Integrating local context in global biodiversity assessments

Juan Gallego-Zamorano

Integrating local context in global biodiversity assessments Juan Gallego-Zamorano

Integrating local context in global biodiversity assessments

Juan Gallego-Zamorano

ISBN:	978-94-6458-796-8
Cover and chapter design:	Bruna Roqué | https://www.brunaroque.com/
Lay-out:	Publiss | www.publiss.nl
Print:	Ridderprint | www.ridderprint.nl

This research was conducted under the auspices of the Graduate School for Socio-Economic and Natural Sciences of the Environment (SENSE)

Integrating local context in global biodiversity assessments

Proefschrift
ter verkrijging van de graad van doctor
aan de Radboud Universiteit Nijmegen
op gezag van de rector magnificus prof. dr. J.H.J.M. van Krieken, volgens
besluit van het college voor promoties
in het openbaar te verdedigen op
vrijdag 27 januari 2023
om 16:30 uur precies

door

Juan Gallego-Zamorano
geboren op 19 februari 1992
te Valladolid, Spanje

Promotor:

Prof. dr. M.A.J. (Mark) Huijbregts

Copromotor:

Dr. A.M. (Aafke) Schipper

Manuscriptcommissie:

Prof. dr. B. (Birka) Wicke

Prof. dr. J.R.M. (Rob) Alkemade (Wageningen University & Research)

Dr. ir. E. (Eelke) Jongejans

Paranimfen:

Caterina Zillien

Kiane de Kleijne

Integrating local context in global biodiversity assessments

Dissertation
to obtain the degree of doctor
from Radboud University Nijmegen
on the authority of the Rector Magnificus prof. dr. J.H.J.M. van Krieken,
according to the decision of the Doctorate Board
to be defended in public on Friday, January 27, 2023
at 4:30 pm

by

Juan Gallego-Zamorano
born on February 19, 1992
in Valladolid, Spain

Supervisor:

Prof. dr. M.A.J. (Mark) Huijbregts

Co-supervisor:

Dr. A.M. (Aafke) Schipper

Manuscript Committee:

Prof. dr. B. (Birka) Wicke
Prof. dr. J.R.M. (Rob) Alkemade (Wageningen University & Research)
Dr. ir. E. (Eelke) Jongejans

Paranymphs:

Caterina Zillien

Kiane de Kleijne

“Dale la vuelta y gíralo

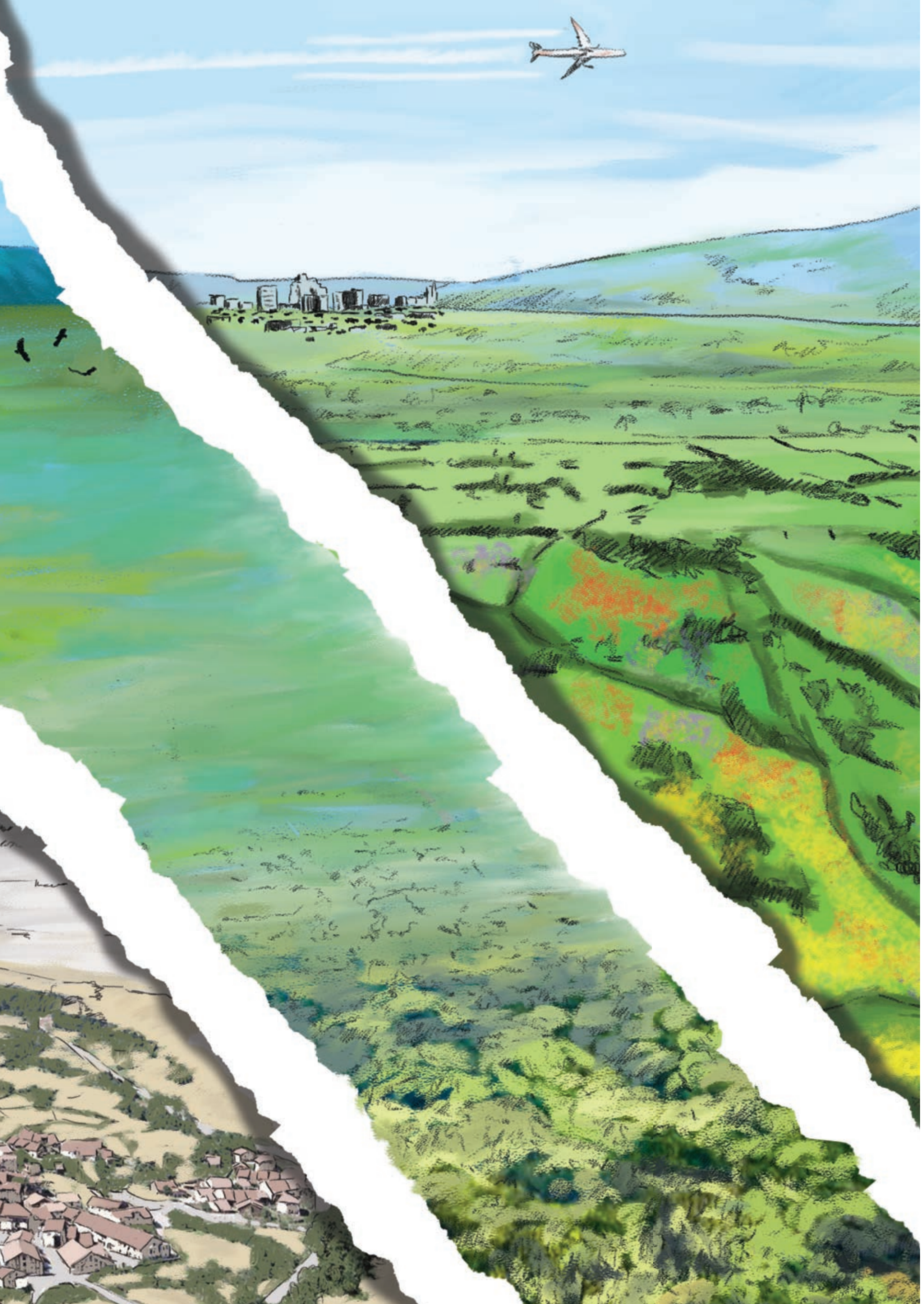
Que lo que parezca solo sea efímero

Dale la vuelta y vívelo

Hazlo a tu manera para que te sea cómodo”

La Pegatina

TABLE OF CONTENTS



CHAPTER 1

INTRODUCTION

1.1 GLOBAL BIODIVERSITY MODELS

Humans have transformed nature to such an extent that the planet may have entered a new geological epoch, the Anthropocene (Crutzen 2006; Corlett 2015). Human activities have significantly altered the global climate, biogeochemical cycles and the biosphere, increasingly threatening global biodiversity. Among the variety of human pressures, land use, overexploitation, pollution, climate change and the introduction of invasive alien species are considered the main threats to global biodiversity (**Figure 1.1**; Maxwell *et al.* 2016; IPBES 2019). In many regions, these threats have increased over time (Dirzo *et al.* 2014; Venter *et al.* 2016) and are expected to further intensify in the future (Tilman *et al.* 2017). The pervasiveness, magnitude, and variety of human pressures have led to around 28% of species across animal and plant taxonomic groups being at risk of extinction according to Red List of the International Union for Conservation of Nature (IUCN 2022).

Global biodiversity and ecosystem models are increasingly used to (i) quantify and understand the underlying causes of biodiversity decline, (ii) make predictions of possible future scenarios, and, ultimately, (iii) evaluate the efficacy of biodiversity policies. These assessments are, in turn, used to underpin (inter)national biodiversity targets and measures, for example via the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). Within the context of IPBES, three broad approaches to global biodiversity modelling are being distinguished, depending on how the relationships between input and output data are represented: correlative modeling, process-based modeling and expert-based modeling (IPBES 2016; **Figure 1.1**). Of these, correlative modelling is probably the best known and most widely applied (IPBES 2016). Based on their approach and the biological level that they address, correlative global biodiversity models (GBMs) can be further classified into three broad types (Alkemade *et al.* 2022):

1. Species-based: these models use individual species data (e.g., habitat preferences, distribution) to assess species occurrence or abundance in relation to environmental factors. These correlate relationships are frequently used to assess the current and future impact of human pressures, such as climate and land-use change, and also to gain understanding of ecological niche limits. This method is used by models such as Map of Life (Powers & Jetz 2019), AIM-Biodiversity (Ohashi *et al.* 2019), or InSiGHTS (Visconti *et al.* 2016; Baisero *et al.* 2020).

2. Community- or assemblage-based: these models calculate assemblage-level metrics, such as species richness or mean species abundance, from empirical observations of species assemblages and correlate these metrics to environmental factors. These models are particularly useful when resources (e.g., time or financial) are limited, when data is spatially sparse or when the knowledge on individual species is incomplete. Examples of these models include PREDICTS, which focuses on the effects of land use on the local abundance or diversity of species (Newbold *et al.* 2015; Purvis *et al.* 2018); BILBI, which assess impacts of human pressures on biodiversity based on compositional similarity (beta diversity) in relation to climate change and land use (Hoskins *et al.* 2020); and GLOBIO, which quantifies the impacts of several human pressures, such as infrastructures, climate change, land use, nitrogen deposition, habitat fragmentation, and hunting pressure, on local biodiversity intactness (Alkemade *et al.* 2009; Schipper *et al.* 2020).

3. Area-based: these models use species-area relationships (SAR) to quantify regional to global species loss due to habitat loss by land use. They are particularly useful to quantify impacts on species richness at large spatial scales. Classic SAR models assume that habitat modified by human activities is completely hostile to all species, while more recent versions of the SAR model (e.g., the countryside SAR) acknowledge that some species might persist in anthropogenic or modified habitat (Chaudhary & Brooks 2017; Martins & Pereira 2017).

Although these models are regularly used for assessing and projecting the impacts of human pressures on biodiversity (Leclère *et al.* 2020; Schipper *et al.* 2020), there are various shortfalls and challenges that require further development in order to improve large-scale biodiversity assessments, which may eventually aid our ability to halt the current biodiversity crisis.

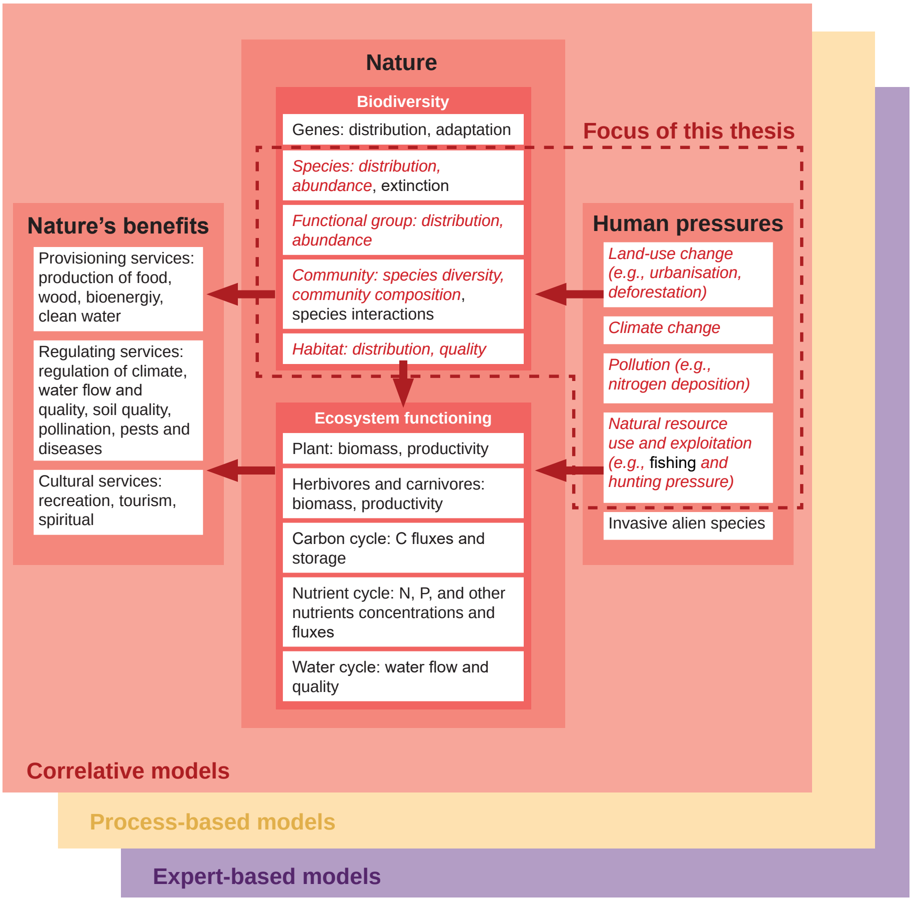


Figure 1.1 Schematic representation of the different types of models of relevance to IPBES based on how they model the relationships between direct human drivers and nature. The overall focus of the thesis is demarcated by the dashed line and the specific pressures and biodiversity response variables covered by the different chapters are in red italic letters. Figure modified from IPBES (2016).

1.2 CHALLENGES IN GLOBAL BIODIVERSITY MODELLING

Multiple pressures

Modelling biodiversity responses to human pressures across large spatial extents comes with various challenges. First, current GBMs mostly focus on land use and climate change (Kim *et al.* 2018), which are recognized as two major pressures on biodiversity worldwide (Maxwell *et al.* 2016). However, other pressures, including overexploitation, pollution, and the introduction of invasive alien species are major additional threats to biodiversity, particularly in specific regions and at the local scale (Pereira *et al.* 2012; Pimm *et al.* 2014; Maxwell *et al.* 2016). Moreover, recent research has revealed that human pressures tend to be highly spatially correlated, i.e., multiple threats acting in the same region (Bowler *et al.* 2020). This cumulation of threats may further jeopardize biodiversity (Brook *et al.* 2008; Darling & Côté 2008; Côté *et al.* 2016; Orr *et al.* 2020). For example, many vertebrate species in the tropics are threatened by a combination of overexploitation and habitat loss (deforestation) (Brodie *et al.* 2015; Symes *et al.* 2018; Romero-Muñoz *et al.* 2019). Currently, the only GBM that includes multiple pressures on biodiversity in addition to land use and climate change is the GLOBIO model (Alkemade *et al.* 2009; Schipper *et al.* 2020). Therefore, a more systematic consideration of the impacts of other human pressures than land use and climate change is highly needed in global biodiversity modelling.

Context dependency

Another challenge for GBMs is that they need to be generic enough to be widely applicable, yet specific enough to account for relevant spatial heterogeneity in ecological responses. Local ecological studies investigating the same question or process may reach different conclusions depending on local conditions (Catford *et al.* 2022). This disparity in conclusions is typically due to context-dependencies, i.e., local environmental conditions or species traits that influence the relationships that researchers observe. For example, the impact of nitrogen deposition on plant species richness is typically greater in warmer sites, in habitats that are nutrient-poor, and where buffer capacity against acidification is low (Bobbink *et al.* 2010; Midolo *et al.* 2019). Another example is provided by the response of dung beetles to land-cover change, which is stronger for diurnal than nocturnal species (Nichols *et al.* 2013). Accounting for context-specific conditions, in terms of both environmental characteristics and species' traits, may, therefore, improve the predictive power of GBMs and our understanding of how biodiversity responds to different pressures (Catford *et al.* 2022). By design, species-based models are able to account for spatial variability in species occurrence, while community- and area-based models are typically based on average, aggregated responses. For example, GLOBIO uses global biodiversity response relationships that are independent of the local context (Alkemade *et al.* 2009; Schipper *et al.* 2020). Quantitative meta-regression modelling represents a promising approach to synthesize empirical data from local studies into generic response relationships, controlling for methodological heterogeneity (e.g., differences in sampling efforts and methods), while considering context-dependencies by accounting for different biotic and abiotic moderators (Gurevitch *et al.* 2018). Therefore, meta-regression modelling is a possible way to improve the extent to which GBMs can account for context-dependencies while keeping their global applicability (Verburg *et al.* 2016; Catford *et al.* 2022).

Data shortfalls

Global biodiversity modelling is also challenged by taxonomic and spatial bias in empirical data needed for the parameterization (Hortal *et al.* 2015). Most of our knowledge about the trends in biodiversity is coming from certain taxonomic groups, such as mammals or birds, and from specific world regions, with a bias toward Europe, North America and Australia (Pereira *et al.* 2012; Hortal *et al.* 2015; Di Marco *et al.* 2017). To obtain a more holistic view of the state of global biodiversity, it is important to develop models able to infer answers for understudied taxonomic groups and regions. Meta-regression models that account for context-specific conditions have great potential also for extrapolation across regions and species (e.g., trait-based models; Wong *et al.* 2019). These models can be used to infer biodiversity responses to human pressures in undersampled regions or for undersampled species if pressure levels, relevant environmental conditions and species traits are known (Wong *et al.* 2019). Trait-based models refer to the use of functional traits (i.e., functional properties of individuals such as body mass or feeding guild) to assess ecological responses (Webb *et al.* 2010; Wong *et al.* 2019). If a trait responds to a human pressure, the response can be extrapolated to species or species groups with the same trait without considering the taxonomic identity of the species, making trait-based models highly applicable for extrapolation. For example, as hunting pressure is typically higher for large-sized mammal and bird species, a trait-based approach including body mass allows to estimate hunting impacts on species for which empirical hunting impact estimates are lacking (Benítez-López *et al.* 2017, 2019). Similarly, incorporating relevant climatic and habitat variables into (meta-regression) models enables researchers to investigate the state of biodiversity in less studied areas.

1.3 AIMS AND SCOPE OF THE THESIS

In this thesis I aim to improve the modelling of terrestrial biodiversity responses to global environmental change in the light of the challenges mentioned above. To that end, I specifically aim to:

1. Develop context-specific biodiversity response relationships for understudied pressures and species groups, which can be used to extrapolate across species and regions.
2. Apply new response relationships to quantify the combined impact of multiple human pressures across large spatial extents.

To achieve these aims, I integrate local contextual information (environmental conditions and species traits) into quantitative meta-analytical models that assess ecological responses to human pressures and apply such models in broad-scale multi-pressure impact assessments. In the thesis, I cover multiple human pressures, with a focus on direct drivers of biodiversity loss that are important yet more poorly represented in GMBs than climate change and land use (nitrogen enrichment, linear infrastructures and hunting). I further cover multiple species groups, including less studied groups (invertebrates or reptiles), and I include context variables representing environmental characteristics and species' traits that are supposed to modify the relationships between the pressures and biodiversity **(Figure 1.1, Table 1.1)**.

1.4 OUTLINE OF THE THESIS

Chapters 2 and 3 develop new response relationships for understudied pressures and taxonomic groups (**Table 1.1**). Specifically, chapter 2 quantifies the effect of nitrogen addition on terrestrial invertebrates, focusing on arthropods and nematodes. Chapter 3 develops trait-based response relationships to assess the impacts of linear infrastructure on major vertebrate species groups (mammals, birds, reptiles, and amphibians) and quantifies group-specific infrastructure effect zones that can be used in spatially explicit impact assessments. Chapters 4 and 5 apply context-specific response relationships for quantifying the combined effect of multiple human pressures on biodiversity (**Table 1.1**). Chapter 4 is a global assessment of the combined effect of land use and nitrogen deposition on plant species richness. In this chapter, a context-specific response relationship for nitrogen enrichment is integrated into a SAR-based model for land-use impacts, expanding the applicability of SAR models. Chapter 5 is a pantropical assessment of the combined effect of land use and hunting on the distributions of tropical mammals, based on their body mass and habitat preferences. Chapters 2, 3 and 5 use a trait-based approach which enables the prediction of anthropogenic threats to less known species (or group of species). Finally, Chapter 6 discusses the findings from the previous chapters and offers general implications and recommendations for future research and biodiversity assessments.

Table 1.1 Overview of the scope of the chapters of this thesis. Model type refers to the three broad types of global biodiversity models: species-based, assemblage-based, and area-based models.

Chapter	Model type	Taxonomic group(s)	Pressure (s)	Metric(s)	Method	Context	
						Environmental variables	Species traits
2	- Species based - Assemblage based	- Arthropods - Nematodes	Nitrogen enrichment	- Abundance - Richness	Meta-regressions	- Mean annual temperature - Mean annual precipitation - Soil cation exchange capacity - Habitat type	- Metamorphosis mode - Feeding guild
3	Species based	- Mammals - Birds - Reptiles - Amphibians	Linear infrastructures	Abundance	Meta-regressions	- Habitat type	- Body mass - Feeding guild
4	- Assemblage based - Area based	Plants	- Land use - Nitrogen enrichment	Richness	- Meta-regressions - Species area relationships	- Mean annual temperature - Soil cation exchange capacity	
5	Species based	Mammals	- Land use - Hunting	Distribution	- Meta-regressions - Species distribution models		- Body mass - Habitat preferences

CHAPTER 2

CONTEXT-DEPENDENT RESPONSES OF TERRESTRIAL INVERTEBRATES TO ANTHROPOGENIC NITROGEN ENRICHMENT

Submitted to Global Change Biology

Authors

Juan Gallego-Zamorano[1]*, Melinda M.J. de Jonge[1], Katharina Runge[1], Steven H. Huls[2], Jiaqi Wang[1], Mark A.J. Huijbregts[1], Aafke M. Schipper[1,3]

[1] Department of Environmental Science, Radboud Institute for Biological and Environmental Sciences (RIBES), Nijmegen, The Netherlands

[2] Department of Plant Ecology and Physiology, Radboud Institute for Biological and Environmental Sciences (RIBES), Nijmegen, The Netherlands

[3] PBL Netherlands Environmental Assessment Agency, The Hague, The Netherlands

ABSTRACT

Anthropogenic increases in nitrogen (N) concentrations through the use of fertilizers are affecting plant diversity and ecosystems worldwide, but relatively little is known about N impacts on terrestrial invertebrate communities. Here, we conducted a meta-analysis of 4,365 observations from 126 publications reporting the effect of N enrichment on the diversity (number of taxa) or abundance (number of individuals per taxon) of terrestrial arthropods or nematodes. We found that the response of invertebrates to N enrichment is highly dependent on both species traits and local climate. The abundance of arthropods with incomplete metamorphosis, such as many agricultural pests, increased in response to N enrichment, while those exhibiting complete or no metamorphosis, such as many pollinators and detritivores, declined from N enrichment levels larger than about 100 kg/ha/yr, particularly in warmer climates. These contrasting and context-dependent responses may explain why we detected no overall response of arthropod richness. For nematodes, the abundance response to N enrichment was dependent on mean annual precipitation and varied between feeding guilds. We observed a consistently negative relationship between nematode abundance and N enrichment in drier areas, as well as a general decline in nematode richness with increasing N addition. These N-induced changes in invertebrate communities could have consequences for various ecosystem functions and services, including those contributing to human food production.

2.1 INTRODUCTION

The anthropogenic increase of nitrogen (N) in the environment, through the use of nitrogen fertilizers or fossil fuel combustion, has large consequences for the structure and functioning of ecosystems (Bobbink *et al.* 2010; Fowler *et al.* 2013; WallisDeVries & Bobbink 2017). For example, elevated N levels promote the establishment and growth of generalist nitrophilous plant species (Bobbink *et al.* 2010; WallisDeVries & Bobbink 2017). The increased prevalence of nitrophilous plants may result in the competitive exclusion of other species, which in turn may lead to an overall decrease in plant species diversity (Isbell *et al.* 2013; Vellend *et al.* 2017; Midolo *et al.* 2019). Increasing N availability can also lead to an imbalance of other essential nutrients such as calcium (Ca) or phosphorus (P) (Lucas *et al.* 2011; Penuelas *et al.* 2020). These changes in plant diversity and nutrient availability are expected to affect terrestrial invertebrate communities through different pathways, such as changes in the reproductive habitat, food quality and microclimate (Nijssen *et al.* 2017; Stevens *et al.* 2018; David *et al.* 2019; Vogels *et al.* 2020). For example, higher and denser vegetation, due to the proliferation of nitrophilous plants, may hamper the mating or deposition of eggs of invertebrates by reducing the amount of bare soil, mating sites and nesting localities (Nijssen *et al.* 2017).

Previous research on the effects of N on invertebrates has mostly focused on small scales or specific species groups (e.g., Haddad *et al.* 2000; Guo-liang *et al.* 2007; Taboada *et al.* 2016). These studies have indicated that the response of invertebrates to N enrichment depends on the species' ecological traits (Fagan *et al.* 2002; Griffith & Grinath 2018; Vogels *et al.* 2020; Borer & Stevens 2022). For example, species with high N body content, such as old-evolved insects (e.g., *Odonata*) or predatory arthropods (e.g., *Araneae*), have high N requirements and are thus expected to increase in abundance if N availability increases (Fagan *et al.* 2002; Vogels *et al.* 2020). Responses to N enrichment may change also with local environmental conditions (WallisDeVries & Van Swaay 2006; Sun *et al.* 2013; Hiltpold *et al.* 2017; Peguero *et al.* 2021). For example, precipitation may mitigate the impacts of N on soil fauna by reducing N accumulation in the soil (Wei *et al.* 2012; Sun *et al.* 2013). Because of the dependencies on species traits and environmental conditions, local studies typically fall short in revealing the general response of invertebrate communities to N enrichment (Nijssen *et al.* 2017; Vogels *et al.* 2020; Borer & Stevens 2022). A recent study that synthesized local experimental data on the effects of N on invertebrates, concluded that N enrichment typically leads to declines in abundance but has no effect on invertebrate diversity (Nessel *et al.* 2021). While this study was the first to synthesize the effects of N on terrestrial invertebrates, it did not evaluate how the effects depend on the amount of N added. Given that the impact of N may change not only depending on species traits or local environmental conditions but also the added quantities (Nijssen *et al.* 2017; Vogels *et al.* 2020), there is a clear need to synthesize and generalize findings of local experiments along a gradient of N addition.

Here, we aim to identify the extent to which the amount of N enrichment affects terrestrial invertebrate richness and abundance, and to explore the role of traits and environmental conditions by synthesizing data from local experimental studies across the globe. We focused on arthropods and nematodes, which were the best-represented groups in the N enrichment experiments. To that end, we compiled a database of 4,365 observations from 126 publications on the effect of experimental N enrichment on arthropod or nematode richness (number of taxa) or abundance (number of individuals per taxon). We then analyzed the data according to a meta-analytical approach controlling for dependencies across and within studies and, where possible, for phylogenetic relatedness among invertebrate groups (Chamberlain *et al.* 2012; Cinar *et al.* 2022). We first assessed the overall response of richness and abundance to N enrichment, independent of the amount of N, using random-effect meta-analysis. Then, we established meta-regression models to investigate changes in arthropod or nematode richness or abundance in relation to the amount of N added, while considering the potential influence of experimental duration, feeding guild, metamorphosis mode, habitat type, and climate and soil variables (i.e., temperature, precipitation and cation exchange capacity (CEC)). This is the first study providing global estimates of the context-dependent relationships between the local richness or abundance of terrestrial invertebrates and increasing levels of N addition.

2.2 METHODS

Literature search

In April 2021, we used the Web of Science, Scopus, ProQuest, and Open Thesis and Dissertations databases to search for primary studies in published and grey literature in all languages. We used a combination of “OR” and “AND” statements with terms related to N enrichment experiments and the richness or abundance of invertebrates (see the complete search strings in **Appendix S2.1**). Additionally, we identified potentially relevant studies by cross-referencing or via e-mail alerts until January 2022 (**Figure S2.1**).

Inclusion criteria

We selected publications suitable for data extraction based on the following inclusion criteria:

- The publication reports on the effect of experimental N enrichment on terrestrial invertebrates (including soil macrofauna), including terrestrial invertebrates in ecosystems that might be subject to occasional floodings, like salt marshes.
- The publication reports measures of terrestrial invertebrate richness or abundance at the species, genus, family, order, class or phylum level of terrestrial invertebrates for at least one level of N enrichment (treatment) and for a control site (no N addition).
- The levels of N addition are provided as or can be converted to N addition rates in kilograms per hectare per year (kg/ha/yr).

We excluded studies where N addition was combined with other interventions, such as changing temperatures, litter removal, grazing, fire manipulation, or in combination with the addition of other nutrients (e.g., phosphorous) unless the study contained plots that differed only in terms of the N addition level. We also excluded studies of invertebrates along a gradient of N deposition without experimental addition of N. The literature search yielded 6,680 unique publications, of which we selected 126 for data extraction, including publications in English, Spanish, or Chinese (**Figure S2.1**).

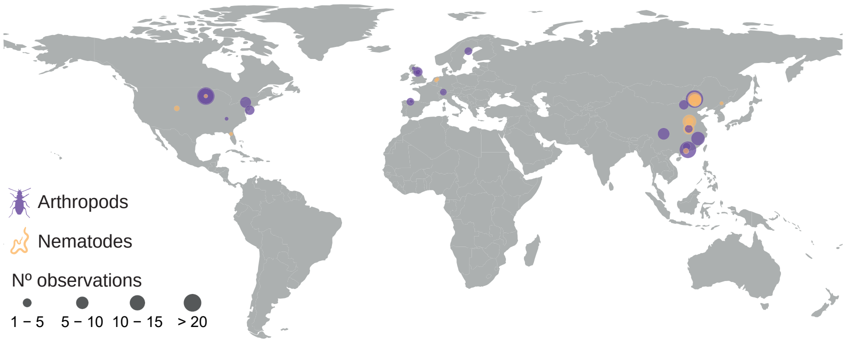
Data extraction

We structured the data into data source (i.e., publication), study and taxon (at the lowest taxonomic level possible). We distinguished multiple studies within a source if it included comparisons of invertebrates in multiple locations or at multiple points in time (e.g., re-surveys), each with a corresponding control plot.

Per study, we extracted the mean taxonomic richness (richness, from now on) and abundance per taxon (abundance, from now on) for treatment and control plots. We also extracted the standard deviation of the mean and the sample size. We extracted the data from text and tables, or graphs using WebPlotDigizer (https://automeris.io/WebPlotDigitizer/). If the mean or the standard deviation were not reported, we calculated them from the standard error, median, range, and/or interquartile range if provided, following Wan, Wang, Liu, & Tong (2014). From each source, we also collected the geographical location, experimental design (i.e., the yearly amount of N addition, experimental duration, type of N fertilizer and plot size) and habitat type. We classified the habitat types into three classes based on the information provided by the authors, i.e., forests, non-forest (including grasslands, shrublands, and wetlands), and cultivated (including croplands and tree plantations).

In our final database, the majority of the observations (i.e., pairwise comparisons between treatment and control) were from arthropods (169 pairwise comparisons for richness, and 2,670 for abundance) and nematodes (66 for richness, and 1,460 for abundance), while annelids (2 for richness, and 25 for abundance) and molluscs (0 for richness, and 6 for abundance) were poorly represented. Therefore, we restricted the analysis to arthropods and nematodes (**Figure 2.1**). For these groups together, we included 34 publications reporting on richness, published between 1998 and 2021 and containing 61 studies and 235 pairwise comparisons from seven countries. The N addition values for the richness dataset ranged from 10 to 1,035 kg/ha/yr in experiments with a duration ranging between 1 and 36 years (**Figure S2.3**). For abundance, we included 126 publications, published between 1970 and 2021, containing 414 studies and 4,130 pairwise comparisons from 23 countries. Insects were the most represented group in the abundance dataset of arthropods (1,775 observations, **Figure S2.2a**), followed by arachnids (436 observations) and collembolans (308 observations). The N addition values for the abundance dataset ranged from 0.75 to 1,875 kg/ha/yr in experiments with a duration ranging between 1 and 36 years (**Figure S2.3**).

a) Richness



b) Abundance

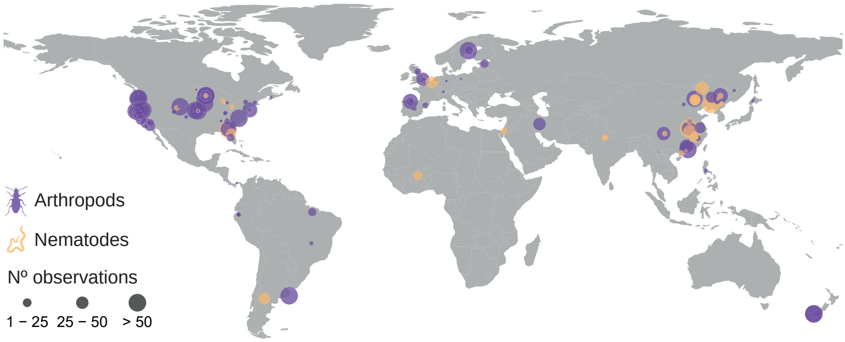


Figure 2.1 Locations of the data sources for a) the richness of arthropods (N = 169 observations) and nematodes (N = 66 observations) and b) the abundance of arthropods (N = 2,670 observations) and nematodes (N = 1,460 observations). The size of each point indicates the number of observations per source. Silhouettes are public domain obtained from “phylopic” (www.phylopic.org).

Effect size

For each study and N level, we calculated the effect size as the natural logarithm of the response ratio (*lnRR*), i.e., the natural logarithm of the ratio of the richness and abundance at the treated site ($\widetilde{A}_T$) and the richness and abundance at the control site ($\widetilde{A}_C$). To account for small sample sizes (e.g., less than 5 replicates), we applied a bias correction to the effect sizes according to the Delta method (lnRRΔ) by Lajeunesse, (2015):

$$lnRR^{\Delta} = ln\left(\frac{\widetilde{A}_T}{\widetilde{A}_C}\right) + \frac{1}{2}\left(\frac{SD_T^2}{n_T\widetilde{A}_T^2} - \frac{SD_C^2}{n_C\widetilde{A}_C^2}\right) \qquad \text{Equation 2.1}$$

Where SD_T^2 is the sampling variance of the mean richness or abundance at the treated site and SD_C^2 is the sampling variance of the mean richness or abundance in the control site. Effect sizes are therefore negative ($\ln RR^{\Delta} < 0$) or positive ($\ln RR^{\Delta} > 0$) if richness or abundance estimates are lower or higher, respectively, at a certain N addition level than in the control plot. In some treatment or control sites, there were zero individuals, precluding the effect size calculation. To circumvent this, we calculated adjusted sample means (Ã) following Pustejovsky (2015) as:

$$\tilde{A} = \begin{cases} \bar{A} \ if \ \bar{A} > 0 \\ 1/(2nD) \ if \ \bar{A} = 0 \end{cases} \qquad \text{Equation 2.2}$$

where $\bar{A}$ is the mean richness or abundance, *n* is the sample size of the corresponding mean and *D* corrects for the scale on which the richness or abundance are reported. For example, if abundance is measured as the number of individuals, D is equal to 1 because this is the minimum number of individuals that is possible to count; if abundance is reported as density (e.g., individuals/m^2), D is equal to the area sampled.

For each effect size $lnRR^{\Delta}$ we established a weighting factor as the inverse of the corresponding sampling variance $\mathrm{VAR}(lnRR^{\Delta})$, calculated as:

$$\mathrm{VAR}(lnRR^{\Delta}) = \frac{SD_T^2}{n_T\tilde{\mathrm{A}}_T^2} + \frac{SD_C^2}{n_C\tilde{\mathrm{A}}_C^2} + \frac{1}{2}\left(\frac{SD_T^4}{n_T^2\tilde{\mathrm{A}}_T^4} + \frac{SD_C^4}{n_C^2\tilde{\mathrm{A}}_C^4}\right) \qquad \text{Equation 2.3}$$

When no variance estimate was reported or if the reported variance was equal to zero we used the “Bracken1992” approach to impute the SD, using the coefficient of variation from all complete cases to impute SDs (Bracken 1992). For the richness of arthropods, 8% of the SDs in the control and the treatment were missing; and for the richness of nematodes, 2% of the SDs in the control and the treatment were missing. For the abundance of arthropods, 41% of the SDs were missing for the control and the treatment plots; for the abundance of nematodes, SDs were missing for 28% of the controls and 31% of the treatments.

Meta-analysis

We used a random-effects meta-analysis to estimate the mean impact of N enrichment on arthropod and nematode richness and abundance in our dataset. We accounted for three sources of non-independence among effect sizes. First, we accounted for between-source variability by adding “Source” as random intercept. Second, we controlled for non-independence due to multiple treatments per study sharing the same control by using a variance-covariance matrix where the diagonal includes the sampling variances and the off-diagonals of the matrix represent the shared variance (covariance) among the effect sizes due to the common control (Olkin & Gleser 2009; Lajeunesse 2011). Finally, for arthropods, we accounted for phylogenetic non-independence by including a phylogenetic tree at the level of order (**Figure S2.2b**), which was the lowest taxonomic level possible based on the information provided across the studies (Chamberlain *et al.* 2012; Cinar *et al.* 2022). We obtained the phylogenetic tree based on the Open Tree Taxonomy (Rees & Cranston 2017) and the Open Tree of Life (Hinchliff *et al.* 2015) and we estimated branch lengths following Grafen & Hamilton (1989). For nematodes, the majority of the studies did not include phylogenetic information and the phylogeny of nematodes is still unresolved (Kern *et al.* 2020), so we could not control for phylogenetic non-independence. In all analyses, we accounted for in-between observation variability by including the observation level as a random effect (Nakagawa & Santos 2012).

Meta-regressions

To determine how richness and abundance respond to the amount of nitrogen added, we established and compared multiple meta-regression models relating the $\ln RR^{\Delta}$ to the amount of N added in the experiments (kg/ha/year) and potential moderators. We selected moderators that are expected to influence the response of invertebrates to N based on literature (**Table S2.1**). In total, we included eight moderators in the analysis: 1) the annual amount of N deposited from the atmosphere (kg/ha/year); 2) the duration of the experiment (i.e., number of years of N addition); 3) invertebrate feeding guild; 4) mean annual temperature (MAT; °C); 5) mean annual precipitation (MAP; mm/month); 6) soil CEC (cmol/kg); 7) habitat type (forests, non-forest, and cultivated); and for arthropods, 8) the type of metamorphosis that they perform during their life cycle.

We extracted yearly atmospheric N deposition values from the global maps from Ackerman, Chen, & Millet, (2018). We linearly interpolated the values for the missing years in the maps (i.e., 1987-1993, 1997-2003, 2007-2013) to match the yearly N deposition to the year of the experiment. For observations before 1984, we used the atmospheric N deposition value reported for 1984 (4% of all observations). Similarly, we obtained the mean annual temperature and mean annual precipitation of the study period in each source by averaging monthly values for each location from the global Climate Research Unit database, which covers the period 1901-2020 (Harris *et al.* 2020). We extracted estimates of CEC from the 250-m resolution global SoilGrids data (Hengl *et al.* 2017) by averaging values at the soil depths of 0–5, 5–15 and 15–30 cm. We classified feeding guild based on the original information from the articles or following www.bugguide.org. If a source provided data on a high taxonomic level (e.g., order or family) with species feeding on different resources but the authors did not provide the feeding guild of the group, then we assigned the category “unknown”. For metamorphosis type, we classified each order of arthropods as (i) complete metamorphosis, (ii) incomplete-gradual metamorphosis, or (iii) no metamorphosis (Capinera 2008).

For each taxon and metric (richness and abundance) we tested the effect of N enrichment on its own (linear and quadratic effect) and in interaction with the moderators. Before the analysis, we $\log_{10}$-transformed the N addition and N deposition values as they presented a strong positive skewness (**Figure S2.3**), and tested for collinearity between the continuous moderators with Pearson correlation (**Figure S2.4**). We tested all possible combinations of N addition and the moderators, excluding models that included highly correlated moderators (i.e., Pearson correlation > 0.8 or < -0.8), like MAT and MAP in the richness dataset (**Figure S2.4**). For the richness analyses, we excluded the categorical variables of metamorphosis (for arthropods) and feeding guild as it was not possible to classify the high taxonomic levels into the different categories. We selected the most parsimonious combination of moderators based on the corrected Akaike Information Criterion (AICc) estimated by the maximum likelihood (ML) method and then used the restricted maximum likelihood (REML) to estimate the regression coefficients of the best model (**Table S2.1**, **Table S2.2**, **Table S2.3** and **Table S2.4**; Cinar, Umbanhowar, Hoeksema, & Viechtbauer, (2021)). We assessed whether the heterogeneity in the true effects was related to the moderators in the models using omnibus tests (Q_M). For each model, we calculated the marginal and conditional R^2 to quantify the amount of heterogeneity explained by fixed effects only and by the entire model, respectively (Nakagawa & Schielzeth 2013). Within the random effects, we also calculated the I^2 of each level to assess the proportion of heterogeneity relative to the total amount of heterogeneity in the observed effects explained by each level (Nakagawa & Santos 2012). Additionally, we checked profile likelihood plots to ensure that the best models identified the variance components and had no converge problems (**Figure S2.11**, **Figure S2.12**). We report the results as the percentage change in richness or abundance $(\%\ change = (e^{lnRR^{\Delta}} - 1) * 100)$.

We performed all analyses with R version 4.0.2, using the R package "metafor" v.3.1-34 to fit the models (Viechtbauer 2010) and "orchaRd" v.0.0.0.9 to calculate the I^2 (Nakagawa *et al.* 2021). We used the R package 'rotl' v.3.0.5 (Michonneau *et al.* 2016) and 'ape' v.5.2 (Paradis & Schliep 2019) to retrieve phylogenetic relationships of arthropods and calculate the branch lengths. We used the R package "ggplot2" v.3.3.5 (Wickham 2016) to make the plots.

Robustness of results

We checked for publication bias, i.e., a bias in peer-reviewed journals to publishing statistically significant results, with contour-enhanced funnel plots (Peters *et al.* 2008) and Egger tests for each taxon and metric (Nakagawa & Santos 2012). For the Egger tests, we modelled the $lnRR^{\Delta}$ as a function of the precision (1/SE) using source and observation as random effects (Nakagawa & Santos 2012).

We tested the sensitivity of our results to differences in the quality of the data sources by re-running our best models only with the highest quality sources. To that end, we assigned each effect size a quality score based on the following criteria:

1. The authors reported the mean and a measure of the variance of the mean (variance, standard deviation, standard error, confidence interval) or the variance measure could be derived from the raw data (1 point). No measure of variance could be extracted or calculated (0 points).

2. The authors reported a direct measure of abundance (1 point), such as the number of individuals, or only an indirect measure of abundance (0 points), such as the abundance of nests.

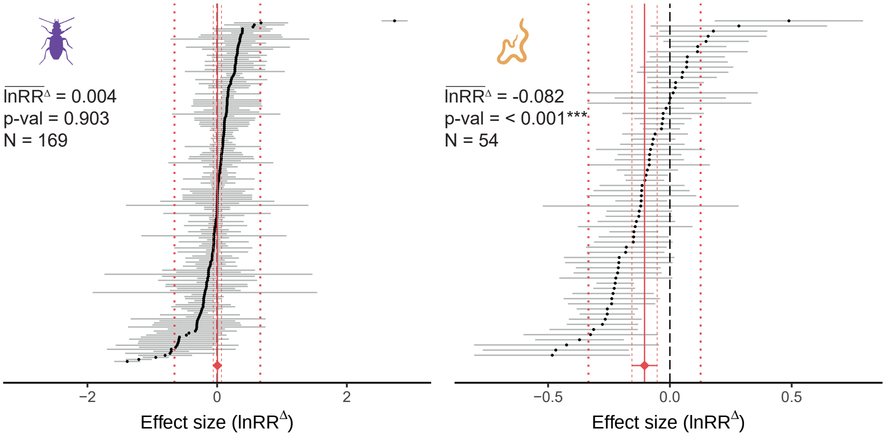
For the analysis with the highest quality sources, we included 1,848 observations (77% of total observations) for the abundance of arthropods and 157 observations (93% of total observations) for their richness; for nematodes, we included 1,158 observations for abundance (80% of total observations) and 53 for richness (80% of total observations). Moreover, we tested the effect of including the phylogeny of arthropods by refitting the best model without the phylogenetic relationships.

2.3 RESULTS

Overall effects of N enrichment

The random-effects model revealed a negative effect of N enrichment on the richness of nematodes (mean: -7.9%, CI: -11.5 – -4.2%; **Figure 2.2a**) and a positive effect of N enrichment on the abundance of arthropods (mean: 18.4%, 95% confidence interval (CI): 6.2 – 31.7%; **Figure 2.2b**). We did not find a response for the richness of arthropods (mean: 0.4%, CI: -5.8 – 7.0%; **Figure 2.2a**) nor for the abundance of nematodes (mean: -9.8%, CI: -27.8 – 12.7%; **Figure 2.2b**). Responses varied considerably between the individual studies, as indicated by the wide prediction intervals (**Figure 2.2**). The funnel plots and the Egger tests did not reveal publication bias (**Figure S2.5**).

a) Richness



b) Abundance

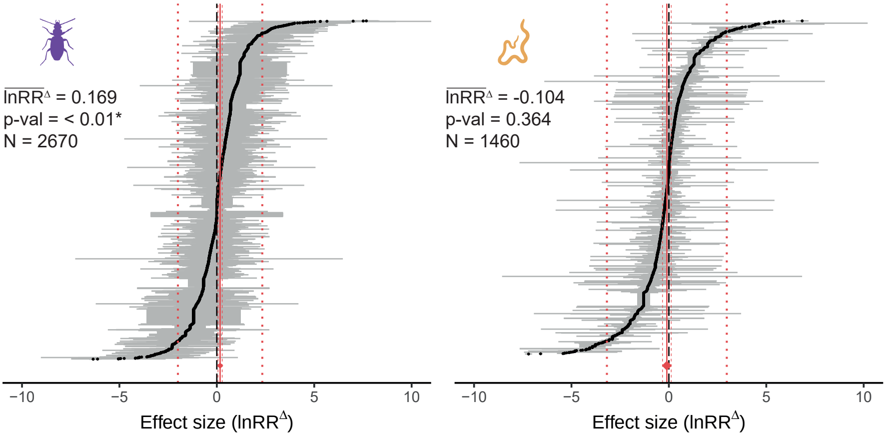


Figure 2.2 Forest plots of a) richness and b) abundance of arthropods (left) and nematodes (right). Effect sizes (lnRR$^{\Delta}$) are the black dots with 95% confidence intervals (CI) in grey. The vertical black dashed line at 0 indicates no change in abundance or richness compared to the control sites (no nitrogen added). Estimated mean lnRR$^{\Delta}$ and p-values of the random effects model are given. The red diamond and solid red line denote the average effect of the null model; dashed red lines indicate the 95% confidence interval of the average effect; dotted red lines represent the prediction interval indicating where 95% of future observations are expected to fall. Silhouettes are public domain obtained from “phylopic” (www.phylopic.org).

Richness response to increasing N addition

The best-supported model explaining the richness of arthropods was the null model, excluding the amount of N addition and any moderators. Further, the average response did not differ from zero (p-value = 0.90; **Figure 2.3a**, **Table S2.2**, **Table S2.3**). Including only high-quality data sources did not change this finding (**Figure S2.6**). The diversity of nematodes was best explained by the amount of N addition, including its quadratic term (Q_M = 14.96, p-value < 0.001; **Figure 2.3b**, **Table S2.4**, **Table S2.5**). The model predicted that the diversity of nematodes was consistently lower in the treated than the control plots, decreasing from -6% with ~50 kg/ha/yr to -30% with ~590 kg/ha/yr. We found the same trend when refitting the model based on high-quality publications only (**Figure S2.7**).

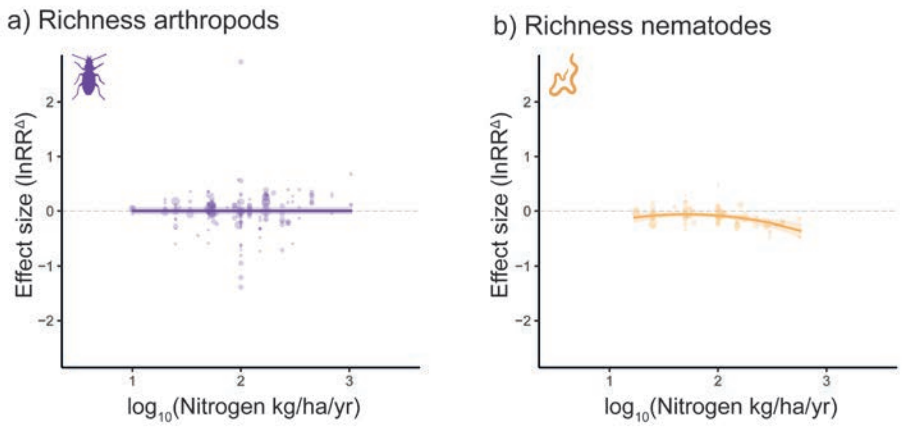


Figure 2.3 Best-supported models explaining the richness of a) arthropods and b) nematodes in relation to the amount of N addition (in kg/ha/yr). Shaded ribbons represent the 95% confidence intervals. The dashed line at 0 indicates no change in richness compared with the control sites (no nitrogen added). Point size represents observation weight. Silhouettes are public domain obtained from “phylopic” (www.phylopic.org).

Arthropod abundance response to increasing N addition

The abundance of arthropods was best explained by a quadratic response to N addition in interaction with metamorphosis type and mean annual temperature (MAT; $Q_M = 60.00$, p-value = < 0.001; **Figure 2.4**, **Table S2.6**, **Table S2.7**). Arthropods with complete metamorphosis declined in abundance from N additions of more than 100 kg/ha/year in warm climates, but not in cold climates. The abundance decline in warmer conditions was corroborated based on the data subset including only high-quality effect sizes (**Figure S2.8b**). Arthropods performing an incomplete-gradual metamorphosis showed a consistent increase in abundance in response to N, with particularly pronounced increases at N addition levels above approximately 100 kg/ha/yr, especially in colder areas (**Figure 2.4**). We found the same response when including only high-quality observations (**Figure S2.8b**). In contrast, arthropods without metamorphosis showed a negative relationship to the amount of N added, with abundance declines from levels of approximately 100 kg/ha/yr. However, this negative response was much less pronounced when we refitted the model based on high-quality effect sizes only (**Figure S2.8b**). The results did not change when the phylogenetic relationships among arthropod orders were excluded from the model (**Figure S2.9**).

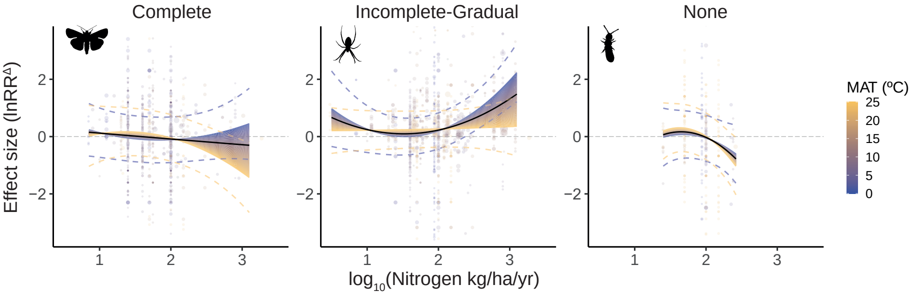


Figure 2.4 Best-supported model explaining the abundance of arthropods in relation to the amount of N addition. Dashed lines represent the 95% confidence interval for the highest (25 °C, yellow) and lowest (0 °C, blue) value of mean annual temperature (MAT) within the dataset. The solid black line represents the response corresponding with the average MAT (10 °C). The dashed line at 0 indicates no change in abundance compared with the control plots (no nitrogen added). Point size represents observation weight. Silhouettes are public domain obtained from "phylopic" (www.phylopic.org).

Nematode abundance response to increasing N addition

The best-supported model explaining the abundance of nematodes included the amount of N addition in interaction with mean annual precipitation (MAP) and feeding guild (Q_M = 62.93, p-value = < 0.001; **Figure 2.5**, **Table S2.8**, **Table S2.9**). In general, nematodes showed a positive relationship to N enrichment in wet areas and a negative relationship in dry areas, while the slope of the response varied between feeding guilds (**Figure 2.5**). With a mean annual precipitation of 80 mm/month (i.e., the mean across the dataset), we found positive response relationships for bacterivores, herbivores and predator-omnivores, with the bacterivores and herbivores increasing in abundances from N enrichment levels of about 100 kg/ha/yr. In contrast, plant-parasites and fungivores showed a negative response relationship to N, with fungivore abundance consistently lower in treated than control sites (**Figure 2.5**). We found the same responses when using only the high-quality observations (**Figure S2.10b**).

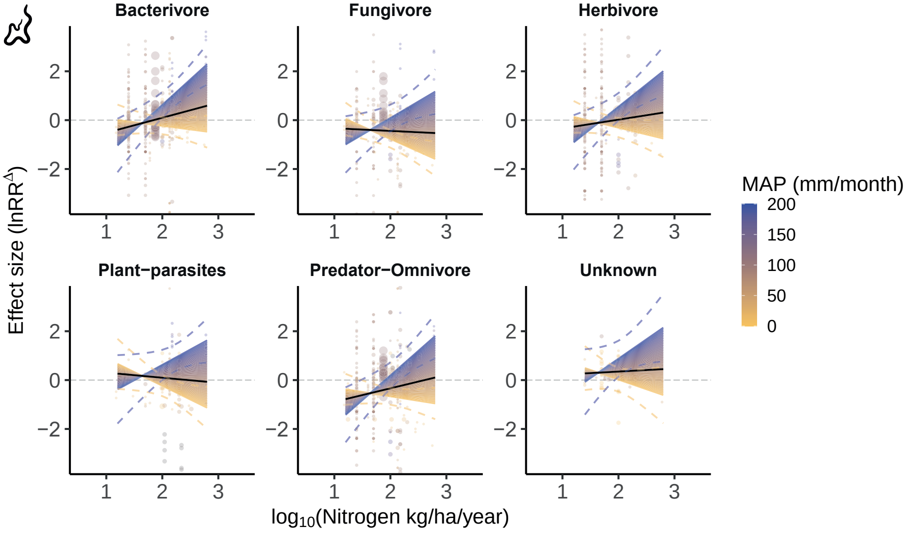


Figure 2.5 Best-supported model explaining nematode abundance in relation to the amount of N addition. Dashed lines represent the 95% confidence interval for the highest (blue) and lowest (yellow) value of mean annual precipitation (MAP). The solid black line represents the values for the average MAP (80 mm/month) of the dataset. The dashed line at 0 indicates no change in abundance compared with the control plots (no nitrogen added). Point size represents observation weight. Silhouette is a public domain obtained from “phylopic” (www.phylopic.org).

2.4 DISCUSSION

The increasing environmental concentrations of N due to anthropogenic activities are affecting plant diversity and ecosystems worldwide, but relatively little is known about N impacts on invertebrates. Based on a novel and extensive database of the findings of local N addition experiments across the globe, we demonstrate that information on species traits and climate conditions is essential to explain the response of invertebrates to anthropogenic N enrichment. We found that arthropods undergoing incomplete metamorphosis, such as true-bugs (*Hemiptera*), grasshoppers (*Orthoptera*) and spiders (*Araneae*), increase in abundance with increasing N addition, while arthropods that undergo complete metamorphosis showed a tendency to decline, particularly if we consider only high-quality observations. This difference may reflect that arthropods with incomplete metamorphosis have relatively large N requirements, while those with complete metamorphosis require more P (Fagan *et al.* 2002; Denno & Fagan 2003; Vogels *et al.* 2020; Villar-Argaiz *et al.* 2021). The increase in N concentrations may decrease the amount of available P (Lucas *et al.* 2011; Penuelas *et al.* 2020; Vogels *et al.* 2020), which may explain the negative response of arthropods with complete metamorphosis as they require P-rich molecules, such as RNA and ribosomes, to create new proteins. The N-induced abundance decrease of arthropods without metamorphosis, which are mostly represented by springtails (*Collembola*) in our database (**Figure S2.2**), may reflect the effect of acidification (Nijssen *et al.* 2017). Although springtails may benefit from increasing N via the increase of litter biomass, this positive effect might be overruled by the decrease in pH, to which springtails are very sensitive (Ke *et al.* 2004; Jänsch *et al.* 2005).

Our results further suggest that local temperature modifies the responses of arthropods to increasing N. In general, impacts of N on arthropod abundance were larger in warmer areas, which is in line with recent findings of larger impacts of N on invertebrate abundance in tropical than in temperate regions (Nessel *et al.* 2021). Synergistic impacts of warming and N enrichment on invertebrate fauna have been reported before. For example, the decline in butterfly species in the Netherlands has been ascribed to the combination of climate warming and the excess of N, which increases plant growth and hence microclimatic cooling during spring, ultimately reducing the development of thermophilous butterflies (WallisDeVries & Van Swaay 2006). Moreover, a recent study found that increased

N availability reduced springtail abundance while increasing oribatid mites, but under long-term drought, the positive effect of N was consistently removed (Peguero *et al.* 2021). However, as the interactive effects of N enrichment and climatic variables are still poorly studied (Porter *et al.* 2013; Nijssen *et al.* 2017), we recommend further research (e.g., multi-factorial experiments) to disentangle the underlying mechanisms.

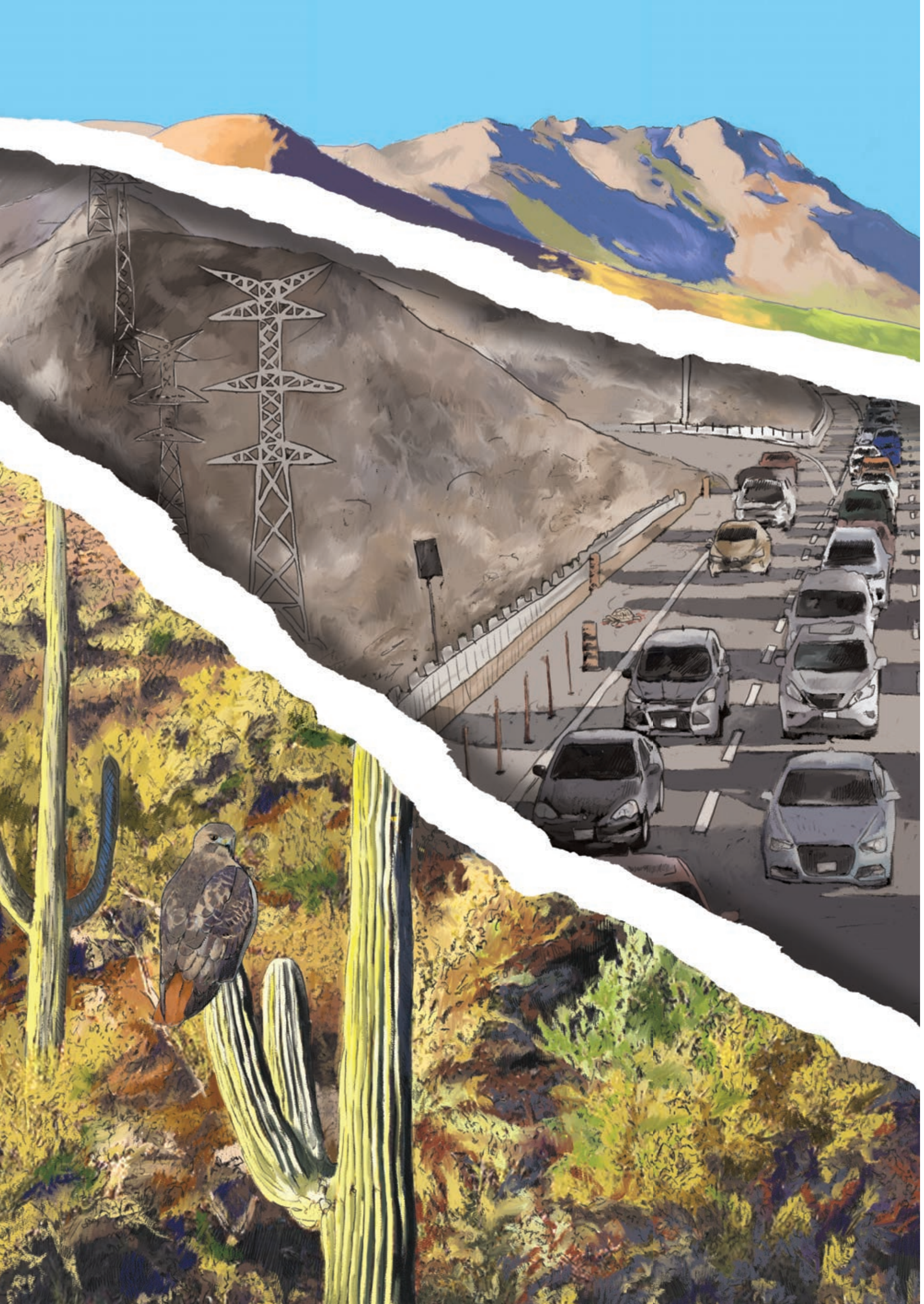
The contrasting responses of the different arthropod groups and the modulating effect of local climate may explain why we did not find an overall response of arthropod richness to N enrichment, as increases in the diversity of some groups may compensate for declines in others (Dornelas *et al.* 2014). The lack of response of arthropod richness to N addition is in line with recent research finding no support for an effect of N on invertebrate richness (Nessel *et al.* 2021). However, we found a clear overall decline in nematode richness with N enrichment. This might reflect that sensitive species are outcompeted by a few generalists benefitting from N addition, such as fast colonizing bacterivores (Bongers & Bongers 1998; Bongers 1999; Song *et al.* 2016; Shaw *et al.* 2019). In addition, nematode richness might be further reduced by high levels of N due to the increase in toxic N-compounds in the soil, such as ammonium, as well as the decrease in pH (Wei *et al.* 2012; Sun *et al.* 2013; Song *et al.* 2016; Shaw *et al.* 2019).

Our results point to a modulating effect of precipitation on nematode abundance responses to N enrichment, which has been previously reported by local studies (Sun *et al.* 2013; Hiltpold *et al.* 2017; Wang *et al.* 2021; Cui *et al.* 2022). In general, nematode abundance showed a negative relationship to N enrichment in dry areas and a positive relationship in wet conditions. This positive relationship may reflect that the addition of N enhances resource availability while the rain prevents the accumulation of toxic N-compounds through leaching and also increases the moisture in the soil, which is essential for the ecology of nematodes (Sun *et al.* 2013; Song *et al.* 2016; Hiltpold *et al.* 2017; Cui *et al.* 2022). The negative response relationship for N addition in drier conditions suggests that accumulation of N in the soil may flip the effects of N enrichment from positive to negative under drier climates. The response of nematode abundance to N enrichment was also dependent on their feeding guild. N enrichment may change the food composition in the soil from fungi-based to bacteria-based, decreasing the abundance and diversity of fungi (Treseder 2004, 2008; Shaw *et al.* 2019). These changes may explain why we found, on average, larger impacts of N addition on fungivores than on bacterivores (**Figure 2.5**, **Table S2.9**), which tend to thrive when N availability increases (Bongers & Bongers 1998; Bongers 1999; Song *et al.* 2016; Shaw *et al.* 2019). The negative average response of predator-omnivore nematodes may reflect that they are generally less tolerant to disturbances due to their longer life cycles (Bongers & Bongers 1998; Bongers 1999; Song *et al.* 2016). Finally, N availability may increase nitrophilous plants and nutrient-rich cells in their roots, which may benefit herbivore nematodes.

In the last decade, there have been many studies reporting invertebrate declines in various locations and world regions (Wagner 2020). It is, however, not yet clear whether this decline holds everywhere nor what are the drivers behind it (Simmons *et al.* 2019; Wagner 2020). The results of our study indicate that the anthropogenic enrichment of N may contribute to the decline of insects (i.e., arthropods with full metamorphosis), such as beetles, bees, butterflies or ants, as well as nematode diversity. This in turn may affect important ecosystem services such as pollination, pest control, or nutrient cycling. At the same time, N-induced increases in nematode herbivores and arthropods undergoing incomplete metamorphosis (such as grasshoppers, locusts, aphids or leafhoppers), may have negative consequences for food production, as these groups include agricultural pest species (Chen & Ruberson 2008). Since there is still a growing demand for the use of N fertilizers globally (FAO 2019), the impacts of N on invertebrate communities may be exacerbated in the future and may get amplified by climate change (Borer & Stevens 2022; Cui *et al.* 2022). Counteracting or mitigating measures of both N emissions and global warming is needed if invertebrate community integrity and ecosystem functioning are to be maintained (Nijssen *et al.* 2017; Stevens *et al.* 2018).

2.5 ACKNOWLEDGEMENTS

We are grateful to A. Taboada for sharing the data with us, to A. Sánchez-Tójar for useful advice on the phylogenetic analyses, and to J.J. Vogels for valuable discussion of the results. We are also thankful to all the scientists, data collectors and their funders that make their data publicly available. This study contributes to the GLOBIO project (www.globio.info).



CHAPTER 3

THE IMPACTS OF LINEAR INFRASTRUCTURE ON TERRESTRIAL VERTEBRATE POPULATIONS: A TRAIT-BASED APPROACH

Published in Global Change Biology, 28 (24), 7217– 7233

Authors

Melinda M.J. de Jonge[1*], Juan Gallego-Zamorano[1], Mark A.J. Huijbregts[1], Aafke M. Schipper[1,2], Ana Benítez-López[1,3,4]

[1]Department of Environmental Science, Radboud Institute for Biological and Environmental Sciences (RIBES), Radboud University, Nijmegen, The Netherlands

[2] PBL Netherlands Environmental Assessment Agency, The Hague, The Netherlands

[3]Integrative Ecology Group, Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas (EBD-CSIC), Sevilla, Spain

[4] Department of Zoology, Faculty of Sciences, University of Granada, Granada, Spain

ABSTRACT

While linear infrastructures, such as roads and power lines, are vital to human development, they may also have negative impacts on wildlife populations up to several kilometres into the surrounding environment (infrastructure-effect zones, IEZ). However, species-specific IEZs are not available for the vast majority of species, hampering global assessments of infrastructure impacts on wildlife. Here, we synthesized 253 studies worldwide to quantify the magnitude and spatial extent of infrastructure impacts on the abundance of 792 vertebrate species. We also identified the extent to which species traits, infrastructure type and habitat modulate IEZs for vertebrate species. Our results reveal contrasting responses across taxa based on the local context and species traits. Carnivorous mammals were generally more abundant in the proximity of infrastructure. In turn, medium to large sized non-carnivorous mammals (> 1 kg) were less abundant near infrastructure across habitats, while their smaller counterparts were more abundant close to infrastructure in open habitats. Bird abundance was reduced near infrastructure, with larger IEZs for non-carnivorous than for carnivorous species. Furthermore, birds experienced larger IEZs in closed (carnivores: ~ 130 m, non-carnivores: > 1 km) compared to open habitats (carnivores: ~ 70 m, non-carnivores: ~ 470 m). Reptiles were more abundant near infrastructure in closed habitats but not in open habitats, where abundances were reduced within an IEZ of ~ 90 m. Finally, IEZs were relatively small in amphibians (< 30 m). These results indicate that infrastructure impact assessments should differentiate IEZs across species and local contexts in order to capture the variety of responses to infrastructure. Our trait-based synthetic approach can be applied in large-scale assessments of the impacts of current and future infrastructure developments across multiple species, including those for which infrastructure responses are not known from empirical data.

3.1 INTRODUCTION

Linear infrastructures such as roads, railways and power lines are vital to human development and span across a large part of the earth's surface (Dulac 2013; Meijer *et al.* 2018). For example, by 2010 there were over 40 million km of paved roads and almost 1 million km of railway tracks globally (Dulac 2013). Linear infrastructure is expected to significantly increase in the coming decades, especially in developing, biodiversity-rich nations (Dulac 2013; Laurance *et al.* 2014). However, linear infrastructure has documented negative impacts on biodiversity (Benítez-López *et al.* 2010; van der Ree *et al.* 2015). As many future infrastructure projects are planned in some of the world's remaining wilderness areas such as tropical forests (Laurance *et al.* 2014; Meijer *et al.* 2018), it is important to synthesize, quantify and understand the impacts of linear infrastructure on biodiversity. This will help not only to evaluate potential negative consequences of future infrastructure developments, but also to design and prioritise mitigation measures.

Infrastructure construction and use affect wildlife through various processes, with habitat destruction and fragmentation, and increased mortality being the most obvious (van der Ree *et al.* 2015). Additionally, infrastructure use may degrade the surrounding habitat through chemical and noise pollution and the creation of habitat edges (Forman & Alexander 1998; van der Ree *et al.* 2015). Further, infrastructure may pose a barrier to species' movement, potentially limiting gene flow between conspecifics and reducing access to important food resources (Forman & Alexander 1998; Holderegger & Di Giulio 2010; van der Ree *et al.* 2015; Skuban *et al.* 2017). As a result, linear infrastructure may affect wildlife populations up to several kilometers into the surrounding environment. This impact zone is commonly known as the road-effect zone in road ecology (Forman & Alexander 1998), and here we expand the term to infrastructure-effect zone (IEZ) to encompass also other types of infrastructure.

While impacts have been most extensively studied for paved roads, various studies report that wildlife populations are also affected by other infrastructure, including railways and unpaved roads (Benítez-López *et al.* 2010; Maynard *et al.* 2016; Barrientos *et al.* 2019) as well as power and pipe lines (Richardson *et al.* 2017; Biasotto & Kindel 2018; D'Amico *et al.* 2018). For example, power line collisions and electrocutions have been identified as one of the main avian mortality causes, especially for raptors (Biasotto & Kindel 2018). However, the impact of different types of infrastructure on the surrounding wildlife may vary, e.g., paved roads may have a higher impact on wildlife than unpaved roads because they are often wider and are more intensively used (van der Ree *et al.* 2015). Infrastructure impacts may further depend on the characteristics of the surrounding habitat. Closed habitats, like forests, are usually more affected by edge effects (Khamcha *et al.* 2018), while noise and air pollution travel further in open habitats (Forman & Alexander 1998; Benítez-López *et al.* 2010; van der Ree *et al.* 2015).

Infrastructure impacts also differ between species (Benítez-López *et al.* 2010; Rytwinski & Fahrig 2012; van der Ree *et al.* 2015). Species with low reproductive rates and long generation times may be disproportionately impacted by infrastructure collisions and mortality as their populations recover more slowly than populations of species with high reproductive rates (Forman *et al.* 2003; Rytwinski & Fahrig 2011). Additionally, species with large home ranges are more likely to encounter infrastructure thus increasing the chance of mortality (Forman *et al.* 2003; Rytwinski & Fahrig 2011; but see Pfeifer *et al.* 2017). As home range size and reproductive rate are related to body size (Hendriks 2007; Tucker *et al.* 2014), large species are expected to be disproportionately affected by infrastructure (Rytwinski & Fahrig 2011, 2012). In contrast, small species may be more abundant in infrastructure verges due to changes in the vegetation or because their larger predators are less abundant (Forman & Alexander 1998; Ascensão *et al.* 2012; Planillo *et al.* 2018; Ouédraogo *et al.* 2020). Lastly, carnivores may be more affected than herbivores as they generally have larger home ranges and lower reproductive rates (Hendriks 2007; Tucker *et al.* 2014). However, some carnivores may be attracted to infrastructure for resources, such as carrion or small mammals that live in the verges (Forman & Alexander 1998; Morelli *et al.* 2014; Planillo *et al.* 2018).

Despite these context-dependencies, the impacts of linear infrastructure on biodiversity have so far been assessed based on aggregated biodiversity indicators (Benítez-López *et al.* 2010; Torres *et al.* 2016), or for a limited number of species only (e.g., Andrasi *et al.* 2021; Carter *et al.* 2022). These limitations typically result from a lack of data on species-specific responses to infrastructure rather than a lack of recognition that infrastructure impacts may differ between habitats, infrastructure types and species (Tulloch *et al.* 2019). While various studies have investigated the interplay between species traits and infrastructure impacts, none have systematically quantified the relationship between species traits and infrastructure-effect zones. Recently, Tulloch *et al*., (2019) proposed using expert opinions to delineate species-specific infrastructure-effect zones for various types of infrastructure. However, the plethora of local empirical studies spanning many species from various taxa offers the possibility of employing a trait-based meta-analytical approach to quantify the impacts of linear infrastructure across vertebrate species.

Here we quantified the magnitude and spatial extent of linear infrastructure impacts on the abundance of terrestrial vertebrates (mammals, birds, amphibians, reptiles). We performed an extensive meta-analysis of 253 studies, from 110 primary sources, spanning 160, 443, 97 and 92 species of mammals, birds, reptiles and amphibians, respectively. We used meta-regression models to identify the extent to which species traits (i.e. body size and diet), infrastructure type (i.e. paved roads, unpaved roads, pipelines, power lines) and habitat (i.e. open or closed) modulate infrastructure effects on vertebrate abundance. We hypothesized that large vertebrates are most negatively impacted by infrastructure, with paved roads having a larger impact than unpaved roads, followed by pipe and power lines (**Table 3.1**). Additionally, we expected narrower IEZs but with larger abundance declines in closed compared to open habitats. Finally, we expected carnivorous species to be more abundant in the proximity of roads because of their use as feeding grounds (roadkills) or as corridors for dispersal

Table 3.1 Moderators included in our meta-regression models with expected relationships, background, taxonomic groups for which each moderator is included and source of data source.

Predictor variable	Hypothesis	Terms	Taxonomic group (data source)
Distance (m, $\log_{10}$-transformed)	– The negative impacts of infrastructure on the surroundings, such as noise and chemical pollution, decrease with increasing distance from infrastructure (Forman & Alexander 1998; van der Ree *et al.* 2015). – Some animals make use of infrastructure corridors which may lead to increased abundances at very close distances (Andersen *et al.* 2017; Ouédraogo *et al.* 2020). Expectation: Abundances decrease with increasing distance in the direct vicinity of infrastructure but increase steadily thereafter.	Distance + Distance^2	All (from source)
Diet (% use of vertebrates, fish and scavenging)	– Carnivorous mammals and birds reportedly feed on roadkilled carrion (Morelli *et al.* 2014). Scavenging birds may be able to detect carcasses in infrastructure clearings more easily than those in the habitat interior (Lambertucci *et al.* 2009). Birds of prey have been spotted perching close to infrastructure before hunting on rodents or other species which are more abundant in the proximity of infrastructure (Morelli *et al.* 2014). Species with diets consisting of a larger percentage of vertebrates or scavenging may be more likely to venture close to the infrastructure than those with a small percentage of vertebrate use. Expectation: Attraction to infrastructure with increasing percentage of diet consisting of vertebrates.	Distance x Diet + Distance^2 x Diet	Birds: (EltonTraits) Mammals: (EltonTraits) Reptiles & Amphibians: Not included
Mean body mass (g, $\log_{10}$-transformed)	– Large species have low reproductive rates and may be more negatively impacted by infrastructure as their populations recover slowly from population declines (Rytwinski & Fahrig 2012). – Larger species have larger home ranges leading them to interact with infrastructure more often which makes them more susceptible to traffic collisions or electrocution from power lines (Rytwinski & Fahrig 2012; D'Amico *et al.* 2018). – Infrastructure verges may provide a refuge for small vertebrates (Morelli *et al.* 2014; Ouédraogo *et al.* 2020). – Large birds have lower song frequencies which have a higher overlap with the frequency of traffic noise (Francis 2015). Expectation: Large species are more affected and experience larger effect zones.	Distance x BM + Distance^2 x BM	Mammals: (EltonTraits) Birds: (EltonTraits) Reptiles: (Feldman *et al.* 2016) Amphibians: (Santini *et al.* 2018, 2018, estimated from snout-vent-length)

Predictor variable	Hypothesis	Terms	Taxonomic group (data source)
Infrastructure type 3(4)-levels - paved roads - unpaved roads - non-traffic (includes power lines for mammals, reptiles and amphibians) - power lines (birds only)	– Roads have an additional negative impact from traffic disturbance (noise, light, chemical emissions) and traffic mortality (van der Ree *et al.* 2015; Richardson *et al.* 2017). – Traffic volume and speed is higher on paved than unpaved roads leading to more disturbance as well as higher traffic mortality (Forman & Alexander 1998). – Paved road surfaces might be avoided (Brehme *et al.* 2013; Ascensão *et al.* 2016; Chen & Koprowski 2016). – Power lines might add to mortality rates for birds (Biasotto & Kindel 2018; D'Amico *et al.* 2018). Expectation: Paved roads have a larger impact than unpaved roads which in turn have a larger impact than non-traffic infrastructure such as seismic lines, pipeline and power lines.	InfraType	All (from source)
Habitat 2-levels -open -closed	– Noise and chemical pollution travel further in open habitats potentially increasing the width of the infrastructure effect-zone (van der Ree *et al.* 2015). – Edge effect may be more pronounced in closed habitats leading to larger effects close to the infrastructure (van der Ree *et al.* 2015). Expectation: Negative impact near infrastructure is larger in closed habitats, but effect-zone is wider in open habitats.	Distance x Habitat + Distance^2 x Habitat	All (from source)

3.2 METHODS

Data collection

Literature search

We collated data from studies included in a previous meta-analysis on infrastructure impacts on biodiversity (Benítez-López *et al.* 2010) and complemented it by searching for additional data in peer-reviewed literature in the ISI Web of Science and Google Scholar in April 2020 using the following search terms: (vertebrate* OR *bird* OR *fauna OR reptil* OR lizard* OR snake* OR turtle* OR tortoise* OR crocodil* OR amphibia* OR frog* OR toad* OR salamander* OR mammal*) AND (infrastruct* OR road$ OR motorway* OR highway* OR "train track" OR railway* OR "transmission line" OR power$line* OR "seismic line" OR pipeline*) AND (disturbance* OR effect* OR impact* OR distance* OR proximity OR avoidance OR influence) AND (density OR abundan* OR encounter$ OR population$ OR count$ OR persistence). We also used ProQuest Dissertations and Theses repository (https://www.proquest.com/products-services/dissertations/) and Open Access Theses and Dissertations repository (https://oatd.org/) to search for additional grey literature. We also used a "snowball" method, in which we reviewed the references of all included papers to identify additional relevant studies based on their title and whether they were cited in a context that suggested they collected data on infrastructure impacts on vertebrates. While we used an English-based literature search, studies in Spanish (Delgado et al., 2004; Vargas-Salinas et al., 2011), German (Ballasus & Sossinka, 1997) and Portuguese (Bager & da Rosa, 2012) retrieved from the original dataset by (Benítez-López et al., 2010) or via cross-referencing were also included. Full details of the literature search and modifications of the search string to the specifications of each database can be found in the Supplementary Materials (S1 Search Strategy).

Inclusion criteria

After an initial screening based on title and abstract, we selected publications that met the following inclusion criteria:

a. The authors reported on the effect of linear infrastructure on nearby populations of birds, mammals, reptiles or amphibians.

b. The authors reported abundances or densities at species or genus level.

c. The authors reported abundances or densities from at least one site close to the infrastructure and one undisturbed and more distant site. Alternatively, the authors reported abundances at several distances from the infrastructure (with a minimum of two distances), where the one furthest away is considered a control, undisturbed site.

The initial title and abstract screening was done by MMJdJ, AB-L and MAJH. When in doubt about the relevance of a particular study, the authors discussed among each other to reach consensus about its transfer to the next screening phase. Full-text screening and data extraction was split between JG-Z and MMJdJ. We evaluated inter-observer agreement between the two screeners by calculating Cohen's kappa (κ) based on a random selection of 50 sources ($\kappa = 0.92$).

The search string and database from Benítez-López *et al.,* (2010) yielded 5,794 unique publications from which we selected 809 publications based on the title and abstract. We added an additional 5 sources through cross-referencing (See Fig S1 in the Supplementary Information for a PRISMA flow diagram showing the screening process). Based on full-text screening we selected 110 publications published between 1979 - 2020 for data extraction. A list of all data sources is provided in the SI.

Data extraction

We structured the data into data source (i.e. publication), study and species, where a single data source may contain one or more studies, depending on whether data is reported for one or more infrastructure types or distinct locations. A study contains one or more species for which abundances are reported at least in one site close by infrastructure (disturbed), and one site further away or in a designated control area (control) in relation to a specific infrastructure. Paired sites (disturbed and control) were always reported within the same study, had similar biophysical (habitat) characteristics, and reported species abundance using the same sampling method.

From each study, we extracted the mean abundance of each species at each distance from the infrastructure, the standard deviation of the mean abundance, and the sample size. We extracted the data from text and tables when possible, or from graphs using WebPlotDigizer (https://automeris.io/WebPlotDigitizer/). When the study reported medians instead of means or range or interquartile range instead of the standard deviation, we calculated the mean and standard deviation following Wan *et al.* (2014). Abundances were reported as various metrics including: number of individuals, population density (individuals/ha), group density (groups/ha), trapping rates (individuals per trapping effort), dropping or scat density (scats/ha), nest densities (nests/ha) or territory density (territories/ha). When abundances were reported in distance intervals we took the middle distance point of the interval as the input distance.

We also extracted the following study characteristics: type of infrastructure (e.g., dirt road, secondary paved road, highway, power line, seismic line, pipeline, logging tracks), habitat (e.g., grassland, cropland, shrubland, tropical forest, temperate forest), location (continent, country), geographic coordinates (longitude, latitude) and year(s) in which the empirical data collection was done. We classified the type of infrastructure into (i) paved roads (including highways), (ii) unpaved roads (dirt roads, gravel roads), and (iii) non-traffic infrastructure (trails, seismic lines, pipelines, power lines). For birds, we included power lines as a separate category as we expect an additional impact from power line collisions compared to other non-traffic infrastructure (Biasotto & Kindel 2018). We classified habitat type into open (grasslands, croplands, shrublands) and closed (forests). If geographical coordinates were not provided by the authors, we retrieved them by geo-referencing maps or descriptions of the study area in the paper using Google Earth.

Our final database contained 3,912 pairwise abundance comparisons between disturbed and non-disturbed areas distributed across 26 countries and 6 continents (**Figure 3.1**). Of these, 863 comparisons were for mammals (160 species in 17 orders and 38 families), 2,471 for birds (443 species in 22 orders and 88 families), 362 for reptiles (97 species in 2 orders and 22 families) and 216 for amphibians (92 species in 2 orders and 16 families). Distance to infrastructure ranged from 0 to 4,500 m for mammals, from 0 to 3,485 m for birds, from 0 to 1,600 m for reptiles and from 0 to 120 m for amphibians. The majority of the comparisons came from paved roads (53% of all comparisons) and closed habitats (69% of all comparisons; we found no data from open habitats for amphibians; see Tables S3.1 - S3.4 for an overview of the number of effect sizes per habitat and infrastructure type).

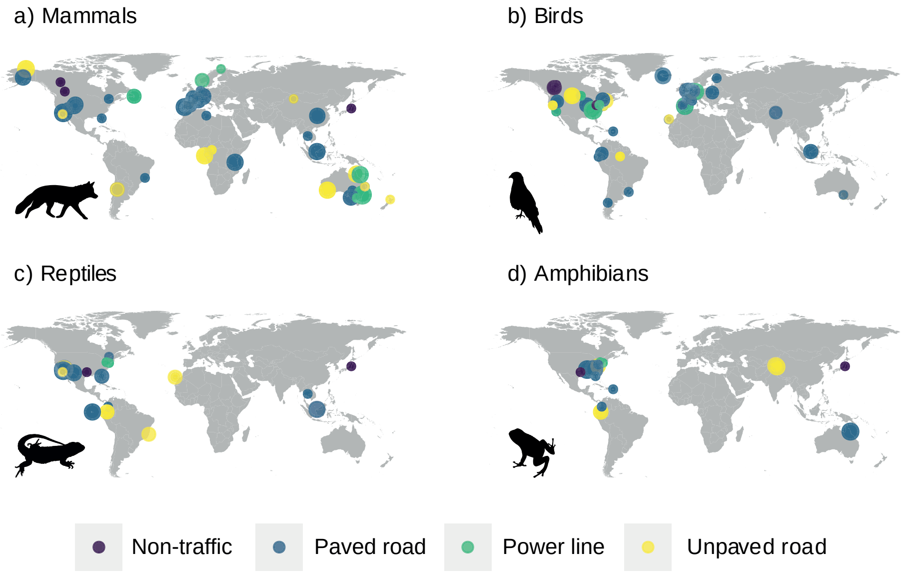


Figure 3.1 Spatial distribution of studies included in our meta-analysis for each species group. Size of points is proportional to the number of species included in each study. Power lines are shown separately but were combined with non-traffic infrastructure for mammals, reptiles and amphibians in all analyses. Silhouettes are public domain obtained from "phylopic" (www.phylopic.org).

Species traits

We gathered data on mean body mass (g) and diet (% of diet consisting of vertebrates, fish or scavenging) for mammals and birds from the EltonTraits database (Wilman *et al.* 2014). We calculated the mean body mass for amphibians from mean snout-vent-length (SVL) using the allometric relationships developed by Santini *et al.* (2018). We extracted mean SVL from Santini *et al.* (2018) and AmphibiaWeb (AmphibiaWeb 2016; https://amphibiaweb.org). We obtained mean body mass of reptiles from allometric relationships with SVL or total length (Feldman *et al.* 2016). When abundances were given on the genus level (e.g., *Cephalophus sp.*) or were aggregated for multiple species within a genus (e.g., *Felis sylvestris & F. catus*), we calculated the mean body mass and diet (% of diet consisting of vertebrates, fish or scavenging) across all species in the genus or aggregated group (9% of mammals, <1% of birds).

Body masses in our database ranged from 3.6 to $3.9*10^{6}$ g for mammals, 4.3 to $1.1*10^{4}$ g for birds, 0.7 to $3.5*10^{4}$ g for reptiles, and $1.4*10^{-3}$ to $3.1*10^{2}$ g for amphibians (**Figure S3.2**). Most mammal and bird species in our database were non-carnivorous, i.e. with 0% of the diet consisting of other vertebrates or scavenging (63% of mammals and 73% of birds) and only 8% of mammals and 6% of birds had a diet consisting of ≥ 80% vertebrates, fish or scavenging (**Figure S3.3**). While percent diet is a continuous variable in our models, we present most of our results for non-carnivorous and carnivorous species as defined above.

Effect size

For each study *i*, species *s* and distance from infrastructure *d*, we calculated the effect size as the natural logarithm of the response ratio (LRR_{isd}), i.e., the logarithm of the ratio of the mean abundance at the affected site ($\bar{A}_{isd}$) and the mean abundance at the control site ($\bar{A}_{isc}$). Because many of the included studies had a small sample size, we applied a small sample bias correction to the effect sizes following the Delta method (LRR^{Δ}; Lajeunesse, 2015):

$$LRR^{\Delta}_{isd} = log\left(\frac{\bar{A}_{isd}}{\bar{A}_{isc}}\right) + \frac{1}{2}\left(\frac{SD^2_{isd}}{n_{isd}\bar{A}^2_{isd}} - \frac{SD^2_{isc}}{n_{isc}\bar{A}^2_{isc}}\right)$$

Equation 3.1

where SD_{isd}^2 is the sampling variance of the mean abundance at the affected site and SD_{isc}^2 is the sampling variance of the mean abundance in the control site. Effect sizes are therefore negative ($LRR < 0$) or positive ($LRR > 0$) if abundance estimates are lower or higher, respectively, near infrastructure. In some cases, a species was not detected in areas close to the infrastructure or the control area, precluding calculation of the effect size. To circumvent this, we used the truncated sample means ($\tilde{A}$) following Pustejovsky (2015):

$$\tilde{A} = \begin{cases} \bar{A} & if \quad \bar{A} > 0 \\ 1/(2nD) & if \quad \bar{A} = 0 \end{cases}$$

Equation 3.2

where *n* is the sample size of the corresponding mean and *D* corrects for the scale on which the abundance is reported (e.g., *D* is equal to 1 when outcomes are reported as total number of individuals averaged over *n* samples while *D* is equal to the number of trap-nights when outcomes are reported as number of individuals per trap night averaged over *n* samples). Treatment or control mean was equal to zero for 20%, 19%, 20% and 26% of the comparisons for mammals, birds, reptiles and amphibians, respectively.

Observed effect sizes (LRR^{Δ}) were weighed by the inverse of their corresponding sampling variances, which were calculated as:

$$\mathrm{VAR}(LRR^{\Delta}_{isd}) = \frac{SD^2_{isd}}{n_{isd}\tilde{A}^2_{isd}} + \frac{SD^2_{isc}}{n_{isc}\tilde{A}^2_{isc}} + \frac{1}{2}\left(\frac{SD^4_{isd}}{n^2_{isd}\tilde{A}^4_{isd}} + \frac{SD^4_{isc}}{n^2_{isc}\tilde{A}^4_{isc}}\right) \qquad \text{Equation 3.3}$$

When no variance estimate was reported, or if the reported variance was equal to zero, we estimated it by assuming that the data follow a Poisson distribution so that $\tilde{A} = SD^2$ (22, 63, 26, and 54% of response ratios for mammals, birds, reptiles and amphibians, respectively).

Analysis

Overall impacts of infrastructure

We ran four multilevel random-effects meta-analyses to estimate the overall impact of infrastructure (regardless of its proximity or any context-dependent factors or species traits) on mammal, bird, reptile and amphibian abundances, respectively. We included observation ID as a random effect (σ_1^2) to account for residual heterogeneity. We also included species (σ_3^2) nested in order or family (σ_2^2) and study (σ_5^2) nested in source (σ_4^2) as random effects to account for non-independence of response ratios and assess variance between sources, studies, orders, families and species. We included order for mammals and birds because body mass is conserved within orders for these groups (Böhning-Gaese & Oberrath 1999; Smith *et al.* 2004). For reptiles and amphibians, there were too few orders, two for each group, to include as random effects term and body mass can vary substantially between families within the same order (Mesquita *et al.* 2016; Phung *et al.* 2020). To control for non-independence due to multiple treatments per study sharing the same control, we used the full variance-covariance matrix in our analysis following Olkin & Gleser (2009) and Lajeunesse (2011). We assessed residual heterogeneity of the meta-analyses using the weighted least squares extension of Cochran’s Q-test (Q_E).

Influence of distance, habitat type, infrastructure type and species traits

We first examined the relationship between the LRR^{Δ} and distance to infrastructure and derived overall infrastructure effect-zones (IEZs, distance to infrastructure where the modelled $LRR^{\Delta} = 0$) for each of the four species groups using single mixed-effects meta-regressions. We $\log_{10}$-transformed distance to infrastructure and included it as both a linear and a quadratic term to account for possible non-linear responses. Next, we ran multiple mixed-effects meta-regressions for each taxonomic group to examine variations in the relationship between LRR^{Δ} and distance while controlling for the effects of habitat type, infrastructure type, body size (g, $\log_{10}$-transformed) and diet (% of diet consisting of vertebrates, fish or scavenging, only for mammals and birds). For body size, diet and habitat we also included interaction terms with distance as we expected that the relationship between infrastructure impacts and distance are modulated by these moderators (see details in **Table 3.1**). We included infrastructure type only as main effect (see details in **Table 3.1**). Prior to the analysis, we tested for collinearity between body mass and diet for mammals (Spearman *rho* = 0.07, **Figure S3.3a**) and birds (Spearman *rho* = 0.56, **Figure S3.3b**). For each taxon we selected the most parsimonious model based on the Akaike Information Criterion (AICc) calculated from the full log-likelihood (Verbyla 2019). For the selected models, we evaluated model fit by calculating the marginal and conditional explained heterogeneity (R_m^2 and R_c^2; Nakagawa & Schielzeth 2013) and quantified the amount of heterogeneity explained by the moderators using the omnibus test (Q_M). We also tested main effects of individual moderators and interactions with Q_M, where interaction terms were dropped to test the main effects. Lastly, we checked profile likelihood plots to ensure the identifiability of the variance components (σ_1^2: observation-level variability, σ_2^2: order or family-level variability, σ_3^2: species-level variability, σ_4^2: source-level variability, σ_5^2: study-level variability; **Figure S3.4-S3.7**). Models are deemed non-identifiable when there is more than one likely parametrization of the variance components, which results in a multimodal or flat profile (Raue *et al.* 2009).

Results are reported as LRR^{Δ}, percentage abundance change (percentage change = $(\exp(LRR^{\Delta}) - 1) * 100$) or width of infrastructure effect-zone (IEZ). All models were fitted with REML (Restricted Maximum Likelihood) using the package metafor v3.0-2 in R4.0.1 (Viechtbauer 2010). We used ggplot2 v3.3.3 (Wickham 2016) and pals v1.7 (Wright 2021) for data visualization, and foreach v1.5.1 (Walling 2020b) and doParallel v1.0.16 (Walling 2020a)to run models in parallel for model selection. All R code as well as the final database will be made publicly available at https://github.com/MelindadeJonge/InfraMetaAnalysis upon publication.

Robustness of results

Publication bias

We assessed publication bias using Funnel plots and Egger tests for each species group (Egger *et al.* 1997). We performed Egger tests by modelling meta-analytic residuals as a function of precision (1/SE) and extracting the modelled intercept.

Sensitivity to small sample means

The LRR^{Δ} is sensitive to cases where the mean abundance of either the affected or control site is near zero (Lajeunesse 2015). Therefore, we tested the robustness of our results to small sample means by selecting LRR^{Δ} for which the small-sample corrected standardized mean of both the control and infrastructure site passed Geary's rule (Lajeunesse 2015):

$$\frac{\tilde{A}}{SD}\left(\frac{4n^{3/2}}{1+4n}\right) \geq 3 \qquad \text{Equation 3.4}$$

This selection reduced the number of effect sizes to 279 (33% of effect sizes) for mammals, 943 (38%) for birds, 140 (39%) for reptiles, and 63 (29%) for amphibians. We compared the results of the random-effects meta-analysis using the selected data set to the results obtained from the complete database.

Imputation of sampling variance

To test the robustness of our results to the imputation of missing sampling variances we also imputed missing SD using the "Bracken1992" and the "HotDeckNN" approach and compared the random-effects meta-analysis results with our default approach for imputing missing SD ("Poisson"). With the "Bracken1992" approach, missing SD are estimated from the SD to mean ratio from all studies with complete information (Bracken 1992; Lajeunesse *et al.* 2013). The "HotDeckNN" approach uses Rubin & Schenker (1991) resampling approach to fill missing SD with SD of studies with complete information that have a similar mean (Lajeunesse *et al.* 2013). For the "HotDeckNN" approach we imputed missing SD 100 times leading to 100 meta-analytical estimates. We also compared the results from the three imputation methods with the results from the subset of the data for which SDs were available. We used the package metagear v0.7 (Lajeunesse 2016) to impute standard deviations based on the "Bracken1992" and "HotDeckNN" approach.

Study quality

To test the sensitivity of our results to the quality of the data sources we assigned each effect size quality score based on the following criteria:

a. The authors reported abundances on the species level or these could be derived from the raw data (1 point). The authors reported abundance on the genus level (0 points).

b. The authors reported abundances in undisturbed sites or the authors reported abundances at a distance from the infrastructure that was equal to or larger than the home range of the species as reported by the authors (1 point). The largest distance between a sampling site and the infrastructure was smaller than the reported home range of the species or the home range of the species was not specified (0 points).

We repeated our random-effects meta-analysis three times: once while including all effect sizes, once excluding effect sizes based on abundances aggregated over multiple species (a = 0, mammals: 1%, birds: 4%, reptiles: 0%, amphibians: 0%) and once excluding effect sizes for which the control site was not explicitly defined as undisturbed or at larger distances from infrastructure than the species' home range (b = 0, mammals: 64%, birds: 89%, reptiles: 56%, amphibians: 66%).

3.3 RESULTS

Overall effects of infrastructure

We found evidence of decline in species abundance across all infrastructure sites when compared to the corresponding control sites for amphibians, but not for mammals, birds and reptiles (LRR^{Δ} [95% CI] of mammals: 0.07 [-0.15 ⍰ 0.30]; birds: -0.13 [-0.33 ⍰ 0.06]; reptiles: -0.03 [-0.22 ⍰ 0.17]; amphibians: -0.22 [-0.41 ⍰ -0.02]). Cochran's Q (Q_E) indicated significant residual heterogeneity for all species groups (**Table S3.5**). When we removed LRR^{Δ} with small sample means our results were similar to those from the full database but had larger confidence intervals (**Table S3.6**). We found no evidence of publication bias for any of the four species groups (**Figure S3.8**). Mean response ratios were similar for all imputation approaches (**Table S3.7**), and when studies were excluded based on the quality criteria (**Figure S3.9**).

Influence of distance to infrastructure

Across species, habitats and infrastructure types, we found that the observed LRR^{Δ} were non-linearly related to distance to infrastructure ($\log_{10}$-transformed) in all four species groups (**Figure 3.2**, **Table S3.5**). Mammal abundances were increased by 23% at 1 m from infrastructure, declined to -2% within the first 40 m, and then increased again leading to infrastructure effect-zones (IEZs) of 105 m (**Figure 3.2a**, **Table S3.5**). Similarly, bird abundances were increased by 11% at 1 m from infrastructure and declined to -18% over the first 35 m with an overall IEZ of 655 m (**Figure 3.2b**, **Table S3.5**). Reptile abundances followed a similar pattern but were reduced by 20% near infrastructure with an IEZ of 48 m (**Figure 3.2c**, **Table S3.5**). Abundances of amphibians were reduced by about -52% at a distance of 1 m to infrastructure, but increased rapidly with distance from infrastructure, yielding an IEZ of 27 m (**Figure 3.2d**, **Table S3.5**).

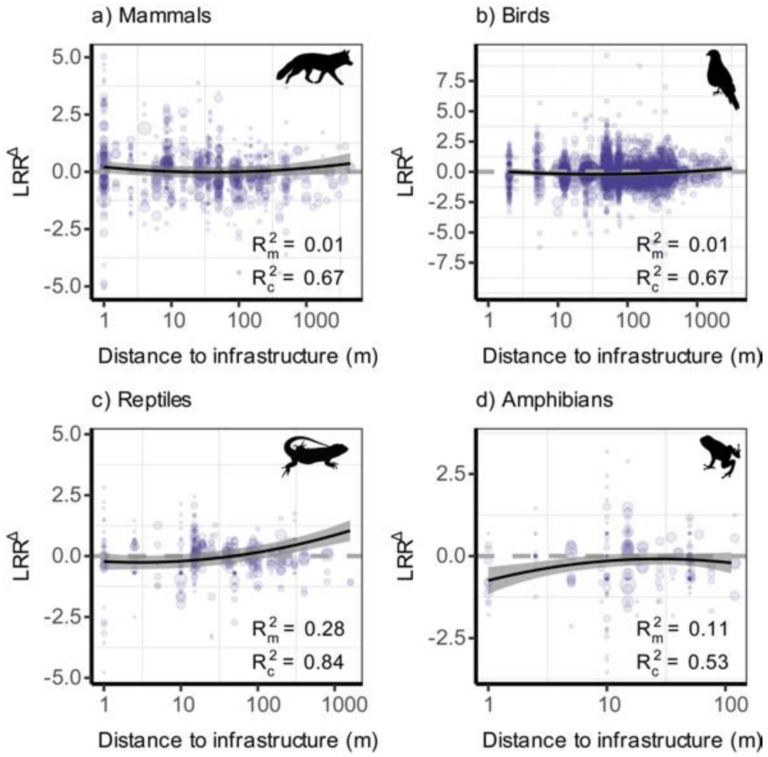


Figure 3.2 Change in species abundance (LRR$^{\Delta}$, natural logarithm of response ratio between abundance at infrastructure site and abundance at control site) as a function of distance to infrastructure for mammals (a), birds (b), reptiles (d) and amphibians (d). Models were fitted using multilevel meta-regression models with distance to infrastructure ($\log_{10}$-transformed, including quadratic term for birds and reptiles) as moderator and observation ID, source ID, study ID (nested in source ID), order ID (or family ID for reptiles and amphibians) and species ID (nested in order or family) as random effects. Size of data points is proportional to the natural logarithm of the inverse of the sampling variance. Grey bands represent the 95% CI of the modelled relationship between LRR$^{\Delta}$ and distance to infrastructure. LRR$^{\Delta} < 0$ indicates abundance decline, LRR$^{\Delta} > 0$ indicates abundance increase and LRR$^{\Delta}$=0 indicates no change (dashed grey line). Silhouettes are public domain obtained from "phylopic" (www.phylopic.org).

Influence of species traits, infrastructure type and habitat characteristics

IEZs varied across species based on their body mass and diet, and according to the environmental context (infrastructure type and habitat type). The moderators of infrastructure impacts differed among the four species groups (**Table 3.2**, **Table S3.8-S3.11**). Infrastructure impacts on mammal abundance were best explained by body mass, diet and habitat, and their interactions with distance to infrastructure, which collectively accounted for 9% of the heterogeneity in the observations (**Table 3.2**, **Table S3.8**). Further heterogeneity was attributed to differences between species (49%) and data sources (15%; **Table S3.12**). As expected, the percentage of vertebrates, fish and scavenging in the diet was positively related to abundance responses in mammals. Carnivorous mammals (80% of diet consisting of vertebrates, fish and scavenging) were more abundant near infrastructure and became less abundant at larger distances (**Figure 3.3**). The positive effect of infrastructure on carnivorous mammals was more apparent for small-sized carnivores than for large-sized carnivores and persisted over larger distances (small carnivores: 107 m, large carnivores: 21 m), with little variation between close and open habitats. In turn, abundance responses of non-carnivorous (0% vertebrates, fish and scavenging) mammals varied between habitat types and body size, with small-sized species (< 1 kg) having higher abundance in the proximity of infrastructure in open habitats, and larger species having reduced abundances in both open and closed habitat types. IEZs varied between 2 and 603 m for small-sized and large-sized non-carnivores, respectively, with variations among habitat types (**Table 3.3**).

Table 3.2 Parameter estimates plus 95% confidence intervals and p-values of AICc selected meta-regression model for each mammals, birds, reptiles and amphibians. Distance: distance to infrastructure (m, $\log_{10}$-transformed), BM: mean body mass (g, $\log_{10}$-transformed), Habitat (open/closed, categorical), InfraType (paved road/power line/unpaved road/non-traffic, categorical). Cochran's Q test for residual heterogeneity (Q_E), Omnibus test of moderators (Q_M), marginal explained variance (R_m^2) and conditional explained (R_c^2) are given for the model. Omnibus tests are also performed for each of the moderators where main effects were tested after dropping interactions.

	Moderator	Estimate (95% CI)	$p_{estimate}$	Q_M (d.f.)	p_{QM}
Mammals					
$Q_{M,9}$= 74 ($p < .0001$)	Intercept	-0.00 (-0.45, 0.45)	*.994*		
$Q_{E,853}$= 6029 ($p < .0001$)	Distance	0.45 (0.02, 0.88)	*.040*	5.92 (2)	*.052*
R_m^2 = 0.09, R_c^2 = 0.75	Distance²	-0.16(-0.32, -0.02)	*.030*		
	Diet	0.02 (0.01, 0.03)	*<.001*	9.71 (1)	*.002*
	BM	-0.08 (--0.26, 0.10)	*.377*	1.41 (1)	*.236*
	Habitat (open)	0.29(-0.050, 0.632)	*.095*	0.29 (1)	*.591*
	Distance x Diet	-0.01 (-0.01, -0.00)	*<.001*	23.82 (1)	*<.001*
	Distance x BM	-0.20(--0.37, -0.03)	*.020*	23.67 (2)	*<.001*
	Distance² x BM	0.09(0.04, 0.14)	*<.001*		
	Distance x Habitat (open)	-0.23(-0.37, -0.08)	*.002*	9.34 (1)	*.002*
Birds					
$Q_{M,8}$= 62 ($p < .001$)	Intercept	0.05 (-0.32, 0.42)	*.795*		
$Q_{E,2462}$= 26188 ($p < .001$)	Distance	-0.04 (-0.13, 0.04)	*.302*	6.65 (1)	*.010*
R_m^2 = 0.04, R_c^2 = 0.66	Diet	-0.01 (-0.02, -0.01)	*.001*	1.43 (1)	*.232*
	Habitat (open)	-0.47 (-0.87, -0.06)	*.024*	3.59 (1)	*.058*
	InfrastructureType (paved road)	-0.45 (-0.80, -0.10)	*.011*	6.63 (3)	*.085*
	InfrastructureType (power line)	-0.29 (-0.70, 0.13)	*.172*		
	InfrastructureType (unpaved road)	-0.32 (-0.75, 0.12)	*.151*		
	Distance x Diet	0.01 (0.01, 0.01)	*<.001*	23.44 (1)	*<.001*
	Distance x Habitat (open)	0.34 (0.20, 0.54)	*<.001*	18.84 (1)	*<.001*
Reptiles					
$Q_{M,4}$ = 64 ($p < .001$)	Intercept	0.18 (-0.27, 0.63)	*.432*		
$Q_{E,357}$= 1335 ($p < .001$)	Distance	-0.44 (-0.87, -0.00)	*.048*	57.30 (2)	*<.001*
R_m^2 = 0.31, R_c^2 = 0.84	Distance²	0.15 (0.03, 0.28)	*.025*		
	Habitat (open)	-0.67 (-1.25, -0.08)	*.017*	0.19 (1)	*.661*
	Distance x Habitat (open)	0.38 (0.09, 0.67)	*.009*	6.81 (1)	*.009*
Amphibians					
$Q_{M,2}$ = 9 ($p = .013$)	Intercept	-0.74(-1.15, -0.33)	*.000*		
$Q_{E,213}$ = 1407 ($p < .001$)	Distance	0.91 (0.21, 1.62)	*.011*	8.74 (2)	*.013*
R_m^2 = 0.11, R_c^2 = 0.53	Distance²	-0.32 (-0.64, 0.00)	*.051*		

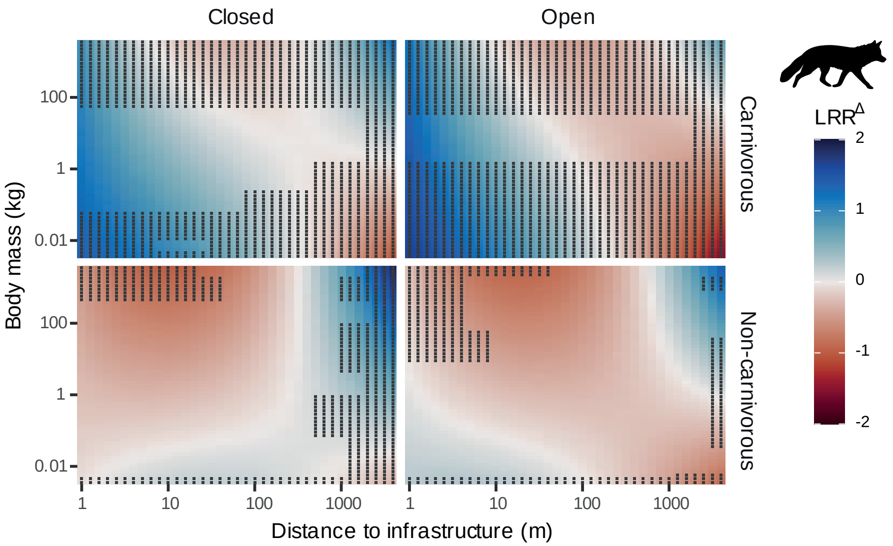


Figure 3.3 Change in species abundance (LRR^{Δ}) as a function of distance to infrastructure and body mass for carnivorous (upper panels, 80% of diet from vertebrates or scavenging) and non-carnivorous mammals (lower panels, 0% of diet from vertebrates or scavenging) in closed (left panels) and open habitats (right panels) based on the best model (See **Table 2** for parameter estimates and R^2 values). Plots show the predicted LRR^{Δ} due to infrastructure from the final model as colour gradient ranging from blue (abundance increase, $LRR^{\Delta} > 0$) to red (abundance decrease, $LRR^{\Delta} < 0$) where white represents no change in abundance ($LRR^{\Delta} = 0$). Dots indicate extrapolation areas. Silhouettes are public domain obtained from "phylopic" (www.phylopic.org).

Table 3.3 Infrastructure effect zones (IEZ) plus 95% confidence intervals estimated by final models (**Table 3.2**) for small (10th percentile of body masses), medium and large (90th percentile of body masses) reptiles, carnivorous (80% of diet consisting of vertebrates, fish or scavenging) mammals and birds and non-carnivorous (0% of diet consisting of vertebrates, fish or scavenging) birds and mammals. IEZ estimates for birds correspond to paved roads. $^{+}$ indicates a positive effect of infrastructure on the abundance within the IEZ. No IEZ was calculated for non-carnivorous birds in open habitats as the modelled response ratios did not increase as a function of distance to infrastructure. See also **Figure S3.11** for a continuous representation of IEZs as a function of diet and body mass for mammals.

Class	Diet	Body mass	Open IEZ (m) [95% CI]	Closed IEZ (m) [95% CI]
Mammals	Carnivore	Small (100 g)	68 (24, 1840)$^{+}$	107 (31, -)$^{+}$
Mammals	Carnivore	Medium (3,000 g)	36 (10, -)$^{+}$	47 (9, -)$^{+}$
Mammals	Carnivore	Large (30,000 g)	21 (6, -)$^{+}$	22 (4, -)$^{+}$
Mammals	Non-carnivore	Small (10 g)	76 (0, 5203)$^{+}$	2 (0, -)
Mammals	Non-carnivore	Medium (2,000 g)	1 (0, 11)$^{+}$	224 (39, 1303)
Mammals	Non-carnivore	Large (400,000 g)	603 (167, 1870)	295 (79, 892)
Birds	Carnivore	-	67 (34, 132)	130 (46, 491)
Birds	Non-carnivore	-	469 (75, 6590)	-
Reptiles	-	-	92 (10, 368)	3 (0, -)$^{+}$
Amphibians	-	-	27 (7, -)	27 (7, -)

Infrastructure impacts on birds were modulated by diet, habitat type and infrastructure type and followed a linear relationship with the log10 transformed distance to infrastructure (**Table 3.2**, **Table S3.9**). Fixed effects explained only 4% of the heterogeneity between observed effect sizes with further variation attributed to differences between studies (30%), species (22%) and orders (9%) (**Table S3.12**). Bird abundances were lower near paved roads than near unpaved roads and power lines, and were highest near other non-traffic infrastructure (seismic lines, pipelines, trails) (**Table 3.2**; **Figure 3.4**, **Figure S3.10**). Furthermore, carnivorous birds experienced larger abundance reductions but smaller IEZs than non-carnivorous birds. Likewise, abundance reductions near infrastructure were higher in open habitats but extended over shorter distances compared to closed habitats. In closed habitats, abundances declined to -78% and -33% for carnivorous and non-carnivorous birds, respectively. The corresponding IEZ for carnivorous birds was 130 m while no IEZ could be calculated for non-carnivores. In turn, abundances of carnivorous birds in open habitats were reduced by -86% with an IEZ of 67 m while non-carnivorous birds were reduced by -58% with an IEZ of 469 m (**Table 3.3**).

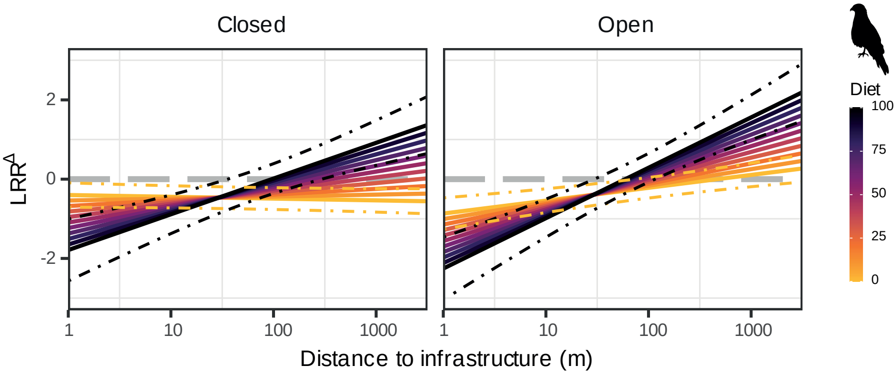


Figure 3.4 Change in species abundance (LRR$^{\Delta}$) as a function of distance to infrastructure and diet (% of diet consisting of vertebrates or scavenging, indicated by color) for birds in closed (left panel) and open (right panel) habitats based on the best model (See **Table 2** for parameter estimates and R^2 values). Dashed lines represent the 95% confidence interval for 0 and 100% of diet consisting of vertebrates or scavenging. LRR$^{\Delta}$ < 0 indicates abundance decline, LRR$^{\Delta}$ > 0 indicates abundance increase and LRR$^{\Delta}$ = 0 indicates no change (dashed grey line). Silhouettes are public domain obtained from "phylopic" (www.phylopic.org).

For reptiles, the relationship between LRR^{Δ} and distance to infrastructure was only modulated by habitat type, which explained about 31% of the heterogeneity (**Table 3.2**, **Table S3.10**). Additional heterogeneity in response ratios was attributed to differences between species (27%) and data sources (25%; **Table S3.12**). In closed habitats, abundance ratios of reptiles increased with +20% near infrastructure compared to control areas and decrease to 0% in the first 5 m (**Figure 3.5**). In contrast, reptile abundances in open habitats were reduced by -39% near infrastructure, with an IEZ of 92 m (**Table 3.3**). Lastly, amphibian responses were not related to body mass or infrastructure type. Instead, only distance to infrastructure and its quadratic term were retained in the final model (**Figure 3.2d**, **Table 3.2**, **Table S3.11**). However, the variance components of the model suggest a large variability between individual species (42%; **Table S3.12**).

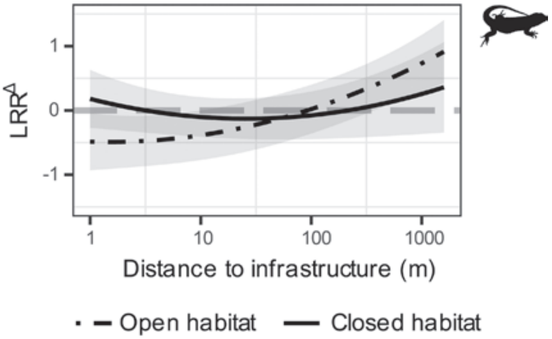


Figure 3.5 Change in species abundance (LRR^{Δ}) as a function of distance to infrastructure for reptiles in closed (solid line) and open (dot-dashed line) habitats based on the best model (See **Table 2** for parameter estimates and R^2 values). Grey bands represent the 95% CI of the modelled relationship between LRR^{Δ} and distance to infrastructure. $\text{LRR}^{\Delta}<0$ indicates abundance decline, $\text{LRR}^{\Delta}>0$ indicates abundance increase and $\text{LRR}^{\Delta}=0$ indicates no change (dashed grey line). Silhouettes are public domain obtained from "phylopic" (www.phylopic.org).

3.4 DISCUSSION

The development of linear infrastructure is pervasive across the globe and is one of the main drivers of global change. Yet, the impacts of linear infrastructure on species abundance have not been comprehensively quantified. Here we contribute to our understanding of the impacts of linear infrastructure on terrestrial vertebrates by synthesizing the findings from local studies across the world. We performed a meta-analysis of reported changes in species-specific abundance in the proximity of infrastructure for mammals, birds, reptiles and amphibians. However, as infrastructure impacts vary between species and environmental context, across-species averages may not give an adequate representation of IEZs and changes in population abundance. To address this, we used a trait-based approach to reveal general functional responses to infrastructure applicable to a wide range of species. We also accounted for differences in environmental characteristics, such as habitat type and infrastructure type. We found that infrastructure impacts were modulated by diet (birds and mammals), body size (mammals), habitat type (birds, mammals and reptiles) and infrastructure type (birds).

Our results yield a relatively small average IEZ for mammals (~ 100 m) which is substantially lower than previous estimates (5 km, Benítez-López *et al.* 2010). These diverging results likely stem from the use of different biodiversity metrics. Benítez-López *et al.* (2010) employed an aggregated biodiversity indicator (mean species abundance; MSA) which was truncated so that positive responses (increased abundances) were not included. Our meta-regression indicates that infrastructure effects on mammal populations are more nuanced and depend on both biological traits and the environmental context. We report contrasting responses of carnivorous and non-carnivorous mammals, with the former being more abundant near infrastructure, whereas the latter consistently display avoidance responses. Indeed, carnivores of varying body sizes are reportedly observed in the vicinity of roads because they are attracted to roadkill carcasses or because they use infrastructure verges as movement corridors (Andersen *et al.* 2017; Planillo *et al.* 2018). Avoidance responses by non-carnivorous mammals depend on their body size and the type of habitat. Medium to large-sized non-carnivorous mammal species were more affected over larger distances than smaller species. Because medium and large-sized species usually have larger home ranges than small-sized species, they may encounter infrastructure more frequently (Rytwinski & Fahrig 2012; Tucker *et al.* 2014). Here we show that these responses may be exacerbated in open habitats (IEZ ~ 600 m) where visibility is higher than in closed habitats (IEZ ~ 300 m). If infrastructure is perceived as a threat similar to predation risk (Frid & Dill 2002), we would expect that animals in open habitats, where anti-predator vigilance is more effective, forage at larger distances from infrastructure than in closed habitats, where higher alertness and quick fleeing responses might be more beneficial (Duffett *et al.* 2020). Small-sized species, in turn, have smaller home ranges and may even use infrastructure verges as a habitat or refuge from predators (Ascensão *et al.* 2012; Ouédraogo *et al.* 2020), particularly in open habitats (**Table 3.3**).

Birds were generally more negatively affected by infrastructure than mammals, leading to an average IEZ of about 650 m, which is similar to recently reported road effect-zones in Great Britain (500 - 700 m, Cooke *et al.* 2020). Paved roads had the largest impact, followed by power lines and other non-traffic infrastructure. Previous evidence has linked high traffic volumes and traffic speed on paved roads to high levels of chemical and noise pollution, as well as traffic mortality (van der Ree *et al.* 2015), which have detrimental effects on birds (noise: Grade & Sieving 2016; roadkills: Grilo *et al.* 2020). Variation between bird species' responses was related to diet, with carnivores experiencing smaller IEZs (~ 100 m) than non-carnivorous birds (~ 470 m). While raptors were less abundant near infrastructures, their small IEZ might indicate that areas near infrastructure may act as complementary hunting grounds due to the potential increase of small mammals (Lambertucci *et al.* 2009). Further, our results indicate that the impact of linear infrastructures is greater in closed compared to open habitats. Species in closed habitats tend to have lower frequency vocalizations than those in open habitats where low-frequency sounds degrade faster (Boncoraglio & Saino 2007), and may be thus more impacted by low-frequency traffic noise due to greater spectral overlap (Francis *et al.* 2011; Francis 2015). Finally, in contrast to our expectations, we did not find a relationship between mean body size and infrastructure impacts (**Table 3.1**, **Table 3.2**). This might be explained by the overrepresentation of passerines in our database, 83% and 51% of all observations in closed and open habitats, respectively. Passerines, which are generally small birds, heavily rely on vocal communications with high song complexity, making them especially sensitive to traffic noise (Catchpole & Slater 2003; Francis *et al.* 2011).

We provide the first estimates of the IEZ across many species of reptiles. Reptile responses were highly variable with positive responses in closed habitats but negative responses in open habitats. The derived IEZs in open habitats (~ 90 m) were smaller but of the same order as those previously reported for single species (e.g., Tanner & Perry 2007: 200 m, *Microlophus albemarlensis*; Peaden *et al.* 2016: 203 - 306 m, *Gopherus agassizii*). In closed habitats, reptiles may use infrastructure sites for thermoregulation because of increased ground temperatures and solar radiation due to clearings in the forest canopy (Sullivan 1981; Meiri *et al.* 2013;

Tuff *et al.* 2016). While we expected that large reptiles would be more affected by infrastructure, we found no evidence of infrastructure impacts being modulated by body mass. This might be explained by opposing relationships between biological traits that affect reptile sensitivity to infrastructure and body size. Previous evidence indicate that thermal biology may play an important role in modulating ectotherm responses to infrastructure, which increases surface temperatures and lowers humidity in the surrounding habitat (van der Ree *et al.* 2015; Tuff *et al.* 2016). Reptile sensitivity to infrastructure may therefore decrease with optimal body temperature, which is in turn positively related to body size (Meiri *et al.* 2013; Nowakowski *et al.* 2018). Similar considerations may explain our findings for amphibians. While small amphibians generally have faster life histories, they are also more sensitive to dehydration and have lower critical body temperatures than larger-bodied species (Tracy *et al.* 2010; Pfeifer *et al.* 2017; Nowakowski *et al.* 2018; Liu *et al.* 2021). Our results for amphibians should, however, be interpreted with caution as the maximum distance to infrastructure (120 m), as well as the average distance of the control sites (200 m), is smaller than previously reported amphibian IEZs, which are however based on distributional data and habitat preferences instead of abundance estimates (e.g., Eigenbrod *et al.* 2009: 600 - 1000 m; Hamer *et al.* 2021: 1000 m).

A considerable proportion of heterogeneity in our analysis was related to differences between species, suggesting other species traits may explain variability in infrastructure impacts. Examples of traits that may be included if data become available are call frequency and the potential to shift vocal frequencies (birds and amphibians; Francis 2015; Liu *et al.* 2021), larval habitat (amphibians; Liu *et al.* 2021), migratory status (all species groups; Southwood & Avens 2010; Beebee 2013; Cooke *et al.* 2020; Grilo *et al.* 2020), foraging behaviour (e.g., active or ambush predation for reptiles and ground, understory, aerial or aquatic for birds; Meiri *et al.* 2013; Francis 2015) and habitat guild (e.g., aquatic, fossorial, terrestrial or arboreal; reptiles and amphibians; Tracy *et al.* 2010; Meiri *et al.* 2013). Another interesting research direction would be to investigate species traits that affect how well species adapt to anthropogenic environments such as habitat specificity and relative brain size (Fristoe *et al.* 2017; Keinath *et al.* 2017; Santini *et al.* 2019; Liu *et al.* 2021). Furthermore, for mammals, birds and amphibians, a considerable amount of heterogeneity was captured by the source and study level random effects, indicating a role for study design specifications or location-specific factors. For example, mortality rates as well as chemical and noise pollution scale with traffic intensity and speed (van der Ree *et al.* 2015). Similarly, climatic conditions such as wind speed and direction, affect how hydrological, chemical and noise impact travel into the surrounding environment (van der Ree *et al.* 2015). Yet, such information is not consistently reported and could therefore not be included in our analysis.

Besides changes in abundance, alternative metrics such as mortality rates, demographic rates, and gene flow between populations may provide additional insight into the processes that underlie infrastructure impacts (Holderegger & Di Giulio 2010; Ascensão *et al.* 2016; González-Suárez *et al.* 2018; Teixeira *et al.* 2020). For example, attraction to roads may lead to increased mortality rates in carnivorous mammals and reptiles with active foraging strategies (Sosa & Schalk 2016; González-Suárez *et al.* 2018). As a result, our reported positive responses to infrastructure for carnivores may translate into reduced long-term population persistence if collision rates in an area exceed the population growth rate (Ceia-Hasse *et al.* 2017; Planillo *et al.* 2018; Grilo *et al.* 2021). Furthermore, the majority of studies in our dataset originated from North-America and Western Europe, and we found no studies originating from Southern and Western Asia and Eastern-Europe. As a result, many species endemic to those regions were not included in our analysis while many future infrastructure projects are planned in those areas (Laurance 2015; Meijer *et al.* 2018). Future studies should aim at including search strings in other languages to include more non-English literature to cover the currently under-represented regions (Konno *et al.* 2020; Barrientos *et al.* 2021). Additionally, easily measurable responses, such as roadkills, may be collected in citizen-science projects and can provide valuable information for species and geographic locations that are under-represented in population-level studies (Périquet *et al.* 2018; Valerio *et al.* 2021).

While we have performed the most comprehensive synthesis study on infrastructure impacts on species abundances of terrestrial vertebrates, our study has some limitations. As it is commonly the case in ecology and biodiversity research (Martin *et al.* 2012; Hughes *et al.* 2021), the majority of the studies in our dataset originate from North America and Western Europe, and we found no studies originating from Southern and Western Asia and Eastern Europe. As a result, species endemic to those regions were not included in our analysis, while many future infrastructure projects are planned in those areas (Laurance *et al.* 2015; Meijer *et al.* 2018). This geographical bias is, to some extent, a reflection of our English-language-based literature search (Amano *et al.* 2021). Future studies addressing global infrastructure impacts on biodiversity should aim at including search strings in other languages to include more non-English literature to cover currently under-represented regions and species (Konno *et al.* 2020; Amano *et al.* 2021; Barrientos *et al.* 2021). Further, most of the studies we included use a control-impact (CI) or space-for-time design, which is arguably less robust for capturing changes in biodiversity than before-after control-impact (BACI) studies (Christie *et al.* 2019). Yet, we prioritized maximizing sample size and taxonomic representativeness over having a few BACI studies focused on a limited number of species and locations. Finally, while we only compared paired disturbed and control sites with similar habitat types and vegetation characteristics, we cannot fully dismiss potential confounding effects of site differences resulting from, for example, past land use or natural spatial species turnover. The latter is, however, less likely at the spatial scale of our analyses, which involve pairwise comparisons within a few hundred meters. Both of these limitations are common in other space-for-time meta-analyses and are impossible to assess without having long-term studies with the same study design as the one reported in the primary studies.

To our knowledge, this is the first study to perform a meta-analysis of changes in abundance in proximity to infrastructure and IEZs using species-specific abundances for mammals, birds, reptiles and amphibians. Our results suggest that infrastructure impacts are highly variable between species and habitat contexts, which should be taken into account in multi-species infrastructure assessments. So far, most large-scale assessments of the current infrastructure network have used a generic IEZ for all species (Ibisch *et al.* 2016; Torres *et al.* 2016; Schipper *et al.* 2020). Instead, our models can be applied across species and habitats by accommodating variable IEZs based on species traits and the distribution of habitat and infrastructure types within their geographic range. Such an approach may also reflect how the composition of a community could change in terms of individual species as well as functional diversity. Moreover, our results can be used to assess the impacts on biodiversity of planned infrastructure projects. Massive expansions of the global infrastructure network are expected within the next decades to give access to traffic and energy-related infrastructure in poor and currently disconnected areas following UN Sustainable Development Goals 7 & 9 (SDG7, SDG9; Fuso Nerini *et al.* 2018; Thacker *et al.* 2019). However, because many of these developments are planned in key areas for biodiversity they are in conflict with SDG15, which aims for halting land degradation and biodiversity loss (Thacker *et al.* 2019; Narain *et al.* 2020; Baste *et al.* 2021). The most prominent example, China's Belt Road Initiative (BRI), potentially intersects up to 1500 key biodiversity areas across Asia, Europe and Africa (Li & Shvarts 2017; Narain *et al.* 2020). These areas can be important habitats for already endangered species including rhinoceros, orangutans, elephants and tigers (Alamgir *et al.* 2019; Carter *et al.* 2022). Similar concerns exist for infrastructure developments in other regions, such as South-America (Laurance 2015; Ascensão *et al.* 2022). Quantitative assessments of the impacts of future infrastructure on biodiversity are the first step in re-aligning SDG9 with SDG15 by informing spatial planning and mitigation and compensation policies (zu Ermgassen *et al.* 2019; Milner-Gulland *et al.* 2021). However, these assessments should also consider indirect effects of new infrastructure such as increased hunting pressure in newly accessible areas, habitat fragmentation, land encroachment, and exotic-species invasions (Torres *et al.* 2016; Benítez-López *et al.* 2017, 2019; Ceia-Hasse *et al.* 2017; Laurance & Arrea 2017; Liu *et al.* 2019). Only with a holistic approach that encompasses the myriad impacts of infrastructure on wildlife we may be able to effectively tackle the loss of biodiversity linked to current and future infrastructure networks.

3.5 ACKNOWLEDGEMENTS

AB-L was supported by an EMERGIA grant (EMERGIA20_00252) from the Junta de Andalucía.

CHAPTER 4

CHANGES IN PLANT SPECIES RICHNESS DUE TO LAND USE AND NITROGEN DEPOSITION ACROSS THE GLOBE

**Published in Diversity and Distributions,
28 (4): 745-755**

Authors

Juan Gallego-Zamorano[1], Mark A.J. Huijbregts[1], Aafke M. Schipper[1, 2]

[1]Department of Environmental Science, Radboud Institute for Biological and Environmental Sciences (RIBES), Radboud University, Nijmegen, The Netherlands

[2]PBL Netherlands Environmental Assessment Agency, The Hague, The Netherlands

ABSTRACT

Aim

The effects of land use and atmospheric nitrogen (N) deposition on plant species richness are typically studied in isolation. Here we quantified the combined effects of these two pressures on terrestrial plant species richness at a 0.25° spatial resolution across the globe.

Location

Global.

Methods

We first used local monitoring and experimental data to determine the proportional changes in plant species richness in relation to different land-use types and N addition levels according to a meta-analytical approach. We then developed a new multi-pressure species-area relationship (mp-SAR) model to combine the site-level responses resulting from the meta-analyses with global land use and N deposition maps to calculate changes in plant species richness at a resolution of 0.25° across the globe.

Results

Both pressures combined resulted in an average plant species richness decline of 26% (± 12% SD) across the grid cells. The combined impact was the largest in Europe, with an average decline of 34% (± 8%), and the smallest in South America (16% ± 11%). Overall, species declines due to land use were considerably larger (19% ± 11%) than declines due to N deposition (6% ± 6%).

Main conclusions

Our new species-area model allows for systematic large-scale assessments of the combined effects of multiple pressures on species richness based on easily retrievable input data. Overall, land use is a more important driver of plant species richness decline than N deposition, but N deposition may have considerable additional impact in specific regions of Europe, Asia and North America. These findings imply that conservation efforts should simultaneously tackle both pressures to ensure their effectiveness in preserving plant biodiversity.

4.1 INTRODUCTION

Terrestrial plant communities are key to global biogeochemical cycles, the distribution of terrestrial animal biodiversity and the provision of benefits to people, including carbon sequestration and water regulation (Franklin *et al.* 2016; Vellend *et al.* 2017). Hence, it is crucial to understand how plant communities will change in response to human pressures on the environment. Land use and atmospheric nitrogen (N) deposition are two important pressures that affect plant biodiversity worldwide (Bobbink *et al.* 2010; Franklin *et al.* 2016). The human use of land, for example for residential, industrial or agricultural purposes, typically comes with the conversion or disturbance of the original natural habitat. This in turn may decrease the number of plant species compared to undisturbed habitats (Gerstner *et al.* 2014a; Newbold *et al.* 2015; Vellend *et al.* 2017). Some low-intensity types of land use (e.g. occasional logging, cities with a low human population density) may be characterized by plant species richness similar to or even higher than plant species richness in undisturbed vegetation. However, conversion of natural vegetation to agricultural land, which is the dominant human land use by far, typically results in species richness declines (Newbold *et al.* 2015; Vellend *et al.* 2017).

The effects of atmospheric N deposition (i.e., the input of reactive N from the atmosphere to the biosphere) on plant species richness are more equivocal, as both increases and decreases in species richness have been observed. In general, increases in plant species richness tend to occur in response to relatively low amounts of N deposition in regions where N is scarce, for example in remote areas (Bobbink *et al.* 2010). The number of species may also increase in well-buffered soils with high pH and cation exchange capacity, where the decline of sensitive species is slower and new species might colonize (Dise *et al.* 2011; Stevens *et al.* 2011; Van den Berg *et al.* 2011). In contrast, higher values of N input may lead to decreases in plant species richness, with soil eutrophication and acidification as important underlying mechanisms (Stevens *et al.* 2010; Vellend *et al.* 2017). Specifically, eutrophication may disproportionally promote the growth of nitrophilous plant species, which then outcompete others for light and resources, leading to an overall decrease in plant species richness (Lawrence 2003; Dise *et al.* 2011; Stevens *et al.* 2018; Midolo *et al.* 2019). Soil acidification may lead to reductions in plant species richness particularly in soils with already low pH, as the pool of species adapted to low pH is relatively small (Bobbink *et al.* 2010; Stevens *et al.* 2010, 2018; Dise *et al.* 2011).

The emission and deposition of N are typically enhanced by land use-related activities such as fertilizer application (and volatilized livestock excreta), fossil fuel combustion (e.g. vehicle emissions), electricity production, or seasonal fires (Bobbink *et al.* 2010; Dise *et al.* 2011; McClean *et al.* 2011; Fowler *et al.* 2013). Hence, land use and associated activities act as a source of N emissions, while (semi-)natural areas are the sinks (Deng *et al.* 2019; Lv *et al.* 2019), resulting in spatial correlations between both pressures (McClean *et al.* 2011; Bowler *et al.* 2020). Thus, landscapes characterized by high-intensity human land use might be characterized by disproportional cumulative declines of plant species richness, because the direct on-site land-use impacts are complemented by impacts of increased N deposition in remaining (semi)-natural habitats. Yet, the landscape-level effects of both pressures combined are rarely studied and have, to our knowledge, never been assessed at a continental to global extent.

Here we aimed to quantify the relative and combined effects of land use and N deposition on landscape-level plant species richness across the globe. To that end, we developed an approach based on the countryside species-area relationship (cSAR) model, which has been used to study impacts of land use on biodiversity (Pereira *et al.* 2014; Gerstner *et al.* 2017). The cSAR model quantifies changes in species richness due to land use, accounting for the affinity of species to different human-modified habitats (Pereira *et al.* 2014). We extended the cSAR to account also for the effect of nitrogen deposition, arriving at a new multi-pressure species-area relationship (mp-SAR) model. We accounted for the effect of nitrogen deposition by quantifying the proportion of plant species able to persist under different levels of N addition, similar to how land-use impacts are quantified in the cSAR. We determined the proportional changes in plant species richness for different land-use types and N deposition values through meta-analyses of local monitoring data obtained from the literature. We then combined the site-level responses with global land use and N deposition maps in the new mp-SAR framework to provide estimates of changes in plant species richness at a resolution of 0.25° (about 25 km at the equator) worldwide.

4.2 METHODS

General approach

Our multi-pressure SAR (mp-SAR) model calculates the change in species richness within a spatial unit (grid cell) based on the areas within that spatial unit affected by different pressures combined with the affinity of the species group to these pressures, as follows (where *j* and *k* denote two different pressures):

$$RSR_{new} = \left(\frac{\sum h_{j,k} A_{j,k}}{A_{tot}}\right)^{z}$$ Equation 4.1

Where RSR_{new} is the relative species richness compared to a reference situation (natural habitat), A_{tot} is the total area of the spatial unit, $A_{j,k}$ is the area within that unit that is subject to pressures *j* and *k*, $h_{j,k}$ represents the affinity of the species group to pressures *j* and *k*, and *z* is the slope of the species-area relationship. Following the countryside SAR model, the affinity $h_{j,k}$ is derived from the ratio between species richness in a human-modified habitat and an original or natural situation (Pereira *et al.* 2014):

$$h_{j,k} = \left(\frac{\bar{S}_{j,k}}{\bar{S}_{n}}\right)^{1/z}$$ Equation 4.2

Where $\bar{S}_{j,k}$ represents the average number of species in the habitat modified by the pressures *j* and *k*, and $\bar{S}_{n}$ represents the average number of species in the natural habitat. The affinity value is higher than 1 if the number of species is higher in the modified than the natural habitat. Ideally, the affinity of species groups to the combination of pressures *j* and *k* is determined based on observational or experimental data covering both pressures simultaneously (e.g., data from multi-factorial experiments). As these data are scarce, we propose to retrieve the affinity to pressure combinations from single-pressure studies based on the assumption that the pressures act independently, implying that we can apply response addition (Plackett & Hewlett 1952; Vinebrooke *et al.* 2004) as:

$$h_{j,k} = \left[\left(\frac{\bar{S}_{j}}{\bar{S}_{n}}\right) x \left(\frac{\bar{S}_{k}}{\bar{S}_{n}}\right)\right]^{1/z}$$ Equation 4.3

Note that this is a generic equation that also applies if one of the two pressures is absent, as then the corresponding species richness ratio equals 1.

To quantify the impacts of land use and N deposition on plant diversity across the globe, we first assembled local monitoring and experimental data representing relative plant species richness in relation to different land-use types ($\bar{S}_j/\bar{S}_n$ in **Equation 4.3**) and to different levels of N addition ($\bar{S}_k/\bar{S}_n$ in **Equation 4.3**).

We then applied the mp-SAR (**Equation 4.1**) by quantifying the areas affected by land use, N deposition, and both pressures combined within each 0.25º grid cell ($A_{j,k}$ in **Equation 4.1**) and the combined affinity to land use and N deposition in that grid cell ($h_{j,k}$ in **Equation 4.1**, **Equation 4.3**), using slope values (z) specific to the biome that the grid cell belongs to. We further detail each of these steps below.

Quantifying plant species richness responses to land use

To quantify the response of plant species richness to land use ($\bar{S}_j/\bar{S}_n$ in **Equation 4.3**), we first merged four existing databases with comparisons of plant species richness between specific land-use types and natural habitats (de Baan *et al.* 2013; Elshout *et al.* 2014; Gerstner *et al.* 2014b; Hudson *et al.* 2014). As these datasets together cover publications up to 2015, we searched for additional, more recent publications (from 2015 to 2020) using the following search key within the ISI Web of Knowledge database:

(TS = ((“land use”) AND (plant OR plants) AND (“species richness” OR “species composition” OR “species abundance”))) AND LANGUAGE: (English OR Catalan OR Portuguese OR Spanish)

A total of 1,109 publications resulted from the search string, of which we selected 201 for full-text screening and 25 for data extraction. We selected publications that included at least one pairwise comparison of plant species richness in a given land-use type and plant species richness in a nearby natural habitat. If a publication included comparisons in multiple locations and for multiple species groups (e.g. vascular plants and woody vegetation), we distinguished multiple studies within the same publication. Our final database included 75 publications and 80 studies, with publication dates ranging from 1997 to 2019, and a total of 201 pairwise comparisons (**Figure S4.1**). A list of the data sources is found in **Appendix S4.1**. We categorized the different land use types and intensities following Hudson et al. (2014), whereby we merged some categories (**Table 4.1**).

Table 4.1 Classification of land use types and intensities (modified from Hudson et al. (2014)).

Land use	Description
Primary vegetation	Natural (original) vegetation with no evidence of prior destruction and minor (if any) disturbance by humans. It can be forest or non-forest.
Secondary vegetation	Regenerating vegetation upon the destruction of the primary vegetation with currently minor disturbance by humans.
Plantations	Plantations of trees or shrubs for subsistence or commercial use. Including extensively managed or mixed timber, fruit/coffee, oil-palm, or rubber plantations in which native understorey and/or other native tree species are tolerated, which are not treated with pesticide or fertilizer, and which have not been recently (< 20 years) clear-felled; and monoculture fruit/coffee/rubber plantations with pesticide input, or mixed species plantations with pesticide inputs. Present signs of clear-felling (trees of different or same ages).
Pastures: Minimal-intensity use	Pasture with minimal inputs of fertilizer and pesticide, and with low stock density (*not* high enough to cause significant disturbance or to stop the regeneration of vegetation).
Pastures: Light- and high-intensity use	Pasture either with significant input of fertilizer or pesticide and/or with high stock density (high enough to cause significant disturbance or to stop the regeneration of vegetation). Including other managements like ploughing, or slash and burning.
Croplands: Minimal-intensity use	Cropland characterized by small fields, mixed crops, crop rotation, little or no inorganic fertilizer use, little or no pesticide use, little or no ploughing, little or no irrigation, little or no mechanization.
Croplands: Light-intensity use	Cropland typically showing some but not many of the following features: large fields, annual ploughing, inorganic fertilizer application, pesticide application, irrigation, no crop rotation, mechanization, monocultures.
Croplands: High-intensity use	Monoculture croplands typically showing many of the following features: large fields, annual ploughing, inorganic fertiliser application, pesticide application, irrigation, mechanization, no crop rotation.
Urban	Urban areas, including villages and extensively managed green areas in cities.

To estimate the plant species richness response to different land-use types, we performed a meta-analysis of the natural logarithm of the response ratios (*RR*) as extracted from the studies (Hedges *et al.* 1999):

$$ln(RR) = ln\left(\frac{\bar{S}_{j,i}}{\bar{S}_{n,i}}\right) \qquad \text{Equation 4.4}$$

Where $\bar{S}_{j,i}$ and $\bar{S}_{n,i}$ represent the mean species richness in a land-use type *j* and the corresponding natural habitat *n* for a study *i*, respectively. Thus, the log response ratio quantifies the proportionate response of plant species richness to land use, based on an effect size measure standardized across studies (Hedges et al. 1999). We analysed the ln RR in relation to land-use type using linear mixed-effects models fitted with the package "metafor" (Viechtbauer 2010). Following Konstantopoulos (2011), we included a random intercept with each observation nested within study and publication to account for the possibility that the underlying true effects within grouping level are not homogeneous. Moreover, we accounted for non-independence of observations sharing a common natural reference through the variance-covariance matrix (Lajeunesse 2011). To account for uncertainties in the observations, we used the inverse of the variance of each observation per study *i* to weight the ln *RR*, with the variance calculated as (Hedges et al., 1999):

$$\sigma^2(RR) = \frac{SD_{j,i}^2}{N_{j,i}\bar{S}_{j,i}^2} + \frac{SD_{n,i}^2}{N_{n,i}\bar{S}_{n,i}^2} \qquad \text{Equation 4.5}$$

Where $SD_{h,i}^2$ and $SD_{n,i}^2$ represent the standard deviations of $\bar{S}_{h,i}$ and $\bar{S}_{n,i}$, respectively, and $N_{h,i}$ and $N_{n,i}$ are the sample sizes (Hedges *et al.* 1999). For studies that did not report estimates of variation (34% of the studies), we imputed the *SD* with the "Bracken1992" method using the coefficient of variation from all complete cases (Bracken & Sinclair 1992). Finally, we investigated whether our results are influenced by publication bias, i.e., a bias in peer-refereed journals to publishing statistically significant results (Nakagawa & Santos 2012). To assess possible publication bias, we used a funnel plot and an Egger's test to assess the funnel plot's asymmetry using the meta-analytic residuals with our multi-level random effect structure and the precision (1/SE) as covariate (Nakagawa & Santos 2012; Fernández-Castilla *et al.* 2021). We did not find signals of publication bias (Egger's test p-value = 0.26, **Figure S4.2**) suggesting that our model outcomes are representative (**Figure S4.2**). For prediction purposes, we used the average estimates from the model (**Figure 4.1**, **Table S4.1**) to calculate the land-use affinities (**Equation 4.2**).

Quantifying plant species richness responses to nitrogen deposition

To quantify the response of plant species richness to N deposition ($\bar{S}_k/\bar{S}_n$ in **Equation 4.3**), we used the database underlying a recent global meta-analysis of the impacts of N on (semi-) natural vegetation (Midolo *et al.* 2019), assuming that the experimental addition of nitrogen is representative of atmospheric deposition. This database includes data from 48 studies reporting N-addition experiments performed between 1990 and 2018. We calculated the log response ratio (ln *RR*) between species richness in treatment plots and control plots (**Equation 4.4**), resulting in a total of 220 pairwise comparisons (**Figure S4.1**). N-addition levels in the treatments ranged between 3.75 and 572 kg of N ha^{-1} yr^{-1}. Following the most parsimonious model from Midolo et al. (2019), we fitted a meta-regression model linking the response of site-level plant species richness to the annual amount of N added as well as relevant modifiers (**Figure S4.3**) i.e., the duration of N addition (years), the mean annual temperature (MAT, in ^{o}C) interacting with N addition, and the soil cation exchange capacity (CEC, in centimole per kilogram). We log$_{10}$-transformed all continuous moderators except the MAT to reduce positive skewness. We retrieved the MAT data from the Climate Research Unit matching the corresponding year of the experiments (Harris *et al.* 2020) and the CEC averages across soil depths of 0–5, 5–15, and 15–30 cm from the SoilGrids database at 250 m resolution (Hengl *et al.* 2017). For the random structure of the model, we nested individual ln *RR* estimates within the experiment grouping-level to account for the possibility that the underlying true effects within experiments are not homogeneous. Moreover, as we did for the land-use model, we accounted for the non-independence of observations with a shared control and weighted the observations using the inverse of the variance (**Equation 4.5**).

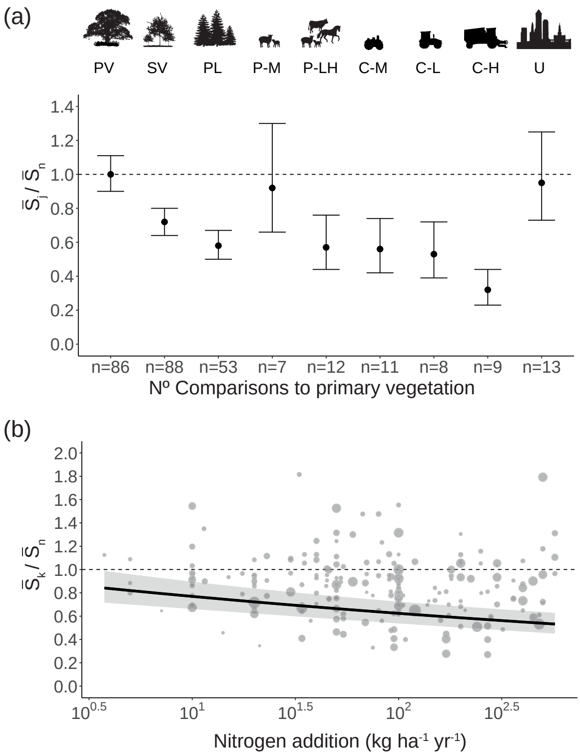


Figure 4.1 Effects of a) land use and b) nitrogen addition (in kg ha^{-1} yr^{-1}) on site-level plant species richness , expressed as plant species richness under influence of a given land use type ($\bar{S}_j$) or level of nitrogen addition ($\bar{S}_k$ relative to the plant species richness in a natural habitat ($\bar{S}_n$). The horizontal dashed lines indicate no change in species richness compared with the natural habitat. In a), PV = primary vegetation and corresponds to the natural habitat, SV = secondary vegetation, PL = plantation forest, P-M and P-LH = pastures minimally and lightly-highly used, respectively, C-M, C-L, C-H = croplands minimally, lightly, highly used respectively, and U = urban areas. Error bars indicate the 95% confidence intervals and in the x-axis, n denotes the number of observations per land-use type. In b), the solid line represents the model predictions for a duration of 32 years (to link up with the model application), assuming median values of the other moderators (i.e. mean annual temperature, and cation exchange capacity). The shaded areas denote the 95% confidence interval, and the point size represents observation weight. Response plots for other values of mean annual temperature and cation exchange capacity are provided in **Figure S4.3**.

We applied the mp-SAR to quantify the combined effects of land use and N deposition on plant species richness at a 0.25º x 0.25º resolution (~25 km) globally, using biome-specific slopes (z-values, **Table S4.2**) obtained from Gerstner, Dormann, Václavík, et al., (2014) combined with the global biome distribution from Dinerstein et al. (2017). To quantify the areas of different land-use types per grid cell, we used the LUH2 dataset for 2015 (Hurtt *et al.* 2020). From the LUH2 dataset we derived the proportions of different land types, including natural vegetation (primary forest and non-forest), secondary vegetation (forest and non-forest), pasture, rangeland, cropland (C3 annual, perennial and N-fixing crops; C4 annual and perennial crops), and urban per 0.25° resolution cell. We classified pastures in the LUH2 as lightly-highly intensively used pastures and rangelands as minimally used pastures, to link up with our land-use categories (**Table 4.1**; **Figure 4.1**). We assigned the use intensity of croplands using the amount of N application (kg ha^{-1} yr^{-1}) as retrieved from the LUH2 data for the year 2015 (Schipper *et al.* 2020). To that end, we classified cropland use intensity as minimal (<100 kg ha^{-1} yr^{-1}), light (100-250 kg ha^{-1} yr^{-1}), or high (> 250 kg ha^{-1} yr^{-1} ; Temme & Verburg, (2011)).

To quantify the amount of N deposition, we used the recently published global maps from Ackerman et al. (2018) with N deposition (both oxidized and reduced N) for the years 1984-1986, 1994-1996, 2004-2006, and 2014-2016 at a 2 x 2.5° resolution. To calculate the site-level species richness responses (**Figure 4.1b**) needed to assess the affinities (**Equation 4.3**), we used the average N deposition over the period of 1984-2015 (matching the LUH2 year) and a corresponding duration of 32 years. Before averaging, we linearly interpolated the values for the missing years (i.e. 1987-1993, 1997-2003, 2007-2013). We then resampled the new long-term average N deposition map to a 0.25° resolution using a bilinear interpolation (**Figure S4.4**). To include the modifying effects of CEC and mean annual temperature on plant species richness responses to N deposition, we obtained CEC values at a 250 m resolution as averages across soil depths of 0–5, 5–15, and 15–30 cm from SoilGrids (**Figure S4.4**, Hengl et al., 2017) and resampled the map to a 0.25° resolution by averaging the values. Similarly, we averaged monthly temperature values for each year in the period 1984-2015 from the global Climate Research Unit database, then averaged over the years and resampled the result to a 0.25° resolution using a bilinear interpolation (**Figure S4.4**, Harris et al., 2020).

In the model application, we assumed that N deposition only affects (semi-)natural vegetation, i.e. primary and secondary vegetation (**Table 4.1**, **Figure 4.1**), assuming that changes in plant species richness in pastures, croplands, plantations, and urban areas are driven by the direct effects of land use (Schipper *et al.* 2020) and because Midolo et al., (2019) only assessed the effect of N on (semi-)natural vegetation plots. Hence, we assume that only secondary vegetation is affected by the combined effect of land use and N deposition. Further, we applied the model only to grid cells within its applicability domain according to a Multivariate Environmental Similarity Surface analysis (MESS, Elith et al. (2010)). The MESS analysis measures the similarity in explanatory variable values between any grid cell in the projection dataset and the values in the dataset used to train the model, such that positive and negative values denote cells that are within and outside of the applicability domain, respectively (**Figure S4.6**). We applied the model only to grid cells within the applicability domain for all variables (N deposition, MAT, CEC, and land use, i.e. ~33% of all 0.25° resolution cells in the world, **Figure S4.5**).

We performed all analyses in R 3.6.3 (R Core Team & R Development Core Team 2020). We used the packages "metafor" (Viechtbauer 2010) and "metagear" (Lajeunesse 2016) for the meta-analysis and data imputation; "tidyverse" for data manipulation and visualization (Wickham *et al.* 2019); "sf" (Pebesma 2018), "raster" (Hijmans 2020), "rgdal" (Bivand *et al.* 2019) and "gdalUtils" (Greenberg & Mattiuzzi 2020) for spatial analysis; "dismo" (Hijmans *et al.* 2017) for the MESS analysis; and "cruts" (Taylor *et al.* 2020) to extract the Climate Research Unit data.

4.3 RESULTS

Worldwide, land use and N deposition combined resulted in a species richness decline of 26 ± 12% (mean ± standard deviation) across the analysed grid cells (**Figure 4.2**, **Table S4.3**). Europe was the most impacted continent with an average species decline of 34% (± 8%) due to both pressures combined, while South America was the least impacted continent (16% ± 11%) (**Figure 4.2**). In North America, Africa, and Asia the average impact of the two pressures combined was 25% (± 11%), 22% (± 12%), and 26% (± 12%), respectively (**Figure 4.2**, **Table S4.3**). Land use was the main driver of species decline globally and per continent, with a global average impact of 19% (± 11%) species decline, whereas N deposition corresponded with a global average decline of 6% (± 6%).

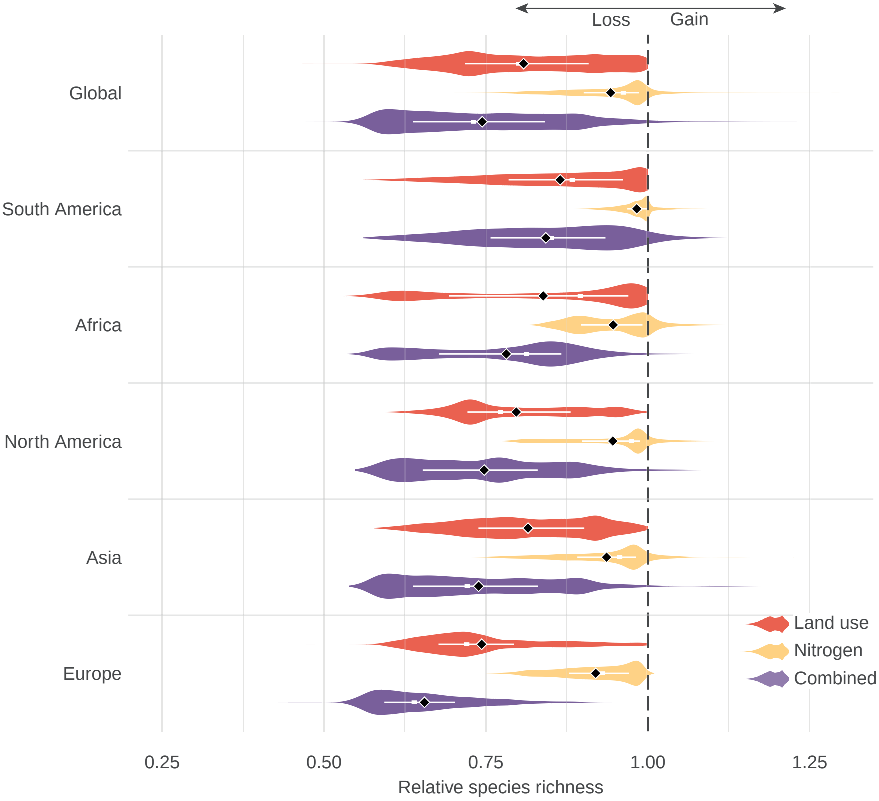


Figure 4.2 Changes in plant species richness across the 0.25° grid cells within the model's applicability domain due to land use, nitrogen and their combined effect globally and per continent. Density plots show the distribution of the data; the white horizontal lines inside the density plots show the interquartile ranges; the thick white square is the median; and the black diamond is the mean. Values are provided in **Table S4.3**. Note: width of violins is adjusted for visualization purposes.

We identified high species declines due to land use in eastern North America (USA), eastern South America (Brazil), eastern Africa (Uganda and Kenya), western Europe (France, the Netherlands and UK), and eastern Asia (China, **Figure 4.3a**). Areas highly affected by N deposition included eastern North America (USA), northern and western Europe (northern Italy, the Netherlands, southern Sweden and Finland), central Africa (Congo basin), and eastern Asia (China, **Figure 4.3b**). The areas most impacted by both pressures combined were western Europe and eastern Asia, followed by eastern North America and central Africa (**Figure 4.3c**).

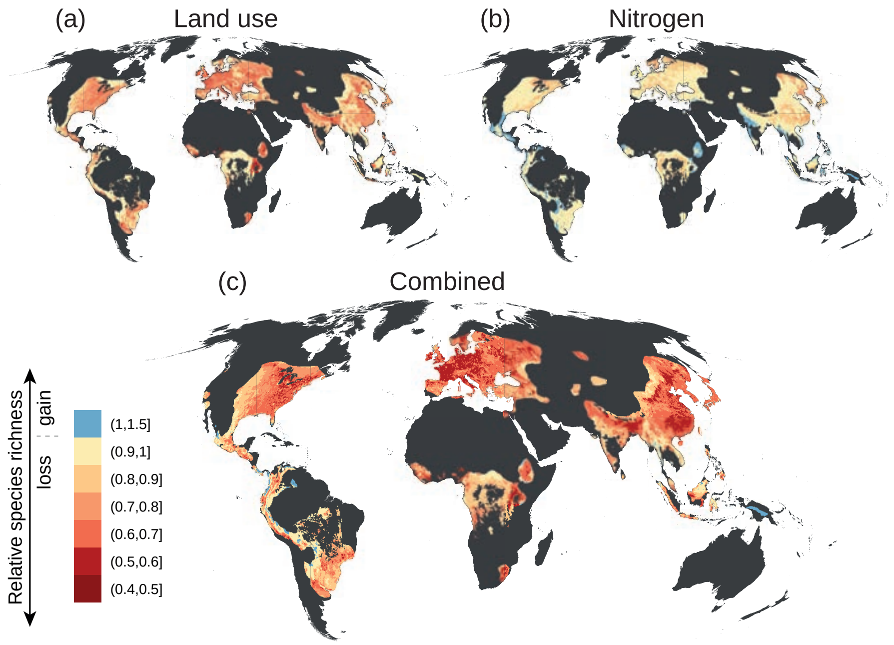


Figure 4.3 Geographical patterns of changes in relative plant species richness due to the effects of a) land use, b) nitrogen deposition and c) both pressures combined. Grey areas are outside the applicability domain of the model (67%, **Figure S4.5**).

In 11% of the cells, N deposition resulted in increases in species richness (**Figure 4.2**, **Figure 4.3b**), reflecting low N deposition (on average 5 kg ha^{-1} yr^{-1}), high mean annual temperature (on average 24 °C) and high CEC (on average 24 cmol kg^{-1}). For the two pressures combined, we found increases in species richness in only 2% of the cells, reflecting the negative impact of land use (**Figure 4.2**, **Figure 4.4**, **Table S4.4**).

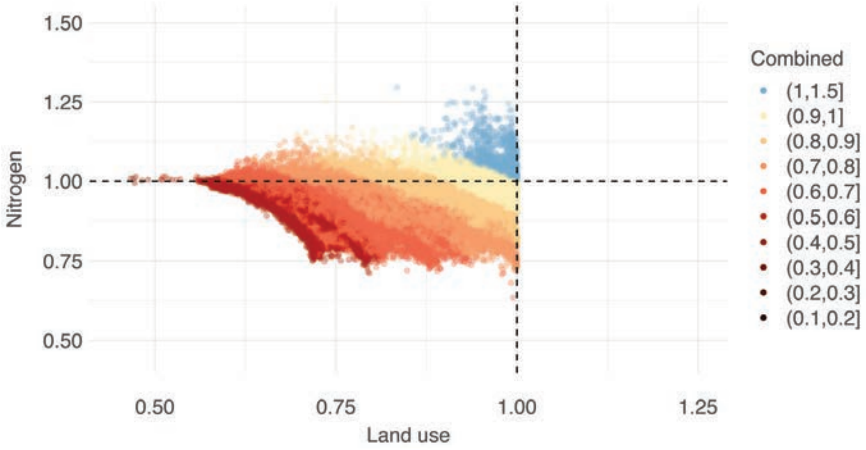


Figure 4.4 Relative species richness per 0.25° grid cell within the applicability domain due to land use, nitrogen deposition and their combined effect (represented by the color coding). Note that the axes have different ranges.

4.4 DISCUSSION

In this study we developed and applied a novel SAR-based model to quantify the effects of land use and N deposition on plant species richness in 0.25° grid cells across the globe. As for any SAR-based model, our results reflect projected changes in plant species richness rather than actual (instantaneous) losses or gains (Pereira *et al.* 2014), because losses or gains of species in response to environmental change typically occur with a lag time (leading to 'extinction debt' or 'colonization credit', respectively; Hanski & Ovaskainen, (2002)). This delay is currently not accounted for by SAR models (Lewis 2006), which implies that our estimates are not directly comparable to empirical observations. However, our model is based on comprehensive meta-analyses of site-level effects of both N deposition (Midolo *et al.* 2019) and land use (de Baan *et al.* 2013; Newbold *et al.*

2015), providing a solid basis for the mp-SAR and our results. We estimated that on average across the globe, landscape-level plant species richness might eventually be reduced by 26% due to the combined effects of land use and N deposition, with land use being the main driver. The latter is in line with previous research at smaller scales (i.e. local to country scale), identifying land use as more important driver of plant species composition than N deposition (McClean *et al.* 2011; Xu *et al.* 2012). Our meta-analysis and final results also confirm the findings of previous studies showing the typically negative effects of land use on local biodiversity (de Baan *et al.* 2013; Gerstner *et al.* 2014a; Newbold *et al.* 2015).

Although we found the highest levels of N deposition and impacts in certain regions in Asia (**Figure 4.2**; **Figure 4.3**; **Figure S4.7**), we observed the largest continental-level N-induced declines in plant species richness in Europe. Our mean estimate of 8% (± 6%) N-induced plant species decline in Europe is in line with the 10-20% decline in plant species richness as previously reported for European shrublands, grasslands and forest ecosystems (Dise *et al.* 2011). Apart from declines in plant species richness due to N deposition, we found net species (richness) increases as a result of low levels of N deposition in tropical montane areas in Costa Rica, Peru, Cambodia, and Vietnam. N deposition can play a key role in modulating the species richness in tropical regions (Lu *et al.* 2014; Perring *et al.* 2018). Especially in tropical montane areas, N is still a limiting factor (Bobbink *et al.* 2010; Perring *et al.* 2018) and thus low values of N deposition may increase plant species richness. However, the increase in species richness due to N deposition is typically caused by the colonization of generalist nitrophilous species (Lawrence 2003; Dise *et al.* 2011; Perring *et al.* 2018). These colonization events and the overall increase in species richness may mask the decrease of specialist species that are outcompeted, as well as the resulting ecosystem homogenization (Stevens *et al.* 2010; Perring *et al.* 2018). Moreover, possible future agricultural intensification as well as an increasing prevalence of seasonal fires to create and prepare agricultural land may increase N deposition levels in tropical regions (Chen *et al.* 2010; Bauters *et al.* 2018), which may turn plant species richness increases to declines. To better understand the effects of nitrogen addition on plant biodiversity, future research should include additional characteristics of the plant communities (e.g. abundance of individual species, or species turnover), because species richness may mask diverging responses of individual species (Fleishman *et al.* 2006; Schipper *et al.* 2016).

Our approach is not without uncertainties. First, we assumed a time frame of 32 years of cumulative N deposition based on the N deposition data available (Ackerman *et al.* 2018). However, impacts may accumulate over longer times, resulting in larger declines (**Figure S4.3**; Midolo et al., (2019)). Further, we assumed a constant level of N deposition across the 32 years, thus not accounting for recent reductions in N deposition as observed for example in Europe. The potential recovery of vegetation communities upon reductions in N inputs is, however, typically slow or may not take place at all as long as the remaining inputs are above critical levels (Dise *et al.* 2011; Stevens 2016). Second, we made several assumptions with regard to the combined effects of land use and nitrogen deposition. For secondary vegetation, we assumed that land use and N deposition act independently and that species' sensitivities to both pressures are uncorrelated, which justifies calculating the combined effect based on the assumption of response addition (Plackett & Hewlett 1952; Vinebrooke *et al.* 2004). However, the assumption of uncorrelated sensitivity might be too simplistic. For example, N-tolerant generalist plant species might be tolerant also to land cover change, while certain specialist species might be sensitive to both pressures. In case of positively correlated sensitivities to both pressures, the response addition approach leads to an overestimation of their combined effect (Vinebrooke *et al.* 2004). If we assume no further decline of species richness due to N deposition in secondary vegetation (i.e. the land cover type assumed to be affected by both pressures), the average decline changes from 6% for the combined effect of both pressures to 5% for land use only (**Figure S4.6**). For cropland, pastures, plantations and urban areas, we assumed that the direct effects of land use override the effects of atmospheric nitrogen deposition. We made this assumption because experimental data was not available to quantify nitrogen impacts in these land-use types (Midolo *et al.* 2019). However, N deposition may still have an additional impact on plant species richness in these land-use types, particularly if nitrogen input from alternative sources (e.g., manure or artificial fertilizers) is low (Kleijn *et al.* 2009; Wüst-Galley *et al.* 2021). To improve our model, it would be highly beneficial to collect and analyse experimental or monitoring data that allow for quantifying and disentangling the separate and combined effects of N enrichment (from both deposition and fertilization) and land use (excluding fertilization) on plant species richness in comparison to natural habitat. This need is most prominent for croplands or pastures, which make up a large share of the anthropogenic land. Finally, we note that we applied our model only to grid cells within its applicability domain (i.e. 33% of all the 0.25° cells in the world), which is not necessarily a representative sample of the globe as a whole. Applied to the entire globe, our model predicts lower species declines on average, due to the inclusion of areas with low N deposition levels and little land use (global mean species decline of 18% instead of 26%; **Figure S4.7** and **Figure S4.8**). However, the global mean impact of nitrogen deposition remains similar (**Figure S4.8**) and land use remains the main driver of plant species richness decline.

Our study provides a new methodology to quantify impacts of multiple pressures on landscape-level plant species richness. Our new mp-SAR approach can be expanded to predict the combined effect of other human pressures, such as climate change or invasive species, which are currently lacking in the SAR framework (Hanski *et al.* 2013; Pereira *et al.* 2014). The required affinity values can be quantified based on experimental data, based on field observations obtained along a pressure gradient, or a combination of experimental and monitoring data, provided that the data include also records in natural habitat (Koricheva & Gurevitch 2014). Given the paucity of studies quantifying impacts of multiple pressures (Franklin *et al.* 2016; Bonebrake *et al.* 2019; Bowler *et al.* 2020), our current methodology may fill a gap and, ultimately, help to underpin conservation policies. Tackling multiple pressures would certainly increase the effectiveness of conservation policies and can even be imperative for success, as removing a dominant pressure could simply reveal the impacts of remaining pressures without a net biodiversity gain (Bonebrake *et al.* 2019; Bowler *et al.* 2020). For example, our results suggest that restoring agricultural land to natural vegetation may not be fully effective in regions with high levels of N deposition, such as eastern Asia, the United States and Europe. The consistent negative impact of land use together with the long-term effect of N deposition in those areas point at a need to tackle both pressures simultaneously if nature is to be conserved or restored, for example through a combination of alternative farming practices (e.g., organic farming), dietary changes (notably a reduction of meat consumption) and targeted N emission reduction measures (Dise *et al.* 2011; Mace *et al.* 2018; Pe'er *et al.* 2020). These efforts may need to be supplemented by active restoration measures to speed up or even enable the recovery of damaged habitats (Stevens 2016). Mitigating or reducing the combined impacts of N deposition and land use on plant communities is not only needed to halt the ongoing decline of biodiversity, but also the associated services to human society.

4.5 ACKNOWLEDGEMENTS

This study was conducted as part of the GLOBIO project (www.globio.info). We are thankful to Martijn Schaap for pointing us at global N deposition maps and to Gabriele Midolo for helping us to model the impact of N deposition on plants. We thank Melinda de Jonge for helping us to double-check our classification of observations into different land-use classes.

CHAPTER

5

COMBINED EFFECTS OF LAND USE AND HUNTING ON DISTRIBUTIONS OF TROPICAL MAMMALS

Published in Conservation Biology, 34 (5): 1271-1280

Authors

Juan Gallego-Zamorano[1*], Ana Benítez-López[1,2], Luca Santini[1,4], Jelle P. Hilbers[1,3], Mark A.J. Huijbregts[1], Aafke M. Schipper[1,3]

[1]Department of Environmental Science, Institute for Wetland and Water Research, Faculty of Science, Radboud University, P.O. Box 9010, NL-6500 GL, Nijmegen, The Netherlands

[2]Integrative Ecology Group, Estación Biológica de Doñana (EBD-CSIC), Av. Americo Vespucio S/N, 41092 Sevilla, Spain

[3]PBL Netherlands Environmental Assessment Agency, P.O. Box 30314 NL-2500 GH, The Hague, The Netherlands

[4]National Research Council, Institute of Research on Terrestrial Ecosystems (CNR-IRET), Via Salaria km 29.300, 00015, Monterotondo (Rome), Italy

ABSTRACT

Land use and hunting are 2 major pressures on biodiversity in the tropics. Yet, their combined impacts have not been systematically quantified at a large scale. We estimated the effects of both pressures on the distributions of 1,884 tropical mammal species by integrating species' range maps, detailed land-use maps (1992 and 2015), species-specific habitat preference data, and a hunting-pressure model. We further identified areas where the combined impacts were greatest (hotspots) and least (coolspots) to determine priority areas for mitigation or prevention of the pressures. Land use was the main driver of reduced distribution of all mammal species considered. Yet, hunting pressure caused additional reductions in large-bodied species' distributions. Together, land use and hunting reduced distributions of species by 41% (SD 30) on average (year 2015), with an overlap between impacts of only 2% on average. Land use contributed more to the loss of distribution (39% on average) than hunting (4% on average). However, hunting reduced the distribution of large mammals by 29% on average; hence, large mammals lost a disproportional amount of area due to the combination of both pressures. Gran Chaco, the Atlantic Forest, and Thailand had high levels of impact across the species (hotspots of area loss). In contrast, the Amazon and Congo basin, the Guianas, and Borneo had relatively low levels of impact (coolspots of area loss). Overall, hunting pressure and human land use increased from 1992 to 2015 and corresponding losses in distribution increased from 38% to 41% on average across the species. To effectively protect tropical mammals, conservation policies should address both pressures simultaneously because their effects are highly complementary. Our spatially detailed and species-specific results may support future national and global conservation agendas, including the design of post-2020 protected-area targets and strategies

5.1 INTRODUCTION

Overexploitation and habitat loss due to agricultural activities are major pressures on biodiversity in the tropics (Maxwell *et al.* 2016). Recent estimates indicate mammal populations have been reduced by more than 80% and by 30% due to hunting pressure and land-use change, respectively (Almeida-Rocha *et al.* 2017; Benítez-López *et al.* 2017). So far, most research has focused on quantifying the impacts of these two pressures separately (Almeida-Rocha *et al.* 2017; Benítez-López *et al.* 2017, 2019; Lima *et al.* 2018), yet both threats typically act simultaneously. For example, deforestation and associated infrastructural development can improve hunters' access to previously remote intact areas (Fa & Brown 2009; Abernethy *et al.* 2013; Laurance *et al.* 2017). Global conservation targets and actions also typically address one of the two pressures (e.g., Aichi Targets 4 and 5 (CBD 2010)) and may thus fall short in addressing overall conservation goals. Hence, studies addressing the combined impacts of land use and hunting are urgently needed.

Only a few researchers have quantified the combined effect of both pressures on tropical mammals (Brodie *et al.* 2015; Romero-Muñoz *et al.* 2019). These authors found that the relative and combined effects of the two pressures differ among species and geographic areas, highlighting the relevance of looking at both pressures simultaneously to design effective conservation actions. However, previous studies were limited to a single region or based on a few species, and the combined effects of both pressures have not yet been comprehensively assessed across multiple mammal species at a large spatial extent. This information is urgently required for informing large-scale conservation planning and prioritization by identifying disproportionally affected areas as well as pristine places where species are still relatively safe (hotspots vs coolspots; e.g., Allan *et al.* (2019)).

We quantified the combined impact of land use and hunting on the geographic distributions of 1,884 tropical mammal species. While land use may result in reductions in distribution due to habitat loss, hunting can lead to extirpations (i.e. local extinctions) in areas that are otherwise suitable (Wilkie *et al.* 2011; Benítez-López *et al.* 2017). Both pressures thus lead to a reduction in the distribution of wildlife species, which may compromise their persistence (Brook *et al.* 2008; Allan *et al.* 2019). We mapped habitat loss due to land use by combining species' geographic range maps with land-use maps and species-specific habitat-preference data. We quantified reductions of the distribution of each species due to hunting pressure as a function of distance to hunters' access points, human population density, and body size of the species, which are major determinants of hunting impacts (Benítez-López *et al.* 2017, 2019). Finally, we quantified reductions in the distribution due to both pressures combined and evaluated possible changes in the impacts of these pressures over the past decades (1992 to 2015).

5.2 METHODS

Species selection and initial distribution

We selected mammal species with at least 95% of their geographic ranges in the tropics. We retrieved maps of the geographical ranges of all terrestrial mammal species from the IUCN (IUCN 2017) and clipped these to the tropics based on the recently updated biomes map by Dinerstein *et al.* (2017). We considered four tropical biomes: Tropical and Subtropical Moist Broadleaf Forests, Tropical and Subtropical Dry Broadleaf Forests, Tropical and Subtropical Coniferous Forests, and Tropical and Subtropical Grasslands, Savannas, and Shrublands. This selection yielded 1,884 species. Because geographic range maps are rather coarse representations of the distributions of species, we refined the range maps based on the species' elevation limits and habitat (Brooks *et al.* 2019) (**Figure 5.1**). For elevation we used the MERIT Digital Elevation Model (Yamazaki *et al.* 2017) at 10 arc-sec resolution (~300 m at the equator) and selected areas within the elevation limits of the species as defined by the International Union for Conservation of Nature (IUCN 2017). For species lacking information on elevation limits, we assumed they occur across the entire elevational gradient within their range. We then filtered out unsuitable natural areas based on species' habitat preferences and a natural land-cover map. We compiled the natural land-cover map (10 arc-seconds resolution) by combining a land-use map for 1992 (see below) with a map of potential natural vegetation (PNV) (Hengl *et al.* 2018). We used the cells with natural land cover from our 1992 land-use map and assigned the vegetation type from the PNV map to the remaining (i.e., anthropogenic land uses) cells. We preferred this combined map for natural land cover over using only the PNV map because of the higher spatial resolution of the land-use map (10 arc-seconds as opposed to 30 arc-seconds) and its more refined classification of natural land-cover types. We then removed cells with unsuitable natural land cover from the species' ranges based on species-specific information on habitat preferences as provided by the IUCN Habitat Classification Scheme (level 2) and on a cross-walk between the IUCN habitat classes and the natural land-cover classes (**Appendix S5.2**, **Table S5.3**; Santini et al. 2019). The area remaining within the occurrence range of a species after the elevation and land-cover filtering constituted our initial distribution estimate (i.e., baseline distribution) (**Figure 5.1**).

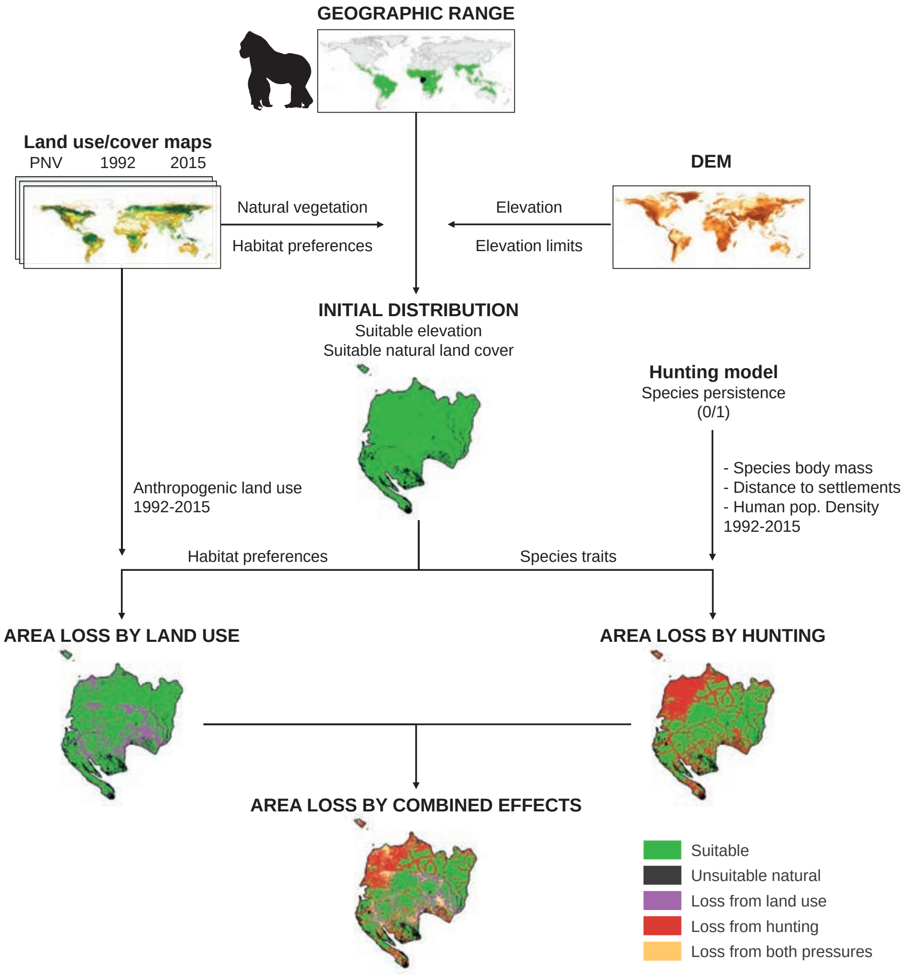


Figure 5.1 Steps in the model of distribution loss for an example species (Western gorilla Gorilla gorilla) (DEM, digital elevation model; suitable, areas suitable for the species; unsuitable natural, natural land cover not suitable for the species). Final map is total area of distribution loss of the species.

Area loss due to land use

For each species, we quantified area loss relative to their initial distribution due to land use based on land-use maps for the years 1992 and 2015 (**Figure 5.1**, **Table S5.3**). We compiled the land-use maps with the land-use allocation routine from the GLOBIO 4 model (Schipper *et al.* 2020), in which we combined country-level total areas of forestry and pasture with the recently released European Space Agency (ESA) climate-change initiative (CCI) land-cover maps (ESA 2017). These maps represent a consistent series of yearly land-cover maps from 1992 to 2015 at a 10 arc-seconds resolution. Cropland and urban areas are included in these maps, but pastures and forestry areas are not because they cannot be distinguished from natural grassland and forests (yet can be unsuitable for many species (Barona *et al.* 2010)). We, therefore, retrieved country-level total areas of pasture and forestry representative for 1992 and 2015 from the Food and Agriculture Organisation (FAO 2016) and downscaled these onto the ESA maps for these same years with the GLOBIO 4 land-use allocation routine (see **Appendix S5.1** for details, and Schipper *et al.* (2020)). Within each species' distribution, we then quantified the total area of the anthropogenic land-use types (i.e. urban areas, croplands, pastures, and forestry) unsuitable for the species based on species-specific habitat preferences (**Figure 5.1**, **Table S5.3**) in the absence of any other pressure such as hunting. We considered the area loss due to land use as the sum of the cells lost due to all four land-use types together.

Area loss by hunting pressure

To account for hunting pressure, we estimated the areas within each species' initial distribution where it would likely be extirpated due to hunting. We used a mixed-effects model with a binomial error distribution to quantify the species-specific probability of persistence under hunting pressure as a function of various key determinants of hunting pressure, namely the distance to hunters' access points (settlements), human population density, and the species' body mass. We fitted the model based on a database with 3,281 mammal abundance estimates of 296 species (from 51 families and 14 orders) from 163 studies and 114 papers that systematically compared abundance between hunted and unhunted sites within the tropics (Benítez-López *et al.* 2017, 2019). Estimates were only included in this database if confounding factors were (virtually) absent or the same in the hunted area and the unhunted control site (Benítez-López *et al.* 2017). This database is the most extensive database of the impact of hunting on species abundance in the tropics, in terms of location coverage (37 countries) and number of species (see above), and it covers the majority of families and the body mass range of our selection of tropical mammals (**Figure S5.1**, Benítez-López *et al.* (2017, 2019)). To estimate loss of distribution due to hunting, we transformed abundance data into occurrence (abundance > 0, n=2,873) and extirpation (abundance = 0, n=408). We retrieved the distance to access points from the hunting database (Benítez-López *et al.* 2017, 2019), human population density (matched as closely as possible to the year of the study) from CIESIN (2017), and body mass from the EltonTraits database (Wilman *et al.* 2014). We $\log_{10}$-transformed the continuous predictor variables before model fitting and included quadratic terms to account for potential nonlinear relationships. We specified as random effects country, study (typically encompassing the data from one article, but some articles report on multiple studies), and species to account for between-country variation in hunting laws and policies, culture, taboos, and traditions (Ngoufo & Waltert 2014; Bobo *et al.* 2015) and to control for nonindependence in the data from the same study or species (Benítez-López *et al.* (2019)). Finally, we selected the most parsimonious model based on the Akaike information criterion (Table S5.1). The best model included distance to settlements and its quadratic term, human population density, and species' body mass.

We then used the best model to predict for each tropical species the probability of persistence under hunting pressure within its distribution at a 30 arc-sec (~1km) resolution. Our predictions were based on the taxonomic identity of the species (captured by the random-effect intercept species) and its body mass (species' vulnerability to hunting pressure) combined with the distribution of context-dependent drivers of hunting pressure in the species' initial distribution (i.e., country, captured by the random-effect intercept country; distance to settlements; and human population density). We retrieved data on human population density specific to 1992 (average between 1990 and 1995) and 2015 from CIESIN (CIESIN & CIAT 2005; CIESIN 2017) and a raster map of distance to the nearest settlement from Benitez-Lopez *et al.* (2019). This represented a static view of the location of human settlements. To estimate the impacts of hunting on the distribution of the species, we binarized the probabilities of occurrence of each species as predicted by the hunting model (1 = species potentially present and 0 = species extirpated). We binarized the predictions based on a probability threshold that maximized the true skills statistic (TSS) (Allouche *et al.* 2006), which assesses the predictive power of the model based on the sensitivity and specificity values (TSS = sensitivity + specificity – 1). The TSS ranges from -1 (all predictions are wrong) to 1 (all predictions are correct). The binarization resulted in species-specific 30 arc-sec maps of potential area loss due to hunting pressure within the initial species' distribution (**Figure 5.1**). Finally, we resampled the hunting-impact maps (30 arc-sec) to the same spatial resolution as the land-use impact maps (10 arc-sec).

Combined impacts of both pressures

To quantify the total reduction in the species' distributions, we overlaid the maps of both pressures and identified the area lost due to hunting only, land use only, and the overlap of the two pressures (**Figure 5.1**). We then calculated the combined impact of both pressures relative to the initial distribution for each species as:

$$P_{\mathrm{loss},i} = \left(\frac{A_{\mathrm{loss},i,\mathrm{LU}} + A_{\mathrm{loss},i,\mathrm{H}} - A_{\mathrm{loss},i,\mathrm{LU}\cap\mathrm{H}}}{A_i}\right) * 100 \qquad \text{Equation 5.1}$$

where $P_{\mathrm{loss},i}$ is the area loss due to both pressures combined relative to the initial distribution (percentage) of species *i*, $A_{\mathrm{loss},i,\mathrm{LU}}$ is the area loss (square kilometers) due to land use only, $A_{\mathrm{loss},i,\mathrm{H}}$ is the loss (square kilometers) due to hunting only, $A_{\mathrm{loss},i,\mathrm{LU}\cap\mathrm{H}}$ is the overlap in loss between the two pressures (square kilometers), and A_i is the initial distribution (square kilometers).

We grouped our area-loss results by species group based on body size: very small (< 0.1 kg, *n*= 979 species), small (0.1 - 1 kg, *n*= 532), medium (1 - 10 kg, *n*= 291), and large (> 10 kg, *n*=82). We further calculated the average area loss across mammals from different continents (the Americas, Africa, and Asia). Finally, we compared the area losses from 1992 to 2015 to identify possible changes in the magnitude and relative importance of the two pressures over time.

Hotspots and coolspots of area loss

We defined hotspots and coolspots of area loss as areas with great (>90%) or small (<10%) distribution loss due to the combined pressures across the species per

0.25º (~25 km) grid-cell (for computation and visualization purposes). Within each 0.25º cell, we divided the cumulative area lost by the cumulative initial area across all the species present in that cell:

$$P_{\text{loss},y} = \frac{\sum_{i=1}^{n} A_{\text{loss},i,y}}{\sum_{i=1}^{n} A_{i,y}} \qquad \text{Equation 5.2}$$

where $P_{\text{loss},y}$ is the average area loss (percentage) in cell y (0.25º resolution ~ 25 km), $A_{\text{loss},i,y}$ is the area loss of species i in cell y (km^2), and $A_{i,y}$ is the initial area of species i within cell y (km^2). All the calculations were done using a Mollweide equal-area projection in R 3.5.3 (R Development Core Team 2016).

5.3 RESULTS

Area loss due to land use and hunting pressure

On average across the species, distributions of the species declined 41% (SD 30) due to the combined impacts of hunting and land use (2% overlap between the two pressures; **Table S5.2**). Land use resulted in an average loss of 39% of the initial distribution (SD 30) and hunting in a loss of 4% (SD 11). The smallest mammal species (< 0.1 kg) were mostly affected by land use (loss of 42% SD 31) (**Figure 5.2**), whereas area losses estimated for large species (> 10 kg) were due to both land use (40% SD 26) and hunting pressure (29% SD 21). Hunting was the main pressure for 30% of the large species (**Figure S5.5**). As a result, large mammals were the most affected group overall, showing an average area loss of 53% (SD 24) (**Figure 5.2**) due to both pressures combined.

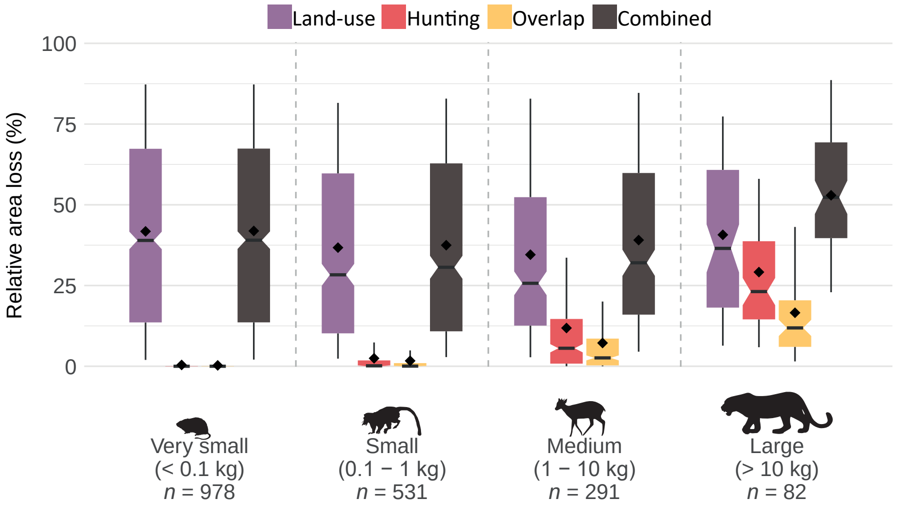


Figure 5.2 For 2015 distribution losses of 1,884 species due to land use and hunting pressure (combined, sum of both pressures minus their overlap; diamonds, mean values per group; lower and upper box boundaries, 25th and 75th percentiles, respectively; thick horizontal line, median; notch, 95% CI around the estimate of the median; whiskers, 10-90% percentiles). Summary statistics are in **Table S5.2**.

Geographical patterns of area loss

Areas of great distribution loss (hotspots) across the species were identified in the Gran Chaco, Atlantic Forest, El Cerrado, northwestern part of South America, East Africa, Madagascar, Thailand, and Java. Areas with small loss (coolspots) were in the Amazon Basin, the Guianas, the Congo Basin, central Borneo, and Papua New Guinea (**Figure 5.3**).

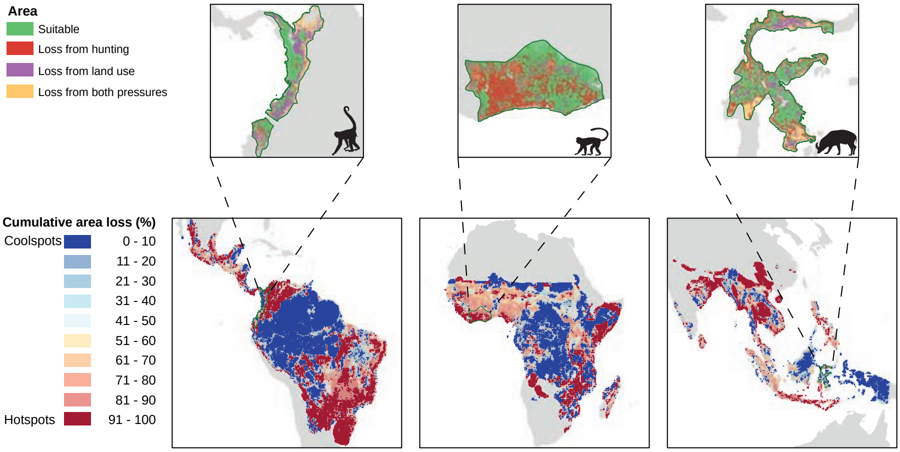


Figure 5.3 Upper panels, loss of distribution due to hunting, land use, and both for the brown-headed spider monkey (Ateles fusciceps), Lowe's monkey (Cercopithecus lowei), and Sulawesi babirusa (Babyrousa celebensis) (from left to right) (suitable, areas suitable for the species). Lower panels, cumulative distribution loss of 1,884 tropical mammal species due to land use and hunting relative to the cumulative area of their initial distribution.

Estimated area losses were the greatest in Africa (average loss 46% [SD 30]), followed by America (40% SD 31) and Asia (37% SD 28 **Figure 5.4**, **Table S5.2**). Land use was the main driver of area loss on all continents, resulting in average losses ranging from 35% in Asia to 45% in Africa (**Figure 5.4a**). These losses were mainly driven by croplands in Africa and Asia (26% SD 24 and 28% SD 23 loss) and by pastures in America (24% SD 22 loss). Mammal species were predicted to be extirpated by hunting across 5% (SD 13) of their initial distribution in Asia (**Figure 5.4a**) and 3-4% on the other continents (**Table S5.2**). When looking only at medium and large species, up to 16% (SD 20) of the initial distribution was under high hunting pressure in Asia and 15% (SD 18) and 13% (SD 17) in Africa and America, respectively (**Figure 5.4b**, **Table S5.2**).

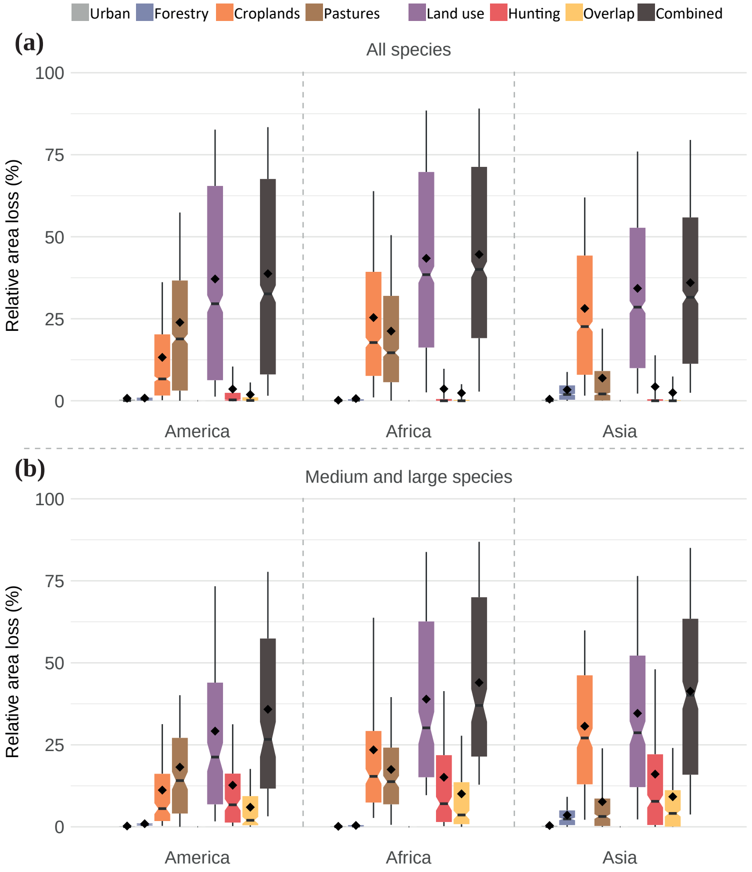


Figure 5.4 Losses in distribution size for (a) all species and (b) only medium (1-10 kg) and large mammals (>10 kg) due to land use and hunting pressure across the species by continent in 2015 (combined, sum of losses due to land use and hunting minus the overlapping areas; diamonds, mean values per group; lower and upper box boundaries, 25th and 75th percentiles; thick horizontal line, median; notch, 95% CI around estimate of the median; whiskers, 10-90% percentile). Summary statistics are in **Table S5.2**.

Changes over time

Losses in distribution increased from a mean of 38% (SD 31) in 1992 to 41% (SD 30) in 2015 (**Figure S5.3**, **Table S5.2**). Some species increased their distribution (i.e., 423 species), for example, in Ethiopia where the area of pasture decreased from 448,000 km^2 in 1992 to 288,000 km^2 in 2015 (FAO 2016). Yet, most species experienced further loss (i.e., 1,387 species), mainly driven by land-use change (**Figure 5.5**, **Figure S5.3**). For medium-sized species, hunting pressure also increased over time, leading to additional reductions in distribution. Large species also experienced increases in the impacts of both pressures; increases were larger for hunting than for land-use impacts (**Figure 5.5**).

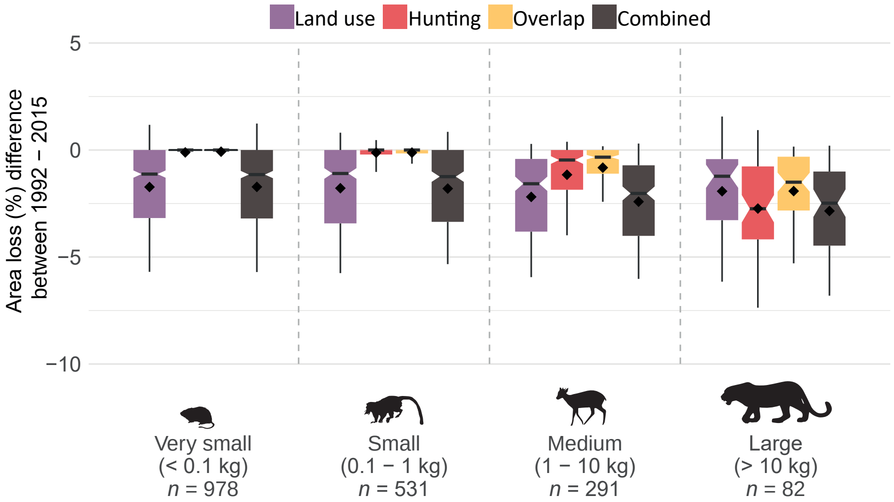


Figure 5.5 Changes in distribution-size losses due to land use and hunting pressure from 1992 to 2015 (negative values, loss of area from 1992 to 2015; positive values, gain of area; diamonds, mean values per group; lower and upper box boundaries, 25th and 75th percentiles, thick horizontal line, median; notch, 95% CI around the estimate of the median; whiskers, 10-90% percentile). Summary statistics in **Table S5.2**.

5.4 DISCUSSION

To our knowledge, we are the first to quantify the combined impact of land use and hunting pressure on the distributions of mammals across the entire tropical region. Our results suggest that tropical mammals lost on average 40% of their distribution due to these two pressures combined (**Figure 5.2**, **Figure 5.4** and **Figure 5.5**), whereby land use is responsible for the largest share (39%) (**Figure 5.2**, **Figure 5.4**, **Figure S5.5**). This is in agreement with a recent analysis of threats to biodiversity based on IUCN threat status information, showing that more species are threatened by crop and livestock farming than by hunting (Maxwell *et al.* 2016). However, our results also indicate hunting is a major pressure on large mammals (**Figure S5.5**), extirpating populations across ~30% of their distribution on average (**Figure 5.2**), confirming that hunting renders larger species locally extinct (Ripple *et al.* 2016, 2019).

For the largest species, the increase in hunting impacts was larger than the increase in land-use impacts (from 1992 to 2015, **Figure 5.5**). We further found that the impacts of both pressures are highly species-specific (**Figure 5.2**, **Figure 5.3**, **Figure S5.5**). For example, Lowe's monkey (*Cercopithecus lowei*), a generalist species, was primarily affected by hunting (but see Linder & Oates (2011)), whereas the brown-headed spider monkey (*Ateles fusciceps*), a forest specialist, was affected most by deforestation and land-use change. We found a relatively small overlap between the impacts of the two pressures (**Figure 5.2**, **Figure 5.4** and **Figure 5.5**, **Table S5.2**), reflecting that hunting mainly takes place in remaining areas of natural habitat that are not yet affected by land use (Ripple *et al.* 2016, 2019; Benítez-López *et al.* 2017, 2019). Hence, both pressures are largely complementary in yielding losses in the distribution of the species. As a result, large mammals in particular lost a disproportional amount of area due to both pressures combined (**Figure 5.2**, **Figure S5.5**). Overall, we considered our area loss estimates conservative (optimistic) because we did not account for additional effects of land use, such as fragmentation or edge effects, that may cause small area remnants to be functionally lost (Pe'er *et al.* 2014). Additionally, we did not consider access points other than settlements (e.g. roads), and we accounted only for hunting impacts that cause extirpations, whereas many hunted mammal populations could be largely reduced without necessarily being extirpated (Benítez-López *et al.* 2017, 2019). These reduced populations might become functionally extinct (i.e., nonviable or no longer contributing to ecosystem functioning) before being totally extirpated from an area. Consequently, the effect of hunting may be larger than estimated here, in line with the finding that our model predicted larger hunting impacts with a higher threshold for binarizing the predicted probabilities of occurrence (i.e., using a threshold corresponding with minimizing the error of predicting local extinctions) (**Figure S5.2**).

Our results further showed clear spatial variation in the effects of the two pressures. At the level of continents, we found that pasture may remove 24% of natural habitat in South America, whereas only 7% may be removed in Asia (**Figure 5.4a**, **Table S5.2**), reflecting that extensive grazing is one of the major drivers of deforestation in America (Barona *et al.* 2010). Furthermore, hunting impacts were bigger in Asia and Africa than in America (**Figure 5.4b**, **Table S5.2**), where bushmeat hunting is largely driven by demand for medicinal products, ornamentals, or trophy products (Ripple *et al.* 2016) and species are accessible and have higher population densities. In some areas with high distribution loss (hotspots) there were very few tropical species (e.g., southern Africa [Angola] and central China) (**Figure 5.3**, **Figure S5.4**). Yet, hotspots of loss also occurred in species-rich areas, such as some parts of South America, East Africa, and Southeast Asia (**Figure 5.3**, **Figure S5.4**). Our results are in line with previous research demonstrating that tropical mammals in the Gran Chaco, the Atlantic Forest, and Java are threatened by both land-use change and hunting (Symes *et al.* 2018; Romero-Muñoz *et al.* 2019).

In contrast, the Amazon and Congo basins, the Guianas, Borneo, and Papua New Guinea had relatively small loss of distribution across the species (coolspots), which is in line with results of previous efforts to map human impacts on biodiversity (Venter *et al.* 2016; Allan *et al.* 2019; Benítez-López *et al.* 2019; Schipper *et al.* 2020). With the ongoing increase of human activities in tropical areas, remaining intact places may be compromised in the future (Watson *et al.* 2018; Allan *et al.* 2019). Indeed, our results show that both land use and hunting pressure increased over the past decades (**Figure 5.5**, **Figure S5.3**). Therefore, we suggest conservation efforts focus on reducing or mitigating these pressures in hotspots and prevent further degradation in coolspots of loss, which is an urgent priority for current global efforts to halt the ongoing biodiversity crisis (Watson *et al.* 2018). Limiting the construction of new roads and enforcing laws against illegal deforestation, hunting, and wildlife trade may contribute to this goal (Peres 2005; Ripple *et al.* 2016).

In 2020 the Convention on Biological Diversity will adopt a post-2020 global biodiversity framework, which calls for evidence-based conservation targets and strategies (CBD 2019). Our results demonstrate the importance of accounting for the combined effect of land use and hunting on medium and large species because their effects are highly complementary (i.e., the two pressures affect different parts of the species' distribution and their relative importance differs among species) (Brodie *et al.* 2015; Symes *et al.* 2018). The magnitude of the impacts combined with the poor level of protection of remaining wilderness areas (Di Marco *et al.* 2019) point to the need to increase the level of protection if tropical mammals are to be conserved (Peres 2005; Geldmann *et al.* 2019). Protected areas need to be strengthened, for example, through law enforcement, effective prosecution, and community engagement (Geldmann *et al.* 2019) to ensure their effectiveness in halting both pressures simultaneously and protect tropical mammals more effectively.

5.5 ACKNOWLEDGMENTS

We thank P. Visconti and M. Čengić for their contributions to the habitat cross-walk. We thank M. Busana and S. Hoeks for helping out with improving the efficiency of the code. We are thankful to Phylopic (www.phylopic.org) for providing nice free silhouettes and especially to Lukasiniho and T. Michael Keesey. J.H. and A.S. were supported by the GLOBIO project (www.globio.info). A.B.L. was supported by a Juan de la Cierva-Incorporación grant (IJCI-2017-31419) from the Spanish Ministry of Science, Innovation and Universities.

CHAPTER 6

SYNTHESIS

6.1 INTRODUCTION

The central aim of this thesis was to advance global biodiversity modeling by 1) developing context-specific biodiversity response relationships for understudied human pressures that allow for extrapolation across regions and/or species (groups), and 2) demonstrating how to use meta-analytical response relationships to assess the combined impacts of multiple human pressures on biodiversity across large spatial extents. Chapters 2 and 3 developed quantitative trait-based meta-analytical models to estimate the impact of nitrogen addition on invertebrates (**Chapter 2**) and linear infrastructures on vertebrates (**Chapter 3**) while accounting for the environmental context. In chapters 4 and 5, similar quantitative meta-analytical models were developed and applied to quantify the relative and combined impacts of land use and nitrogen deposition on plant species richness globally (Chapter 4), and of land use and hunting pressure on the distributions of mammals in the tropics (Chapter 5). This final chapter synthesizes the findings of the previous chapters in relation to the aims of the thesis. Specifically, this chapter discusses the context-dependent response relationships developed and used in different chapters (section 6.2) and the challenges and advances of multi-pressure impact modelling (section 6.3). Finally, section 6.4 provides overall conclusions of the thesis and recommendations for future research.

6.2 CONTEXT-DEPENDENT RESPONSE RELATIONSHIPS

Compared to climate change and land use, other human pressures on biodiversity, such as overexploitation or pollution, have received much less attention in global biodiversity assessments. In this thesis, meta-analytical models were developed and used to quantify the impact of nitrogen enrichment on invertebrates (Chapter 2) and plants (Chapter 4), effects of linear infrastructure on several vertebrate groups (Chapter 3) and the impact of hunting on mammals in the tropics (Chapter 5). Differences between environmental circumstances and between species modify the biodiversity response to human pressures. Indeed, all chapters demonstrate that ecological responses to a given human pressure depend on local environmental conditions and/or species traits (**Table 6.1**). For example, impacts of nitrogen addition on the abundance of invertebrates were clearly different depending on the local temperature (**Fig. 6.1b**) and between species groups (**Fig. 6.1c**).

Table 6.6 Overview of the context variables considered in each chapter and the variables remaining after model selection.

Chapter	Model type	Taxonomic group(s)	Variables considered	Variables selected
2	- Species based - Assemblage based	- Arthropods - Nematodes	- Mean annual temperature - Mean annual precipitation - Soil cation exchange capacity - Habitat type - Metamorphosis mode - Feeding guild	Arthropods: - Mean annual temperature - Metamorphosis mode Nematodes: - Mean annual precipitation - Feeding guild
3	Species based	- Mammals - Birds - Reptiles - Amphibians	- Habitat type - Body mass - Feeding guild	Mammals: - Habitat type - Body mass - Feeding guild Birds: - Habitat type - Feeding guild Reptiles: - Habitat type Amphibians: - None
4	- Assemblage based - Area based	Plants	- Mean annual temperature - Soil cation exchange capacity	- Mean annual temperature - Soil cation exchange capacity
5	Species based	Mammals	- Body mass	- Body mass

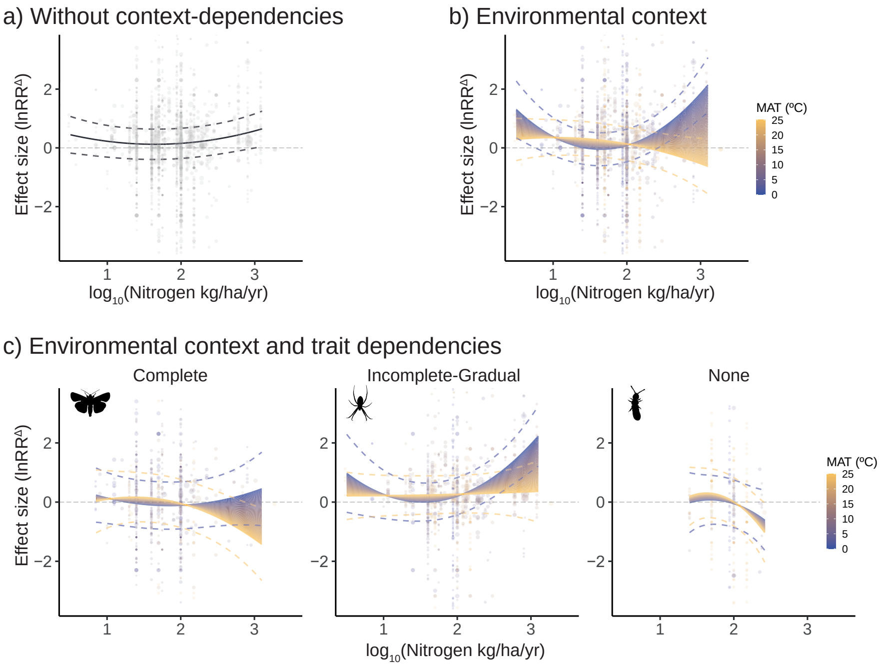


Figure 6.1 Abundance of arthropods in relation to a) the amount of nitrogen addition only, b) nitrogen addition and mean annual temperature (MAT) and c) nitrogen addition, MAT and arthropod metamorphosis types (best-supported model selected in Chapter 2). Dashed lines represent the 95% confidence interval for the highest (25 ºC, yellow) and lowest (0 ºC, blue) value of mean annual temperature (MAT) within the dataset. The dashed line at 0 indicates no change in abundance compared with the control plots (no nitrogen added). Point size represents observation weight. Silhouettes are public domain obtained from "phylopic" (www.phylopic.org).

Relevant environmental moderators identified in this thesis include climatic factors, such as temperature or precipitation (Chapters 2 and 4), but also habitat type or soil buffer capacity (Chapters 3 and 4). Local climate turned out important for the responses of plants and invertebrates to nitrogen enrichment (Chapters 2 and 4). For example, the impact of nitrogen enrichment on invertebrates was higher in areas with higher temperatures and lower precipitation, which may be explained by the faster grow of nitrophilous plants and the accumulation of toxic nitrogen compounds for invertebrates (**Chapter 2, Fig. 6.1b, c**). Under the assumption that the spatial comparison between sites in different local climates would detect the same biodiversity response as if climate change would occur in those sites ('space-for-time substitution'), my results indicates that impacts of nitrogen pollution might be amplified with climate change. This is in line with the results of multi-factorial experiments studying the response of biodiversity to nutrient enrichment and climate change (Song *et al.* 2016; Peguero *et al.* 2021; Wang *et al.* 2021; Cui *et al.* 2022). For vertebrates such as mammals, birds and reptiles, I found that habitat type moderated the abundance response to linear infrastructure (Chapter 3), with greater impacts in closed habitats, such as forests. In contrast, habitat type was not selected as a relevant variable for the effect of nitrogen on invertebrates. This unexpected result might be due to the low variability in habitat types in the database used in Chapter 2, i.e., most of the observations were made in non-forest habitats such as grasslands. Further, the primary data sources did not provide detailed information about the different habitat types, which prevented us from implementing a more detailed habitat classification. Still it is expected that nitrogen effects on plants vary between habitats and functional groups (Bobbink *et al.* 2010; Midolo *et al.* 2019), which probably extrapolates to invertebrates as well (Vogels *et al.* 2020).

My thesis also shows the relevance of including species traits in biodiversity models. Body mass is a key functional trait that correlates with many other species properties, e.g., home range size, metabolic rate, or flight speed (Steven 2004; Alerstam *et al.* 2007; Tucker *et al.* 2014). Here I found that it is also one of the traits determining the sensitivity of species to human pressures like linear infrastructures (Chapter 3) and hunting (Chapter 5; Benítez-López *et al*., (2017)). In general, these chapters show that larger species are more sensitive to human pressures than smaller ones, in line with other studies (e.g. Cardillo *et al*. 2005). Large-sized species tend to have lower growth rates (Fenchel 1974; Cardillo *et al.* 2005) and population densities (Damuth 1981; Santini *et al.* 2022), and are also more prone to encounter humans in fragmented habitats as they have relatively large home ranges (Cardillo *et al.* 2005; Tucker *et al.* 2014). These characteristics make large-sized species more vulnerable to human threats (Chapters 3 and 5), resulting in a higher risk of extinction (Cardillo *et al.* 2005; Hilbers *et al.* 2016; Ripple *et al.* 2017, 2019). Another important trait in the context of ecological responses to human pressures is the feeding guild of species (Chapters 2 and 3). Carnivores were one of the major trophic groups affected by nitrogen enrichment (i.e., carnivorous nematodes, Chapter 2), linear infrastructure (i.e., carnivorous mammals and birds, Chapter 3), and hunting (Benítez-López *et al.* 2019). Nutrient enrichment can change the quality of prey by creating an imbalance of nutrients in ecosystems (Vogels *et al.* 2020). These changes in food quality can negatively affect carnivorous invertebrates as they need high-quality prey to meet their strong energetic requirements (Carbone *et al.* 2007; Vogels *et al.* 2020). Carnivorous vertebrates typically have wide home ranges to increase their chances of finding prey and tend to occur in low densities (Carbone *et al.* 2007; Santini *et al.* 2022). These characteristics make carnivores susceptible to negative impacts of human pressures (Ripple *et al.* 2014).

Other traits such as reproductive rate, brain size or ecological specialization can be also important in understanding the impact of human pressures on biodiversity. For example, specialist species are generally more affected by anthropogenic changes in the ecosystem than generalists, due to their narrower ecological niche (Clavel *et al.* 2011; Keinath *et al.* 2017; Vogels *et al.* 2020; Viana & Chase 2022). However, there is still limited information about the ecological specialization of species or other possibly relevant traits (e.g., reproductive rate, mobility or brain size), especially for understudied groups. In the case of terrestrial invertebrates, for instance, only the metamorphosis mode and the feeding guild could be included in the assessment of responses to nitrogen addition (Chapter 2), due to a lack of information about other traits. Moreover, even for well-studied groups, such as mammals or birds, we could only include information about their body size or feeding guild (Chapter 3), as other traits that could modulate their response to linear infrastructure are still not available for many species. This highlights the need to increase the availability of trait data not only for understudied groups but also for relatively well-studied (vertebrate) species. Expanding recently established traits databases, such as GlobalAnts (Parr *et al.* 2017) or LepTraits (Shirey *et al.* 2022) for ants and butterflies and the recently published traits databases for mammals (Soria *et al.* 2021) and birds (Tobias *et al.* 2022), would certainly help future studies of how human pressures are affecting different aspects of biodiversity.

6.3 COMBINED IMPACTS OF MULTIPLE PRESSURES

One of the key aims of current ecological research is to understand biodiversity responses to multiple human pressures (Didham *et al.* 2007; Darling & Côté 2008; Côté *et al.* 2016; Bowler *et al.* 2020; Orr *et al.* 2020). Ideally, multi-pressure impacts would be revealed from quantitative meta-analyses based on multi-factorial studies assessing the separate and combined impacts of multiple pressures. However, despite the increasing number of studies assessing biodiversity responses to multiple pressures in different ecological systems (e.g., terrestrial systems: Ma et al. (2020); aquatic systems: Lange et al. (2018)), there is not sufficient data to systematically infer biodiversity responses to all relevant combinations of pressures. To overcome this limitation, Chapters 4 and 5 relied on combining single-pressure response relationships with geospatial data on pressures and moderators in order to perform a multi-pressure assessment including land use in combination with nitrogen deposition (Chapter 4) and with hunting (Chapter 5). Chapter 4 followed an assemblage-based approach and made two main assumptions with regard to the combined impacts of the two pressures. First, it was assumed that some locations are affected by only one of the two pressures, i.e., it was assumed that anthropogenic habitats such as croplands or urban areas are not affected by nitrogen deposition as the land use is considered the main driver of species richness loss in these human-modified areas (Schipper *et al.* 2020). Second, for locations affected by both pressures, such as secondary forests, it was assumed that species' sensitivities to both pressures are uncorrelated, and thus that the response to these pressures combined can be quantified by response addition (Vinebrooke *et al.* 2004). However, the assumption of uncorrelated sensitivity may be overly simplistic. For example, generalist species might be more resilient to multiple pressures compared to specialist species, which are usually more sensitive to changes (Clavel *et al.* 2011). This assumption of additive effects could thus lead to an overestimation of the combined impact of both pressures (Vinebrooke *et al.* 2004). Nevertheless, it has been suggested that this simple assumption provides quantitatively reasonable estimates (Altenburger *et al.* 2013). In addition, I found only small differences in the impact estimates when assuming no additional impacts of nitrogen deposition in secondary vegetation (Fig. S4.6). Chapter 5 uses a species-based approach to quantify the separate and combined impacts of land use and hunting. Similar to other species-based GBMs, e.g., InSiGHTS (Visconti *et al.* 2016; Baisero *et al.* 2020), we assumed that an area was suitable only if both pressures were absent, allowing the occurrence of a species. Using this method, I discovered that the areas impacted by hunting and land use had only 2% overlap on average across the species, demonstrating that the two pressures affect different parts of the distributions of tropical mammals, as previously suggested at smaller scales (Brodie *et al.* 2015; Romero-Muñoz *et al.* 2019).

Land use is commonly considered the main current threat to biodiversity worldwide (Newbold *et al.* 2015; Maxwell *et al.* 2016). However, this does not necessarily hold for all species groups and locations (Bellard *et al.* 2022). For example, I found that the impact of nitrogen addition on plant species richness may outweigh the impacts of land use in relatively cold areas (Chapter 4, Fig. 6.2a) and that impact of hunting may outweigh land-use impacts on large tropical mammals (Chapter 5; Fig. 6.2b). Ranking human pressures is commonly done in biodiversity assessments that aim to support policy-making. For example, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), the International Union for Conservation of Nature (IUCN), or the World Wide Fund for Nature (WWF) regularly publish rankings of human pressures (Purvis *et al.* 2019; Almond *et al.* 2020; IUCN 2022). However, as shown in this thesis and also recently highlighted by Bellard et al. (2022), pressure ranking may change depending on the spatial extent considered (local to global) and the local context. Quantifying the context-dependencies of biodiversity impacts helps to improve pressure rankings, which in turn may help to increase the effectiveness of broad-scale biodiversity policies. Macro-ecological assessments, such as the ones performed in Chapters 4 and 5, improve our understanding of how humans are affecting ecological patterns at large scales and can guide global conservation actions (see also Santini *et al.* 2021). Yet, more research is needed to further improve the quantification of the combined effects of multiple pressures and how they interact with each other under different circumstances to jeopardize biodiversity.

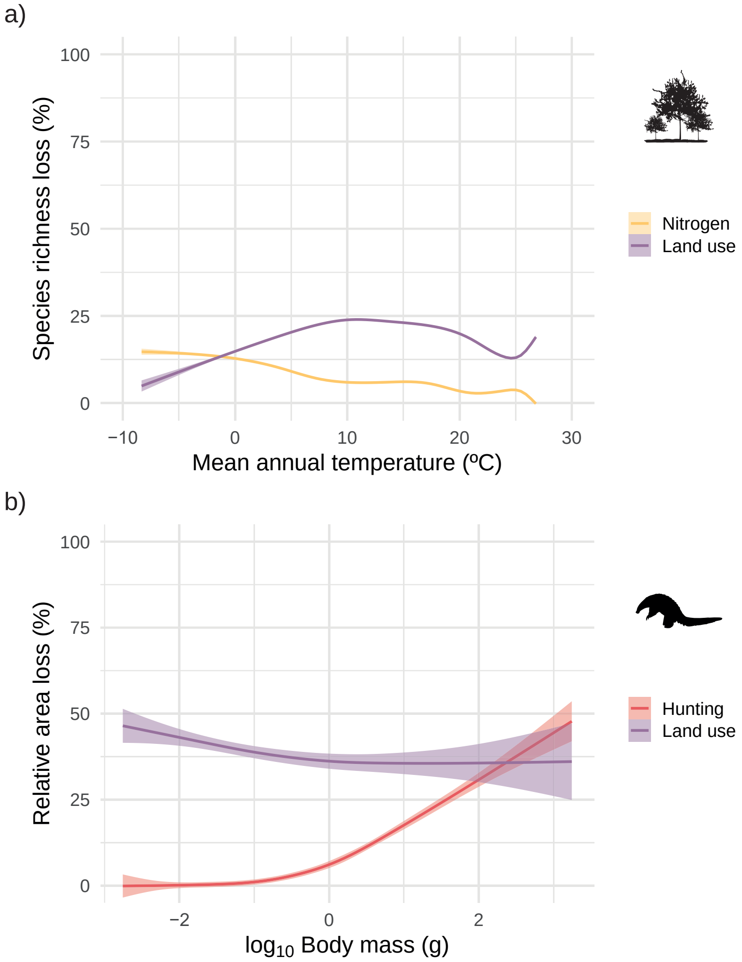


Figure 6.2 The impacts of a) nitrogen deposition and land use on plant species richness in relation to mean annual temperature (environmental context), and b) hunting pressure and land use on the distributions of tropical mammals in related to their body mass (species trait context). Plots are based on a) the grids within the applicability domain of the model developed in Chapter 4 and b) the species-specific results for the mammal species included in Chapter 5. Lines represent a generalized additive model (gam) smoother with the shaded areas representing the 95% confidence limits. Silhouettes are public domain obtained from “phylopic” (www.phylopic.org).

6.4 CONCLUSIONS AND RECOMMENDATIONS

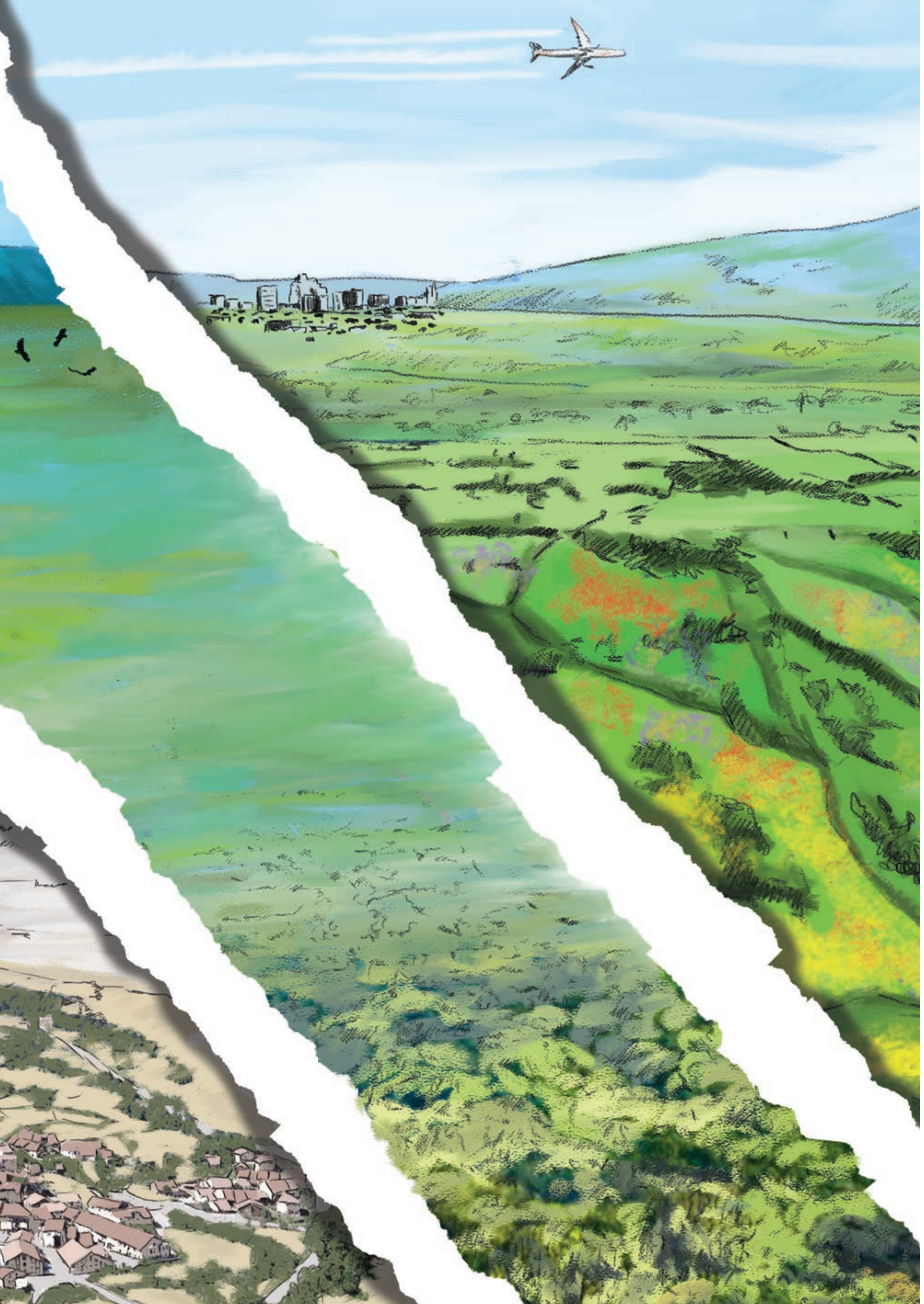
The following conclusions are drawn from the research done in my thesis:

- The impacts of hunting, nitrogen enrichment or linear infrastructure on biodiversity depend on local environmental conditions and species traits;
- Interactive effects between human pressures and their local context can be quantified through meta-analytical models with environmental and trait variables included;
- Models accounting for environmental and trait dependencies can be used to predict the impact of human pressures in understudied areas and for understudied species;
- While land use is a dominant pressure on biodiversity, impacts of nitrogen enrichment or hunting can exceed the impacts of land use for certain species and under certain environmental conditions.

Based on the findings of this thesis, the following recommendations for future research and conservation are:

- Future global or large-scale biodiversity models should aim to account for context-dependent responses to human pressures;
- More extensive databases of traits influencing species' environmental responses (e.g., mobility or ecological specialization) should be established in order to improve the development of traits-based biodiversity models;
- More multi-factorial (experimental or observational) studies should be conducted to better quantify the interactive effect of human pressures on biodiversity;
- More quantitative meta-analytical models should be developed to increase our understanding of biodiversity responses to understudied human pressures;
- Conservation policies and strategies should address multiple pressures simultaneously to effectively halt the ongoing biodiversity crisis.

The current global change comes with challenges that we can only address with measures backed up by science. The need for broadly applicable, adequate biodiversity models to help and guide conservation policies is clear. My thesis forms part of ongoing efforts to understand and inform how human pressures affect global biodiversity, with the ultimate aim to better guide biodiversity policy and conservation.



APPENDIX

A

APPENDIX CHAPTER 2

Appendix S2.1: Search strings

Date of search: 12.03.2021

Web of Science: 5,516

(TS=((“nitrogen deposition” OR “N deposition” OR “nitrogen addition*” OR “N addition*” OR “deposit* of N*” OR “addition* of N*” OR “N* treatment*” OR “N* load*”)

AND

(“species richness” OR “abund*” OR “richn*” OR “composition” OR “number” OR “biodiversity”)

AND

(“insect*” OR “arthropod*” OR “pollinat*” OR “invertebr*” OR “*hopper*” OR “*bug*” OR “spider*” OR “katydi*” OR “crick*” OR “locus*” OR “beet*” OR “larv*” OR “*fly” OR “*flies” OR “midges” OR “tick*” OR “mite*” OR “lepidop*” OR “arac*” OR “myriap*” OR “coleop*” OR “odon*” OR “amphip*” OR “acrid*” OR “carabid*” OR “hemipt*” OR “coccoid*”)))

All languages and All databases:

- Web of Science Core Collection
- BIOSIS Citation Index
- Chinese Science Citation DatabaseSM
- Current Contents Connect
- Data Citation Index
- Derwent Innovations Index
- KCI-Korean Journal Database
- MEDLINE®
- Russian Science Citation Index
- SciELO Citation Index
- Zoological Record

Scopus: 1,488

TITLE-ABS-KEY ((“nitrogen deposition” OR “N deposition” OR “nitrogen addition*” OR “N addition*” OR “deposit* of N*” OR “addition* of N*” OR “N* treatment*” OR “N* load*”) AND (“species richness” OR “abund*” OR “richn*” OR “composition” OR “number” OR “biodiversity”) AND (“insect*” OR “arthropod*” OR “pollinat*” OR “invertebr*” OR “*hopper*” OR “*bug*” OR “spider*” OR “katydi*” OR “crick*” OR “locus*” OR “beet*” OR “larv*” OR “*fly” OR “*flies” OR “midges” OR “tick*” OR”mite*” OR “lepidop*” OR “arac*” OR “myriap*” OR “coleop*” OR “odon*” OR “amphip*” OR “acrid*” OR “carabid*” OR “hemipt*” OR “coccoid*”)) AND (LIMIT-TO (SUBJAREA , “AGRI”) OR LIMIT-TO (SUBJAREA , “BIOC”) OR LIMIT-TO (SUBJAREA , “ENVI”) OR LIMIT-TO (SUBJAREA , “CHEM”) OR LIMIT-TO (SUBJAREA , “EART”) OR LIMIT-TO (SUBJAREA , “CENG”) OR LIMIT-TO (SUBJAREA , “Undefined”))

ProQuest: 66

noft(“nitrogen deposition” OR “N deposition” OR “nitrogen addition*” OR “N addition*” OR “deposit of N*” OR “addition of N*” OR “N treatment*” OR “N load*”) AND noft(“species richness” OR “abund*” OR “richn*” OR “composition” OR “number” OR “biodiversity”) AND noft(“insect*” OR “arthropod*” OR “pollinat*” OR “invertebr*” OR “hopper*” OR “bug*” OR “spider*” OR “katydi*” OR “crick*” OR “locus*” OR “beet*” OR “larv*” OR “dragonfl*” OR “butterfl*” OR “fly” OR “flies” OR “midges” OR “tick*” OR “mite*” OR “lepidop*” OR “arac*” OR “myriap*” OR “coleop*” OR “odon*” OR “amphip*” OR “acrid*” OR “carabid*” OR “hemipt*” OR “coccoid*”)

Open Thesis and Dissertations: 7

(“nitrogen deposition” OR “N deposition” OR “nitrogen addition*” OR “N addition*” OR “deposit* of N*” OR “addition* of N*” OR “N* treatment*” OR “N* load*”) AND (“species richness” OR “abund*” OR “richn*” OR “composition” OR “number” OR “biodiversity”) AND (“insect*” OR “arthropod*” OR “pollinat*” OR “invertebr*” OR “*hopper*” OR “*bug*” OR “spider*” OR “katydi*” OR “crick*” OR “locus*” OR “bee*” OR “larv*” OR “*fly” OR “*flies” OR “midges” OR “tick*” OR “mite*” OR “lepidop*” OR “arac*” OR “myriap*” OR “coleop*” OR “odon*” OR “amphip*” OR “acrid*” OR “carabid*” OR “hemipt*” OR “coccoid*”)

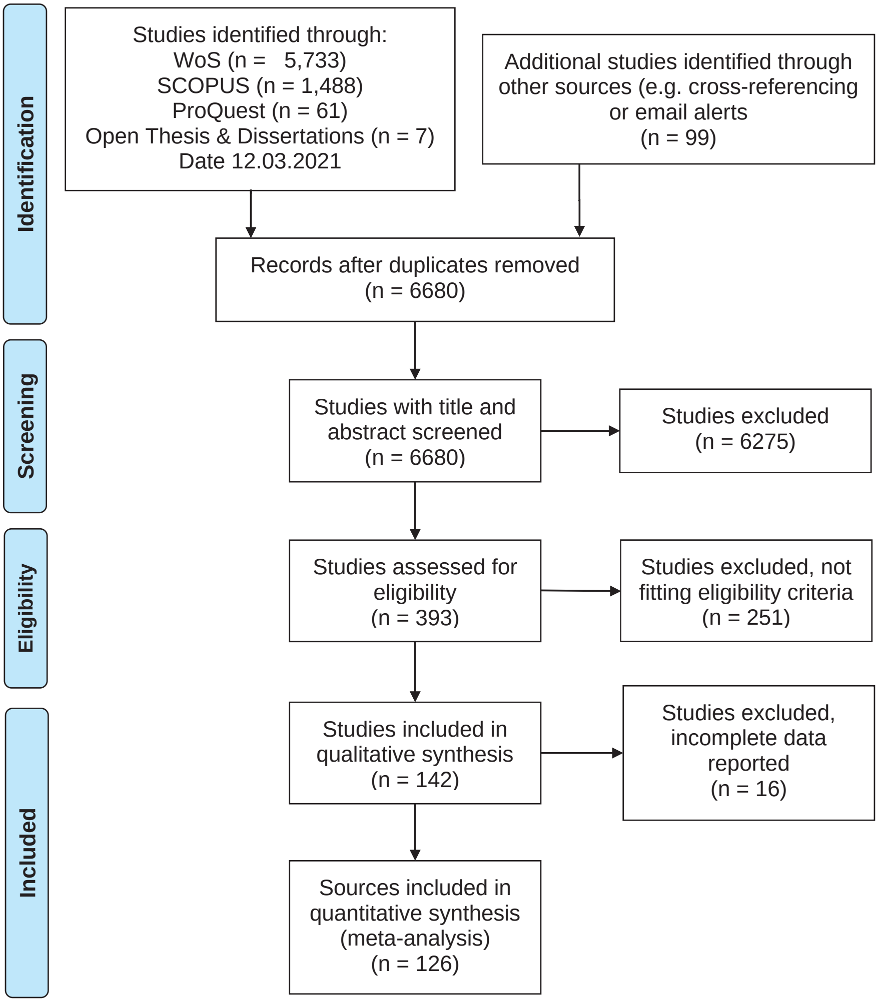


Figure S2.1 PRISMA plot

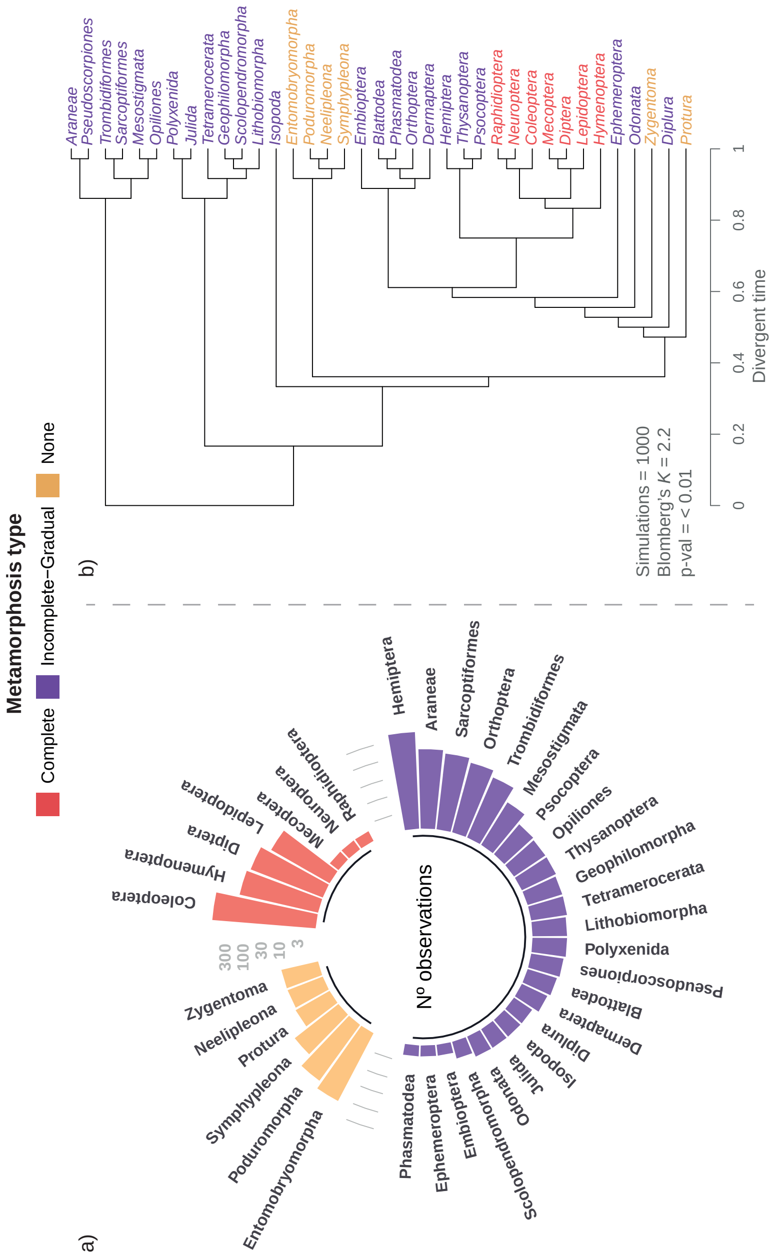


Figure S2.2 a) Number of observations per order (in the log-scale for visualization purposes) and b) phylogenetic tree of the orders of arthropods coloured by the metamorphosis type of the Order. Phylogenetic signal for the metamorphosis type tested within the orders using the Blomberg's *K* statistic (Blomberg *et al.* 2003) which resulted in a strong signal (Blomberg's K = 2.5, p-value = < 0.01). We used the package "phytools" v.0.7-47 (Revell 2012) to test the phylogenetic signal.

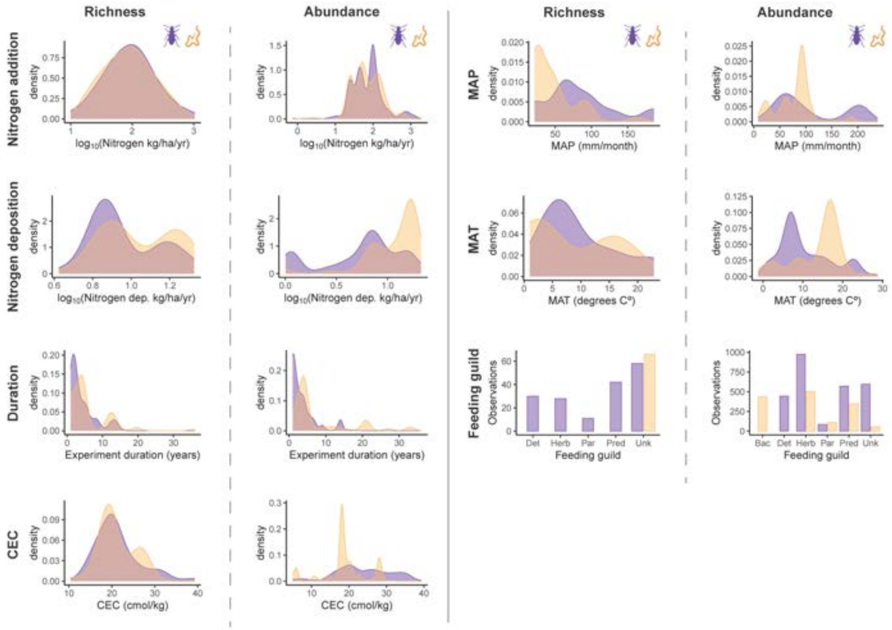
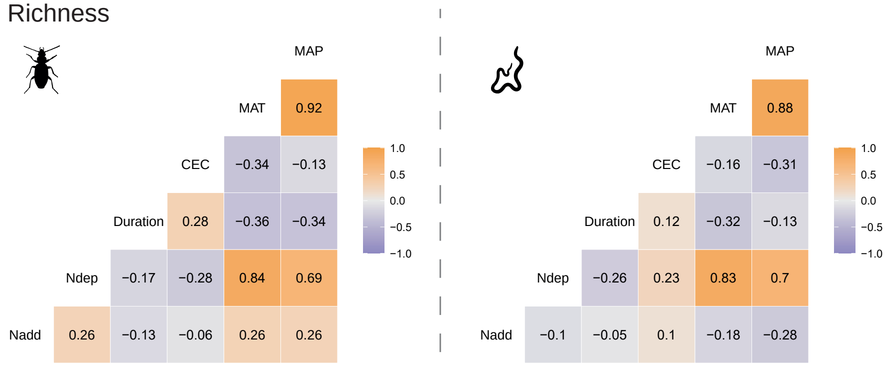


Figure S2.3 Density plots and the number of observations for each moderator tested in the richness and the abundance dataset per phylum. CEC = cation exchange capacity; MAP = mean annual precipitation; MAT = mean annual temperature; For the feeding guild group: Bac = Bacterivores, Det = Detritivores, Herb = Herbivores-Fungivores, Par = Parasites, Pred = Predators-Omnivores, Unk = Unknown. Silhouettes are public domain obtained from "phylopic" (www.phylopic.org).

a) Richness



b) Abundance

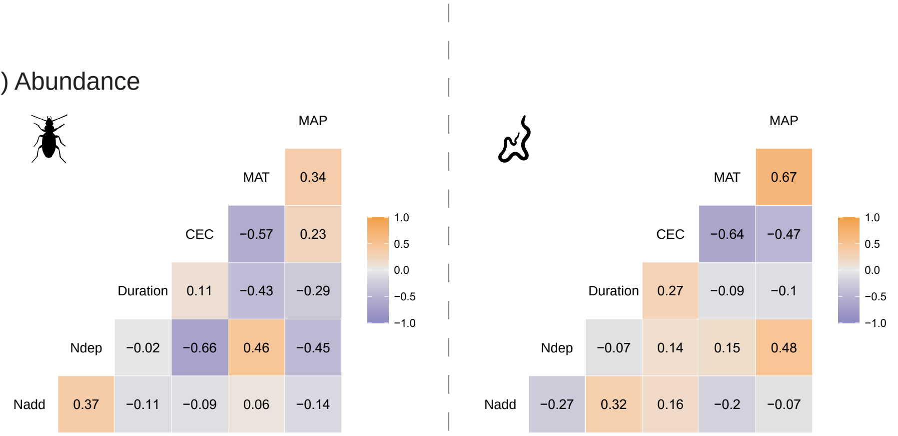
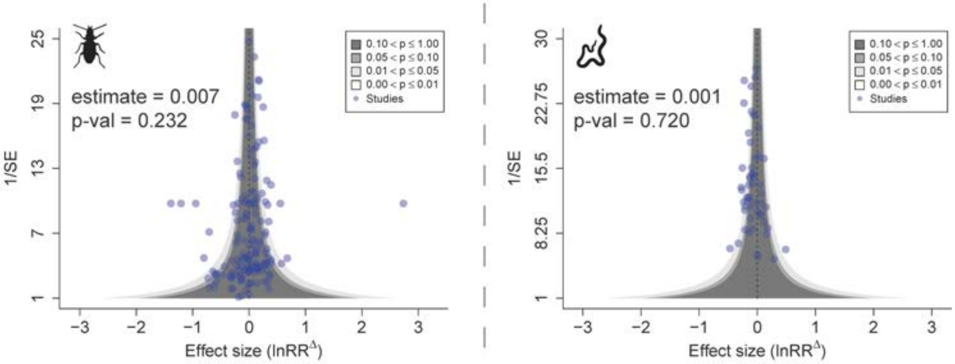


Figure S2.4 Pearson correlation plots for continuous variables in the a) richness and b) abundance database of arthropods and nematodes. Silhouettes are public domain obtained from “phylopic” (www.phylopic.org).

a) Richness



b) Abundance

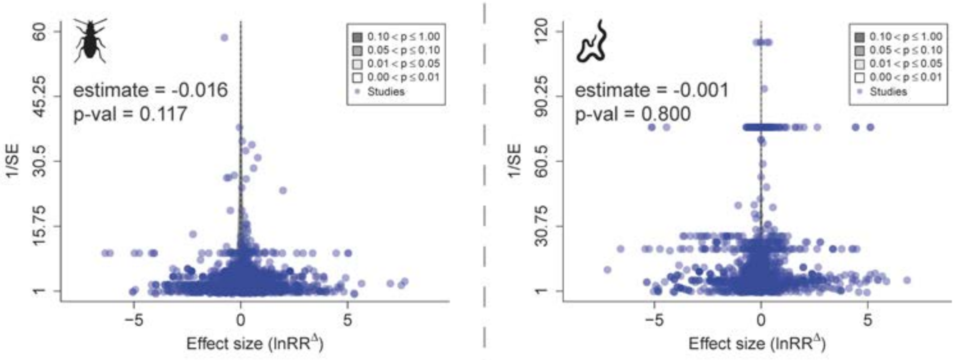


Figure S2.5 Contour-enhanced funnel plots for the a) richness and b) abundance of arthropods and nematodes to check publication bias. If missing studies appear to be in areas of statistical non-significance (i.e. dark areas) then this would suggest that there could be publication bias. If studies are missing in the statistical significance area (i.e. white area) this would suggest that the asymmetry is due to other factors than publication bias (Peters *et al.* 2008). Precision is indicated as the inverse of the standard error (1/SE). Egger's test suggests that there is no publication bias (p-value > 0.05, Nakagawa & Santos, (2012)). Silhouettes are public domain obtained from "phylopic" (www.phylopic.org).

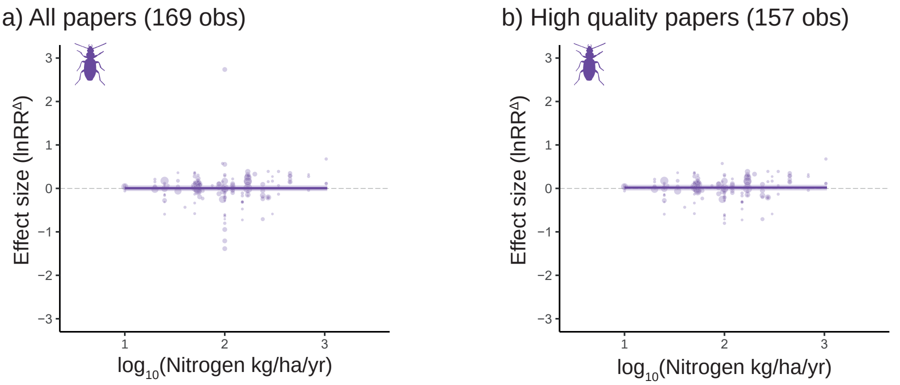


Figure S2.6 Best model for the taxonomic richness of arthropods when using the a) the full dataset and b) only the high-quality sources of data. Shaded ribbons represent the 95% confidence intervals. The dashed line at 0 indicates no change in abundance or richness compared with the control points (0 kg/ha/yr). Point size represents observation weight. Silhouettes are public domain obtained from "phylopic" (www.phylopic.org).

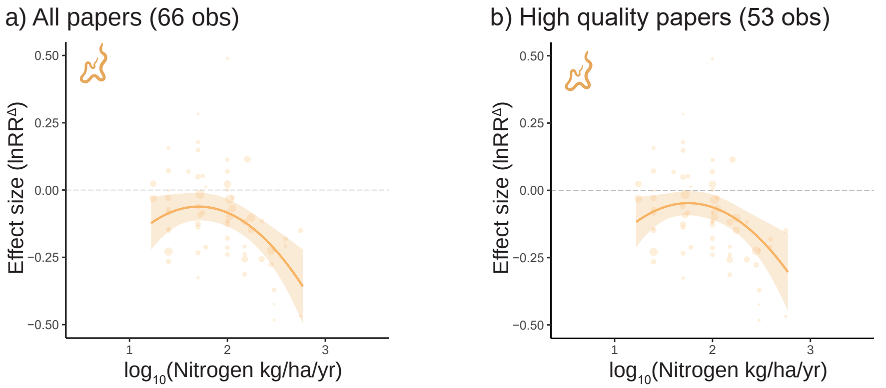


Figure S2.7 Best model for the taxonomic richness of nematodes when using a) the full dataset and b) only the high-quality sources of data. Shaded ribbons represent the 95% confidence intervals. The dashed line at 0 indicates no change in abundance or richness compared with the control points (0 kg/ha/yr). Silhouettes are public domain obtained from "phylopic" (www.phylopic.org).

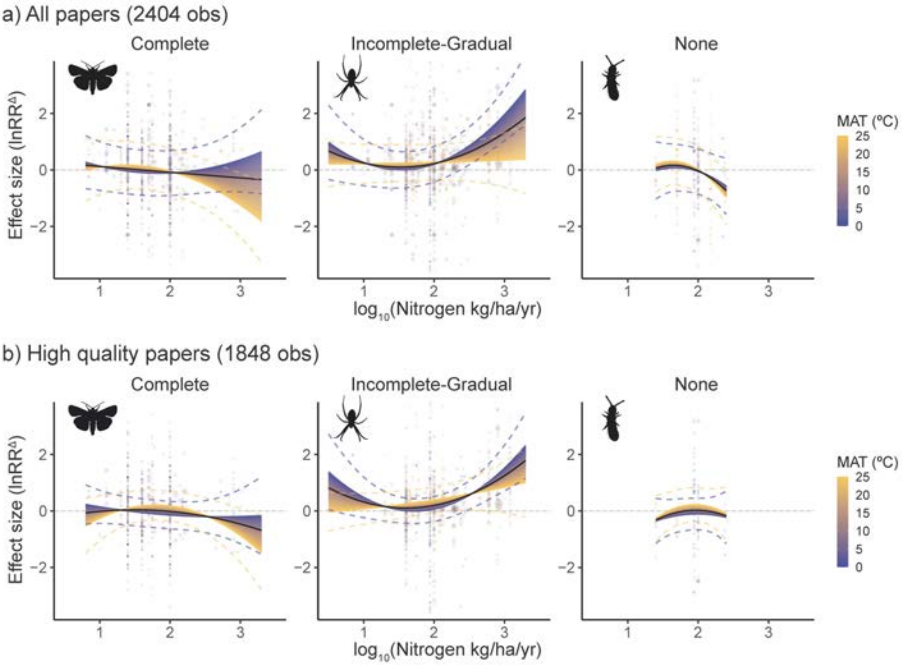


Figure S2.8 Best model for the abundance of arthropods when using the a) the full dataset and b) only the high-quality sources of data. Dashed lines represent the 95% confidence interval for the highest (yellow) and lowest (blue) value of mean annual temperature (MAT in °C). The solid black line represents the values for the average MAT. The dashed line at 0 indicates no change in abundance compared with the control plots (no nitrogen added). Point size represents observation weight. Silhouettes are public domain obtained from "phylopic" (www.phylopic.org).

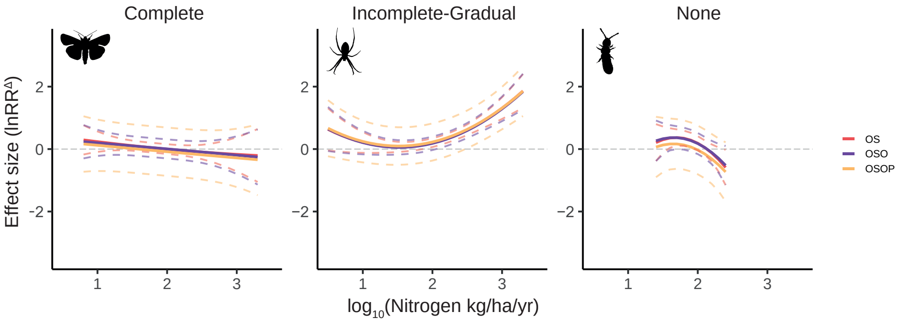
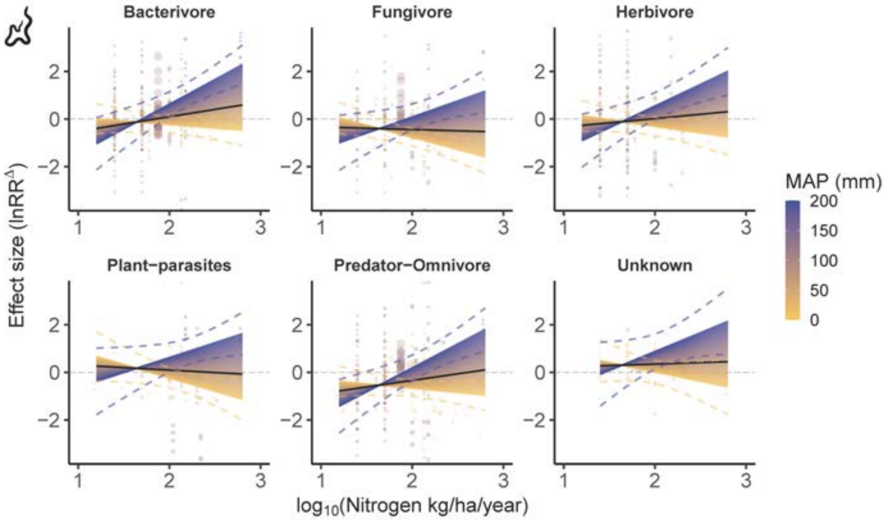


Figure S2.9 Comparison of the random effect structure for the best model for the abundance of arthropods keeping the mean annual temperature at the average value (10 °C). Differences are between the model including only the Observation and Source level of variation (OS), including also the *Order* level as random effect only (OSO), and including also phylogenetic relationships among *Orders* (OSOP). Silhouettes are public domain obtained from "phylopic" (www.phylopic.org).

a) All papers (1460 obs)



b) High quality papers (1162 obs)

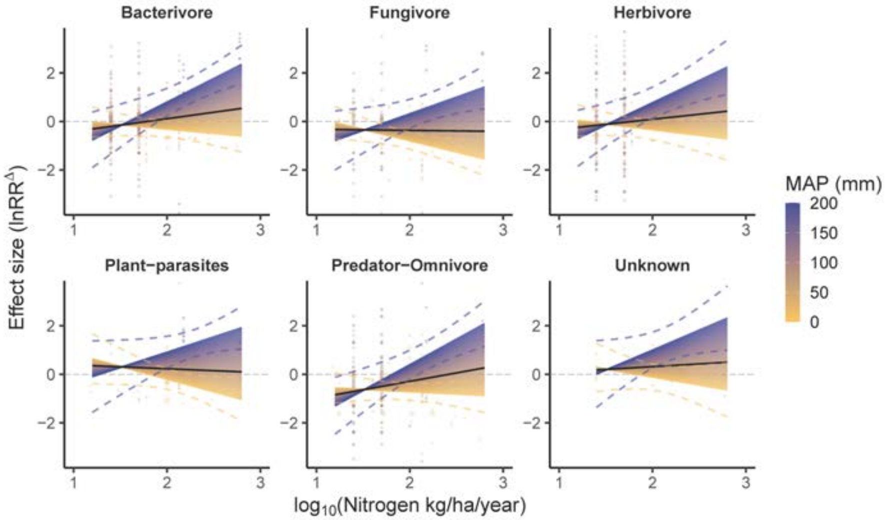


Figure S2.10 Best model for the abundance of nematodes when using a) the full dataset and b) only the high-quality sources of data. The dotted lines represent the 95% confidence interval for the highest and lowest value of mean annual precipitation (MAP). The dashed line at 0 indicates no change in abundance or richness compared with the control points (0 kg/ha/yr). Silhouettes are public domain obtained from “phylopic” (www.phylopic.org).

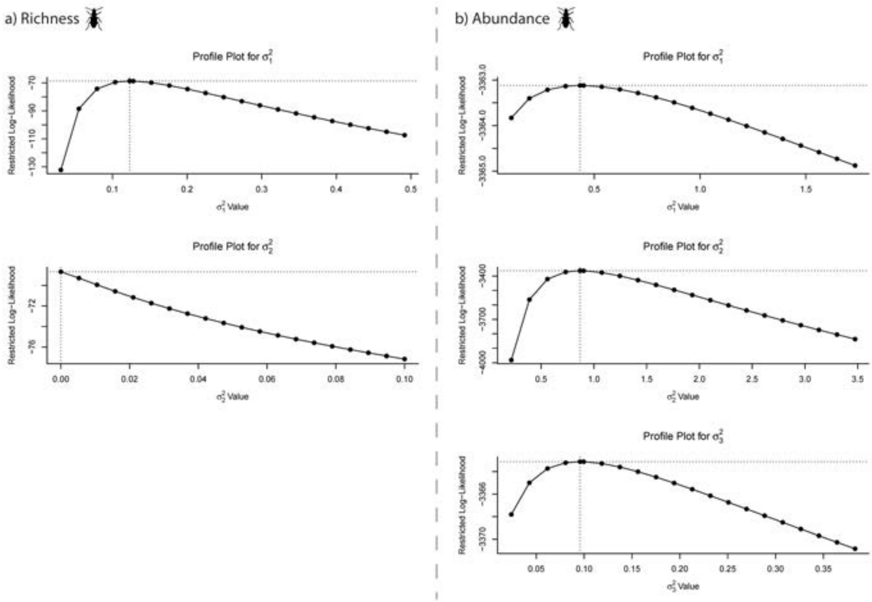


Figure S2.11 Profile plots for the best model selected for arthropod a) richness and b) abundance. For a) σ_1^2 = observation-level variability, σ_2^2 = source-level variability. For b) σ_1^2 = *order*-level variability, σ_2^2 = observation-level variability, σ_3^2 = source-level variability. All source of variability shows a peak meaning that the models converged. Silhouettes are public domain obtained from "phylopic" (www.phylopic.org).

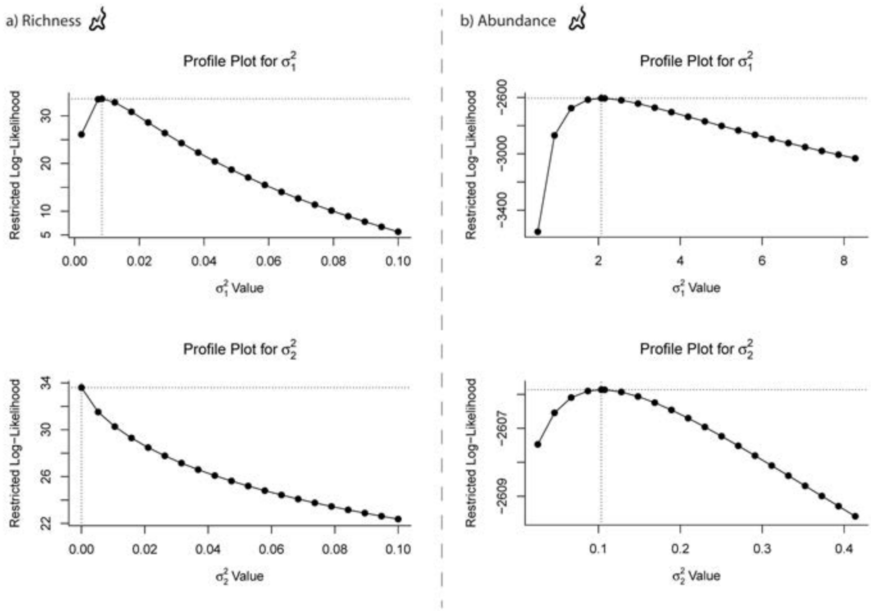


Figure S2.12 Profile plots for the best model selected for nematode a) richness and b) abundance. σ_1^2 = observation-level variability, σ_2^2 = source-level variability. All source of variability shows a peak meaning that the models converged. Silhouettes are public domain obtained from “phylopic” (www.phylopic.org).

Table S2.1 Main factors that might influence invertebrates' response to increased N in the ecosystems.

Moderator	**Rationale**
Nitrogen addition (kg/ha/year)	N addition might remove the general N limitation of ecosystems and thus increase the abundance of invertebrates (Nijssen *et al.* 2017; Stevens *et al.* 2018; Vogels *et al.* 2020). Alternatively, the excess of N might create an imbalance of other nutrients (e.g. P or C) which might decrease the abundance of invertebrates (Vogels *et al.* 2020). Invertebrate richness might decrease due to the proliferation of generalist species able to adapt to the N-rich conditions, outcompeting specialists and decreasing the general invertebrate diversity (Stevens *et al.* 2018; Shaw *et al.* 2019; Vogels *et al.* 2020).
Atmospheric nitrogen deposition (kg/ha/year)	Higher losses from N addition are expected in sites with low atmospheric N deposition where species are adapted to low amounts of N.
Duration of experiment (years)	In the short term, N might be beneficial as it relaxes nutrient limitations and can increase the abundance and taxonomic richness of invertebrates. In the long-term, only certain groups of invertebrates might be able to survive the excess of N due to its accumulation in the ecosystem. Therefore, both abundances and taxonomic richness are expected to decrease in the long term (Nijssen *et al.* 2017; Stevens *et al.* 2018; Vogels *et al.* 2020).
Feeding guild	Herbivores might experience an increase in abundance due to the proliferation of nitrophilous plants (Stevens *et al.* 2018; Vogels *et al.* 2020). However, their taxonomic richness might decrease if generalist species proliferate and outcompete specialists. Predators and omnivores might benefit from the increase in herbivores and also increase their populations. Parasites might experience a decrease if their hosts disappear from the ecosystem. Detritivores might experience an abundance and taxonomic richness increase if there is more decomposed material available due to N. However, if the environment becomes too acidic they might decrease due to the toxic effect of N (Stevens *et al.* 2018; Vogels *et al.* 2020). For nematodes, bacterivore species are expected to increase as they are normally opportunistic and fast colonizers species, while predator-omnivore species normally decrease as they are more sensitive to disturbances and they have longer lives (Bongers & Bongers 1998; Bongers 1999; Sun *et al.* 2013; Shaw *et al.* 2019). Moreover, the bacterial-fungal ratio might be altered with N addition and fungi might decrease, which ultimately might decrease the abundance of fungivore nematodes (Treseder 2004, 2008; Wallenstein *et al.* 2006).
Mean annual temperature (ºC)	Increasing temperatures lead to drier microhabitats, exacerbating the effect of N due to its accumulation, and reducing the abundance of invertebrates in general (WallisDeVries & Van Swaay 2006; Blankinship *et al.* 2011; Porter *et al.* 2013). Moreover, N and climatic warming can cause microclimatic cooling and hence, negatively affect thermophilous insect species (WallisDeVries & Van Swaay 2006). Increasing temperatures can also make the movement of soil fauna more difficult due to drier soils and thus be also negative for them (Blankinship *et al.* 2011; Porter *et al.* 2013; Hiltpold *et al.* 2017).

Moderator	Rationale
Mean annual precipitation (mm/month)	High precipitation can remove N from the soil. Therefore, it is expected that in places with higher mean annual precipitation, the effect of N addition would be less if N is added in low quantities. Moreover, water can facilitate the movement of soil fauna so it should be beneficial for them, especially for nematodes (Porter *et al.* 2013; Sun *et al.* 2013; Hiltpold *et al.* 2017; Griffith & Grinath 2018; Cui *et al.* 2022).
Soil CEC (cmol/kg)	High CEC means a higher buffer capacity of the ecosystem so changes in invertebrates will be less pronounced where CEC is higher (Nijssen *et al.* 2017; Stevens *et al.* 2018; Vogels *et al.* 2020).
Habitat	Invertebrates in sensitive habitats to N addition such as natural grasslands or forests are supposed to experience larger changes due to N addition than in habitats such as croplands where N availability is higher (Bobbink *et al.* 2010; Vogels *et al.* 2020).
Metamorphosis type	Increasing N might create an imbalance of other essential nutrients in the environment such as Phosphorus (P) or Calcium (C). Arthropods performing a complete metamorphosis have a high concentration of P-rich molecules that allow them to group fast and reshape their body during metamorphosis (Elser *et al.* 2003; Woods *et al.* 2004; Alfsnes *et al.* 2017; Villar-Argaiz *et al.* 2021). Therefore, they may decrease due to the imbalance of P and other essential nutrients for their metamorphosis created by increasing N. In contrast, arthropods performing an incomplete or gradual metamorphosis have more N in their body compared to P because the lack of metamorphosis and their slow growth rate (Fagan *et al.* 2002; Denno & Fagan 2003; Martinson *et al.* 2008; Wiesenborn 2011; Alfsnes *et al.* 2017; Villar-Argaiz *et al.* 2021). Therefore, as they have high N requirements (N limited), they are expected to increase with increasing N availability. Moreover, arthropods with no metamorphosis are expected to benefit from increasing N as N is normally a limiting element in nature.

Table S2.2 Model selection for the taxonomic richness of arthropods when controlling for the heterogeneity between observations and sources. Models are ordered from low to high AICc. I^2 denotes the proportion of heterogeneity relative to the total amount of heterogeneity in the observed effects explained by each random effect level. mR^2 and cR^2 are the marginal (only fixed effects) and conditional (fixed and random effects) R^2. Only the 10 models with the lowest AICc are shown.

Fixed effects	I^2 total	I^2 RowID	I^2 Source	AICc	mR^2	cR^2
~1	0.92	0.92	0	147.13	0.00	0.00
~logNadd2	0.92	0.92	0	148.19	1.02	1.02
~logNadd	0.92	0.92	0	148.43	0.78	0.78
~logNadd * CEC	0.92	0.92	0	149.53	3.78	3.78
~logNadd + logNadd2	0.92	0.92	0	149.81	1.54	1.54
~logNadd * CRU_MAT_mean	0.92	0.92	0	151.64	2.20	2.20
~logNadd * logNdep	0.92	0.92	0	151.79	1.77	1.77
~logNadd * CRU_MAP_mean	0.92	0.92	0	152.00	1.71	1.71
~logNadd * Duration_Years	0.92	0.92	0	152.12	1.34	1.34
~(logNadd + logNadd2) * CEC	0.92	0.92	0	152.63	5.38	5.38

Table S2.3 Parameter estimates with their standard error (SE), 95% confidence intervals (CI lower limit and CI upper limit) and p-value using the restricted maximum likelihood (REML) for the best model selected by AICc for the taxonomic richness of arthropods. Cochran's Q test (Q), marginal (mR^2) and conditional (cR^2) explained variance are given for the model. Asterisks indicate significance level: *** indicates p-value < 0.001, ** indicates p-value < 0.01, * indicates p-value < 0.05, n.s. indicates p-value > 0.05.

Arthropods richness (REML)	Moderator	Estimate	SE	CI.low	CI.up	p-value
Q(df = 168) = 1545.63***	Intercept	0.00	0.03	-0.06	0.07	0.90
$mR^2 = 0.00$						
$cR^2 = 0.00$						

Table S2.4 Model selection for the taxonomic richness of nematodes when controlling for the heterogeneity between observations and sources. Models are ordered from low to high AICc. I^2 denotes the proportion of heterogeneity relative to the total amount of heterogeneity in the observed effects explained by each random effect level. mR^2 and cR^2 are the marginal (only fixed effects) and conditional (fixed and random effects) R^2.

Fixed effects	I^2 total	I^2 RowID	I^2 Source	AICc	mR^2	cR^2
~logNadd + logNadd2	0.66	0.50	0.16	-74.52	30.68	47.44
~(logNadd + logNadd2) * CEC	0.62	0.59	0.03	-72.84	46.92	49.56
~(logNadd + logNadd2) * CRU_MAP_mean + (logNadd + logNadd2) * CEC	0.59	0.59	0.00	-71.78	56.08	56.08
~(logNadd + logNadd2) * CRU_MAT_mean	0.62	0.62	0.00	-71.30	44.50	44.50
~logNadd * logNdep + logNadd * CRU_MAP_mean	0.62	0.62	0.00	-71.25	44.06	44.06
~(logNadd + logNadd2) * logNdep + (logNadd + logNadd2) * CEC	0.59	0.59	0.00	-70.96	53.79	53.79
~(logNadd + logNadd2) * logNdep + (logNadd + logNadd2) * CRU_MAP_mean	0.59	0.59	0.00	-70.80	55.04	55.04
~logNadd2	0.68	0.55	0.13	-70.44	18.82	34.53
~(logNadd + logNadd2) * Duration_Years	0.64	0.58	0.06	-70.38	39.87	45.52
~logNadd * Duration_Years	0.65	0.65	0.00	-70.09	32.85	32.85

Table S2.5 Parameter estimates with their standard error (SE), 95% confidence intervals (CI lower limit and CI upper limit) and p-value using the restricted maximum likelihood (REML) for the best model selected by AICc for the taxonomic richness of nematodes. Cochran's Q test for residual heterogeneity (QE), Omnibus test of moderators (QM), marginal (mR^2) and conditional (cR^2) explained variance are given for the model. Asterisks indicate significance level: *** indicates p-value < 0.001, ** indicates p-value < 0.01, * indicates p-value < 0.05, n.s. indicates p-value > 0.05.

Nematodes richness (REML)	Moderator	Estimate	SE	CI.low	CI.up	p-value	QM
QE(df = 63) = 185.24***	Intercept	-0.82	0.33	-1.47	-0.17	0.01	
mR^2 = 30.68	Nadd	0.89	0.35	0.21	1.57	0.01	QM(df = 2) = 14.95**
cR^2 = 47.44	$Nadd^2$	-0.26	0.09	-0.44	-0.09	0.00	

Table S2.6 Model selection for the abundance of arthropods when controlling for the heterogeneity between observations, sources and phylogenetic relationships between orders of arthropods. Models are ordered from low to high AICc. I^2 denotes the proportion of heterogeneity relative to the total amount of heterogeneity in the observed effects explained by each random effect level. mR2 and cR2 are the marginal (only fixed effects) and conditional (fixed and random effects) R^2. Only the 10 models with the lowest AICc are shown.

Fixed effects	I^2 total	I^2 RowID	I^2 Source	I^2 Order	AICc	mR^2	cR^2
~(logNadd + logNadd2) * CRU_MAT_mean + (logNadd + logNadd2) * Metamorphosis	0.94	0.68	0.06	0.19	7713.13	6.02	31.29
~(logNadd + logNadd2) * Metamorphosis	0.94	0.68	0.08	0.18	7713.14	5.34	31.28
~(logNadd + logNadd2) * CRU_MAT_mean + (logNadd + logNadd2) * CRU_MAP_mean + (logNadd + logNadd2) * Metamorphosis	0.94	0.68	0.06	0.20	7713.39	6.44	32.54
~(logNadd + logNadd2) * logNdep + (logNadd + logNadd2) * CRU_MAT_mean + (logNadd + logNadd2) * Metamorphosis	0.94	0.69	0.06	0.19	7715.21	6.36	31.33
~(logNadd + logNadd2) * logNdep + (logNadd + logNadd2) * CRU_MAT_mean + (logNadd + logNadd2) * CRU_MAP_mean + (logNadd + logNadd2) * Metamorphosis	0.94	0.68	0.06	0.20	7716.04	6.6	32.6
~(logNadd + logNadd2) * CRU_MAP_mean + (logNadd + logNadd2) * Metamorphosis	0.94	0.67	0.08	0.19	7716.05	5.55	32.03
~(logNadd + logNadd2) * CRU_MAT_mean + (logNadd + logNadd2) * CEC + (logNadd + logNadd2) * Metamorphosis	0.94	0.69	0.05	0.19	7717.03	6.05	30.98
~(logNadd + logNadd2) * logNdep + (logNadd + logNadd2) * CRU_MAT_mean + (logNadd + logNadd2) * CEC + (logNadd + logNadd2) * Metamorphosis	0.93	0.70	0.05	0.18	7717.11	6.34	30.23
~(logNadd + logNadd2) * logNdep + (logNadd + logNadd2) * Metamorphosis	0.94	0.68	0.08	0.18	7717.23	5.6	31.91
~(logNadd + logNadd2) * Duration_Years + (logNadd + logNadd2) * CRU_MAT_mean + (logNadd + logNadd2) * CRU_MAP_mean + (logNadd + logNadd2) * Metamorphosis	0.94	0.67	0.07	0.20	7717.98	6.45	33.27

Table S2.7 Parameter estimates with their standard error (SE), 95% confidence intervals (CI lower limit and CI upper limit) and p-value using the restricted maximum likelihood (REML) for the best model selected by AICc for the abundance of arthropods. Nadd: nitrogen addition (kg/ha/yr, log10 transformed), Metamorphosis (Complete/Incomplete-Gradual/None, categorical), mean annual temperature (MAT, ºC). Cochran's Q test for residual heterogeneity (QE), Omnibus test of moderators (QM), marginal (mR^2) and conditional (cR^2) explained variance are given for the model. Asterisks indicate significance level: *** indicates p-value < 0.001, ** indicates p-value < 0.01, * indicates p-value < 0.05, n.s. indicates p-value > 0.05.

Arthropods abundance (REML)	**Moderator**	**Estimate**	**SE**	**CI.low**	**CI.up**	**p-value**	**QM**
QE(df = 2392) = 24959.96***	Intercept	1.10	0.93	-0.71	2.92	0.23	
QM(df = 11) = 59.99***	Nadd	-1.32	0.96	-3.21	0.56	0.17	QM(df = 2) = 1.91 n.s
mR^2 = 6.02	Nadd^2	0.36	0.27	-0.17	0.89	0.18	
cR^2 = 31.29	MAT	-0.08	0.05	-0.18	0.02	0.13	QM(df = 1) = 2.26 n.s
	Metamorphosis (Incomplete-Gradual)	1.04	0.97	-0.87	2.95	0.29	QM(df = 6) = 2.81 n.s
	Metamorphosis (None)	-4.53	4.13	-12.63	3.56	0.27	
	Nadd : MAT	0.11	0.06	0.00	0.22	0.04	QM(df = 2) = 6.43 *
	Nadd^2 : MAT	-0.04	0.02	-0.07	-0.01	0.02	
	Nadd : Metamorphosis (Incomplete-Gradual)	-1.46	0.95	-3.33	0.40	0.12	QM(df = 4) = 35.85***
	Nadd : Metamorphosis (None)	5.51	4.33	-2.98	13.99	0.20	
	Nadd^2 : Metamorphosis (Incomplete-Gradual)	0.55	0.24	0.08	1.02	0.02	
	Nadd^2 : Metamorphosis (None)	-1.61	1.14	-3.83	0.62	0.16	

Table S2.8 Model selection for the abundance of nematodes when controlling for the heterogeneity between observations and sources. Models are ordered from low to high AICc. I^2 denotes the proportion of heterogeneity relative to the total amount of heterogeneity in the observed effects explained by each random effect level. mR^2 and cR^2 are the marginal (only fixed effects) and conditional (fixed and random effects) R^2.

Fixed effects	**I^2 total**	**I^2 RowID**	**I^2 Source**	**AICc**	**mR^2**	**cR^2**
~logNadd * Feeding_GuildUsed + logNadd * CRU_MAP_mean	1.00	0.95	0.05	5297.09	6.40	10.84
~logNadd * logNdep + logNadd * Feeding_GuildUsed + logNadd * CRU_MAP_mean	1.00	0.96	0.04	5297.82	6.74	10.13
~logNadd * logNdep + logNadd * Feeding_GuildUsed + logNadd * CRU_MAT_mean + logNadd * CRU_MAP_mean	1.00	0.96	0.04	5298.83	7.44	11.05
~logNadd * Feeding_GuildUsed + logNadd * CRU_MAT_mean + logNadd * CRU_MAP_mean	1.00	0.95	0.05	5298.96	6.96	11.75
~logNadd * logNdep + logNadd * Feeding_GuildUsed + logNadd * CRU_MAT_mean + logNadd * CRU_MAP_mean + logNadd * CEC	1.00	0.96	0.04	5301.08	7.71	11.06
~logNadd * Duration_Years + logNadd * Feeding_GuildUsed + logNadd * CRU_MAP_mean	1.00	0.95	0.05	5301.11	6.28	10.99
~logNadd * Feeding_GuildUsed + logNadd * CRU_MAP_mean + logNadd * CEC	1.00	0.95	0.05	5301.45	6.31	11.26
~logNadd * logNdep + logNadd * Feeding_GuildUsed + logNadd * CRU_MAP_mean + logNadd * CEC	1.00	0.96	0.04	5302.33	6.61	10.52
~logNadd * Feeding_GuildUsed + logNadd * CRU_MAT_mean + logNadd * CRU_MAP_mean + logNadd * CEC	1.00	0.94	0.06	5302.35	7.37	12.49
~logNadd * logNdep + logNadd * Duration_Years + logNadd * Feeding_GuildUsed + logNadd * CRU_MAP_mean	1.00	0.96	0.04	5302.42	6.58	10.65

Table S2.9 Parameter estimates with their standard error (SE), 95% confidence intervals (CI lower limit and CI upper limit) and p-value using the restricted maximum likelihood (REML) for the best model selected by AICc for the abundance of nematodes. Nadd: nitrogen addition (kg/ha/yr, log10 transformed), FG: Feeding guild (Bacterivore/Fungivore/Herbivore/Parasite/Predator-Omnivore/Unknown, categorical), MAP: Mean Annual Precipitation (mm). Cochran's Q test for residual heterogeneity (QE), Omnibus test of moderators (QM), marginal (mR^2) and conditional (cR^2) explained variance are given for the model. Asterisks indicate significance level: *** indicates p-value < 0.001, ** indicates p-value < 0.01, * indicates p-value < 0.05, n.s. indicates p-value > 0.05.

Nematodes abundance (REML)	**Moderator**	**Estimate**	**SE**	**CI.low**	**CI.up**	**p-value**	**QM**
QE(df = 1430) = 1492399.18***	Intercept	0.46	0.74	-0.98	1.90	0.53	
QM(df = 13) = 62.69***	Nadd	-0.36	0.36	-1.06	0.34	0.32	QM(df = 1) = 0.99 n.s
mR^2 = 6.39	FG (Fungivore)	0.91	0.68	-0.41	2.24	0.18	QM(df = 5) = 5.66 n.s
cR^2 = 10.85	FG (Herbivore)	0.43	0.63	-0.80	1.67	0.49	
	FG (Parasite)	1.65	1.12	-0.54	3.84	0.14	
	FG (Predator-Omnivore)	-0.31	0.60	-1.48	0.86	0.61	
	FG (Unknown)	1.23	1.40	-1.52	3.98	0.38	
	MAP	-0.02	0.01	-0.04	0.00	0.01	QM(df = 1) = 6.52*
	Nadd : FG (Fungivore)	-0.73	0.36	-1.42	-0.03	0.04	QM(df = 5) = 0.29 n.s
	Nadd : FG (Herbivore)	-0.26	0.36	-0.96	0.45	0.48	
	Nadd : FG (Parasite)	-0.82	0.53	-1.85	0.20	0.12	
	Nadd : FG (Predator-Omnivore)	-0.06	0.32	-0.70	0.57	0.85	
	Nadd : FG (Unknown)	-0.49	0.70	-1.86	0.87	0.48	
	Nadd : MAP	0.01	0.00	0.01	0.02	0.00	QM(df = 1) = 12.18***

APPENDIX CHAPTER 3

Web of Science

We searched ISI Web of Science in April 2020 using the following search string in the field “Topic (TS)”:

TS=((vertebrate* OR *bird* OR *fauna OR reptil* OR lizard* OR snake* OR turtle* OR tortoise* OR crocodil* OR amphibia* OR frog* OR toad* OR salamander* OR mammal*) AND (infrastruct* OR road$ OR motorway* OR highway* OR “train track” OR railway* OR “transmission line” OR power$line* OR “seismic line” OR pipeline*) AND (disturbance* OR effect* OR impact* OR distance* OR proximity OR avoidance OR influence) AND (density OR abundan* OR encounter$ OR population$ OR count$ OR persistence))

Google Scholar

We searched Google Scholar in April 2020 using a modification of the original search string, as Google Scholar does not allow wild cards or Boolean terms. We split the original search string into eight substrings and removed wildcards:

- (reptile|lizard|snake|turtle|tortoise|crocodile)
  (infrastructure|road|motorway|highway|”train track”|railway)
  (disturbance|effect|impact|distance|proximity|avoidance|influence)
  (density|abundance|encounter|population|count|persistence)

- (reptile|lizard|snake|turtle|tortoise|crocodile)
  (“transmission line”|”power line”| “seismic line”|pipeline)
  (disturbance|effect|impact|distance|proximity|avoidance|influence)
  (density|abundance|encounter|population|count|persistence)

- (amphibian|frog|toad|salamander)
  (infrastructure|road|motorway|highway|”train track”|railway)
  (disturbance|effect|impact|distance|proximity|avoidance|influence)
  (density|abundance|encounter|population|count|persistence)

- (amphibian|frog|toad|salamander)(“transmission
  line”|”power line”| “seismic line”|pipeline)
  (disturbance|effect|impact|distance|proximity|avoidance|influence)
  (density|abundance|encounter|population|count|persistence)

- (bird|mammal)
  (infrastructure|road|motorway|highway|”train track”|railway)
  (disturbance|effect|impact|distance|proximity|avoidance|influence)
  (density|abundance|encounter|population|count|persistence)
- (bird|mammal)(“transmission line”|”power line”| “seismic line”|pipeline)
  (disturbance|effect|impact|distance|proximity|avoidance|influence)
  (density|abundance|encounter|population|count|persistence)
- (avifauna|herpetofauna|vertebrate)(“transmission
  line”|”power line”| “seismic line”|pipeline)
  (disturbance|effect|impact|distance|proximity|avoidance|influence)
  (density|abundance|encounter|population|count|persistence)
- (avifauna|herpetofauna|vertebrate)
  (infrastructure|road|motorway|highway|”train track”|railway)
  (disturbance|effect|impact|distance|proximity|avoidance|influence)
  (density|abundance|encounter|population|count|persistence)

We collected the first 100 hits for each search string for title and abstract screening.

ProQuest Dissertations and Theses repository

We searched all fields except full text with the following search string:

(vertebrate* OR bird* OR avifauna OR herpetofauna OR reptil* OR lizard* OR snake* OR turtle* OR tortoise* OR crocodil* OR amphibia* OR frog* OR toad* OR salamander* OR mammal*) AND (infrastruct* OR road OR roads OR motorway* OR highway* OR “train track” OR railway* OR “transmission line” OR power*line* OR “seismic line” OR pipeline*) AND (disturbance* OR effect* OR impact* OR distance* OR proximity OR avoidance OR influence) AND (density OR abundan* OR encounter* OR population OR population* OR count OR counts OR persistence)

Open Access Theses and Dissertations

We searched “Any field” with the same search string as used in ProQuest:

(vertebrate* OR bird* OR avifauna OR herpetofauna OR reptil* OR lizard* OR snake* OR turtle* OR tortoise* OR crocodil* OR amphibia* OR frog* OR toad* OR salamander* OR mammal*) AND (infrastruct* OR road OR roads OR motorway*

OR highway* OR “train track” OR railway* OR “transmission line” OR power*line* OR “seismic line” OR pipeline*) AND (disturbance* OR effect* OR impact* OR distance* OR proximity OR avoidance OR influence) AND (density OR abundan* OR encounter* OR population OR population* OR count OR counts OR persistence)

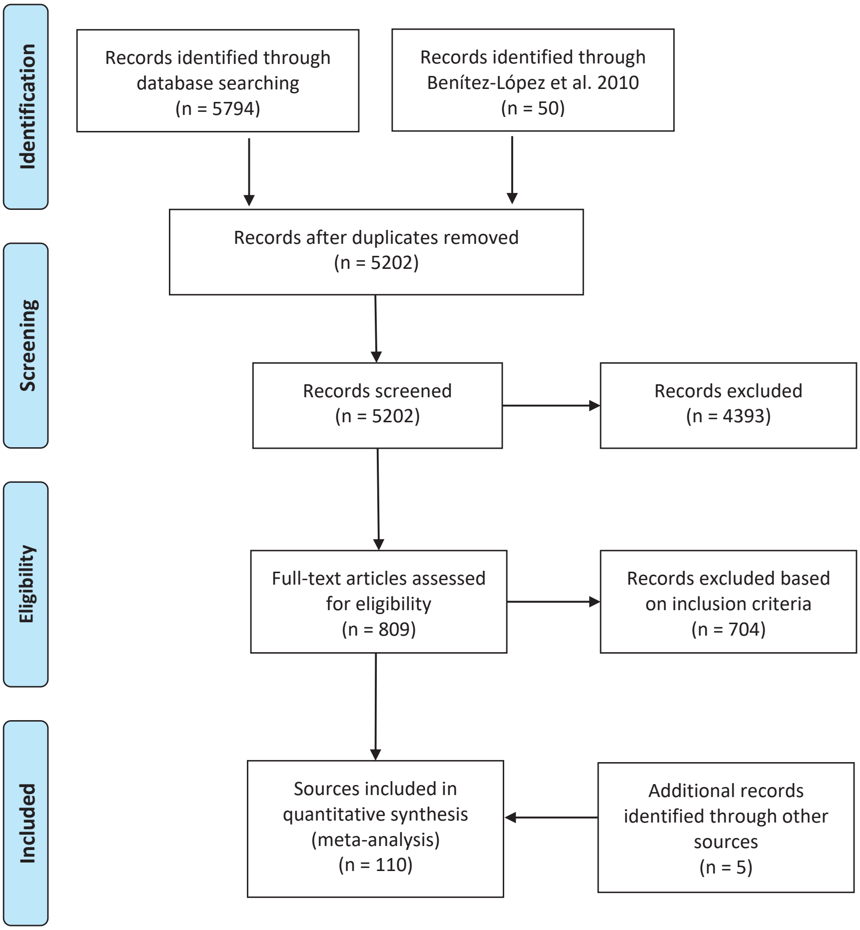


Figure S3.1 PRISMA flow-chart showing the number of primary sources identified during our literature search and the number of sources retained included during the first and second screening and the final number of primary sources included in the analysis. From the final 110 sources, 30 were obtained from Benítez-López et al. 2010.

- (bird|mammal)
  (infrastructure|road|motorway|highway|”train track”|railway)
  (disturbance|effect|impact|distance|proximity|avoidance|influence)
  (density|abundance|encounter|population|count|persistence)
- (bird|mammal)(“transmission line”|”power line”| “seismic line”|pipeline)
  (disturbance|effect|impact|distance|proximity|avoidance|influence)
  (density|abundance|encounter|population|count|persistence)
- (avifauna|herpetofauna|vertebrate)(“transmission
  line”|”power line”| “seismic line”|pipeline)
  (disturbance|effect|impact|distance|proximity|avoidance|influence)
  (density|abundance|encounter|population|count|persistence)
- (avifauna|herpetofauna|vertebrate)
  (infrastructure|road|motorway|highway|”train track”|railway)
  (disturbance|effect|impact|distance|proximity|avoidance|influence)
  (density|abundance|encounter|population|count|persistence)

We collected the first 100 hits for each search string for title and abstract screening.

ProQuest Dissertations and Theses repository

We searched all fields except full text with the following search string:

(vertebrate* OR bird* OR avifauna OR herpetofauna OR reptil* OR lizard* OR snake* OR turtle* OR tortoise* OR crocodil* OR amphibia* OR frog* OR toad* OR salamander* OR mammal*) AND (infrastruct* OR road OR roads OR motorway* OR highway* OR “train track” OR railway* OR “transmission line” OR power*line* OR “seismic line” OR pipeline*) AND (disturbance* OR effect* OR impact* OR distance* OR proximity OR avoidance OR influence) AND (density OR abundan* OR encounter* OR population OR population* OR count OR counts OR persistence)

Open Access Theses and Dissertations

We searched “Any field” with the same search string as used in ProQuest:

(vertebrate* OR bird* OR avifauna OR herpetofauna OR reptil* OR lizard* OR snake* OR turtle* OR tortoise* OR crocodil* OR amphibia* OR frog* OR toad* OR salamander* OR mammal*) AND (infrastruct* OR road OR roads OR motorway*

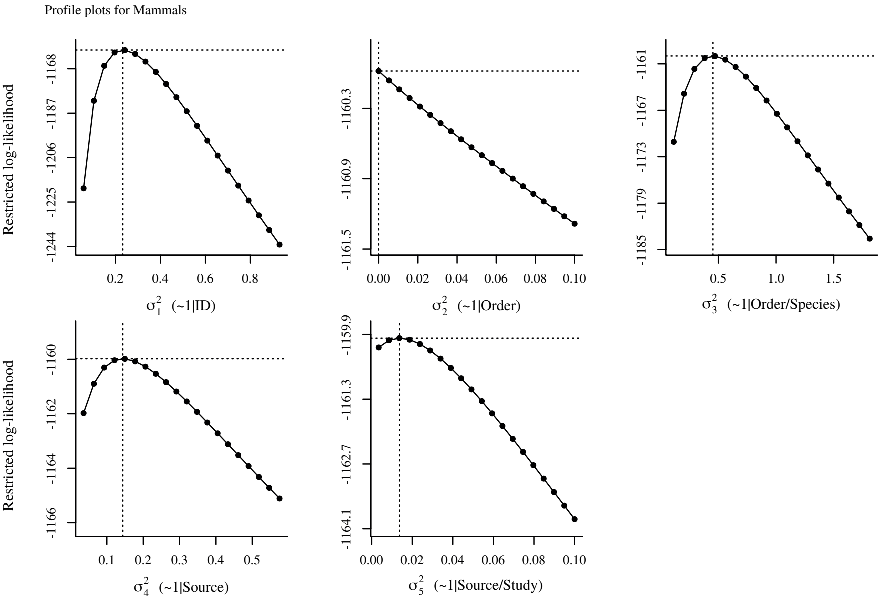


Figure S3.4 Profile likelihood plots of the variance components in the final model for mammals. σ^2_1: between-effect size variability, σ^2_2: between-order variability, σ^2_3: between-species variability, σ^2_4: between-sources variability, σ^2_5: between-study variability.

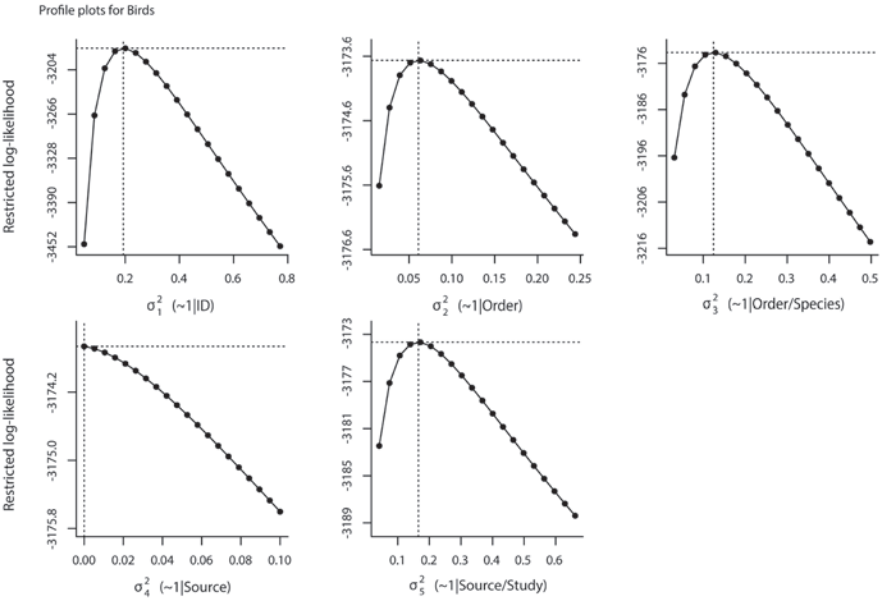


Figure S3.5 Profile likelihood plots of the variance components in the final model for birds. σ^2_1: between-effect size variability, σ^2_2: between-order variability, σ^2_3: between-species variability, σ^2_4: between-sources variability, σ^2_5: between-study variability.

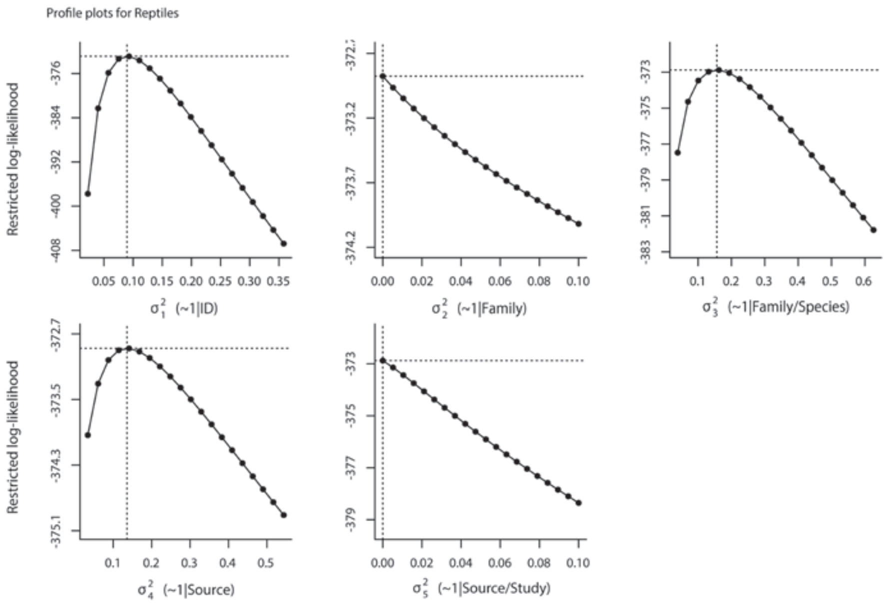


Figure S3.6 Profile likelihood plots of the variance components in the final model for reptiles. σ^2_1: between-effect size variability, σ^2_2: between-family variability, σ^2_3: between-species variability, σ^2_4: between-sources variability, σ^2_5: between-study variability.

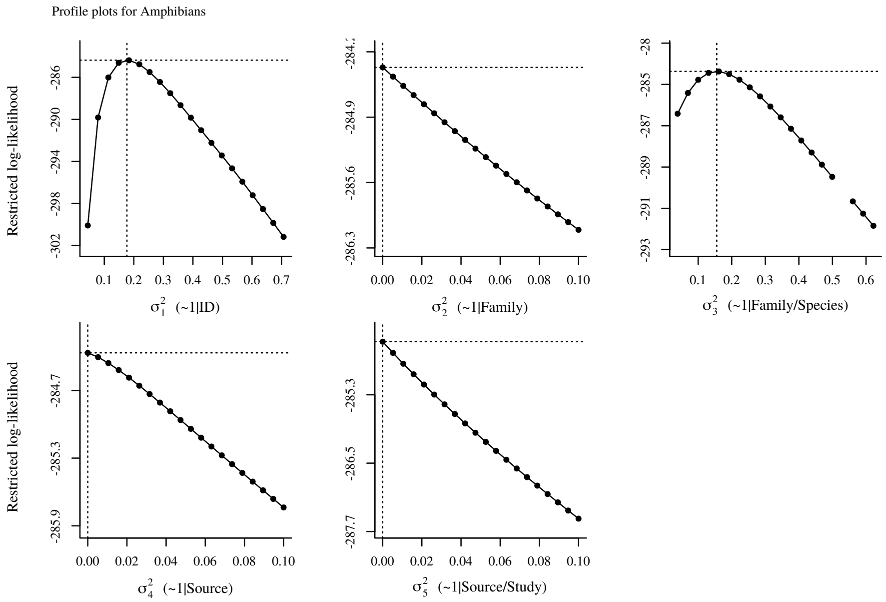


Figure S3.7 Profile likelihood plots of the variance components in the final model for amphibians. σ^2_1: between-effect size variability, σ^2_2: between-family variability, σ^2_3: between-species variability, σ^2_4: between-sources variability, σ^2_5: between-study variability.

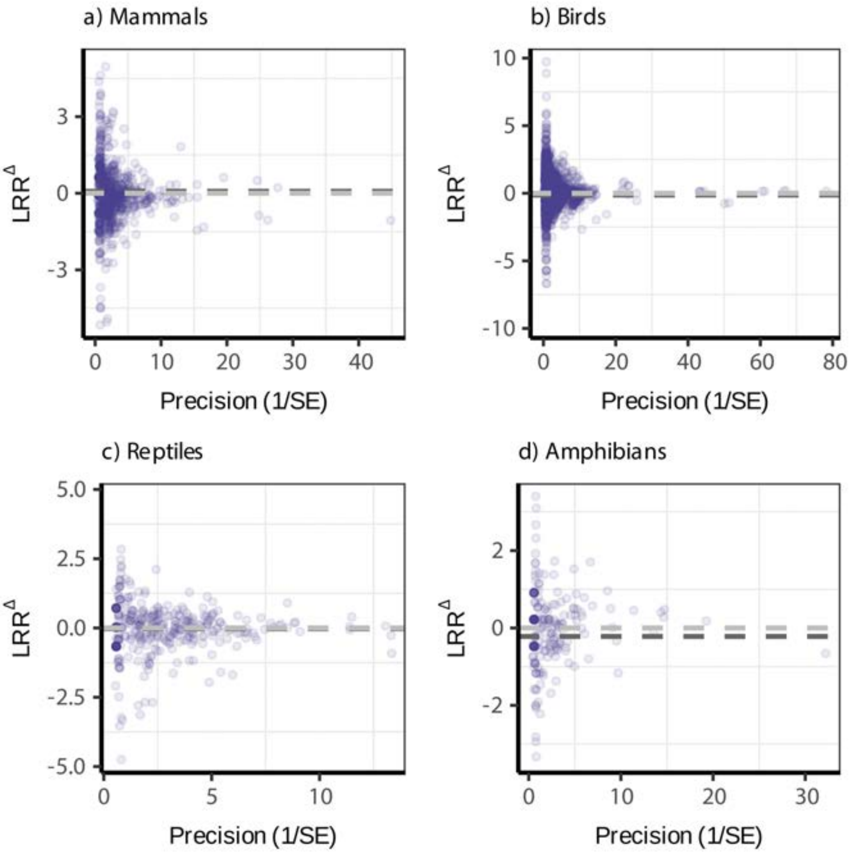


Figure S3.8 Funnel plots of the meta-analytic residuals for a) mammals, b) birds, d) reptiles and d) amphibians. Dashed lines indicate residual LRRΔ = 0 (zero line, light gray) and weighted mean effect size (dark gray). Egger test for mammals: intercept = -0.03 (95% CI: -0.27, 0.22, p=0.81). Egger test for birds: intercept = -0.-7 (95% CI: -0.27, 0.14, p=0.51). Egger test for reptiles: intercept = -0.03 (95% CI: -0.25, 0.19, p=0.82). Egger test for amphibians: intercept = -0.05 (95% CI: -0.21, 0.29, p=0.73).

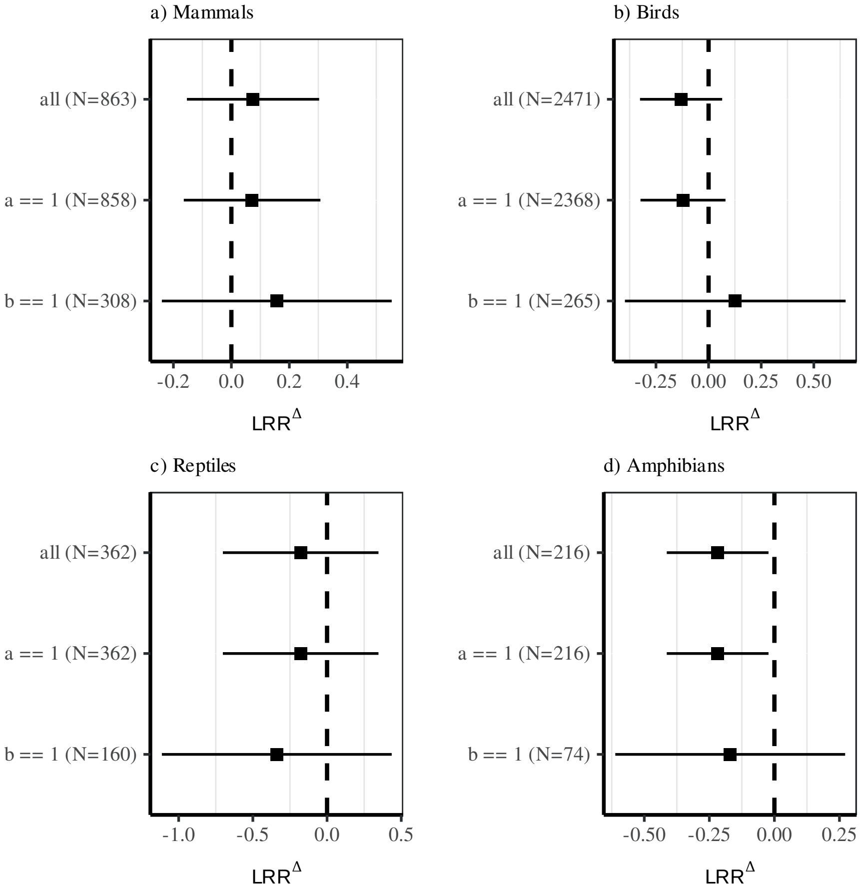


Figure S3.9 Forest plots for a) mammals, b) birds, c) reptiles and d) amphibians showing the robustness of the mean weighted effect sizes to exclusion of studies with different quality levels. all: all studies included, a == 1: excluding studies reporting abundances aggregated over 2 or more species or on genus level and b == 1: excluding studies for which the control site was not explicitly defined as undisturbed or at distances from infrastructure larger than the species' home range. Number of retained effect sizes is indicated between brackets for each quality level (N). Dashed line indicates $LRR^{\Delta} = 0$.

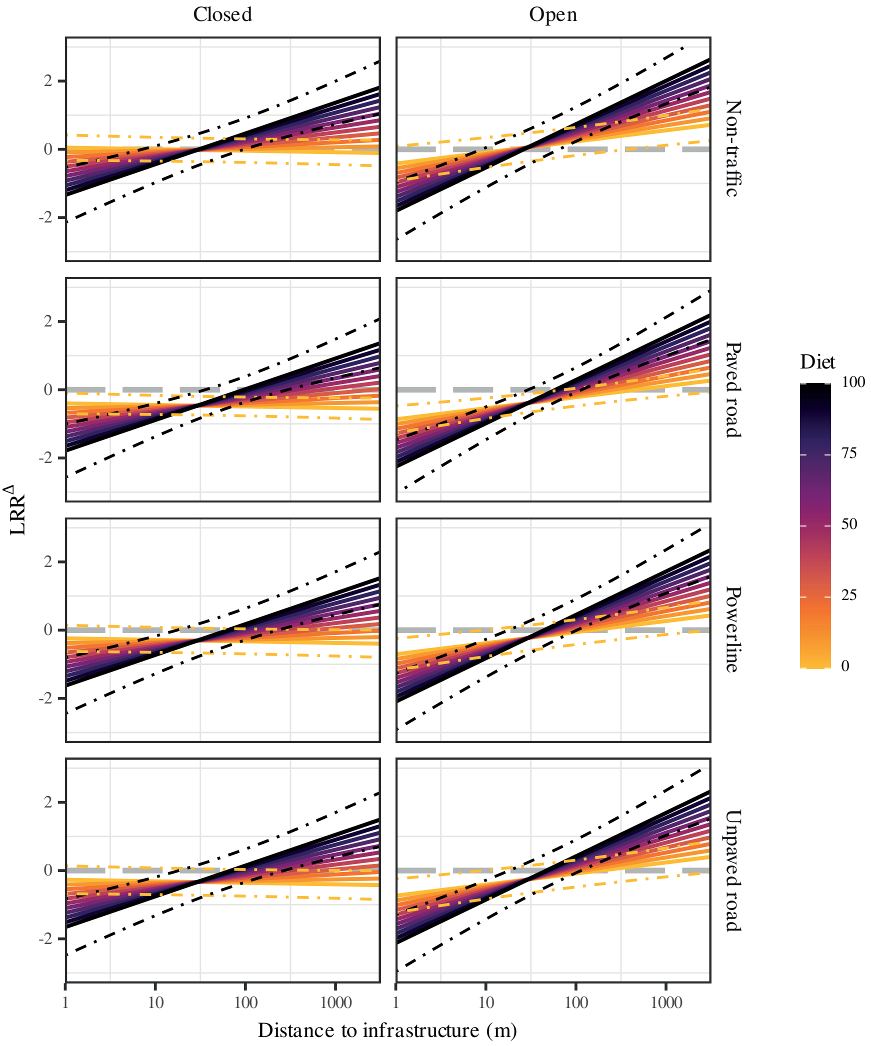


Figure S3.10 Change in species abundance (LRR$^{\Delta}$) as a function of distance to infrastructure and diet (% of diet consisting of vertebrates or scavenging, indicated by color) for birds in closed (left panel) and open (right panel) habitats for all four infrastructure types (rows, See **Table 3.2** for model information). Dashed lines represent the 95% confidence interval for 0 and 100% of diet consisting of vertebrates or scavenging. LRR$^{\Delta}$<0 indicates abundance decline, LRR$^{\Delta}$>0 indicates abundance increase and LRR$^{\Delta}$=0 indicates no change (dashed grey line).

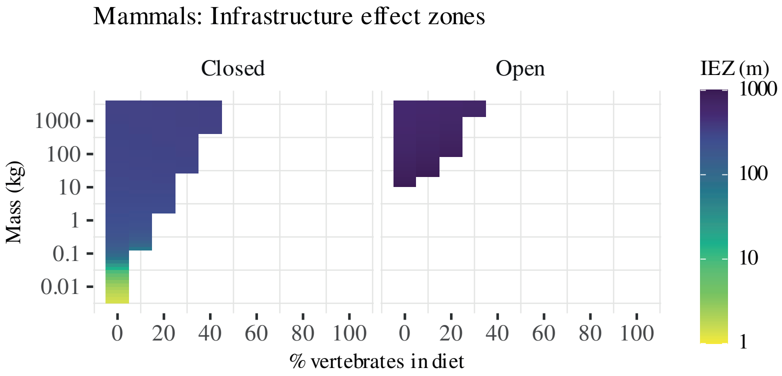


Figure S3.11 Estimated infrastructure effect zone (IEZ, m) for mammals as a function of body mass and diet (% of diet from vertebrates or scavenging) in closed (left panel) and open (right panel) habitats. Areas in white represent combinations of species traits and habitat type with positive responses to infrastructure.

Table S3.1 Number of effect sizes for mammals split to habitat and infrastructure type. Note that non-traffic infrastructure and power lines are combined into a single 'non-traffic' category in the analysis.

	Paved roads	**Unpaved roads**	**Non-traffic**	**Power line**	***Total***
Open	182	45	-	7	*234*
Closed	291	180	65	93	*629*
Total	*473*	*125*	*65*	*100*	*863*

Table S3.2 Number of effect sizes for birds split to habitat and infrastructure type.

	Paved roads	**Unpaved roads**	**Non-traffic**	**Power line**	***Total***
Open	562	115	-	92	*769*
Closed	679	43	227	753	*1702*
Total	*1241*	*158*	*227*	*845*	*2471*

Table S3.3 Number of effect sizes for reptiles split to habitat and infrastructure type. Note that non-traffic infrastructure and power lines are combined into a single 'non-traffic' category in the analysis.

	Paved roads	**Unpaved roads**	**Non-traffic**	**Power line**	***Total***
Open	180	7	-	-	*187*
Closed	95	37	35	8	*175*
Total	*275*	*44*	*35*	*8*	*362*

Table S3.4 Number of effect sizes for amphibians split to habitat and infrastructure type. Note that non-traffic infrastructure and power lines are combined into a single 'non-traffic' category in the analysis.

	Paved roads	**Unpaved roads**	**Non-traffic**	**Power line**	***Total***
Open	-	-	-	-	**-**
Closed	99	91	19	7	*216*
Total	*99*	*91*	*19*	*7*	*216*

Table S3.5 Parameter estimates and 95% confidence intervals and results of Omnibus Q-test (Q_M) of random-effects meta-analysis and distance only mixed-effects meta-analysis for each taxon. k indicates the number of effect sizes included in the analysis. Asterisks indicate significance level for Q_M: *** indicates p-value < 0.001, ** indicates p-value < 0.01, * indicates p-value < 0.05, n.s. indicates p-value > 0.05.

	Mammals (*k=863*)				**Birds (*k=2471*)**				**Reptiles (*k=362*)**				**Amphibians (*k=216*)**			
	Mean effect	*95% CI*	*AIC*	Q_M	*Mean effect*	*95% CI*	*AIC*	Q_M	*Mean effect*	*95% CI*	*AIC*	Q_M	*Mean effect*	*95% CI*	*AIC*	Q_M
LRR^{Δ} ~ 1	0.07	-0.15, 0.30	2425	-	-0.13	-0.33, 0.06	6461	-	-0.03	-0.22, 0.17	827	-	-0.22	-0.41, -0.02	594	
LRR^{Δ} ~ 1	0.14	-0.10, 0.39	2426	$1.6^{n.s}$	-0.32	-0.56, -0.08	6456	6.9^{**}	-0.45	-0.75, -0.16	789	47.5^{***}	-0.51	-0.85, -0.18	592	4.6^{*}
+ log(D)	-0.05	-0.13, 0.03			0.10	0.03, 0.17			0.35	0.25, 0.44			0.24	0.02, 0.46		
LRR^{Δ} ~ 1	0.21	-0.05, 0.47	2423	6.1^{*}	0.10	-0.30, 0.50	6452	13.5^{**}	-0.22	-0.55, 0.12	784	57.3^{***}	-0.74	-1.15, -0.33	590	8.7^{*}
+ log(D)	-0.28	-0.51, -0.06			-0.39	-0.76, -0.01			-0.16	-0.54, 0.22			0.91	0.21, 1.62		
+ $\log(D)^2$	0.09	0.01, 0.17			0.12	0.03, 0.22			0.17	0.05, 0.30			-0.32	-0.63, 0.00		

Table S3.6 Parameter estimates and 95% confidence intervals, number of effect sizes (k) and results of Cochran's Q-test (QE) of random-effects meta-analysis based on the full dataset (all LRR^{Δ}) and on a subset of the data for which Geary's diagnostic ≥ 3 (selected LRR^{Δ}). Asterisks indicate significance level for QE: *** indicates p-value < 0.001, ** indicates p-value < 0.01, * indicates p-value < 0.05, n.s. indicates p-value > 0.05.

	Mammals				**Birds**				**Reptiles**				**Amphibians**			
	Mean effect	*95% CI*	*k*	Q_E	*Mean effect*	*95% CI*	*k*	Q_E	*Mean effect*	*95% CI*	*k*	Q_E	*Mean effect*	*95% CI*	*k*	Q_E
All LRR^{Δ}	0.07	-0.15, 0.30	863	8410^{***}	-0.13	-0.33, 0.06	2471	26890^{***}	-0.03	-0.22, 0.17	362	1455^{***}	-0.22	-0.41, -0.02	216	1407^{***}
Selected LRR^{Δ}	-0.04	-0.25, 0.17	279	6646^{***}	-0.02	-0.22, 0.17	943	15242^{***}	-0.20	-0.50, 0.10	140	1052^{***}	-0.17	-0.38, 0.05	63	1213^{***}

Table S3.7 Results of random-effects meta-analysis under different SD imputation methods. Numbers between brackets indicate the percentage of effect sizes with imputed SDs.

	Mammals (22%)		**Birds (63%)**		**Reptiles (26%)**		**Amphibians (54%)**	
	Mean effect	*95% CI*	*Mean effect*	*95% CI*	*Mean effect*	*95% CI*	*Mean effect*	*95% CI*
No imputation	-0.02	-0.40, 0.36	-0.01	-0.29, 0.28	0.09	-0.14, 0.33	0.01	-0.18, 0.19
Poisson	0.07	-0.15, 0.30	-0.13	-0.33, 0.06	-0.03	-0.22, 0.17	-0.22	-0.41, -0.02
Bracken	0.06	-0.17, 0.29	-0.22	-0.43, 0.00	-0.00	-0.20, 0.19	-0.33	-0.59, -0.08
HotDeckNN (median)	0.06	-0.17, 0.29	-0.20	-0.42, 0.02	-0.01	-0.21, 0.20	-0.25	-0.48, -0.02
HotDeckNN (mean)	0.06	-0.17, 0.29	-0.20	-0.42, 0.02	-0.01	-0.21, 0.20	-0.24	-0.47, -0.01

Table S3.8 Results of mixed-effects meta-regression model selection for mammals with Akaike information criterium (AICc) and difference from the lowest AICc (ΔAICc). Only the 10 models with the lowest AICc and those with only one moderator are shown for simplicity.

Fixed effects	**AICc**	**ΔAICc**
~logD * Diet + logD * Habitat + logD * logBM + logD^2 * logBM	2374.6	-
~logD * Diet + logD * Habitat + logD^2 * Habitat + logD * logBM + logD^2 * logBM	2375.4	0.8
~logD * Diet + logD^2 * Diet + logD * Habitat + logD * logBM + logD^2 * logBM	2376.7	2.1
~logD * Diet + logD^2 * Diet + logD * Habitat + logD^2 * Habitat + logD * logBM + logD^2 * logBM	2377.5	2.9
~logD * Diet + logD * logBM + logD^2 * logBM + logD * Habitat + InfraType	2378.1	3.5
~logD * Diet + logD * logBM + logD^2 * logBM + logD * Habitat + logD^2 * Habitat + InfraType	2378.9	4.3
~logD * Diet + logD * logBM + logD^2 * logBM	2380.2	5.6
~logD * Diet + logD^2 * Diet + logD * logBM + logD^2 * logBM + logD * Habitat + InfraType	2380.2	5.6
~logD * Diet + logD^2 * Diet + logD * logBM + logD^2 * logBM + logD * Habitat + logD^2 * Habitat + InfraType	2381.1	6.4
~logD * Diet + logD * logBM + logD^2 * logBM + Habitat	2382.0	7.4
~Diet	2415.8	41.2
~logD + logD^2	2423.3	48.7
~1	2425.3	50.7
~logD	2425.7	51.1
~logBM	2426.4	51.8
~Habitat	2426.6	51.9
~InfraType	2429.2	54.5

Table S3.9 Results of mixed-effects meta-regression model selection for birds with Akaike information criterium (AICc) and difference from the lowest AICc (ΔAICc). Only the 10 models with the lowest AICc and those with only one moderator are shown for simplicity.

Fixed effects	AICc	ΔAICc
~logD * Diet + logD * Habitat + InfraType	6420.2	0.0
~logD * Diet + logD * logBM + logD * Habitat + InfraType	6420.3	0.2
~logD * Diet + logD * Habitat	6420.5	0.3
~logD * Diet + logD * Habitat + logD * logBM	6420.9	0.7
~logD * Diet + logD^2 + logD * Habitat + InfraType	6421.7	1.5
~logD * Diet + logBM + logD * Habitat + InfraType	6422.0	1.8
~logD * Diet + logD * logBM + logD * Habitat + InfraType + logD^2	6422.1	2.0
~logD * Diet + logD^2 + logD * Habitat	6422.2	2.0
~logD * Diet + logD * Habitat + logBM	6422.3	2.1
~logD * Diet + logD * logBM + logD^2 * logBM + logD * Habitat + InfraType	6422.6	2.5
~logD + logD^2	6451.9	31.8
~logD	6456.3	36.1
~Habitat	6460.4	40.2
~1	6461.2	41.0
~logBM	6461.7	41.6
~Diet	6461.9	41.7
~InfraType	6466.2	46.0

Table S3.10 Results of mixed-effects meta-regression model selection for reptiles with Akaike information criterium (AICc) and difference from the lowest AICc (ΔAICc). Only the 10 models with the lowest AICc and those with only one moderator are shown for simplicity.

Fixed effects	AICc	ΔAICc
~logD * Habitat + logD^2	781.6	0.0
~logD * Habitat + logD^2 + logBM	781.6	0.0
~logD * logBM + logD^2 + logD * Habitat	782.3	0.7
~logD * logBM + logD^2 * logBM + logD * Habitat	782.8	1.2
~logD * Habitat + logD^2 * Habitat	783.0	1.4
~logD * Habitat + logD^2 * Habitat + logBM	783.2	1.6
~logD + logD^2 + InfraType	783.4	1.8
~logD + logD^2 + logBM + InfraType	783.8	2.2
~logD * logBM + logD * Habitat + logD^2 * Habitat	783.9	2.4
~logD * Habitat + logBM	784.4	2.8
~logD + logD^2	784.5	2.9
~logD	789.4	7.9
~logBM	826.5	44.9
~1	826.8	45.2
~Habitat	828.9	47.3
~InfraType	829.5	47.9

Table S3.11 Results of mixed-effects meta-regression model selection for amphibians with Akaike information criterium (AICc) and difference from the lowest AICc (ΔAICc).

Fixed effects	AICc	ΔAICc
~logD + $\log D^2$	590.4	0.0
~logD + $\log D^2$ + logBM	590.7	0.3
~logD * logBM + $\log D^2$	591.7	1.4
~logD	591.9	1.5
~logD * logBM + $\log D^2$ * logBM	592.0	1.6
~logD + logBM	592.5	2.2
~1	594.2	3.8
~logD * logBM	594.2	3.8
~logD + $\log D^2$ + InfraType	595.0	4.7
~logBM	595.3	4.9
~logD + $\log D^2$ + logBM + InfraType	595.3	5.0
~logD + InfraType	596.0	5.6
~InfraType	596.0	5.6
~logD + logBM + InfraType	596.2	5.8
~logD * logBM + $\log D^2$ + InfraType	596.6	6.3
~logD * logBM + $\log D^2$ * logBM + InfraType	596.8	6.5
~logD * logBM + InfraType	597.6	7.3

Table S3.12 Estimates of variance components (σ_1^2: observation-level variability, σ_2^2: order or family - level variability, σ_3^2: species-level variability, σ_4^2: source–level variability, σ_5^2: study-level variability) of the final model selected based on the AICc for mammals, birds, reptiles and amphibians.

	Mammals	Birds	Reptiles	Amphibians
σ_1^2 (residual)	0.2325	0.1940	0.0902	0.1767
σ_2^2 (order/family)	0.0000	0.0505	0.0000	0.0000
σ_3^2 (species)	0.4529	0.1242	0.1517	0.1555
σ_4^2 (source)	0.1437	0.0000	0.1400	0.0000
σ_5^2 (study)	0.0138	0.1702	0.0000	0.0000

Figure S4.1 Geographical distribution of the studies included in the meta-analysis of land-use effects and the meta-analysis of nitrogen addition effects. Point size represents the number of response ratios (RR, observations) available from each study.

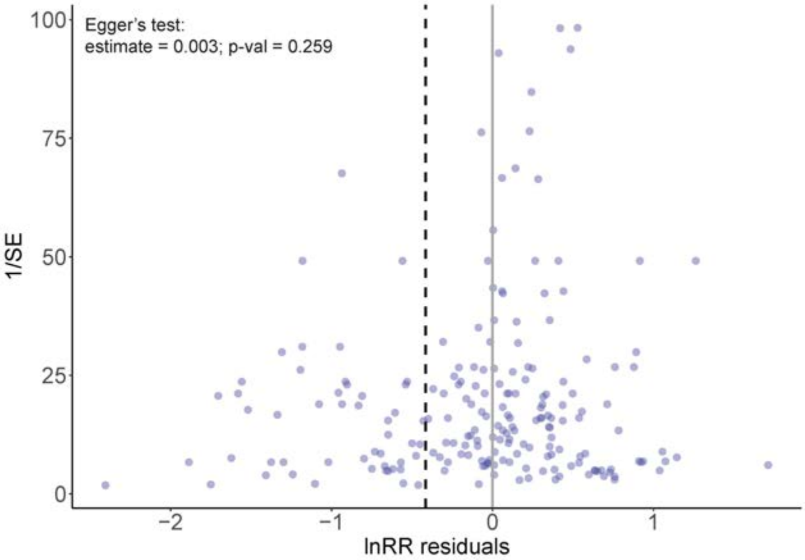


Figure S4.2 Funnel plot for the null model of the land-use meta-analysis to check publication bias. The inverse of the standard error (1/SE) indicates the precision of the observations. The solid line (grey) indicates RR = 0 and the dashed line (black) the weighted mean effect size. Egger's test suggests that there is no publication bias (p-value > 0.05, Nakagawa & Santos (2012)).

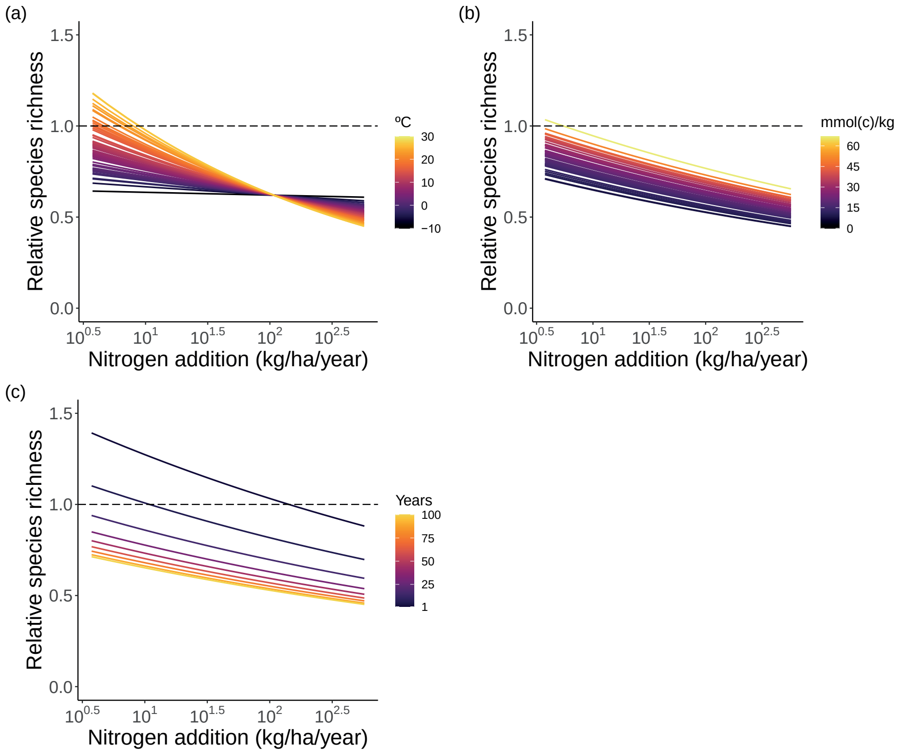
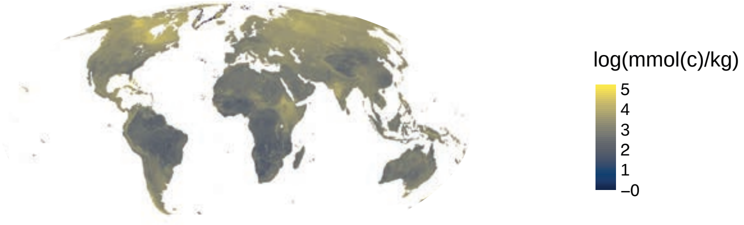


Figure S4.3 Responses of plant species richness to nitrogen addition considering a) mean annual temperature (MAT), b) cation exchange capacity (CEC), and c) duration of nitrogen addition. Predictions for MAT and CEC (a, b) are made based on the median value for the other variable and a cumulative duration of 32 years of nitrogen addition. Predictions for duration (c) are made based on median values of MAT and CEC.

(a) Mean annual temperature 1984–2015

(b) Cation exchange capacity



(c) Nitrogen deposition 1984–2015

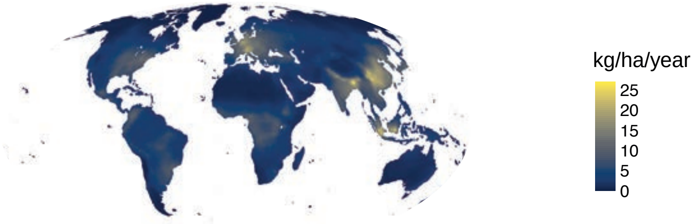


Figure S4.4 Input variables for the nitrogen impact model. For visualization purposes, cation exchange capacity is expressed on a log-scale.

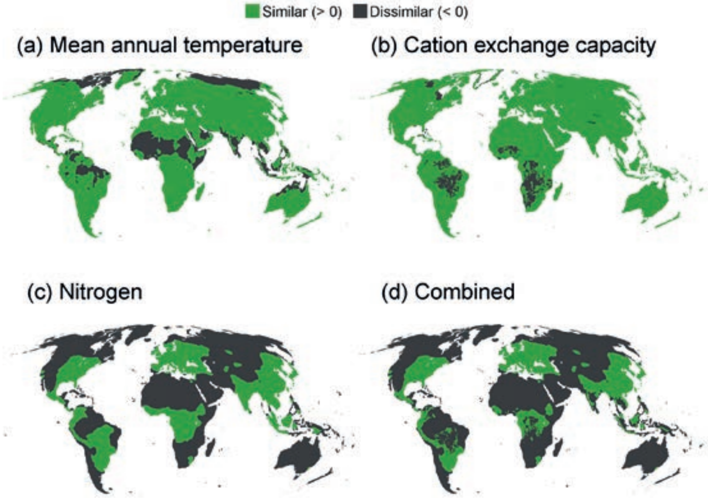


Figure S4.5 Applicability domain of the nitrogen meta-analysis model calculated using Multivariate Environmental Similarity Surface analysis (MESS) for the input moderators in the model, including a) mean annual temperature (MAT), b) cation exchange capacity (CEC), c) mean nitrogen deposition across 1984-2015 (N), and d) all the moderators combined. Positive values (green) represent grid cells with covariate values within the range of values in the database used to establish the response relationships (so, inside the applicability domain) and negative values (black) represent cells outside the applicability domain. For land use we did not include a MESS map because all the categories in the land use input map (LUH2) are included in our meta-analysis.

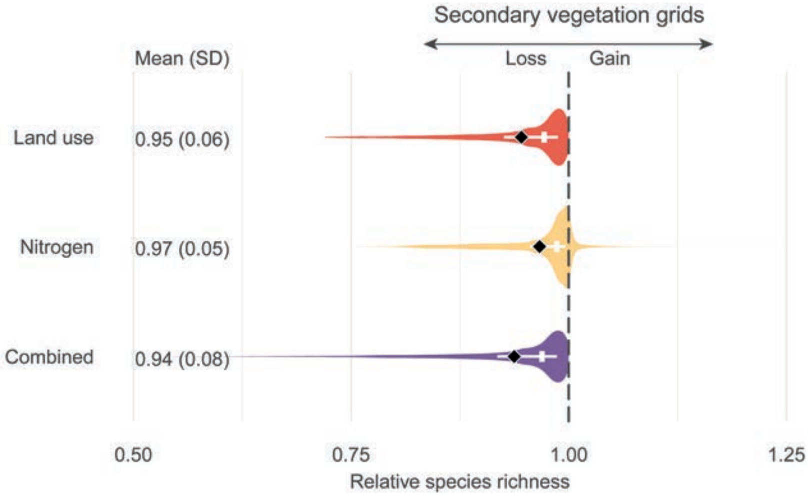


Figure S4.6 Changes in plant species richness in relation to land use (top), nitrogen deposition (centre) and the combination of both pressures (bottom) across the 0.25° grid cells in secondary vegetation only. Values above 1 represent an increase in the number of species, whereas values below 1 reflect species richness declines. Density plots show the distribution of the data; the white horizontal lines inside the density plots show the interquartile ranges; the thick white square is the median; and the black diamond is the mean.

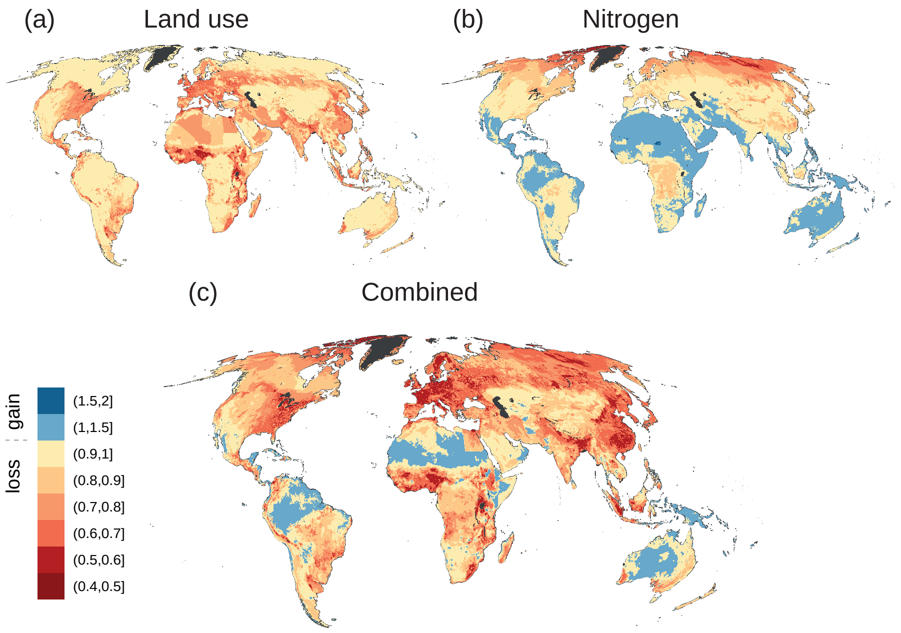


Figure S4.7 Geographical patterns of changes in plant species richness due to the effects of a) land use, b) nitrogen deposition (for a duration of 32 years) and c) both pressures combined without considering the model's applicability domain. Values above 1 represent an increase in the number of species; values below 1 represent a decline.

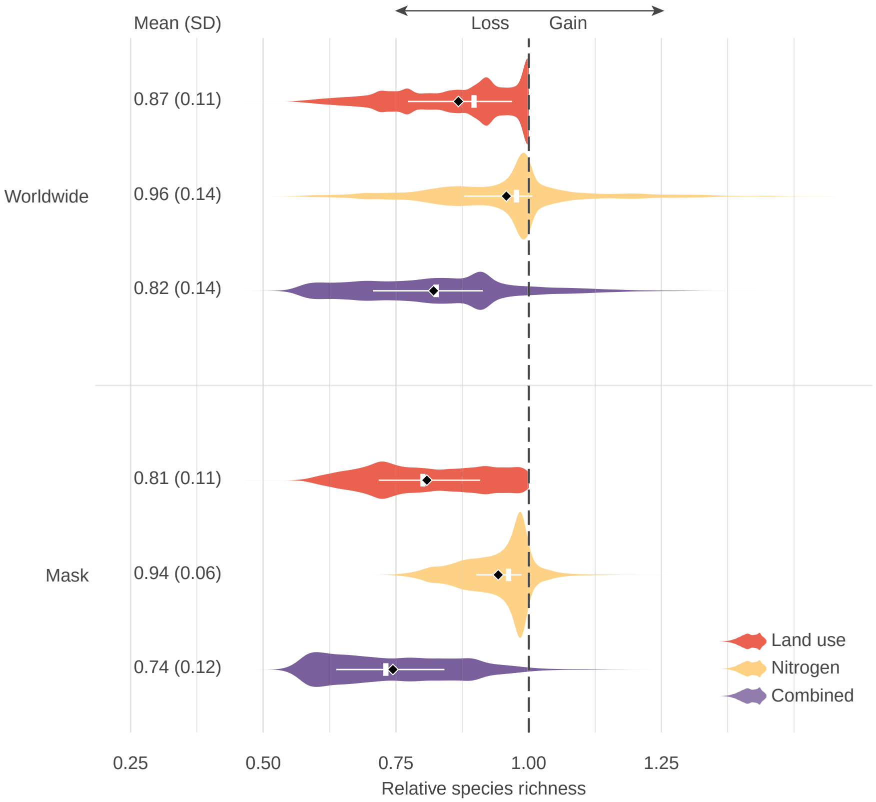


Figure S4.8 Changes in plant species richness across the 0.25° grid cells worldwide (top panel; values corresponding to **Figure S7**) and across grid cells within the model's applicability domain bottom panel; values corresponding to **Figure 2** in the main text) due to land use, nitrogen and their combined effect. Density plots show the distribution of the data; the white horizontal lines inside the density plots show the interquartile ranges; the thick white square is the median; and the black diamond is the mean.

Table S4.1 Estimates of the relative species richness change per land use type derived from the meta-analysis. Response ratio (RR) estimates and 95% confidence intervals (CI) for relative species richness obtained from the meta-analysis that included 75 publications, with publication dates ranging between 1997 and 2019, and a total of 201 pairwise comparisons.

Land use type	RR	CI-lower	CI-upper
Primary vegetation	1	0.9	1.11
Cropland - Intense use	0.32	0.23	0.44
Cropland - Light use	0.53	0.39	0.72
Cropland -Minimal use	0.56	0.42	0.74
Pasture - Light to intense use	0.57	0.44	0.76
Pasture - Minimal use	0.92	0.66	1.3
Plantation forest	0.58	0.5	0.67
Secondary vegetation	0.72	0.64	0.8
Urban	0.95	0.73	1.25

Table S4.2 Biome-specific slopes of species-area relationships for terrestrial plants (Gerstner *et al.* 2014b).

Biome name	Slope (z-value)
Boreal Forests/Taiga	0.078
Deserts & Xeric Shrublands	0.205
Flooded Grasslands & Savannas	0.37
Mediterranean Forests, Woodlands & Scrub	0.28
Montane Grasslands & Shrublands	0.215
Temperate Broadleaf & Mixed Forests	0.161
Temperate Conifer Forests	0.127
Temperate Grasslands, Savannas & Shrublands	0.144
Tropical & Subtropical Coniferous Forests	0.454
Tropical & Subtropical Dry Broadleaf Forests	0.126
Tropical & Subtropical Grasslands, Savannas & Shrublands	0.31
Tropical & Subtropical Moist Broadleaf Forests	0.212
Tundra	0.25

Table S4.3 Relative species richness per continent and pressure. Values represent the mean (standard deviation), minimum, and maximum values of relative species richness compared to the original situation due to land use, nitrogen deposition, and their combined effect.

Continent	Pressure	Mean (sd)	Min	Max
Global	Combined	0.74 (0.12)	0.43	1.23
	Nitrogen	0.94 (0.06)	0.63	1.30
	Land use	0.81 (0.11)	0.47	1.00
North America	Combined	0.75 (0.11)	0.55	1.23
	Nitrogen	0.95 (0.07)	0.76	1.30
	Land use	0.80 (0.10)	0.57	1.00
South America	Combined	0.84 (0.11)	0.56	1.14
	Nitrogen	0.98 (0.03)	0.85	1.14
	Land use	0.86 (0.11)	0.56	1.00
Europe	Combined	0.66 (0.08)	0.43	0.95
	Nitrogen	0.92 (0.06)	0.75	1.01
	Land use	0.74 (0.09)	0.47	1.00
Africa	Combined	0.78 (0.12)	0.48	1.22
	Nitrogen	0.95 (0.06)	0.82	1.29
	Land use	0.84 (0.14)	0.47	1.00
Asia	Combined	0.74 (0.12)	0.54	1.22
	Nitrogen	0.94 (0.07)	0.63	1.23
	Land use	0.82 (0.10)	0.58	1.00

Table S4.4 Numbers and percentages of cells with increases and decreases of plant species richness.

Pressure	Total	Increase	Decrease	No Change	Increase (%)	Decrease (%)
Combined	64,036	1,111	62,925	0	0.02	0.98
Nitrogen	64,036	6,614	57,104	318	0.11	0.89
Land use	64,036	0	63,915	121	0.00	1.00

APPENDIX CHAPTER 5

Appendix S5.1. Description of the land-use allocation by the GLOBIO model

The GLOBIO model (version 4) includes a 10 arc-seconds (~300m resolution at the equator) land-use allocation procedure to capture the spatial heterogeneity of land use (Kim *et al.* 2018). Three types of inputs are required: 1) regional totals or demands ("claims") of each land-use type, expressed in terms of area (km^2); 2) a base map with the natural land cover, and 3) map layers quantifying the suitability of each grid cell for each land-use type. In this study, we distinguished five anthropogenic land-use types that match the IUCN habitat classification scheme, i.e., arable land, pastureland, plantations, urban areas and secondary vegetation (tropical heavily degraded former forest). For arable lands and urban areas, we directly used the ESA's CCI land cover maps for the years 1992 and 2015. Because the ESA's land cover map does not include data on pastures and plantations, we used data from the FAO to obtain the claims for those land use types. The FAO provides total areas (km^2) of different land use practices per country and year. For pasture and rangeland we used area of *Permanent and Temporary meadows and pastures*, and for plantations the area of *Planted forest*, based on country-specific data reported for 1992 and 2015 (FAO 2016). We then used the GLOBIO 4 allocation routine to allocate the claims of pasture and forestry (in which forestry takes precedence over pasture), using the corresponding suitability layers (Kim *et al.* 2018) and using the ESA CCI maps of the respective years as a base maps. Thus, in essence we superimposed pasture and forestry land onto the ESA CCI land-cover maps of 1992 and 2015. Further details on the GLOBIO land-use allocation routine can be found in Schipper *et al.* (2020).

Appendix S5.2. Description of the crosswalk between the GLOBIO land-use map and the IUCN habitat classification

We created this crosswalk in a two-step procedure. We first made an initial connection between the GLOBIO land-use classes and the level 1 and 2 classes of the Habitat Classification Scheme of the IUCN (IUCN 2015), based on similarities in definitions (i.e. vegetation types and climate). Second, to further refine the initial cross-walk, we matched the definitions of the IUCN habitats with the biomes from Dinerstein et al. (2017) and identified which land-use classes felt inside the different biomes. In addition, to account for habitats occurring at high altitudes (e.g. Forest-

Subtropical/Tropical Moist Montane (IUCN habitat 1.9), occurs generally above c.1200m), we used a high-resolution digital elevation map to identify the land uses occurring over the threshold of 1200 m that the IUCN defines.

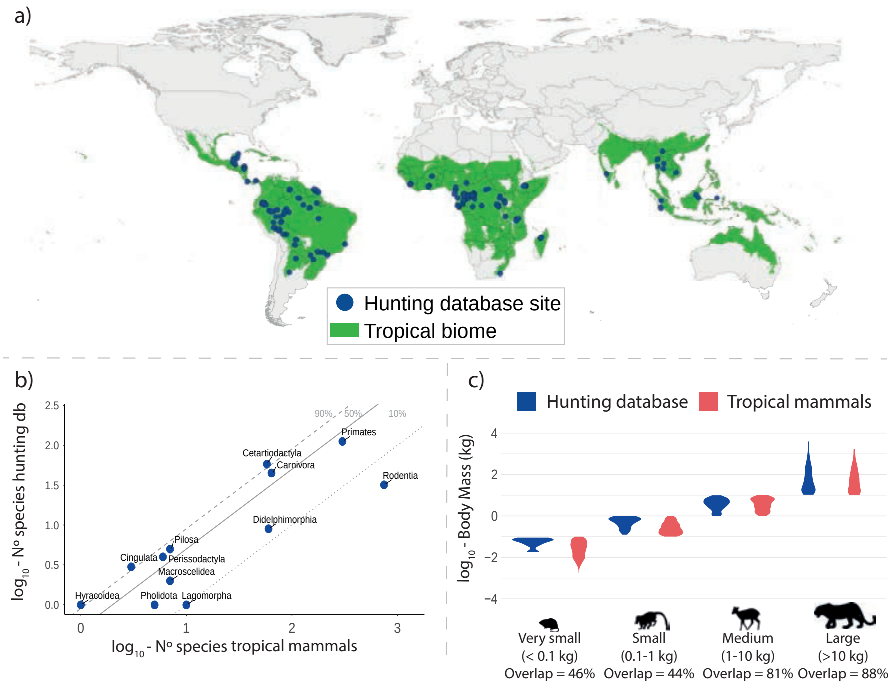


Figure S5.1 Comparison between the hunting database and the selection of tropical mammals in terms of a) location, b) number of species and c) body mass coverage. a) Location of study sites in the hunting database and the coverage of the tropical biome that we used to subset the selection of tropical mammals. b) Relationship between the number of species represented in our database (N = 296) and the number of tropical species for which we extrapolated our models (N = 1,884) for 12 orders. Lines show proportions of 10%, 50% and 90% (dotted, solid, dashed, respectively) representation. c) Violin plot showing the representation and percentage overlap between the hunting database and the selection of tropical mammals by different body size groups.

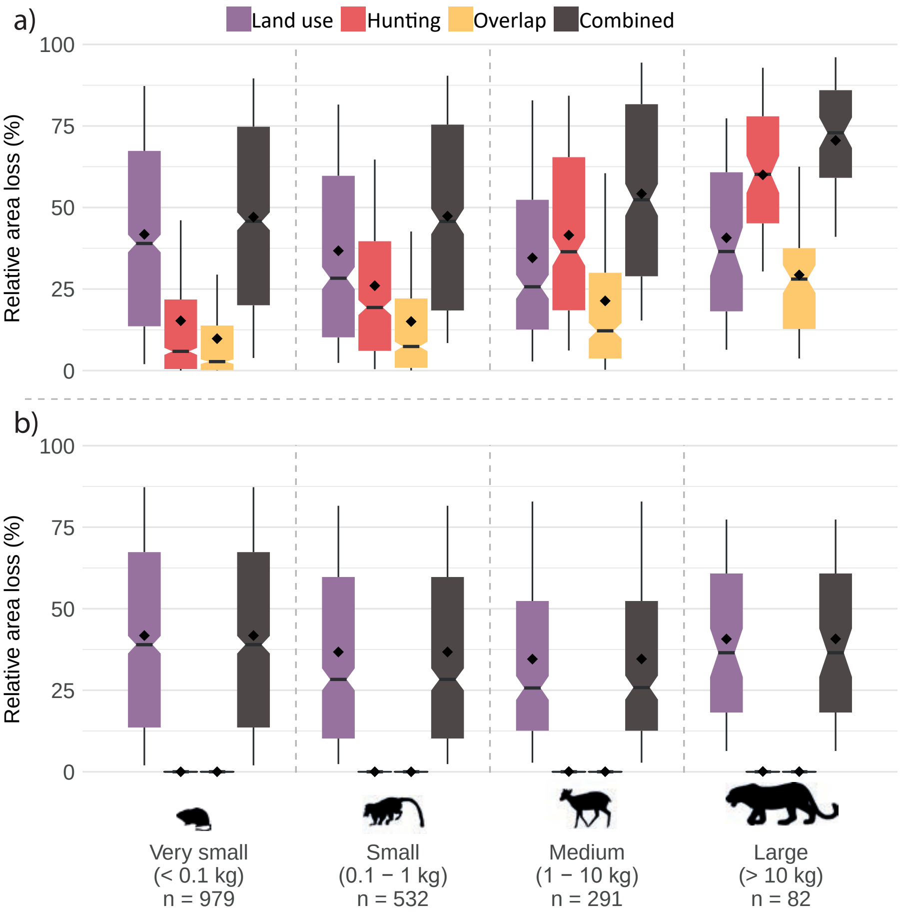


Figure S5.2 Reductions in distribution (%) by land use and hunting with two different thresholds for the hunting model based on a) maximum specificity (minimizing the error of predicting local extinction) and b) maximum sensitivity (minimizing the error of predicting occurrence). The model performance of these scenarios was measured by the TSS which ranges between -1 (all predictions are wrong) and 1 (all predictions are correct). In both scenarios the TSS was lower than obtained with maximizing both sensitivity and specificity (as presented in the main text), i.e., we obtained TSS of 0.55 for a) and 0.10 for b), compared to a TSS of 0.72 for the default model.

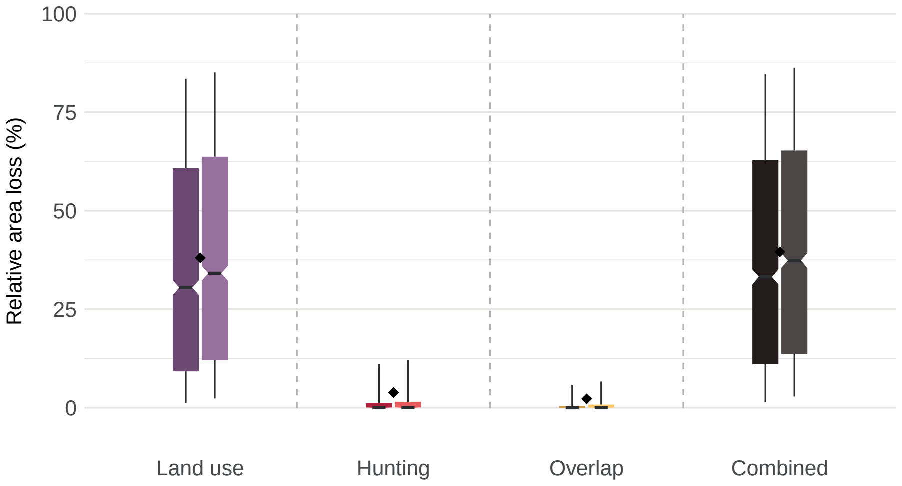


Figure S5.3 Losses in species' distributions (%) due to land use and hunting pressure for 1992 (left-hand boxes) and 2015 (right-hand boxes). The combined effect is the result of the sum of the losses due to land use and hunting minus the overlapping areas. The black diamonds represent the mean values per group; lower and upper box boundaries are 25th and 75th percentiles, the black thick line inside the box is the median, the notch represents the 95% confidence interval around the median and the whiskers the 10-90% percentile.

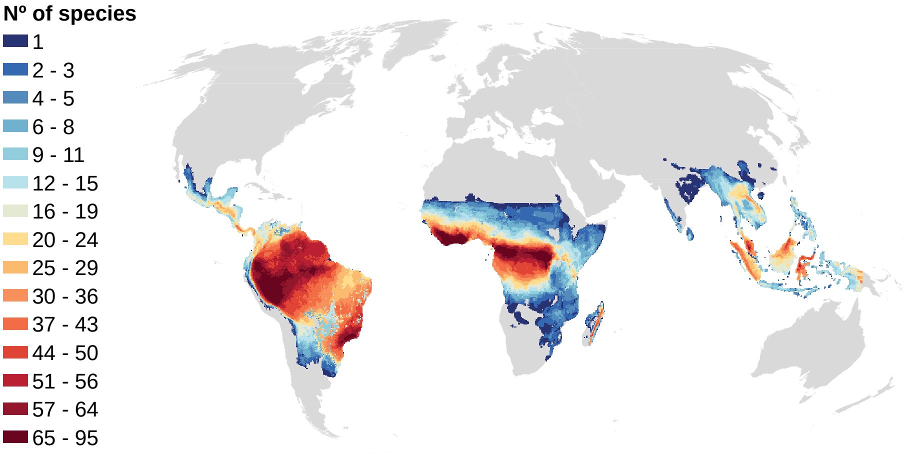


Figure S5.4 Number of species per 0.25° grid cell (~25 km) in the tropical biomes included in our analysis.

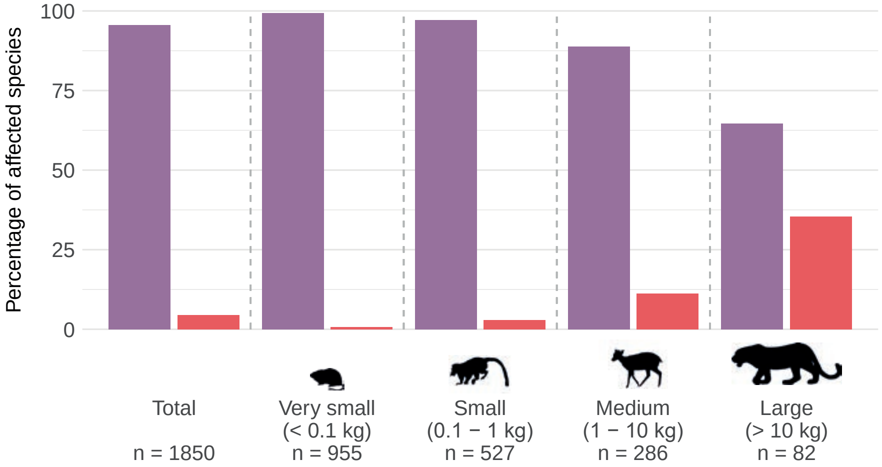


Figure S5.5 Relative number of species (%) per body mass group affected by land use (purple bar) or hunting pressure (red bar) as main driver of losses in distribution for the year 2015. Per species the main driver was calculated as the pressure that removed the most area relative to its extent of suitable area. Species that were not affected by either pressure or equally affected were discarded. The percentage is calculated based on the number of species per body mass group.

Table S5.1 Model selection results for the binomial hunting model. AIC was used to select the best model, which was applied to calculate the hunting pressure per species. BM: body mass, Dist: distance to hunters' access points, PopDens: human population density. Random effects were species identity, country of the study and study identity.

Variables	Df	logLik	AIC	ΔAIC
BM + Dist + Dist2 + PopDens	8	-977.53	1971.06	0
BM + Dist + Dist2 + PopDens + PopDens2	9	-977.52	1973.04	1.98
BM + Dist + Dist2	7	-980.9	1975.81	4.75
Dist + Dist2 + PopDens	7	-987.69	1989.38	18.32
Dist + Dist2 + PopDens + PopDens2	8	-987.68	1991.36	20.31
Dist + Dist2	6	-991.44	1994.88	23.83
BM + Dist + PopDens + PopDens2	8	-993.14	2002.28	31.22
BM + Dist	6	-999.64	2011.28	40.22
Dist + PopDens + PopDens2	7	-1003.2	2020.4	49.34
Dist	5	-1009.91	2029.82	58.77
BM + PopDens	6	-1086.59	2185.19	214.13
BM + PopDens + PopDens2	7	-1086.94	2187.89	216.83
PopDens	5	-1095.5	2201.01	229.95
PopDens + PopDens2	6	-1095.4	2202.8	231.75
BM	5	-1099.01	2208.02	236.96
Null model (only random effects)	4	-1107.24	2222.48	251.42

Table S5.2 Mean values and standard deviation of area loss by different pressures. Mean values and standard deviation of area loss by different pressures for different body size groups, continents, and years. Size- and continent-specific values are for the year 2015.

Grouping	Size	N	Combined	Overlap	Hunting	Land use	Croplands	Pastures	Forestry	Urban
Size	large	82	52.95 ± 24.34	16.56 ± 16.47	29.16 ± 21.31	40.70 ± 26.44	25.83 ± 21.77	16.42 ± 17.51	2.46 ± 4.02	0.32 ± 0.93
	medium	291	39.07 ± 28.90	7.20 ± 12.46	11.84 ± 16.77	34.55 ± 28.63	23.92 ± 21.76	12.75 ± 15.20	2.47 ± 3.91	0.41 ± 0.88
	small	532	37.42 ± 30.24	1.68 ± 5.18	2.46 ± 6.75	36.67 ± 30.11	20.59 ± 20.49	17.36 ± 21.43	1.99 ± 2.96	0.90 ± 4.82
	very small	979	41.86 ± 30.83	0.27 ± 1.68	0.41 ± 2.09	41.73 ± 30.85	23.33 ± 22.68	18.56 ± 21.49	2.03 ± 4.56	0.59 ± 2.41
Continent	Africa	570	46.19 ± 30.57	2.79 ± 8.93	4.02 ± 11.40	44.97 ± 30.77	26.30 ± 23.57	21.73 ± 21.39	0.84 ± 3.50	0.24 ± 0.65
	America	647	39.50 ± 31.32	1.93 ± 5.24	3.45 ± 8.81	38.03 ± 31.35	13.74 ± 15.34	24.05 ± 22.66	0.97 ± 1.48	0.98 ± 4.58
	Asia	667	37.04 ± 28.28	2.65 ± 8.54	4.52 ± 12.62	35.24 ± 27.93	28.48 ± 23.11	6.78 ± 11.52	4.30 ± 5.12	0.65 ± 2.57
Total	2015	1884	40.65 ± 30.27	2.45 ± 7.71	4.00 ± 11.07	39.14 ± 30.25	22.76 ± 21.93	17.23 ± 20.55	2.11 ± 4.05	0.64 ± 3.12
	1992	1884	38.35 ± 30.52	2.05 ± 6.64	3.59 ± 10.27	36.82 ± 30.47	21.58 ± 21.82	16.88 ± 20.60	1.25 ± 2.99	0.34 ± 1.91

Table S5.3 Cross-walk from IUCN habitat classes to ESA CII and GLOBIO classes

IUCN Code	IUCN Description	ESA Code	ESA Description	GLOBIO Code	GLOBIO Description	Natural/ Anthropogenic
1.1	Forest – Boreal	60	Tree cover, broadleaved, deciduous, closed to open (>15%)	60	Tree cover, broadleaved, deciduous, closed to open (>15%)	Natural
1.1	Forest – Boreal	61	Tree cover, broadleaved, deciduous, closed (>40%)	61	Tree cover, broadleaved, deciduous, closed (>40%)	Natural
1.1	Forest – Boreal	62	Tree cover, broadleaved, deciduous, open (15-40%)	62	Tree cover, broadleaved, deciduous, open (15-40%)	Natural
1.1	Forest – Boreal	70	Tree cover, needleleaved, evergreen, closed to open (>15%)	70	Tree cover, needle-leaved, evergreen, closed to open (>15%)	Natural
1.1	Forest – Boreal	71	Tree cover, needleleaved, evergreen, closed (>40%)	71	Tree cover, needle-leaved, evergreen, closed (>40%)	Natural
1.1	Forest – Boreal	72	Tree cover, needleleaved, evergreen, open (15-40%)	72	Tree cover, needle-leaved, evergreen, open (15-40%)	Natural
1.1	Forest – Boreal	80	Tree cover, needleleaved, deciduous, closed to open (>15%)	80	Tree cover, needle-leaved, deciduous, closed to open (>15%)	Natural
1.1	Forest – Boreal	81	Tree cover, needleleaved, deciduous, closed (>40%)	81	Tree cover, needle-leaved, deciduous, closed (>40%)	Natural
1.1	Forest – Boreal	82	Tree cover, needleleaved, deciduous, open (15-40%)	82	Tree cover, needle-leaved, deciduous, open (15-40%)	Natural
1.1	Forest – Boreal	90	Tree cover, mixed leaf type (broadleaved and needleleaved)	90	Tree cover, mixed leaf type (broadleaved and needle-leaved)	Natural
1.2	Forest – Subarctic	60	Tree cover, broadleaved, deciduous, closed to open (>15%)	60	Tree cover, broadleaved, deciduous, closed to open (>15%)	Natural
1.2	Forest – Subarctic	62	Tree cover, broadleaved, deciduous, open (15-40%)	62	Tree cover, broadleaved, deciduous, open (15-40%)	Natural
1.2	Forest – Subarctic	70	Tree cover, needleleaved, evergreen, closed to open (>15%)	70	Tree cover, needle-leaved, evergreen, closed to open (>15%)	Natural
1.2	Forest – Subarctic	72	Tree cover, needleleaved, evergreen, open (15-40%)	72	Tree cover, needle-leaved, evergreen, open (15-40%)	Natural

IUCN Code	IUCN Description	ESA Code	ESA Description	GLOBIO Code	GLOBIO Description	Natural/ Anthropogenic
1.2	Forest – Subarctic	80	Tree cover, needleleaved, deciduous, closed to open (>15%)	80	Tree cover, needle-leaved, deciduous, closed to open (>15%)	Natural
1.2	Forest - Subarctic	82	Tree cover, needleleaved, deciduous, open (15-40%)	82	Tree cover, needle-leaved, deciduous, open (15-40%)	Natural
1.3	Forest – Subantarctic	60	Tree cover, broadleaved, deciduous, closed to open (>15%)	60	Tree cover, broadleaved, deciduous, closed to open (>15%)	Natural
1.3	Forest – Subantarctic	62	Tree cover, broadleaved, deciduous, open (15-40%)	62	Tree cover, broadleaved, deciduous, open (15-40%)	Natural
1.3	Forest – Subantarctic	70	Tree cover, needleleaved, evergreen, closed to open (>15%)	70	Tree cover, needle-leaved, evergreen, closed to open (>15%)	Natural
1.3	Forest – Subantarctic	72	Tree cover, needleleaved, evergreen, open (15-40%)	72	Tree cover, needle-leaved, evergreen, open (15-40%)	Natural
1.3	Forest – Subantarctic	80	Tree cover, needleleaved, deciduous, closed to open (>15%)	80	Tree cover, needle-leaved, deciduous, closed to open (>15%)	Natural
1.3	Forest – Subantarctic	82	Tree cover, needleleaved, deciduous, open (15-40%)	82	Tree cover, needle-leaved, deciduous, open (15-40%)	Natural
1.4	Forest – Temperate	50	Tree cover, broadleaved, evergreen, closed to open (>15%)	50	Tree cover, broadleaved, evergreen, closed to open (>15%)	Natural
1.4	Forest – Temperate	60	Tree cover, broadleaved, deciduous, closed to open (>15%)	60	Tree cover, broadleaved, deciduous, closed to open (>15%)	Natural
1.4	Forest – Temperate	61	Tree cover, broadleaved, deciduous, closed (>40%)	61	Tree cover, broadleaved, deciduous, closed (>40%)	Natural
1.4	Forest – Temperate	62	Tree cover, broadleaved, deciduous, open (15-40%)	62	Tree cover, broadleaved, deciduous, open (15-40%)	Natural
1.4	Forest – Temperate	70	Tree cover, needleleaved, evergreen, closed to open (>15%)	70	Tree cover, needle-leaved, evergreen, closed to open (>15%)	Natural
1.4	Forest – Temperate	71	Tree cover, needleleaved, evergreen, closed (>40%)	71	Tree cover, needle-leaved, evergreen, closed (>40%)	Natural
1.4	Forest – Temperate	72	Tree cover, needleleaved, evergreen, open (15-40%)	72	Tree cover, needle-leaved, evergreen, open (15-40%)	Natural

IUCN Code	IUCN Description	ESA Code	ESA Description	GLOBIO Code	GLOBIO Description	Natural/ Anthropogenic
1.4	Forest – Temperate	80	Tree cover, needleleaved, deciduous, closed to open (>15%)	80	Tree cover, needle-leaved, deciduous, closed to open (>15%)	Natural
1.4	Forest – Temperate	81	Tree cover, needleleaved, deciduous, closed (>40%)	81	Tree cover, needle-leaved, deciduous, closed (>40%)	Natural
1.4	Forest – Temperate	82	Tree cover, needleleaved, deciduous, open (15-40%)	82	Tree cover, needle-leaved, deciduous, open (15-40%)	Natural
1.4	Forest – Temperate	90	Tree cover, mixed leaf type (broadleaved and needleleaved)	90	Tree cover, mixed leaf type (broadleaved and needle-leaved)	Natural
1.4	Forest – Temperate	100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	Natural
1.5	Forest - Subtropical/ Tropical Dry	50	Tree cover, broadleaved, evergreen, closed to open (>15%)	50	Tree cover, broadleaved, evergreen, closed to open (>15%)	Natural
1.5	Forest - Subtropical/ Tropical Dry	60	Tree cover, broadleaved, deciduous, closed to open (>15%)	60	Tree cover, broadleaved, deciduous, closed to open (>15%)	Natural
1.5	Forest - Subtropical/ Tropical Dry	61	Tree cover, broadleaved, deciduous, closed (>40%)	61	Tree cover, broadleaved, deciduous, closed (>40%)	Natural
1.5	Forest - Subtropical/ Tropical Dry	62	Tree cover, broadleaved, deciduous, open (15-40%)	62	Tree cover, broadleaved, deciduous, open (15-40%)	Natural
1.5	Forest - Subtropical/ Tropical Dry	70	Tree cover, needleleaved, evergreen, closed to open (>15%)	70	Tree cover, needle-leaved, evergreen, closed to open (>15%)	Natural
1.5	Forest - Subtropical/ Tropical Dry	72	Tree cover, needleleaved, evergreen, open (15-40%)	72	Tree cover, needle-leaved, evergreen, open (15-40%)	Natural
1.5	Forest - Subtropical/ Tropical Dry	80	Tree cover, needleleaved, deciduous, closed to open (>15%)	80	Tree cover, needle-leaved, deciduous, closed to open (>15%)	Natural
1.5	Forest - Subtropical/ Tropical Dry	90	Tree cover, mixed leaf type (broadleaved and needleleaved)	90	Tree cover, mixed leaf type (broadleaved and needle-leaved)	Natural
1.6	Forest - Subtropical/ Tropical Moist Lowland	50	Tree cover, broadleaved, evergreen, closed to open (>15%)	50	Tree cover, broadleaved, evergreen, closed to open (>15%)	Natural
1.6	Forest - Subtropical/ Tropical Moist Lowland	60	Tree cover, broadleaved, deciduous, closed to open (>15%)	60	Tree cover, broadleaved, deciduous, closed to open (>15%)	Natural

IUCN Code	IUCN Description	ESA Code	ESA Description	GLOBIO Code	GLOBIO Description	Natural/ Anthropogenic
1.6	Forest - Subtropical/ Tropical Moist Lowland	61	Tree cover, broadleaved, deciduous, closed (>40%)	61	Tree cover, broadleaved, deciduous, closed (>40%)	Natural
1.6	Forest - Subtropical/ Tropical Moist Lowland	62	Tree cover, broadleaved, deciduous, open (15-40%)	62	Tree cover, broadleaved, deciduous, open (15-40%)	Natural
1.6	Forest - Subtropical/ Tropical Moist Lowland	70	Tree cover, needleleaved, evergreen, closed to open (>15%)	70	Tree cover, needle-leaved, evergreen, closed to open (>15%)	Natural
1.6	Forest - Subtropical/ Tropical Moist Lowland	80	Tree cover, needleleaved, deciduous, closed to open (>15%)	80	Tree cover, needle-leaved, deciduous, closed to open (>15%)	Natural
1.6	Forest - Subtropical/ Tropical Moist Lowland	90	Tree cover, mixed leaf type (broadleaved and needleleaved)	90	Tree cover, mixed leaf type (broadleaved and needle-leaved)	Natural
1.7	Forest - Subtropical/ Tropical Mangrove Vegetation Above High Tide Level	160	Tree cover, flooded, saline water	160	Tree cover, flooded, fresh or brackish water	Natural
1.7	Forest - Subtropical/ Tropical Mangrove Vegetation Above High Tide Level	170	Tree cover, flooded, saline water	170	Tree cover, flooded, saline water	Natural
1.7	Forest - Subtropical/ Tropical Mangrove Vegetation Above High Tide Level	180	Shrub or herbaceous cover, flooded, fresh/saline/brakish water	180	Shrub or herbaceous cover, flooded, fresh/saline/brackish water	Natural
1.8	Forest - Subtropical/ Tropical Swamp	160	Tree cover, flooded, fresh or brakish water	160	Tree cover, flooded, fresh or brackish water	Natural
1.9	Forest - Subtropical/ Tropical Moist Montane	50	Tree cover, broadleaved, evergreen, closed to open (>15%)	50	Tree cover, broadleaved, evergreen, closed to open (>15%)	Natural
1.9	Forest - Subtropical/ Tropical Moist Montane	60	Tree cover, broadleaved, deciduous, closed to open (>15%)	60	Tree cover, broadleaved, deciduous, closed to open (>15%)	Natural
1.9	Forest - Subtropical/ Tropical Moist Montane	61	Tree cover, broadleaved, deciduous, closed (>40%)	61	Tree cover, broadleaved, deciduous, closed (>40%)	Natural

IUCN Code	IUCN Description	ESA Code	ESA Description	GLOBIO Code	GLOBIO Description	Natural/ Anthropogenic
1.9	Forest - Subtropical/ Tropical Moist Montane	62	Tree cover, broadleaved, deciduous, open (15-40%)	62	Tree cover, broadleaved, deciduous, open (15-40%)	Natural
1.9	Forest - Subtropical/ Tropical Moist Montane	70	Tree cover, needleleaved, evergreen, closed to open (>15%)	70	Tree cover, needle-leaved, evergreen, closed to open (>15%)	Natural
1.9	Forest - Subtropical/ Tropical Moist Montane	71	Tree cover, needleleaved, evergreen, closed (>40%)	71	Tree cover, needle-leaved, evergreen, closed (>40%)	Natural
1.9	Forest - Subtropical/ Tropical Moist Montane	90	Tree cover, mixed leaf type (broadleaved and needleleaved)	90	Tree cover, mixed leaf type (broadleaved and needle-leaved)	Natural
2.1	Savanna – Dry	110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	Natural
2.1	Savanna – Dry	120	Shrubland	120	Shrubland	Natural
2.1	Savanna – Dry	121	Evergreen shrubland	121	Evergreen shrubland	Natural
2.1	Savanna – Dry	122	Deciduous shrubland	122	Deciduous shrubland	Natural
2.1	Savanna – Dry	130	Grassland	130	Grassland	Natural
2.2	Savanna – Moist	180	Shrub or herbaceous cover, flooded, fresh/saline/brakish water	180	Shrub or herbaceous cover, flooded, fresh/saline/brackish water	Natural
2.2	Savanna – Moist	100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	Natural
2.2	Savanna – Moist	110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	Natural
3.1	Shrubland – Subarctic	120	Shrubland	120	Shrubland	Natural
3.1	Shrubland – Subarctic	121	Evergreen shrubland	121	Evergreen shrubland	Natural
3.1	Shrubland – Subarctic	122	Deciduous shrubland	122	Deciduous shrubland	Natural
3.2	Shrubland – Subantarctic	120	Shrubland	120	Shrubland	Natural
3.2	Shrubland – Subantarctic	121	Evergreen shrubland	121	Evergreen shrubland	Natural
3.2	Shrubland – Subantarctic	122	Deciduous shrubland	122	Deciduous shrubland	Natural

IUCN Code	IUCN Description	ESA Code	ESA Description	GLOBIO Code	GLOBIO Description	Natural/ Anthropogenic
3.3	Shrubland – Boreal	120	Shrubland	120	Shrubland	Natural
3.3	Shrubland – Boreal	121	Evergreen shrubland	121	Evergreen shrubland	Natural
3.3	Shrubland – Boreal	122	Deciduous shrubland	122	Deciduous shrubland	Natural
3.4	Shrubland – Temperate	100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	Natural
3.4	Shrubland – Temperate	110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	Natural
3.4	Shrubland – Temperate	120	Shrubland	120	Shrubland	Natural
3.4	Shrubland – Temperate	121	Evergreen shrubland	121	Evergreen shrubland	Natural
3.4	Shrubland – Temperate	122	Deciduous shrubland	122	Deciduous shrubland	Natural
3.5	Shrubland - Subtropical/ Tropical Dry	100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	Natural
3.5	Shrubland - Subtropical/ Tropical Dry	110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	Natural
3.5	Shrubland - Subtropical/ Tropical Dry	120	Shrubland	120	Shrubland	Natural
3.5	Shrubland - Subtropical/ Tropical Dry	121	Evergreen shrubland	121	Evergreen shrubland	Natural
3.5	Shrubland - Subtropical/ Tropical Dry	122	Deciduous shrubland	122	Deciduous shrubland	Natural
3.6	Shrubland - Subtropical/ Tropical Moist	100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	Natural
3.6	Shrubland - Subtropical/ Tropical Moist	110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	Natural
3.6	Shrubland - Subtropical/ Tropical Moist	120	Shrubland	120	Shrubland	Natural
3.6	Shrubland - Subtropical/ Tropical Moist	121	Evergreen shrubland	121	Evergreen shrubland	Natural

IUCN Code	IUCN Description	ESA Code	ESA Description	GLOBIO Code	GLOBIO Description	Natural/ Anthropogenic
3.7	Shrubland - Subtropical/ Tropical High Altitude	100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	Natural
3.7	Shrubland - Subtropical/ Tropical High Altitude	110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	Natural
3.7	Shrubland - Subtropical/ Tropical High Altitude	120	Shrubland	120	Shrubland	Natural
3.7	Shrubland - Subtropical/ Tropical High Altitude	121	Evergreen shrubland	121	Evergreen shrubland	Natural
3.7	Shrubland - Subtropical/ Tropical High Altitude	122	Deciduous shrubland	122	Deciduous shrubland	Natural
3.7	Shrubland - Subtropical/ Tropical High Altitude	150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	Natural
3.8	Shrubland - Mediterranean-type Shrubby Vegetation	120	Shrubland	120	Shrubland	Natural
3.8	Shrubland - Mediterranean-type Shrubby Vegetation	121	Evergreen shrubland	121	Evergreen shrubland	Natural
3.8	Shrubland - Mediterranean-type Shrubby Vegetation	122	Deciduous shrubland	122	Deciduous shrubland	Natural
4.1	Grassland – Tundra	130	Grassland	130	Grassland	Natural
4.1	Grassland – Tundra	140	Lichens and mosses	140	Lichens and mosses	Natural
4.1	Grassland – Tundra	150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	Natural
4.1	Grassland – Tundra	152	Sparse shrub (<15%)	152	Sparse shrub (<15%)	Natural
4.1	Grassland – Tundra	180	Shrub or herbaceous cover, flooded, fresh/saline/brakish water	180	Shrub or herbaceous cover, flooded, fresh/saline/brackish water	Natural
4.2	Grassland – Subarctic	130	Grassland	130	Grassland	Natural

IUCN Code	IUCN Description	ESA Code	ESA Description	GLOBIO Code	GLOBIO Description	Natural/ Anthropogenic
4.2	Grassland – Subarctic	140	Lichens and mosses	140	Lichens and mosses	Natural
4.2	Grassland – Subarctic	150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	Natural
4.2	Grassland – Subarctic	180	Shrub or herbaceous cover, flooded, fresh/saline/brakish water	180	Shrub or herbaceous cover, flooded, fresh/saline/brackish water	Natural
4.3	Grassland – Subantarctic	130	Grassland	130	Grassland	Natural
4.4	Grassland – Temperate	130	Grassland	130	Grassland	Natural
4.5	Grassland - Subtropical/ Tropical Dry	130	Grassland	130	Grassland	Natural
4.6	Grassland - Subtropical/ Tropical Seasonally Wet/Flooded	180	Shrub or herbaceous cover, flooded, fresh/saline/brakish water	180	Shrub or herbaceous cover, flooded, fresh/saline/brackish water	Natural
4.7	Grassland - Subtropical/ Tropical High Altitude	130	Grassland	130	Grassland	Natural
5.1	Wetlands (inland) - Permanent Rivers/ Streams/Creeks (includes waterfalls)	210	Water bodies	210	Water bodies	Natural
5.1	Wetlands (inland) - Tundra Wetlands (incl. pools and temporary waters from snowmelt)	210	Water bodies	210	Water bodies	Natural
5.11	Wetlands (inland) - Alpine Wetlands (includes temporary waters from snowmelt)	210	Water bodies	210	Water bodies	Natural
5.12	Wetlands (inland) - Geothermal Wetlands	210	Water bodies	210	Water bodies	Natural

IUCN Code	IUCN Description	ESA Code	ESA Description	GLOBIO Code	GLOBIO Description	Natural/ Anthropogenic
5.13	Wetlands (inland) - Permanent Inland Deltas	210	Water bodies	210	Water bodies	Natural
5.14	Wetlands (inland) - Permanent Saline, Brackish or Alkaline Lakes	210	Water bodies	210	Water bodies	Natural
5.15	Wetlands (inland) - Seasonal/Intermittent Saline, Brackish or Alkaline Lakes and Flats	210	Water bodies	210	Water bodies	Natural
5.16	Wetlands (inland) - Permanent Saline, Brackish or Alkaline Marshes/Pools	210	Water bodies	210	Water bodies	Natural
5.17	Wetlands (inland) - Seasonal/Intermittent Saline, Brackish or Alkaline Marshes/Pools	210	Water bodies	210	Water bodies	Natural
5.18	Wetlands (inland) - Karst and Other Subterranean Hydrological Systems (inland)	NA	NA	255	NA	Natural
5.2	Wetlands (inland) - Seasonal/Intermittent/ Irregular Rivers/ Streams/Creeks	210	Water bodies	210	Water bodies	Natural
5.3	Wetlands (inland) - Shrub Dominated Wetlands	180	Shrub or herbaceous cover, flooded, fresh/saline/brakish water	180	Shrub or herbaceous cover, flooded, fresh/saline/brackish water	Natural
5.4	Wetlands (inland) - Bogs, Marshes, Swamps, Fens, Peatlands	180	Shrub or herbaceous cover, flooded, fresh/saline/brakish water	180	Shrub or herbaceous cover, flooded, fresh/saline/brackish water	Natural

IUCN Code	IUCN Description	ESA Code	ESA Description	GLOBIO Code	GLOBIO Description	Natural/ Anthropogenic
5.5	Wetlands (inland) - Permanent Freshwater Lakes (over 8ha)	210	Water bodies	210	Water bodies	Natural
5.6	Wetlands (inland) - Seasonal/Intermittent Freshwater Lakes (over 8ha)	210	Water bodies	210	Water bodies	Natural
5.7	Wetlands (inland) - Permanent Freshwater Marshes/Pools (under 8ha)	210	Water bodies	210	Water bodies	Natural
5.8	Wetlands (inland) - Seasonal/Intermittent Freshwater Marshes/ Pools (under 8ha)	210	Water bodies	210	Water bodies	Natural
5.9	Wetlands (inland) - Freshwater Springs and Oases	210	Water bodies	210	Water bodies	Natural
6	Rocky areas (eg. inland cliffs, mountain peaks)	200	Bare areas	200	Bare areas	Natural
6	Rocky areas (eg. inland cliffs, mountain peaks)	201	Consolidated bare areas	201	Consolidated bare areas	Natural
8.1	Desert – Hot	200	Bare areas	200	Bare areas	Natural
8.1	Desert – Hot	201	Consolidated bare areas	201	Consolidated bare areas	Natural
8.1	Desert – Hot	202	Unconsolidated bare areas	202	Unconsolidated bare areas	Natural
8.1	Desert – Hot	150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	Natural
8.1	Desert – Hot	151	Sparse tree (<15%)	151	Sparse tree (<15%)	Natural
8.1	Desert – Hot	152	Sparse shrub (<15%)	152	Sparse shrub (<15%)	Natural

IUCN Code	IUCN Description	ESA Code	ESA Description	GLOBIO Code	GLOBIO Description	Natural/ Anthropogenic
8.1	Desert – Hot	153	Sparse vegetation herbaceous cover (<15%)	153	Sparse herbaceous cover (<15%)	Natural
8.2	Desert – Temperate	200	Bare areas	200	Bare areas	Natural
8.2	Desert – Temperate	201	Consolidated bare areas	201	Consolidated bare areas	Natural
8.2	Desert – Temperate	202	Unconsolidated bare areas	202	Unconsolidated bare areas	Natural
8.2	Desert – Temperate	150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	Natural
8.2	Desert – Temperate	151	Sparse tree (<15%)	151	Sparse tree (<15%)	Natural
8.2	Desert – Temperate	152	Sparse shrub (<15%)	152	Sparse shrub (<15%)	Natural
8.2	Desert – Temperate	153	Sparse vegetation herbaceous cover (<15%)	153	Sparse herbaceous cover (<15%)	Natural
8.3	Desert – Cold	200	Bare areas	200	Bare areas	Natural
8.3	Desert – Cold	201	Consolidated bare areas	201	Consolidated bare areas	Natural
8.3	Desert – Cold	202	Unconsolidated bare areas	202	Unconsolidated bare areas	Natural
8.3	Desert – Cold	150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	Natural
8.3	Desert – Cold	151	Sparse tree (<15%)	151	Sparse tree (<15%)	Natural
8.3	Desert – Cold	152	Sparse shrub (<15%)	152	Sparse shrub (<15%)	Natural
8.3	Desert – Cold	153	Sparse vegetation herbaceous cover (<15%)	153	Sparse herbaceous cover (<15%)	Natural
8.3	Desert – Cold	140	Lichens and mosses	140	Lichens and mosses	Natural
14.1	Artificial/Terrestrial - Arable Land	10	Cropland, rainfed	10	Cropland, rainfed	Anthropogenic
14.1	Artificial/Terrestrial - Arable Land	11	Cropland, rainfed, Herbaceous cover	11	Cropland, rainfed, Herbaceous cover	Anthropogenic
14.1	Artificial/Terrestrial - Arable Land	12	Cropland, rainfed, Tree or shrub cover	12	Cropland, rainfed, Tree or shrub cover	Anthropogenic

IUCN Code	IUCN Description	ESA Code	ESA Description	GLOBIO Code	GLOBIO Description	Natural/ Anthropogenic
14.1	Artificial/Terrestrial - Arable Land	20	Cropland, irrigated or post-flooding	20	Cropland, irrigated or post-flooding	Anthropogenic
14.1	Artificial/Terrestrial - Arable Land	20	Cropland, irrigated or post-flooding	2	Cropland	Anthropogenic
14.1	Artificial/Terrestrial - Arable Land	20	Cropland, irrigated or post-flooding	231	Medium intensity cropland	Anthropogenic
14.1	Artificial/Terrestrial - Arable Land	20	Cropland, irrigated or post-flooding	232	High intensity cropland	Anthropogenic
14.2	Artificial/Terrestrial – Pastureland	130	Grassland	3	Pasture	Anthropogenic
14.2	Artificial/Terrestrial – Pastureland	130	Grassland	4	Rangeland	Anthropogenic
14.3	Artificial/Terrestrial – Plantations	12	Cropland, rainfed, Tree or shrub cover	5	Forestry	Anthropogenic
14.4	Artificial/Terrestrial - Rural Gardens	30	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)	30	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)	Anthropogenic
14.4	Artificial/Terrestrial - Rural Gardens	40	Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%)	40	Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%)	Anthropogenic
14.5	Artificial/Terrestrial - Urban Areas	190	Urban areas	190	Urban areas	Anthropogenic
14.6	Artificial/Terrestrial - Subtropical/Tropical Heavily Degraded Former Forest	30	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)	5	Forestry	Anthropogenic
14.6	Artificial/Terrestrial - Subtropical/Tropical Heavily Degraded Former Forest	30	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)	6	Secondary vegetation	Anthropogenic

B

LITERATURE CITED

Abernethy, K.A., Coad, L., Taylor, G., Lee, M.E. & Maisels, F. (2013). Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. *Philos. Trans. R. Soc. B Biol. Sci.*, 368, 20120303–20120303.

Ackerman, D.E., Chen, X. & Millet, D.B. (2018). Global nitrogen deposition (2°× 2.5° grid resolution) simulated with GEOS-Chem for 1984-1986, 1994-1996, 2004-2006, and 2014-2016.

Alamgir, M., Campbell, M.J., Sloan, S., Suhardiman, A., Supriatna, J. & Laurance, W.F. (2019). High-risk infrastructure projects pose imminent threats to forests in Indonesian Borneo. *Sci. Rep.*, 9, 140.

Alerstam, T., Rosén, M., Bäckman, J., Ericson, P.G.P. & Hellgren, O. (2007). Flight Speeds among Bird Species: Allometric and Phylogenetic Effects. *PLOS Biol.*, 5, e197.

Alfsnes, K., Leinaas, H.P. & Hessen, D.O. (2017). Genome size in arthropods; different roles of phylogeny, habitat and life history in insects and crustaceans. *Ecol. Evol.*, 7, 5939–5947.

Alkemade, R., van Bussel, L.G.J., Rodríguez, S.L. & Schipper, A.M. (2022). Global biodiversity assessments need to consider mixed multifunctional land-use systems. *Curr. Opin. Environ. Sustain.*, 56, 101174.

Alkemade, R., van Oorschot, M., Miles, L., Nellemann, C., Bakkenes, M. & ten Brink, B. (2009). GLOBIO3: A Framework to Investigate Options for Reducing Global Terrestrial Biodiversity Loss. *Ecosystems*, 12, 374–390.

Allan, J.R., Watson, J.E.M., Di Marco, M., O'Bryan, C.J., Possingham, H.P., Atkinson, S.C., *et al.* (2019). Hotspots of human impact on threatened terrestrial vertebrates. *PLOS Biol.*, 17, e3000158.

Allouche, O., Tsoar, A. & Kadmon, R. (2006). Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.*, 43, 1223–1232.

Almeida-Rocha, J.M. de, Peres, C.A. & Oliveira, L.C. (2017). Primate responses to anthropogenic habitat disturbance: A pantropical meta-analysis. *Biol. Conserv.*, 215, 30–38.

Almond, R.E.A., Grooten, M. & Peterson, T. (2020). *Living Planet Report 2020-Bending the curve of biodiversity loss*. World Wildlife Fund.

Altenburger, R., Backhaus, T., Boedeker, W., Faust, M. & Scholze, M. (2013). Simplifying complexity: Mixture toxicity assessment in the last 20 years. *Environ. Toxicol. Chem.*, 32, 1685–1687.

Amano, T., Berdejo-Espinola, V., Christie, A.P., Willott, K., Akasaka, M., Báldi, A., *et al.* (2021). Tapping into non-English-language science for the conservation of global biodiversity. *PLOS Biol.*, 19, e3001296.

AmphibiaWeb. (2016). Information on amphibian biology and conservation. *Berkeley, Calif. Amphib.*

Andersen, G.E., Johnson, C.N., Barmuta, L.A. & Jones, M.E. (2017). Use of anthropogenic linear features by two medium-sized carnivores in reserved and agricultural landscapes. *Sci. Rep.*, 7, 11624.

Andrasi, B., Jaeger, J.A.G., Heinicke, S., Metcalfe, K. & Hockings, K.J. (2021). Quantifying the road-effect zone for a critically endangered primate. *Conserv. Lett.*, 14, e12839.

Ascensão, F., Clevenger, A.P., Grilo, C., Filipe, J. & Santos-Reis, M. (2012). Highway verges as habitat providers for small mammals in agrosilvopastoral environments. *Biodivers. Conserv.*, 21, 3681–3697.

Ascensão, F., D'Amico, M. & Barrientos, R. (2022). No planet for Apes? Assessing global priority areas and species affected by linear infrastructures. *Int. J. Primatol.*, 43, 57–73.

Ascensão, F., Mata, C., Malo, J.E., Ruiz-Capillas, P., Silva, C., Silva, A.P., *et al.* (2016). Disentangle the Causes of the Road Barrier Effect in Small Mammals through Genetic Patterns. *PLoS One*, 11, e0151500.

de Baan, L., Alkemade, R. & Koellner, T. (2013). Land use impacts on biodiversity in LCA: a global approach. *Int. J. Life Cycle Assess.*, 18, 1216–1230.

Baisero, D., Visconti, P., Pacifici, M., Cimatti, M. & Rondinini, C. (2020). Projected Global Loss of Mammal Habitat Due to Land-Use and Climate Change. *One Earth*, 2, 578–585.

Barona, E., Ramankutty, N., Hyman, G. & Coomes, O.T. (2010). The role of pasture and soybean in deforestation of the Brazilian Amazon. *Environ. Res. Lett.*, 5, 024002.

Barrientos, R., Ascensão, F., Beja, P., Pereira, H.M. & Borda-de-Água, L. (2019). Railway ecology vs. road ecology: similarities and differences. *Eur. J. Wildl. Res.*, 65, 12.

Barrientos, R., Ascensão, F., D'Amico, M., Grilo, C. & Pereira, H.M. (2021). The lost road: Do transportation networks imperil wildlife population persistence? *Perspect. Ecol. Conserv.*, 19, 411–416.

Baste, I.A., Watson, R.T., Brauman, K.I., Samper, C. & Walzer, C. (2021). Making peace with nature: a scientific blueprint to tackle the climate, biodiversity and pollution emergencies.

Bauters, M., Drake, T.W., Verbeeck, H., Bodé, S., Hervé-Fernández, P., Zito, P., *et al.* (2018). High fire-derived nitrogen deposition on central African forests. *Proc. Natl. Acad. Sci.*, 115, 549–554.

Beebee, T.J.C. (2013). Effects of Road Mortality and Mitigation Measures on Amphibian Populations. *Conserv. Biol.*, 27, 657–668.

Bellard, C., Marino, C. & Courchamp, F. (2022). Ranking threats to biodiversity and why it doesn't matter. *Nat. Commun.*, 13, 2616.

Benítez-López, A., Alkemade, R., Schipper, A.M., Ingram, D.J., Verweij, P.A., Eikelboom, J.A.J., *et al.* (2017). The impact of hunting on tropical mammal and bird populations. *Science*, 356, 180–183.

Benítez-López, A., Alkemade, R. & Verweij, P.A. (2010). The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. *Biol. Conserv.*, 143, 1307–1316.

Benítez-López, A., Santini, L., Schipper, A.M., Busana, M. & Huijbregts, M.A.J. (2019). Intact but empty forests? Patterns of hunting-induced mammal defaunation in the tropics. *PLOS Biol.*, 17, e3000247.

Van den Berg, L.J.L., Vergeer, P., Rich, T.I.M.C.G., Smart, S.M., Guest, D.A.N. & Ashmore, M.R. (2011). Direct and indirect effects of nitrogen deposition on species composition change in calcareous grasslands. *Glob. Chang. Biol.*, 17, 1871–1883.

Biasotto, L.D. & Kindel, A. (2018). Power lines and impacts on biodiversity: A systematic review. *Environ. Impact Assess. Rev.*, 71, 110–119.

Bivand, R., Keitt, T. & Rowlingson, B. (2019). rgdal: bindings for the "geospatial" data abstraction library.

Blankinship, J.C., Niklaus, P.A. & Hungate, B.A. (2011). A meta-analysis of responses of soil biota to global change. *Oecologia*, 165, 553–565.

Blomberg, S.P., Garland JR., T. & Ives, A.R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, 57, 717–745.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., *et al.* (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecol. Appl.*, 20, 30–59.

Bobo, K.S., Aghomo, F.F.M. & Ntumwel, B.C. (2015). Wildlife use and the role of taboos in the conservation of wildlife around the Nkwende Hills Forest Reserve; South-west Cameroon. *J. Ethnobiol. Ethnomed.*, 11, 2.

Böhning-Gaese, K. & Oberrath, R. (1999). Phylogenetic effects on morphological, life-history, behavioural and ecological traits of birds. *Evol. Ecol. Res.*, 1, 347–364.

Boncoraglio, G. & Saino, N. (2007). Habitat Structure and the Evolution of Bird Song: A Meta-Analysis of the Evidence for the Acoustic Adaptation Hypothesis. *Funct. Ecol.*, 21, 134–142.

Bonebrake, T.C., Guo, F., Dingle, C., Baker, D.M., Kitching, R.L. & Ashton, L.A. (2019). Integrating proximal and horizon threats to biodiversity for conservation. *Trends Ecol. Evol.*, 34, 781–788.

Bongers, T. (1999). The Maturity Index, the evolution of nematode life history traits, adaptive radiation and cp-scaling. *Plant Soil*, 212, 13–22.

Bongers, T. & Bongers, M. (1998). Functional diversity of nematodes. *Appl. Soil Ecol.*, 10, 239–251.

Borer, E.T. & Stevens, C.J. (2022). Nitrogen deposition and climate: an integrated synthesis. *Trends Ecol. Evol.*

Bowler, D.E., Bjorkman, A.D., Dornelas, M., Myers-Smith, I.H., Navarro, L.M., Niamir, A., *et al.* (2020). Mapping human pressures on biodiversity across the planet uncovers anthropogenic threat complexes. *People Nat.* , 2, 380–394.

Bracken, M.B. (1992). Statistical methods for analysis of effects of treatment in overviews of randomized trials. *Eff. care newborn infant*, 13–20.

Bracken, M.B. & Sinclair, J.C. (1992). *Effective care of the newborn infant.* Oxford: Oxford University Press.

Brehme, C.S., Tracey, J.A., Mcclenaghan, L.R. & Fisher, R.N. (2013). Permeability of Roads to Movement of Scrubland Lizards and Small Mammals. *Conserv. Biol.*, 27, 710–720.

Brodie, J.F., Giordano, A.J., Zipkin, E.F., Bernard, H., Mohd-Azlan, J. & Ambu, L. (2015). Correlation and persistence of hunting and logging impacts on tropical rainforest mammals. *Conserv. Biol.*, 29, 110–121.

Brook, B., Sodhi, N. & Bradshaw, C. (2008). Synergies among extinction drivers under global change. *Trends Ecol. Evol.*, 23, 453–460.

Brooks, T.M., Pimm, S.L., Akçakaya, H.R., Buchanan, G.M., Butchart, S.H.M., Foden, W., *et al.* (2019). Measuring Terrestrial Area of Habitat (AOH) and Its Utility for the IUCN Red List. *Trends Ecol. Evol.*, 34, 977–986.

Capinera, J.L. (2008). *Encyclopedia of entomology*. Springer Science & Business Media.

Carbone, C., Teacher, A. & Rowcliffe, J.M. (2007). The Costs of Carnivory. *PLOS Biol.*, 5, e22.

Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., *et al.* (2005). Multiple Causes of High Extinction Risk in Large Mammal Species. *Science*, 309, 1239–1241.

Carter, N., Killion, A., Easter, T., Brandt, J. & Ford, A. (2022). Road development in Asia: Assessing the range-wide risks to tigers. *Sci. Adv.*, 6, eaaz9619.

Catchpole, C.K. & Slater, P.J.B. (2003). *Bird song: biological themes and variations*. Cambridge university press.

Catford, J.A., Wilson, J.R.U., Pyšek, P., Hulme, P.E. & Duncan, R.P. (2022). Addressing context dependence in ecology. *Trends Ecol. Evol.*, 37, 158–170.

CBD. (2010). *Decision adopted by the Conference of the Parties to the Convention on Biological Diversity at its Tenth Meeting*.

CBD. (2019). *Post-2020 Global biodiversity framework: Discussion paper*.

Ceia-Hasse, A., Borda-de-Água, L., Grilo, C. & Pereira, H.M. (2017). Global exposure of carnivores to roads. *Glob. Ecol. Biogeogr.*, 26, 592–600.

Chamberlain, S.A., Hovick, S.M., Dibble, C.J., Rasmussen, N.L., Van Allen, B.G., Maitner, B.S., *et al.* (2012). Does phylogeny matter? Assessing the impact of phylogenetic information in ecological meta-analysis. *Ecol. Lett.*, 15, 627–636.

Chaudhary, A. & Brooks, T.M. (2017). National Consumption and Global Trade Impacts on Biodiversity. *World Dev.*

Chen, H.L. & Koprowski, J.L. (2016). Differential effects of roads and traffic on space use and movements of native forest-dependent and introduced edge-tolerant species. *PLoS One*, 11.

Chen, Y., Randerson, J.T., Van Der Werf, G.R., Morton, D.C., Mu, M. & Kasibhatla, P.S. (2010). Nitrogen deposition in tropical forests from savanna and deforestation fires. *Glob. Chang. Biol.*, 16, 2024–2038.

Chen, Y. & Ruberson, J.R. (2008). Impact of variable nitrogen fertilisation on arthropods in cotton in Georgia, USA. *Agric. Ecosyst. Environ.*, 126, 281–288.

Christie, A.P., Amano, T., Martin, P.A., Shackelford, G.E., Simmons, B.I. & Sutherland, W.J. (2019). Simple study designs in ecology produce inaccurate estimates of biodiversity responses. *J. Appl. Ecol.*, 56, 2742–2754.

CIESIN. (2017). *Center for International Earth Science Information Network, Ciesin Columbia University. Gridded Population of the World, Version 4 (GPWv4): Population Density, Revision 10*. NASA Socioeconomic Data and Applications Center (SEDAC).

CIESIN & CIAT. (2005). *Center for International Earth Science Information Network - CIESIN - Columbia University Centro Internacional de Agricultura Tropical - CIAT. Gridded Population of the World, Version 3 (GPWv3): Population Density Grid*. NASA Socioeconomic Data and Applications Center (SEDAC), Palisades, NY.

Cinar, O., Nakagawa, S. & Viechtbauer, W. (2022). Phylogenetic multilevel meta-analysis: A simulation study on the importance of modelling the phylogeny. *Methods Ecol. Evol.*, 13, 383–395.

Cinar, O., Umbanhowar, J., Hoeksema, J.D. & Viechtbauer, W. (2021). Using information-theoretic approaches for model selection in meta-analysis. *Res. Synth. Methods*, 12, 537–556.

Clavel, J., Julliard, R. & Devictor, V. (2011). Worldwide decline of specialist species: toward a global functional homogenization? *Front. Ecol. Environ.*, 9, 222–228.

Cooke, S.C., Balmford, A., Donald, P.F., Newson, S.E. & Johnston, A. (2020). Roads as a contributor to landscape-scale variation in bird communities. *Nat. Commun.*, 11, 3125.

Corlett, R.T. (2015). The Anthropocene concept in ecology and conservation. *Trends Ecol. Evol.*, 30, 36–41.

Côté, I.M., Darling, E.S. & Brown, C.J. (2016). Interactions among ecosystem stressors and their importance in conservation. *Proc. R. Soc. B Biol. Sci.*, 283, 20152592.

Crutzen, P.J. (2006). The "anthropocene." In: *Earth system science in the anthropocene*. Springer, pp. 13–18.

Cui, S., Han, X., Xiao, Y., Wu, P., Zhang, S., Abid, A., *et al.* (2022). Increase in rainfall intensity promotes soil nematode diversity but offset by nitrogen addition in a temperate grassland. *Sci. Total Environ.*, 825, 154039.

D'Amico, M., Catry, I., Martins, R.C., Ascensão, F., Barrientos, R. & Moreira, F. (2018). Bird on the wire: Landscape planning considering costs and benefits for bird populations coexisting with power lines. *Ambio*, 47, 650–656.

Damuth, J. (1981). Population density and body size in mammals. *Nature*, 290, 699–700.

Darling, E.S. & Côté, I.M. (2008). Quantifying the evidence for ecological synergies. *Ecol Lett*, 11, 1278–1286.

David, T.I., Storkey, J. & Stevens, C.J. (2019). Understanding how changing soil nitrogen affects plant–pollinator interactions. *Arthropod. Plant. Interact.*, 13, 671–684.

Deng, O., Zhang, S., Deng, L., Lan, T., Luo, L., Gao, X., *et al.* (2019). Atmospheric dry nitrogen deposition and its relationship with local land use in a high nitrogen deposition region. *Atmos. Environ.*, 203, 114–120.

Denno, R.F. & Fagan, W.F. (2003). Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology*, 84, 2522–2531.

Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T.A. & Ewers, R.M. (2007). Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol. Evol.*, 22, 489–496.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., *et al.* (2017). An ecoregion-based approach to protecting half the terrestrial realm. *Bioscience*, 67, 534–545.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345, 401–406.

Dise, N.B., Ashmore, M., Belyazid, S., Bleeker, A., Bobbink, R., de Vries, W., *et al.* (2011). Nitrogen as a threat to European terrestrial biodiversity. In: *The European Nitrogen Assessment: Sources, Effects and Policy Perspectives* (eds. Bleeker, A., Grizzetti, B., Howard, C.M., Billen, G., van Grinsven, H., Erisman, J.W., et al.). Cambridge University Press, Cambridge, pp. 463–494.

Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., *et al.* (2014). Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. *Science*, 344, 296 LP – 299.

Duffett, D., D'Amico, M., Mulero-Pázmány, M. & González-Suárez, M. (2020). Species' traits as predictors of avoidance towards roads and traffic. *Ecol. Indic.*, 115, 106402.

Dulac, J. (2013). Global land transport infrastructure requirements. *Paris Int. Energy Agency*, 20, 2014.

Egger, M., Smith, G.D., Schneider, M. & Minder, C. (1997). Bias in meta-analysis detected by a simple, graphical test. *BMJ*, 315, 629 LP – 634.

Eigenbrod, F., Hecnar, S.J. & Fahrig, L. (2009). Quantifying the Road-Effect Zone. *Ecol. Soc.*, 14.

Elith, J., Kearney, M. & Phillips, S. (2010). The art of modelling range-shifting species. *Methods Ecol. Evol.*, 1, 330–342.

Elser, J.J., Acharya, K., Kyle, M., Cotner, J., Makino, W., Markow, T., *et al.* (2003). Growth rate–stoichiometry couplings in diverse biota. *Ecol. Lett.*, 6, 936–943.

Elshout, P.M.F., van Zelm, R., Karuppiah, R., Laurenzi, I.J. & Huijbregts, M.A.J. (2014). A spatially explicit data-driven approach to assess the effect of agricultural land occupation on species groups. *Int. J. Life Cycle Assess.*, 19, 758–769.

ESA. (2017). *Land Cover CCI Product User Guide Version 2.0*.

Fa, J.E. & Brown, D. (2009). Impacts of hunting on mammals in African tropical moist forests: a review and synthesis. *Mamm. Rev.*, 39, 231–264.

Fagan, W.F., Siemann, E., Mitter, C., Denno, R.F., Huberty, A.F., Woods, H.A., *et al.* (2002). Nitrogen in Insects: Implications for Trophic Complexity and Species Diversification. *Am. Nat.*, 160, 784–802.

FAO. (2016). *FAOSTAT Land domain*. Food and Agriculture Organization of the Nations.

FAO. (2019). *World fertilizer trends and outlook to 2022*. Rome.

Feldman, A., Sabath, N., Pyron, R.A., Mayrose, I. & Meiri, S. (2016). Body sizes and diversification rates of lizards, snakes, amphisbaenians and the tuatara. *Glob. Ecol. Biogeogr.*, 25, 187–197.

Fenchel, T. (1974). Intrinsic rate of natural increase: The relationship with body size. *Oecologia*, 14, 317–326.

Fernández-Castilla, B., Declercq, L., Jamshidi, L., Beretvas, S.N., Onghena, P. & Van den Noortgate, W. (2021). Detecting selection bias in meta-analyses with multiple outcomes: a simulation study. *J. Exp. Educ.*, 89, 125–144.

Fleishman, E., Noss, R.F. & Noon, B.R. (2006). Utility and limitations of species richness metrics for conservation planning. *Ecol. Indic.*, 6, 543–553.

Forman, R.T.T. & Alexander, L.E. (1998). Roads and Their Major Ecological Effects. *Annu. Rev. Ecol. Syst.*, 29, 207-C2.

Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., *et al.* (2003). *Road ecology: science and solutions*. Island press.

Fowler, D., Coyle, M., Skiba, U., Sutton, M.A., Cape, J.N., Reis, S., *et al.* (2013). The global nitrogen cycle in the twenty-first century. *Philos. Trans. R. Soc. B Biol. Sci.*, 368.

Francis, C.D. (2015). Vocal traits and diet explain avian sensitivities to anthropogenic noise. *Glob. Chang. Biol.*, 21, 1809–1820.

Francis, C.D., Ortega, C.P. & Cruz, A. (2011). Noise Pollution Filters Bird Communities Based on Vocal Frequency. *PLoS One*, 6, e27052.

Franklin, J., Serra-Diaz, J.M., Syphard, A.D. & Regan, H.M. (2016). Global change and terrestrial plant community dynamics. *Proc. Natl. Acad. Sci.*, 113, 3725 LP – 3734.

Frid, A. & Dill, L. (2002). Human-caused Disturbance Stimuli as a Form of Predation Risk. *Conserv. Ecol.*, 6.

Fristoe, T.S., Iwaniuk, A.N. & Botero, C.A. (2017). Big brains stabilize populations and facilitate colonization of variable habitats in birds. *Nat. Ecol. Evol.*, 1, 1706–1715.

Fuso Nerini, F., Tomei, J., To, L.S., Bisaga, I., Parikh, P., Black, M., *et al.* (2018). Mapping synergies and trade-offs between energy and the Sustainable Development Goals. *Nat. Energy*, 3, 10–15.

Geldmann, J., Manica, A., Burgess, N.D., Coad, L. & Balmford, A. (2019). A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures. *Proc. Natl. Acad. Sci.*, 201908221.

Gerstner, K., Dormann, C.F., Stein, A., Manceur, A.M. & Seppelt, R. (2014a). Effects of land use on plant diversity – A global meta-analysis. *J. Appl. Ecol.*, 51, 1690–1700.

Gerstner, K., Dormann, C.F., Václavík, T., Kreft, H., Seppelt, R. & Pearman, P. (2014b). Accounting for geographical variation in species–area relationships improves the prediction of plant species richness at the global scale. *J. Biogeogr.*, 41, 261–273.

Gerstner, K., Levers, C., Kuemmerle, T., Václavík, T., Pereira, H.M. & Seppelt, R. (2017). Assessing land-use effects on European plant diversity using a biome-specific countryside species–area model. *Divers. Distrib.*, 23, 1193–1203.

González-Suárez, M., Zanchetta Ferreira, F. & Grilo, C. (2018). Spatial and species-level predictions of road mortality risk using trait data. *Glob. Ecol. Biogeogr.*, 27, 1093–1105.

Grade, A.M. & Sieving, K.E. (2016). When the birds go unheard: highway noise disrupts information transfer between bird species. *Biol. Lett.*, 12, 20160113.

Grafen, A. & Hamilton, W.D. (1989). The phylogenetic regression. *Philos. Trans. R. Soc. London. B, Biol. Sci.*, 326, 119–157.

Greenberg, J.A. & Mattiuzzi, M. (2020). gdalUtils: wrappers for the geospatial data abstraction library (GDAL) utilities.

Griffith, K.A. & Grinath, J.B. (2018). Interactive effects of precipitation and nitrogen enrichment on multi-trophic dynamics in plant-arthropod communities. *PLoS One*, 13, e0201219.

Grilo, C., Borda-de-Água, L., Beja, P., Goolsby, E., Soanes, K., le Roux, A., *et al.* (2021). Conservation threats from roadkill in the global road network. *Glob. Ecol. Biogeogr.*, 30, 2200–2210.

Grilo, C., Koroleva, E., Andrášik, R., Bíl, M. & González-Suárez, M. (2020). Roadkill risk and population vulnerability in European birds and mammals. *Front. Ecol. Environ.*, 18, 323–328.

Guo-liang, X., Jiang-ming, M., Sheng-lei, F., Gundersen, P., Guo-yi, Z. & Jing-Hua, X. (2007). Response of soil fauna to simulated nitrogen deposition: A nursery experiment in subtropical China. *J. Environ. Sci.*, 19, 603–609.

Gurevitch, J., Koricheva, J., Nakagawa, S. & Stewart, G. (2018). Meta-analysis and the science of research synthesis. *Nature*, 555, 175–182.

Haddad, N.M., Haarstad, J. & Tilman, D. (2000). The effects of long-term nitrogen loading on grassland insect communities. *Oecologia*, 124, 73–84.

Hamer, A.J., Barta, B., Bohus, A., Gál, B. & Schmera, D. (2021). Roads reduce amphibian abundance in ponds across a fragmented landscape. *Glob. Ecol. Conserv.*, 28, e01663.

Hanski, I. & Ovaskainen, O. (2002). Extinction debt at extinction threshold. *Conserv. Biol.*, 16, 666–673.

Hanski, I., Zurita, G.A., Bellocq, M.I. & Rybicki, J. (2013). Species-fragmented area relationship. *Proc Natl Acad Sci U S A*, 110, 12715–12720.

Harris, I., Osborn, T.J., Jones, P. & Lister, D. (2020). Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Sci. Data*, 7, 109.

Hedges, L. V, Gurevitch, J. & Curtis, P.S. (1999). The meta-analysis of response rations in experimental ecology. *Ecology*, 80, 1150–1156.

Hendriks, A.J. (2007). The power of size: A meta-analysis reveals consistency of allometric regressions. *Ecol. Modell.*, 205, 196–208.

Hengl, T., Mendes de Jesus, J., Heuvelink, G.B.M., Ruiperez Gonzalez, M., Kilibarda, M., Blagotić, A., *et al.* (2017). SoilGrids250m: Global gridded soil information based on machine learning. *PLoS One*, 12, e0169748.

Hengl, T., Walsh, M.G., Sanderman, J., Wheeler, I., Harrison, S.P. & Prentice, I.C. (2018). Global mapping of potential natural vegetation: an assessment of machine learning algorithms for estimating land potential. *PeerJ*, 6, e5457.

Hijmans, R.J. (2020). raster: Geographic data analysis and modeling.

Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2017). dismo: species distribution modeling.

Hilbers, J.P., Schipper, A.M., Hendriks, A.J., Verones, F., Pereira, H.M. & Huijbregts, M.A.J. (2016). An allometric approach to quantify the extinction vulnerability of birds and mammals. *Ecology*, 97, 615–626.

Hiltpold, I., Johnson, S.N., Bayon, R.-C. Le & Nielsen, U.N. (2017). Climate Change in the Underworld: Impacts for Soil-Dwelling Invertebrates. *Glob. Clim. Chang. Terr. Invertebr.*, Wiley Online Books.

Hinchliff, C.E., Smith, S.A., Allman, J.F., Burleigh, J.G., Chaudhary, R., Coghill, L.M., *et al.* (2015). Synthesis of phylogeny and taxonomy into a comprehensive tree of life. *Proc. Natl. Acad. Sci.*, 112, 12764 LP – 12769.

Holderegger, R. & Di Giulio, M. (2010). The genetic effects of roads: A review of empirical evidence. *Basic Appl. Ecol.*, 11, 522–531.

Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M. & Ladle, R.J. (2015). Seven shortfalls that beset large-scale knowledge of biodiversity. *Annu. Rev. Ecol. Evol. Syst.*, 46, 523–549.

Hoskins, A.J., Harwood, T.D., Ware, C., Williams, K.J., Perry, J.J., Ota, N., *et al.* (2020). BILBI: Supporting global biodiversity assessment through high-resolution macroecological modelling. *Environ. Model. Softw.*, 132, 104806.

Hudson, L.N., Newbold, T., Contu, S., Hill, S.L.L., Lysenko, I., De Palma, A., *et al.* (2014). The PREDICTS database: a global database of how local terrestrial biodiversity responds to human impacts. *Ecol Evol*, 4, 4701–4735.

Hughes, A.C., Orr, M.C., Ma, K., Costello, M.J., Waller, J., Provoost, P., *et al.* (2021). Sampling biases shape our view of the natural world. *Ecography*, 44, 1259–1269.

Hurtt, G.C., Chini, L., Sahajpal, R., Frolking, S., Bodirsky, B.L., Calvin, K., *et al.* (2020). Harmonization of global land-use change and management for the period 850--2100 (LUH2) for CMIP6. *Geosci. Model Dev. Discuss.*, 2020, 1–65.

Ibisch, P.L., Hoffmann, M.T., Kreft, S., Pe'er, G., Kati, V., Biber-Freudenberger, L., *et al.* (2016). A global map of roadless areas and their conservation status. *Science*, 354, 1423–1427.

IPBES. (2016). *The methodological assessment report on scenarios and models of biodiversity and ecosystem services.* Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany.

IPBES. (2019). Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.

Isbell, F., Reich, P.B., Tilman, D., Hobbie, S.E., Polasky, S. & Binder, S. (2013). Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. *Proc. Natl. Acad. Sci.*, 110, 11911 LP – 11916.

IUCN. (2015). International union for conservation of nature. Habitat Classification Scheme Version, 3, 1.

IUCN. (2017). *The IUCN Red List of Threatened Species. Version 2017-3*.

IUCN. (2022). *The IUCN Red List of Threatened Species. Version 2022-1.*

Jänsch, S., Amorim, M.J. & Römbke, J. (2005). Identification of the ecological requirements of important terrestrial ecotoxicological test species. *Environ. Rev.*, 13, 51–83.

Ke, X., Yang, Y., Yin, W. & Xue, L. (2004). Effects of low pH environment on the collembolan Onychiurus yaodai. *Pedobiologia*, 48, 545–550.

Keinath, D.A., Doak, D.F., Hodges, K.E., Prugh, L.R., Fagan, W., Sekercioglu, C.H., *et al.* (2017). A global analysis of traits predicting species sensitivity to habitat fragmentation. *Glob. Ecol. Biogeogr.*, 26, 115–127.

Kern, E.M.A., Kim, T. & Park, J.-K. (2020). The Mitochondrial Genome in Nematode Phylogenetics. *Front. Ecol. Evol.*, 8.

Khamcha, D., Corlett, R.T., Powell, L.A., Savini, T., Lynam, A.J. & Gale, G.A. (2018). Road induced edge effects on a forest bird community in tropical Asia. *Avian Res.*, 9, 20.

Kim, H., Rosa, I.M.D., Alkemade, R., Leadley, P., Hurtt, G., Popp, A., *et al.* (2018). A protocol for an intercomparison of biodiversity and ecosystem services models using harmonized land-use and climate scenarios. *Geosci. Model Dev.*, 11, 4537–4562.

Kleijn, D., Kohler, F., Báldi, A., Batáry, P., Concepción, E.D., Clough, Y., *et al.* (2009). On the relationship between farmland biodiversity and land-use intensity in Europe. *Proc. R. Soc. B Biol. Sci.*, 276, 903–909.

Konno, K., Akasaka, M., Koshida, C., Katayama, N., Osada, N., Spake, R., *et al.* (2020). Ignoring non-English-language studies may bias ecological meta-analyses. *Ecol. Evol.*, 10, 6373–6384.

Konstantopoulos, S. (2011). Fixed effects and variance components estimation in three-level meta-analysis. *Res. Synth. Methods*, 2, 61–76.

Koricheva, J. & Gurevitch, J. (2014). Uses and misuses of meta-analysis in plant ecology. *J. Ecol.*, 102, 828–844.

Lajeunesse, M.J. (2011). On the meta-analysis of response ratios for studies with correlated and multi-group designs. *Ecology*, 92, 2049–2055.

Lajeunesse, M.J. (2015). Bias and correction for the log response ratio in ecological meta-analysis. *Ecology*, 96, 2056–2063.

Lajeunesse, M.J. (2016). Facilitating systematic reviews, data extraction, and meta-analysis with the metagear package for R. *Methods Ecol. Evol.*, 7, 323–330.

Lajeunesse, M.J., Koricheva, J., Gurevitch, J. & Mengersen, K. (2013). Recovering missing or partial data from studies: a survey of conversions and imputations for meta-analysis. *Handb. meta-analysis Ecol. Evol.*, 195–206.

Lambertucci, S.A., Speziale, K.L., Rogers, T.E. & Morales, J.M. (2009). How do roads affect the habitat use of an assemblage of scavenging raptors? *Biodivers. Conserv.*, 18, 2063–2074.

Lange, K., Bruder, A., Matthaei, C.D., Brodersen, J. & Paterson, R.A. (2018). Multiple-stressor effects on freshwater fish: Importance of taxonomy and life stage. *Fish Fish.*, 19, 974–983.

Laurance, W.F. (2015). Emerging Threats to Tropical Forests. *Ann. Missouri Bot. Gard.*, 100, 159–169.

Laurance, W.F. & Arrea, I.B. (2017). Roads to riches or ruin? *Science*, 358, 442–444.

Laurance, W.F., Campbell, M.J., Alamgir, M. & Mahmoud, M.I. (2017). Road Expansion and the Fate of Africa's Tropical Forests . *Front. Ecol. Evol.* .

Laurance, W.F., Clements, G.R., Sloan, S., O'Connell, C.S., Mueller, N.D., Goosem, M., *et al.* (2014). A global strategy for road building. *Nature*, 513, 229–232.

Laurance, W.F., Sloan, S., Weng, L. & Sayer, J.A. (2015). Estimating the Environmental Costs of Africa's Massive "Development Corridors." *Curr. Biol.*, 25, 3202–3208.

Lawrence, D. (2003). The response of tropical tree seedlings to nutrient supply: meta-analysis for understanding a changing tropical landscape. *J. Trop. Ecol.*, 19, 239–250.

Leclère, D., Obersteiner, M., Barrett, M., Butchart, S.H.M., Chaudhary, A., De Palma, A., *et al.* (2020). Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature*, 585, 551–556.

Lewis, O.T. (2006). Climate change, species–area curves and the extinction crisis. *Philos. Trans. R. Soc. B Biol. Sci.*, 361, 163–171.

Li, N. & Shvarts, E. (2017). The Belt and Road Initiative: WWF Recommendations and Spatial Analysis. *WWF Brief. Pap. Hong Kong WWF*.

Lima, D.O. de, Lorini, M.L. & Vieira, M.V. (2018). Conservation of grasslands and savannas: A meta-analysis on mammalian responses to anthropogenic disturbance. *J. Nat. Conserv.*, 45, 72–78.

Linder, J.M. & Oates, J.F. (2011). Differential impact of bushmeat hunting on monkey species and implications for primate conservation in Korup National Park, Cameroon. *Biol. Conserv.*, 144, 738–745.

Liu, G., Rowley, J.J.L., Kingsford, R.T. & Callaghan, C.T. (2021). Species' traits drive amphibian tolerance to anthropogenic habitat modification. *Glob. Chang. Biol.*, 27, 3120–3132.

Liu, X., Blackburn, T.M., Song, T., Li, X., Huang, C. & Li, Y. (2019). Risks of biological invasion on the belt and road. *Curr. Biol.*, 29, 499–505.

Lu, X., Mao, Q., Gilliam, F.S., Luo, Y. & Mo, J. (2014). Nitrogen deposition contributes to soil acidification in tropical ecosystems. *Glob. Chang. Biol.*, 20, 3790–3801.

Lucas, R.W., Klaminder, J., Futter, M.N., Bishop, K.H., Egnell, G., Laudon, H., *et al.* (2011). A meta-analysis of the effects of nitrogen additions on base cations: Implications for plants, soils, and streams. *For. Ecol. Manage.*, 262, 95–104.

Lv, J., Buerkert, A., Benedict, K.B., Liu, G., Lv, C. & Liu, X. (2019). Comparison of nitrogen deposition across different land use types in agro-pastoral catchments of western China and Mongolia. *Atmos. Environ.*, 199, 313–322.

Ma, Z., Chen, H.Y.H., Li, Y. & Chang, S.X. (2020). Interactive effects of global change factors on terrestrial net primary productivity are treatment length and intensity dependent. *J. Ecol.*, 108, 2083–2094.

Mace, G.M., Barrett, M., Burgess, N.D., Cornell, S.E., Freeman, R., Grooten, M., *et al.* (2018). Aiming higher to bend the curve of biodiversity loss. *Nat. Sustain.*, 1, 448–451.

Di Marco, M., Chapman, S., Althor, G., Kearney, S., Besancon, C., Butt, N., *et al.* (2017). Changing trends and persisting biases in three decades of conservation science. *Glob. Ecol. Conserv.*, 10, 32–42.

Di Marco, M., Ferrier, S., Harwood, T.D., Hoskins, A.J. & Watson, J.E.M. (2019). Wilderness areas halve the extinction risk of terrestrial biodiversity. *Nature*, 573, 582–585.

Martin, L.J., Blossey, B. & Ellis, E. (2012). Mapping where ecologists work: biases in the global distribution of terrestrial ecological observations. *Front. Ecol. Environ.*, 10, 195–201.

Martins, I.S. & Pereira, H.M. (2017). Improving extinction projections across scales and habitats using the countryside species-area relationship. *Sci Rep*, 7, 12899.

Martinson, H.M., Schneider, K., Gilbert, J., Hines, J.E., Hambäck, P.A. & Fagan, W.F. (2008). Detritivory: stoichiometry of a neglected trophic level. *Ecol. Res.*, 23, 487–491.

Maxwell, S.L., Fuller, R.A., Brooks, T.M. & Watson, J.E.M. (2016). Biodiversity: The ravages of guns, nets and bulldozers. *Nature*, 536, 143–145.

Maynard, R.J., Aall, N.C., Saenz, D., Hamilton, P.S. & Kwiatkowski, M.A. (2016). Road-Edge Effects on Herpetofauna in a Lowland Amazonian Rainforest. *Trop. Conserv. Sci.*, 9, 264–290.

McClean, C.J., van den Berg, L.J.L., Ashmore, M.R. & Preston, C.D. (2011). Atmospheric nitrogen deposition explains patterns of plant species loss. *Glob. Chang. Biol.*, 17, 2882–2892.

Meijer, J.R., Huijbregts, M.A.J., Schotten, K.C.G.J. & Schipper, A.M. (2018). Global patterns of current and future road infrastructure. *Environ. Res. Lett.*, 13, 64006.

Meiri, S., Bauer, A.M., Chirio, L., Colli, G.R., Das, I., Doan, T.M., *et al.* (2013). Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. *Glob. Ecol. Biogeogr.*, 22, 834–845.

Mesquita, D.O., Costa, G.C., Colli, G.R., Costa, T.B., Shepard, D.B., Vitt, L.J., *et al.* (2016). Life-History Patterns of Lizards of the World. *Am. Nat.*, 187, 689–705.

Michonneau, F., Brown, J.W. & Winter, D.J. (2016). rotl: an R package to interact with the Open Tree of Life data. *Methods Ecol. Evol.*, 7, 1476–1481.

Midolo, G., Alkemade, R., Schipper, A.M., Benítez-López, A., Perring, M.P. & De Vries, W. (2019). Impacts of nitrogen addition on plant species richness and abundance: a global meta-analysis. *Glob. Ecol. Biogeogr.*, 28, 398–413.

Milner-Gulland, E.J., Addison, P., Arlidge, W.N.S., Baker, J., Booth, H., Brooks, T., *et al.* (2021). Four steps for the Earth: mainstreaming the post-2020 global biodiversity framework. *One Earth*, 4, 75–87.

Morelli, F., Beim, M., Jerzak, L., Jones, D. & Tryjanowski, P. (2014). Can roads, railways and related structures have positive effects on birds? – A review. *Transp. Res. Part D Transp. Environ.*, 30, 21–31.

Nakagawa, S., Lagisz, M., O'Dea, R.E., Rutkowska, J., Yang, Y., Noble, D.W.A., *et al.* (2021). The orchard plot: Cultivating a forest plot for use in ecology, evolution, and beyond. *Res. Synth. Methods*, 12, 4–12.

Nakagawa, S. & Santos, E.S.A. (2012). Methodological issues and advances in biological meta-analysis. *Evol. Ecol.*, 26, 1253–1274.

Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods Ecol. Evol.*, 4, 133–142.

Narain, D., Maron, M., Teo, H.C., Hussey, K. & Lechner, A.M. (2020). Best-practice biodiversity safeguards for Belt and Road Initiative's financiers. *Nat. Sustain.*, 3, 650–657.

Nessel, M.P., Konnovitch, T., Romero, G.Q. & González, A.L. (2021). Nitrogen and phosphorus enrichment cause declines in invertebrate populations: a global meta-analysis. *Biol. Rev.*

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., *et al.* (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520, 45.

Ngoufo, R. & Waltert, M. (2014). Social norms and cultural services - community belief system and use of wildlife products in the Northern periphery of the Korup National Park, South-West Cameroon . *Chang. Adapt. Socio-Ecological Syst.* .

Nichols, E., Uriarte, M., Bunker, D.E., Favila, M.E., Slade, E.M., Vulinec, K., *et al.* (2013). Trait-dependent response of dung beetle populations to tropical forest conversion at local and regional scales. *Ecology*, 94, 180–189.

Nijssen, M.E., WallisDeVries, M.F. & Siepel, H. (2017). Pathways for the effects of increased nitrogen deposition on fauna. *Biol. Conserv.*, 212, 423–431.

Nowakowski, A.J., Watling, J.I., Thompson, M.E., Brusch IV, G.A., Catenazzi, A., Whitfield, S.M., *et al.* (2018). Thermal biology mediates responses of amphibians and reptiles to habitat modification. *Ecol. Lett.*, 21, 345–355.

Ohashi, H., Hasegawa, T., Hirata, A., Fujimori, S., Takahashi, K., Tsuyama, I., *et al.* (2019). Biodiversity can benefit from climate stabilization despite adverse side effects of land-based mitigation. *Nat. Commun.*, 10, 5240.

Olkin, I. & Gleser, L. (2009). Stochastically dependent effect sizes. *Handb. Res. Synth. meta-analysis*, 357–376.

Orr, J.A., Vinebrooke, R.D., Jackson, M.C., Kroeker, K.J., Kordas, R.L., Mantyka-Pringle, C., *et al.* (2020). Towards a unified study of multiple stressors: divisions and common goals across research disciplines. *Proc. R. Soc. B Biol. Sci.*, 287, 20200421.

Ouédraogo, D.-Y., Villemey, A., Vanpeene, S., Coulon, A., Azambourg, V., Hulard, M., *et al.* (2020). Can linear transportation infrastructure verges constitute a habitat and/or a corridor for vertebrates in temperate ecosystems? A systematic review. *Environ. Evid.*, 9, 13.

Paradis, E. & Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35, 526–528.

Parr, C.L., Dunn, R.R., Sanders, N.J., Weiser, M.D., Photakis, M., Bishop, T.R., *et al.* (2017). GlobalAnts: a new database on the geography of ant traits (Hymenoptera: Formicidae). *Insect Conserv. Divers.*, 10, 5–20.

Pe'er, G., Bonn, A., Bruelheide, H., Dieker, P., Eisenhauer, N., Feindt, P.H., *et al.* (2020). Action needed for the EU Common Agricultural Policy to address sustainability challenges. *People Nat.* , 2, 305–316.

Pe'er, G., Tsianou, M.A., Franz, K.W., Matsinos, Y.G., Mazaris, A.D., Storch, D., *et al.* (2014). Toward better application of minimum area requirements in conservation planning. *Biol. Conserv.*, 170, 92–102.

Peaden, J.M., Tuberville, T.D., Buhlmann, K.A., Nafus, M.G. & Todd, B.D. (2016). Delimiting road-effect zones for threatened species: implications for mitigation fencing. *Wildl. Res.*, 42, 650–659.

Pebesma, E. (2018). Simple features for R: standardized support for spatial vector data. *R J.*, 10, 439–446.

Peguero, G., Folch, E., Liu, L., Ogaya, R. & Peñuelas, J. (2021). Divergent effects of drought and nitrogen deposition on microbial and arthropod soil communities in a Mediterranean forest. *Eur. J. Soil Biol.*, 103, 103275.

Penuelas, J., Janssens, I.A., Ciais, P., Obersteiner, M. & Sardans, J. (2020). Anthropogenic global shifts in biospheric N and P concentrations and ratios and their impacts on biodiversity, ecosystem productivity, food security, and human health. *Glob. Chang. Biol.*, 26, 1962–1985.

Pereira, H., Ziv, G. & Miranda, M. (2014). Countryside Species–Area Relationship as a valid alternative to the Matrix-Calibrated Species–Area model. *Conserv. Biol.*, 28, 874–876.

Pereira, H.M., Navarro, L.M. & Martins, I.S. (2012). Global Biodiversity Change: The Bad, the Good, and the Unknown. *Annu. Rev. Environ. Resour.*, 37, 25–50.

Peres, C.A. (2005). Why We Need Megareserves in Amazonia. *Conserv. Biol.*, 19, 728–733.

Périquet, S., Roxburgh, L., Le Roux, A. & Collinson, W.J. (2018). Testing the value of citizen science for roadkill studies: A case study from South Africa. *Front. Ecol. Evol.*, 6, 15.

Perring, M.P., Diekmann, M., Midolo, G., Schellenberger Costa, D., Bernhardt-Römermann, M., Otto, J.C.J., *et al.* (2018). Understanding context dependency in the response of forest understorey plant communities to nitrogen deposition. *Environ. Pollut.*, 242, 1787–1799.

Peters, J.L., Sutton, A.J., Jones, D.R., Abrams, K.R. & Rushton, L. (2008). Contour-enhanced meta-analysis funnel plots help distinguish publication bias from other causes of asymmetry. *J. Clin. Epidemiol.*, 61, 991–996.

Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., *et al.* (2017). Creation of forest edges has a global impact on forest vertebrates. *Nature*, advance on.

Phung, T.X., Nascimento, J.C.S., Novarro, A.J. & Wiens, J.J. (2020). Correlated and decoupled evolution of adult and larval body size in frogs. *Proc. R. Soc. B Biol. Sci.*, 287, 20201474.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., *et al.* (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, 344, 1246752.

Plackett, R.L. & Hewlett, P.S. (1952). Quantal responses to mixtures of poisons. *J. R. Stat. Soc. Ser. B*, 14, 141–163.

Planillo, A., Mata, C., Manica, A. & Malo, J.E. (2018). Carnivore abundance near motorways related to prey and roadkills. *J. Wildl. Manage.*, 82, 319–327.

Porter, E.M., Bowman, W.D., Clark, C.M., Compton, J.E., Pardo, L.H. & Soong, J.L. (2013). Interactive effects of anthropogenic nitrogen enrichment and climate change on terrestrial and aquatic biodiversity. *Biogeochemistry*, 114, 93–120.

Powers, R.P. & Jetz, W. (2019). Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nat. Clim. Chang.*, 9, 323–329.

Purvis, A., Molnár, Z., Obura, D., Ichii, K., Willis, K., Chettri, N., *et al.* (2019). Chapter 2.2 Status and Trends –Nature.

Purvis, A., Newbold, T., De Palma, A., Contu, S., Hill, S.L.L., Sanchez-Ortiz, K., *et al.* (2018). Chapter Five - Modelling and Projecting the Response of Local Terrestrial Biodiversity Worldwide to Land Use and Related Pressures: The PREDICTS Project. In: *Advances in Ecological Research* (eds. Bohan, D.A., Dumbrell, A.J., Woodward, G. & Jackson, M.). Academic Press, pp. 201–241.

Pustejovsky, J.E. (2015). Measurement-comparable effect sizes for single-case studies of free-operant behavior. *Psychol. Methods*, 20, 342.

R Core Team & R Development Core Team. (2020). R: a language and environment for statistical computing.

Raue, A., Kreutz, C., Maiwald, T., Bachmann, J., Schilling, M., Klingmüller, U., *et al.* (2009). Structural and practical identifiability analysis of partially observed dynamical models by exploiting the profile likelihood. *Bioinformatics*, 25, 1923–1929.

van der Ree, R., Smith, D.J. & Grilo, C. (2015). *Handbook of road ecology*. John Wiley & Sons.

Rees, J.A. & Cranston, K. (2017). Automated assembly of a reference taxonomy for phylogenetic data synthesis. *Biodivers. Data J.*, 5, e12581.

Revell, L.J. (2012). phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, 3, 217–223.

Richardson, M.L., Wilson, B.A., Aiuto, D.A.S., Crosby, J.E., Alonso, A., Dallmeier, F., *et al.* (2017). A review of the impact of pipelines and power lines on biodiversity and strategies for mitigation. *Biodivers. Conserv.*, 26, 1801–1815.

Ripple, W.J., Abernethy, K., Betts, M.G., Chapron, G., Dirzo, R., Galetti, M., *et al.* (2016). Bushmeat hunting and extinction risk to the world's mammals. *R. Soc. open Sci.*, 3, 160498.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., *et al.* (2014). Status and Ecological Effects of the World's Largest Carnivores. *Science*, 343.

Ripple, W.J., Wolf, C., Newsome, T.M., Betts, M.G., Ceballos, G., Courchamp, F., *et al.* (2019). Are we eating the world's megafauna to extinction? *Conserv. Lett.*, 0, e12627.

Ripple, W.J., Wolf, C., Newsome, T.M., Hoffmann, M., Wirsing, A.J. & McCauley, D.J. (2017). Extinction risk is most acute for the world's largest and smallest vertebrates. *Proc. Natl. Acad. Sci.*, 114, 10678.

Romero-Muñoz, A., Torres, R., Noss, A.J., Giordano, A.J., Quiroga, V., Thompson, J.J., *et al.* (2019). Habitat loss and overhunting synergistically drive the extirpation of jaguars from the Gran Chaco. *Divers. Distrib.*, 25, 176–190.

Rubin, D.B. & Schenker, N. (1991). Multiple imputation in health-are databases: An overview and some applications. *Stat. Med.*, 10, 585–598.

Rytwinski, T. & Fahrig, L. (2011). Reproductive rate and body size predict road impacts on mammal abundance. *Ecol. Appl.*, 21, 589–600.

Rytwinski, T. & Fahrig, L. (2012). Do species life history traits explain population responses to roads? A meta-analysis. *Biol. Conserv.*, 147, 87–98.

Santini, L., Antão, L.H., Jung, M., Benítez-López, A., Rapacciuolo, G., Di Marco, M., *et al.* (2021). The interface between macroecology and conservation: Existing links and untapped opportunities. *Front. Biogeogr.*, 13.

Santini, L., Bénitez-López, A., Dormann, C. & Huijbregts, M.A.J. (2022). Population density estimates for terrestrial mammal species. *Glob. Ecol. Biogeogr.*

Santini, L., Benítez-López, A., Ficetola, G.F. & Huijbregts, M.A.J. (2018). Length–mass allometries in amphibians. *Integr. Zool.*, 13, 36–45.

Santini, L., González-Suárez, M., Russo, D., Gonzalez-Voyer, A., von Hardenberg, A. & Ancillotto, L. (2019). One strategy does not fit all: determinants of urban adaptation in mammals. *Ecol. Lett.*, 22, 365–376.

Schipper, A.M., Belmaker, J., de Miranda, M.D., Navarro, L.M., Böhning-Gaese, K., Costello, M.J., *et al.* (2016). Contrasting changes in the abundance and diversity of North American bird assemblages from 1971 to 2010. *Glob. Chang. Biol.*, 22, 3948–3959.

Schipper, A.M., Hilbers, J.P., Meijer, J.R., Antão, L.H., Benítez-López, A., de Jonge, M.M.J., *et al.* (2020). Projecting terrestrial biodiversity intactness with GLOBIO 4. *Glob. Chang. Biol.*, 26, 760–771.

Shaw, E.A., Boot, C.M., Moore, J.C., Wall, D.H. & Baron, J.S. (2019). Long-term nitrogen addition shifts the soil nematode community to bacterivore-dominated and reduces its ecological maturity in a subalpine forest. *Soil Biol. Biochem.*, 130, 177–184.

Shirey, V., Larsen, E., Doherty, A., Kim, C.A., Al-Sulaiman, F.T., Hinolan, J.D., *et al.* (2022). LepTraits 1.0 A globally comprehensive dataset of butterfly traits. *Sci. Data*, 9, 382.

Simmons, B.I., Balmford, A., Bladon, A.J., Christie, A.P., De Palma, A., Dicks, L. V, *et al.* (2019). Worldwide insect declines: An important message, but interpret with caution. *Ecol. Evol.*, 9, 3678–3680.

Skuban, M., Finďo, S., Kajba, M., Koreň, M., Chamers, J. & Antal, V. (2017). Effects of roads on brown bear movements and mortality in Slovakia. *Eur. J. Wildl. Res.*, 63, 82.

Smith, F.A., Brown, J.H., Haskell, J.P., Lyons, S.K., Alroy, J., Charnov, E.L., *et al.* (2004). Similarity of Mammalian Body Size across the Taxonomic Hierarchy and across Space and Time. *Am. Nat.*, 163, 672–691.

Song, M., Li, X., Jing, S., Lei, L., Wang, J. & Wan, S. (2016). Responses of soil nematodes to water and nitrogen additions in an old-field grassland. *Appl. Soil Ecol.*, 102, 53–60.

Soria, C.D., Pacifici, M., Di Marco, M., Stephen, S.M. & Rondinini, C. (2021). COMBINE: a coalesced mammal database of intrinsic and extrinsic traits. *Ecology*, 102, e03344.

Sosa, R. & Schalk, C.M. (2016). Seasonal Activity and Species Habitat Guilds Influence Road-Kill Patterns of Neotropical Snakes. *Trop. Conserv. Sci.*, 9, 1940082916679662.

Southwood, A. & Avens, L. (2010). Physiological, behavioral, and ecological aspects of migration in reptiles. *J. Comp. Physiol. B*, 180, 1–23.

Steven, B. (2004). Keeping an Eye on the Neighbors. *Science*, 306, 238–239.

Stevens, C.J. (2016). How long do ecosystems take to recover from atmospheric nitrogen deposition? *Biol. Conserv.*, 200, 160–167.

Stevens, C.J., David, T.I. & Storkey, J. (2018). Atmospheric nitrogen deposition in terrestrial ecosystems: its impact on plant communities and consequences across trophic levels. *Funct. Ecol.*, 32, 1757–1769.

Stevens, C.J., Duprè, C., Dorland, E., Gaudnik, C., Gowing, D.J.G., Bleeker, A., *et al.* (2010). Nitrogen deposition threatens species richness of grasslands across Europe. *Environ. Pollut.*, 158, 2940–2945.

Stevens, C.J., Manning, P., van den Berg, L.J.L., de Graaf, M.C.C., Wamelink, G.W.W., Boxman, A.W., *et al.* (2011). Ecosystem responses to reduced and oxidised nitrogen inputs in European terrestrial habitats. *Environ. Pollut.*, 159, 665–676.

Sullivan, B. (1981). Observed differences in body temperature and associated behavior of four snake species. *J. Herpetol.*, 15, 245–246.

Sun, X., Zhang, X., Zhang, S., Dai, G., Han, S. & Liang, W. (2013). Soil Nematode Responses to Increases in Nitrogen Deposition and Precipitation in a Temperate Forest. *PLoS One*, 8, e82468.

Symes, W.S., Edwards, D.P., Miettinen, J., Rheindt, F.E. & Carrasco, L.R. (2018). Combined impacts of deforestation and wildlife trade on tropical biodiversity are severely underestimated. *Nat. Commun.*, 9, 4052.

Taboada, A., Marcos, E. & Calvo, L. (2016). Disruption of trophic interactions involving the heather beetle by atmospheric nitrogen deposition. *Environ. Pollut.*, 218, 436–445.

Tanner, D. & Perry, J. (2007). Road effects on abundance and fitness of Galápagos lava lizards (Microlophus albemarlensis). *J. Environ. Manage.*, 85, 270–278.

Taylor, B.M., Parida, B. & Davies, J. (2020). cruts: interface to climatic research unit time-series version 3.21 data.

Teixeira, F.Z., Rytwinski, T. & Fahrig, L. (2020). Inference in road ecology research: what we know versus what we think we know. *Biol. Lett.*, 16, 20200140.

Temme, A.J.A.M. & Verburg, P.H. (2011). Mapping and modelling of changes in agricultural intensity in Europe. *Agric. Ecosyst. Environ.*, 140, 46–56.

Thacker, S., Adshead, D., Fay, M., Hallegatte, S., Harvey, M., Meller, H., *et al.* (2019). Infrastructure for sustainable development. *Nat. Sustain.*, 2, 324–331.

Tilman, D., Clark, M., Williams, D.R., Kimmel, K., Polasky, S. & Packer, C. (2017). Future threats to biodiversity and pathways to their prevention. *Nature*, 546, 73–81.

Tobias, J.A., Sheard, C., Pigot, A.L., Devenish, A.J., Yang, J., Sayol, F., *et al.* (2022). AVONET: morphological, ecological and geographical data for all birds. *Ecol. Lett.*, 5, 581–597.

Torres, A., Jaeger, J.A.G. & Alonso, J.C. (2016). Assessing large-scale wildlife responses to human infrastructure development. *Proc. Natl. Acad. Sci.*, 113, 8472–8477.

Tracy, C.R., Christian, K.A. & Tracy, C.R. (2010). Not just small, wet, and cold: effects of body size and skin resistance on thermoregulation and arboreality of frogs. *Ecology*, 91, 1477–1484.

Treseder, K.K. (2004). A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO2 in field studies. *New Phytol.*, 164, 347–355.

Treseder, K.K. (2008). Nitrogen additions and microbial biomass: a meta-analysis of ecosystem studies. *Ecol. Lett.*, 11, 1111–1120.

Tucker, M.A., Ord, T.J. & Rogers, T.L. (2014). Evolutionary predictors of mammalian home range size: body mass, diet and the environment. *Glob. Ecol. Biogeogr.*, 23, 1105–1114.

Tuff, K.T., Tuff, T. & Davies, K.F. (2016). A framework for integrating thermal biology into fragmentation research. *Ecol. Lett.*, 19, 361–374.

Tulloch, A.I.T., Gordon, A., Runge, C.A. & Rhodes, J.R. (2019). Integrating spatially realistic infrastructure impacts into conservation planning to inform strategic environmental assessment. *Conserv. Lett.*, 12, e12648.

Valerio, F., Basile, M. & Balestrieri, R. (2021). The identification of wildlife-vehicle collision hotspots: Citizen science reveals spatial and temporal patterns. *Ecol. Process.*, 10, 6.

Vellend, M., Baeten, L., Becker-Scarpitta, A., Boucher-Lalonde, V., McCune, J.L., Messier, J., *et al.* (2017). Plant biodiversity change across scales during the Anthropocene. *Annu. Rev. Plant Biol.*, 68, 563–586.

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., *et al.* (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat. Commun.*, 7, 12558.

Verburg, P.H., Dearing, J.A., Dyke, J.G., Leeuw, S. van der, Seitzinger, S., Steffen, W., *et al.* (2016). Methods and approaches to modelling the Anthropocene. *Glob. Environ. Chang.*, 39, 328–340.

Verbyla, A.P. (2019). A note on model selection using information criteria for general linear models estimated using REML. *Aust. N. Z. J. Stat.*, 61, 39–50.

Viana, D.S. & Chase, J.M. (2022). Increasing climatic decoupling of bird abundances and distributions. *Nat. Ecol. Evol.*

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.*, 36, 1–48.

Villar-Argaiz, M., López-Rodríguez, M.J. & Tierno de Figueroa, J.M. (2021). Divergent nucleic acid allocation in juvenile insects of different metamorphosis modes. *Sci. Rep.*, 11, 10313.

Vinebrooke, R.D., Cottingham, K.L., Norberg Jon, M.S., Dodson, S.I., Maberly, S.C. & Sommer, U. (2004). Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of species co-tolerance. *Oikos*, 104, 451–457.

Visconti, P., Bakkenes, M., Baisero, D., Brooks, T., Butchart, S.H.M., Joppa, L., *et al.* (2016). Projecting Global Biodiversity Indicators under Future Development Scenarios. *Conserv. Lett.*, 9, 5–13.

Vogels, J.J., van den Burg, A., van de Waal, D., Weijters, M., Bobbink, R., Nijssen, M., *et al.* (2020). *Imbalanced by overabundance: Effects of Nitrogen deposition on nutritional quality of producers and its subsequent effects on consumers*. VBNE, Vereniging van Bos- en Natuurterreineigenaren.

Wagner, D.L. (2020). Insect Declines in the Anthropocene. *Annu. Rev. Entomol.*, 65, 457–480.

Wallenstein, M.D., McNulty, S., Fernandez, I.J., Boggs, J. & Schlesinger, W.H. (2006). Nitrogen fertilization decreases forest soil fungal and bacterial biomass in three long-term experiments. *For. Ecol. Manage.*, 222, 459–468.

Walling, M. (2020a). doParallel: Foreach Parallel Adaptor for the 'parallel' Package. R package version 1.0.16.

Walling, M. (2020b). foreach: Foreach Looping Construct for R. R package version 1.5.1.

WallisDeVries, M.F. & Bobbink, R. (2017). Nitrogen deposition impacts on biodiversity in terrestrial ecosystems: Mechanisms and perspectives for restoration. *Biol. Conserv.*, 212, 387–389.

WallisDeVries, M.F. & Van Swaay, C.A.M. (2006). Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. *Glob. Chang. Biol.*, 12, 1620–1626.

Wan, X., Wang, W., Liu, J. & Tong, T. (2014). Estimating the sample mean and standard deviation from the sample size, median, range and/or interquartile range. *BMC Med. Res. Methodol.*, 14, 135.

Wang, H., Liu, G., Huang, B., Wang, X., Xing, Y. & Wang, Q. (2021). Long-term nitrogen addition and precipitation reduction decrease soil nematode community diversity in a temperate forest. *Appl. Soil Ecol.*, 162, 103895.

Watson, J.E.M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., *et al.* (2018). The exceptional value of intact forest ecosystems. *Nat. Ecol. Evol.*, 2, 599–610.

Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.I. & LeRoy Poff, N. (2010). A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecol. Lett.*, 13, 267–283.

Wei, C., Zheng, H., Li, Q., Lü, X., Yu, Q., Zhang, H., *et al.* (2012). Nitrogen Addition Regulates Soil Nematode Community Composition through Ammonium Suppression. *PLoS One*, 7, e43384.

Wickham, H. (2016). *ggplot2: elegant graphics for data analysis*. springer.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., *et al.* (2019). Welcome to the {tidyverse}. *J. Open Source Softw.*, 4, 1686.

Wiesenborn, W.D. (2011). Nitrogen content in riparian arthropods is most dependent on allometry and order. *Florida Entomol.*, 94, 71–80.

Wilkie, D.S., Bennett, E.L., Peres, C.A. & Cunningham, A.A. (2011). The empty forest revisited. *Ann. N. Y. Acad. Sci.*, 1223, 120–128.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027.

Wong, M.K.L., Guénard, B. & Lewis, O.T. (2019). Trait-based ecology of terrestrial arthropods. *Biol. Rev.*, 94, 999–1022.

Woods, H.A., Fagan, W.F., Elser, J.J. & Harrison, J.F. (2004). Allometric and Phylogenetic Variation in Insect Phosphorus Content. *Funct. Ecol.*, 18, 103–109.

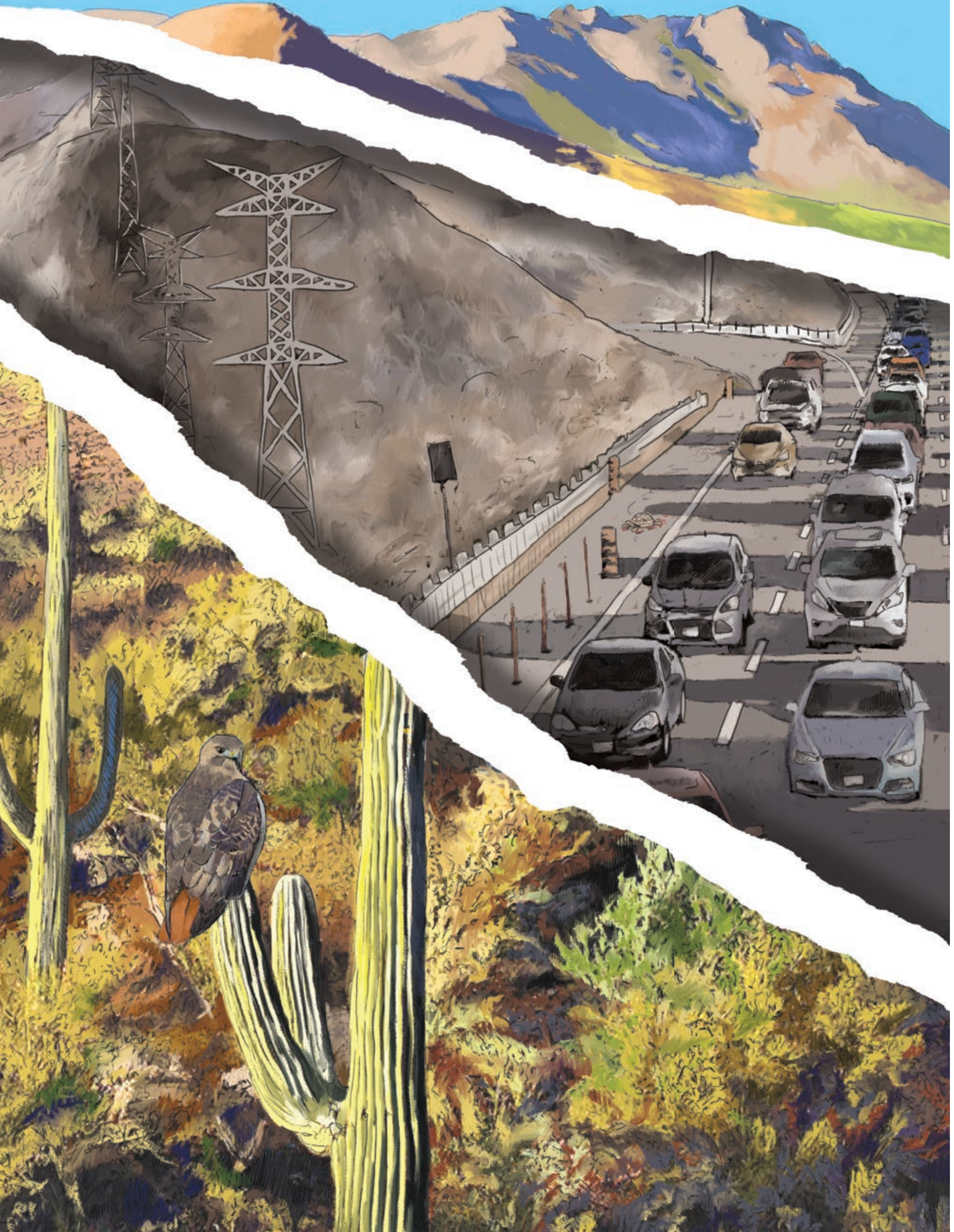
Wright, K. (2021). pals: Color Palettes, Colormaps and Tools to Evaluate Them. R package version 1.7.

Wüst-Galley, C., Volk, M. & Bassin, S. (2021). Interaction of climate change and nitrogen deposition on subalpine pastures. *J. Veg. Sci.*, 32, e12946.

Xu, Z.W., Wan, S.Q., Ren, H.Y., Han, X.G. & Jiang, Y. (2012). Influences of land use history and short-term nitrogen addition on community structure in temperate grasslands. *J. Arid Environ.*, 87, 103–109.

Yamazaki, D., Ikeshima, D., Tawatari, R., Yamaguchi, T., O'Loughlin, F., Neal, J.C., *et al.* (2017). A high-accuracy map of global terrain elevations. *Geophys. Res. Lett.*, 44, 5844–5853.

zu Ermgassen, S.O.S.E., Utamiputri, P., Bennun, L., Edwards, S. & Bull, J.W. (2019). The Role of "No Net Loss" Policies in Conserving Biodiversity Threatened by the Global Infrastructure Boom. *One Earth*, 1, 305–315.



SUMMARY, SAMENVATTING, RESUMEN

C

SUMMARY

Global biodiversity models (GBMs) are essential to assess the global status of biodiversity and support biodiversity policy. However, current GBMs are limited in the selection of human pressures they consider as well as the extent to which they account for the context-dependence of biodiversity responses to human pressures. Moreover, GBMs are challenged by data shortfalls, as the availability of biodiversity data differs greatly among species (groups) and world regions. This thesis aims to improve the way GBMs assess biodiversity responses to human pressures by 1) developing new context-specific response relationships for understudied pressures that allow for extrapolation to understudied species and/or regions, and 2) demonstrating how to use these types of models to quantify the combined impacts of multiple human pressures at large scales. Ultimately, this thesis advances our understanding of how human pressures are affecting terrestrial biodiversity worldwide.

Current GBMs are mostly focused on quantifying the impacts of land use and climate change on terrestrial biodiversity. Chapters 2 and 3 present new context-specific biodiversity response relationships for two underrepresented pressures (nitrogen enrichment and linear infrastructure). Both chapters show that the responses of biodiversity to these pressures are highly context-dependent. Chapter 2 compiled a new global dataset of 4,365 observations from 126 papers reporting the effect of nitrogen enrichment on the richness or abundance of arthropods or nematodes. Meta-analytical models were established to explore these effects along a gradient of nitrogen addition levels and in relation to environmental conditions and species traits. The response of arthropod abundance to nitrogen addition was mostly driven by their metamorphosis mode and, to a lesser extent, by the local mean annual temperature. The abundance of arthropods with full metamorphosis (including pollinators) showed a decrease when nitrogen increased, especially in warmer climates, while those with incomplete metamorphosis (including agricultural pests) increased. The response of nematode abundance to nitrogen enrichment differed between feeding groups and was modulated by local annual precipitation, with consistent abundance declines in drier areas. Moreover, arthropod richness did not show a response to nitrogen addition, but nematode richness consistently declined. Chapter 3 synthesized 253 studies worldwide quantifying the magnitude and spatial extent of the impacts of linear infrastructure (e.g., roads, powerlines)

on the abundance of 792 vertebrate species, including mammals, birds, reptiles and amphibians. Carnivorous and small herbivorous mammals (e.g., rodents) were more abundant in the proximity of infrastructure while medium and large herbivores decreased, especially in open habitats. Bird abundances were reduced near infrastructure with larger effect zones (i.e., spatial extent of the impacts) for non-carnivorous than for carnivorous species. Moreover, birds in closed habitats such as forests were more impacted than birds in open areas. Reptiles were more abundant near infrastructure in closed habitats but not in open habitats. Finally, the abundance of amphibians was reduced by approximately half in the proximity of infrastructure, but the impact disappeared around 30 meters away.

Chapters 4 and 5 present spatially explicit multi-pressure biodiversity impact assessments based on innovative combinations of biodiversity response relationships and geospatial pressure data. Chapter 4 provides the first global assessment of the combined effect of land use and nitrogen deposition on plant species richness. A new species-area model was developed to integrate the responses of plant communities to both land use and nitrogen deposition and assess resulting changes in plant species richness in 0.25-degree grid cells (about 25x25 km) worldwide. The model results revealed a global mean species richness loss of 26% due to both pressures combined, with land use being the main driver. Both impacts had considerable geographic variation, with Europe being the most impacted continent and South America the least. Chapter 5 presents the first pantropical assessment of the combined effect of land use and hunting on the distributions of tropical mammals (1,884 species). Species range maps were combined with detailed land-use maps (~300 m resolution), species-specific habitat preference data, and novel hunting impact relationships based on an extensive pantropical database of local hunting-induced extinctions (3,281 observations). On average, the species lost approximately 40% of their distribution due to the combined effect of both pressures. Land use was the main driver of loss but hunting greatly impacted large-sized species. Moreover, the two pressures were highly complementary, affecting different parts of species' ranges, and their impact increased from 1992 to 2015. The chapter also provides a pantropical map identifiying the areas where the impacts were greatest (hotspots) and least (coolspots) to determine priority areas for mitigation or prevention of the pressures.

Based on the findings of this thesis it was concluded that trait-based meta-analytical models are an effective tool for quantifying the context-dependent impacts of human pressures on biodiversity. These models are widely applicable as they can assess large-scale impacts across multiple environments and species, including those without empirical data on their responses to human pressures. Moreover, the meta-analytical response relationships can be integrated in multi-pressure biodiversity models in order to systematically quantify the relative and combined impacts of multiple human pressures. Therefore, the tools and results of this thesis can help to more comprehensively assess human impacts on terrestrial biodiversity worldwide and, ultimately, better guide future national and global conservation agendas, including the post-2020 global biodiversity framework.

SAMENVATTING

Mondiale biodiversiteitsmodellen zijn essentieel voor het bepalen van de staat van instandhouding van de mondiale biodiversiteit en het ondersteunen van biodiversiteitsbeleid. De huidige modellen zijn echter onvolledig in de drukfactoren die ze meenemen en in de mate waarin ze rekening houden met het feit dat effecten van milieudruk op biodiversiteit afhankelijk zijn van de context. Bovendien wordt de ontwikkeling van deze modellen bemoeilijkt door tekorten aan data, aangezien de beschikbaarheid van biodiversiteitsgegevens sterk verschilt tussen soort(groep)en en werelddelen. Dit proefschrift heeft tot doel om mondiale biodiversiteitsmodellen te verbeteren door 1) het ontwikkelen van nieuwe contextspecifieke responsrelaties voor relatief slecht vertegenwoordigde drukfactoren, en 2) te demonstreren hoe dit soort relaties gebruikt kunnen worden om de gecombineerde effecten van meerdere drukfactoren op biodiversiteit te bepalen. Op deze manier bevordert dit proefschrift ons begrip van de invloed van milieudruk op de terrestrische biodiversiteit wereldwijd.

Bestaande mondiale biodiversiteitsmodellen zijn vooral gericht op het kwantificeren van de effecten van landgebruik en klimaatverandering op terrestrische biodiversiteit. Hoofdstukken 2 en 3 presenteren nieuwe contextspecifieke biodiversiteitsresponsrelaties voor twee relatief slecht vertegenwoordigde drukfactoren (eutrofiëring (stikstof) en lineaire infrastructuur). Beide hoofdstukken laten zien dat de respons van biodiversiteit op deze drukfactoren in hoge mate contextafhankelijk is. Hoofdstuk 2 is gebaseerd op een nieuwe mondiale dataset van 4.365 waarnemingen uit 126 studies die de effecten van stikstoftoename op de aantallen of diversiteit van geleedpotigen of nematoden (aaltjes) hebben onderzocht. Met behulp van meta-analytische regressiemodellen zijn de effecten van stikstoftoename gekwantificeerd in relatie tot omgevingscondities en soortkenmerken. De respons van geleedpotigen op stikstoftoevoeging was voornamelijk afhankelijk van de wijze van metamorfose (gedaanteverwisseling) en, in mindere mate, de lokale jaargemiddelde temperatuur. Geleedpotigen met volledige metamorfose (inclusief bestuivers) namen in aantal af bij een toename van stikstof, vooral bij hogere temperaturen, terwijl geleedpotigen met onvolledige metamorfose (inclusief plaagsoorten) in aantal toenamen. Effecten van stikstof op aantallen aaltjes waren afhankelijk van hun voedselkeuze en de lokale jaarlijkse neerslag, met consistent negatieve effecten in drogere gebieden. De diversiteit van geleedpotigen was niet afhankelijk van stikstof, terwijl de diversiteit van aaltjes afnam. Hoofdstuk 3 is gebaseerd op een synthese van 253 studies die het effect hebben onderzocht van de aanwezigheid van lineaire infrastructuur (zoals wegen, hoogspanningsleidingen) op de aantallen van 792 gewervelde soorten, waaronder zoogdieren, vogels, reptielen en amfibieën. Vleesetende en kleine plantenetende zoogdieren (bijvoorbeeld knaagdieren) waren talrijker in de nabijheid van infrastructuur, terwijl middelgrote en grote herbivoren minder voorkwamen, vooral in gebieden met een open vegetatiestructuur. Vogels waren minder talrijk in de nabijheid van infrastructuur, met name waar het niet-vleesetende soorten betrof. Daarnaast waren de negatieve effecten van infrastructuur op vogels sterker in gebieden met een gesloten vegetatiestructuur, zoals bossen, dan in open gebieden. Reptielen waren talrijker in de buurt van infrastructuur in gebieden met een gesloten vegetatiestructuur, maar niet in open gebieden. Amfibieën waren ongeveer de helft minder talrijk in de nabijheid van infrastructuur, maar dit effect reikte niet verder dan ongeveer 30 meter.

Hoofdstukken 4 en 5 presenteren ruimtelijk expliciete analyses van de gecombineerde effecten van verschillende menselijke drukfactoren op biodiversiteit op basis van innovatieve combinaties van biodiversiteitsresponsrelaties en ruimtelijk expliciete data van milieudruk. Hoofdstuk 4 beschrijft de eerste mondiale studie naar het gecombineerde effect van landgebruik en stikstofdepositie op de soortenrijkdom van planten. Hiertoe zijn responsrelaties voor landgebruik en stikstofdepositie geïntegreerd in een nieuw ontwikkeld soort-oppervlaktemodel waarmee veranderingen in plantensoortenrijkdom kunnen worden gekwantificeerd in gridcellen van 0.25^{o} (ongeveer 25x25 km). Het mondiaal gemiddeld verlies aan plantensoortenrijkdom bedroeg 26%, met landgebruik als de belangrijkste oorzaak. De effecten van beide drukfactoren vertoonden aanzienlijke geografische variatie, waarbij Europa het meest getroffen continent was en Zuid-Amerika het minst. Hoofdstuk 5 presenteert de eerste pantropische analyse van het gecombineerde effect van landgebruik en jacht op de verspreiding van tropische zoogdieren (1.884 soorten). Hiertoe zijn verspreidingskaarten van de soorten gecombineerd met gedetailleerde landgebruikskaarten (~300 m resolutie), soortspecifieke habitatvoorkeuren en nieuwe responsrelaties voor de effecten van jacht op het voorkomen van zoogdieren, afgeleid op basis van een pantropische database met 3.281 waarnemingen. Gemiddeld genomen is het verspreidingsgebied van de onderzochte soorten met ongeveer de 40% afgenomen als gevolg van landgebruik en jacht. Landgebruik bleek de belangrijkste oorzaak van dit verlies, maar met name voor grote soorten is jacht ook een belangrijke factor. Daarnaast bleken landgebruik en jacht aan te grijpen op verschillende delen van het verspreidingsgebied en zijn de effecten in toegenomen tussen 1992 en 2015. Het hoofdstuk voorziet in een pantropische kaart van de effecten van beide drukfactoren ten behoeve van het aanwijzen van prioritaire gebieden voor beschermingsmaatregelen.

Op basis van de bevindingen van dit proefschrift kan worden geconcludeerd dat het afleiden van meta-analytische responsrelaties een veelbelovende benadering is voor het kwantificeren van contextafhankelijke, grootschalige effecten van drukfactoren op biodiversiteit. Deze responsrelaties kunnen worden gebruikt ten behoeve van extrapolatie naar verwante gebieden of soort(groep) en waarvoor weinig empirische gegevens beschikbaar zijn. Bovendien kunnen de meta-analytische responsrelaties worden geïntegreerd in ruimtelijk expliciete biodiversiteitsmodellen waarmee de relatieve en gecombineerde effecten van verschillende drukfactoren kunnen worden gekwantificeerd. Hiermee vormt dit proefschrift een belangrijke stap voor het beter kwantificeren van de menselijke impact op de wereldwijde terrestrische biodiversiteit en het onderbouwen van nationale en mondiale natuurbeschermingsagenda's, inclusief het mondiale post-2020 raamwerk voor biodiversiteit.

RESUMEN

Los modelos de biodiversidad global (GBM, por sus siglas en inglés) son esenciales para evaluar el estado de la biodiversidad e informar las políticas de conservación. Sin embargo, la mayoría de los GBM presentan ciertas limitaciones ya que: 1) no tienen en cuenta cómo las presiones humanas pueden variar su impacto dependiendo del contexto local, es decir, en qué manera las características y condiciones locales modifican las relaciones impacto-respuesta observadas por los investigadores (o variaciones locales); 2) no cuantifican los impactos combinados de múltiples presiones, y 3) tienen carencias para incorporar las respuestas de las especies para las cuales no existe suficiente información ecológica. Por lo tanto, esta tesis tiene como objetivo mejorar la forma en que los GBM evalúan las respuestas de la biodiversidad a las presiones humanas mediante: 1) el desarrollo de nuevas relaciones de respuesta para presiones humanas infravaloradas que permitan además su extrapolación a regiones y/o especies poco estudiadas, y 2) demostrar cómo utilizar estos tipos de modelos para combinar el impacto de múltiples presiones humanas a gran escala. En última instancia, la tesis ayuda a mejorar nuestra comprensión de cómo los impactos humanos están poniendo en peligro la biodiversidad terrestre en todo el mundo.

Actualmente, los GBM se centran mayoritariamente en cuantificar el impacto del cambio climático y de los cambios en el uso del territorio. En los capítulos 2 y 3 se han desarrollado nuevas relaciones de respuesta para presiones y grupos taxonómicos poco estudiados, teniendo en cuenta las posibles variaciones locales que modifiquen la respuesta de la biodiversidad. Ambos capítulos muestran que, efectivamente, la respuesta de la biodiversidad depende en gran medida de las condiciones locales. En el capítulo 2 se ha compilado un nuevo conjunto de datos a escala global con 4,365 observaciones pareadas, correspondientes a 126 artículos, que estudian el efecto del enriquecimiento de nitrógeno en la riqueza y/o abundancia de artrópodos y/o nematodos. Se han establecido modelos meta-analíticos para explorar los cambios en la biodiversidad a lo largo de un gradiente de niveles de adición de nitrógeno y en relación con las condiciones ambientales locales y los rasgos biológicos de las especies. La respuesta de la abundancia de artrópodos a la adición de nitrógeno está mediada principalmente por su tipo de metamorfosis y, en menor medida, por la temperatura media anual a escala local. La abundancia de artrópodos con metamorfosis completa (p. ej., polinizadores)

se reduce a medida que aumentan los niveles de nitrógeno, especialmente en climas más cálidos, mientras que aquellos con metamorfosis incompleta (p. ej., especies consideradas como plaga) aumentan con mayores niveles de nitrógeno. La respuesta de la abundancia de nematodos al enriquecimiento de nitrógeno varía entre grupos tróficos y está modulada por la precipitación media anual a escala local, de forma que la disminución de la abundancia de nematodos resulta siempre mayor en áreas más secas. Además, la riqueza de artrópodos no muestra una respuesta a la adición de nitrógeno, pero la riqueza de nematodos disminuye consistentemente con el aumento de los niveles de nitrógeno. En el capítulo 3 se sintetizan 253 estudios que cuantificaron la magnitud del impacto y el área afectada por infraestructuras lineales (es decir, las zonas de efecto de infraestructuras lineales como carreteras o líneas de alta tensión) sobre la abundancia de 792 especies de vertebrados, incluyendo mamíferos, aves, reptiles y anfibios. Con respecto al efecto en mamíferos, los carnívoros y los herbívoros de menor tamaño (p. ej., micro-mamíferos) aumentan en abundancia en las proximidades a infraestructuras, mientras que los herbívoros de tamaño mediano y grande disminuyen, especialmente en hábitats abiertos. La abundancia de aves se reduce en la proximidad de infraestructuras, con zonas de efecto más extensas para las especies no carnívoras que para las carnívoras. Además, las aves en hábitats cerrados tales como bosques, se ven más afectadas que las aves asociadas a áreas abiertas. Por su lado, los reptiles son más abundantes cerca de infraestructuras en hábitats cerrados, pero no en hábitats abiertos. Finalmente, la abundancia de anfibios se redujo aproximadamente a la mitad en las proximidades a infraestructuras, pero el impacto desapareció alrededor de los 30 metros de distancia.

Los impactos combinados de presiones humanas sobre la biodiversidad terrestre todavía están infra-representados en los GBM, pero existe una preocupación creciente sobre cómo los efectos interactivos de múltiples presiones pueden poner aún más en peligro la biodiversidad. En los capítulos 4 y 5 se desarrollan metodologías novedosas para combinar varias presiones humanas mediante el uso de modelos meta-análiticos y datos geoespaciales recientes. El capítulo 4 proporciona la primera evaluación global del efecto combinado del uso del territorio y la deposición de nitrógeno en la riqueza relativa de especies de plantas. Se ha desarrollado un nuevo modelo de relación “especies-área” (SAR, por sus siglas en inglés) para, primero, integrar las respuestas de las comunidades de plantas tanto al cambio de uso del territorio como a la deposición de nitrógeno y, segundo, evaluar los cambios resultantes en la riqueza de especies de plantas por todo el mundo, en cuadrículas de 0.25 grados (unos 25x25 km). Globalmente, los resultados indican una pérdida media de riqueza de especies del 26% debido a ambas presiones combinadas, siendo el uso del territorio el principal responsable de la pérdida de especies. Ambos impactos tienen una variación geográfica considerable, siendo Europa el continente más afectado y América del Sur el que menos. Por último, el capítulo 5 establece la primera evaluación a escala pan-tropical del efecto combinado del uso del territorio y la caza sobre la distribución de mamíferos tropicales (1,884 especies evaluadas). Para la evaluación, se ha utilizado mapas de distribución de especies en combinación con mapas de uso del territorio espacialmente explícitos (con una resolución de aproximadamente 300 metros), datos de preferencia de hábitat específicos de las especies, y un extenso meta-análisis pan-tropical de extinciones locales inducidas por la caza (con 3,281 observaciones). En promedio, se ha estimado que el 40% del área óptima original para los mamíferos tropicales se ha perdido debido al efecto combinado de ambas presiones. El uso del territorio es el principal factor de la pérdida de área de distribución de mamíferos, pero la caza tiene un gran impacto en las especies de mayor tamaño. Además, estas dos presiones se muestran como altamente complementarias, afectando diferentes partes del área de distribución de las especies, y aumentando desde los años 90 (entre los años 1992 y 2015). Asimismo, se ha elaborado un mapa pan-tropical que identifica zonas críticas de pérdida de área debido a la combinación de ambas presiones (puntos calientes o *hotspots* en inglés) y zonas que aún se encuentran poco afectadas y que actúan como refugio para las especies (puntos fríos o *coolspots* en inglés). Este mapa facilita la delimitación de áreas prioritarias para la mitigación o prevención de ambas presiones a escala pan-tropical.

Sobre la base de los resultados de esta tesis, se concluye que los modelos meta-analíticos que incluyen rasgos biológicos de las especies y variables ambientales a escala local son una herramienta eficaz para cuantificar de qué manera el impacto de las presiones humanas sobre la biodiversidad varía dependiendo del contexto local. Además, estos modelos son ampliamente aplicables, ya que pueden evaluar impactos a gran escala en múltiples entornos y especies, incluso para aquellas especies para las cuales se carece de datos empíricos sobre sus respuestas a las presiones humanas. Asimismo, los métodos utilizados para combinar los efectos de varias presiones constituyen un paso importante de cara a la cuantificación sistemática de los impactos de múltiples presiones humanas en los modelos de biodiversidad global. Por lo tanto, las herramientas y los resultados de esta tesis pueden ayudar a evaluar de manera más holística los impactos humanos sobre la biodiversidad terrestre y, en última instancia, servir de hoja de ruta para informar las agendas nacionales y globales de conservación, incluyendo el marco de trabajo para la biodiversidad global post-2020.

CV

D

On February 19th 1992 I was born in Valladolid, Spain. I grew up in a small but beautiful town called El Escorial, northwest of Madrid, in the Sierra de Guadarrama. When I was a child I could not go much to the field because of health problems, but my passion and curiosity for nature did not stop me from learning as much as I could about nature's wonders. During my high school at the Real Colegio Alfonso XII, my favourite class was, of course, Biology. In 2010 (the International Year of Biodiversity) I graduated from high school, and during that summer, I was lucky to join my first field campaign, focused on assessing the impact of a thermal powerplant on freshwater biodiversity. I enjoyed the monitoring of biodiversity so much, that I immediately decided to pursue the BSc in Biology at the Complutense University of Madrid. During my studies, I discovered the world of birds and butterflies and decided to increase my knowledge by joining different monitoring projects. In my last year of the BSc, I got awarded with an Erasmus grant to do my thesis in Helsinki and I decided to do it at the Natural History Museum of Finland. Although until that time I was mostly interested in fieldwork, I decided to focus my thesis on analyzing long-term data to learn about statistics and spatial analysis. During my time in Finland, I was also lucky to get my first two jobs as a field assistant at the University of Helsinki. It was amazing to discover Finland's nature by doing fieldwork. After Finland, I graduated as a biologist in Madrid in 2015 and decided to do an MSc in Nature Conservation in Prague. During my year in Prague, I got three nice opportunities. First, I learned about GIS and remote-sensing analysis, which I really enjoyed; second, I monitored fire salamanders in the Czech Republic to assess their status in relation to a deadly virus; and third, I got the chance to obtain a double MSc with Cranfield University in the UK. In 2016, I moved to the UK and started my second MSc in Environmental Data Science. During that year I learnt different programming languages, did a 4-months group project for the Flood and Coastal Committee of East Anglia, and did my MSc thesis at the Natural History Museum of London. My time at the Natural History Museum was truly a dream. Thanks to my thesis, I got amazed by data analyses so I decided to start applying for PhDs in global biodiversity assessments. However, after completing my MSc, I also felt like going back to the field, so I first went to Mexico to capture and monitor birds of prey in what it is the biggest migration of raptors on Earth, the Veracruz River of Raptors. After (almost) two amazing months in Mexico, I started my PhD at the Environmental Science Department of Radboud University in November 2017. Here, I specialized in developing and applying (meta-analytical) models for quantifying human impacts on biodiversity across scales. I also kept myself busy in the field and I became a certified bird ringer by the Dutch Centre for Avian Migration and Demography at the Ooijse Graaf station. Almost five years after the start of my PhD project, I feel that I grew in so many aspects, from professional and intellectual to personal, that I cannot express it with words. Now that I am finished, I feel ready to apply all my knowledge and experiences to my true passion, NATURE.

PUBLICATION LIST

E

PEER-REVIEWED JOURNAL ARTICLES

Published or accepted

Baláz, V., Solský, M., Lastra González, D., Havlıková, B., **Gallego-Zamorano, J.**, González Sevilleja, C., Torrent, L., & Vojar, J. (2018). First survey of pathogenic fungus Batrachochytrium salamandrivorans in wild and captive amphibians in the Czech Republic. Salamandra, 54, 87–91.

Beaujean, S., Nor, A. N. M., Brewer, T., **Gallego-Zamorano, J.**, Dumitriu, A. C., Harris, J., & Corstanje, R. (2021). A multistep approach to improving connectivity and co-use of spatial ecological networks in cities. Landscape Ecology, 36(7), 2077-2093.

Benítez-López, A., Santini, L., **Gallego-Zamorano, J.**, Milá, B., Walkden, P., Huijbregts, M. A., & Tobias, J. A. (2021). The island rule explains consistent patterns of body size evolution in terrestrial vertebrates. Nature Ecology & Evolution, 5(6), 768-786.

de Jonge, M. M., **Gallego-Zamorano, J.**, Huijbregts, M. A., Schipper, A. M., & Benítez-López, A. (2022). The impacts of linear infrastructure on terrestrial vertebrate populations: A trait-based approach. Global Change Biology, 28 (24), 7217-7233.

Duplouy, A., Woestmann, L., **Gallego-Zamorano, J.** & Saastamoinen, M. (2018). Impact of male condition on his spermatophore and consequences for female reproductive performance in the Glanville fritillary butterfly. Insect Science, 25.

Gallego-Zamorano, J., Benítez-López, A., Santini, L., Hilbers, J. P., Huijbregts, M. A., & Schipper, A. M. (2020). Combined effects of land use and hunting on distributions of tropical mammals. Conservation Biology, 34(5), 1271-1280.

Gallego-Zamorano, J., Huijbregts, M. A., & Schipper, A. M. (2022). Changes in plant species richness due to land use and nitrogen deposition across the globe. Diversity and Distributions, 28(4), 745-755.

Gallego-Zamorano, J., Hokkanen, T., & Lehikoinen, A. (2018). Climate-driven synchrony in seed production of masting deciduous and conifer tree species. Journal of Plant Ecology, 11(2), 180-188.

Plumptre, A. J., Baisero, D., Belote, R. T., Vázquez-Domínguez, E., Faurby, S., Jędrzejewski, W., ...**Gallego-Zamorano, J**., & Boyd, C. (2021). Where might we find ecologically intact communities?. Frontiers in Forests and Global Change, 26.

Sevilleja, C. G., Van Langevelde, F., **Gallego-Zamorano, J.,** Bassignana, C. F., & Wynhoff, I. (2022). Sod translocation to restore habitats of the myrmecophilous butterfly Phengaris (Maculinea) teleius on former agricultural fields. Ecology and evolution, 12(9), e9293.

Simmons, B. I., Balmford, A., Bladon, A. J., Christie, A. P., De Palma, A., Dicks, L. V., **Gallego-Zamorano, J.**, ... & Finch, T. (2019). Worldwide insect declines: An important message, but interpret with caution. Ecology and Evolution, 9(7), 3678-3680.

Submitted

Gallego-Zamorano, J., de Jonge, M., Runge, K., Huls, S., Wang, J., Huijbregts, M.A.J. & Schipper, A.M. Context-dependent responses of terrestrial invertebrates to anthropogenic nitrogen enrichment.

Santini, L., Tobias, J., Callaghan, C., **Gallego-Zamorano, J.**, Benítez-López, A. Global patterns and predictors of avian population density.

CONFERENCES

Effects of hunting and land cover change on tropical mammals. British Ecological Society-Macroecology 2018.

European bee abundances are modulated by local and landscape context interactions. Netherlands Annual Ecology Meeting 2019.

Effects of hunting and land use on tropical mammals. Netherlands Annual Ecology Meeting 2019.

Hunting pressure complements land use in reducing available habitat of tropical mammals. International Congress of Conservation Biology 2019

Assessing the combined effect of N-deposition and land use on plant species richness. Netherlands Annual Ecology Meeting 2020.

Differential effects of nitrogen addition on terrestrial invertebrates. NWO Life 2022.

Context-dependent responses of terrestrial invertebrates to anthropogenic nitrogen enrichment. European Congress of Conservation Biology 2022.

ACKNOWLEDGEMENTS

F

People tend to think that a PhD is just 4 or 5 years of work. For me, the PhD journey has been much more than just work, it has been a massive personal and professional development, and it started long before I arrived at Radboud University. Many people have contributed making this journey a part of my life that I could never forget (in a good way) and helped me to achieve the realization of this thesis. This section is for all of you (bear with me, it might be longer than a paper).

Aafke, I believe that you still remember our first encounter at the Natural History Museum of London. That was probably one of the luckiest moments in my life. You immediately showed your interest and trust in me, which soon after, resulted in offering me this PhD. I will be always thankful for that opportunity and all your guidance during these years (related or not to the PhD). You have taught me so many things that I cannot select one, but on top of all the valuable lessons, you helped me to grow as a researcher and as a person; I couldn't be more grateful for that. What I accomplished in this thesis would not have ever been possible without you. You helped me to give shape to my crazy ideas, and to polish them into papers that I could only dream of (especially the text!). We managed to create an amazing team which I am sure I will miss; although I am also sure that our paths will cross each other in the future.

Mark, I cannot be happier about what we managed to achieve, both professionally and personally, in these years. Perseverance is the only way to achieve great things, I believe that in our relationship that is what made you never quit on me and what made me never quit on you. It took us long to build trust in each other but once we managed, I really enjoyed working with you. You helped me to strengthen my thoughts and to defend them with the conviction that only knowledge and science can provide. I am especially grateful for all those quick chats that we had in the last years of the PhD (even when you were extremely busy) that helped me to keep pushing in the right direction and finish everything smoothly.

It is never easy to start working in a new place (a new country) and even less starting a PhD but you, Ana and Luca, made me feel at home from the very beginning. Thank you so much for "standing me on your shoulders", because, for me, you are truly giant scientists. You also helped and supported me during this journey, even in the worst moments, as if I were one of your own students. I owe you so much that I will never be able to pay it back, not even with 1000 more papers together. Laura, you also helped me to feel Nijmegen as my home (although you felt that it was not yours anymore), thank you!. I want to especially remark the Benítez-López & Santini (2018) Scotland project of "hunting" Marlee Tucker to our Nijmegen crew, you brought who became one of my biggest pillars during these years. Marlee, although you are not in any of my chapters, without your support and friendship I would have never ever finished this thesis. Since the very first moment, I noticed that our relationship was something "sospechoso" and felt very connected to you. Every moment with you was, is and will be "delightful" because you are always there to help and listen to me, thanks for being as you are. I am sure we will keep having moments and adventures together for long (I owe you that you could not attend my defence personally).

I, of course, need to thank all the people at the Environmental Science department of Radboud University. From the coffee talks to the department activities, Daniel, Selwyn, Coline, Michela, Melinda, Mirza, Caterina, Tamara, Kiane, Fiona, Jelle, Steef, Mitchell, Cristiana, Irene, Koen, Francesco, Anne...(big etc!) you all gave me strength to keep working every day on this thesis until I finished it. All the bad moments of the PhD are less if you have nice people around, and all of you are extremely nice people! The administrative people, Gina and Henny, you simply make the life easier for all the new people arriving at the department, thank you for all your help with the bureaucracy. Then I want to mention some special people that will last in my mind always. Daniel, I will certainly miss our deep talks when the department was empty already, I will also miss your dad-jokes which became truly dad-jokes with Tiago! Selwyn and Coline or Coline and Selwyn, our trip through Scotland is probably one of my best moments of the PhD, we really learnt how to put up a tent in seconds and how to survive with tins under the rain. Thank you for all the good moments together from the dinners and discussions to the trips, Bosnia is another unforgettable memory! Mirza, you are simply such a good person that you deserve everything, thank you for teaching me so much at the beginning and for showing me your amazing culture! I can say that you showed me one of my current favourite bands (Dubioza kolektiv). Melinda, the last years working together were a win-win for me, you helped me to be as thorough as possible and I think I helped you to be more pragmatic with things, thank you so much for everything (including the master class about making beer! Joost you rock!). Kiane, I guess that hippies are attracted to each other, your hugs are pure energy that made me start my days with a smile. I admire you in so many aspects that I cannot list them, thanks for being such a good friend and paranimfen. Mitchell, my borrelman, I always enjoyed our talks which ~80% of the time were with a beer. Since the A1 course, we knew that drinks will join us and so we run the department borrels as the best borrelteam ever! Steef, keep organizing events for the department because that creates our family atmosphere, thanks for it! Cristiana, believe it or not you were a big support in the last year of my PhD, thank you so much for everything (especially the amazing chocolate!). Jelle and Veerle, thank you so so much for all the moments together, I hope that your Spanish soul will keep lighting forever (maybe we will see each other in Spain in the future!). Por último, Caterina e Iván, vosotros me habéis transportado a España cuando más lo necesitaba, con cada paella, hamburguesa, charla, me habéis ayudado a sacar energía para terminar. Sois de lo mejor que he conocido en estos años, ¡gracias de todo corazón!

Time for some words for two of the most special and unexpected reunions of my life. Francesca, such a coincidence that after 4 years of our Helsinki adventure, we both ended up in Nijmegen. You are one of those people that give brightness to life; every time that we meet you enlightened me to keep enjoying what I was doing. You certainly gave me the strength that I needed for finishing this thesis. Coni, from Chichicaxtle to Nijmegen, who could say that? The dinners, the Wingspan, but especially the birding days with you and Devin certainly helped me to keep pushing. Hopefully, we will have many more of those days in the future (in any continent).

I could not have finished this PhD, which was purely computer-based, without expending long hours in the field. My passion for birds got stronger in these years thanks to you Bram, Ward, Ruud, and Joost. Thanks to all of you, I completed one of my dreams, becoming an official bird-ringer. The Ooijse Graaf will always be in my mind. Moreover, in these years I discovered another passion, butterflies (vlinders!). Irma and Chris (and Cristina), you showed me this fantastic world from which I will never escape. It was such a pleasure to go butterfly-watching with you around Europe that I could be doing 15min counts for a month or more, like in Madeira! Thank you so much for everything (not only the butterflies)!

This PhD is not only the result of 4 years of work, my research career started back in Madrid in 2010 where I did my Bachelor's in Biology. Javi, tu siempre me animaste a volar alto y me diste las alas para hacerlo, jamás te estaré lo suficientemente agradecido por todos tus consejos y enseñanzas. Aunque nunca hayas sido mi supervisor directo, siempre te he considerado mi mentor. Part of the scientist that I am is thanks to everyone that believed in me during my stay in Finland. Aleksi, you and all the HeLLO group welcomed me in Helsinki as I could ever imagine being a bachelor student. You made me fall in love with (surprisingly) data and R! You taught me how to make good science and you have been always there when I needed you, even years after I left Finland. I could not be happier for finding you when I decided to start living abroad, thanks a lot! Sara, Diego, Ed, and Andy, you were a huge example of good scientists and better people, thank you so much for sharing so many things with me. Similarly, Ricardo and Alvaro, you were extremely nice to me (and Cristina) and is always a pleasure to meet you around the world! Oscar, the Finnish people introduced us, and since then, you have been always there to advise me and encourage me, thank you so much for all your support! Mar and Marjo, you trusted in me and gave me my first jobs as a biologist, which encouraged me to keep doing science and resulted in this thesis, thanks! My stay in Prague was short but some people made it extremely worth it, and I am pleased that I met them. Vitek, you taught me for the first time one of my favourite topics, geospatial analysis! I enjoyed so much every hour of the GIS class that I decided to keep learning it. Jiri, you showed me the fantastic world of salamanders which I love now. Moreover, thanks to the efforts of Peter and Lukáš I finished going to the UK where I had the privilege of working at probably one of the best places in the world, the Natural History Museum of London. Adriana, you were such a dedicated supervisor that I cannot thank you for all your lessons (I still owe you publishing my thesis!). Andy, for me you are one of the greatest scientists that I have ever met, but more importantly, you were as kind and supportive to me as you are with your son (although you do not like birds!). Thanks to both of you, I finished finding the best PhD that I could ever imagine.

I must also thank all the inspiration that Future For Nature and Future For Nature-Academy gave me during all these years. My passion for nature exponentially grew with each meeting, event or award. You are all great young conservationists! I am sure you will continue engaging people to fight for nature with your passion and inspiring stories! I am especially thankful to you Ignas, Rascha, Onnika, and all the FFN-Academy from Nijmegen, we nailed our Academy-Day.

Tiempo para dirigirme a la gente con la que más comparto mis pensamientos y modo de ser, "mis" biólogos y biólogas. Desde la Complu hasta la CULS pasando por Helsinki, siempre me habéis apoyado en todo lo que he hecho y sois mi mayor fuente de inspiración, amigos y amigas que mantendré durante toda la vida. Gracias a vosotros y vosotras, he conseguido terminar uno de mis sueños. Luci, la petirroja que siempre está atenta a cada paso que doy. Desde que te conocí has estado en cada momento importante de mi vida, ¡hasta te lees mis artículos! Gracias por siempre estar ahí. Álvaro, eres de las personas más transparentes que conozco y con las que mejor me lo paso siempre, luchador como pocos, cada vez que hablamos de todos tus proyectos, me inspiras. Siempre has sido un apoyo enorme en cada uno de mis pasos y en esta tesis igual, ¡eres un grande, José! Sergio, del odio (fugaz) al amor, desde el primer momento de la carrera hemos estado juntos y siempre lo estaremos. Tú has sido de las pocas personas que ha venido a visitarme en todos los países en los que he vivido y eso siempre me ha dado fuerzas, ¡gracias! Nuestro sueño de convertirnos en grandes científicos cada día está más cerca, esta tesis es para mí el primer paso, ¡ahora te toca a ti! Adri, eres posiblemente la persona más trabajadora que conozco, ¡tu energía es arrolladora! A pesar de las mil cosas al día que haces, siempre has sacado tiempo para mí cuando te lo he pedido ¡hasta desde el otro lado del mundo! Gracias por inspirarme y enseñarme que cualquier cosa se consigue con esfuerzo, esta tesis es un ejemplo. Santi, desde El Escorial hasta Georgia o Nijmegen, nunca ha habido quién nos pare en aquello de perseguir nuestros sueños. Gracias por todos los momentos juntos. Guille y Sarita, gracias por iluminarme con vuestro conocimiento en cada conversación, seguid siendo tan inquietos porque no hay nada mejor que una mente crítica y gente que te la despierte. Beto, contigo pude descansar de la tesis y volver con más fuerzas para empezar una nueva etapa, esas dos semanas en Baja fueron fantásticas ¡gracias mostri! Lejos de casa conocí a un tipo muy especial, con una barba y un corazón tan grande como el de un misticeto. Héctor, tu amor por la vida se contagia, y siempre que hemos hablado me has "envenenado" de esa energía tan fuerte que te caracteriza (¡gracias!), ¡ojalá hubiese más personas como tú por el mundo! En la ciudad más bonita del mundo (Praga), conocí a una "batwoman" catalana que me marcó para siempre. Laura, seguramente eres la persona más importante que conocí en República Checa. Contigo he aprendido muchísimo sobre murciélagos, recetas, y la vida en general. ¡Gracias por aguantar todas mis bromas y por darme momentos inolvidables!

Jon, desde que te conocí siempre me ha alucinado tu capacidad de encontrar ideas para hacer nuevos proyectos. Cada conversación contigo ha sido y será un ¡disfrute! Eres de los mejores pajareros y científicos que conozco, y estoy seguro que en un futuro sacaremos ese Science, Nature, o Journal of whatever que tanto nos gustaría. Y para cerrar este apartado de gente espectacular, gracias a ese grupo de pajareros locos y enamorados de los búhos, los Brinzaleros. En especial a Patri, Raúl, Raquel, Alberto, Iván, y Patcat, cada momento que paso con vosotros (ojalá pudiera pasar más) deseo que sea infinito, gracias por ser tan buenos conmigo. En definitiva, gracias a todos por ser parte de mi vida.

Gracias a mis amigos de El Escorial. Fran, Pablo, Deivid, Diegui, aunque no sepáis estrictamente a lo que me dedico, siempre estáis ahí cuando vuelvo a casa y eso es mucho. Lo mismo que tú, Sandra, gracias por escucharme siempre que lo necesito. A los fuenlabreños, Vero y Casta, gracias por los Catanes, las risas, y en definitiva los momentos juntos; no sé cómo habéis aguantado mis chapas sobre la tesis. Bruna, tu conseguiste plasmar mis ideas en una realidad que superó mis expectativas, esta tesis no luciría tanto sin tu talento en ella, gracias por haber convertido mis capitulos en obras de arte. Albis, aunque nos conocimos en el pueblo, nuestras vidas han evolucionado lejos de él, pero siempre paralelas. Ahora eres de las personas más importantes de mi vida y que más apoyo me ha dado estos años. Poco puedo decir que no sepas, simplemente, gracias por ser.

Nada de lo que he hecho en esta tesis, ni de lo que hago, pudiera ser posible sin el apoyo incondicional de mi familia. Papá, Mamá, Dani, sin duda parte de esta tesis es vuestra porque soy como soy y he llegado hasta aquí, gracias a vosotros. A pesar de la distancia siempre os siento cerca y siempre me apoyáis en todo (incluyendo mis aventuras por el mundo). Gracias por quererme tal y como soy. Sois el “seguro” que todo hijo y hermano quisiera en el caso de fallar, pero que nunca se necesita porque vuestro cariño le hace volar. ¡Os quiero! Igualmente, el cariño por parte de la familia Sevilleja, Julia, Sara, Isma, Sergio y David (no puedo poner a todos los Sevilleja porque si no, no termino) siempre me ha hecho evadirme de la tesis cuando lo necesitaba y me ha dado fuerzas para volver a retomarla. ¡Gracias por vuestro apoyo y por acogerme como a uno más siempre! (aunque no pueda estar mucho en casa por las gatas). Y por supuesto, gracias a la parte más reciente de mi familia, Gala. Aunque nos conocemos desde hace poco, siento como si hubiésemos crecido juntos, y estos últimos meses de tesis me has apoyado como tal, ¡qué alegría tenerte!

Para terminar, las últimas palabras que escribo de mi tesis tienen que ir dirigidas a la persona que día tras día ha estado a mi lado. Cristina, tú eres la compañera de viaje que cualquiera desearía. Gracias a la energía, el apoyo, y la luz que me has dado durante estos años, esta tesis ha sido mucho más sencilla. En verdad, cualquier cosa me resulta sencilla desde que estás en mi vida. Supongo que tener siempre pájaros en la cabeza y mariposas en el estómago, hace que uno pueda volar sin esfuerzo. Asique, ¡sigamos volando juntos hacia nuevas aventuras y sueños! ¡Te re-quiero!

This thesis research has been carried out under the research data management policy of the Radboud Institute for Biological and Environmental Sciences, accessed at www.ru.nl/ribes.

CHAPTER 2

Gallego-Zamorano, Juan et al. (2022), Data from Context-dependent responses of terrestrial invertebrates to anthropogenic nitrogen enrichment, Dryad, Dataset, https://doi.org/10.5061/dryad.pnvx0k6r4

CHAPTER 3

De Jonge, Melinda (2022), Data from: Advances in large-scale multi-species impact assessments: chapter 3. DANS: https://doi.org/10.17026/dans-xcw-zyvh

CHAPTER 4

Gallego-Zamorano, Juan; Huijbregts, Mark; Schipper, Aafke (2022), Changes in plant species richness due to land use and nitrogen deposition across the globe, Dryad, Dataset, https://doi.org/10.5061/dryad.f1vhhmgx7

CHAPTER 5

Gallego-Zamorano, J. (Radboud University); Benitez Lopez, dr A. (Radboud University); Santini, dr. L. (Radboud University); Huijbregts, prof. dr. M.A.J. (Radboud University); Schipper, dr. A.M. (Radboud University) (2020): Data from: Combined effects of land use and hunting on distributions of tropical mammals. DANS. https://doi.org/10.17026/dans-zah-vs6x

SENSE

Netherlands Research School for the
Socio-Economic and Natural Sciences of the Environment

D I P L O M A

for specialised PhD training

The Netherlands research school for the
Socio-Economic and Natural Sciences of the Environment
(SENSE) declares that

Juan Gallego-Zamorano

born on 19th February 1992 in Valladolid Spain

has successfully fulfilled all requirements of the
educational PhD programme of SENSE.

Nijmegen, 27 January 2023

Chair of the SENSE board	The SENSE Director
Prof. dr. Martin Wassen	Prof. Philipp Pattberg

The SENSE Research School has been accredited by the Royal Netherlands Academy of Arts and Sciences (KNAW)

KONINKLIJKE NEDERLANDSE
AKADEMIE VAN WETENSCHAPPEN

The SENSE Research School declares that Juan Gallego-Zamorano has successfully fulfilled all requirements of the educational PhD programme of SENSE with a work load of 51.9 EC, including the following activities:

SENSE PhD Courses

- Environmental research in context (2018)
- Research in context activity: ‘Organising the Future For Nature Academy day’ (2020)

Other PhD and Advanced MSc Courses

- Zero Inflated Models in R, PE&RC and SENSE (2018)
- Scientific Writing for PhD Candidates, Radboud University (2018)
- University Teaching Qualification 1, Radboud University (2018)
- Masterclass Git, GitHub and Markdown in a R-environment, Royal Netherlands Meteorological Institute (2018)
- Scientific writing for PhD candidates, Radboud University (2019)
- Animal Movement Analysis, PE&RC (2019)
- Grant writing and Presenting for funding committees, Radboud University (2020)
- Meta-analysis, Maastricht University (2021)
- Education in a Nutshell, Radboud University (2022)

Management and Didactic Skills Training

- Organising Journal club for the Environmental Science Group, Radboud University (2018)
- Organising different events related to conservation biology the for Future For Nature Academy day, Radboud University (2018-20209)
- Teaching in the BSc courses ‘Man and the Environment (2017-2021), Introduction to R (2018-2021) and ‘Geographic Information Systems’ (2020-2021), and the MSc course ‘Biodiversity and Ecological Assessment (2018-2021)

Oral Presentations

- *Effects of hunting and land cover change on tropical mammals*. British Ecological Society-Macroecology 10-11 July 2018, St.Andrews, United Kingdom
- *European bee abundances are modulated by local and landscape context interactions*. Netherlands Annual Ecology Meeting , 12-13 February 2019, Lunteren, The Netherlands
- *Hunting pressure complements land use in reducing available habitat of tropical mammals*. International Congress of Conservation Biology, 20-25 July 2019, Kuala Lumpur, Malaysia
- *Differential effects of nitrogen addition on terrestrial invertebrates*. European Congress of Conservation Biology 22-26 August 2022, Prague, Czech Republic.

SENSE coordinator PhD education

Dr. ir. Peter Vermeulen