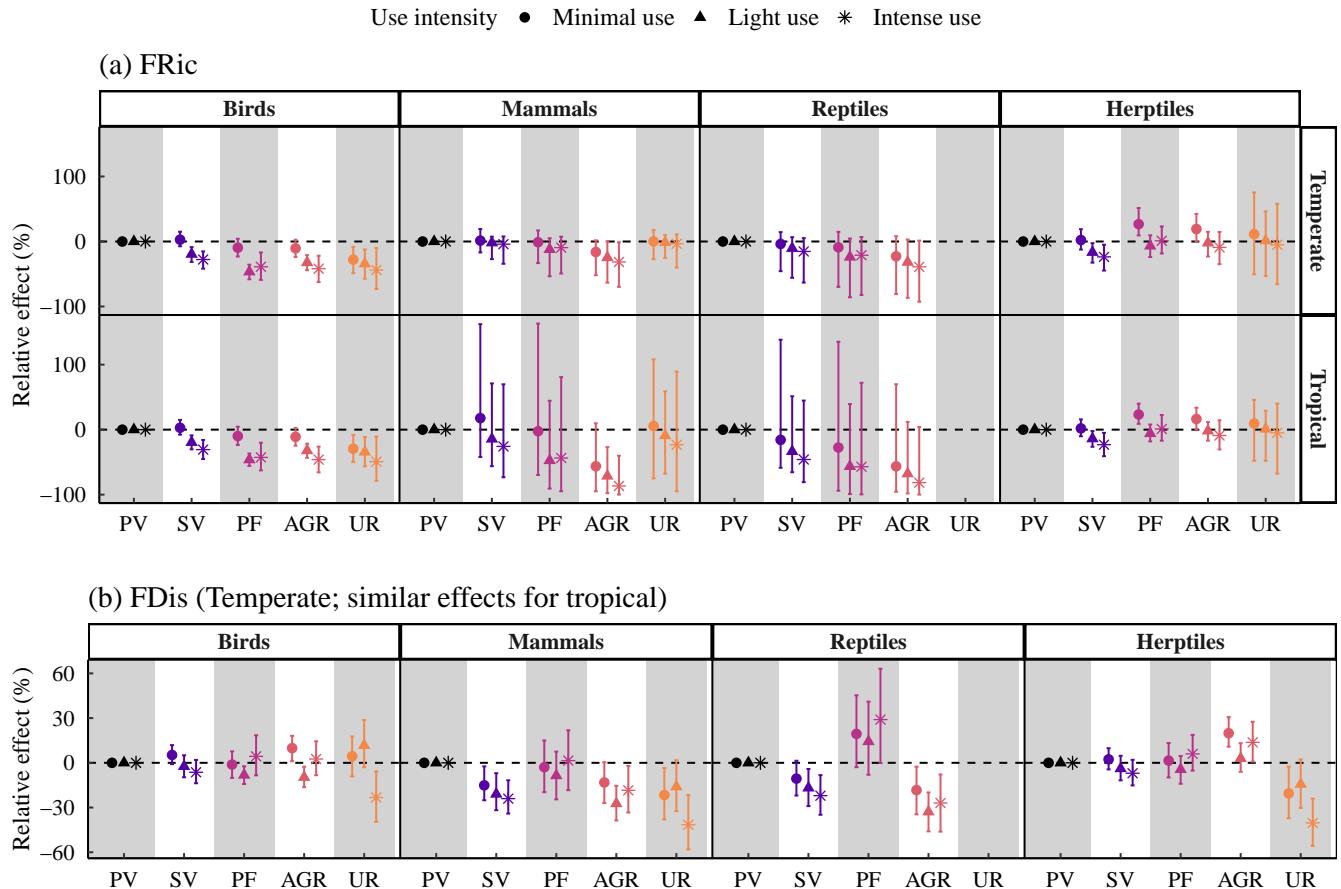
**Figure S3.19: Effects of land use, land-use intensity and region on FRic (a) and FDis (b), for the subset of species with complete trait data (i.e., excluding species with less than 100% trait completeness), with geographical range size as an additional trait considered in the calculation of functional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



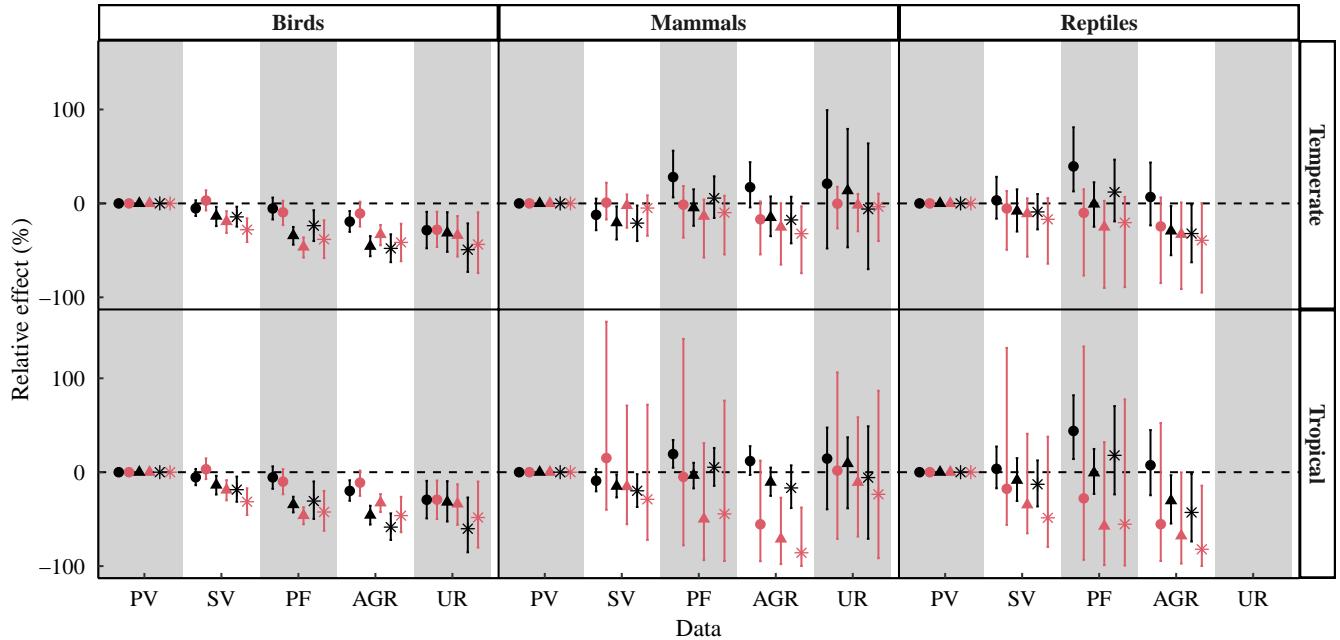
**Figure S3.21: Effects of land use and land-use intensity on FRic (a) and FDis (b), obtained when re-sampling primary vegetation sites twenty independent times.** I fixed the sample size for primary vegetation sites at 50. For FRic, we fitted Model 1a (see main text, Chapter 3), which included the effects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



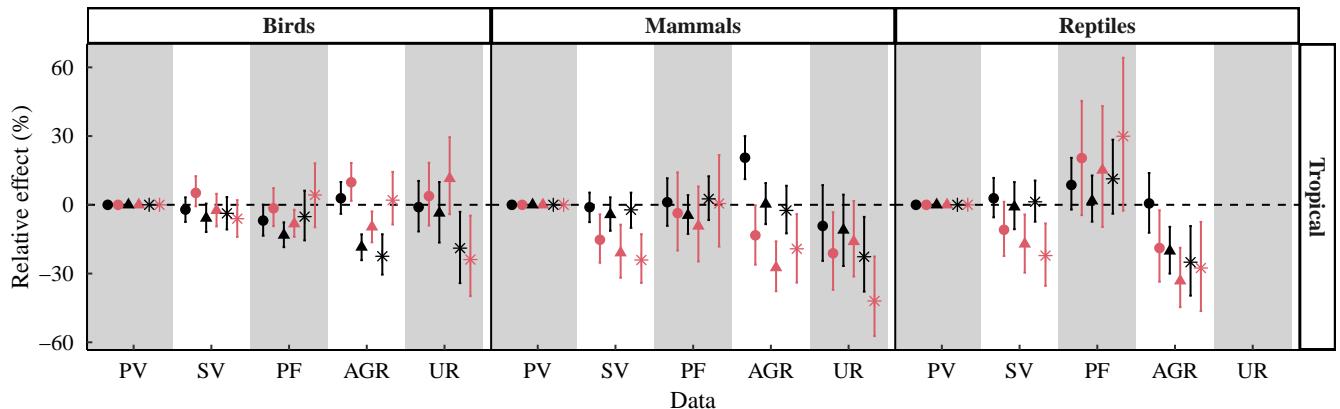
**Figure S3.22: Effects of land use, land-use intensity and taxonomic class on FRic (a) and FDis (c), for the subset of species with complete trait data (i.e., excluding species with less than 100% trait completeness).** Effects are plotted as a % difference relative to the reference land use (primary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

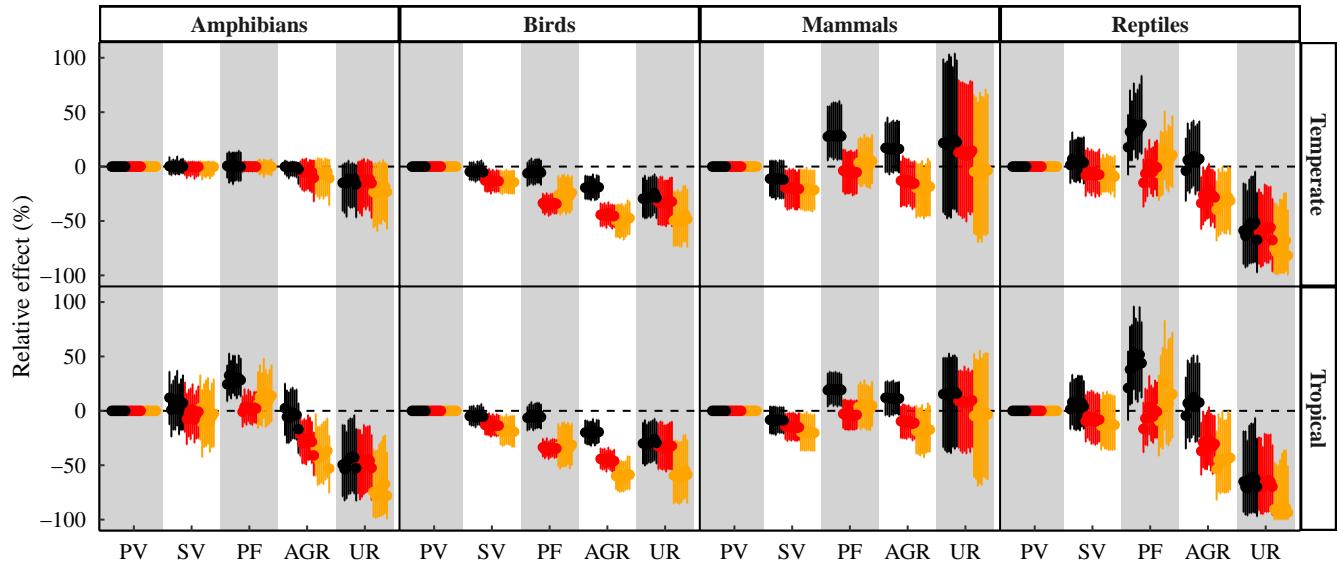


(a) FDis

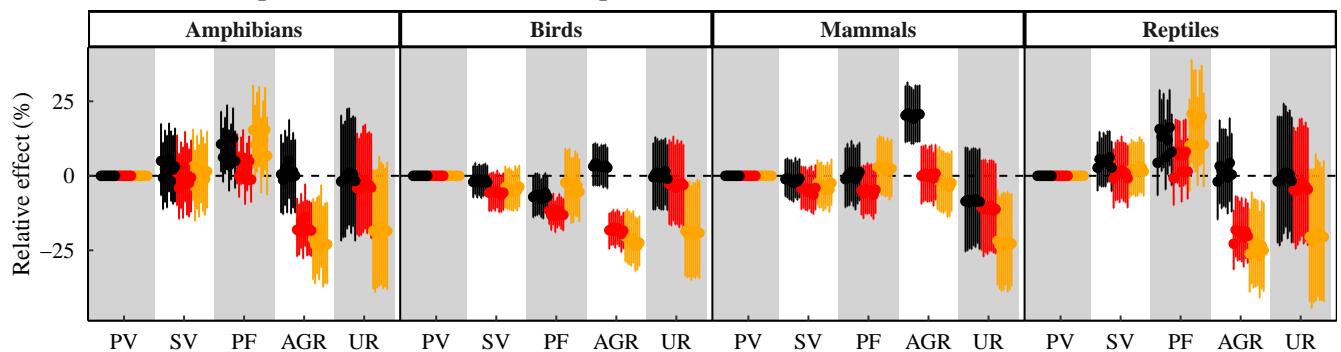


**Figure S3.23: Effects of land use, region, land-use intensity and taxonomic class on FRic and FDis obtained with the imputed trait data (black points) or with the complete data subsets (red points).** Effects are plotted as a % difference relative to the reference land use (primary vegetation, PV).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

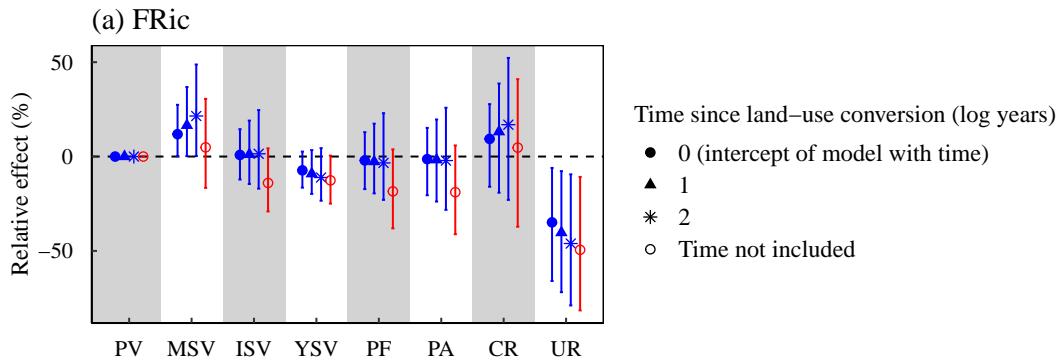
- For FRic, the best-fitting model includes the main effects of land use and time since land-use conversion, but no interaction between these predictors. The model's summary (Table S3.6) show that time since conversion has a significant negative effect on FRic, but the relationship between FRic and time 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**

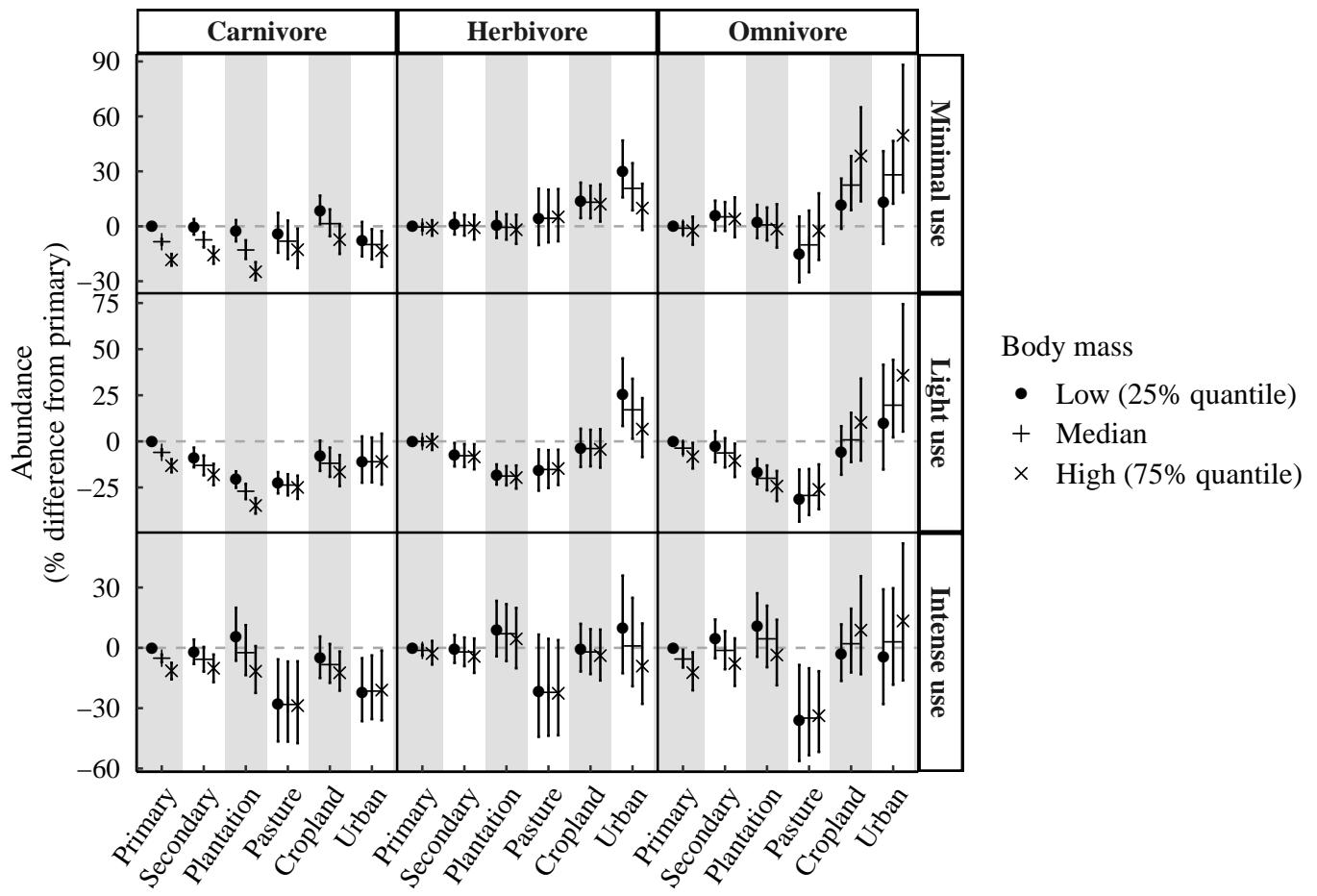
# Appendix 4: Supporting information for Chapter 5

**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.

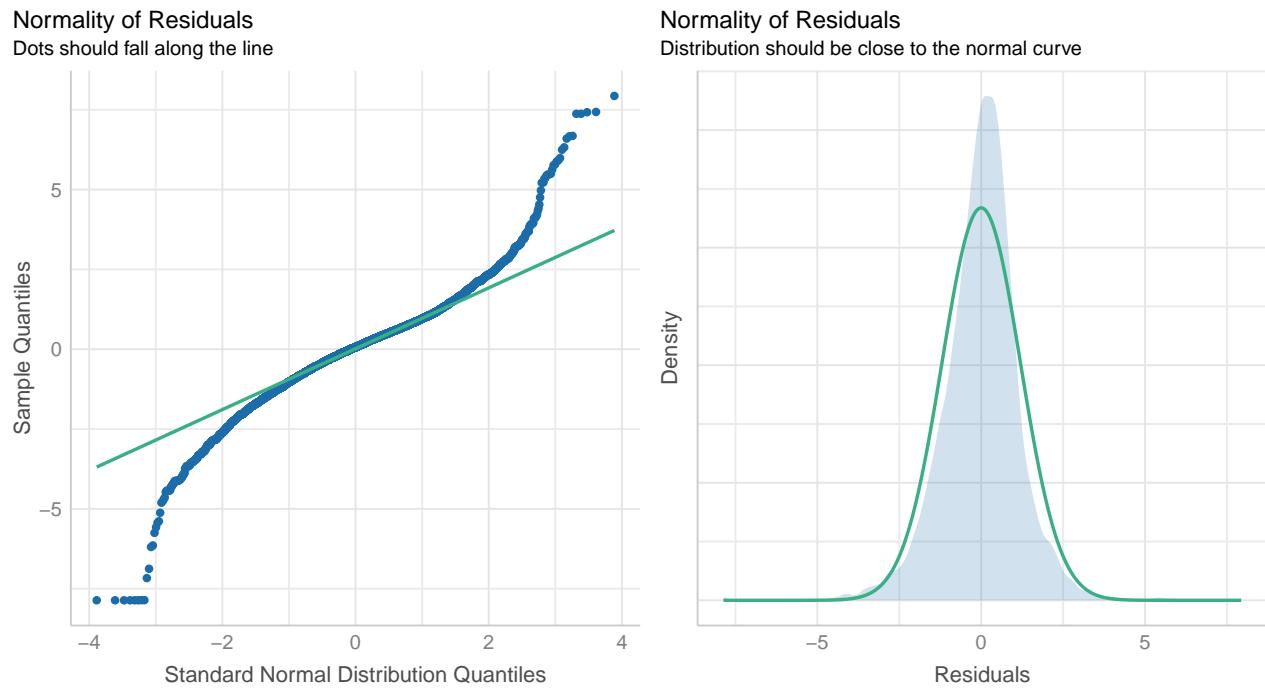
| Class             | RMR data   | Coverage for PREDICTS species | Phylogenetic signal (Pagel's $\lambda$ , $\pm 95\%$ CI) |
|-------------------|--|-------------------------------|---|
| <b>Amphibians</b> | 126 species from Stark et al. (2020)   | 16/379 species (4%)           | 0.89 (0.86-0.91)  |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

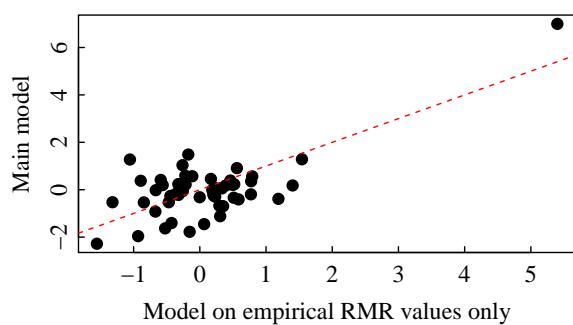


**Figure S5.2: Effects of land use, land-use intensity, trophic group, body mass and their interactions on assemblage-level total abundance**, estimated from the model specified in Fig. S1. The predictions are rescaled with reference to minimally used primary vegetation, considered to be the undisturbed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

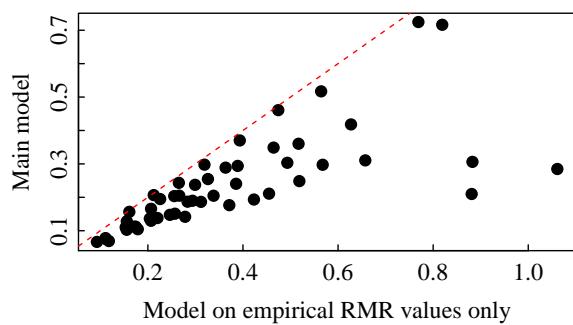


**Figure S5.3:** Diagnostic plots (qq-plot and residual distribution) for the linear mixed-effects model looking at the effects of land use, land-use intensity, trophic group and their interactions on assemblage-level total RMR. The diagnostic plots were obtained with the 'performance' R package (Lüdecke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

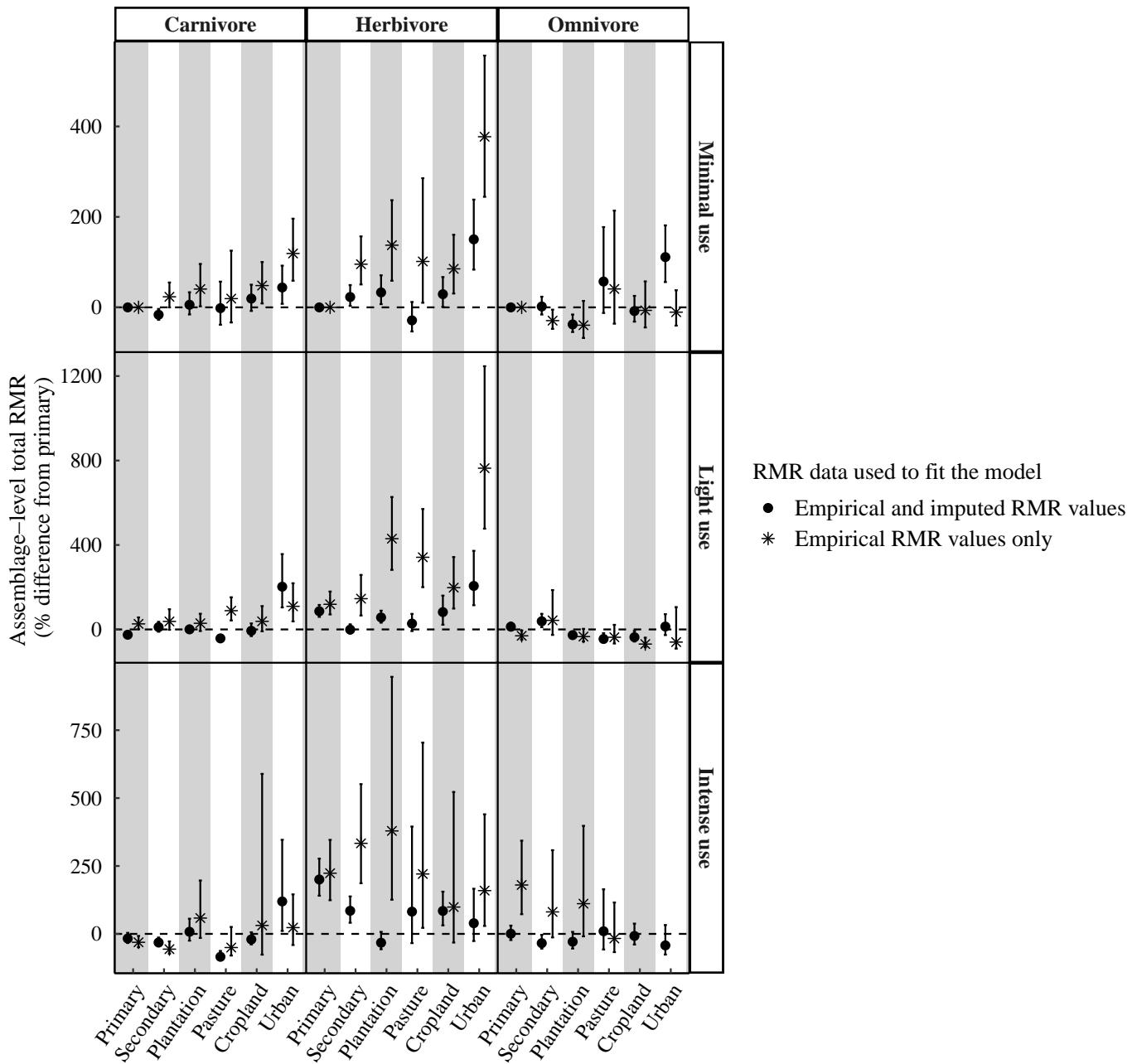
**(a) Coefficient estimates**



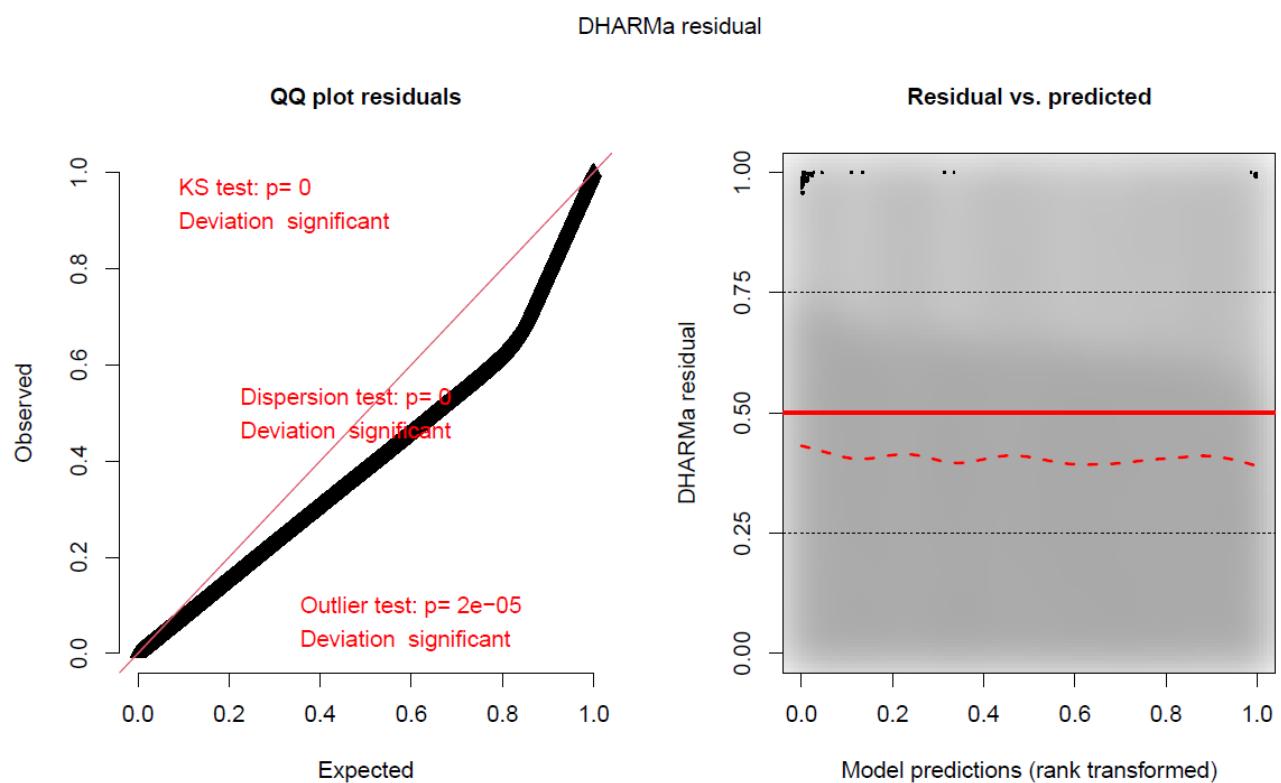
**(b) Standard error estimates**



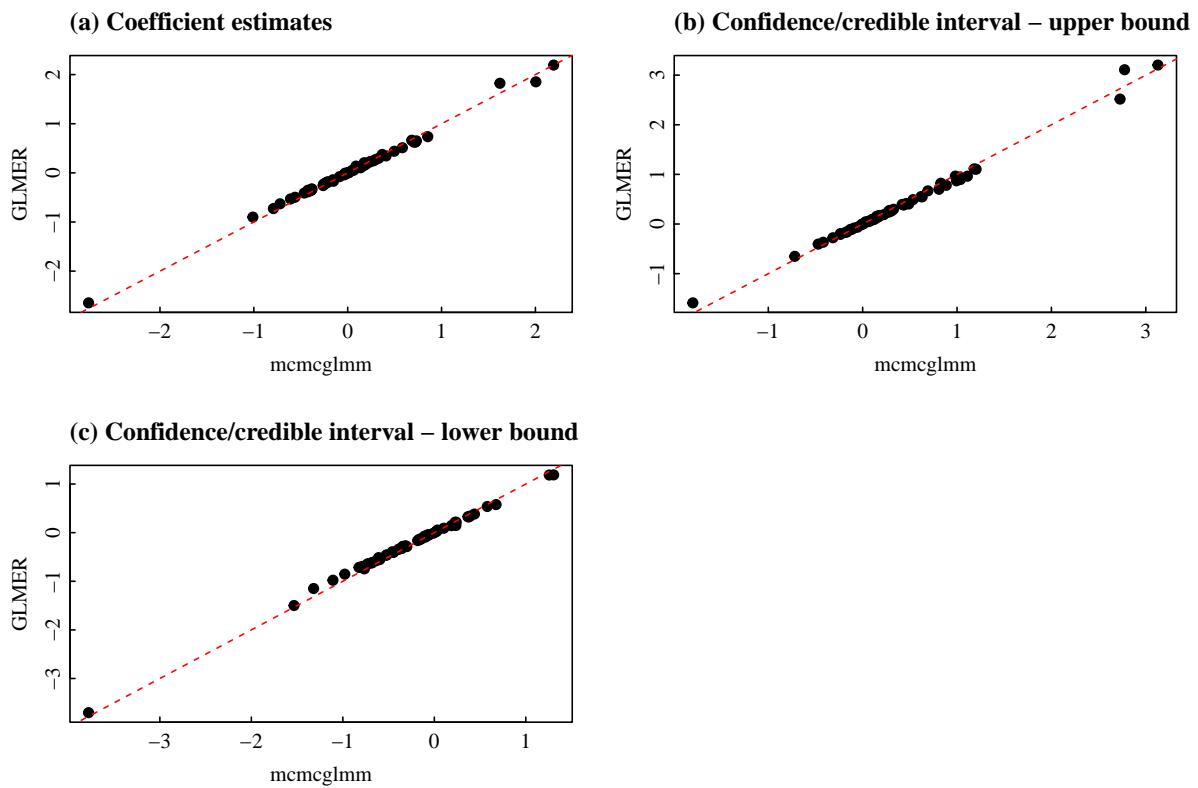
**Figure S5.4: Estimates for the models looking at the effects of land use, land-use intensity, trophic group and their interactions on assemblage-level total RMR.** I plotted the estimates from the model fitted on the empirical and imputed RMR values (presented in the main text) on the y-axis, and the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

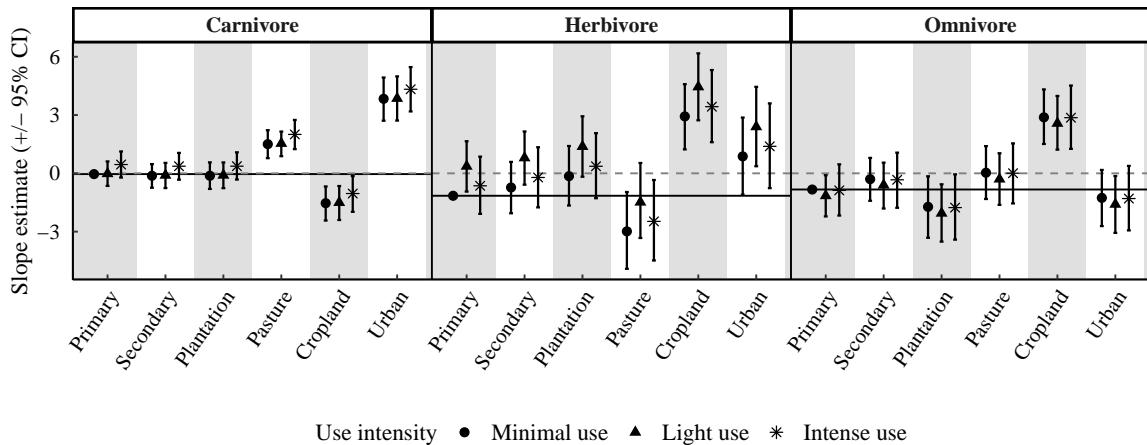


**Figure S5.6:** Diagnostic plots for the generalised mixed-effects model looking at the effects of land use, land-use intensity, trophic group, residual RMR and their interactions on species' probability of occurrence. The diagnostic plots were obtained with the 'DHARMA' R package (Hartig, 2021).

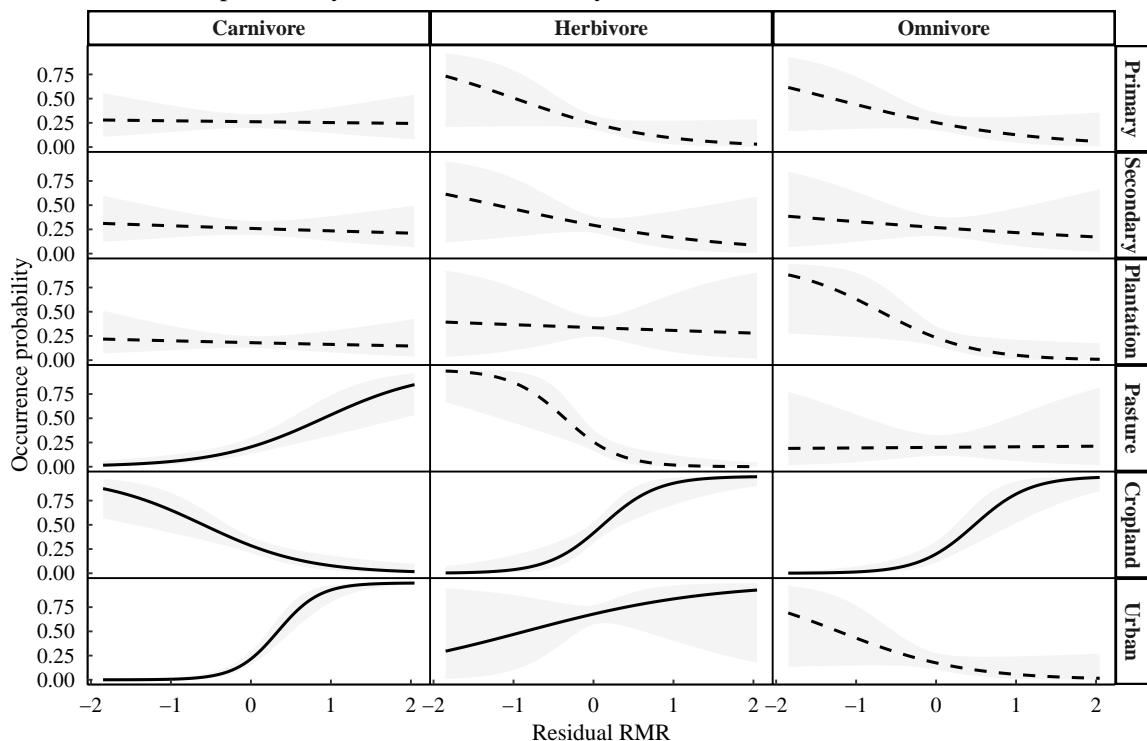


**Figure S5.7:** Model's coefficients from the occurrence model fitted using the 'lme4' package (Bates et al., 2015) against coefficients from the model fitted using a Bayesian framework with the 'MCMCglmm' package (Hadfield, 2010). The models were fitted to investigate the effects of land use, land-use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