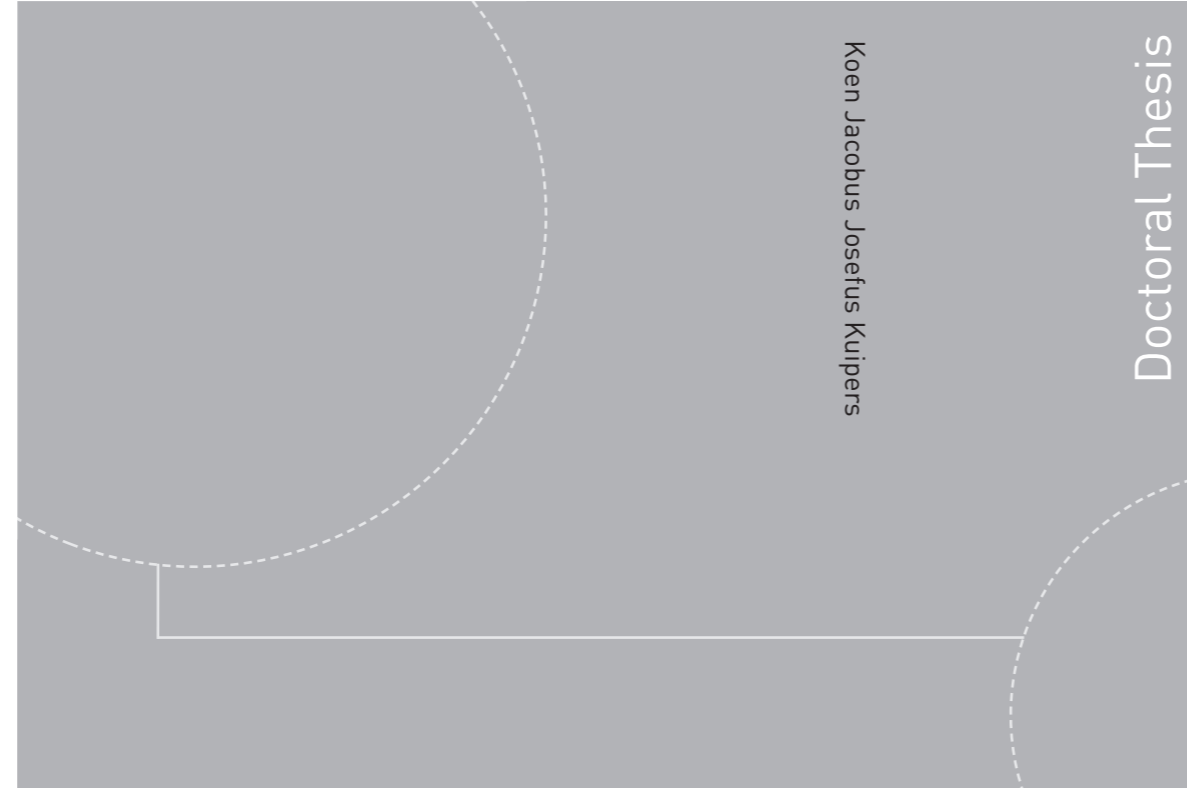


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Koen Jacobus Josefus Kuipers

**Predicting global habitat conversion
and fragmentation effects on
terrestrial vertebrate species richness
with species-area models within the
life cycle impact assessment
framework**

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Thesis for the degree of Philosophiae Doctor

Trondheim, August 2020

Norwegian University of Science and Technology
Faculty of Engineering
Department of Energy and Process Engineering



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Preface

The thesis has been submitted to the Faculty of Engineering Science in partial fulfilment of the degree of Philosophiae Doctor. This work was carried out at the Industrial Ecology Programme and the Department of Energy and Process Engineering at the Norwegian University of Science and Technology in Trondheim, Norway, in the period 2016-2020.

Koen Jacobus Josephus Kuipers

Trondheim, April 2020

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Then, thanks to my colleagues, most of whom became my close friends. I am unsure whether the RBK matches, (overambitious) ski- or occasional cabin trips made me feel Norwegian or emphasised my foreignness, but I do know that I really enjoyed the years spent in Trondheim. Alex, Eivind, Dan, Cristina, the Jans, John, Lorenzo, Helene, Martin, Magnus, Maren, Otavio, Philomena, Romain, and all others, mange takk! Furthermore, I must acknowledge the importance of my colleagues in the LCIA group. The labyrinth of impact assessment models frequently made our heads spin and jointly attempting to unravel them has been fun, funny, and educational.

Also, I really appreciated the visits from my friends and family members who cared to cross the North Sea! I am delighted that there are too many names to name, and sad about those who last-minute could not make it over to Norway due to current travel restrictions. Of course, special thanks to Isabelle, who visited me more than anyone else and whose company I always love.

Finally, I would like to thank my family. Marius and Gertrude, thanks for having been so closely involved in all decisions that led me to where I am now. Pap, mam, and Lot, our shared humour never failed to cheer me up, especially when I needed it!

Abstract

Habitat change is the single largest threat to global biodiversity. Mainly caused by human land use, this results in the loss and fragmentation of natural habitat and subsequent losses of species. The relevance of halting and reversing biodiversity loss caused by habitat change is recognised by international efforts, such as the Aichi biodiversity targets or the Sustainable Development Goals (SDGs, specifically, SDG 15). A variety of studies and assessments is needed to guide strategies to reach these goals and to assess whether we are on the right track for reaching them. In this light, a quantitative understanding of the effects of human land use is essential.

Environmental decision-support tools can help to channel such information into decision-making processes, thereby helping to guide actions and strategies to minimise biodiversity impacts. Life cycle assessment (LCA) is such a tool that comprehensively assesses impacts along complete value chains. However, currently available life cycle impact assessment (LCIA) models for global land use impacts on species richness consider the effects of habitat conversion only and neglect the additional effects of habitat fragmentation. This means that land use impacts may be systematically underestimated in current LCAs. To more completely capture impacts related to land use, both habitat conversion and fragmentation effects should be considered. This thesis contributes to improving the LCIA characterisation of land use impacts by developing a novel method that considers the combined effects of habitat conversion and fragmentation.

I investigated possible options for including the consideration of fragmentation effects within the LCA framework (Chapter 2). Based on a species-area relationship (SAR) approach, I developed a model that considers the global combined effects of habitat conversion and fragmentation on regional (non-flying) mammal species richness (Chapter 3). Fragmentation effects are estimated from changes in habitat connectivity based on the number and size of habitat patches, permeability of the matrix separating the patches, and species dispersal distances. The results suggest that neglecting fragmentation effects results in an average underestimation of land use impacts of about 10%. This reflects the relevance of considering fragmentation in addition to habitat conversion. In addition to regional species losses, we are interested global species extinctions. Hence, I developed an approach for indicating the potential effect of regional species loss on global species extinctions in a taxon- and regionally-specific manner (Chapter 4). The results highlight focal regions for the conservation of global species richness. A combination of the SAR model including fragmentation and the estimation of the global extinction probabilities results in a novel LCIA land use characterisation method (Chapter 5). This spatially differentiated LCIA model for land use impacts on species richness is globally applicable and considers the combined effects of habitat conversion and fragmentation on amphibians, reptiles, birds and mammals. Overall, these characterisation factors improve the potential for characterising impacts of land use in LCAs more completely.

The limitations regarding a global approach like the one proposed here is that it generalises impacts over larger scales, potentially not accurately reflecting local responses to habitat conversion or dispersal behaviour of specific species. Nevertheless, large-scale studies may help to identify global trends or to trace impacts spanning across regions. Hence, LCA biodiversity assessments are best suited for comparative analyses at larger scales. This thesis is an important step forward to more completely cover the aspects of land use impacts on species richness in LCA.

Publications

This thesis is based on the four articles listed below as primary publications. Two of these articles have been published in the Journal of Life Cycle Assessment and Environmental Science and Technology, respectively. One of these articles is being prepared for submission at Proceedings of the National Academy of Sciences of the United States of America and one is being prepared for submission at Science of the Total Environment.

The articles listed as secondary publications are related to, but not included in this thesis. One of these articles has been published in Science of the Total Environment and the other is being prepared for submission.

Primary publications

Kuipers KJJ, RF May, BJ Graae, F Verones. 2019. Reviewing the potential for including habitat fragmentation to improve life cycle impact assessments for land use impacts on biodiversity. *International Journal of Life Cycle Assessment* 24: 2206-2219.

Author contribution: Literature review and writing.

Kuipers KJJ, S Hellweg, F Verones. 2019. Potential consequences of regional species loss for global species richness: a quantitative approach for estimating global extinction probabilities. *Environmental Science & Technology* 53: 4728-4738.

Author contribution: Research design, modelling, data analysis, and writing.

Kuipers KJJ, JP Hilbers, J Garcia-Ulloa, BJ Graae, R May, F Verones, MAJ Huijbregts, AM Schipper. In preparation. Effects of habitat conversion and fragmentation on mammal species richness worldwide. To be submitted to Proceedings of the National Academy of Sciences of the United States of America.

Author contribution: Research co-design, data collection, modelling, data analysis, and writing.

Kuipers KJJ, R May, F Verones. In preparation. Considering habitat conversion and fragmentation in characterisation factors for land use impacts on vertebrate species richness. To be submitted to Science of the Total Environment.

Author contribution: Research design, modelling, data analysis, and writing

Secondary publications

Dorber M, **KJJ Kuipers**, F Verones. 2020. Global characterization factors for terrestrial biodiversity impacts of future land inundation in life cycle assessment. *Science of the Total Environment* 712(134582).

Author contribution: Assisted in partial method development, contributed to writing

Lekve-Bjelle E, **KJJ Kuipers**, F Verones, R Wood. In preparation. Trends in national biodiversity footprints of land use. Submitted to *Ecological Economics* (ECOLEC_2020_1305).

Author contribution: Assisted in partial method development and writing

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Chapter 1: Introduction

Chapter 1: Introduction

1.1. Global land use and its effect on species richness

The sharp rise in the global extinction rate relative to pre-human levels is a key indicator of the Anthropocene (Crutzen 2002; Dirzo et al. 2014), where global human activity leaves virtually no ecosystem unaffected (Sanderson et al. 2002). Roughly 25% of the studied terrestrial species are currently threatened with extinction according to the International Union for Conservation of Nature's (IUCN) Red List criteria (IPBES 2019; IUCN 2019). Of the terrestrial vertebrates, amphibians are under highest pressure with 41% of the amphibian species threatened with extinction, followed by mammals (25%), reptiles (19%), and birds (13%) (IUCN 2019). Current extinction rates are estimated to be a factor 100-1,000 larger compared to rates between and similar to those during previous mass extinction events (Barnosky et al. 2011; Pimm et al. 2014), suggesting that we are currently in the midst of the sixth mass extinction (Ceballos et al. 2015, 2017).

Most of the steep increases in extinction risks and sharp declines in species richness can be directly attributed to anthropogenic pressures. The main direct pressures are, in order of relevance, habitat conversion, climate change, overexploitation, pollution, and the introduction of invasive species (Pereira et al. 2012; IPBES 2019). The importance of protecting ecosystems is recognised globally and reflected in international agreements and targets such as the Aichi biodiversity targets (CBD 2010) and the Sustainable Development Goals (SDGs) (UN 2019). Yet, none of these anthropogenic pressures have been effectively mitigated at the global scale and rather show increasing trajectories over recent decades (Butchart et al. 2010; Tittensor et al. 2014; Johnson et al. 2017).

Habitat conversion, the pressure with the largest relative global impact is addressed in Aichi targets 5, 7, and 11 and SDG 15. It is largely caused by the increase of human land use at the cost of natural habitat (MEA 2005; Tilman et al. 2017). This land cover change is so vast and rapid that it is distinctly visible from space, continuously monitored by satellite imagery. 77% of the ice-free land has been modified by the direct effects of human activities (Watson et al. 2016, 2018; Allan et al. 2017), mostly due to agricultural expansion (Foley et al. 2005; Ellis and Ramankutty 2008; Ramankutty et al. 2008; Gibbs et al. 2010). For example, global forests are estimated to cover only 62% of their original (i.e., pre-human) extent (Steffen et al. 2015). To illustrate this rapid change, Fig. 1 shows the Amazon forest cover in 1985 and 2015, revealing the magnitude of deforestation in southern parts of the Amazon over the last 30 years.

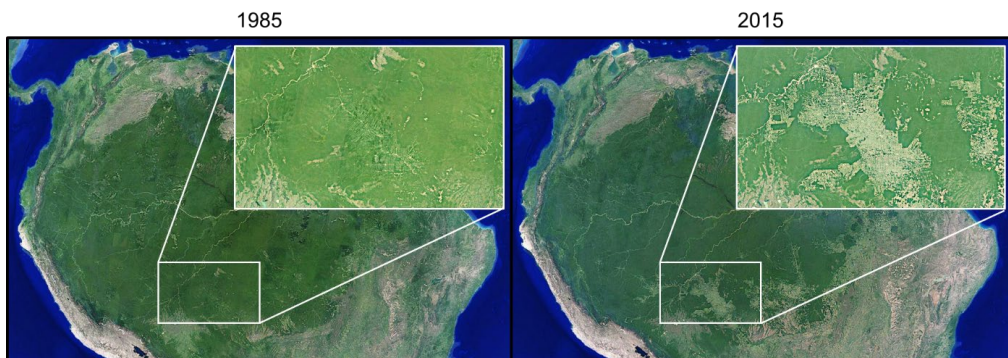


Figure 1. Deforestation in the Amazon between 1985 (Landsat) and 2015 (Copernicus) (Google Earth).

Globally, habitat conversion has been estimated to reduce local species richness by an average of 14% (Newbold et al. 2015). On a regional level, habitat conversion and fragmentation disrupt natural species ranges. Insufficient habitat availability and connectivity may threaten long-term survival, meaning that some species are committed to extinction unless their habitats are restored (Hanski and Ovaskainen 2000, 2002; Haddad et al. 2015). Such time-delayed extinctions are known as the extinction debt (Tilman et al. 1996).

Biodiversity hotspots form regions that are specifically vulnerable and relevant for global species richness (Myers et al. 2000; Marchese 2015). Pimm and Raven (2000) projected that even if deforestation in tropical forest hotspots would have halted in 2000, these hotspots eventually lose 18% of their species by 2100 due to induced habitat loss prior to 2000.

Habitat conversion does not only lead to loss of habitat, it typically also leads to fragmentation of the natural land cover (Ibisch et al. 2016; Taubert et al. 2018; Jacobson et al. 2019), dividing the remaining habitat into smaller and more isolated fragments. Fragmentation reduces the available habitat beyond just the area converted as species may not be able to reach all fragments. Besides negatively affecting habitat connectivity, habitat fragmentation increases species communities' exposure to external threats along habitat edges, putting many specialist species at risk as their environmental niches diminish (Ewers and Didham 2005; Fischer and Lindenmayer 2007). This issue of habitat fragmentation can be exemplified with the current global forest cover: more than 70% of the world's forest area is within 1 km of its edge (Krauss et al. 2010; Haddad et al. 2015), and only 20% of the tropical forest area constitutes intact fragments larger than 500 km² (Potapov et al. 2017).

Fragmentation effects, independent of habitat loss, are hard to isolate and quantify due to differentiated species responses (Fahrig 2003, 2017) and the relationship between habitat conversion and fragmentation (e.g., fragmented landscapes tend to comprise little habitat) (Bartlett et al. 2016). This has led to considerable debate on the contribution of fragmentation effects relative to the effects of habitat loss only (Fahrig 2013, 2015; Villard and Metzger 2014; Hanski 2015; Fletcher et al. 2018; Fahrig et al. 2019). Nevertheless, global meta- and comparative analyses show that fragmented ecosystems are characterised by lower species richness and higher species extinction risks (Haddad et al. 2015; Crooks et al. 2017; Pfeifer et al. 2017; Tucker et al. 2018). The mechanisms of fragmentation influencing species richness are discussed in more detail in chapter 2 of this thesis.

Understanding the individual and combined effects of habitat conversion and fragmentation is important for the development of strategies to effectively mitigate or reverse land use impacts on ecosystems. Modelling the effects of habitat conversion and fragmentation on species richness contributes to the improved understanding of patterns of biodiversity loss and informs environmental decision-making about potential impacts or effects of mitigation or restoration strategies.

1.2. Modelling global habitat loss and fragmentation impacts on species richness

Incomplete regional and taxonomic data and lags in species responses to environmental changes make it difficult to measure the global impacts of anthropogenic land use on species richness. Modelling approaches help to uncover general patterns ensuing habitat conversion and fragmentation and can be used to predict effects of past, current, or future land use on species richness at the global scale.

The species-area relationship (SAR) describes the relationship between increasing number of species with increasing area on the regional level, typically in a power function (Arrhenius 1921; Dengler 2009). The rationale for this positive correlation is that larger sample areas tend to

contain a higher diversity of habitat niches accommodating different species (Connor and McCoy 1979; Triantis et al. 2003) and that the equilibrium of species immigration and extinction rates in large, well-connected sample sites results in higher species richness compared to smaller sample sites (MacArthur and Wilson 1963, 1967; Whittaker et al. 2017).

Modern land use tends to reduce land cover heterogeneity and the size and connectivity of natural “habitat islands” in a homogenous “sea” of human-modified land cover. SARs are therefore commonly used to estimate the effect of habitat conversion on regional species richness as natural habitat is converted into human land use types (Keil et al. 2015). Habitat conversion may not lead to immediate species loss, meaning that the region may hosts more species than expected until the extinction debt has been paid, elevating the probabilities of extinction for all species in the region (Martins and Pereira 2017; IPBES 2019).

Several SAR varieties exist that differentiate between land-use and land cover types. The matrix-calibrated (Koh and Ghazoul 2010) and countryside SAR (Pereira and Daily 2006) are prime examples that are commonly used in conservation research that account for habitat heterogeneity by respectively adjusting the SAR slope or area variables depending on the suitability of the landscape elements to the regional species community (discussed further in chapter 2). The countryside SAR has been used in several studies to quantify the effects of global land use on plant and vertebrate species richness (Chaudhary and Brooks 2018, 2019; Marques et al. 2019). Due to data limitations, these global approaches have so far not extended across other taxonomic groups.

Although these SAR models consider the size of various land cover types and the magnitude of their change, they do not consider the explicit spatial configuration of the different land types, thus neglecting fragment distributions and permeability of the land cover separating habitat fragments (i.e., the matrix). Consequently, traditional SAR models may not adequately capture the relationship between the remaining habitat area and species richness in fragmented landscapes (Rybicki and Hanski 2013). Thus, fragmentation effects, relating to habitat availability due to reduced connectivity, are not captured by species-area models (Matthews et al. 2014).

Metapopulation theory describes the viability of a network of habitat fragments to sustain species populations based on minimum species area requirements, fragment sizes, and dispersal across the fragments (Hanski 1998). The metapopulation capacity is a measure for the capacity of a landscape to support species populations (Hanski and Ovaskainen 2000) and can be used in combination with species-area models to consider habitat connectivity in fragmented landscapes (Hanski et al. 2013).

Network analysis is used as another method for measuring habitat connectivity (Saura and Pascual-Hortal 2007), which can be used to quantify effects of land cover change on connectivity (Bodin and Saura 2010) and effectively available habitat (Saura et al. 2011). This approach is often used for quantifying the connectivity of protected areas (Saura et al. 2017). In chapter 3, a SAR model that incorporates network analysis is used to consider the combined effects of habitat conversion and fragmentation ensuing human land-use on mammal species richness at the global scale.

Habitat conversion and fragmentation impacts are geographically heterogeneous as both pressures and responses to these pressures differ per region and species community (Matias et al. 2014; Haddad et al. 2015). Although regional species loss gives an indication about the global extent of land-use impacts, declines in regional species richness do not necessarily lead to global extinctions. Extinctions in regions hosting high numbers of threatened and endemic species are more likely to cause global extinctions compared to extirpations in regions with few threatened

and endemic species (Orme et al. 2005). Therefore, the distribution of endemic and threatened species richness is relevant for prioritisation strategies and targeting conservation efforts (Kier et al. 2009). Consequently, predicting global extinction rates from global anthropogenic land-use requires above-mentioned regionalised models combined with a method to translate regional impacts into global extinctions. A method for such conversion is discussed in chapter 4.

Knowledge on global land-use impacts on species richness can be used to develop strategies to meet the global biodiversity targets or to monitor the progress towards meeting these targets. Incorporating this knowledge into decision-support tools can make it available to policy makers and can aid the development of comprehensive strategies for meeting several sustainability targets simultaneously, while considering potential trade-offs between them.

1.3. Life cycle assessment

To progress towards meeting global sustainability and biodiversity targets, comprehensive actions are needed that can address various targets to prevent trade-offs from reducing one specific impact. This requires assessments available to policy-makers that quantify impacts in a consistent manner. This is the objective of quantitative impact assessments, which channel knowledge arising from modelling approaches such as discussed above into impact indicators, reflecting specific changes in environmental conditions resulting from human pressures (Ness et al. 2007). The use of impact indicators intends to ease the interpretation and comparison of consequences of human impacts without getting lost in the totality of specific effects of anthropogenic activities.

Life cycle assessment (LCA) is such a comprehensive decision-support tool that considers various pressures and impacts at the global scale. It is widely used—e.g. for E.U. and national policy (European Commission 2003, 2005a, b), environmental product declarations (Flanigan et al. 2013), and company-level assessments (Clavreul et al. 2017; Shahmohammadi et al. 2018)—for assessing the impacts of products or processes over entire value chains (ISO 2006). This means that the impacts associated with a product or process are the sum of all the impacts occurring during resource extraction, production, transportation, use, and disposal phases. LCA can be used to i) compare the environmental impacts of similar products, ii) identify where in the product's life cycle the highest impacts occur, and iii) assess which impacts are dominant in the product's life cycle (Hellweg and Mila i Canals 2014). Hence, LCA can inform policy and decision makers about product alternatives to minimise environmental impacts, identify impact hotspots both technically and geographically, and assess potential trade-offs between different impact types when trying to minimise a specific impact. Therefore, LCA is often used for creating strategies to reduce the environmental impacts of products, consumption, or activities.

The strength of LCA is that it can estimate the contribution of various impacts simultaneously. Hence, impacts that occur through emissions (e.g., greenhouse gas emissions) and wastes (e.g., ammonia leaching), as well as the degradation (e.g., habitat conversion) and depletion of natural resources (e.g., extraction of rare earth elements) can be compared throughout all life cycle stages.

LCA consists of four stages. The first and last stages comprise the goal and scope definition and the interpretation of the results, respectively. The second and third phases constitute the modelling of the impacts related to the product or process. The second phase comprises the development of the life cycle inventory (LCI), constituting all physical and energy flows throughout all life cycle stages. This includes the emissions and wastes into the environment as well as the and degradation and depletion of natural resources.

The third stage is the life cycle impact assessment (LCIA), which transforms the LCI environmental pressures occurring along the value chain into impact indicators. To get to these indicators, the physical flows from or into the natural environment are multiplied with so-called characterisation factors (Hauschild and Huijbregts 2015). For land-use, the physical flow represents the area of land used of a certain land-use type (de Souza et al. 2015). The corresponding characterisation factor represents the species richness impact per-area land-use of the respective land-use type. The land-use type-specific impacts are calculated based on SAR approaches and converted into per-area impacts (Curran et al. 2016). LCA methods are still under development and over the last decades, modelling of land-use impacts evolved from simple taxonomically generic species-area models (de Schryver and Goedkoop 2008) to more sophisticated regionally and taxonomically specific species-area models (Chaudhary et al. 2015; Chaudhary and Brooks 2018). Because data on the spatial distribution and responses to human land-use is globally and comprehensively available for amphibians, birds, mammals, and reptiles only, the LCA land-use characterisation factors consider these vertebrate species groups exclusively. The development of LCA land-use impact modelling is discussed in detail in chapter 2.

Current LCA land-use impact modelling considers the effects of habitat conversion, but neglects additional fragmentation effects on species richness. This means that the land-use impacts may be systematically underestimated in LCA studies. Hence, developing an impact method that does consider fragmentation effects in addition to the effects of habitat conversion will improve the characterisation of land-use impacts in this decision-support tool. Chapter 5 proposes a novel method for characterising land-use impacts on species richness considering the combined effects of habitat conversion and fragmentation ready for use in LCA. This life cycle impact assessment method can be used in other decision-support tools as well, like environmentally extended input output analyses (EEIOA), which often rely on the same impact modelling approaches as those developed for LCA (Chaudhary and Kastner 2016; Verones et al. 2017; Marques et al. 2019).

1.4. Thesis contribution

Although habitat fragmentation research has expanded substantially over the recent decades (Ewers and Didham 2005; Fischer and Lindenmayer 2007; Didham et al. 2012), few generic models to predict the effects on global species richness that can be applied across taxonomic groups, habitats, and regions (e.g., Hanski et al. 2013; Thompson et al. 2017) have been developed. Moreover, new developments in fragmentation research have not been included regularly in impact assessment tools, leading to a potential underestimation of land-use impacts in impact assessments (discussed in chapter 2) and decision-making processes.

This thesis aims to develop a globally applicable method based on species-area models to quantify impacts of both habitat loss and fragmentation on regional and global terrestrial vertebrate species richness that can be readily used in impact assessments to support environmentally informed decision-making.

The research goals are:

1. Identify possibilities of incorporating fragmentation effects in the life cycle impact assessment (LCIA) for the application in LCA and EEIOA (Chapter 2).
2. Develop a model to predict habitat loss and fragmentation effects on vertebrate species richness (Chapter 3).
3. Develop a method to translate regional species loss into potential global species loss (Chapter 4).

4. Develop a set of characterisation factors ready for implementation in operational LCA and EEIOA (Chapter 5).

In chapter 2, fragmentation effects on species richness are identified and the potential for including these in LCA is discussed. In chapter 3, a regionally specific method for predicting the effects of habitat loss and fragmentation is developed and this method is globally applied to predict the effects of habitat loss and fragmentation on regional mammal species richness. Furthermore, the potential consequence of ignoring fragmentation is quantified. In chapter 4 a method for translating regional species loss into global extinctions is developed. In chapter 5, the framework described in chapter 2, the habitat loss and fragmentation impact model of chapter 3, and the regional species loss to global species extinction conversion factors of chapter 4 are combined to develop LCIA land-use characterisation factors that consider the combined effects of habitat conversion and fragmentation at the global scale.

Together, this thesis aims to contribute towards improved understanding of fragmentation effects and capability to predict these effects in decision-oriented tools like LCA.

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Chapter 2: Reviewing the potential for including habitat fragmentation to improve life cycle impact assessments for land use impacts on biodiversity

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Reviewing the potential for including habitat fragmentation to improve life cycle impact assessments for land use impacts on biodiversity

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Abstract

Purpose The biosphere is progressively subjected to a variety of pressures resulting from anthropogenic activities. Habitat conversion, resulting from anthropogenic land use, is considered the dominant factor driving terrestrial biodiversity loss. Hence, adequate modelling of land use impacts on biodiversity in decision-support tools, like life cycle assessment (LCA), is a priority. State-of-the-art life cycle impact assessment (LCIA) characterisation models for land use impacts on biodiversity translate natural habitat transformation and occupation into biodiversity impacts. However, the currently available models predominantly focus on total habitat loss and ignore the spatial configuration of the landscape. That is, habitat fragmentation effects are ignored in current LCIA models with the exception of one recently developed method.

Methods Here, we review how habitat fragmentation may affect biodiversity. In addition, we investigate how land use impacts on biodiversity are currently modelled in LCIA and how missing fragmentation impacts can influence the LCIA model results. Finally, we discuss fragmentation literature to evaluate possible methods to include habitat fragmentation into advanced characterisation models.

Results and discussion We found support in available ecological literature for the notion that habitat fragmentation is a relevant factor when assessing biodiversity loss. Moreover, there are models that capture fragmentation effects on biodiversity that have the potential to be incorporated into current LCIA characterisation models.

Conclusions and recommendations To enhance the credibility of LCA biodiversity assessments, we suggest that available fragmentation models are adapted, expanded and subsequently incorporated into advanced LCIA characterisation models and promote further efforts to capture the remaining fragmentation effects in LCIA characterisation models.

Keywords Life cycle assessment (LCA) · LCIA · Characterisation model · Characterisation factor · Habitat loss · Spatial configuration landscape · Species-area relationship (SAR) · Terrestrial ecosystems

1 Introduction

The biosphere is progressively subjected to increasing pressures (both in number and intensity) resulting from

anthropogenic activities (Rockström et al. 2009a, b; Newbold et al. 2015). These pressures can be direct (e.g. land use, pollution or overexploitation) and indirect (e.g. climate change or the introduction of invasive species) effects of human activities (Bellard et al. 2012; Pereira et al. 2012; Moritz and Agudo 2013; Newbold et al. 2016b). The current intensity and rate of environmental change are so vast that many species cannot adequately adapt to match the new environment and neither escape by migration to more suitable regions (Chevin et al. 2010). This has led to unprecedented declines in species populations and an increase in global biodiversity loss (Dirzo et al. 2014). Pimm et al. (2014) estimated that current extinction rates are roughly three orders of magnitude higher than fossil (i.e. pre-human) extinction rates. In effect, this leads to severe deterioration of the biosphere integrity.

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Anthropogenic land use (i.e. land transformation and occupation), resulting in habitat degradation (e.g. homogenisation), loss and fragmentation, is considered the dominant factor for terrestrial biodiversity loss (MEA 2005; de Souza et al. 2015; Newbold et al. 2016a). Natural habitat degradation, loss and fragmentation are distinct processes associated with diverse effects on ecosystems. Habitat degradation and habitat loss per se refer to the change in hospitability of the modified landscape elements (i.e. from natural to modified habitat). Habitat fragmentation is the process whereby habitat modification results in the division of continuous habitat into smaller, isolated habitat fragments separated by a matrix of modified territory (McGarigal and Cushman 2002; Fahrig 2003; Ewers and Didham 2005). That is, habitat fragmentation refers to the change in the average size, shape and spatial arrangement of the landscape elements. Fragmentation effects can be strong or weak and positive or negative, depending on the species (Fahrig 2017). The combination of the quality and spatial configuration of the landscape elements determines the ecological quality of the landscape (Fahrig 2003; Haddad et al. 2017b).

Large-scale and intensive land use jeopardises the ecological quality of landscapes globally, resulting in regional and global biodiversity loss. Severe loss of biodiversity potentially compromises the resilience of ecosystem functions and related ecosystem services (e.g. pollination) on which human well-being ultimately depends (Curran et al. 2016; Newbold et al. 2016a).

Due to its global relevance, modelling of land use impacts on biodiversity is considered a priority in decision-support tools like life cycle assessment (LCA) (Curran et al. 2016). LCA is a widely applied tool to systematically evaluate the cradle-to-grave environmental impacts of products or services to identify impact hotspots and promote options for reductions of environmental impacts (Hellweg and Mila i Canals 2014).

In recent years, efforts to improve the representation of land use impacts on biodiversity in LCA have led to the development of taxonomic and regionally specific characterisation models in life cycle impact assessment (LCIA) (de Baan et al. 2013b; Chaudhary et al. 2015). Most characterisation models, which generate so-called characterisation factors (CFs) for translating land use change from the life cycle inventory (LCI) into biodiversity loss metrics, are based on concepts from ecology and island biogeography theory (MacArthur and Wilson 1963, 1967). The currently available characterisation models focus solely on habitat degradation and area loss and do not include fragmentation effects that refer to the spatial configuration of the landscape (de Souza et al. 2015; Curran et al. 2016; Teixeira et al. 2016a). However, empirical research (Watling and Donnelly 2006; Krauss et al. 2010; Haddad et al. 2015) and theory (e.g. island theory or metapopulation theory) (MacArthur and Wilson 1967; Hanski 1999; Cook et al. 2002; Ewers and Didham

2005; Leroux et al. 2017), as well as habitat fragmentation models (Wahlberg et al. 1996; Hanski and Ovaskainen 2000; Hanski et al. 2013; Matias et al. 2014; Thompson et al. 2017), confirm the significance of habitat fragmentation in biodiversity assessments. Larrey-Lassalle et al. (2018b) were the first to address this gap in LCIA characterisation models and recently developed a novel LCIA method that accounts for forest isolation effects on birds in selected ecoregions.

The aim of this paper is (i) to discuss the relation between landscape configuration and biodiversity; (ii) to review current practices in LCIA characterisation modelling of land use impacts on biodiversity; (iii) to evaluate the need for specifying the landscape configuration in biodiversity assessments within LCA and (iv) to identify how future research can contribute to reach this goal.

2 Spatial configuration of the landscape and biodiversity

When discussing landscape elements, it is common to distinguish between the binary categories of hospitable habitat and hostile matrix (Haila 2002; Watling and Donnelly 2006). However, in reality the landscape consists of a gradient from hospitable to inhospitable areas that are conceived differently per species, obscuring a clear distinction between habitat and matrix elements (Haila 2002; Fischer and Lindenmayer 2007). Analogous to island biogeography theory and species-area relationships (SAR), we refer here to undisturbed natural habitat simply as habitat and to any anthropogenically modified habitat as matrix. The ecological quality of a matrix element can range from hospitable (e.g. similar to the natural habitat) to hostile (e.g. in high contrast with the natural habitat), depending on the affinity of the local species with the matrix element (Watling and Donnelly 2006; Prugh et al. 2008; Chaudhary et al. 2015). Since there is a gradient between hospitable and inhospitable matrix elements, it is not strictly correct to apply the term matrix for elements that are relatively hospitable (Ewers and Didham 2005). However, we apply this terminology to make a clear distinction between undisturbed (i.e. habitat) and disturbed (i.e. matrix) landscape components.

Anthropogenic habitat fragmentation is the division of continuous habitat into habitat fragments separated by a matrix of human-transformed land cover (Haddad et al. 2015) and thus involves changes in the landscape composition and structure. Although habitat loss and habitat fragmentation are often confounded, they are distinct processes accompanied by different ecological effects (McGarigal and Cushman 2002). The effect of habitat fragmentation is highly dependent on the hostility of the matrix, which affects the species' dispersal ability and severity of edge effects near borders between habitat fragments and the matrix (Fahrig and Merriam 1994; Ewers and Didham 2005; Fischer and Lindenmayer 2007). Habitat

fragmentation might have detrimental effects on specialist species (i.e. species with strong adaptation to an environmental niche), but may have varying effects on generalist species (i.e. species occurring in a broader range of environmental conditions) (Martensen et al. 2012; Estavillo et al. 2013; Betts et al. 2014). Hence, local increase in biodiversity is nowadays witnessed in some locations due to the introduction of invasive and generalist species. However, this can go at the cost of rare specialist species, leading to biodiversity loss on the global scale (Bender et al. 1998; Pardini et al. 2010; Fahrig 2017).

Fragmentation effects are commonly grouped under five categories that together describe the spatial attributes of the landscape patches: (1) patch area, (2) edge effects, (3) patch shape, (4) patch isolation and (5) matrix structure (Fahrig 2003; Ewers and Didham 2005). Here, we will discuss the implications of these fragmentation elements for biodiversity on the landscape scale. This scale comprises various habitat and matrix types.

Patch area Habitat fragmentation results in splitting continuous habitats into separated habitat patches, leading to a decrease in the average size of the remaining, natural habitat patches (Fig. 1a, b). This has additional impacts on biodiversity, independent of habitat loss per se. Small fragment areas impose a limit to population size and can impede recolonization rates. There are various mechanisms through which small populations are vulnerable to local extinction. Although these processes rarely act independently, they can be divided into four categories: (1) environmental stochasticity (e.g. seasonal or annual fluctuations in food supply), (2) natural catastrophes (e.g. floods or fires), (3) demographic stochasticity (e.g. fluctuations in sex ratios) and (4) reduced genetic diversity (e.g. genetic drift) (Wilcox and Murphy 1985; Ewers and Didham 2005; Fischer and Lindenmayer 2007; Swift and Hannon 2010; Leroux et al. 2017). A combination of increased extinction risks and decreased recolonization rates may lead to local extinctions.

Edge effects Splitting up habitat patches does not only result in an increase in number of patches and a decrease in average patch size but also result in increasing habitat edge relative to the remaining habitat interior (Fig. 1c, d). Habitat edges form a buffer zone or transition area between the habitat and matrix, where the nature of species interactions is altered due to overlaps of species from distinct habitats. The severity of the edge effects is partly determined by the contrast between the habitat and surrounding matrix (Ewers and Didham 2007; Laurance 2008). Also, the penetration depth of edge effects can vary widely, from tens of metres to several kilometres (depending on the habitat type and targeted species) (Fischer and Lindenmayer 2007). Species may respond differently to fragment edge and fragment interior areas. Specialist species often prefer to dwell in fragment interiors whereas generalist species

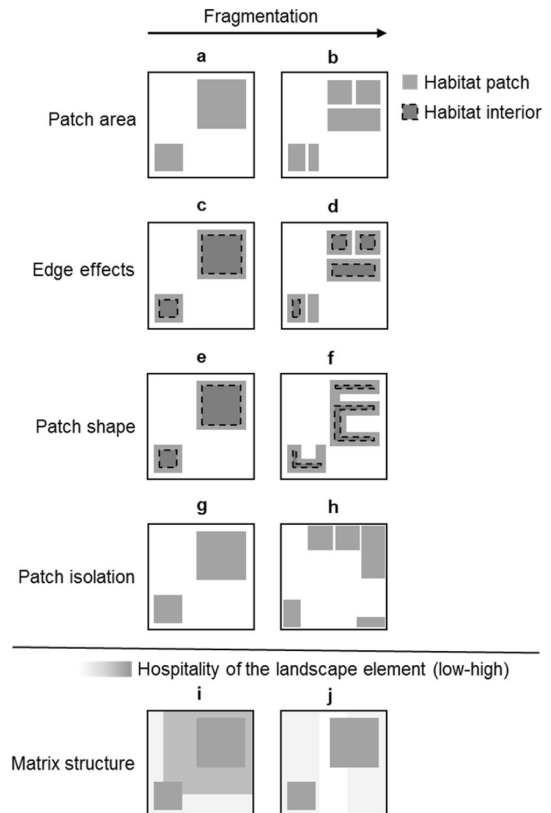


Fig. 1 Patch area, edge effects, patch shape, patch isolation and matrix structure. The total amount of habitat is identical in every figure; the total amount of habitat edge and interior varies; the hospitality of the landscape elements displays the contrast between the elements and the permeability of the landscape

prefer edge areas, even though mortality rates may be higher at edges compared with fragment interiors (Andren and Angelstam 1988). A decrease in the ratio of core to edge habitat leads to a reduction in the available habitat of core-dwelling species, increasing their extinction risk. On the local (e.g. road verges, forest edges, at tree lines or where communities in other ways meet) scale, species diversity is often higher in the edges due to species overlap from the various habitat types (Kark and van Rensburg 2006). However, when looking at the regional (i.e. landscape) scale, rare and more specialised species are generally resident in habitat interiors. Hence, increasing habitat edge might lead to an increase in biodiversity at the local scale, but to a decrease in biodiversity at the regional or global scale as the core specialists disappear.

Patch shape Fragments with complex shapes have a relatively high proportion of edge area. The convoluted nature of complex shapes can result in the division of interior habitat into

several interior areas separated by edge-affected habitat, imposing restrictions to the population size of core-dwelling species (Fig. 1e, f). Several small, separated interiors would have an average species density that is lower than a single continuous interior of the same total area (Ewers and Didham 2005, 2007). On the other hand, complexly shaped fragments are colonised more frequently than compact patches since the larger proportional amount of edge increases the probability that dispersing species encounter the patch (Ewers and Didham 2007). Following the same logic, emigration rates are also more likely in complex fragment shapes. The combination of increased immigration and emigration leads to an increase in turnover rate of individuals, increasing demographic variability in complex fragments and higher local species richness of generalist species (Ewers and Didham 2007). Furthermore, predation rates are often higher around the habitat exterior due to the abundant movement of species and reduced possibilities to search cover for prey species.

Patch isolation The most commonly studied effect of habitat fragmentation is the isolation of habitat fragments in space and time relative to other habitat patches (Fig. 1g, h). The level of isolation is dependent on the geographical location of the habitat fragment relative to other similar habitat fragments (e.g. the distance); the characteristics of the matrix (e.g. the presence and quality of dispersal routes) (Fahrig and Merriam 1994) and the dispersal capability of the species within the landscape (Ewers and Didham 2005; Thompson et al. 2017). Fragment isolation negatively affects species dispersal and consequentially their distribution patterns (Laurance 2008). Impeded dispersal and altered distribution patterns increases the species' vulnerability to extinction (Watling and Donnelly 2006).

Matrix structure The quality of the matrix significantly influences the severity of edge effects and largely determines the degree of isolation (Fig. 1i, j). Edge effects are more severe when the contrast between the landscape elements is higher. The degree of isolation of the landscape elements is higher when the elements are separated by a relatively hostile matrix. Nevertheless, habitat remnants are not necessarily the only landscape elements that provide resources. Hence, the matrix can both strengthen and mitigate the intensity of fragmentation effects (Ewers and Didham 2005). A landscape with an impenetrable and inhospitable matrix is likely to be subjected to the extinction of metapopulations (the collection of local populations inhabiting spatially distinct habitat patches) (Moilanen and Hanski 1998). A landscape with a matrix structure that allows for dispersal is likely to retain metapopulations, also when the colonisation-extinction dynamics are affected.

These above-mentioned mechanisms indicate that it is not only the total amount of habitat in a landscape but also the

spatial configuration of the landscape that matters for regional biodiversity. Fragmented landscapes involve several fragmentation effects simultaneously. Furthermore, responses to the various fragmentation effects differ per species. It is therefore difficult to determine the relative importance of each fragmentation effect for biodiversity in general terms. Nevertheless, some authors have tried to synthesise results of studies on single fragmentation effects on individual species. Ibáñez et al. (2014) found both positive and negative effects of change in patch connectivity, edge area and patch sizes in their meta-analysis of fragmentation effects on plant species diversity. They found that the average effect sizes of the fragmentation effects differ only marginally, and the effect size ranges indicate that the relative importance of the fragmentation effect is context dependent. A synthesis of various fragmentation experiments, performed by Haddad et al. (2015) reveals similar results on the effect sizes and ranges of patch size, edge area and patch isolation effects.

3 LCIA characterisation models for land use impacts on biodiversity: retrospective and state-of-the-art

3.1 Species-area relationship models in LCIA

The conventional LCA endpoint (or damage) indicator for damage to ecosystem quality is biodiversity loss. Although biodiversity is a multifaceted concept that encompasses different hierarchical levels of life (e.g. genes, species, populations, communities and ecosystems) and their various attributes (i.e. composition, function and structure) (Niemi and McDonald 2004; Curran et al. 2011, 2016; de Baan et al. 2013b), assessments in LCA have mainly focused on species richness, i.e. the community-level species number. The main reasons for this are data availability and the relative unambiguity regarding the interpretation of the indicator (Milà i Canals et al. 2007; Curran et al. 2011; de Souza et al. 2015; Teixeira et al. 2016b).

LCIA characterisation models for land use impacts on biodiversity evolved from spatially and taxonomically generic models using the traditional species-area relationship (SAR) concept (Köllner 2000; Goedkoop and Spriensma 2001; Köllner 2002; de Schryver and Goedkoop 2008; Koellner and Scholz 2008; Schmidt 2008; de Schryver et al. 2010), to spatially and taxonomically explicit models (de Baan et al. 2013a, 2015) using the matrix-calibrated SAR (de Baan et al. 2013b) and the countryside SAR (Chaudhary et al. 2015; Chaudhary and Brooks 2018). Using (variations of) the SAR allows for the quantification of species richness impacts if a habitat is converted into a human-modified area (i.e. land use types).

The SAR, often related to the island biogeography theory of MacArthur and Wilson (1963, 1967), denotes a power relationship between the amount of area (A) of an ecosystem and the number of species (S) it can facilitate (Eq. (1)):

$$S = c \cdot A^z \quad (1)$$

where c and z are constants dependent on the environmental conditions and characteristics of the species in the ecosystem that indicate the maximum species density per area unit and the slope of the species-area curve, respectively.

The traditional SAR assumes that no species persist on human-modified land, i.e. assuming a binary landscape of either habitat or non-habitat (i.e. the matrix). The matrix-calibrated SAR model (Koh and Ghazoul 2010) predicts lower species extinction risks compared with the traditional SAR when the new habitat or land use type is hospitable for some species groups. The suitability of the matrix is dependent on its relative share p of each land use type i and sensitivity σ of the taxonomic group g to each land use type i of total n types of the total converted land area (Eq. (2)) (Koh and Ghazoul 2010; Koh et al. 2010).

$$S_g = c \cdot A^z \cdot \sum_i p_i \cdot \sigma_{g,i} \quad (2)$$

However, even though the matrix-calibrated SAR tries to incorporate the fact that some species can persist in non-natural habitat, mathematically the number of species in a landscape will always be zero if all natural habitat is gone. In other words, without any natural habitat left, all species would go extinct locally, also in hospitable matrix types.

The countryside SAR (Pereira and Daily 2006) predicts that species adapted to human-modified habitats also survive in the absence of their natural habitat (Proença and Pereira 2013) by incorporating the affinity h of taxonomic group g with habitat or land use type i of n types (Eq. (3)) (Pereira and Daily 2006).

$$S_g = c \cdot \left(\sum_i^n h_{g,i} \cdot A_i \right)^z \quad (3)$$

The LCIA model based on the countryside SAR developed by Chaudhary et al. (2015) is currently operational in the LC-IMPACT method and is recommended by the Life Cycle Initiative hosted by UN environment for hotspot analysis (Frischknecht et al. 2016).

Hanski et al. (2013) developed the species-fragmented area relationship (SFAR, Eq. (4)): another SAR model variety that includes some fragmentation effects. The SFAR accounts for habitat patch isolation in a fragmented landscape by expanding the traditional SAR model with a measure for landscape fragmentation derived from metapopulation theory (metapopulation capacity, λ) and a

measure for the species' sensitivity to habitat fragmentation (b).

$$S = c \cdot A^z \cdot e^{-b/\lambda} \quad (4)$$

The metapopulation capacity captures the impact of landscape structure on metapopulation persistence (Hanski and Ovaskainen 2000). The metapopulation capacity of a landscape increases with the total amount of available habitat, but decreases with increasing fragmentation (Rybicki and Hanski 2013). It is based on the number of habitat patches in the landscape, the Euclidean distance between these patches and species dispersal characteristics. Thereby, the metapopulation capacity accounts for patch area isolation, but ignores patch shape, edge and matrix effects.

Larrey-Lassalle et al. (2018a) developed a methodology to derive the metapopulation capacity (λ) of a specific habitat type at the ecoregion level. Based on the ecoregion-level metapopulation capacity, they developed regionally specific CFs (Larrey-Lassalle et al. 2018b) for forest-dwelling bird species in the selected ecoregions by combining the countryside SAR (Chaudhary et al. 2015) with the SFAR (Hanski et al. 2013), thereby forming a countryside SFAR characterisation model (Eq. (5)).

This countryside SFAR accounts for the amount of available habitat A in ecoregion j , the affinity h of taxon g to habitat or land use type i , patch isolation λ in ecoregion j and the sensitivity b of taxon g to patch isolation (Eq. (5)).

$$S_{g,j} = c \cdot \left(\sum_i^n h_{g,i,j} \cdot A_{i,j} \right)^z \cdot e^{-b_g/\lambda_{g,j}} \quad (5)$$

With their countryside SFAR, Larrey-Lassalle et al. (2018b) were the first to explicitly account for the effects of forest patch isolation in land use LCIA modelling. However, their model is limited to forest habitat fragmentation and forest-dwelling bird species located in hotspots for forest biodiversity.

3.2 Reflections on land use characterisation models and fragmentation effects

Most above-mentioned characterisation models capture effects of the conversion from habitat to various land use types as well as conversions between land use types. The most basic models (Köllner 2000, 2002; Koellner and Scholz 2008; Schmidt 2008; de Baan et al. 2013a) do not go further than this. That is they assess local biodiversity impacts at the patch level and hence refer to α diversity (i.e. the species diversity of a specific site). These local impacts cannot always be aggregated to regional impacts, because biodiversity damage in the patch does not necessarily equate biodiversity damage on the landscape level. To make their models applicable to regions instead of patches, some have developed regional CFs

(Goedkoop and Spriensma 2000; de Schryver and Goedkoop 2008; de Schryver et al. 2010; de Baan et al. 2013b; Chaudhary et al. 2015) to classify the impacts of patch conversion in the region. These regional CFs refer to γ diversity (i.e. the total species richness in the landscape). So far, only de Baan et al. (2013b) and Chaudhary et al. (2015) developed CFs that refer to global species richness losses.

Table 1 provides an overview of the characterisation models with species richness indicators, showing that many indicators refer to alpha (i.e. plot scale) diversity in specific geographical areas, using land use effects on vascular plants as a proxy for overall species richness impacts.

The multi-habitat models consider the share of various habitat types in the landscape, but do not account for the shape and accessibility of the habitat types (i.e. the spatial configuration). Thus, although some of the above-mentioned characterisation models do consider habitat heterogeneity, only the countryside SFAR accounts for the spatial landscape configuration. However, the scope of the countryside SFAR is limited to patch isolation and neglects other fragmentation effects. Furthermore, the

countryside SFAR model described above focuses on birds and forest habitat in selected ecoregions only and does not incorporate a method to translate regional biodiversity loss into global biodiversity loss. Generally, there is a difference in ecological dynamics of a large, continuous habitat patch and of various isolated habitat patches of the same type, even though the total share of the habitat type relative to the whole landscape is the same. This can have consequences for the validity of the models since inaccessible habitat patches do not contribute to the total available habitat amount for a certain group of species.

4 Consequences of excluding fragmentation effects

Habitat conversion is a non-random process and typically spreads from human settlements and infrastructure (Laurance 2008). Habitat loss spreading from infrastructure typically causes habitat fragmentation, implying that anthropogenic habitat conversion is likely to cause fragmentation. Therefore, not accounting for fragmentation effects in LCIA

Table 1 LCIA land use characterisation models for species richness indicators

Characterisation model	Scale	Geographical coverage	Taxonomic specificity	Landscape heterogeneity	Spatial configuration effects
Köllner (2000)	Local (α)	Local (Swiss lowlands, Switzerland)	Plants as proxy	–	No
Lindeijer (2000)	Local (α)	Global (biomes)	Plants as proxy	–	No
Goedkoop and Spriensma (2000)	Local (α), regional (γ)	Local (Swiss lowlands, Switzerland)	Plants as proxy	Yes	No
Köllner (2002)	Local (α)	Local (Swiss Plateau, Germany, Alpine region)	Plants as proxy	–	No
Vogtländer (2004)	Local (α)	Local (Netherlands)	Plants as proxy	–	No
Koellner and Scholz (2008)	Local (α)	Local (Switzerland)	Plants as proxy	–	No
Schmidt (2008)	Local (α)	Local (Denmark, Indonesia, Malaysia)	Plants as proxy	–	No
de Schryver and Goedkoop (2008)	Local (α), regional (γ)	Local (UK)	Plants as proxy	Yes	No
de Schryver et al. (2010)	Local (α), regional (γ)	Local (UK)	Plants as proxy	Yes	No
Geyer et al. (2010)	Local (α), regional (γ)	Local (San Joaquin Valley, USA)	Vertebrates	Yes	No
de Baan et al. (2013a)	Local (α)	Global (biomes)	Arthropods, invertebrates, plants, vertebrates	–	No
de Baan et al. (2013b)	Local (α), regional (γ)	Global (ecoregions)	Amphibians, birds, mammals, plants, reptiles	Yes	No
Mueller et al. (2014)	Local (α)	Global (biomes)	Plants as proxy	–	No
de Baan et al. (2015)	Local (α)	Local (East Africa)	Mammals	–	No
Chaudhary et al. (2015)	Local (α), regional (γ), global	Global (ecoregions)	Amphibians, birds, mammals, plants, reptiles	Yes	No
Larrey-Lassalle et al. (2018b)	Regional (γ)	Global (selected ecoregions)	Birds	Yes	Patch isolation (forest)

land use impact categories can result in underestimations of biodiversity impacts. Underestimating biodiversity impacts in highly fragmented landscapes will lead to misleading results in LCIA biodiversity impact assessments.

Both matrix-calibrated SAR and countryside SAR models consider matrix effects to some extent by adjusting the species-area curve according to the matrix quality and by allowing a fraction of the original species to persist in the modified landscape, respectively. Thereby, these methods overcome the main deficit of applying island biogeography theory and the classical SAR to terrestrial landscapes, where terrestrial fragments are treated as ‘real islands’ in a hostile matrix. However, all three SAR models only look at the total amount of habitat and matrix types in the landscape without specifying the spatial structure of these landscape elements, thereby ignoring the edge effects, shape and isolation of the landscape elements (Whittaker et al. 2005; Laurance 2008; Hanski et al. 2013). In effect, even though the matrix quality is included in the matrix-calibrated and countryside SAR, this information is not used to incorporate dispersal and isolation effects. That is the matrix-calibrated SAR and the countryside SAR do consider differing matrix qualities (Fig. 1i, j), but do not link the spatial configuration of the matrix and habitat elements to fragmentation effects like edge effects and patch isolation. Hence, since island biogeography theory and most SAR models do not explicitly take into account the spatial configuration of heterogeneous terrestrial habitat fragments, methodological advancements are needed to adequately capture land use effects on biodiversity in a more comprehensive manner (Cook et al. 2002; Whittaker et al. 2005).

The countryside SFAR considers patch isolation by incorporating the distance between habitat fragments and species’ dispersal characteristics. However, the countryside SFAR does not consider the quality of the matrix for the patch isolation, which can lead to an underestimation of the degree of fragmentation. For example patch isolation is dependent not only on the distance between the patches but also on the hostility and structure (e.g. presence of barriers) of the matrix. Since a change in biodiversity dynamics is influenced by an interplay between habitat loss and fragmentation effects, a model that focuses on a single component of land use change may not capture its full effects on biodiversity (Leroux et al. 2017).

Despite theoretical and empirical support, there is also scepticism regarding the relative importance of habitat fragmentation per se compared with the total habitat area for biodiversity assessments (Fahrig 2003, 2017; Jackson and Fahrig 2016; Fahrig et al. 2019). Fahrig (2013) proposed the controversial habitat amount hypothesis, which suggests that the total amount of suitable habitat outweighs the spatial configuration of the landscape as an

explanatory variable for species diversity. Contradicting evidence from other studies (e.g. Wahlberg et al. 1996; Cook et al. 2002; Prugh et al. 2008), this view implies that the matrix quality and habitat isolation do not significantly affect species diversity, relative to the effect of total available habitat. This hypothesis stems from the notion that species respond differently to fragmentation—some species prefer edge areas and heterogeneous landscapes, whereas others prefer homogeneous interiors. Hence, fragmentation may favour some groups of species at the cost of others, resulting in no net change of biodiversity, depending on the (taxonomic) group of species studied. As the habitat amount hypothesis denies the relevance of species response mechanisms to landscape change (e.g. responses to patch shape, edge effects and patch isolation), the theory has been met with opposition from theoretical perspectives (Hanski 2015; Fletcher et al. 2018) and empirical evidence (e.g. Lindgren and Cousins 2017). The habitat amount hypothesis is supported by Melo et al. (2017), who tested the hypothesis on small mammals in the South American savannah. They identified some natural habitat types as matrix (e.g. savannah grassland) and based the degree of habitat isolation on the distance between habitat patches only, thereby ignoring matrix permeability. This suggests a sample design relatively favourable to prove the habitat amount hypothesis. Similar to Melo et al. (2017), Haddad et al. (2017a) tested the habitat amount hypothesis in controlled experiments in the USA and UK for plant and arthropod species, respectively. They, however, concluded that both amount and configuration of habitat affect species richness, thereby rejecting the habitat amount hypothesis. Torrenta and Villard (2017) tested the habitat amount hypothesis on birds in fragmented forests in Ontario, Canada, and supported the conclusions from Haddad et al. (2017a).

The perspective of the habitat amount hypothesis would support the application of the classical SAR model to terrestrial habitat fragments, but would not acknowledge the benefit of incorporating matrix effects in the matrix-calibrated SAR and the countryside SAR. Furthermore, it would reject the relevance of any other model capturing species’ responses to habitat fragmentation.

Considering the vast amount of research on fragmentation effects, the habitat amount hypothesis shows that habitat amount is probably the most important variable for predicting species diversity, but has so far been unable to provide sufficient evidence to ignore the spatial structure of the landscape. As ecologists acknowledge the relevance of fragmentation effects, demonstrated by the vast amount of studies on habitat fragmentation, so should the LCIA land use characterisation models for biodiversity impacts to more accurately assess how anthropogenic land use affects species diversity.

5 Potentials for representing habitat fragmentation effects

Incorporating habitat fragmentation effects in LCIA models for land use impacts on biodiversity can be complicated by the limited availability of model input parameters provided by the LCI. Furthermore, the models should be designed for species richness indicators to allow assessment of fragmentation effects on multiple species at once and not for single species such as the incidence function model (Wahlberg et al. 1996). Hence, not all fragmentation models are suitable for LCIA purposes.

Since anthropogenic land transformation and occupation are translated to biodiversity loss, it is straightforward to focus on models that incorporate fragmentation effects into SAR models. Tjørve (2002) was one of the first to consider multiple habitats in one theoretical SAR model instead of treating habitat as one continuous patch. The data intensity for implementing the multi-habitat model proposed by Tjørve (2002) is relatively high since the number of habitat patches, as well as the number of unique species per habitat patch in the landscape, should be provided. As this data is not readily available for every habitat patch globally, Tjørve's multi-habitat model (Tjørve 2002) is not applicable for LCIA characterisation models for land use impacts on (global) biodiversity.

Nevertheless, Tjørve's (2002) novel method inspired others to incorporate spatial aspects on the landscape level into adapted SAR models. Examples of models that incorporate the concept of habitat variability are the matrix-calibrated SAR (Koh and Ghazoul 2010) and the countryside SAR (Pereira and Daily 2006) that have been mentioned earlier. As mentioned before, these two models incorporate spatial aspects implicitly by considering varying habitat types in the landscape, but do not incorporate spatial configurations explicitly by considering the spatial structure of the landscape.

Arnillas et al. (2017) developed a model similar to Tjørve's multi-habitat SAR, by designing a SAR model considering the number, size and isolation of the habitat patches in the landscape together with the proportion of unique species per habitat patch and their dispersal characteristics. However, as the model proposed by Arnillas et al. (2017) is similar to Tjørve's (2002) multi-habitat model in terms of data requirements, the concept is not readily applicable in the LCA context.

Metapopulation theory has its roots in island biogeography theory and metapopulation models can potentially be related to SARs. Spatially explicit metapopulation models describe the presence of species across a network of habitat fragments (Leroux et al. 2017). A higher number and total area of connected habitat fragments predict higher species survival rates (Hanski 1999). Inversely, if progressive fragmentation

exceeds metapopulation persistence thresholds, species extinctions are predicted.

Table 2 summarises the challenges, data requirements and potential adaptations of the current LCIA characterisation models to incorporate fragmentation effects, which are discussed in more detail in Sections 5.1 and 5.2.

5.1 Patch area and isolation

The countryside SFAR developed by Larrey-Lassalle et al. (2018b) is a good step towards the incorporation of patch area and isolation effects into LCIA land use characterisation models for biodiversity loss. Although their model has been developed for birds in forest habitat in a selection of ecoregions only, their methodology can be used to incorporate patch area and isolation effects for various taxa in all the terrestrial ecoregions, including various habitat types.

Ecoregions typically contain various vegetation types (e.g. deciduous forest, coniferous forest, shrubland, grassland or cropland). Hence, basing the degree of fragmentation of an ecoregion on solely one vegetation type is inaccurate. There are roughly two methods to account for fragmentation using the metapopulation capacity in ecoregions containing a variety of vegetation: (1) using the dominant vegetation type as an indicator for the degree of fragmentation of the landscape, as Larrey-Lassalle et al. (2018a) did, or (2) calculating the metapopulation capacity for each vegetation type separately and deriving the average metapopulation capacity value (weighing the vegetation types based on size or number of species it contains). Furthermore, the method developed to estimate the metapopulation capacity per ecoregion can be applied to ecoregions other than those selected by Larrey-Lassalle et al. (2018a) to develop a globally applicable characterisation model.

Species have varying dispersal characteristics and respond heterogeneously to habitat isolation. That is the metapopulation capacity, λ , and the species sensitivity to habitat fragmentation, b , are species specific. Generating taxonomically specific countryside SFAR models including other taxonomic groups involves the specification of the average taxonomic dispersal characteristics and sensitivity to fragmentation.

One flaw of the metapopulation capacity is that it does not take into account the contribution of the matrix to habitat fragmentation. That is the permeability of the matrix does not influence the degree of isolation of the habitat fragments. A high contrasting matrix might amplify habitat isolation, whereas a low contrasting matrix might weaken habitat isolation. Therefore, integrating the species affinity (h) with the matrix and the metapopulation capacity (based on patch area, Euclidian distance between patches and species' dispersal characteristics) should influence the fragmentation effect on biodiversity.

Table 2 Challenges and opportunities regarding the incorporation of fragmentation effects into SAR models

Fragmentation effect category	Challenges	Data requirements	Potential adaptations
Patch area and number	Incorporate effects of several patches into SAR models without double-counting species that exist in several patches	Size and number of habitat patches	Incorporate metapopulation capacity; replace the total amount of area (<i>A</i>) in the SAR by a parameter indicating the amount of habitat a species can effectively utilise
Edge effects	Identify amount of interior and edge area; determine average species response to edge area	Amount of interior and edge area; species affinity with interior and edge areas	Reduce the amount of area (<i>A</i>) in the SAR by the amount of edge area species cannot utilise
Patch shape	Identify shape of patches	Shape of habitat patches	Replace the total amount of area (<i>A</i>) in the SAR by a value indicating the patch area a species can utilise
Patch isolation	Identify the amount of habitat species can utilise in the region	Distance between patches; species dispersal capacity	Incorporate metapopulation capacity; replace the total amount of area (<i>A</i>) in the SAR by a parameter indicating the amount of habitat a species can effectively utilise
Matrix structure	Identify the permeability of the matrix elements; link the matrix permeability to patch isolation	Spatial configuration of the landscape; species-specific permeability of matrix types	Incorporate matrix permeability into the patch isolation variable

5.2 Patch shape and edge effects

Koh et al. (2010) took the matrix-calibrated SAR model one step further to more explicitly account for the spatial structure of the landscape by incorporating taxon-specific responses to edge effects. They developed two variants that trade off data requirements with prediction accuracy: (1) a landscape-specific model and (2) a generic model.

Both models take into account the total amount of edge in the landscape A_{edge} and include a taxon-specific response factor to estimate how the species in the landscape are affected by the total amount of edge. The landscape-specific model is based on the actual amount of edge in the landscape (Eq. (6)) (Koh et al. 2010):

$$A_{edge} = \delta_g \cdot \sum_j^M \beta_j \tag{6}$$

where β represents the edge-affected area of fragment j , M the total number of fragments and δ the edge effect on taxonomic group g . Incorporating this into the matrix-calibrated SAR (Eq. (2)) results in Eq. (7) (Koh et al. 2010):

$$S_g = c_g \cdot (A - A_{edge})^{z_g \cdot \sum_i^n p_i \cdot \sigma_{g,i}} \tag{7}$$

Here, the number of species S of taxonomic group g is calculated based on the total amount of habitat A and habitat edge A_{edge} by using the SAR constants c and z , the share p of matrix type i in the landscape and the sensitivity σ of taxonomic group g to this matrix type. By assessing the landscape-specific edge-affected area, patch shape effects are explicitly incorporated in the landscape-specific model.

The generic model of Koh et al. (2010) (Eq. (8)) does not specify the patch shape and assumes that each fragment is

approximately circular in shape and similar in size. The only input parameters needed are the amount of habitat, A , the number of fragments, k , and the average edge-penetration distance, ε . With these assumptions, the total amount of edge can be estimated as:

$$A_{edge} = \pi \cdot \varepsilon \cdot \left(2 \cdot \sqrt{\frac{A}{\pi \cdot k}} - \varepsilon \right) \cdot \delta \cdot k \tag{8}$$

Incorporating this into the matrix-calibrated SAR (Eq. (2)) is equal to Eq. (7). Both the landscape-specific and generic models could also be incorporated into the countryside SAR (Eq. (9)) (Koh et al. 2010):

$$S_g = c_g \cdot \left(\sum_i^n h_{g,i} \cdot A_i - A_{edge} \right)^{z_g} \tag{9}$$

where S is the number of species and c and z are the SAR constants of taxonomic group g . Factor h indicates the taxon’s affinity with landscape element i , and A and A_{edge} indicate the total area of the landscape element and the landscape element’s edge, respectively.

Incorporating edge effects into the SAR models requires (1) empirical data from the landscape such as the total amount of edge area or the number of fragments and (2) generic data on taxon-specific responses to habitat edges and the average edge-penetration distance. Estimating the amount of edge per landscape and estimating average edge effects can be done based on currently available data, such as satellite data or databases such as BIOFRAG, a global database for analysing biodiversity responses to forest fragmentation (Pfeifer et al. 2014). Obtaining information on generic taxon-specific responses to habitat edges and

the average edge-penetration distance is difficult and ambiguous, as the response to edge effects may differ substantially from species to species.

5.3 Future research on incorporating fragmentation effects into LCIA models

Table 3 summarises the attempts to incorporate fragmentation effects into SAR models. This shows that there is potential to account for edge, patch isolation and matrix structure effects in LCIA characterisation models by incorporating the models proposed by Koh et al. (2010) and Hanski et al. (2013). Incorporating patch area and number and patch shape remains a challenge as the model proposed by Tjørve (2002) has high data input requirements and as there has been so far no attempt to incorporate patch shape effects into SAR models.

Adapted SAR models like Eq. (5) and Eq. (9) could be used to include fragmentation effects into the current LCIA land use characterisation models for biodiversity loss. For example, the models in Eq. (5) and Eq. (9) could be integrated to capture patch shape, area, isolation and edge effects. These fragmentation-adapted SAR models include more parameters than the conventional countryside SAR and therefore require more data input. To make such models operational in LCAs, these data inputs should, however, be incorporated in the LCIA.

That is, in the case of the edge effects, the total amount of edge (β) per landscape element in each landscape unit (e.g. land patch type per ecoregion) as well as the taxon-specific responses to habitat edges (δ) should be assessed empirically

or estimated (e.g. using the number of habitat patches, k , to estimate the total amount of edge, β). For incorporating the metapopulation capacity, the metapopulation capacity (λ) of each landscape (e.g. ecoregion) as well as the taxon-specific response to patch isolation (b) should be assessed or estimated. This could be done based on an adapted version of the method proposed by Larrey-Lassalle et al. (2018a) and applied to all ecoregions, major habitat types and taxonomic groups. Generating representative values for all these parameters globally is subject for further research.

Data to fill in the gaps mentioned above can be obtained from empirical research, remote sensing, modelling or databases like PREDICTS, a global database of how local terrestrial biodiversity responds to human impacts (Hudson et al. 2014, 2016), and BIOFRAG (Pfeifer et al. 2014). Databases like PREDICTS and BIOFRAG could potentially be used to obtain information for δ and b , whereas remote sensing sources, such as satellite imagery of GlobCover 2009 (Bontemps et al. 2011), could be used to obtain values for λ .

The matrix structure can mitigate or strengthen fragmentation effects. Generally, the greater the contrast between the habitat patch and the matrix, the more severe the fragmentation effect. Including the effect of the matrix structure on edge effects could be done by differentiating the severity of edge effects (b) in neighbouring habitat and matrix types that are alike and in those that are relatively distinct. Including the effect of the matrix structure on patch isolation could be done by including matrix hostility and the occurrence of migration barriers in the metapopulation capacity (λ).

Table 3 Fragmentation effects incorporated in SAR models

Fragmentation effect category	Mechanism	Incorporated in life cycle impact assessment characterisation model	Species-area relationship model attempt (outside life cycle impact assessment)	Model
Patch area and number	More and smaller patches (smaller populations)	–	Tjørve (2002); Amillas et al. (2017)	Multi-habitat SAR
Edge effects	Increasing habitat edge relative to interior (selective pressures)	–	Koh et al. (2010)	Edge-corrected SAR
Patch shape	Division interior habitat and altering colonisation and immigration rates (selective pressures and higher species turnover)	–	–	–
Patch isolation	Hampering species dispersal and (re)colonisation (increased species vulnerability)	Larrey-Lassalle et al. (2018b)	Hanski et al. (2013)	Countryside SFAR*, SFAR*
Matrix structure	Strengthening or mitigating fragmentation effects	Matrix quality incorporated; matrix structure not linked to edge effects or patch isolation	Hanski et al. (2013); Koh and Ghazoul (2010); Pereira and Daily 2006	SFAR*, matrix-calibrated SAR**, countryside SAR**

* SFAR and countryside SFAR account for the spatial structure of the matrix through the metapopulation capacity, λ . The degree of contrast between landscape elements is not linked to edge effects or patch isolation

** Matrix-calibrated SAR and countryside SAR account for the hospitability of the matrix elements, but do not link the matrix characteristics to edge or patch isolation effects

Apart from providing input parameters for the models described above, further methodological improvements can be developed, such as linking matrix quality with patch isolation in the calculation of the metapopulation capacity. Another subject for future research is to think about how the LCI and LCIA should be integrated to assess land use impacts, including fragmentation, on biodiversity. The LCI typically provides data on the amount of land area transformed and/or occupied and not about the spatial characteristics of these land use patches. In the adapted models described above, the degree of fragmentation is assigned to the respective landscape a priori, meaning that land use impacts in already fragmented regions would be higher compared with regions with low degrees of fragmentation. That is the models are not designed to translate land transformation and occupation from the LCI into fragmentation effects. It is preferable to keep the input requirements from the LCI as low as possible to ease the work for LCA practitioners. For assessing the in situ effects of anthropogenic activities, other tools than LCA such as risk assessments are preferred.

6 Conclusions

Recent efforts to develop novel theories and models for biodiversity impacts signify the increasing acknowledgement that anthropogenic impacts on ecosystems are one of the major current environmental challenges, which result in biodiversity loss and a decrease in ecosystem resilience, quality and services. Methodological improvements of LCIA characterisation models for land use impacts in biodiversity have led to significant advancements regarding translating land use into biodiversity loss in the LCA framework over the last decades, e.g. from regional assessments for vascular plants to regionally and taxonomically specific global models. Nevertheless, the spatial configuration of landscape elements is not comprehensively taken into consideration in state-of-the-art LCIA characterisation models, even though habitat fragmentation alters the dynamics of the landscape through changes in patch shapes and sizes, amount of habitat edge, matrix structure and patch isolation. Although fragmentation is context specific and fragmentation effects differ per species (i.e. fragmentation effects can be weak or strong and positive or negative, depending on the species), theory and empirical data suggest that fragmentation effects should not be overlooked (Watling and Donnelly 2006; Krauss et al. 2010; Haddad et al. 2015; Lindgren and Cousins 2017; Torrenta and Villard 2017). What is more, habitat fragmentation is not uniform across the globe, but tends to spread from human settlements, meaning that some regions are more strongly affected by fragmentation effects and considering spatial aspects is thus key.

Incorporating fragmentation effects into LCIA characterisation models is not an easy task. Limited data input from the

LCI restricts the potential specificity of the characterisation models and may obstruct the use of some SAR models (e.g. multi-habitat SAR models). Moreover, scant species- and region-specific data availability complicates the generation of parameters specifying the species' response to various fragmentation effects, such as the species' affinity with the habitat and land use types (h), response to edge effects (δ), response to habitat isolation (b) and dispersal characteristics.

Furthermore, fragmentation consequences are more easily determined at the local scale than at the global scale. Increased edge area might lead to increase in species diversity on the local scale, whereas this local increase in species diversity might mean a decrease in species diversity at the global scale if the increased species diversity is caused by generalist species occurring across various locations at the cost of specialist species occurring only at the local scale. For globally applicable characterisation factors, edge effects on the global scale should be considered.

Nevertheless, various models capturing fragmentation effects have the potential to be incorporated into LCIA characterisation models. Elaborating the LCIA characterisation models by introducing parameters related to the spatial configuration of the landscape and the related species responses (e.g. β or k , δ , λ and b) requires additional data input. A major challenge will therefore lie in our ability to work with the currently available data to generate global-, regional- and taxonomic-specific parameters and models to capture the effects of habitat fragmentation. Not acknowledging fragmentation effects in LCIA characterisation models for land use impacts on biodiversity may, however, lead to an inadequate assessment of the LCA biodiversity impacts. Hence, including these effects has the potential to improve the credibility of the LCIA land use characterisation models.

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Chapter 3: Global effects of habitat conversion and fragmentation on regional mammal species richness

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Global effects of habitat conversion and fragmentation on regional mammal species richness

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Abstract

Human-induced habitat conversion is a key driver of biodiversity loss. While various studies quantified the global biodiversity impact of habitat conversion itself, the additional effect of habitat fragmentation has not yet been quantified globally. Here, we estimated the combined effect of habitat conversion and fragmentation on the number of mammal species committed to extinction in 807 of the world's terrestrial ecoregions. We developed a new species-area model that integrates both differences in habitat suitability and connectivity, allowing for consistent modelling of land type suitability and matrix permeability across all ecoregions. On average across the ecoregions, eight mammal species are committed to go extinct due to the current conversion of habitat, with a maximum loss of 101 species. Palearctic, Afrotropic, and Indomalayan ecoregions were predicted to be the most affected and Oceanic and Australasian ecoregions the least, both in terms of absolute and relative numbers of predicted extinctions. We found that, on average, 9% of the species loss is caused by fragmentation, up to a maximum of 90%. We further found a strong positive correlation between habitat conversion and fragmentation effects, reflecting that more habitat conversion generally brings about more fragmentation. Our results imply that impacts of habitat conversion are clearly underestimated if fragmentation is neglected, indicating that conservation and restoration measures should address both habitat conversion and fragmentation.

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Chapter 4: Potential consequences of regional species loss for global species richness: a quantitative approach for estimating global extinction probabilities

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Potential Consequences of Regional Species Loss for Global Species Richness: A Quantitative Approach for Estimating Global Extinction Probabilities

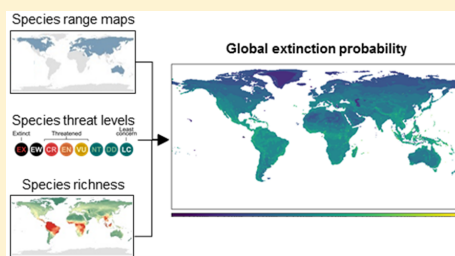
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Supporting Information

ABSTRACT: Because the biosphere is highly heterogeneous, species diversity impacts are typically assessed at local or regional scales. Because regional species richness impact metrics refer to different species compositions, they cannot be easily compared or aggregated to global impacts. Translating regional species richness impacts into global impacts allows for comparisons between impacts and facilitates the estimation of global species extinctions. This requires a conversion (or weighting) factor that takes into account the characteristics of regionally specific species compositions. We developed a methodology for deriving such conversion factors based on species' habitat ranges, International Union for Conservation of Nature threat levels, and species richness. We call these conversion



factors global extinction probabilities (GEPs) of the reference location or region. The proposed methodology allows for the calculation of GEPs for any spatial unit and species group for which data on spatial distribution are available and can be implemented in methodologies like life cycle impact assessment. Furthermore, the GEPs can be used for the identification of conservation hot spots. The results of the proposed GEPs (for various taxonomic groups) show that the risk that regional species loss may result in global species extinctions significantly differs per region and informs where irreversible biodiversity impacts are more likely to occur.

1. INTRODUCTION

Human activities progressively affect ecosystems, causing biodiversity loss and alterations, ultimately threatening the biosphere's integrity globally.^{1–4} These ecosystem changes are severe, and comparing current species extinction rates to those during and between the previous five mass extinction events indicates that we have entered a sixth mass extinction.^{5–11} Furthermore, human influence is considered to be currently the dominating factor driving environmental change, and some argue that this pushed us into a new geological epoch, the Anthropocene.^{8,12–15}

Humans have the capacity to influence trends regarding ecosystem change, indicating that conservation efforts may significantly reduce biodiversity loss.^{3,4,16,17} The biosphere is a highly heterogeneous system,¹⁸ and to organize international conservation efforts effectively, biodiversity hot spots are identified for the establishment of priority areas for the protection of ecosystems.¹⁹ The identification of these hot spots is based on a number of characteristics, including species range sizes, species vulnerabilities, and species richness.^{20,21} Furthermore, because anthropogenic stressors are not uniformly distributed, international conservation efforts require environmental assessments to inform where impacts are

happening and how these could be mitigated.²² Approaches that help to assess these impacts need to be spatially explicit, because nature changes widely in space and differences in environmental conditions and species richness and composition need to be reflected. In addition, most anthropogenic impacts take place along global value chains, substantiating the need for global, spatially explicit assessments to trace these impacts along complete value chains.

Life cycle assessment (LCA) is such a method that quantifies potential impacts of product systems along global value chains.²³ Spatially explicit life cycle impact assessments (LCIAs) estimate, *inter alia*, regionally specific species loss. Local or regional species richness impacts (e.g., species loss) cannot be easily aggregated or compared for several reasons. First, many species occur across various regions. Hence, regional species loss does not necessarily lead to global species loss.²⁴ Therefore, aggregating regional species loss across regions may lead to double counting of species. Second, some

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regions host more threatened species than others.²⁵ It is more likely that regional losses in those regions lead to global extinctions than in regions associated with fewer threatened species. Third, statistically, there are more threatened species present in locations characterized by high species density compared to locations characterized by low species density.² Consequently, impacts occurring in high-diversity locations are more likely to lead to global extinctions than impacts occurring in low-density locations.

Hence, to assess or compare the environmental footprints of cross-regional value chains, regional species richness impacts should be converted into globally comparable and summable impacts.²⁶ A first attempt in doing so was carried out by Verones et al.,²⁷ who created factors (so-called vulnerability scores) to convert regional species richness impacts into potentially global species extinctions at the ecoregion scale. However, they created conversion factors for only four terrestrial taxonomic groups (amphibians, birds, mammals, and reptiles), thereby omitting marine and freshwater species. Moreover, the sum of their regionally specified (i.e., ecoregion) conversion factors is >1, meaning that the application of these vulnerability scores allows for a prediction of >100% species loss if this is not corrected for.

We develop a methodology for deriving scores—based on species range sizes, species vulnerabilities, and species richness—indicating the extent to which regional species loss in the respective area may contribute to global species loss. We call these scores global extinction probabilities (GEPs) and generate them for marine, terrestrial, and freshwater species groups on the local (i.e., $0.05^\circ \times 0.05^\circ$ grid) and ecoregion scale. As the sum of all area scores equals 1, the methodology predicts 100% global species extinction if regional species loss is 100% in all regions. In effect, these area scores can be used to translate fractions of species lost per region into potential global species extinctions in ecosystem assessments and tools like LCA. Furthermore, these GEPs can assist in the identification of priority conservation areas. Effectively, GEPs can be used as weighting factors to weight regional species diversity impacts (in terms of regional fraction of species lost) to assess its global implications.

It is important to note that the GEP should be interpreted as a proxy of global species extinctions if regional extinctions occur. That is, a GEP of 0.1 would mean that if all species would disappear from a region, global species diversity would be reduced by 10%.

2. MATERIALS AND METHODS

The presented methodology builds upon the proposed vulnerability scores from Verones et al.,²⁷ which have been applied by Verones et al.^{28–30} and Chaudhary et al.,^{31–34} and incorporates concepts like the extent of occurrence,³⁵ endemic richness,^{36–38} range rarity,^{20,37,39} and International Union for Conservation of Nature's (IUCN's) Red List of threatened species.⁴⁰ The identification and quantification of priority conservation areas and GEPs require spatial data on global species distributions and species threat levels and the identification of administrative spatial units (e.g., countries or ecoregions).

2.1. Quantifying the Global Extinction Probabilities (GEPs). Because species respond heterogeneously to anthropogenic pressures, species richness impact assessments are often tailored to taxonomic groups. For this reason, we generate GEPs for various taxonomic groups in marine,

terrestrial, and freshwater environments. Apart from individual taxonomic groups, the GEPs can be calculated for any other specific species groups. When using the GEPs to translate regional species loss into potential global species extinctions, it is important that the GEP refers to the same species group(s) and spatial unit to which the regional species loss refers. For instance, translating mammal extinctions in Madagascar into global mammal extinctions requires a GEP referring to mammals in Madagascar; using a GEP that refers to vertebrate species in East Africa is not appropriate.

Calculating GEPs requires data on species ranges, threat levels, and distributions. The first step in the calculation process is to rasterize each species range individually, basing the cell values on the occurrence of the species in that location [0.0–1.0 (Table 1)] and a value of 0 in the cells where the

Table 1. Weighting Scheme for Species Occurrence in Total Distribution

presence	cell value
extant	1.0
probably extant	0.5
possibly extant	0.5
possibly extinct	0.1
extinct	0.0
presence uncertain	0.0

species is not present (gridding based on overlap with the center of the cell). The occurrence value of the species in the cell is 1 if the species is extant and progressively lower as the uncertainty about its presence increases (section 2.2). We restricted the occurrence of marine species to marine ecoregions, terrestrial species to terrestrial ecoregions, and freshwater species to freshwater bodies. We did not refine the geographical range based on elevation and habitat preferences because of the limited availability of data regarding these preferences for all species. Second, range rarity is calculated by dividing all species' cell values by the global sum of the cell values of its distribution, resulting in cell values that represent a fraction of the total species' occurrence. Hence, individual cell values of species with small ranges are relatively high compared to those of species with widespread ranges. Third, all species rasters are aggregated, weighting each species raster based on the species' threat level (Table 2 and sections 2.3 and 2.5). Cells that contain a relatively high number of threatened species with small ranges will have relatively high values. Fourth, all cell values in the aggregated raster are divided by

Table 2. IUCN Red List Threat-Level Quantification Schemes

IUCN's Red List threat level	linear scheme	categorical scheme	logarithmic scheme
extinct	0.0	0.0	0.0
extinct in the wild	0.0	0.0	0.0
regionally extinct	0.0	0.0	0.0
critically endangered	1.0	8.0	1.0
endangered	0.8	6.0	1.0×10^{-1}
vulnerable	0.6	4.0	1.0×10^{-2}
lower risk	0.4	2.0	1.0×10^{-3}
near threatened	0.4	2.0	1.0×10^{-3}
data deficient	0.2	2.0	1.0×10^{-4}
least concern	0.2	1.0	1.0×10^{-4}

the sum of all species' threat levels, resulting in cell values that individually represent a fraction of the total; i.e., the sum of all cell values of the species group is 1. These cell values represent the GEP per grid cell (in arc degrees).

This process is illustrated in eq 1, where o is the occurrence value of species s in cell p and TL is the threat level of species s .

$$\text{GEP}_p = \frac{\sum_s \frac{o_{p,r} \times \text{TL}_s}{\sum_p o_{p,r}}}{\sum_s \text{TL}_s} \quad (1)$$

The result is an aggregated cell-level map for each species group. The cell values can be interpreted as proxies for the contribution of regional species extirpations in the cell location that lead to global species extinctions. Hence, cells with high values should receive high priority for the conservation of global species richness. Thereby, GEPs provide an important component for the quantification and ranking of areas of importance for the conservation of global species richness.

Upscaling the cell-level map to the desired spatial units involves the aggregation of all cells in the spatial unit. That is, the value of the spatial unit is the sum of all the cells it contains, as shown in eq 2

$$\text{GEP}_r = \sum_p \frac{\sum_s \frac{o_{p,r} \times \text{TL}_s}{\sum_p o_{p,r}}}{\sum_s \text{TL}_s} \quad (2)$$

where r denotes the spatial unit (e.g., ecoregion). The global sum of the values (GEPs) of all spatial units is 1. These values can be interpreted in a manner analogous to that used for the cell-level GEPs, but instead of referring to a single cell, the GEPs refer to a larger spatial unit. Because the ecoregion-level GEPs are aggregated cell-level GEPs, large ecoregions will generally have higher GEPs. Conceptually, this makes sense as the GEP quantifies the contribution of species extirpations in a region to global species extinctions.

2.2. Species Distribution Data. Spatially explicit data of species ranges are extracted from the IUCN's Red List spatial data⁴¹ and BirdLife's species distribution data.⁴²

For the marine environment, we selected all marine areas on continental shelves, as specified by the World Wildlife Fund (WWF) marine ecoregions of the world.⁴³ We assessed five taxonomic groups individually for which species-specific spatial data were available: chondrichthyes (1088 species), corals (1476 species), marine fish (2562 species), marine mammals (125 species), and seagrasses (6365 species). For the terrestrial environment, we selected all terrestrial areas, as specified by the WWF terrestrial ecoregions of the world.⁴⁴ We assessed four taxonomic groups individually: amphibians (6490 species), birds (11120 species), mammals (5303 species), and reptiles (4923 species). All bird species, i.e., marine, terrestrial, and freshwater birds, are assessed together, as all bird species need terrestrial habitat for breeding. For the freshwater environment, we selected all freshwater areas, as specified by the WWF freshwater ecoregions of the world.⁴⁵ We assessed seven taxonomic groups combined: crabs (1257 species), crayfish (498 species), freshwater fish (6410 species), molluscs (1406 species), freshwater plants (1323 species), odonata (1476 species), and freshwater shrimps (699 species). Note that any environment and any (combination of) species group(s) could be chosen with the proposed methodology, as long as spatial data and species threat levels are available.

The IUCN⁴¹ and BirdLife⁴² data distinguish six categories of species occurrences in the species' spatial data: (1) extant, (2) probably extant, (3) possibly extant, (4) possibly extinct, (5) extinct, and (6) presence uncertain. We use these categories as a weighting factor for the importance of each local occurrence for the total species distribution. The weighting scheme is based on the weighting scheme used by Pouzols et al.⁴⁶ for their global conservation priority maps (Table 1). We use weighting to exclude locations where species are currently no longer present and to make locations where species presence is uncertain less important. Disregarding this type of weighting may skew species distributions to regions where the species are no longer present.

2.3. Species Threat-Level Data. The IUCN's Red List of Threatened Species⁴¹ is used to determine the threat level of the species. The IUCN's Red List distinguishes 10 threat-level categories: (i) extinct, (ii) extinct in the wild, (iii) regionally extinct, (iv) critically endangered, (v) endangered, (vi) vulnerable, (vii) lower risk, (viii) near threatened, (ix) data deficient, and (x) least concern. These categories are used as a weighting factor for the importance of each species relative to other species in the same species group. Furthermore, it is used to exclude species distributions in locations where these species have become extinct (categories i–iii). The default weighting scheme is based on the weighting scheme used by Pouzols et al.⁴⁶ (Table 2, linear scheme column, values from 0 to 8).

2.4. Spatial Resolution and Scale. To be able to do calculations with the species distribution maps from IUCN and BirdLife, the shapefiles of all species' distributions (polygons) are rasterised. The size of the raster cells can be chosen arbitrarily. Small raster cells increase the level of detail but involve longer computation times. Here, a grid size of $0.05^\circ \times 0.05^\circ$ (approximately 5.5 latitude km \times 5.6 longitude km near the equator) was chosen, following Verones et al.²⁸

For practical reasons for those wanting to apply the GEPs, the cell-level maps are also aggregated to administrative or ecologically homogeneous spatial units (e.g., countries or ecoregions). These can be chosen arbitrarily, as long as the spatial units are larger than the grid cells. Here, the WWF ecoregions of the world were chosen as the spatial units. These comprise 232 distinct marine,⁴³ 827 terrestrial,⁴⁴ and 449 freshwater ecoregions.⁴⁵ These ecoregions reflect biogeographic classifications of the complex distribution of the Earth's natural communities and are therefore, from an ecological perspective, more appropriate to use for priority conservation areas and GEPs than administrative units like countries.

2.5. Sensitivity of Threat-Level Parametrization. In the aggregation process, the weighting of the species based on the IUCN's Red List threat-level classification²⁵ requires conversions from the qualitative classification to an arbitrary quantitative classification. We adopted the nonlinear quantification scheme of Pouzols et al.⁴⁶ for the species threat levels, ranging from 0 to 8. However, as this quantification is arbitrary, other quantification schemes could be chosen. Verones et al.^{27,28,30} and de Baan et al.²⁴ used, for example, a linear approach for their quantification schemes of the IUCN's Red List threat levels.

To estimate the sensitivity of these arbitrary parameter choices, we performed the analysis mentioned above with three distinct IUCN Red List threat-level quantification (parametrization) schemes: (1) a linear approach based on that of

Verones et al.^{27,28,30} and de Baan et al.,²⁴ (2) a categorical approach based on that of Pouzols et al.,⁴⁶ as introduced above, and (3) a logarithmic approach based on that of Butchart et al.⁴⁷ to include a case in which particular attention is paid to species that are relatively close to extinction (Table 2).

The sensitivity of the choice of quantification scheme is analyzed by assessing the magnitude of the differences between the ecoregion GEP results when adopting the different threat-level quantification schemes. Maps are produced to qualitatively assess the differences between the different parameter schemes, and box plots are used to show the distribution of the GEP values for each quantification scheme.

2.6. Analyzing Spatial Patterns of Range Rarity and Threat Levels Individually. The GEP merges range rarity, species threat levels, and species richness. The IUCN's Red List threat levels are determined on the basis of whether the species meets certain criteria. Most of these criteria refer to the total number of individuals, the size and number of subpopulations, and fluctuations therein.⁴⁸ In addition, criterion B of the IUCN's Red List classification scheme⁴⁸ refers to combinations of size, fragmentation, and decline of and fluctuation in the extent of occurrence and the total number of individuals and the number and size of subpopulations. Consequently, information about the size of the species' geographical range may enter the GEP twice.

To check whether combining the two indicators leads to double counting of range size, we calculate mean range rarity^{20,37,39} and mean threat-level scores for terrestrial mammals and derive Spearman correlation coefficients, as the data are not normally distributed (Figure S9), for range rarity and mean threat-level scores with the linear, categorical, and logarithmic parametrization schemes.

Mean range rarity (MRR) is the average range rarity in the grid cell across all species in the species class, as illustrated in eq 3

$$\text{MRR}_p = \frac{\sum_{s=1}^n \frac{a_{s,p}}{n_p}}{n_p} \quad (3)$$

where n is the number of species present in grid cell p . Similar to the GEP, the range rarity is based on presence in a cell (Table 1).

Similarly, the mean threat level (MTL) is the average threat level in the grid cell across all species in the species class, as illustrated in eq 4.

$$\text{MTL}_p = \frac{\sum_{s=1}^n \text{TL}_{s,p}}{n_p} \quad (4)$$

For the correlation coefficients, the cell-level mean range rarity and mean threat levels are aggregated to the ecoregion level by calculating the average MRR and MTL of the cells contained in the ecoregion. There are a few outliers (always islands, which typically host endemic species) in both the ecoregion-level mean range rarity and mean threat level of terrestrial mammals. We tested the correlation for all ecoregions.

2.7. Case Study. To demonstrate the application and effect of the GEP, the terrestrial mammal GEPs (using the categorical parametrization scheme for TL values) have been used in combination with spatially explicit (ecoregions) characterization factors, developed by Chaudhary and

Brooks,⁴⁹ indicating the predicted number of mammal species going extinct per square meter of land used (occupied) for agriculture. We converted their characterization factors for regional mammal extinctions into fractions of regionally disappeared mammal species by dividing the species loss data by regional species richness in each ecoregion (Table S4). The converted characterization factors in terms of regional fractions of mammal extinctions per square meter were then multiplied by the corresponding GEPs (categorical parametrization scheme) to calculate potential global fractions of mammal extinctions per square meter.

Subsequently, we ranked the ecoregion-specific characterization factors based on predicted fractions of regional extinctions and predicted fractions of global extinctions and compared the rankings to illustrate how including the GEP can shift the severity of the impacts spatially when translating regional species diversity impacts into global species diversity impacts.

3. RESULTS AND DISCUSSION

3.1. Cell-Level GEPs. The cell-level GEPs of marine fish, terrestrial mammals, and freshwater groups are shown in Figure 1; maps of the other species groups can be found in Figures S1–S3. All species groups show similar patterns: the differences between maximum and minimum cell values are high (4–9 orders of magnitude); cell values can differ substantially, even on local scales; and cells near the equator have generally higher values compared to those of moderate latitudes because species density and the number of endemic species are generally high near the tropics.

Furthermore, marine fish have high GEPs close to coastal areas relative to marine areas farther from the coasts. This also holds for most other marine groups (Figure S1). As most fisheries occur close to coastal areas, this indicates that there is an increased risk of marine species extinctions. The distribution of marine mammal GEPs shows a pattern different from that of the GEP distributions of most other species. Instead of having high cell values near the equator, marine mammal GEPs are generally higher at moderate latitudes. For some marine groups, the cell-level GEPs appear to be absent in some regions (e.g., sub-Antarctic regions for marine fish). This can mean that either there are no species of that species group in those regions or there are no data on species of that species group in those regions.

For terrestrial areas, only the birds group has species occurring everywhere, while mammal species span across all terrestrial areas with the exception of Antarctica. Islands, especially those near the equator, have distinctively high GEPs. This is mainly due to relatively high levels of species richness near the equator and because islands generally host a high number of endemic species.³⁸ In addition, this may be due to the relatively high number and share of endangered species in the tropics (Figure S7).²⁵ A combination of a high number of both endemic and endangered species is also possible. Differences in GEP cell values are more pronounced for amphibians and reptiles than for birds and mammals. This can be explained by amphibians and reptiles having generally smaller ranges being more confined to specific habitats, whereas birds and mammals have generally more widespread distributions across a great variety of habitats.²⁵

The distribution of GEPs of freshwater species is similar to the distribution of terrestrial species (i.e., generally higher values near the tropics and lower values in Arctic regions).

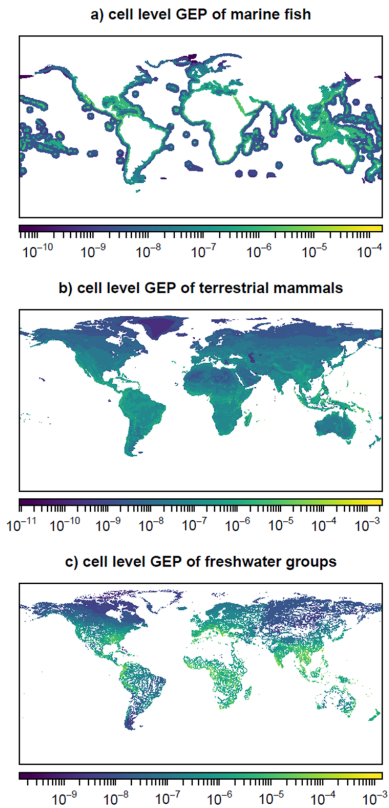


Figure 1. Cell-level GEPs of (a) marine fish, (b) terrestrial mammals, and (c) freshwater groups (legend scaled logarithmically). The maps use the marine,⁴³ terrestrial,⁴⁴ and freshwater⁴⁵ ecoregions of the world and the Global Lakes and Wetlands Database⁵⁰ to delineate borders.

Nevertheless, in contrast to the GEPs of terrestrial species, the eastern part of the United States is highlighted by high GEP values for the freshwater groups.

3.2. Ecoregion-Level GEPs. As ecoregion-level GEPs are aggregations of the cell-level GEPs, the ecoregion-level GEP maps convey similar patterns (Figure 2) (high GEP values near the equator). Differences between the maximum and minimum values of ecoregion GEPs are not as extreme as the differences between the cell-level GEPs. Maps of the other species groups can be found in Figures S4–S6, and complete lists of all ecoregion GEPs can be found in Tables S2–S4.

Relatively large ecoregions contain a high number of cells. Consequently, the GEP of a relatively large ecoregion can be high in comparison to that of a smaller ecoregion, even though the average individual cell values might be relatively low. Conceptually, this makes sense: large ecoregions are generally more likely to contain more species in total than small ecoregions; therefore, if all species would be lost in a large ecoregion, this is likely to have relatively large consequences for global biodiversity loss. Nevertheless, these results show that ecoregion size is not the dominating factor, as the ecoregions with the highest species density, smallest species

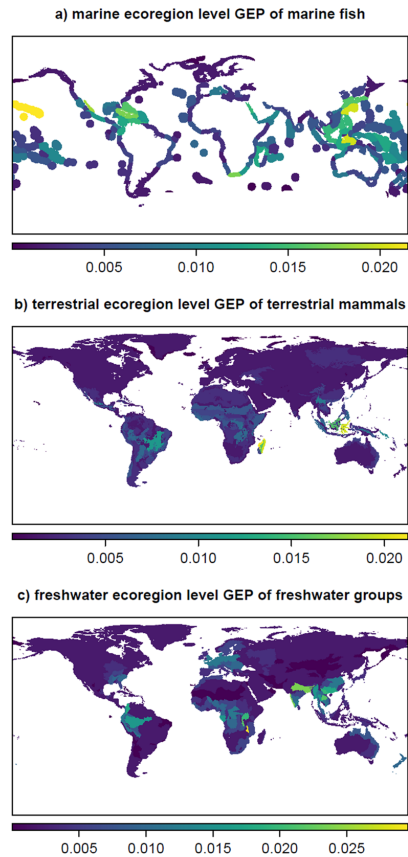


Figure 2. Ecoregion-level GEPs of (a) marine fish, (b) terrestrial mammals, and (c) freshwater groups (legend scaled linearly). The maps use the marine,⁴³ terrestrial,⁴⁴ and freshwater⁴⁵ ecoregions of the world to delineate borders.

ranges, and highest number of threatened species stand out, often located near the equator, no matter the size of the ecoregion.

However, although large ecoregions may have relatively high GEPs, the actual number of species lost in large ecoregions is often relatively low because chances are smaller that a species becomes extinct across a large region compared to a small region. In the species–area curve, relating the size of natural habitat to species richness,^{51,52} this is represented by the flattening of the curve with an increase in area. Hence, during estimation of potential global extinctions in large ecoregions, the relatively low number of species lost regionally may be combined with a high GEP, indicating that if these species become extinct in this large region, it is relatively likely that they become extinct globally.

3.3. Application. The results shown above should be interpreted carefully. GEPs can be interpreted as approximations of the percentage of species gone extinct globally if all species in a specific location or region will be lost. It is important to note that the GEP does not estimate actual species extinctions but that it approximates the consequences

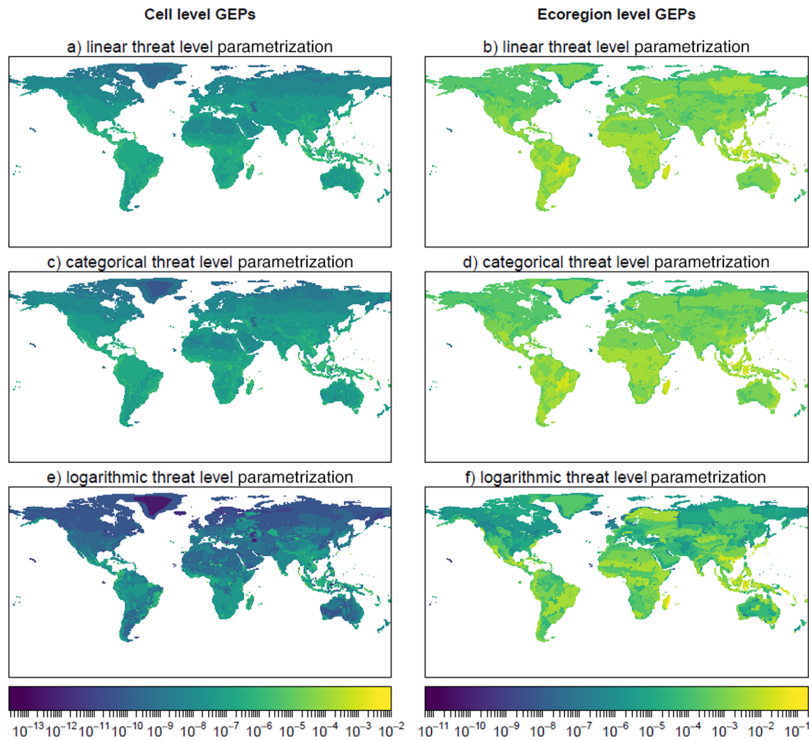


Figure 3. GEPs on cell and terrestrial ecoregion levels of terrestrial mammals calculated with different parameter schemes (legend scaled logarithmically). The maps use the terrestrial⁴⁴ ecoregions of the world to delineate borders.

of fractions of species that disappear per region for global species diversity. That is, the GEP can be used as a stand-alone hot spot indicator when used at homogeneous spatial resolutions (e.g., cell level), but to become an appropriate impact indicator for global extinction risks at the ecoregion level, it needs to be combined with fractions of regionally lost species. Essentially, the GEP informs about the potential irreversibility of impacts if the local or regional ecosystems are exposed to pressures and consequently lose species richness.

Hence, GEPs can serve several purposes. They can be used as indicators of potentially vulnerable areas in terms of global species loss, and they can be used as conversion factors to translate fractions of regional species lost into potential global species extinctions in combination with impact assessments to estimate global biodiversity impacts due to anthropogenic pressures. If the GEPs are used as conversion factors to translate regional species loss (e.g., fraction of species within a region that potentially disappeared) into potential global species extinctions, it is important that the GEPs refer to the same spatial unit to which the regional species loss refers. Potential global species extinctions or global fractions that potentially disappeared are calculated by multiplying the regional fractions that potentially disappeared by the GEP corresponding to the same taxonomic group and spatial unit, as shown in the case study. When used in this context, the GEP indicates the extent to which regional fractions of species lost contribute to global species extinctions.

GEPs can also be used in contexts different from translating regional species loss into potentially global species extinctions, for example, to identify priority conservation areas. The WWF terrestrial ecoregions are classified into three conservation status categories: (1) critical or endangered (54% of the terrestrial ecoregions), (2) vulnerable (27% of the terrestrial ecoregions), and (3) relatively stable or intact (19% of the terrestrial ecoregions).^{44,53} The ecoregion conservation status is related to anthropogenic pressures (e.g., habitat loss, the degree of fragmentation, and estimates of future threat and degree of protection), whereas the GEPs are related to species compositions (species richness, geographical distributions, and threat levels) isolated from any pressures. Combining the ecoregion conservation status index (anthropogenic threats) with ecoregion GEPs (potential irreversibility of prospective impacts) may enhance the understanding of anthropogenic impacts on ecosystems and aid in the identification of priority areas for global biodiversity conservation.

3.4. Sensitivity of Threat-Level Parametrization. The different parametrization schemes for parametrizing the IUCN's Red List threat levels of species give different weights to endangered species. In the linear parametrization scheme, the differences between the lowest (least concern = 0.2) and highest (critically endangered = 1.0) threat-level values are smallest (factor of 5 difference). The differences are greatest in the logarithmic parametrization scheme, where the least concern category is parametrized as 1.0×10^{-4} and the critically endangered category as 1.0 (factor of 1.0×10^4

difference). This means that cells containing endangered species become more important compared to cells not containing endangered species with the logarithmic parametrization scheme.

Calculating the GEPs with the different parametrization schemes does not alter the pattern. The main difference is that the regional differences are more pronounced with the logarithmic parametrization scheme (on the cell and ecoregion level). The linear and categorical categorization schemes result in very similar GEP distributions. This is illustrated in Figure 3, where the cell- and ecoregion-level GEPs of terrestrial mammals are shown under the three different parametrization schemes. The logarithmic parametrization scheme puts an even stronger focus on areas near the equator. Complete lists of all ecoregion GEPs calculated with the three distinct parametrization schemes can be found in Tables S2–S4.

Figure 4 displays box plots of the ecoregion GEP distributions. This shows that varying the parametrization

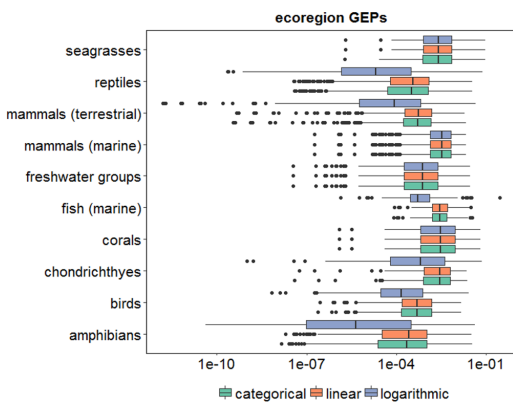


Figure 4. Box plots of ecoregion GEP distributions under the various parametrization schemes.

scheme has no significant effect for the distributions of GEPs for corals, marine mammals, seagrasses, and freshwater groups. For the other groups, the ecoregion GEP value can differ more substantially when adopting the different parametrization schemes.

Furthermore, Figure 4 illustrates that the GEP distribution is very similar under the categorical and linear scheme but that the GEP values are more distinct when the logarithmic parametrization scheme is used.

Figures 3 and 4 indicate that the pattern of the GEP distribution becomes more pronounced when using a logarithmic parametrization scheme. The general direction of GEPs calculated according to the three schemes remains the same. It should be stressed that these parametrization schemes have been chosen arbitrarily. We cannot conclude which parametrization scheme would be more appropriate to use, but we can conclude that the GEPs show the same pattern, regardless of which parametrization scheme is used. This underlines that the spatial pattern of GEPs is fairly robust but that the individual GEP values are approximations.

3.5. Assessing Spatial Patterns of Range Rarity and Threat Levels Individually. To assess whether combining range rarity and threat levels leads to double counting, we

calculated mean range rarity and mean threat-level scores for terrestrial mammals and analyzed the degree of similarity between the two indicators.

The mean range rarity and mean threat-level maps for terrestrial mammals can be found in Figure S7. In the mean range rarity, mostly islands stand out (e.g., Madagascar, Caribbean Islands, Azores, Solomon Islands, and Papua New Guinea), whereas Arctic and sub-Arctic regions tend to have relatively low values. Furthermore, the mean range rarity map shows a smooth gradient between slightly higher values around tropical and subtropical regions (with the exception of the Sahara) and lower values in the Northern Hemisphere.

The mean threat level is equally distributed with some location-specific extremes. Arctic and some coastal regions tend to stand out in terms of high values. In contrast to the mean range rarity, islands tend to have relatively low values and the Sahara is characterized by higher mean threat levels compared to those of its surrounding regions. The mean threat level with logarithmic parametrization primarily shows the distribution of critically endangered and endangered species, as the other species become almost irrelevant for the mean threat-level score. Hence, this parametrization shows more pronounced regional differences compared to the distribution of the mean threat levels related to the linear and categorical parametrizations.

Table 3 shows Spearman (ρ) correlation coefficients for the mean range rarity and mean threat level averaged to the

Table 3. Spearman Correlation Coefficients for Mean Range Rarity and Mean Threat Levels of Terrestrial Mammals at the Ecoregion Level

parametrization scheme	Spearman ρ
mean threat level (linear)	0.370
mean threat level (categorical)	0.364
mean threat level (logarithmic)	0.435

ecoregion level. One outlier (Ogasawara subtropical moist forest) affects the correlation for mean range rarity and mean threat level (logarithmic); because of the low total number of species on this island, most are endemic and threatened (leading to very high mean range rarity and high mean threat-level scores, especially under the logarithmic parametrization scheme). The scatter plot in Figure S8 shows how extreme the outlier of the Ogasawara subtropical moist forest ecoregion is. Nevertheless, the results presented in Table 3 suggest that there is weak to moderate correlation⁵⁴ between mean range rarity and mean threat level (for all parametrization schemes). Considering Figures S7 and S8 and the correlation coefficients in Table 3, we can conclude that range rarity and threat levels capture distinct aspects related to extinction probabilities.

Essentially, the IUCN's Red List classification indicates how close a species is to extinction and criterion B specifically describes how critical intact habitat is for the species' persistence. As the threat levels are determined on the basis of whether species meet any in the set of criteria, criterion B is not necessarily relevant for all species. Range rarity alone fails to capture the likelihood that endangered species with large ranges are more likely to become extinct than nonthreatened species with large ranges as species with large ranges are not necessarily abundant throughout the whole range. For example, the endangered giant otter's (*Pteronura brasiliensis*) extent of occurrence stretches over approximately one-third of

South America, but the small number of total individuals and subpopulations increases the risk that local extirpation leads to global extinction.

On the other hand, the threat level alone fails to capture the likelihood that nonthreatened species with small ranges are more likely to become extinct than nonthreatened species with large ranges if these species become extinct locally. For example, the green mango (*Anthracothorax viridis*) is endemic to Puerto Rico so local extinction in Puerto Rico is likely to result in global extinction, even though the Green Mango is currently listed as “least concern”.

Combining both range rarity and threat level in the GEP attributes the lowest risk to locations hosting nonthreatened species with large geographical ranges, medium risks to locations hosting nonthreatened species with small geographical ranges and endangered species with large geographical ranges, and highest risks to locations hosting endangered species with small geographical ranges.

Considering both range rarity and threat levels also conforms with other methods identifying locations that are critical for global biodiversity such as key biodiversity areas (KBAs),⁵⁵ important bird and biodiversity areas (IBAs), and alliance for zero extinction sites (AZEs).⁵⁶

3.6. Case Study. The GEPs can be used with any set of data for translating fractions of regional species extinctions into global species extinctions, as long as the spatial resolution and the taxonomic group referring to the extinctions correspond with the same spatial resolution and taxonomic group of the GEPs. One example is to use the GEPs in combination with predicted net changes in local species richness.^{10,17,57–61} Another example is to use the GEPs in combination with characterization factors indicating fractions of species that have regionally disappeared in life cycle impact assessments.

Combining the ecoregion-level GEPs for terrestrial mammals with the ecoregion-specific characterization factors for agricultural land use impacts per square meter on regional mammal species diversity, developed by Chaudhary and Brooks,⁴⁹ results in characterization factors for global mammal species diversity impacts (Table S5). The ranking of these regional and global ecoregion characterization factors differs substantially, indicating that regional species diversity impacts do not reflect global species diversity impacts. These rankings, presented in Tables S1 and S5, show that, e.g., the Enriquillo wetlands ecoregion ranks sixth in terms of regional mammal species diversity impacts per square meter of land used for agriculture. However, for the global impacts, this ecoregion ranks 373rd, meaning that these relatively high regional extinctions are not strongly contributing to global species extinctions. This may be explained by intensive agricultural land use but small numbers of endemic and threatened species in this region.

Conversely, the Mentawai Islands rain forest ecoregion is characterized by relatively low regional mammal diversity impacts (ranked 72nd) compared to global diversity impacts (ranked sixth) due to agricultural land use. This can be explained by the large numbers of mammal species that are endemic to these islands and relatively large numbers of threatened species in this region, whereas the land use-related pressures exerted on these local populations might not be as severe.

Figure 5 shows the ranking on a map, where the colors indicate the rank of the ecoregion regarding the regional mammal species diversity impacts per square meter of

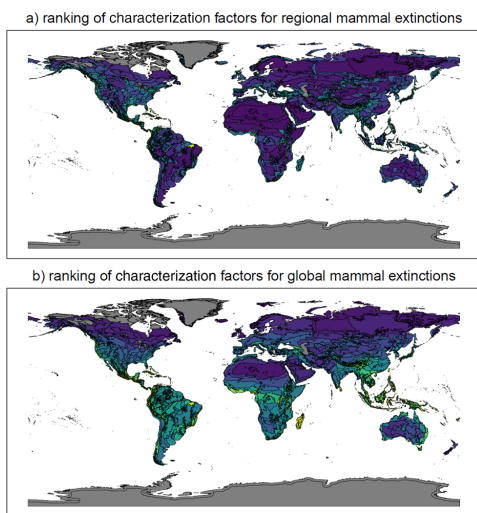


Figure 5. Ranking of ecoregion characterization factors (PDF mammal species per square meter of agricultural land use) for (a) regional diversity impacts and (b) global diversity impacts. Yellow indicates high rank, blue low rank, and gray regions for which no data were available. The maps use the terrestrial⁴⁴ ecoregions of the world to delineate borders.

agricultural land use (Figure 5a) and the global mammal species diversity impacts (Figure 5b). These maps show that agricultural land use impacts in the tropics cause the greatest impacts in terms of global species extinctions, whereas the impacts on regional species extinctions are more scattered across specific ecoregions.

Chaudhary and Brooks⁴⁹ also attempted to capture global species diversity impacts by considering species endemic to the region only. In another study,³² they considered all species and used a factor (vulnerability score³¹) to flag regions hosting large numbers of threatened and endemic species. Using the vulnerability score is appropriate for use in combination with absolute regional species extinctions, whereas the GEP is designed for use in combination with fractions of species that regionally disappeared.

This case study on agricultural land use impacts on regional and global mammal species diversity shows how regional species diversity and global diversity impacts can differ spatially and how the methods using the GEP can differ from other methods trying to capture global species diversity impacts.

3.7. Critical Appraisal of the Method and Data. The GEPs proposed here have been limited to species groups for which IUCN species range maps are available. The included species are by no means exhaustive. First, spatial data are not available for all known species within the included species groups. Second, there is consensus that there are probably many species that are unknown.⁶ Third, the IUCN does not have species range maps available for all species groups (e.g., bacteria, fungi, and insects). Thus, the GEPs should be updated as more data become available.

Furthermore, the accuracy of the species distribution data differs substantially per species. The species distribution data may indicate the extent of occurrence or the area of occupancy, depending on the species. For example, the range of the giant

otter (*P. brasiliensis*) stretches over approximately one-third of South America in one continuous patch. This range, indicating the extent of occurrence, also covers areas currently unsuitable as habitat for the giant otter. In contrast, the range of the Asian elephant (*Elephas maximus*) stretches over approximately one-third of Southeast Asia in numerous discontinuous patches, indicating the area of occupancy of the Asian elephant in these locations. Following our modeling approach, the average cell value will be lower for the giant otter than for the Asian elephant because its total range is larger. This discrepancy in the accuracy of species distribution data is due to the availability of data and cannot be solved easily.

The proposed method for estimating range rarity is based on the presence or absence in a cell (in arc degrees). This means that the range rarity is not based on the actual size of the total species range, as area sizes per cell vary over different latitudes. Hence, range rarity is not included as a fraction of the total range size area but as a fraction of the total locations (i.e., cells) in which the species is present.

The threat-level parameter values have been set arbitrarily, as there is no method for quantifying how more likely it is that endangered species become extinct compared to nonthreatened species. This arbitrary parametrization introduces uncertainty into the model. Although choosing different parametrization schemes is an attempt to capture part of the uncertainty, an uncertainty range cannot be quantified because these parameter values have been set arbitrarily. Similarly, due to limited data availability, uncertainty regarding the species distribution data can also not be quantified.

Nevertheless, the GEP can be useful for assessments in species diversity trends and ecological impact assessments at large scales. The magnitude of human activities has led to impacts on global scales. However, as specific anthropogenic and environmental pressures and species assemblages differ substantially by region, the ecological responses to these pressures differ, as well. Assessing the global implications of spatially differentiated trends in and impacts on biodiversity requires a conversion factor like the GEP.

The main spatial patterns of GEPs conform with other species diversity maps indicating potential vulnerability to extinction^{6,21,36,38} and maps identifying priority conservation areas.^{6,16,19,21,46} All maps show relatively high values around the tropics and especially high values on tropical islands. Other areas that stand out in most maps are northwest South America, Madagascar, the Himalayas, and Southeast Asia. This correspondence with existing maps supports the idea that the GEP captures extinction risks into a factor that can be used to translate regional species diversity loss into global species diversity loss.

The simple methodology, based on quantitative data and categories such as the distribution of species, their geographical ranges, and their threat levels, results in location-specific GEPs that sum to 1. This means that if all species are lost regionally, all species will also be globally extinct. This theoretical logic is important when applying a conversion or weighting factor like the GEP at global scales.

The GEP is easy to use in species diversity assessments as it is used as a multiplication factor with regional species diversity impacts (as done in the case study). The GEP is available globally at a fine resolution ($0.05^\circ \times 0.05^\circ$) that can be aggregated to any larger spatial unit. The GEPs cover marine, terrestrial, and freshwater realms and various taxonomic groups. That is, the GEP is additive, scalable, and comparable

globally across various realms and taxonomic groups. This means that the GEPs can be used for many different studies focusing on different realms, species groups, and locations. Having one factor that can be used across various impact assessments can foster the coherence between these assessments.

■ ASSOCIATED CONTENT

3 Supporting Information

The Supporting Information is available free of charge on the ACS Publications website at DOI: 10.1021/acs.est.8b06173.

Cell-level (Figures S1–S3) and ecoregion-level (Figures S4–S6) GEPs of all taxonomic groups considered in this study, including chondrichthyes, corals, marine fish, marine mammals, seagrasses, amphibians, birds, terrestrial mammals, reptiles, and freshwater groups; mean range rarity and mean threat-level maps of terrestrial mammals (Figure S7); scatter plots of the relation between mean range rarity and mean threat-level scores per ecoregion (Figure S8); density figures of the distribution of the MRR and MTL data; and a ranking of the GEP, regional, and global characterization factors per ecoregion (Table S1) (PDF)

Marine, terrestrial, and freshwater GEP tables (Tables S2–S4, respectively), containing GEP values for each taxonomic group (i.e., all groups mentioned above) and each parametrization scheme (i.e., linear, categorical, and logarithmic schemes), and agricultural land use impacts on regional and global mammal species extinctions (Table S5) (XLSX)

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Chapter 5: Considering habitat conversion and fragmentation in characterisation factors for land use impacts on vertebrate species richness

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Considering habitat conversion and fragmentation in characterisation factors for land-use impacts on vertebrate species richness

To be submitted to Science of the Total Environment

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Abstract

Human land use is one of the primary threats to terrestrial species richness and is considered a priority for meeting global sustainability and biodiversity targets. Decision-support tools, such as life cycle assessment (LCA), are widely used for developing strategies to achieve such objectives. Currently available life cycle impact assessment (LCIA) methods apply the countryside species-area relationship (c-SAR) to quantify habitat conversion impacts on species richness. However, additional effects of habitat fragmentation are yet ignored in these assessments. We use the species-habitat relationship (SHR), an adaptation of the c-SAR that considers both habitat conversion and fragmentation effects, to develop a new set of land-use characterisation factors for 702 terrestrial ecoregions (in 238 countries), four land-use types (urban, cropland, pasture, and forestry), and four taxonomic groups (amphibians, birds, mammals, and reptiles; plus the aggregate of these vertebrate groups). The SHR generally predicts higher per-area impacts of land-use than the impacts estimated by the c-SAR (a median relative difference of +9%), indicating that land-use impacts may be systematically underestimated when ignoring fragmentation effects. Whereas per-area impacts of land-use on regional species richness are highest in temperate regions, reflecting the diminished extent of natural habitat, per-area impacts of land-use on global species richness are highest in the subtropics, reflecting the importance of tropical regions and islands to global vertebrate species diversity. The large variety in magnitude of land-use impacts across the world's regions emphasizes the importance of regionalised assessments. The set of characterisation factors proposed here can be readily used in environmental decision-making.

Keywords: Life cycle assessment (LCA), life cycle impact assessment (LCIA), land-use, fragmentation, species-area relationship (SAR), biodiversity

This article is awaiting publication and is not included in NTNU Open

Chapter 6: Discussion and conclusion

Chapter 6: Discussion and conclusion

6.1. Scientific relevance and contribution

6.1.1. Embedding the thesis in the current research landscape

The Aichi biodiversity targets, set up to protect and conserve natural systems, expire this year and most of the targets will not have been reached. To be able to meet biodiversity targets for the next decades, such as those defined in the sustainable development goals (SDGs) and in the potential follow up of the Aichi biodiversity targets, a quantitative understanding of human impacts on biodiversity is required to be able to effectively mitigate the total impacts (Leadley et al. 2014; Tittensor et al. 2014; Steffen et al. 2015; IPBES 2019). Empirical assessments provide information on local responses, but global assessments require modelling techniques to uncover responses at larger scales and estimate impacts where no species-response data is present.

As explained earlier in this thesis, several global land-use impact assessment models exist today using different types of species-area relationships (SARs) (Pereira and Daily 2006; Koh and Ghazoul 2010; Hanski et al. 2013). However, none of these models consider fragmentation methods, in addition to the effects of habitat conversion, at the global scale. Consequently, LCIA models based on these models may miss part of the impacts caused by land-use, as elaborated upon in chapter 2. One method exists within the framework of LCA that includes fragmentation. Larrey-Lassalle (2018) proposed a method for characterising land-use impacts including fragmentation based on the countryside SAR (Pereira and Daily 2006) and the species fragmented-area relationship (SFAR) (Hanski et al. 2013). However, due to the challenges to generalise this method across regions, habitat types, and taxa, it is only developed for birds in ecoregions covering forest biodiversity hotspots.

This thesis has contributed to developing a method characterising impacts of habitat conversion and fragmentation across the four terrestrial vertebrate taxa at the global scale within the life cycle impact assessment (LCIA) framework. It follows the recommendations of the Life Cycle Initiative (Joliet et al. 2018) and is designed for potential implementation in LCIA methodologies such as ReCiPe or LC-IMPACT (Huijbregts et al. 2017; Verones et al. 2020), which are collections of coordinated impact assessments. This is the first global model of this kind, representing a significant advancement within this research field (Table 1).

Table 1. Overview of LCIA land-use characterisation models and some of their characteristics relevant for this thesis.

Model	SAR type	Global coverage	Average and marginal CFs	Fragmentation effects included	Taxonomic coverage	LCIA method that uses underlying models
(de Baan et al. 2013)	Matrix-calibrated SAR	✓	✓	X	Amphibians, reptiles, birds, mammals, plants*	ReCiPe; IMPACT World+
(Chaudhary et al. 2015)	Countryside SAR	✓	✓	X	Amphibians, reptiles, birds, mammals, plants*	LC-IMPACT; Life Cycle Initiative
(Larrey-Lassalle et al. 2018)	Countryside SFAR	X	X	✓	Birds**	-
Thesis chapter 5	SHR	✓	✓	✓	Amphibians. Reptiles, birds, mammals	-

* Characterisation factors for global plant species loss are not available (only regional loss).

** Characterisation factors for regional species loss only.

Overall, this thesis provides several new contributions within and beyond the field of LCIA.

1) Development and application of the SHR

The species-habitat relationship (SHR), proposed in chapter 3, is a species-area model variant that considers habitat area, connectivity, and suitability to assess impacts on regional species richness regarding the change in any of these three aspects. To facilitate its global application across taxonomic groups, parameter data requirements of the SHR model are minimised. Compared to the countryside SAR (Pereira and Daily 2006), the SHR requires additional information on i) the regional spatial configuration of the land types; ii) median dispersal distances; and iii) the permeability of the matrix, although this last aspect can be harmonised with and based on the same data as the habitat suitability parameter of the countryside SAR. In chapter three, the SHR is applied to estimate the impacts of global habitat conversion and fragmentation on regional mammal species richness only. This is the first study that systematically addresses the combined and individual effects of habitat conversion and fragmentation on regional species richness at the global scale. This indicated that the effects of habitat conversion are dominant, but that ignoring fragmentation leads to a systematic underestimation (of an average of approximately 10%) of land-use impacts. The novel finding of the SHR application highlights the relevance for incorporating fragmentation effects in global land-use impact assessments.

2) Development of an approach to assess global extinctions

Chapter 3 addresses the quantification of habitat conversion and fragmentation effects on regional species richness. However, as biodiversity is heterogeneously distributed, impacts on regional species do not contribute equally to global species richness change (Orme et al. 2005; Kier et al. 2009). Hence, to address targets regarding global biodiversity, global impact assessments should differentiate between the contribution of regional impacts and global impacts (Verones et al. 2015). A method to translate regional species richness impacts to global species extinctions is proposed and applied to various taxonomic groups in chapter 4. This is the first approach designed to directly translate regional relative species extinctions into global relative species extinctions of taxa across marine, aquatic, and terrestrial environments. The results indicate that the geographical relevance for global biodiversity impacts differs substantially across regions. This means that strategies to mitigate regional or global species richness impacts should consider this spatial differentiation. Furthermore, by considering species richness, endemism, and threat levels and covering a wide range of marine (chondrichthyes, coals, marine fish, marine mammals, and seagrasses), aquatic (crabs, crayfish, freshwater fish, molluscs, freshwater plants, odonatan, and freshwater shrimps), and terrestrial (amphibians, reptiles, mammals, birds) taxonomic groups, the global extinction probability (GEP) complements the global biodiversity hotspots that have not covered all abovementioned taxa (Myers et al. 2000; Orme et al. 2005; Marchese 2015).

3) Development of updated land-use characterisation factors

Chapter 5 integrates the modelling approaches of chapters three and four to develop a new regionalised LCIA method for the characterisation of land-use impacts on vertebrate species richness. In contrast to previous LCIA methods (Chaudhary et al. 2015; Chaudhary and Brooks 2018; Larrey-Lassalle et al. 2018), this approach considers the combined effects of habitat conversion and fragmentation across all terrestrial vertebrate species classes globally (excluding bats).

By considering the combined effects of habitat conversion and fragmentation, the new method characterises impacts associated with human land-use more completely. Moreover, the new LCIA method considers already-fragmented regions to be more vulnerable to land-use impacts than

regions characterised by largely continuous land types (Ewers and Didham 2005; Rybicki and Hanski 2013). This means that impact assessments employing the approach proposed here recognise relatively high impacts in regions that are vulnerable due to the fragmentation of its landscape. This was previously not recognised in global LCIA methods.

The newly proposed characterisation factors (CFs) are in line with the recommendations for LCIA CF development by i) addressing biodiversity impacts in terms of potentially disappeared fraction of species (PDF); ii) being spatially and taxonomically-differentiated; iii) representing both regional and global impacts; and iv) providing both average and marginal characterisation factors (Verones et al. 2017a; Jolliet et al. 2018).

The proposed land-use impact assessment method fills the research gap regarding the systematic quantification of habitat conversion and fragmentation effects on species richness globally within the LCIA framework. Therefore, the methods and results presented can directly contribute to global biodiversity assessments and achieving conservation targets.

6.1.2. Practical relevance

Addressing global habitat conversion and fragmentation effects on terrestrial vertebrate species richness is relevant for assessments assessing the global biodiversity status and trends therein (IPBES 2019), as well as for determining conservation goals (CBD 2010; Johnson et al. 2017; UN 2019), and for the strategies to meet global biodiversity targets (Ricketts and Imhoff 2003; Phalan et al. 2011; Pouzols et al. 2014; Saura et al. 2017). The results of chapter 3 contribute to such assessments of the global status and trends regarding biodiversity by assessing the magnitude of global land-use impacts on regional mammal species richness.

Information on the contribution of fragmentation effects relative to the effects of habitat conversion inform about the potential effects of land management strategies to mitigate impacts on or restore species richness. In relation to the “land sparing” and “land sharing” debate (Phalan et al. 2011; Simons and Weisser 2017), the results on the relative contribution of fragmentation effects suggest that protecting natural habitat is more effective than optimising habitat connectivity. Nevertheless, the results indicate that minimising habitat fragmentation or improving connectivity can contribute to reducing land-use impacts, suggesting that land sharing (Simons and Weisser 2017) and the establishment of corridors (Damschen et al. 2006) can support conservation efforts if protection of natural habitat is not an option.

Even though the SHR has been applied to non-flying mammals only in chapter 3, the concept can be applied to other taxonomic groups as well (e.g., chapter 5). The SHR can be used for the development of large-scale strategies to reduce land-use impacts or restore the quality of the landscape. By applying the SHR directly to land-use scenarios (Schipper et al. 2020), biodiversity impacts related to the scenarios can be assessed and used for optimisation strategies to maximise land-use output and minimise biodiversity impacts. This means that the SHR can be used for regional land-use planning or for the spatial design of protected areas (Saura et al. 2017). The SHR has been developed for the global scale and generalises habitat suitability and dispersal capacities at the ecoregion-level. Hence, one should be cautious with applying the SHR for small-scale applications as this may require more detailed assessments of specific habitat suitability and dispersal behaviour.

To address biodiversity conservation at the global level, GEPs can be used for the prioritisation and identification of protected areas (Pouzols et al. 2014; Veach et al. 2017). Likewise, they contribute to the half-earth discussion (Wilson 2016) regarding the effective protection of global biodiversity by protection half of the earth’s surface (Dinerstein et al. 2017; Pimm et al. 2018; Ellis 2019). Moreover, the GEPs can be directly applied to regional species richness impacts to

assess their global relevance, as done in chapter 5. This is done by multiplying the GEP of a certain region and taxonomic group with the relative regional species loss of the corresponding taxon and region. That is, GEPs can be readily implemented in various impact assessments regarding regional species richness and have already been used for assessing global impacts of land inundation (Dorber et al. 2019a, b). As the GEPs cover a variety of taxa in marine, freshwater, and terrestrial realms, they facilitate consistent modelling of global species loss across the various impact pathways within the LCIA framework.

The integration of the SHR and GEP into LCIA CFs indicates large regional differences in the per-area impacts of land-use on biodiversity. This emphasizes the importance of regionalised impact assessments (Mutel et al. 2018). That is, impact assessments should reflect the spatial differences in responses to anthropogenic pressures because the impacts in a specific region are not necessarily representative for the impacts in another.

Since this approach for calculating land-use CFs follows the LCIA recommendations as specified by the Life Cycle Initiative (Verones et al. 2017a; Jolliet et al. 2018), it is harmonised with existing LCIA methods. This ensures that the CFs can be readily used in operational life cycle assessments (LCAs) and potentially integrated into future updates of LCIA methodologies such as ReCiPe or LC-IMPACT (Huijbregts et al. 2017; Verones et al. 2020). LCA practitioners can multiply the CF of a certain land-use type in a certain region with the area of land-use of the corresponding type and in the corresponding region to estimate the biodiversity impact of the land-use activity. Such assessments can inform land-use planning on where land-use can be expected to have relatively high or relative low impacts. Alternatively, it may inform industries where in their value chain highest biodiversity impacts can be expected. It may also enable consumers to compare the biodiversity footprint of similar products.

The applicability of the CFs is not restricted to LCA. Other impact assessments may also rely on LCIA methods, such as environmentally extended input output analyses (EEIOA) that quantify consumption-based environmental pressures based on international trade and national accounts data (Chaudhary and Kastner 2016; Verones et al. 2017b; Marques et al. 2019). Land use data can be linked to such national accounts and by multiplying the land-use area with the CFs, biodiversity impacts embedded in international trade could be estimated. The CFs can also be used for large-scale environmental impact assessments or strategic environmental assessments to assess the land use impacts related to large development projects or strategic decisions, respectively. Hence, although this approach has been developed within the framework of LCIA, it has the potential to advance global impact assessments beyond LCA.

Together, the chapters of this thesis contribute to the understanding of and ability to quantify global habitat conversion and fragmentation impacts related to human land-use on terrestrial vertebrate species richness. Application of the SHR to land-use and land cover maps, use of the GEPs, or utilisation of the CFs in impact assessments could all contribute to monitoring progress towards achieving targets related to the SDG 15 (life on land) (UN 2019), uncovering trends for global assessments such as the Global Assessment Report on Biodiversity and Ecosystem Services (IPBES 2019), and identifying effective land-use planning (Dinerstein et al. 2017).

6.2. Limitations and uncertainty

6.2.1. Parameter limitations and uncertainty

Parameter uncertainty is the uncertainty associated with parameter values, which can result from inaccurate, incomplete, or unrepresentative data (Van Zelm and Huijbregts 2013). The proposed

land-use impact method relies on globally available data on, for example, species distributions, habitat occurrences, dispersal capacities, and land-use and land cover data.

Species distributions were used for the identification of species per ecoregion and to assess species endemism. Species distributions were obtained from the IUCN range maps (IUCN 2019). However, the accuracy of the species ranges may vary substantially, with some ranges accurately representing species occurrence whereas others more coarsely characterise the geographic range of occurrence (Brooks et al. 2019). Hurlbert and Jetz (2007) argued that at resolutions less than 200 km, range maps tend to overestimate the area of occupancy of individual species, leading to a potential mischaracterisation of species occurrence.

The suitability of different land types to the regional species community (as defined by the range maps) is defined as the proportion of species occurring in the land type relative to the total number of species in the regional community. This proportion can be defined based on local observations from comprehensive databases such as PREDICTS (Hudson et al. 2016; Chaudhary and Brooks 2018) or based on IUCN habitat classifications indicating in which habitats species occur (IUCN 2019), as done in this thesis. Local observations may not be available for all taxa or geographic regions, potentially leading to the use of unrepresentative data in regions absent of observations. The use of the IUCN habitat classification scheme, on the other hand, may be spatially inaccurate. For example, species documented to occur in forests may not occur across every forest cover within their range, although this is assumed when the IUCN data is used for estimating habitat suitabilities. The permeability of different land types relies on the same data.

Another factor relevant for the potential dispersal of species between habitat fragments is the median dispersal distance of the species occurring in a certain region and land type. However, dispersal distances are not documented for most terrestrial vertebrates. Because body-mass data is more widely available for birds and mammals (Wilman et al. 2014), the dispersal distances are estimated based on allometric relationships between body mass, home range, and natal dispersal distance (Sutherland et al. 2000; Bowman et al. 2002; Bowman 2003; Hilbers et al. 2016). Although these estimates allow for global species coverage, the estimated dispersal distances may be inaccurate.

The global identification of land-use and land cover types also involves uncertainty. First, it can be challenging to separate human-modified land from natural habitat (e.g., pasture land from natural grasslands) in satellite imagery. Second, seasonal changes may affect the identification of land cover types. There are several land-use and land cover maps (e.g., Ellis et al. 2010; Bontemps et al. 2011; Schipper et al. 2020), that each have different methods for characterising land-use and land cover types. The GLOBIO4 land classification (Schipper et al. 2020) is based on satellite imagery from the European Space Agency (ESA 2017) and land-use data from national or regional statistics. In GLOBIO4, the characterisation of land-use is matched to the land-use statistics by allocating land-use types to those cells with the highest probability so that the total characterised land-use matches the area of the regional land-use statistics. Hence, although the total amount of land-use classified by GLOBIO4 corresponds with total human-modified land, the spatial distribution may not always be accurate.

Species richness impacts are estimated based on predicted species richness in a reference state and in an impacted state. The impacted state is typically the current state of the land-use and land cover. The reference state typically reflects an unimpacted state. Because there is no data on the original land cover prior to human influence, the original land cover is estimated based on present-day climate data (Ramankutty et al. 2010). Furthermore, the suitability of the original land cover to the ecoregion species community is determined based on present-day habitat occurrences. It cannot be assessed whether such reference states adequately reflect the natural

state prior to human influence (Scholes and Biggs 2005). If the species richness in the reference state is overestimated, the predicted impacts are likely to be overestimated as well (and vice versa).

Species-area relationships indicate the rate at which species richness may decrease when the available area decreases. This rate is dependent on the size and evolutionary history of a region (Drakare et al. 2006; Storch et al. 2012; Gerstner et al. 2014). In theory every individual region has its own distinct species-area relationship. We derived SAR slopes that are taxon-, realm-, and ecoregion size-specific based on estimates of universal SAR slopes by Storch et al (2012). However, these slopes have not been tested at the ecoregion-level, potentially resulting in unrepresentative slopes for some regions.

6.2.2. Model limitations and uncertainty

Model uncertainty is the result of the incomplete understanding or oversimplification of a mechanism (Van Zelm and Huijbregts 2013). The impact method for the quantification of land-use effects on species richness is based on a species-area model, centring around the assumption that species richness decreases by decrease in available habitat. Because simple traditional SARs may systematically overestimate extinctions (He and Hubbell 2011), the impact method proposed here is based on the countryside SAR, which considers that part of the regional species community will remain in the human-modified land after conversion of natural habitat (Pereira and Daily 2006; Martins and Pereira 2017). Although considering the suitability of natural and human land types improves the performance of SARs (Proença and Pereira 2013), they do not capture all complex pressure-response mechanisms related to land-use impacts on species richness (Matias et al. 2014; Matthews et al. 2014).

The SHR is an integration of the countryside SAR (Pereira and Daily 2006) and the equivalent connected area (ECA) measure (Saura et al. 2011) by replacing the area variable in the SAR by the ECA. The ECA considers the area of and distance between distinct patches, the permeability of the matrix separating these patches, and the dispersal distance of the group of species in a certain region and land type. Because of the relatively low parameter requirements and global availability of input data, the SHR is a suitable modelling approach for LCA impact methods. The advantage of using the SHR in impact assessments is that it reflects additional impacts if fragmentation occurs. However, the SHR was not rigorously validated against empirical assessments of land-use impacts on species richness (which is partly due to the absence of such data at the ecoregion or global scale). Consequently, although the SHR considers both habitat conversion and fragmentation effects, it cannot be concluded whether it better predicts species richness than the conventional countryside SAR. Hence, it is currently recommended to use it for comparative impact assessments to weigh fragmentation into the comparison and not for calculating absolute species richness.

The global extinction probability (GEP) is a method to translate impacts on regional species richness into potential global species extinctions. It is an approximation that assumes a linear relationship between the number of regionally lost and globally lost species (i.e., 1 every X number of species that becomes lost regionally is likely to be extinct globally too). However global extinctions do not follow such a linear trend in reality, resulting in a potential under- or overestimation of global species extinctions.

6.2.3. Limitations and uncertainty regarding the potential application

Due to the unavailability of comprehensive data on species distributions or other species characteristics for all taxa, the characterisation of land-use impacts has been limited to terrestrial

vertebrates (i.e., amphibians, reptiles, mammals, and birds). Hence, other terrestrial taxa, such as plants, insects, or fungi are not considered. This means that the land-use impact method does not reflect impacts on all species. When applying the CFs in the LCA context to estimate land-use impacts, the impacts can be interpreted as impacts on terrestrial vertebrates only, or as proxies for impacts on total terrestrial species richness.

Life cycle inventory (LCI) data, representing the amount of land used per land-use type during the life cycle of a product, is often provided at a geographically coarse scale. The potential mismatch of the spatial resolution of the LCI data with the spatial resolution of LCIA CFs means that the spatial differentiation in responses reflected in the LCIA CFs cannot be utilised (Mutel et al. 2018). Using regionally-aggregated CFs results in more inaccurate impact predictions. Furthermore, LCA practitioners typically use LCA software to calculate the impacts of products or processes. However, most commercial software tools do currently not support spatial differentiation, preventing the adoption of spatially explicit LCAs.

CFs could only be calculated for regions in which land-use and species data was present. This means that the impact method did not characterise land-use impacts on species richness in some regions. If there is LCI land-use data in such regions that needs to be matched with a CF, a global average CF or a CF interpolated from neighbouring areas could be used (Mutel et al. 2018). However, the use of unrepresentative CFs may result in a mischaracterisation of the impacts.

The land-use CFs indicate per-area species richness impacts. Multiplying the CFs with the LCI data (i.e., land-use area) results in total species richness impacts related to a certain amount of land-use. This means that LCA assumes a linear pressure-response relationship between land-use and species richness impacts (Curran et al. 2011), not considering potential pressure-response thresholds. This is not just the case for land-use impacts, but for all impacts estimated within LCA.

Although the SHR can be used to assess potential positive effects of habitat restoration, CFs only calculate negative effects. This means it is assumed that land-use either does not affect, or negatively affects species richness. For example, CFs are not designed to estimate positive effects of abandoning human-modified land (i.e., a negative LCI land-use value).

LCA assesses biodiversity impacts for each pressure independently, not considering potential interactions between the impacts of various pressures (Curran et al. 2011). This may lead to an underestimation of the total impacts if the impacts of combined pressures are higher than the sum of the impacts related to these pressures individually. Conversely, this may result in an overestimation of the total impacts if the impacts of combined pressures are lower than the sum of the impacts related to these pressures individually.

LCA is meant for comparative analyses to reduce the environmental footprint of products and processes. Hence, land-use impacts calculated by multiplying LCI data with corresponding CFs should not be interpreted as absolute impacts, but rather used comparatively only (Hauschild and Huijbregts 2015).

6.3. Conclusion and outlook

Chapters 2-5 build towards the development of a method characterising species richness impacts of global habitat conversion and fragmentation within the LCIA framework. The thesis highlights the relative relevance of global habitat fragmentation compared to habitat conversion effects on species richness. Furthermore, it emphasizes the regional differentiation both in terms of regional and global impacts. This is the first global approach that systematically characterises the combined effects of habitat conversion and fragmentation, providing an important contribution to potentially improve land-use impact assessments in decision-support tools like LCA or EEIOA.

Further research is required to validate the SHR model performance against empirical data regarding land use impacts on species richness. Other next steps could be extension of the approach to also consider fragmentation effects other than those related to habitat connectivity, such as edge, shape, and matrix spillover effects.

Furthermore, the impact assessment method should be improved as new data becomes available. For example to:

- A) extend the analysis across other taxa (e.g., plants and insects);
- B) increase parameter accuracy, e.g., by refining the species dispersal distance;
- C) reduce model uncertainty, e.g., by adding relevant explanatory variables (if data availability allows for its parametrisation);
- D) refine the land-use and land cover classification and possibly extend or refine the number of land-use and natural land cover classes considered in the model.
- E) differentiate between land use intensities.

This is a first attempt to quantify both global habitat conversion and fragmentation impacts in LCA. As such, it is not meant as the golden standard for characterising fragmentation impacts in LCA. Other approaches are welcome to substantiate, further develop, or challenge the results from this research. Nevertheless, this thesis contributes a starting point for including fragmentation in future global land-use impact assessments. It highlights the potential relevance of fragmentation effects, hopefully stimulating its consideration in LCA; it introduces a model and set of factors to consistently translate regional species loss into potential global species extinctions across terrestrial, freshwater, and marine taxa, facilitating the harmonisation of various LCIA models (e.g., for land use, water use, or eutrophication); it proposes a method for quantifying global fragmentation effects within the LCA framework; and it introduces a set of CFs that can be readily used by LCA practitioners, facilitating the consideration of both habitat conversion and fragmentation in decision-making processes. These developments contribute to significantly advance the level of sophistication of LCA and land use impact assessments.

6.4. References

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SI1 (Supporting Information for chapter 3): Global effects of habitat conversion and fragmentation on regional mammal species richness

Submitted to Proceedings of the National Academy of Sciences of the United States of America

The main article to this supplementary material is awaiting publication and is not included in NTNU Open

SI2 (Supporting Information for chapter 4): Potential consequences of regional species loss for global species richness: a quantitative approach for estimating global extinction probabilities

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Potential consequences of regional species loss for global species richness – a quantitative approach for estimating global extinction probabilities

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Supplementary Information-1

This file includes Figures S1-S9 and table S1.

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Supplementary Information-2

The Supporting Information (including SI-2) is available free of charge on the ACS Publications website at DOI: 10.1021/acs.est.8b06173. SI-2 includes Tables S1-S3 on ecoregion-level marine, terrestrial, and freshwater GEPs, respectively, and Table S4 on the case study.

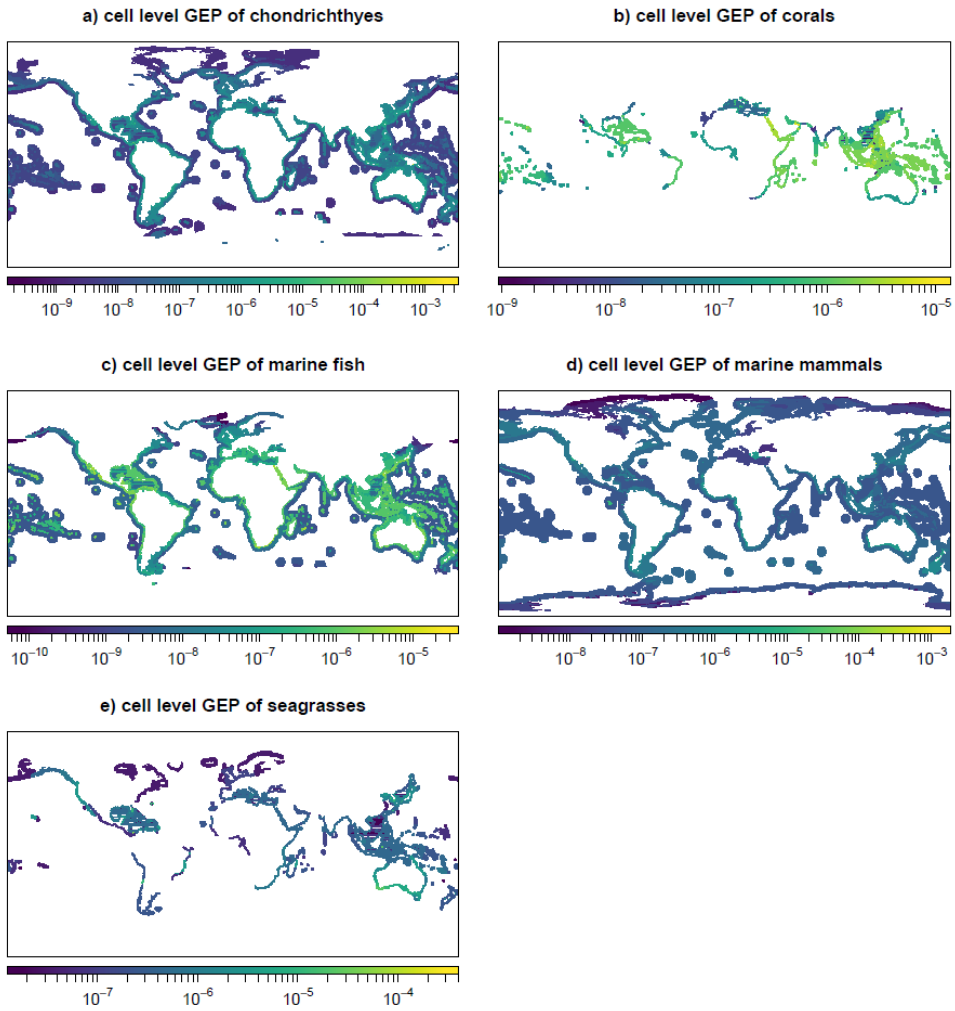


Figure S1. Cell level GEP of marine species groups: a) chondrichthyes, b) corals, c) marine fish, d) marine mammals, and e) seagrasses (legend scaled logarithmically). The maps use the marine ecoregions of the world¹ to delineate borders.

The cell values (GEPs) are calculated by the following equation:

$$GEP_p = \frac{\sum_s \frac{o_{s,p} \cdot TL_s}{\sum_p o_{s,p}}}{\sum_s TL_s}$$

where o is the occurrence of species s in cell p , and TL is the threat level of species s . The sum of all cell level GEPs is 1. All species occurrences outside marine ecoregions are excluded.

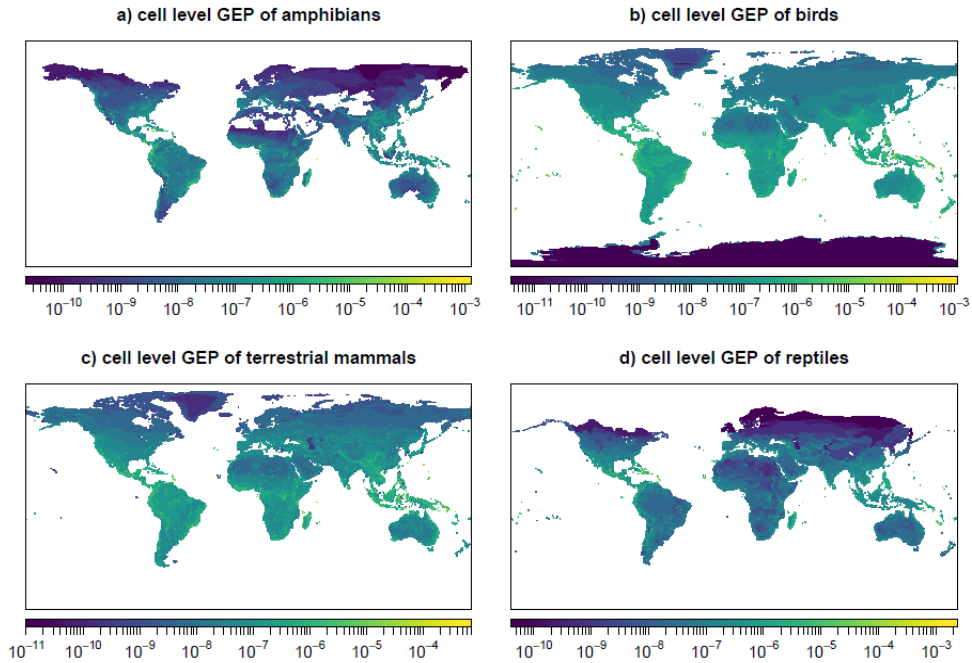


Figure S2. Cell level GEP of terrestrial species groups: a) amphibians, b) birds, c) terrestrial mammals, and d) reptiles (legend scaled logarithmically). The maps use the terrestrial ecoregions of the world² to delineate borders.

The cell values (GEPs) are calculated by the following equation:

$$GEP_p = \frac{\sum_s \frac{o_{s,p} \cdot TL_s}{\sum_p o_{s,p}}}{\sum_s TL_s}$$

where o is the occurrence of species s in cell p , and TL is the threat level of species s . The sum of all cell level GEPs is 1. All species occurrences outside terrestrial ecoregions are excluded.

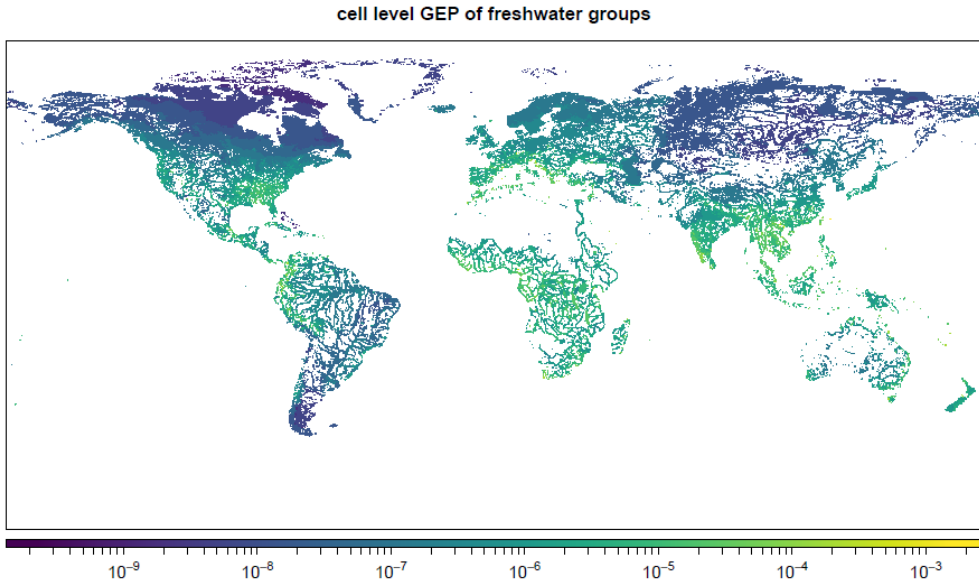


Figure S3. Cell level GEP of freshwater species groups combined (legend scaled logarithmically). The map uses the freshwater ecoregions of the world³ and the Global Lakes and Wetlands Database⁴ to delineate borders.

The cell values (GEPs) are calculated by the following equation:

$$GEP_p = \frac{\sum_s \frac{o_{s,p} \cdot TL_s}{\sum_p o_{s,p}}}{\sum_s TL_s}$$

where o is the occurrence of species s in cell p , and TL is the threat level of species s . The sum of all cell level GEPs is 1. All species occurrences outside freshwater bodies are excluded.

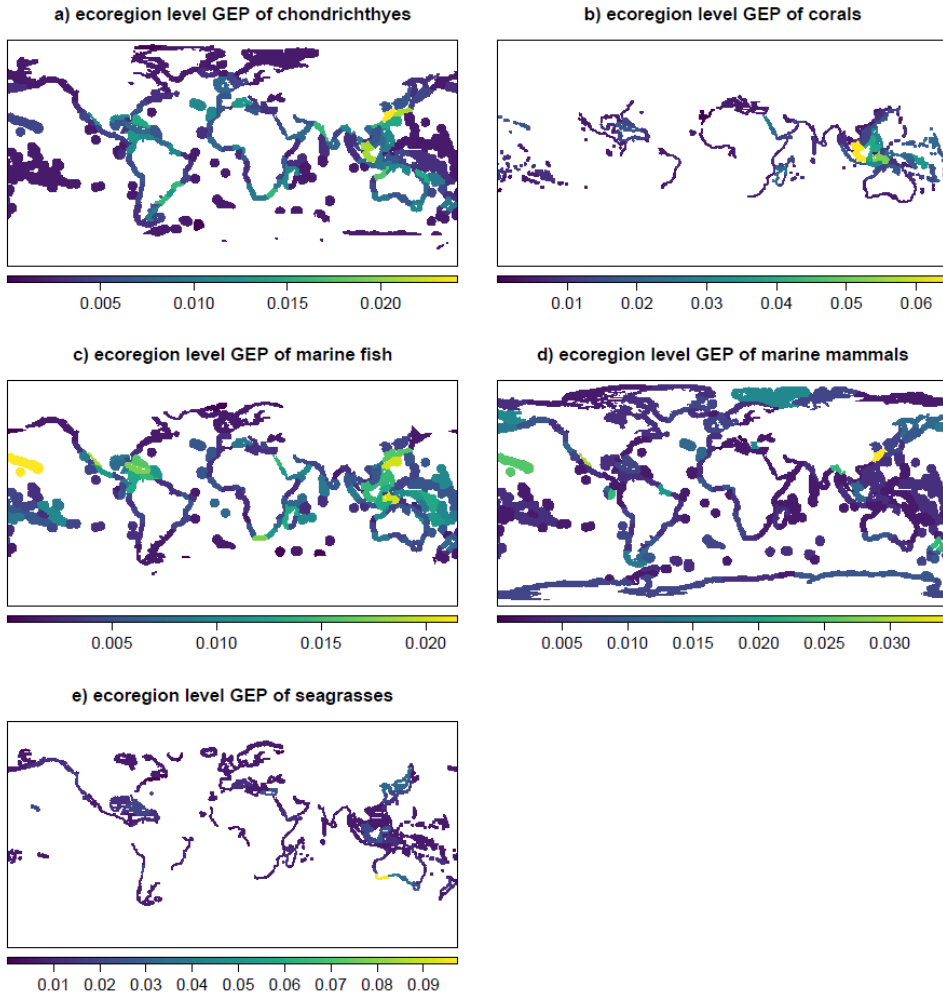


Figure S4. Ecoregion level GEP of marine species groups: a) chondrichthyes, b) corals, c) marine fish, d) marine mammals, and e) seagrasses (legend scaled linearly). The maps use the marine ecoregions of the world¹ to delineate borders.

The ecoregion values (GEPs) are calculated by the following equation:

$$GEP_r = \sum_p \frac{\sum_s \frac{o_{s,p,r} \cdot TL_s}{\sum_{p,r} o_{s,p,r}}}{\sum_s TL_s}$$

where o is the occurrence of species s in cell p and spatial unit r (e.g., ecoregion), and TL is the threat level of species s . The sum of all cell level GEPs is 1. All species occurrences outside marine ecoregions are excluded.

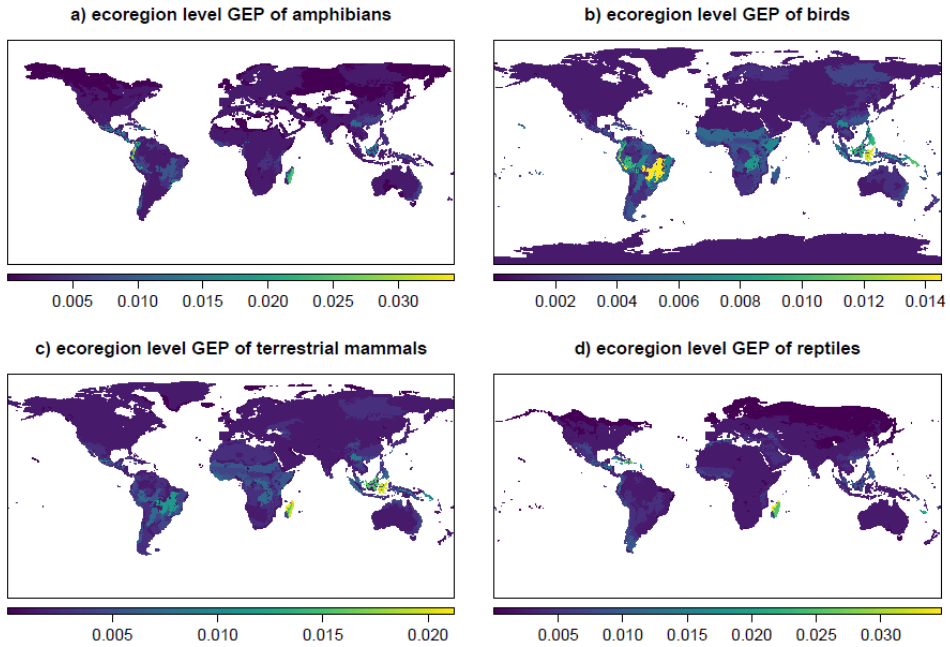


Figure S5. Ecoregion level GEP of terrestrial species groups: a) amphibians, b) birds, c) terrestrial mammals, and d) reptiles (legend scaled linearly). The maps use the terrestrial ecoregions of the world² to delineate borders.

The ecoregion values (GEPs) are calculated by the following equation:

$$GEP_r = \sum_p \frac{\sum_s \frac{o_{s,p,r} \cdot TL_s}{\sum_{p,r} o_{s,p,r}}}{\sum_s TL_s}$$

where o is the occurrence of species s in cell p and spatial unit r (e.g., ecoregion), and TL is the threat level of species s . The sum of all cell level GEPs is 1. All species occurrences outside marine ecoregions are excluded.

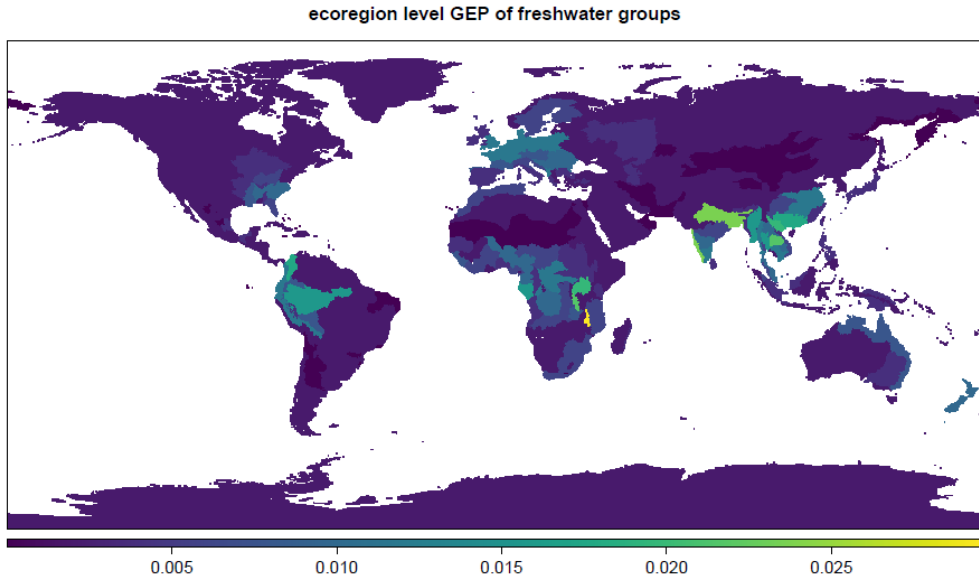


Figure S6. Ecoregion level GEP of freshwater species groups combined (legend scaled linearly). The map uses the freshwater ecoregions of the world³ and the Global Lakes and Wetlands Database⁴ to delineate borders.

The ecoregion values (GEPs) are calculated by the following equation:

$$GEP_r = \sum_p \frac{\sum_s \frac{o_{s,p,r} \cdot TL_s}{\sum_{p,r} o_{s,p,r}}}{\sum_s TL_s}$$

where o is the occurrence of species s in cell p and spatial unit r (e.g., ecoregion), and TL is the threat level of species s . The sum of all cell level GEPs is 1. All species occurrences outside marine ecoregions are excluded.

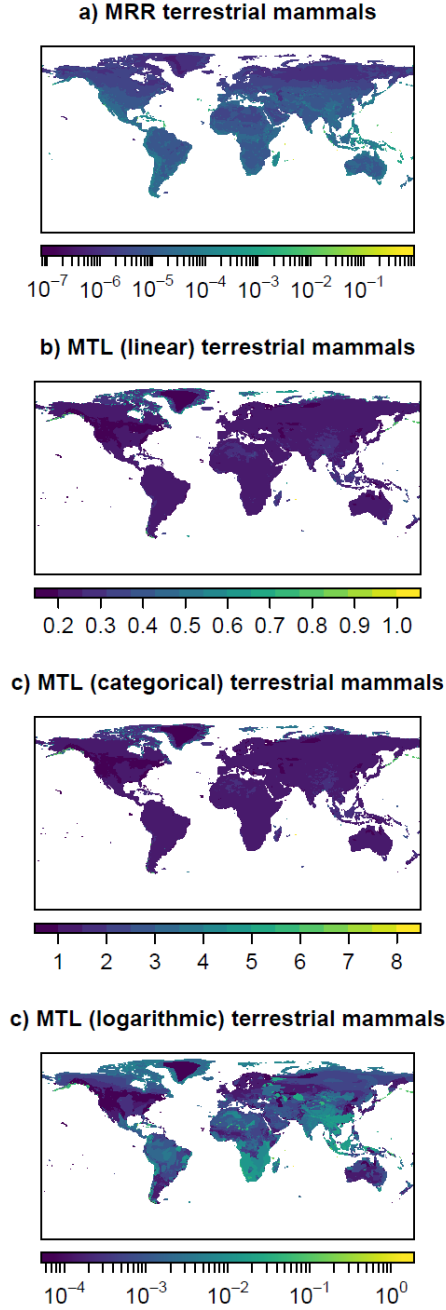


Figure S7. Mean range rarity (MRR) and mean threat levels (MTLs) of terrestrial mammals (legend scaled logarithmically for MRR and MTL logarithmic, and linearly for MTL linear and MTL categorical). The maps use the terrestrial ecoregions of the world² to delineate borders.

The mean range rarity and mean threat levels are calculated by the following equations:

$$MRR_p = \frac{\sum_{s=1}^n \frac{o_{s,p}}{\sum_p o_{s,p}}}{n_p} \text{ and } MTL_p = \frac{\sum_{s=1}^n TL_{s,p}}{n_p},$$

where o is the occurrence of species s in grid cell p , n the number of species in grid cell p , and TL the threat level of species s in grid cell p .

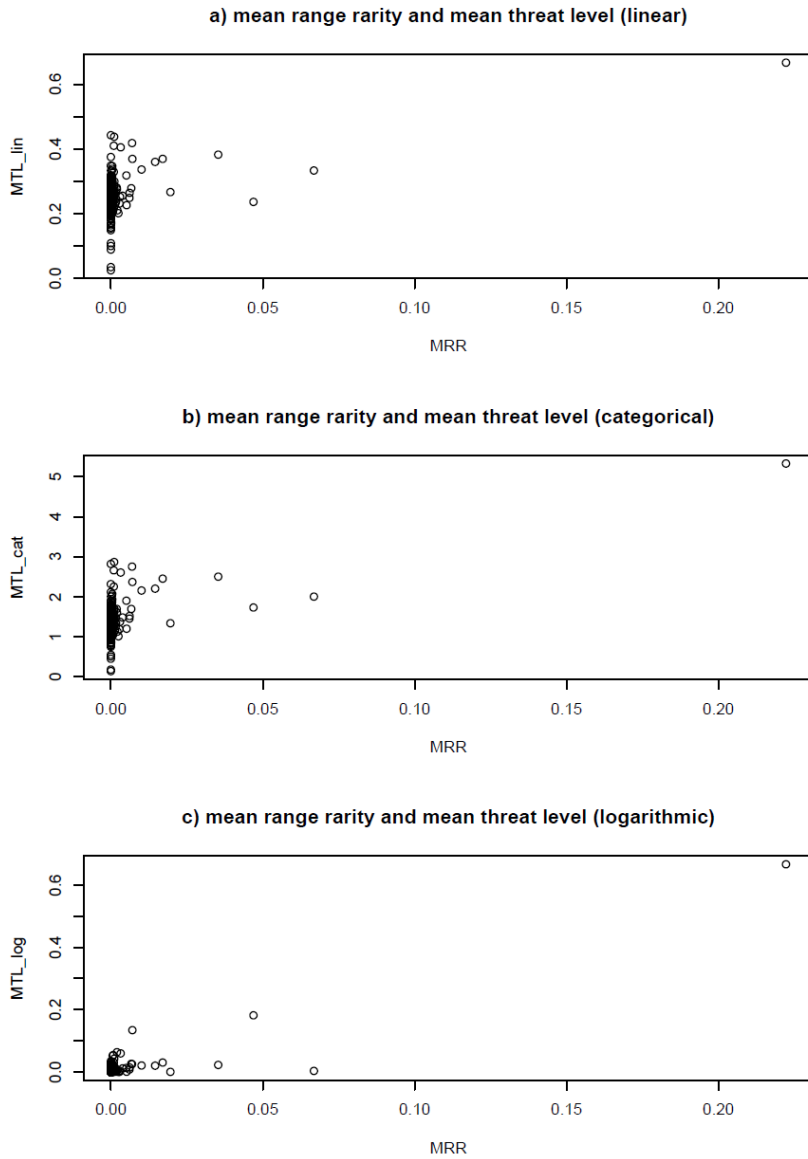


Figure S8. Scatterplots of mean range rarity (MRR) plotted against mean threat levels (MTLs) of terrestrial mammals.

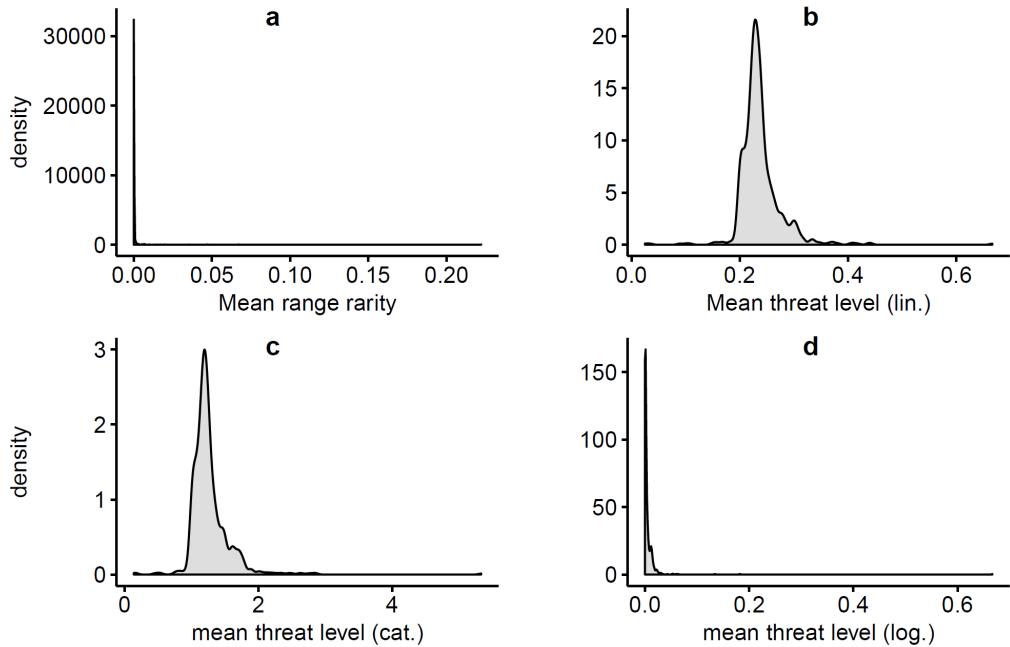


Figure S9. Densities of ecoregion-level a) mean range rarity (MRR), b) mean threat level (MTL) linearly parametrised, c) MTL categorically parametrised, and d) MTL logarithmically parametrised.

The ecoregion-level MRR and MTL data has been tested for normality by analysing the figures above and performing Shapiro-Wilk's tests on each data set. The results indicate that neither of the datasets is normally distributed. For this reason, we used the Pearson's correlation coefficient for analysing the correlation between the MRR and various MTL data.

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Table S1. Rankings [high-low] of the (1) terrestrial mammal GEPs (categorical parametrisation) per ecoregion, (2) agricultural land use impacts on regional mammal species diversity based on Chaudhary and Brooks⁵ [regional PDF mammal species/m²], and (3) agricultural land use impacts on global mammal species diversity [global PDF mammal species/m²].

Ecoregion	code	Rank mammal GEP	Rank regional PDF mammal species/m ²	Rank global PDF mammal species/m ²
Lord Howe Island subtropical forests	AA0109	344	1	1
Christmas and Cocos Islands tropical forests	IM0110	416	2	3
Ogasawara subtropical moist forests	OC0109	345	3	2
Cayos Miskitos-San Andrés and Providencia moist forests	NT0110	790	4	722
Granitic Seychelles forests	AT0113	340	5	4
Enriquillo wetlands	NT0903	783	6	373
Maldives-Lakshadweep-Chagos Archipelago tropical moist forests	IM0125	785	7	552
Cook Islands tropical moist forests	OC0103	786	8	672
Southern Africa mangroves	AT1405	748	9	170
Lesser Antillean dry forests	NT0220	669	10	59
Mount Cameroon and Bioko montane forests	AT0121	88	11	5
Sierra de la Laguna pine-oak forests	NT0307	701	12	97
Leeward Islands moist forests	NT0134	373	13	14
Madagascar ericoid thickets	AT1011	758	14	285
Puerto Rican dry forests	NT0226	749	15	242
Sao Tome, Principe and Annobon moist lowland forests	AT0127	187	16	8
Palau tropical moist forests	OC0110	530	17	33
Madeira evergreen forests	PA0425	685	18	135
Tongan tropical moist forests	OC0114	780	19	649
Pati-a Valley dry forests	NT0225	761	20	384
Chimalapas montane forests	NT0114	733	21	258
Jamaican dry forests	NT0218	498	22	42
Santa Marta páramo	NT1007	712	23	190
Nicobar Islands rain forests	IM0133	118	24	7
Louisiade Archipelago rain forests	AA0110	507	25	48
Windward Islands moist forests	NT0179	419	26	26
South Florida rocklands	NT0164	673	27	150
South Avalon-Burin oceanic barrens	NA0615	789	28	764
Rwenzori-Virunga montane moorlands	AT1013	147	29	10
Hawaii tropical high shrublands	OC0701	795	30	774
Belizian pine forests	NT0302	672	31	158
Eastern Panamanian montane forests	NT0122	692	32	191
Sri Lanka montane rain forests	IM0155	381	33	22
Khangai Mountains conifer forests	PA0512	776	34	583
East African montane moorlands	AT1005	448	35	43
Knysna-Amatole montane forests	AT0115	684	36	192
Sulu Archipelago rain forests	IM0156	560	37	75
South Taiwan monsoon rain forests	IM0171	659	38	162
Admiralty Islands lowland rain forests	AA0101	337	39	19
Marianas tropical dry forests	OC0203	399	40	35
Sierra de los Tuxtlas	NT0161	327	41	20
Yapen rain forests	AA0108	427	42	51
East African halophytics	AT0901	753	43	402
Socotra Island xeric shrublands	AT1318	781	44	706
Cuban cactus scrub	NT1306	548	45	80
Hawaii tropical low shrublands	OC0702	793	46	773
Sumatran tropical pine forests	IM0304	695	47	234
Comoros forests	AT0105	238	48	18
Florida sand pine scrub	NA0513	774	49	622
Biak-Numfoor rain forests	AA0103	95	50	11
Motagua Valley thornscrub	NT1312	742	51	372
Veracruz montane forests	NT0177	568	52	109
Southeastern Iberian shrubs and woodlands	PA1219	772	53	616
Peninsular Malaysian peat swamp forests	IM0145	700	54	265
Sierra de la Laguna dry forests	NT0227	494	55	77
Guayaquil flooded grasslands	NT0905	654	56	202
Rakiura Island temperate forests	AA0407	343	57	39
Santa Marta montane forests	NT0159	455	58	68
Panamanian dry forests	NT0224	716	59	291
Caatinga Enclaves moist forests	NT0106	549	60	100
Sierra Juarez and San Pedro Martir pine-oak forests	NA0526	423	61	64
Cordillera de Merida páramo	NT1005	335	62	44
Trobrind Islands rain forests	AA0125	86	63	12
Chiapas montane forests	NT0113	538	64	113
Trinidad and Tobago moist forests	NT0171	564	65	128
Nansei Islands subtropical evergreen forests	IM0170	34	66	9

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Corsican montane broadleaf and mixed forests	PA1204	778	67	714
Madagascar mangroves	AT1404	313	68	38
Kinabalu montane alpine meadows	IM1001	420	69	71
Veracruz dry forests	NT0233	655	70	244
Mentawai Islands rain forests	IM0127	14	71	6
Bahamian-Antillean mangroves	NT1402	66	72	13
Oaxacan montane forests	NT0146	288	73	40
Southern Mesoamerican Pacific mangroves	NT1407	348	74	56
Northern Mesoamerican Pacific mangroves	NT1404	458	75	90
Cuban pine forests	NT0304	730	76	403
Cuban wetlands	NT0902	454	77	89
Atlantic Coast restingas	NT0102	429	78	81
Cauca Valley dry forests	NT0207	693	79	305
Indus River Delta-Arabian Sea mangroves	IM1403	750	80	480
Mascarene forests	AT0120	237	81	30
San Lucan xeric scrub	NT1314	480	82	118
Andaman Islands rain forests	IM0101	96	83	17
Great Basin montane forests	NA0515	470	84	112
New Caledonia dry forests	AA0202	224	85	31
Samoa tropical moist forests	OC0112	728	86	425
Goadavari-Krishna mangroves	IM1401	743	87	487
Mandara Plateau mosaic	AT0710	754	88	534
Cape Verde Islands dry forests	AT0201	787	89	767
Puerto Rican moist forests	NT0155	574	90	195
Jamaican moist forests	NT0131	176	91	27
Eritrean coastal desert	AT1304	751	92	533
Eastern Zimbabwe montane forest-grassland mosaic	AT1006	501	93	146
Bahamian pine mosaic	NT0301	415	94	107
Southern Atlantic mangroves	NT1406	254	95	50
Guianan freshwater swamp forests	NT0149	734	96	469
Atlantic coastal pine barrens	NA0504	738	97	490
Canary Islands dry woodlands and forests	PA1203	375	98	82
Maranhão Babaçu forests	NT0139	352	99	78
Costa Rican seasonal moist forests	NT0119	311	100	66
Northeastern Brazil restingas	NT0144	674	101	334
Sierra Madre de Chiapas moist forests	NT0162	491	102	155
Araya and Paria xeric scrub	NT1301	557	103	204
Yellow Sea saline meadow	PA0908	762	104	639
Gurupa várzea	NT0126	697	105	366
Banda Sea Islands moist deciduous forests	AA0102	207	106	47
Lake Chad flooded savanna	AT0904	739	107	509
Luzon tropical pine forests	IM0302	194	108	45
Itigi-Sumbu thicket	AT0708	731	109	478
Drakensberg alti-montane grasslands and woodlands	AT1003	711	110	401
Red River freshwater swamp forests	IM0147	512	111	177
Northeast India-Myanmar pine forests	IM0303	609	112	260
Hispaniolan pine forests	NT0305	551	113	207
Sri Lanka lowland rain forests	IM0154	33	114	15
Hawaii tropical moist forests	OC0106	792	115	772
Crete Mediterranean forests	PA1205	397	116	125
Northern California coastal forests	NA0519	520	117	200
Galápagos Islands scrubland mosaic	NT1307	213	118	54
Northern Triangle temperate forests	IM0402	539	119	209
Mediterranean High Atlas juniper steppe	PA1010	675	120	354
Wrangel Island arctic desert	PA1113	487	121	176
Sierra Madre de Oaxaca pine-oak forests	NT0308	43	122	16
Central American montane forests	NT0112	241	123	57
Chiapas Depression dry forests	NT0211	377	124	117
South Malawi montane forest-grassland mosaic	AT1014	604	125	272
Willamette Valley forests	NA0417	509	126	201
Luzon montane rain forests	IM0122	341	127	99
South American Pacific mangroves	NT1405	312	128	83
Orinoco wetlands	NT0906	694	129	397
Niger Delta swamp forests	AT0122	336	130	102
South Sakhalin-Kurile mixed forests	PA0438	720	131	468
East African mangroves	AT1402	475	132	185
Etosha Pan halophytics	AT0902	736	133	549
Buru rain forests	AA0104	307	134	87
Honshu alpine conifer forests	PA0511	401	135	147
Cordillera La Costa montane forests	NT0117	370	136	127
Albany thickets	AT1201	506	137	215
Mindoro rain forests	IM0130	121	138	37
Hawaii tropical dry forests	OC0202	791	139	771
Cyprus Mediterranean forests	PA1206	525	140	233
Hispaniolan dry forests	NT0215	522	141	229

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Qilian Mountains conifer forests	PA0517	570	142	263
Pantanos de Centla	NT0148	617	143	313
Pernambuco coastal forests	NT0151	421	144	167
Jos Plateau forest-grassland mosaic	AT1010	503	145	223
Tehuacán Valley matorral	NT1316	314	146	103
Miskito pine forests	NT0306	612	147	316
Southern Korea evergreen forests	PA0439	735	148	564
Fiji tropical dry forests	OC0201	611	149	315
KwaZulu-Cape coastal forest mosaic	AT0116	571	150	279
Cross-Niger transition forests	AT0106	432	151	186
Sumba deciduous forests	AA0203	598	152	311
Lara-Falcón dry forests	NT0219	493	153	227
Talamancan montane forests	NT0167	119	154	49
Queen Charlotte Islands	NA0525	759	155	670
Magdalena Valley dry forests	NT0221	514	156	246
Aleutian Islands tundra	NA1102	342	157	138
Sundarbans freshwater swamp forests	IM0162	725	158	547
Kamchatka-Kurile taiga	PA0604	771	159	732
Central Range sub-alpine grasslands	AA1002	77	160	32
New Britain-New Ireland montane rain forests	AA0112	541	161	269
Eastern Java-Bali montane rain forests	IM0112	395	162	172
Irrawaddy freshwater swamp forests	IM0116	732	163	571
Guinean mangroves	AT1403	527	164	264
Scandinavian coastal conifer forests	PA0520	766	165	719
Northern Khorat Plateau moist deciduous forests	IM0138	652	166	390
Cordillera Central páramo	NT1004	249	167	86
Appenine deciduous montane forests	PA0401	666	168	421
Palawan rain forests	IM0143	55	169	25
Puget lowland forests	NA0524	594	170	331
Azores temperate mixed forests	PA0403	485	171	241
Eastern Arc forests	AT0109	83	172	41
Jarrah-Karri forest and shrublands	AA1204	317	173	136
Pernambuco interior forests	NT0152	406	174	197
East Afghan montane conifer forests	PA0506	457	175	221
Peninsular Malaysian montane rain forests	IM0144	287	176	120
Hainan Island monsoon rain forests	IM0169	280	177	116
Newfoundland Highland forests	NA0611	784	178	766
Ecuadorian dry forests	NT0214	393	179	196
Cuban moist forests	NT0120	178	180	76
Copper Plateau taiga	NA0604	765	181	725
Sumatran freshwater swamp forests	IM0157	442	182	222
Maputaland-Pondoland bushland and thickets	AT1012	374	183	179
Tasmanian Central Highland forests	AA0411	380	184	188
Zambezi coastal flooded savanna	AT0906	706	185	508
Myanmar Coast mangroves	IM1404	634	186	382
Huon Peninsula montane rain forests	AA0107	309	187	140
Fiji tropical moist forests	OC0105	216	188	92
Catatumbo moist forests	NT0108	434	189	224
New Caledonia rain forests	AA0113	298	190	137
Afghan Mountains semi-desert	PA1301	737	191	630
Chao Phraya lowland moist deciduous forests	IM0108	490	192	261
Ethiopian montane moorlands	AT1008	44	193	28
Bohai Sea saline meadow	PA0902	773	194	752
Mindanao montane rain forests	IM0128	269	195	119
Sinú Valley dry forests	NT0229	391	196	203
Jalisco dry forests	NT0217	117	197	60
Isthmian-Pacific moist forests	NT0130	289	198	134
Helanshan montane conifer forests	PA0508	389	199	205
Tasmanian temperate forests	AA0412	329	200	166
Gulf of California xeric scrub	NA1306	28	201	21
Vanuatu rain forests	AA0126	93	202	55
South Appenine mixed montane forests	PA1218	696	203	499
Mediterranean conifer and mixed forests	PA0513	543	204	309
Tonle Sap freshwater swamp forests	IM0164	643	205	419
Northern Vietnam lowland rain forests	IM0141	349	206	184
Central African mangroves	AT1401	319	207	157
Sundarbans mangroves	IM1406	677	208	473
Orissa semi-evergreen forests	IM0142	718	209	550
Guinean montane forests	AT0114	417	210	235
Marañón dry forests	NT0223	561	211	332
South Western Ghats montane rain forests	IM0151	73	212	52
Lowland fynbos and renosterveld	AT1202	318	213	165
Tamaulipan matorral	NA1311	607	214	375
Cauca Valley montane forests	NT0109	132	215	74
Tian Shan montane conifer forests	PA0521	599	216	367

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South Western Ghats moist deciduous forests	IM0150	202	217	106
Eastern Himalayan subalpine conifer forests	IM0501	195	218	101
Indochina mangroves	IM1402	499	219	296
Angolan montane forest-grassland mosaic	AT1001	552	220	336
Venezuelan Andes montane forests	NT0175	150	221	84
Australian Alps montane grasslands	AA1001	414	222	243
Swan Coastal Plain Scrub and Woodlands	AA1205	665	223	474
Maputaland coastal forest mosaic	AT0119	403	224	237
Nihonkai evergreen forests	PA0427	303	225	159
Serengeti volcanic grasslands	AT0714	647	226	447
Western Java montane rain forests	IM0167	91	227	61
East Deccan dry-evergreen forests	IM0204	713	228	560
Seram rain forests	AA0118	47	229	46
Flint Hills tall grasslands	NA0807	727	230	634
Western Ecuador moist forests	NT0178	266	231	142
Vogelkop montane rain forests	AA0127	152	232	96
Hispaniolan moist forests	NT0127	263	233	143
Tonle Sap-Mekong peat swamp forests	IM0165	593	234	386
Paraguana xeric scrub	NT1313	192	235	123
Orinoco Delta swamp forests	NT0147	559	236	350
Indus Valley desert	IM1302	768	237	748
Northern New Guinea montane rain forests	AA0116	75	238	58
Cook Inlet taiga	NA0603	740	239	673
Hokkaido deciduous forests	PA0423	708	240	566
Pyrenees conifer and mixed forests	PA0433	596	241	394
Bajo dry forests	NT0204	529	242	340
Zambezian Cryptosepalum dry forests	AT0203	603	243	407
Northern transitional alpine forests	NA0521	752	244	708
Fiordland temperate forests	AA0403	745	245	686
Caledon conifer forests	PA0503	770	246	757
Cameroonian Highlands forests	AT0103	16	247	23
Crimean Submediterranean forest complex	PA0416	648	248	470
Trans Fly savanna and grasslands	AA0708	363	249	231
Montane fynbos and renosterveld	AT1203	268	250	161
Queensland tropical rain forests	AA0117	81	251	69
Everglades	NT0904	558	252	364
Central Anatolian steppe	PA0803	629	253	458
New Guinea mangroves	AA1401	398	254	266
Southern Rift montane forest-grassland mosaic	AT1015	160	255	121
Chin Hills-Arakan Yoma montane forests	IM0109	502	256	338
Sulaiman Range alpine meadows	PA1018	676	257	530
Nenjiang River grassland	PA0903	744	258	698
Taiwan subtropical evergreen forests	IM0172	141	259	108
North Western Ghats montane rain forests	IM0135	293	260	194
Malabar Coast moist forests	IM0124	219	261	152
Irrawaddy dry forests	IM0205	546	262	365
Chao Phraya freshwater swamp forests	IM0107	473	263	321
Southern Pacific dry forests	NT0230	278	264	182
Western Himalayan subalpine conifer forests	IM0502	371	265	253
Halmahera rain forests	AA0106	130	266	105
Campos Rupestres montane savanna	NT0703	199	267	148
Gulf of St. Lawrence lowland forests	NA0408	726	268	665
Tasmanian temperate rain forests	AA0413	259	269	171
Kopet Dag semi-desert	PA1319	704	270	592
Rodope montane mixed forests	PA0435	662	271	523
Hobyo grasslands and shrublands	AT1307	606	272	438
Westland temperate forests	AA0414	760	273	736
Amazon-Orinoco-Southern Caribbean mangroves	NT1401	270	274	180
Madagascar spiny thickets	AT1311	78	275	73
Himalayan subtropical broadleaf forests	IM0115	153	276	129
Southern Vietnam lowland dry forests	IM0211	276	277	193
Central and Southern Cascades forests	NA0508	410	278	293
Greater Negros-Panay rain forests	IM0114	56	279	63
Tumbes-Piura dry forests	NT0232	347	280	250
Southern Cone Mesopotamian savanna	NT0909	583	281	418
Inner Niger Delta flooded savanna	AT0903	624	282	471
Sunda Shelf mangroves	IM1405	245	283	174
Western Java rain forests	IM0168	68	284	72
California montane chaparral and woodlands	NA1203	355	285	262
Teral-Duar savanna and grasslands	IM0701	383	286	282
Northern Andean páramo	NT1006	48	287	67
East Saharan montane xeric woodlands	AT1303	621	288	477
Texas blackland prairies	NA0814	690	289	582
Southwest Borneo freshwater swamp forests	IM0153	446	290	329
East Central Texas forests	NA0405	620	291	485

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Northeastern Himalayan subalpine conifer forests	PA0514	384	292	290
Meghalaya subtropical forests	IM0126	378	293	284
Wasatch and Uinta montane forests	NA0530	537	294	391
Mount Lofty woodlands	AA1206	322	295	247
Cross-Sanaga-Bioko coastal forests	AT0107	71	296	79
Klamath-Siskiyou forests	NA0516	362	297	280
Alberta Mountain forests	NA0501	724	298	671
Sierra Madre del Sur pine-oak forests	NT0309	36	299	62
Timor and Wetar deciduous forests	AA0204	154	300	149
Po Basin mixed forests	PA0432	631	301	501
New Britain-New Ireland lowland rain forests	AA0111	189	302	168
Western Zambebian grasslands	AT0724	610	303	488
Naracoorte woodlands	AA1208	632	304	507
Sonoran-Sinaloan transition subtropical dry forest	NA0201	438	305	335
Yucatán dry forests	NT0235	361	306	288
Northern Thailand-Laos moist deciduous forests	IM0139	449	307	342
North Atlantic moist mixed forests	PA0429	767	308	761
Ozark Mountain forests	NA0412	663	309	567
Isthmian-Atlantic moist forests	NT0129	275	310	219
Lesser Sundas deciduous forests	AA0201	69	311	88
North Western Ghats moist deciduous forests	IM0134	573	312	442
Solomon Islands rain forests	AA0119	7	313	29
Sierra Nevada forests	NA0527	382	314	306
Taiheiyō montane deciduous forests	PA0441	332	315	273
Brahmaputra Valley semi-evergreen forests	IM0105	196	316	187
Nigerian lowland forests	AT0123	308	317	248
Guajira-Barranquilla xeric scrub	NT1308	220	318	199
Cardamom Mountains rain forests	IM0106	324	319	268
Hindu Kush alpine meadow	PA1005	671	320	585
Eastern Java-Bali rain forests	IM0113	111	321	126
East African montane forests	AT0108	84	322	104
Cascade Mountains leeward forests	NA0507	650	323	554
Balsas dry forests	NT0205	274	324	228
Alaska Peninsula montane taiga	NA0601	613	325	503
Zambebian halophytics	AT0908	681	326	601
Pantepui	NT0169	379	327	308
Suiphun-Khanka meadows and forest meadows	PA0907	688	328	618
Central American dry forests	NT0209	358	329	299
Western Himalayan broadleaf forests	IM0403	253	330	217
Southern Annamites montane rain forests	IM0152	129	331	145
Illyrian deciduous forests	PA1210	597	332	494
Eastern Cascades forests	NA0512	535	333	426
Khangai Mountains alpine meadow	PA1007	714	334	663
Hokkaido montane conifer forests	PA0510	630	335	526
Northern Annamites rain forests	IM0136	60	336	91
English Lowlands beech forests	PA0421	746	337	730
Veracruz moist forests	NT0176	173	338	183
Caspian Hyrcanian mixed forests	PA0407	369	339	312
Sayan Intermontane steppe	PA0815	709	340	660
Cuban dry forests	NT0213	261	341	230
Okanagan dry forests	NA0522	682	342	625
Sri Lanka dry-zone dry evergreen forests	IM0212	120	343	144
Cordillera Oriental montane forests	NT0118	164	344	181
Northern Triangle subtropical forests	IM0140	157	345	178
Apure-Villavicencio dry forests	NT0201	315	346	277
Elburz Range forest steppe	PA0507	478	347	389
Nebraska Sand Hills mixed grasslands	NA0809	689	348	633
Nile Delta flooded savanna	PA0904	466	349	380
Iberian conifer forests	PA1208	638	350	556
Nelson Coast temperate forests	AA0404	702	351	658
Al Hajar montane woodlands	AT0801	451	352	370
Tarim Basin deciduous forests and steppe	PA0442	656	353	587
Palouse grasslands	NA0813	649	354	579
Pindus Mountains mixed forests	PA1217	523	355	437
Chocó-Darién moist forests	NT0115	72	356	114
Tigris-Euphrates alluvial salt marsh	PA0906	508	357	429
Sierra Madre Oriental pine-oak forests	NA0303	115	358	154
Northern dry deciduous forests	IM0208	623	359	537
Kola Peninsula tundra	PA1106	757	360	755
Monte Alegre várzea	NT0141	360	361	323
Northwestern Andean montane forests	NT0145	52	362	94
Magdalena-Urabá moist forests	NT0137	193	363	211
Paraná flooded savanna	NT0908	402	364	351
Northern Pacific coastal forests	NA0520	516	365	435
Bolivian montane dry forests	NT0206	149	366	189

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Rann of Kutch seasonal salt marsh	IM0901	710	367	677
Edwards Plateau savanna	NA0806	595	368	515
Mesoamerican Gulf-Caribbean mangroves	NT1403	392	369	348
Central Pacific coastal forests	NA0510	240	370	238
California Central Valley grasslands	NA0801	272	371	256
Blue Mountains forests	NA0505	463	372	393
Southern Andean Yungas	NT0165	98	373	153
Myanmar coastal rain forests	IM0132	426	374	369
Dinaric Mountains mixed forests	PA0418	477	375	415
California coastal sage and chaparral	NA1201	180	376	213
Allegheny Highlands forests	NA0401	667	377	628
Madagascar succulent woodlands	AT1312	57	378	111
Sinaloan dry forests	NT0228	148	379	198
Himalayan subtropical pine forests	IM0301	465	380	409
Atlantic coastal desert	PA1304	705	381	682
Yucatán moist forests	NT0181	125	382	173
Yukon Interior dry forests	NA0617	717	383	697
Northeastern coastal forests	NA0411	482	384	424
Qionglai-Minshan conifer forests	PA0518	126	385	175
Trans-Mexican Volcanic Belt pine-oak forests	NT0310	8	386	53
Eastern Anatolian deciduous forests	PA0420	605	387	541
Nujiang Langcang Gorge alpine conifer and mixed forests	PA0516	89	388	151
Western Gulf coastal grasslands	NA0701	576	389	506
Sakhalin Island taiga	PA0607	510	390	460
Kopet Dag woodlands and forest steppe	PA1008	505	391	457
Kaokoveld desert	AT1310	618	392	563
Central Mexican matorral	NA1302	467	393	420
Albertine Rift montane forests	AT0101	11	394	65
Yarlung Tsangpo arid steppe	PA1022	619	395	565
Borneo peat swamp forests	IM0104	232	396	254
Eastern Himalayan broadleaf forests	IM0401	161	397	216
Maracaibo dry forests	NT0222	531	398	483
Sichuan Basin evergreen broadleaf forests	PA0437	479	399	433
Southwest Australia woodlands	AA1210	151	400	210
Euxine-Colchic broadleaf forests	PA0422	577	401	516
South Island temperate forests	AA0410	775	402	765
Saharan halophytics	PA0905	668	403	650
Central American Atlantic moist forests	NT0111	229	404	259
South Deccan Plateau dry deciduous forests	IM0209	171	405	232
Northern tall grasslands	NA0812	703	406	690
Luang Prabang montane rain forests	IM0121	165	407	226
Central British Columbia Mountain forests	NA0509	719	408	711
Sumatran montane rain forests	IM0159	29	409	93
Northwestern Himalayan alpine shrub and meadows	PA1012	412	410	400
Eastern Congolian swamp forests	AT0110	354	411	352
Bolivian Yungas	NT0105	145	412	214
Magdalena Valley montane forests	NT0136	58	413	132
Azerbaijan shrub desert and steppe	PA1305	472	414	443
Emin Valley steppe	PA0806	639	415	613
Red Sea coastal desert	PA1333	635	416	612
Richmond temperate forests	AA0408	779	417	769
Central American pine-oak forests	NT0303	35	418	110
Hengduan Mountains subalpine conifer forests	PA0509	260	419	289
Northern Zanzibar-Inhambane coastal forest mosaic	AT0125	19	420	85
Sundaland heath forests	IM0161	228	421	271
Serra do Mar coastal forests	NT0160	51	422	131
Eastern Cordillera real montane forests	NT0121	38	423	122
Madagascar lowland forests	AT0117	2	424	24
Sulawesi montane rain forests	AA0124	24	425	95
Somali montane xeric woodlands	AT1319	460	426	441
Tyrrhenian-Adriatic Sclerophyllous and mixed forests	PA1222	304	427	328
Mississippi lowland forests	NA0409	615	428	595
Southeastern Papuan rain forests	AA0120	23	429	98
Central Korean deciduous forests	PA0413	495	430	481
Bahia coastal forests	NT0103	54	431	139
Kazakh upland	PA0811	678	432	676
Eastern Great Lakes lowland forests	NA0407	687	433	685
Nihonkai montane deciduous forests	PA0428	177	434	252
Angolan scarp savanna and woodlands	AT1002	575	435	543
Changbai Mountains mixed forests	PA0414	422	436	428
Cantabrian mixed forests	PA0406	321	437	345
Vogelkop-Aru lowland rain forests	AA0128	63	438	156
Ghorat-Hazarajat alpine meadow	PA1004	627	439	619
Atlantic dry forests	NT0202	443	440	448
Northwest Iberian montane forests	PA1216	519	441	510

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Sumatran peat swamp forests	IM0160	201	442	274
Central Anatolian steppe and woodlands	PA0410	468	443	464
Montana Valley and Foothill grasslands	NA0808	616	444	611
Rio Negro campinarana	NT0158	367	445	388
Tenasserim-South Thailand semi-evergreen rain forests	IM0163	140	446	236
Sulawesi lowland rain forests	AA0123	3	447	34
Northern Anatolian conifer and deciduous forests	PA0515	526	448	522
Persian Gulf desert and semi-desert	PA1323	741	449	756
Luzon rain forests	IM0123	62	450	164
California interior chaparral and woodlands	NA1202	182	451	278
Beringia upland tundra	NA1107	633	452	645
Western Himalayan alpine shrub and Meadows	PA1021	528	453	529
Altai steppe and semi-desert	PA0802	587	454	580
Northland temperate kauri forests	AA0406	637	455	651
Piney Woods forests	NA0523	582	456	576
Madagascar dry deciduous forests	AT0202	1	457	36
Qilian Mountains subalpine meadows	PA1015	569	458	568
La Costa xeric shrublands	NT1309	353	459	398
Arizona Mountains forests	NA0503	271	460	325
Eyre and York mallee	AA1203	628	461	646
Mindanao-Eastern Visayas rain forests	IM0129	21	462	115
Qin Ling Mountains deciduous forests	PA0434	255	463	320
Middle Atlantic coastal forests	NA0517	310	464	357
Ucayali moist forests	NT0174	135	465	251
Paropamisus xeric woodlands	PA1322	592	466	607
Southwestern Arabian montane woodlands	AT1321	554	467	562
Iquitos várzea	NT0128	172	468	281
Pacific Coastal Mountain icefields and tundra	NA1117	658	469	684
Southern New Guinea freshwater swamp forests	AA0121	244	470	318
Southern Zanzibar-Inhambane coastal forest mosaic	AT0128	248	471	319
Central Asian riparian woodlands	PA1311	653	472	675
Southwest Iberian Mediterranean sclerophyllous and mixed forests	PA1221	464	473	493
Western Congolian swamp forests	AT0129	217	474	310
Mediterranean acacia-argania dry woodlands and succulent thickets	PA1212	156	475	275
Saharan flooded grasslands	AT0905	346	476	405
Altai montane forest and forest steppe	PA0502	518	477	539
Chhota-Nagpur dry deciduous forests	IM0203	400	478	456
Southern Anatolian montane conifer and deciduous forests	PA1220	428	479	472
Gulf of Oman desert and semi-desert	AT1306	462	480	496
Peninsular Malaysian rain forests	IM0146	18	481	124
Appalachian-Blue Ridge forests	NA0403	461	482	497
Anatolian conifer and deciduous mixed forests	PA1202	608	483	638
Petén-Veracruz moist forests	NT0154	42	484	160
Baltic mixed forests	PA0405	698	485	727
Kamchatka Mountain tundra and forest tundra	PA1105	715	486	733
Tibesti-Jebel Uweinat montane xeric woodlands	PA1331	729	487	753
Alberta-British Columbia foothills forests	NA0502	683	488	710
Kayah-Karen montane rain forests	IM0119	205	489	314
Eastern Guinean forests	AT0111	25	490	141
Altai alpine meadow and tundra	PA1001	547	491	572
Borneo montane rain forests	IM0103	76	492	208
Succulent Karoo	AT1322	170	493	300
Southeastern Indochina dry evergreen forests	IM0210	101	494	245
Upper Midwest forest-savanna transition	NA0415	642	495	678
Sayan Alpine meadows and tundra	PA1016	651	496	688
Colorado Rockies forests	NA0511	500	497	542
Carpathian montane forests	PA0504	471	498	517
Irrawaddy moist deciduous forests	IM0117	200	499	322
Mizoram-Manipur-Kachin rain forests	IM0131	162	500	303
Baja California desert	NA1301	159	501	301
Fraser Plateau and Basin complex	NA0514	657	502	699
Carnarvon xeric shrublands	AA1301	204	503	327
British Columbia mainland coastal forests	NA0506	489	504	535
Arabian Peninsula coastal fog desert	AT1302	413	505	492
Magellanic subpolar forests	NT0402	155	506	302
Southern New Guinea lowland rain forests	AA0122	163	507	307
Northeastern Spain and Southern France Mediterranean forests	PA1215	563	508	606
Guianan Highlands moist forests	NT0124	107	509	257
Italian sclerophyllous and semi-deciduous forests	PA1211	411	510	495
Kamchatka-Kurile meadows and sparse forests	PA0603	542	511	588
Appalachian mixed mesophytic forests	NA0402	459	512	520
Beringia lowland tundra	NA1106	544	513	594

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Highveld grasslands	AT1009	285	514	377
Daba Mountains evergreen forests	PA0417	286	515	379
Namib desert	AT1315	435	516	512
Tamaulipan mezquital	NA1312	496	517	559
Iceland boreal birch forests and alpine tundra	PA0602	777	518	770
Madagascar subhumid forests	AT0118	5	519	70
Western Guinean lowland forests	AT0130	12	520	133
Northern New Guinea lowland rain and freshwater swamp forests	AA0115	90	521	249
Atlantic Equatorial coastal forests	AT0102	114	522	270
South Island montane grasslands	AA1003	721	523	751
Victoria Basin forest-savanna mosaic	AT0721	136	524	297
Taiheiyō evergreen forests	PA0440	146	525	304
Alps conifer and mixed forests	PA0501	233	526	353
Peruvian Yungas	NT0153	26	527	163
Alai-Western Tian Shan steppe	PA0801	580	528	632
Caucasus mixed forests	PA0408	64	529	225
Meseta Central matorral	NA1307	206	530	343
Badghyz and Karabil semi-desert	PA1306	545	531	610
Eastern Australian temperate forests	AA0402	61	532	220
Eastern Mediterranean conifer-sclerophyllous-broadleaf forests	PA1207	277	533	381
Kalaallit Nunaat low arctic tundra	NA1113	755	534	762
South Central Rockies forests	NA0528	483	535	558
Alaska-St. Elias Range tundra	NA1101	636	536	691
Central Andean wet puna	NT1003	108	537	276
Masai xeric grasslands and shrublands	AT1313	333	538	449
Eastern Himalayan alpine shrub and meadows	PA1003	273	539	383
Guianan savanna	NT0707	334	540	454
Solimões-Japurá moist forests	NT0163	306	541	422
Tocantins/Pindare moist forests	NT0170	158	542	326
Narmada Valley dry deciduous forests	IM0207	262	543	376
Marajó várzea	NT0138	433	544	525
Tian Shan foothill arid steppe	PA0818	515	545	600
Beni savanna	NT0702	223	546	360
Purus-Madeira moist forests	NT0157	291	547	408
Drakensberg montane grasslands, woodlands and forests	AT1004	110	548	286
Zambezi flooded grasslands	AT0907	211	549	356
Bahia interior forests	NT0104	41	550	206
Purus várzea	NT0156	185	551	346
Araucaria moist forests	NT0101	174	552	341
Central Afghan Mountains xeric woodlands	PA1309	566	553	647
Kuh Rud and Eastern Iran montane woodlands	PA1009	439	554	540
Caqueta moist forests	NT0107	258	555	387
Ural montane forests and tundra	PA0610	707	556	745
Trans-Baikal conifer forests	PA0609	562	557	643
Cape York Peninsula tropical savanna	AA0703	214	558	362
Northeast China Plain deciduous forests	PA0430	555	559	641
Southeastern conifer forests	NA0529	302	560	431
Southern Great Lakes forests	NA0414	591	561	668
Central Range montane rain forests	AA0105	9	562	130
Aegean and Western Turkey sclerophyllous and mixed forests	PA1201	441	563	553
Esperance mallee	AA1202	227	564	378
Ussuri broadleaf and mixed forests	PA0443	431	565	546
Ethiopian montane forests	AT0112	59	566	240
Angolan Mopane woodlands	AT0702	445	567	561
Chiquitano dry forests	NT0212	252	568	395
Negro-Branco moist forests	NT0143	265	569	406
Pamir alpine desert and tundra	PA1014	481	570	586
Great Lakes Basin desert steppe	PA1316	511	571	624
Einasleigh upland savanna	AA0705	212	572	374
New England-Acadian forests	NA0410	497	573	609
High Monte	NT1010	138	574	333
Lower Gangetic Plains moist deciduous forests	IM0120	297	575	436
Sierra Madre Occidental pine-oak forests	NA0302	124	576	317
Northern mixed grasslands	NA0810	586	577	669
Gobi Lakes Valley desert steppe	PA1315	534	578	642
Western Siberian hemiboreal forests	PA0444	644	579	715
South China-Vietnam subtropical evergreen forests	IM0149	50	580	239
Eastern Anatolian montane steppe	PA0805	139	581	339
Valdivian temperate forests	NT0404	32	582	212
Amur meadow steppe	PA0901	622	583	702
Middle East steppe	PA0812	450	584	575
Yunnan Plateau subtropical evergreen forests	PA0102	167	585	359

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Cantebury-Otago tussock grasslands	AA0801	764	586	768
Wyoming Basin shrub steppe	NA1313	409	587	551
Western Great Lakes forests	NA0416	601	588	693
Atacama desert	NT1303	469	589	599
Guianan piedmont and lowland moist forests	NT0182	243	590	416
Upper Gangetic Plains moist deciduous forests	IM0166	292	591	453
Balkan mixed forests	PA0404	284	592	444
Northeast Siberian coastal tundra	PA1107	686	593	742
Karakoram-West Tibetan Plateau alpine steppe	PA1006	190	594	385
Central tall grasslands	NA0805	553	595	661
Arctic desert	PA1101	747	596	763
Southeast Australia temperate forests	AA0409	87	597	298
Trans-Baikal Bald Mountain tundra	PA1112	660	598	734
Gissaro-Alai open woodlands	PA0808	316	599	486
Ethiopian montane grasslands and woodlands	AT1007	112	600	324
Central Deccan Plateau dry deciduous forests	IM0201	357	601	521
Central U.S. hardwood forests	NA0404	453	602	593
Central and Southern mixed grasslands	NA0803	390	603	545
Jurua-Purus moist forests	NT0133	166	604	368
Mojave desert	NA1308	294	605	463
Southern Andean steppe	NT1008	356	606	518
Da Hinggan-Dzhagdy Mountains conifer forests	PA0505	572	607	679
Napo moist forests	NT0142	79	608	294
Scandinavian Montane Birch forest and grasslands	PA1110	680	609	741
Celtic broadleaf forests	PA0409	679	610	743
Guizhou Plateau broadleaf and mixed forests	PA0101	186	611	392
Pantanal	NT0907	326	612	504
Gibson desert	AA1303	588	613	694
Xingu-Tocantins-Araguaia moist forests	NT0180	198	614	404
Coolgardie woodlands	AA1201	614	615	712
Ethiopian xeric grasslands and shrublands	AT1305	208	616	410
North Central Rockies forests	NA0518	452	617	603
Ordos Plateau steppe	PA1013	492	618	640
Arnhem Land tropical savanna	AA0701	46	619	267
South Siberian forest steppe	PA0817	661	620	739
Japura-Solimoes-Negro moist forests	NT0132	264	621	455
Chilean matorral	NT1201	169	622	396
Sumatran lowland rain forests	IM0158	20	623	218
Southeastern mixed forests	NA0413	407	624	584
Selenge-Orkhon forest steppe	PA0816	524	625	667
Khathiar-Gir dry deciduous forests	IM0206	388	626	570
Muskwa-Slave Lake forests	NA0610	625	627	726
Daurian forest steppe	PA0804	430	628	602
Southern Acacia-Commiphora bushlands and thickets	AT0716	113	629	347
Northern Cordillera forests	NA0613	590	630	705
Southwest Australia savanna	AA1209	386	631	569
Central China loess plateau mixed forests	PA0411	328	632	527
Pilbara shrublands	AA1307	330	633	531
Northwest Russian-Novaya Zemlya tundra	PA1108	699	634	759
Central Indochina dry forests	IM0202	53	635	292
Southern Africa bushveld	AT0717	203	636	434
Murray-Darling woodlands and mallee	AA1207	350	637	557
Pannonian mixed forests	PA0431	394	638	591
Nullarbor Plains xeric shrublands	AA1306	540	639	687
Chukchi Peninsula tundra	PA1104	640	640	737
Mediterranean dry woodlands and steppe	PA1213	267	641	489
Mesopotamian shrub desert	PA1320	456	642	648
Huang He Plain mixed forests	PA0424	387	643	598
Sayan montane conifer forests	PA0519	474	644	657
Eastern forest-boreal transition	NA0406	567	645	703
Sechura desert	NT1315	80	646	337
Central forest-grasslands transition	NA0804	364	647	578
Qaidam Basin semi-desert	PA1324	444	648	644
Central Andean puna	NT1002	122	649	371
Tapajós-Xingu moist forests	NT0168	137	650	399
Namibian savanna woodlands	AT1316	295	651	514
Tibetan Plateau alpine shrublands and meadows	PA1020	366	652	581
Baluchistan xeric woodlands	PA1307	424	653	631
Sonoran desert	NA1310	144	654	412
Zagros Mountains forest steppe	PA0446	210	655	462
Eastern highlands moist deciduous forests	IM0111	221	656	467
Snake-Columbia shrub steppe	NA1309	242	657	482
Northwest Territories taiga	NA0614	626	658	735
Alto Paraná Atlantic forests	NT0150	39	659	295
North Island temperate forests	AA0405	447	660	652

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Central Congolian lowland forests	AT0104	82	661	349
Mid-Continental Canadian forests	NA0608	584	662	718
Mato Grosso seasonal forests	NT0140	197	663	465
Changjiang Plain evergreen forests	PA0415	175	664	451
Zambezian Baikiaea woodlands	AT0726	338	665	573
Northwestern Congolian lowland forests	AT0126	30	666	283
Mediterranean woodlands and forests	PA1214	168	667	446
Uruguayan savanna	NT0710	67	668	344
Eastern Gobi desert steppe	PA1314	440	669	656
Victoria Plains tropical savanna	AA0709	488	670	683
Caspian lowland desert	PA1308	486	671	681
West Saharan montane xeric woodlands	PA1332	517	672	700
Southern Hudson Bay taiga	NA0616	641	673	746
Atlantic mixed forests	PA0402	359	674	605
Okhotsk-Manchurian taiga	PA0606	425	675	653
Southwestern Arabian foothills savanna	AT1320	396	676	637
Espinal	NT0801	250	677	505
Western short grasslands	NA0815	323	678	574
Tian Shan montane steppe and meadows	PA1019	247	679	513
Eastern Australia mulga shrublands	AA0802	436	680	662
Central Andean dry puna	NT1001	183	681	484
Thar desert	IM1304	437	682	664
Central Canadian Shield forests	NA0602	581	683	729
Northern Acacia-Commiphora bushlands and thickets	AT0711	65	684	355
Iberian sclerophyllous and semi-deciduous forests	PA1209	282	685	544
Yamal-Gydan tundra	PA1114	664	686	760
Northern Indochina subtropical forests	IM0137	10	687	255
Central Ranges xeric scrub	AA1302	257	688	524
Nama Karoo	AT1314	127	689	430
Northeastern Congolian lowland forests	AT0124	17	690	287
Borneo lowland rain forests	IM0102	4	691	169
Humid Chaco	NT0708	70	692	363
Guianan moist forests	NT0125	99	693	411
Humid Pampas	NT0803	131	694	440
Uatuma-Trombetas moist forests	NT0173	106	695	417
Manchurian mixed forests	PA0426	279	696	548
Interior Alaska-Yukon lowland taiga	NA0607	536	697	716
Eastern Canadian forests	NA0605	602	698	740
Western Congolian forest-savanna mosaic	AT0723	116	699	427
Junggar Basin semi-desert	PA1317	339	700	617
Registan-North Pakistan sandy desert	PA1326	513	701	709
Western European broadleaf forests	PA0445	331	702	614
South Iran Nubo-Sindian desert and semi-desert	PA1328	408	703	666
Kalahari Acacia-Baikiaea woodlands	AT0709	300	704	577
Midwestern Canadian Shield forests	NA0609	589	705	738
Deccan thorn scrub forests	IM1301	239	706	532
Bering tundra	PA1102	533	707	723
Canadian Aspen forests and parklands	NA0802	521	708	720
Southern Miombo woodlands	AT0719	142	709	466
Southeast Australia temperate savanna	AA0803	351	710	635
Eastern Miombo woodlands	AT0706	92	711	423
Brigalow tropical savanna	AA0702	102	712	432
Llanos	NT0709	109	713	439
Colorado Plateau shrublands	NA1304	226	714	536
Northern Canadian Shield taiga	NA0612	556	715	731
Kazakh forest steppe	PA0809	504	716	721
Northern short grasslands	NA0811	296	717	597
North Tibetan Plateau-Kunlun Mountains alpine desert	PA1011	305	718	608
Low Monte	NT0802	181	719	519
Kimberly tropical savanna	AA0706	105	720	452
Zambezian and Mopane woodlands	AT0725	100	721	450
Great Basin shrub steppe	NA1305	209	722	538
Carpentaria tropical savanna	AA0704	184	723	528
Southeast Tibet shrublands and meadows	PA1017	74	724	414
Cherskii-Kolyma mountain tundra	PA1103	585	725	744
Guinean forest-savanna mosaic	AT0707	37	726	361
Jian Nan subtropical evergreen forests	IM0118	97	727	461
Tirari-Sturt stony desert	AA1309	299	728	626
Great Victoria desert	AA1305	385	729	680
East European forest steppe	PA0419	283	730	615
Madeira-Tapajós moist forests	NT0135	31	731	358
Chihuahuan desert	NA1303	104	732	476
Mitchell grass downs	AA0707	281	733	621
Northwestern thorn scrub forests	IM1303	320	734	654
Southern Congolian forest-savanna mosaic	AT0718	128	735	500

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Central European mixed forests	PA0412	251	736	596
Western Australian Mulga shrublands	AA1310	418	737	704
Southwest Amazon moist forests	NT0166	13	738	330
Eastern Canadian Shield taiga	NA0606	565	739	747
Central Tibetan Plateau alpine steppe	PA1002	225	740	604
Angolan Miombo woodlands	AT0701	94	741	498
Sarmatic mixed forests	PA0436	365	742	696
Patagonian steppe	NT0805	103	743	502
Kazakh semi-desert	PA1318	256	744	627
Central Asian southern desert	PA1312	368	745	701
Kalahari xeric savanna	AT1309	191	746	590
Northern Congolian forest-savanna mosaic	AT0712	85	747	491
Central Persian desert basins	PA1313	290	748	655
Central Asian northern desert	PA1310	215	749	623
Simpson desert	AA1308	230	750	629
Kazakh steppe	PA0810	376	751	707
Red Sea Nubo-Sindian tropical desert and semi-desert	PA1325	404	752	724
Mongolian-Manchurian grassland	PA0813	231	753	636
Taimyr-Central Siberian tundra	PA1111	532	754	754
East Sudanian savanna	AT0705	123	755	555
Caatinga	NT1304	49	756	475
Alashan Plateau semi-desert	PA1302	246	757	659
Pontic steppe	PA0814	134	758	589
Northeast Siberian taiga	PA0605	476	759	750
Great Sandy-Tanami desert	AA1304	301	760	695
Dry Chaco	NT0210	15	761	413
Central Zambezan Miombo woodlands	AT0704	22	762	445
Taklimakan desert	PA1330	235	763	674
West Sudanian savanna	AT0722	45	764	511
Somali Acacia-Commiphora bushlands and thickets	AT0715	27	765	479
South Saharan steppe and woodlands	PA1329	234	766	689
West Siberian taiga	PA0611	405	767	749
Scandinavian and Russian taiga	PA0608	236	768	713
Cerrado	NT0704	6	769	459
North Saharan steppe and woodlands	PA1321	133	770	692
Arabian Desert and East Sahero-Arabian xeric shrublands	PA1303	188	771	717
Sahelian Acacia savanna	AT0713	40	772	620
East Siberian taiga	PA0601	143	773	728
Sahara desert	PA1327	179	774	758
Chatham Island temperate forests	AA0401	801	775	775
Ile Europa and Bassas da India xeric scrub	AT1308	811	776	776
South China Sea Islands	IM0148	799	777	777
Islas Revillagigedo dry forests	NT0216	815	778	778
Juan Fernández Islands temperate forests	NT0401	816	779	779
Western Polynesian tropical moist forests	OC0117	826	780	780
Faroe Islands boreal grasslands	PA0807	794	781	781
Norfolk Island subtropical forests	AA0114	788	782	782
Antipodes Subantarctic Islands tundra	AA1101	802	783	783
Marielandia Antarctic tundra	AN1101	803	784	784
Maudlandia Antarctic desert	AN1102	804	785	785
Scotia Sea Islands tundra	AN1103	805	786	786
Southern Indian Ocean Islands tundra	AN1104	806	787	787
Ascension scrub and grasslands	AT0703	807	788	788
St. Helena scrub and woodlands	AT0720	808	789	789
Amsterdam and Saint-Paul Islands temperate grasslands	AT0802	809	790	790
Tristan Da Cunha-Gough Islands shrub and grasslands	AT0803	810	791	791
Aldabra Island xeric scrub	AT1301	484	792	792
Lake	Lake	218	793	793
Bermuda subtropical conifer forests	NA0301	796	794	794
Arctic coastal tundra	NA1103	722	795	795
Arctic foothills tundra	NA1104	670	796	796
Baffin coastal tundra	NA1105	782	797	797
Brooks-British Range tundra	NA1108	646	798	798
Davis Highlands tundra	NA1109	756	799	799
High Arctic tundra	NA1110	645	800	800
Interior Yukon-Alaska alpine tundra	NA1111	600	801	801
Kalaallit Nunaat high arctic tundra	NA1112	691	802	802
Low Arctic tundra	NA1114	550	803	803
Middle Arctic tundra	NA1115	578	804	804
Ogilvie-MacKenzie alpine tundra	NA1116	579	805	805
Torngat Mountain tundra	NA1118	763	806	806
Cocos Island moist forests	NT0116	812	807	807
Fernando de Noronha-Atol das Rocas moist forests	NT0123	813	808	808
Trindade-Martin Vaz Islands tropical forests	NT0172	814	809	809
San FÁ©lix-San Ambrosio Islands temperate forests	NT0403	817	810	810

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Clipperton Island shrub and grasslands	NT0705	818	811	811
Caribbean shrublands	NT1305	372	812	812
Malpelo Island xeric scrub	NT1311	819	813	813
St. Peter and St. Paul rocks	NT1318	820	814	814
Carolines tropical moist forests	OC0101	325	815	815
Central Polynesian tropical moist forests	OC0102	821	816	816
Eastern Micronesia tropical moist forests	OC0104	822	817	817
Kermadec Islands subtropical moist forests	OC0107	823	818	818
Marquesas tropical moist forests	OC0108	824	819	819
Rapa Nui subtropical broadleaf forests	OC0111	825	820	820
Society Islands tropical moist forests	OC0113	797	821	821
Tuamotu tropical moist forests	OC0115	800	822	822
Tubuai tropical moist forests	OC0116	798	823	823
Yap tropical dry forests	OC0204	723	824	824
Northwestern Hawaii scrub	OC0703	827	825	825
Novosibirsk Islands arctic desert	PA1109	769	826	826
Rock and Ice	Rock and Ice	222	827	827

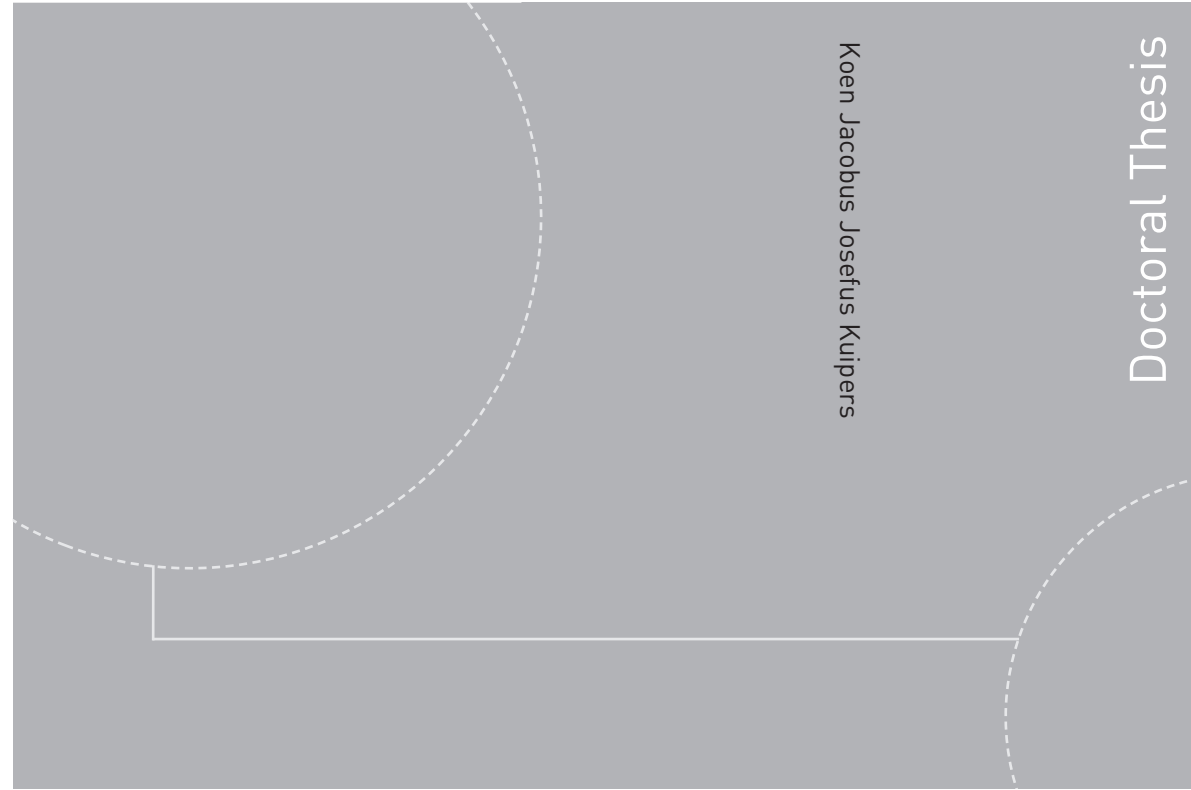
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SI3 (Supporting Information for chapter 5): Considering habitat conversion and fragmentation in characterisation factors for land use impacts on vertebrate species richness

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