Future-Proofing Mammal Conservation in the Face of Climate and Land-Use Change

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I, Chloë Alexia Metcalfe, confirm that the work presented in this thesis is my own. Where information is derived from other sources, I confirm that this has been indicated in the thesis.

Abstract

We are currently witnessing very rapid biodiversity changes, unprecedented in recent history, driven primarily by climate and land-use changes. Conserving biodiversity is crucial for ensuring ecosystem services and maintaining habitat that is resilient to anthropogenic pressures. There are many tools at our disposal to address these challenges, such as the use of protected areas, increasing climate and habitat connectivity, as well as implementing habitat restoration to create suitable habitats for native plant and animal species. It is a combination of approaches that will best prepare us for a future rich in biodiversity. The aims of my thesis are to explore how protected-area characteristics, such as their design, management and size, impact local mammal biodiversity at a global scale, as well as to highlight where best to focus conservation efforts in order to conserve mammal species richness, including through the restoration of natural habitats. I find that there are 11% more mammal species on average in local samples of biodiversity inside protected areas compared to areas without protection. I also show that a greater availability of natural habitats increases total mammal abundance, and that total mammal abundance increases with increased distance inside the border of a protected area. Furthermore, I identify areas that do not contain enough contiguous habitat that is large enough to support the continued survival of mammal species under future climate conditions. These areas are projected to be within future climatically suitable patches, and so may need to be the focus of conservation efforts to expand the area of suitable habitat, and conserve levels of mammal biodiversity. I also explore how hypothetical restoration can increase the land available to support mammal conservation, highlighting areas in South and Central America, Western and Eastern Africa, Eastern and Southeast Asia, as well as large parts of Europe as restoration priorities. These restoration priorities were identified by considering habitat suitability, future climatic suitability and taking into account the minimum area requirements of species. My thesis demonstrates the significance of enhancing the protection of natural habitat, the importance of incorporating climate change together with habitat suitability and species-specific minimum area requirements in future projections of species distributions, as well as where can be considered as hypothetical restoration priorities. Local research can be undertaken to assess the feasibility of these hypothetical restoration areas. As species ranges are projected to significantly change in the face of climate, by using projections of where mammals will be in the year 2070, we can ensure that decisions made for the current environment will foster long-lasting, positive biodiversity outcomes. This research contributes to the understanding of what characteristics are most important for protected areas, and where should be considered as global priorities for conservation and restoration of habitats.

Impact Statement

My doctoral research in the field of biological conservation over the past 4 years has focused on how we can future-proof mammal conservation in the face of anthropogenic pressures such as climate and land-use change. Rapid changes in biodiversity and ecosystems mean that it is crucial that we act in a targeted manner to combat species loss and the disruption to natural processes. What nature provides, both its intrinsic value, and that of ecosystem services such as pollination, resources for food, medicine and provision of livelihoods is truly irreplaceable, and my thesis aims to provide some guidance on where we can start to ensure that we conserve biodiversity into the future.

This thesis provides insight into the effectiveness of protected areas at conserving mammal biodiversity, and how we can enhance their use through increasing their size, and ensuring the wide availability of natural habitat for species. My research also looks at the use of minimal area requirements as a way to show where conservation efforts may need to be targeted, as some future climatically suitable areas do not contain enough contiguous habitat to support species into the future. Finally, I look at terrestrial areas globally that should be considered as priorities for restoration, so as to conserve future mammal biodiversity. I would like to see this work used to inform priorities for local conservation studies that consider the feasibility of implementing habitat restoration on the ground within the identified priority areas, and to see an increase in empirical estimates of species-specific minimum area requirements.

My research over the past 4 years has allowed me to become a specialist in the effectiveness of protected areas. I am a lead author on “Protected Areas and Nature Recovery, achieving the goal to protect 30% of UK and seas for nature by 2030”, a policy briefing paper published though the British Ecological Society (BES) in 2022. After this work ended, I was invited to apply to form part of the BES policy committee, where I continue to provide guidance to inform BES policy work. I also form part of the IUCN World Commission on Protected Areas, where I contribute to discussions on effective Protected Areas, and I am proud to say that I have reviewed an application from a site applying for World Heritage Status.

I have also presented findings from my PhD to a lay audience through blogs: “Why do protected areas matter?” which explored the 30x30 target and was featured on the BES website, and “Bad habits of protected areas” written for the general public and featured on the London NERC DTP website.

I have also presented the results in this thesis during in-person presentations at national and international conferences, which led to invaluable discussions, wider impact and outlook. This included at the: ICCB International Conservation Congress in Kigali, Rwanda, in July 2023, the Joint DTP Conference, From Sea to Sky: A Changing World, at the University of Surrey in September 2022, the World Biodiversity Forum in Davos, Switzerland, in July 2022, the BES Ecology Across Borders conference in Liverpool in December 2021, and Broadly Scientific, addressing London NERC DTP students, at UCL in April 2021. I also presented poster presentations at the BES Annual Meeting in Edinburgh in December 2022, and the Joint DTP Conference, Natural Networks: Connectivity and Inclusivity, at the University of Surrey in September 2021. I ensured that I wrote up a small summary for every conference that I attended to feature in the CBER newsletter, which I ran as the chief editor for two and a half years.

I am passionate about integrating biodiversity into the decision-making process, and have attended Parliamentary Links Day, which aims to strengthen the dialogue between the scientific community, MPs and peers. I have also attended the launch of Wildlife and Countryside Links' progress report on protecting 30% of land and sea by 2030. Both events were at the parliamentary estate, and the invitation to attend came from the BES for my work on as a lead author on the policy briefing paper on protected areas. Furthermore, at the IUCN World Conservation Congress in Marseille I helped draft a document that commented on the wording of target 3 before it is set in policy – the goal for 30% protected area coverage by 2030, this fed into the Marseille Manifesto.

I also undertook a UKRI policy internship at Natural England, where I facilitated workshops with external stakeholders, focussing on knowledge exchange, engagement, and dissemination of key findings before, during and after the events. I also wrote and presented case studies on the implementation of protecting 30% of land and sea by 2030 in the UK, in collaboration with DEFRA; I conducted interviews with independent landowners, The National Trust, and Local Councils, as well as read management and restoration plans. The expertise that I was able to bring to the table was thanks to my PhD research.

Acknowledgements

I told my mum that I wanted to save the rainforests when I was little - she told me, "Then you will". I don't think either of us realised that I would go on to become the first person in our family to attend university and see this all the way through to undertake a Doctoral Degree in Biological Conservation. To get to this stage, I have had the fortune of being supported by a huge number of people. I struggled with dyslexia from a young age, and thanks to my school picking up on this early, I have had multiple specialists involved in my development that have taught me strategies to combat some of my difficulties, but also to embrace my visual mindset and turn it into a strength. Throughout my Primary, Secondary, A-level and University education I have had the benefit of being mentored by inspiring teachers and supervisors. In some way they are all represented in the work that I have been able to present today, thank you to all of you.

My primary supervisor Tim Newbold has been a true lifeline over the last 4 years. He is everything that you could ever hope for in a PhD supervisor. Tim has dedicated so much time to my ideas and encouraged me to push myself and seek out information and solutions for my work. My problem-solving abilities have come on no end, I have learnt new coding techniques for spatial and statistical analysis, and I am confident delivering my research to international and national audiences. Tim really has been a role model to me, and certainly leads by example.

I have also been lucky enough to have Terry Dawson and Nina Bhola on board as secondary and tertiary supervisors. Their ideas and inputs into my work have been invaluable. Terry's wealth of experience in this field really helped with developing some of the ideas behind my work, and I don't think he knows how much the informal chat that we had at the BES annual meeting last Christmas helped keep me going. Nina came on as my Collaborative Award in Science and Engineering (CASE) partner, from UNEP-WCMC. Nina has been instrumental in discussing how my research can have a wider impact on biological conservation, particularly around protected areas. Both of their encouragement and enthusiasm for my work has been fantastic, and I really appreciate all the time that they have given to me. Also, a thank you to Corinna Ravilious (UNEP-WCMC Senior ArcGIS officer), who helped me with some of my ArcPy Code when I was drowning in the thousands of output maps from my R function, and a huge thank you to Helen Doran who acted as an expert mentor throughout the three months of my UKRI Policy Internship at Natural England.

My wife, Mavi, has really proven her worth in gold on this journey. Whenever I have doubted myself, or it has got too much, she has wasted no time in picking me back up, encouraging me to carry on or to take a break. "Si alguien puede hacerlo, eres tú". I can't thank her enough for her support, and I am truly so lucky to have her in my life. I can't wait to see what we achieve together next.

I take a bit of my core family unit with me wherever I go: Grandma's practicality, Grandad's entrepreneurial spirit, Mum's resilience, Dad's hard work, Brother's innovation, Grandad Bob's humour and Irene's adventurous streak. My family have all been a huge support in their own way on my journey to completing my PhD, and I thank them for always being there to back me. I would also like to specifically thank my parents, for always believing in the value of my education. My wider family-in-law have also provided me with encouragement and allowed me the space and time to study on our trips to Spain. My friends outside of university have also been great, and provided much needed breaks from working, as have my friends within my Cohort on the DTP.

My commute into UCL would not have been complete without my morning phone chats with my Grandma and my Mum. These have really been special moments for me that set me up for a day in the CBER office. And lastly a big thank you goes to the CBER office and my colleagues here. CBER really is a special place to work, and I am so lucky to have spent the last 4 years here.

My PhD viva was conducted by Prof Sarah Durant and Dr Regan Early. I thank them both for all the time that they have spent reviewing my thesis, and I really do believe that the final thesis here is much improved thanks to their comments.

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Chapter 2

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I explore the impact of protection status, and protected area characteristics on mammal species richness and abundance in a global study. Supplementary materials for chapter 2 are located straight after this chapter for easy viewing.

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I summarise the main findings of my thesis and assess their contributions to the field.

Appendix

An extract from the policy briefing, “Protected Areas and Nature Recovery. Achieving the goal to protect 30% of UK land and seas for nature by 2030.” which I co-authored.

Metcalfe, C. A. & Schere, C. M. (2022). ‘What is the current state of protected areas and what are their biodiversity trends?’ *Protected Areas and Nature Recovery*. British Ecological Society, p28-33.

Chapter 1

General Introduction

We now live in a world where 77% of terrestrial land has been modified to some extent by humans (Watson et al., 2018). Anthropogenic pressures on the planet have led to widespread biodiversity decline caused by land use change, direct exploitation of natural resources, pollution, climate change and invasive alien species (Jaureguiberry et al., 2022). Various conservation tools have emerged to try to combat such anthropogenic impacts, including protected areas (Hoffmann, 2022). Protected areas are a globally recognised means of conserving nature, managed to safeguard biodiversity, ecosystem services and cultural values (Dudley, 2008). They often reduce the loss of habitats, such as forest habitat (Geldmann et al., 2013), and increase species abundance and richness (Gray et al., 2016).

Designating a multitude of protected areas is insufficient without considering the effectiveness or representativeness of the areas appointed. The success of a protected area can be determined by what happens on both a local scale: such as design (both physical characteristics and management), natural ecosystem processes (Barnes, Craigie, Dudley, & Hockings, 2017), as well as on a more global scale: such as with their placement in the face of climate change (Heikkinen et al., 2020). Overall, protected areas have performed relatively well so far under a changing climate, acting as stepping stones for some species (Thomas & Gillingham, 2015), and facilitating colonisation for others (Gillingham et al., 2015). Indeed, protected areas can mitigate some aspects of climate change, such as through maintaining lower average temperatures than unprotected areas (X. Xu, Huang, Belle, Frenne, & Jia, 2022). The representativeness of protected areas in the face of climate change is very important, as is its ability to conserve a wide variety of ecosystems, habitats, and species. Quantifying the success of a protected area can be difficult as this depends on site specific goals to conservation. However, part of the IUCN's definition of a protected area is to "*achieve the long-term conservation of nature*" – thus it is important to understand how effective protected areas are at conserving biodiversity, so that important characteristics are maintained or enhanced to meet future conservation needs.

There are many ways that the conservation of nature can be monitored, which can include: monitoring local biodiversity through small scale studies that compare biodiversity inside protected areas to comparative sites outside of protection (Coetzee, Gaston, & Chown, 2014), recording the range of habitats that are being protected (Geldmann, Manica, Burgess, Coad, & Balmford, 2019), and monitoring population change in species over time (S. T. Williams, Williams, Lewis, & Hill, 2017), especially for keystone species (da Silva Lins, Gardon, Meyer, & dos Santos, 2017), without whom an ecosystem's function would fundamentally change. Barnes et al. (2017) point out that in using species richness as a biological monitoring tool, it is often ignored that protected areas are frequently established in species rich areas. However, the opposite is also true, for example where protected areas are situated in places of low economic value, often due to being of low suitability for agriculture (L. N. Joppa & Pfaff, 2009; Venter et al., 2018), and these areas are also often areas of lower habitat quality for biodiversity. The biases in protected area placement challenge our ability to assess the effectiveness of protected areas, therefore it is important to consider the specific local context, together with the measure of biodiversity used. Terrestrial protected areas have been shown to conserve a 10.6% increase in species richness and a 14.5% increase in species abundance compared to matched sites of the same land use outside of protection (Gray et al., 2016). However, what exactly contributes to this increase is still unknown. It has been suggested that in order to obtain a holistic view of the effectiveness of a protected area, the following needs to be addressed: size, shape, connectivity and management (Barnes et al., 2017). Some off these will be explored in greater depth in the following section, “Protected Area Design”.

In this thesis, I focus on mammals in exploring the impacts that protected areas have on biodiversity. Mammals are a suitable study group as they are among the best sampled groups of species, allowing us to obtain data on species distributions and traits. Mammals are also present across the globe, sensitive to land use change and fragmentation (Crooks et al., 2017), as well as climate change (Hetem, Fuller, Maloney, & Mitchell, 2014) and anthropogenic pressures (Ceballos, Ehrlich, Soberón, Salazar, & Fay, 2005) - all of which protected areas have the potential to counter. However, it has been noted that protected areas too often fail the world’s mammals by not being large enough, not being interconnected (Berger, 2017), and not having sufficient resources to support effective management (Waldron et al., 2017). Of the 27 orders of extant mammals on the IUCN Red List, those that contain large-bodied species face some of the highest levels of threat to their existence, the order Carnivora being particularly threatened (Bowyer, Boyce, Goheen, & Rachlow, 2019).

Traits can be important considerations in conservation studies, as they can contribute to the resilience of species in the face of environmental changes, and thus to species’ extinction risk. For mammals, habitat breadth (the range of habitat types that a species is capable of occupying), generation length (the age of maturation) and adult body size have emerged as consistent predictors of extinction risk (Chichorro et al., 2022). Conversely, mammal resilience is often improved where species have a generalist diet (Leclerc, Courchamp, & Bellard, 2020), a high rate of reproduction (Capdevila, Stott, et al., 2022) and the capacity to be behaviourally flexible (Júnior, Rios, Dodonov, Vilela, & Japyassú, 2022) - such as through changing migration routes. However, continual exposure to multiple threats can decrease species resilience in the long term (Capdevila, Noviello, McRae, Freeman, & Clements, 2022). Considering mammal species traits can therefore guide targeted and effective conservation strategies, which can help to future proof mammal conservation in the face of climate and land-use change.

Protected Area Design

There are many different types of habitat protection, which can broadly be broken down into 4 categories: statutory protected sites, non-statutory protected sites, protected landscapes, and other effective area-based conservation measures (table

1). Statutory protected sites such as National Parks and Sites of Special Scientific Interest (SSSI), are legally designated sites that have nature conservation as their primary purpose. These protected areas can range from strictly conserved regions, such as those classified under IUCN management categories Ia, Ib, II and III, where the highest levels of biodiversity protection is in effect, to areas designated for sustainable use (Dudley, 2008), such as hunting reserves which allow for regulated hunting to generate proceeds for conservation (IUCN, 2016) or to control species populations (Gortázar & Fernandez-de-Simon, 2022). Non-statutory protected sites such as local wildlife sites can also have nature conservation as their primary purpose, however they don't have legal protection. Examples include local wildlife sites (The Wildlife Trusts, 2024) and community conservancies (Rewilding Africa, 2024). Protected landscapes such as UNESCO Biosphere Reserves, are designated for their cultural, landscape or recreational values, however nature conservation is not the primary purpose (Dudley, 2008). Lastly, other effective area-based conservation measures (OECMs), are areas where conservation is achieved as a by-product of management, or is a secondary objective (Alves-Pinto et al., 2021). Protected area management categories are updated as knowledge advances (Dudley, Parrish, Redford, & Stolton, 2010), however, a designation in one country can have a different interpretation to the same designation in another, and categories themselves can overlap within a specific site.

Table 1: different types of habitat protection with descriptions and some examples of the designations (Bailey et al., 2022; Dudley, 2008).

Types of habitat protection	Description	Examples
Statutory protected sites	Legally designated sites that have nature conservation as a primary purpose.	IUCN categories Ia-VI.
Non – statutory protected sites	Sites that have nature conservation as a primary purpose but that don't have statutory protection.	Local Wildlife Sites.
Protected landscapes	Designated for cultural, landscape or recreational value. Nature conservation not primary purpose.	UNESCO Biosphere Reserve, National Scenic Area.
Other effective area – based conservation measures	Conservation can be delivered as a by-product of management, as a secondary objective or they may be sites that meet protected area criteria but are not reported as a protected area.	Military training grounds, botanical gardens or traditional agricultural systems.

The governance of protected areas determines how power and responsibilities are determined, how decisions are taken, and thus the strengths and challenges faced by the protected area to uphold stakeholders and rightsholder rights (Booker & Franks, 2019; J. Graham, Amos, & Plumptre, 2003). Protected area governance can be grouped into four broad types: governance by government, governance by private individuals and organisations, governance by indigenous peoples or local communities, or governance shared among two or more more of these groups (Borrini-Feyerabend et al., 2013). Protected areas that have good governance, effective management, and sound design and planning in place can apply to become part of the IUCN green list of protected and conserved areas which acts as the gold standard for nature conservation through the use of protected areas (IUCN & World Commission on Protected Areas, 2017).

The success of a protected area comes from a myriad of design characteristics (Başkent, 2023; Coad et al., 2015; Lawton et al., 2010). However, there are existing biases in protected area placement, for example they are often established on lands that will not provide much benefit to the economy if used by humans (L. N. Joppa & Pfaff, 2009; Venter et al., 2018). Rather than putting the economy of humans first, we should realise that our economy is actually nested within nature, and not a separate part of the equation (P. Dasgupta, 2021). One way to effectively place protected areas is through using spatial behaviour of the wildlife that needs protecting; boundaries can be drawn up that include the habitats and resources that a particular species needs (Choi et al., 2019), although this approach would be more complex for larger protected areas. Large protected areas can have benefits, for example if the area that is protected is larger than the home range of the species, then this can have positive impacts, such as increasing species density (Di Franco et al., 2018). However there is also merit in small protected areas, specifically those with a complex border (Wintle et al., 2019). Wintle *et al*. (2019) demonstrates that through ensuring the edges of a protected area create a complex shape, especially in habitat that is more fragmented, greater conservation value is achieved as it increases ecological representativeness of resources for species.

The edge of a protected area, or indeed a transition between any two habitat types, may be subject to edge effects, associated with a change in ecological community structure. Edge effects may manifest, for example, through agricultural incursions, such as cocoa planting encroaching on protected tropical forests (Brobbey, Agyei, & Osei-Tutu, 2020), or slash and burn farming which can lead to uncontrolled wildfires spreading within protected areas (Mistry & Bizerril, 2011). Such agricultural incursions and edge effects in general can cause increased temperature variability, heightened desiccation and wind exposure, which in turn can impact important ecological processes such as nutrient cycling and pollination, and can leave species that are dependent on a certain habitat type vulnerable to predation or with insufficient resources to reproduce (Laurance, 2000). Edge effects impacting protected areas can also arise through livestock incursions, such as cattle illegally grazing inside protected areas (Butt, 2014), which in turn can lead to mortality of large carnivores through conflict with people at protected area borders (Balme, Slotow, & Hunter, 2010; Woodroffe & Ginsberg, 1998). As habitat patches become more fragmented due to agricultural expansion, creation of infrastructure for power and transportation, as well as urbanisation, more areas will be exposed to potentially detrimental edge effects (Li et al., 2022; Mullu, 2016; Newmark, 2008). A global analysis of plant and animal communities at forest edges showed that areas that had never been exposed to habitat disturbance had stronger declines in species richness at habitat edges, than areas that had historically been exposed to habitat disturbance (J. Willmer, Püttker, & Prevedello, 2022). This suggests that protected areas, often established in historically undisturbed habitats, may be more at risk of detrimental edge effects. Understanding and managing activities leading to edge effects can be important to prevent wildlife declines within and surrounding protected area borders.

The interconnectivity of protected areas plays a major role in their effectiveness, high levels of connectivity can facilitate species dispersal (Brennan et al., 2022; S. H. Williams et al., 2019), as well as aid species range shifts in the face of climate change (Littlefield, McRae, Michalak, Lawler, & Carroll, 2017). There are many different ways to quantify connectivity, one example indicator is ProtConn, Protected Connected. This indicator of protected area connectivity was able to show that in 2016 although 14.7% of the world was covered in protected areas, only 9.3% of protected areas were considered connected for animals that on average dispersed 10 km, increasing to 11.7% for animals able to disperse 100 km (Saura, Bastin, Battistella, Mandrici, & Dubois, 2017). This study was completed by calculating the probability of direct dispersal between two protected areas using median dispersal distances of species. A later study looked at the structural connectivity of protected areas, using the human footprint dataset as a resistance layer; this produced a similar connectivity value of intact land between protected areas at an average of 9.7% (Ward et al., 2020). The importance of connectivity of protected areas for species is shown in a case study on jaguar (*Panthera onca*) in West Mexico, where a small protected area provided resources for this species to allow it to continue to move across degraded habitat (Luja, Navarro, Torres Covarrubias, Cortés Hernández, & Vallarta Chan, 2017). The Natura 2000 initiative, a scheme that is specific to Europe, and is composed of more than 26,000 areas that have some level of protection, has been assessed for its connectivity for large carnivores. There were very few protected areas that were within a species maximum dispersal distance, and furthermore no single protected site is large enough to support viable populations of lynx (*Lynx lynx*), wolf (*Canis lupus*) or bear (*Urus arctos*) (apart from one site in Sweden for bear), highlighting the importance of connectivity between protected areas (L. Santini, Boitani, Maiorano, Rondinini, & Roma, 2016).

Not only is the location of a protected area important, but also the type of habitat contained both within and around the protected area. Habitat use of herbivorous mammals has been shown to be linked to the availability of resources in the landscape (Teitelbaum et al., 2015). In research by Teitelbaum et al., the quantity of resources was measured using the normalised difference vegetation index (NDVI), a measure of vegetation health and density, and it was found that in areas with lower resources, herbivorous mammals migrated longer distances. This could be an indication that not only is connectivity of protected areas important, but also the capability of a protected area to provide the resources the wildlife depends upon. Indeed, a high proportion of natural habitat in the land surrounding species has been shown to increase biodiversity in many settings (Outhwaite, Ortiz, Spooner, Dalin, & Newbold, 2022; Ramesh, Kalle, Rosenlund, & Downs, 2016). Protecting areas that incorporate species ranges and resource needs has benefits for many species, especially if large-bodied organisms are used to delineate boundaries, as these organisms often encounter a variety of habitats that are used by a diverse range of species (Caro & Berger, 2019).

Connectivity

Habitat connectivity determines how easy it is for an organism to move through a landscape depending on the types of habitats that are available, and can be particularly important in the context of range shifts driven by climate change. The potential benefits of increased connectivity for biodiversity conservation are well reported in the literature (Anderson, Clark, Olivero, Barnett, & Hall, 2023; de la Peña-Domene & Minor, 2014). Connected landscapes can increase species biodiversity (Brudvig, Damschen, Tewksbury, Haddad, & Levey, 2009), improve access to resources required by species to survive and reproduce (Hodapp, Hillebrand, & Striebel, 2019), support species migrations (Van Moorter, Kivimäki, Panzacchi, & Saerens, 2021), prevent local extinctions (Hooftman, Edwards, & Bullock, 2016), promote genetic diversity within species populations through enabling gene flow (Christie & Knowles, 2015), and enable species (particularly those with low dispersal abilities that are less able to traverse fragmented landscapes) to move between habitat patches (Scriven et al., 2019).

Whilst there are many ways of estimating connectivity, most studies use measures of structural and functional connectivity (Correa Ayram, Mendoza, Etter, & Salicrup, 2016). Structural connectivity is based on the habitat features present within the landscape, whereas functional connectivity also takes into account species traits such as dispersal ability or habitat preference to help determine how connected a landscape is for specific species. There are also many different methods of measuring connectivity. Some of the most common include least cost pathways and graph theory (Correa Ayram et al., 2016). Least cost pathways determine the easiest route between two habitat patches, often by estimating the resistance of the landscape to species' movement, dependent upon the habitats present. Graph theory represents habitat patches within a landscape as nodes, with links between nodes representing species movements. This can help visualise areas that are most important for species movements between patches, determining where conservation efforts should be focussed. The appropriate methods and metrics to use will depend on the conservation objective (Keeley, Beier, & Jenness, 2021).

Connectivity is lost when landscapes become fragmented, which can occur in many ways. Linear infrastructure, such as roads, railways, power lines and fences, can all contribute to dividing landscapes into smaller habitat patches that may become isolated from each other (Biasotto & Kindel, 2018; Fedorca et al., 2020). Land-use change in the form of urbanisation and agricultural expansion are also impacting connectivity at a global scale. In a study on the east coast of the United States of

America, patches that contribute the most to landscape connectivity for a range of terrestrial animals were shown to be most at risk of urbanisation and sea-level rise in the year 2100 (Leonard et al., 2017). Within forested lands in western USA, urbanisation through residential development and roads have caused 4.5% loss of forest, and this is predicted to increase by a further 1.2% by the year 2030, removing key habitat linkages that maintain forest connectivity for 1.7 million km^2 of forest in the area (Theobald, Crooks, & Norman, 2011). The isolation of habitat patches through fragmentation can cause the loss of important ecological interactions, such as plant-pollinator interactions (Ferreira et al., 2020).

Some of the ways in which connectivity can be enhanced include creating habitat corridors that contain a mosaic of habitat types (Travers, Härdtle, & Matthies, 2021), restoring degraded habitats (Banks-Leite, Ewers, Folkard-Tapp, & Fraser, 2020), as well as establishing protected areas (S. H. Williams et al., 2019). These initiatives can contribute to ecosystem resilience - the ability of species within an ecosystem to withstand stressors on their existence, in particular allowing species to respond to the effects of climate change, as discussed in detail in the following section.

Climate Change

Climate change is causing an increase in global average temperatures, increased incidence of climatic extremes, and changes to global rainfall patterns (IPCC, 2023). However, changes in climate are being experienced unevenly across regions of the globe, with some areas being exposed to more extreme conditions, or experiencing more rapid changes than others (Garcia, Cabeza, Rahbek, & Araújo, 2014). Projections of future climates are important as it can help us to plan for different eventualities, or to employ actions that help mitigate detrimental changes. The Intergovernmental Panel on Climate Change (IPCC) is the leading international body for the assessment of climate change and develops future climate change scenarios based on different plausible levels of emissions, with the current generation of scenarios being the Representative Concentration Pathways, (RCPs), and other socioeconomic factors, which are described by the Shared Socio-economic Pathways, (SSPs). Projected climatic changes by the year 2100 range from 1.5°C – 2°C global average warming for strong mitigation scenarios (SSP1/RCP2.6), to greater than 4°C warming for fossil-fuel intensive scenarios (SSP5/RCP8.5) (IPCC, 2023).

The impacts of climate change are widespread. From the pre-industrial period of 1850-1900 to the present day we have seen increases in the frequency and intensity of heavy precipitation, droughts, desertification and dust storms in many regions of the world. Going forward we will continue to see increases in frequency and intensity of extreme rainfall, droughts, and extreme heat events if we continue to emit greenhouse gasses and allow land use change to occur at current levels (Ebi et al., 2020). These events, and events influenced by climate change such as wildfires or tropical cyclones, can lead to detrimental impacts on human physical and mental health such as heat stress, smoke inhalation, and injury/death (Ebi et al., 2020). Climate change is also impacting food security worldwide. A recent study compared the temperature anomaly due to climate change (determined by difference between the mean annual temperature and a 30 year mean annual temperature in each region) to the food insecurity experience scale. This scale looks at the number of people that at all times don't have physical and economic access to sufficient, safe and nutritious foods. The study found that in 2019, every 1°C temperature anomaly led to moderate to severe global food insecurity increasing by 2.14%; furthermore they highlight that countries such as Africa, which are least responsible for greenhouse gas emissions, are experiencing the most negative impact of climate change on food security (S. Dasgupta & Robinson, 2022). Throughout history, significant climatic changes such as drought has affected many aspects of livelihoods, which in turn has led to social unrest (Kaniewski et al., 2020). As we face an uncertain future, addressing climate change is crucial to prevent further disruptions to societies and ecosystems.

Climate change is impacting biodiversity in a number of ways, including causing shifts in species ranges (Pacifici et al., 2020) and increasing biodiversity loss by increasing the number of species considered as threatened by extinction (Habibullah, Din, Tan, & Zahid, 2022). As climate change advances protected areas can be a useful tool in limiting the effects of climate change on biodiversity; they can help species to track suitable climates through protection of climate corridors, and prevent the destruction of habitat in areas projected to be climatically suitable for species in the future. Protected areas need to be designed in a way that considers future climate change, as protected areas may protect different species assemblages than those for which they were originally designed, due to climate driven species turn over within (Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011; Hole et al., 2009). Of the current range of climatic conditions under protection, no country is projected to protect even half of this range of currently protected climates by 2070 (Elsen, Monahan, Dougherty, & Merenlender, 2020), which will cause a key issue in protected area representativeness, as countries are unable to represent the full range of ecosystems and species diversity within their protected areas. Identifying future climate refugia is one method that can help complement the work that current protected areas undertake, increasing climate representativeness. It is those areas that have the slowest moving climates under climate change that will act as the best refugia, and therefore enhance ecological resilience (Arafeh-Dalmau, 2020). A study of 1,010 protected areas in New South Wales Australia looked into whether their borders would incorporate climate refugia modelled for 12 different climate scenarios in 2070 within the region (V. Graham, Baumgartner, Beaumont, Esperon-Rodriguez, & Grech, 2019). They found that only 7 of the protected areas included in this study overlapped with key refuge areas in all 12 scenarios, and that only 363 protected areas were predicted to become refugia in one or more of the climate scenarios for the year 2070. This highlighted the need for more protected areas within the region, that incorporate the climate refugia modelled.

Creating a network of protected areas that are future proofed against climate-induced species range shifts will be key if we are to conserve existing levels of biodiversity. Protected areas now need to be designed anticipating species range shifts, and there are a few studies that begin to identify where protected areas should be in the face of climate change (V. Graham et al., 2019; Stralberg, Carroll, & Nielsen, 2020). However, for those that have already been designated, it is important to ensure that their management is adaptive to climate-change pressures. “Future-Proofing Conservation” management is a newly created concept that aims to do just this and has been trialled in Colombia. It focusses on protected area management that holds the following ideals: to anticipate ecological change and recognise it as a governance issue, create targets that focus on social values and to ensure ongoing learning takes place (Van Kerkhoff et al., 2019).

It is important to note that the effects of climate change on biodiversity can interact with impacts of land-use change in complex ways, and so studies should address land-use change and climate change together if we are to have a more complete vision of the future. Land-use changes such as deforestation can amplify the impacts of climate change creating a reinforcing feedback loop. For example, as the trees and soils that sequester carbon are disturbed by human activities such as logging, urbanisation, and agriculture, they ultimately release their carbon stores back into the environment, further increasing the intensity of climate change (Culas, 2009). Variations in species richness, species compositions and ecosystem functions are best explained when both climate and land-use change and their interactions are taken into consideration, rather than looking at them in isolation (Peters et al., 2019; Sarmento Cabral et al., 2013). A combination of both land-use and climate change is predicted to cause a further 5-16% decrease in suitable habitat availability for mammal species by the year 2050 (Baisero, Visconti, Pacifici, Cimatti, & Rondinini, 2020). Furthermore, as land-use change itself reduces habitat availability, which in turn reduces landscape connectivity, population sizes and dispersal ability of species, the remaining isolated populations will be less resilient to climate change and extreme climatic events (Schulte to Bühne, Tobias, Durant, & Pettorelli, 2021).

Ecosystem services can also be impaired as a result of interactive effects of climate change, ecosystem degradation, increased disaster risk (Munang, Thiaw, Alverson, Liu, & Han, 2013) and land-use change (Hasan, Zhen, Miah, Ahamed, & Samie, 2020). Ecosystem services are ways that the natural environment can provide direct and indirect benefits to human wellbeing and quality of live. They can broadly be broken down into 4 categories: provisioning services such as food, medicines and fresh water, regulating services such as air quality, erosion control and pollination, cultural services such as cultural diversity, ecotourism and education, and supporting services such as photosynthesis, nutrient cycling and soil formation (MEA, 2005). One such example of how climate change can impact ecosystem services are coral reefs. Coral reefs are being damaged through increased CO_2 emissions, which are absorbed by the oceans affecting the pH of water and the rate of coral calcification, the process by which corals grow. Damage to corrals in this way can impact the ecosystem services that they provide such as costal protection from storm surges, nurseries for marine species that local communities may depend on for food, and in turn have a negative effect on biodiversity through increasing extinction rates of species and causing habitat fragmentation (He, Liang, Zeng, Yuan, & Li, 2019). Another example is that of how climate change is negatively impacting pollinator biodiversity, especially in tropical regions, which has direct consequences for food security, such as reduced crop yield (Millard et al., 2023). These examples underscore the urgent need for effective ecosystem management that mitigates the impacts of climate change, amongst other anthropogenic pressures, to help safeguard biodiversity and thus ensure the continued benefits of ecosystem services.

Conclusion

It is clear that in order for biodiversity trends to improve, we need an integrated approach that increases the amount of protected landscapes, restores degraded habitats, and mitigates land-use and climate change (Leclère et al., 2020). These approaches need to be in conjunction with allowing for ecosystem services such as sustainable food production, safe drinking water and many others that contribute to achieving a large proportion of the sustainable development goals. The wider debate on land-sharing verses land-sparing (Grass et al., 2019) is central to discussions on how to manage ecosystems in a way that both achieves biodiversity conservation, as well as delivers the ecosystem services required for human society (Kremen & Merenlender, 2018). Land-sparing describes one extreme of a continuum in which land is set aside for biodiversity conservation with strict rules on its usage, and other land is used intensively for providing resources for humans. At the other extreme, land-sharing describes a situation in which areas of land are sustainably used by humans for extracting resources, while also preserving biodiversity within the same areas, with this biodiversity contributing to human resource extraction through the provision of ecosystem services. For countries to be able to meet their biodiversity commitments, both approaches are likely to be needed; whilst ensuring that landscape connectivity is maintained, with the optimal strategy depending on the specific context of the landscape (Grass et al., 2019).

As anthropogenic pressures, such as habitat destruction and climate change, are driving widespread species decline and range shifts, conservation tools such as protected areas are one way to mitigate these pressures by conserving biodiversity and reducing habitat loss. There are a lack of studies that link terrestrial protected area characteristics to biodiversity outcomes; my thesis aims to address the effectiveness of some of the tools available to aid with future proofing the conservation of mammals. The main research questions of my work are: what characteristics of terrestrial protected areas are most correlated with the highest levels of mammal biodiversity? To what extent do protected areas preserve land that is expected to have suitable climate and habitat for mammal species in the future? Which parts of the world, if restored to natural habitat, have the potential to conserve the most mammal species under future climate change? I start my thesis by addressing how protected areas can improve local measures of mammal biodiversity, move on to identifying areas of the globe that do not contain enough contiguous habitat for mammal conservation under future climate change, and lastly look at what areas can conserve the most mammal species richness by undergoing restoration of natural habitat.

Chapter 2

Local Measures of Mammal Biodiversity vary with Global Terrestrial Protected Area Characteristics

Abstract

Protected areas play a vital role in conserving biodiversity, preventing anthropogenic land-use change and providing important ecosystem services. As we face rapid biodiversity and habitat losses this century, it is essential to understand which characteristics of protected areas make them most effective in preserving habitats and biodiversity. This will enable us to optimise the use of finite resources and improve long term conservation outcomes in the face of climate and land use change. I explore the impact of protection status, and protected area characteristics on terrestrial mammal species richness and abundance in a global study. I find that there are 11% more mammal species on average in local samples of biodiversity inside protected areas compared to areas without protection. Natural habitat within protected areas has a positive effect on total mammal abundance at low and medium elevations, but surprisingly a negative effect on species richness. Effects at high elevations were weaker, and in the opposite directions compared to low and medium elevations. Total mammal abundance also increased with distance inside protected areas, especially in areas with a greater percentage of natural habitat within 100 km of the sample site. Overall, my results suggest that protection status itself is most important for mammal species richness, whereas the spatial characteristics of protected areas are important for both mammal abundance and mammal species richness. Based on my findings, it appears that having large, protected areas with relatively little impact of edges, and generally having high amounts of natural habitat will be beneficial for mammal biodiversity. These results can be used to help policy makers make legislation that fulfils the new internationally agreed biodiversity and sustainable development targets.

Introduction

There are several internationally agreed frameworks and sets of targets aiming to reduce biodiversity losses, including the Sustainable Development Goals (SDGs), and the Kunming-Montreal Global Biodiversity Framework (GBF). Protected areas play a large role in many of the targets in these agreements (Fischborn & Sandwith, 2021; Woodley et al., 2022). It is therefore important to monitor how current protected areas are performing, so that governments and organisations can implement best practice in designating and designing additional protected areas, and increase the effectiveness of existing protected areas. Just under 17% of the world's land surface is currently covered by protected areas (Protected Planet, 2023). Meeting the internationally agreed target of effectively protecting 30% of land and sea by 2030 (Convention of Biological Diversity, 2022) will require both increasing area coverage as well as improving and maintaining the effectiveness of existing protected areas.

The major driver of biodiversity loss to date is land-use change (Biggs & Scholes, 2005; Davison, Rahbek, & Morueta-Holme, 2021; Newbold, 2018). Already, 77% of land (excluding Antarctica) has undergone anthropogenic modification (Watson et al., 2018), and between now and the year 2070 some of the most impacted parts of the globe are projected to undergo an average of 9-17% decadal land-cover change, leading to the endangerment of 1,700 species of birds, mammals and amphibians (Powers & Jetz, 2019). Some of the threats that land-use change can have on biodiversity include habitat loss, fragmentation and degradation (R. J. Fletcher et al., 2018), loss of keystone species as well as interruption of natural ecosystem functions (Liu et al., 2018), together with the potential introduction of invasive species (W. Wang et al., 2016). Protected areas are one of the most effective ways of preventing land-use change (Figueroa & Sánchez-Cordero, 2008), and thus contribute to safeguarding species into the future. We know that protected areas conserve natural habitats (Geldmann et al., 2013), have higher local biodiversity than sites outside their borders (Coetzee et al., 2014; Gray et al., 2016), and provide ecosystem services such as carbon sequestration, water purification and natural hazard mitigation (Castro et al., 2015; Stolton et al., 2015).

There are many important features of protected areas to consider when assessing their effectiveness for biodiversity conservation (Watson, Dudley, Segan, & Hockings, 2014). The Lawton review highlighted a need for "more, bigger, better and joined" terrestrial protected areas to conserve biodiversity effectively now and in the face of future climate change (Lawton, 2010). Since this review, research into how the characteristics of protected areas influence biodiversity outcomes has expanded (Barnes et al., 2017; Ward et al., 2020; Wintle et al., 2019), and studies continue to provide evidence that protected areas can better conserve species when they are larger (Barnes et al., 2017) and more connected (Saura et al., 2019). Protected areas with a more complex border (fractal dimension, also known as border rugosity) also have increased conservation value, as more ecological representativeness is achieved (Wintle et al., 2019). The geographical placement of protected areas is also of great importance, for example to ensure that they encompass the range of environmental conditions required by different species (Wintle et al., 2019), and to enable them to be resilient in the face of climatic changes (Hanson et al., 2020). Protected-area management and governance have also been shown to impact biodiversity (Barnes et al., 2017; Powlen et al., 2021).

As well as protected areas, there are other landscape characteristics that can increase levels of biodiversity. For example, topographically diverse habitats can act as a buffer against pressures such as climate change due to the variety of microclimates present (Suggitt et al., 2018), and areas of high topographical diversity (regardless of the percentage of protected area coverage in these areas) are better at conserving priority species (Cunningham et al., 2021). Furthermore, the landscape matrix of habitat itself is of importance to conservation; structurally similar natural habitat is more often selected for when species utilise an area, regardless of its protection status (Stewart, Darlington, et al., 2019). These studies highlight the complexity of considering a wide range of protected area and landscape characteristics, and disentangling their impact on biodiversity.

The diversity of mammals, and the wide ranging nature of some of them, means that they are likely to be exposed to a wide range of landscape features (Presley et al., 2019), and so may be strongly influenced by the placement and design of protected areas. At present, many protected areas are not large or interconnected enough for the effective conservation of mammal species (Berger, 2017; Bowyer et al., 2019). Furthermore, it has been noted that mammals that face greater fragmentation in their habitat are at a greater risk of extinction (Crooks et al., 2017). A case study of 69 species of large mammals (mostly herbivores) in African protected areas showed that between the years of 1970 and 2005, mammals experienced an average decrease in population size of 59% (Craigie et al., 2010). Although there were multiple reasons for this decline, such studies highlight the need for further research into the characteristics of protected areas, and their influence on biodiversity outcomes.

My global study considers the role in conserving biodiversity of several terrestrial protected-area characteristics important to mammal biodiversity, including a protected area’s size, proximity to another protected area, border rugosity, and strictness of protection as determined by the IUCN management categories. I also test whether measures of biodiversity vary with distance inside a protected area’s border, and with the amount of natural habitat immediately surrounding the sampled site. Furthermore, I explore if site-specific measures of mammal biodiversity are significantly different between protected areas and comparable sites outside of protection. I predict that protected areas have higher mammal biodiversity than areas with no protection. I also predict that protected areas that are larger, more connected, with high border complexity and strict management will have higher mammal species richness and abundance, and also that measures of biodiversity will be higher further inside protected areas, and where surrounding habitat quality is higher.

Methods

Dataset preparation

I downloaded the World Database on Protected Areas (WDPA) for August 2020, which contains the location and size of all globally recognized protected areas and, where known, their management and governance categories (for details, see below). I filtered this dataset to include only protected areas that are predominantly or entirely terrestrial, excluding coastal and marine protected areas (World Database of Protected Areas User Manual 1.6, 2019). The data consist of both polygon (delineating the boundaries of protected areas) and point data (a point on the map at the location of the protected area, which has information such as the size of the protected area, but for which boundaries could not be drawn). Point data represent 9% of all protected areas in the WDPA, and so, following previous recommendations (Bingham et al., 2020), I include these in my analysis of the impact of protection status on mammal biodiversity. However, for my analysis of protected area characteristics, point data have been excluded because for these protected areas I could not estimate border complexity.

Mammal biodiversity data were obtained from the PREDICTS database, which contains local measures of terrestrial biodiversity from habitats under different levels of human land use, collected between 1983 and 2014 (Hudson et al., 2014, 2017). The PREDICTS database has some taxonomic and geographic bias (Purvis et al., 2018), but contains a good representation of mammals with data on 397 species across 11 out of 14 sampled biomes (Hudson et al., 2014). The PREDICTS data are hierarchically structured: within an individual published work (data ‘Sources’) there can be multiple taxonomic groups sampled with different sampling methods, which are accordingly separated into different ‘Studies’, within which there may be spatial clusters (‘Blocks’) of sampled ‘Sites’ (figure 1). Study sites contain the raw measurements, which typically record abundance but sometimes only species occurrence.

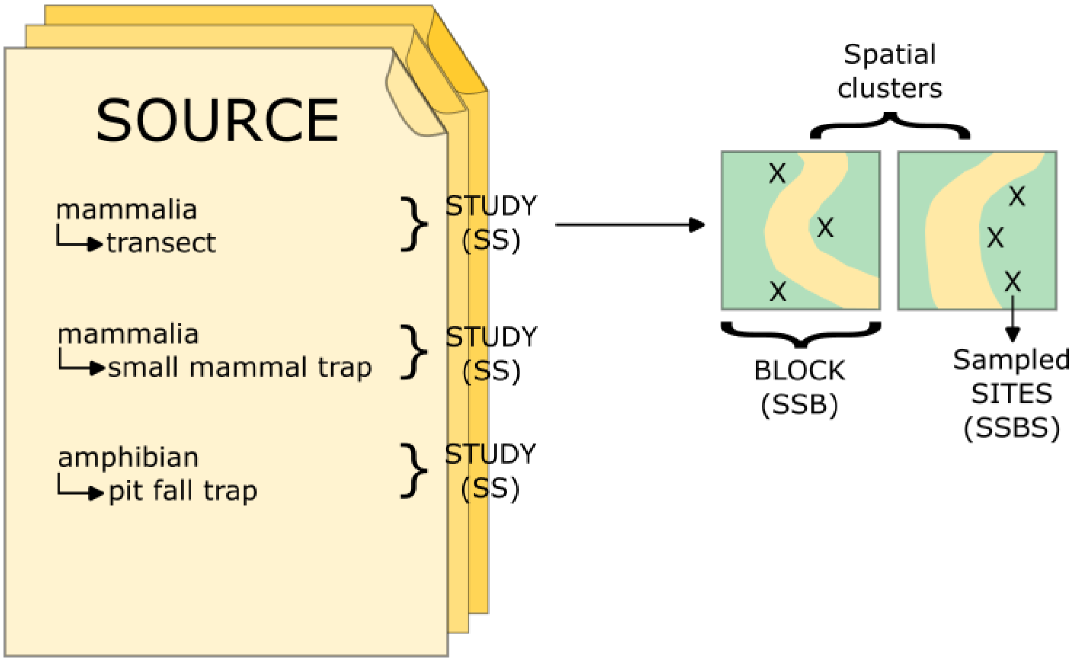


Figure 1. Own depiction of the hierarchical structure of the PREDICTS database. Source: the individual published work from which the data was sourced, which may contain data for multiple taxonomic groups sampled with different sampling methods. Study (SS): a subset of the source, in which the data were sampled using one sampling method, e.g. mammals sampled along a transect. Block (SSB): a spatial cluster of sampled sites within a study. Sites (SSBS): the locations that contain the raw data, typically recording abundance, but sometimes only species occurrences.

Individual studies of biodiversity within the PREDICTS database can use different sampling techniques and apply different levels of sampling effort. To be able to compare biodiversity between studies I use hierarchical models with appropriate random effects (explained below). To account for the differences in sampling effort within a small proportion of the PREDICTS studies, I used the "CorrectSamplingEffort" function from the predictsFunctions package, version 1.0. This corrects any measures of abundance that are effort-sensitive using a linear correction based on the recorded relative sampling effort within each study (Newbold et al., 2014). I also merge sites from the database using the "MergeSites" function in the same package. This combines original locations that have the same coordinates and that also share a number of other properties such as land use. Sites that are merged generally reflect multiple sub-samples within one site, for example, pitfall traps used for trapping small mammals may have been entered as different sites even though they occurred on the same transect. Of the 32,827 biodiversity records for mammal species within the PREDICTS database, 31,524 recorded species abundance, 1,269 species occurrence, and 34 overall mammal species richness. I used the "SiteMetrics" function from the "predictsFunctions" package version 1.0 (Newbold, 2015a) in R version 4.0.5, to combine these biodiversity records into 2,239 sites with biodiversity data on the sampled mammal abundance and species richness. An overview of the dataset preparation is shown in figure 2.

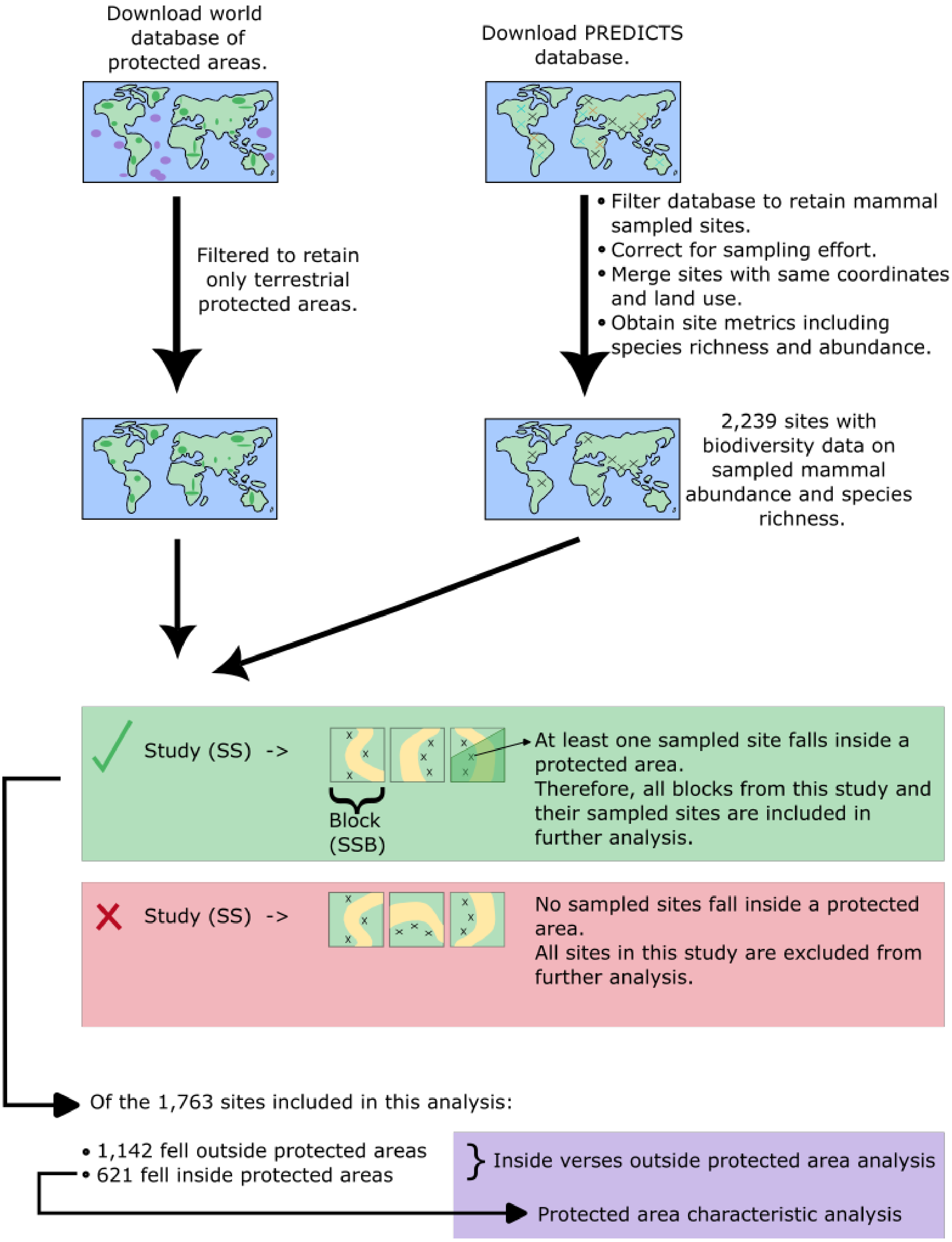


Figure 2. Own depiction of the preparation of the World Database of Protected Areas and the PREDICTS database for use in my study. Green box represents a study that satisfies the conditions to be included in the analysis. Red box represents a study that would not be included in the analysis. Purple box represents the 2 analyses from my study, and the sampled sites that went into each analysis.

I only considered in my analyses sites from studies that included at least one site inside a protected area. This meant that 476 unprotected sites were not included in this analysis as they came from studies that didn't have any sites located within protected areas. Excluding these samples means that any differences detected in analysis are more likely to be because of protection itself, rather than due to differences in broad-scale environmental conditions. Of the 1,763 sites included in this analysis, 621 sites fell inside 64 protected areas worldwide according to the WDPA (figure 3), while 1,142 sites fell outside of protection.

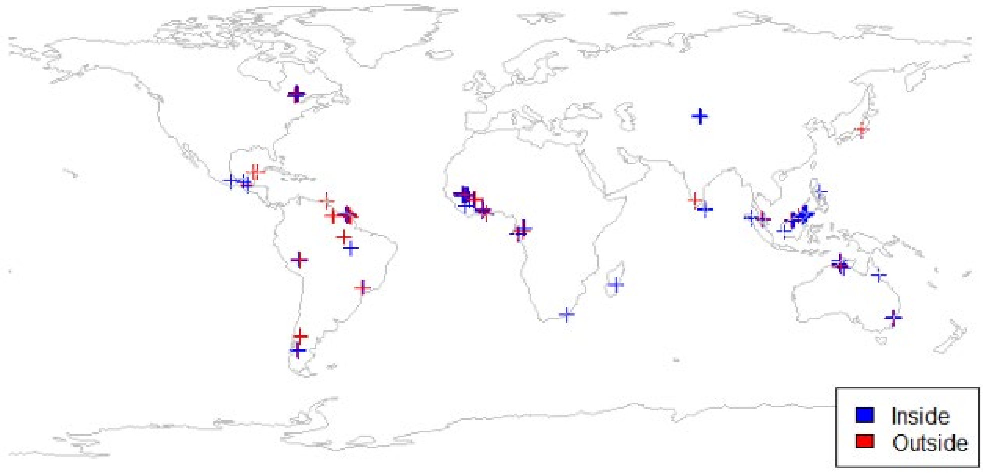


Figure 3. Locations of sites of mammal biodiversity in the PREDICTS database included in this study. "Inside" are sites that are positioned inside of a protected area as recorded in the WDPA. "Outside" are sites that fall outside of protected areas, which were paired with at least one site inside a protected area from the same study. Plotted in the WGS84 geographic coordinate system.

Variables

The strictness of the management of protected areas was based on the International Union for Conservation of Nature (IUCN) management categories (table 1). In line with a previous study (Gray et al., 2016), IUCN categories Ia, Ib and II were combined in a category of 'most restrictive', while categories III, IV, V and VI were combined as 'least restrictive' protected areas. It is important to note that the true strictness of protection for each of these categories varies among countries (Ferraro et al., 2013), which will add some noise to any analyses. I combined the categories 'not applicable' and 'not reported' to form a new category 'unknown'. Sites with this 'unknown' designation were included in the analysis as they accounted for just under half the data, and so removing them would have reduced the statistical power with which to test the effect of the other characteristics considered. There were 4 PREDICTS sites that fell inside more than one protected area due to protected area border overlap. These cases were manually inspected. In all cases, the 2 protected areas that the PREDICTS site fell inside were identical in size, and it was only the IUCN category that differed. In all 4 cases, the site was assigned to the most restrictive IUCN category, as it is assumed that the restrictions from this category would take precedence, and therefore have the greatest impact on the site. I reclassified the five IUCN governance categories as listed in the WDPA (table 2), into four final categories in alignment with the Governance Assessment for Protected and Conserved Areas (Booker & Franks, 2019).

Table 1: IUCN Management Categories and their associated definitions (Dudley et al., 2010). Categories Ia, Ib and II are grouped into the category "most restrictive", and III, IV, V and VI into the category "least restrictive".

IUCN Management Category	Summary	Category for Analysis
Ia: Strict Nature Reserve	Area designated to protect biodiversity or landscape features. Human activities are heavily restricted so that conservation values can be met.	Most restrictive
Ib: Wilderness Area	Large unmodified areas without significant human presence. These areas are protected to preserve their natural condition.	
II: National Park	Large natural areas designated to protect large-scale ecological processes. Open for spiritual, scientific, educational and recreational visits.	
III: Natural Monument or Feature	Areas that protect a natural monument.	Least restrictive
IV: Habitat / Species Management Area	These areas are designated to protected particular species or habitats as reflected by their management plan.	
V: Protected Landscape / Seascape	Areas that are the result of the interaction between people and nature, providing ecological, biological, cultural and scenic value.	
VI: Protected Area with sustainable use of natural resources	These areas may have traditional natural resource management systems in place, which are compatible with nature conservation.	

Table 2: IUCN Governance categories of protected areas and their associated definitions. Categories "federal or national ministry or agency" and "sub-national ministry or agency" were grouped together for my analysis.

IUCN Governance Category	Summary	Category for Analysis
Not reported	Governance category not reported.	Not reported
Federal or national ministry or agency	Federal or national ministry or agency in charge.	State Governance
Sub-national ministry or agency	Sub-national ministry or agency in charge.	
Joint governance	Where two or more groups share authority, either through transboundary, collaborative or joint governance.	Shared Governance
Governance by indigenous people and local communities	Areas established and run by indigenous peoples or local communities.	Community Governance
Governance by private actors	Conservation areas established and run by individual landowners, non-profit organisations or for-profit organisations.	Private Governance

To obtain a measure of border complexity of protected areas, I calculated the fractal dimension (D), which gives a measure of how complex the shape of the perimeter of the protected area is by reference to the area protected (Pászto, Marek, & Tuček, 2011):

$$D = (2*\log(P))/(\log(A))$$

Where P = perimeter length and A = area. Values range between 1 and 2. A value close to 1 indicates that the border is minimally complex and has a more regular shape.

I obtained the percentage of natural and artificial land within a 100-km-radius circular buffer surrounding the sites where samples of biodiversity were conducted. Whilst home range size varies widely among mammal species, 100 km was considered appropriate for this analysis, as it represents an area that can be covered by a typical large mammal in its lifetime (Minor & Lookingbill, 2010; Niculae et al., 2016). In addition, this size buffer is commonly used in spatial studies on small mammals (Giraudoux et al., 2013; Peplinski & Brown, 2020), to account for pressures in the surrounding landscape. The land-use map that I used is constructed of the 47 IUCN terrestrial land uses nested within 8 broader categories – forest, savanna, shrubland, grassland, wetlands, rocky, desert (which for the purposes of this study I combined into 'natural habitat') and artificial land – at a spatial resolution of 1 km (Jung et al., 2020). The 'artificial land' category as used in the Jung et al., 2020 map encompassed the PREDICTS land-use categories: croplands, pasture, urban areas and plantations. The buffers were drawn using the Sinusoidal Projection, which is a pseudocylindrical projection in ArcMap 10.6 representing equal areas with minimal distortion (ArcGIS, 2016b).

In the PREDICTS dataset, each site is attributed to one of a set of land uses and land-use intensities based on the description of the habitat given in the original publications that presented the biodiversity data (Hudson et al., 2014). I considered here only land use, and not land-use intensity, because of the relatively limited sample size and the consideration of multiple other protected-area characteristics: primary vegetation (natural habitat with no evidence of past destruction), secondary vegetation (areas where the natural habitat has previously been destroyed by human land use or extreme natural events, but is now in recovery), pasture (areas used for regular or permanent livestock grazing), urban (human settlements including buildings, parks and gardens), cropland (areas used to grow herbaceous crops) and plantations (areas used to grow woody crops, such as fruit trees, coffee, rubber, timber and oil palm) (Hudson et al., 2014). For the purposes of this study (because of the relatively small sample size of some groups) I combined primary and secondary vegetation into a single category, “natural”, and pasture, urban, cropland and plantation into “artificial”.

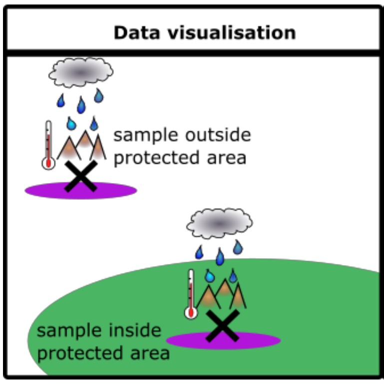
To quantify how connected a protected area is to other protected areas, I measured the distance from the border of a protected area to the border of the nearest other protected area using the “Near Analysis” function in ArcMap 10.6. I also calculated the distance from PREDICTS sites inside protected areas to the border of the protected area using the “Near Table” function. I undertook these calculations using the Azimuthal Equidistant Projection, which is an azimuthal projection that represents scale, direction and distance with minimal distortion (ArcGIS, 2016a).

Elevation, temperature and precipitation were included in my analysis, since they are known to influence broad-scale biodiversity patterns (Antonelli et al., 2018), and thus may confound any inferences about the impact of protection status or protected area characteristics. Elevation was estimated for each sampled site using the elevatr package Version 0.3.4, and annual mean temperature and total annual precipitation from WorldClim Version 2.1 (Fick & Hijmans, 2017). An alternative to including such control variables in the analysis is to create a dataset with matching sites selected to control for the same environmental differences. However, given the incomplete sampling in the PREDICTS database, this would have reduced statistical power to an unacceptable degree. Previous studies of the impact of protected areas on biodiversity using the PREDICTS database have also successfully used the approach that I take (Gray et al., 2016).

Inside verses outside protected area analysis

For my first analysis, I compare mammal biodiversity metrics inside and outside protected areas. As fixed effects, I included whether the PREDICTS site fell inside or outside a protected area according to the WDPA, the predominant land use, elevation, mean annual temperature and total annual precipitation. I considered interaction terms between elevation and mean annual temperature, and between elevation and mean annual precipitation, because climatic variables and elevation have been shown before to have interactive effects on mammal biodiversity (Antonelli et al., 2018).

Elevation was $\log_e$-transformed, scaled and centred, while mean annual temperature and precipitation were also scaled and centred. Study (SS) and spatial block (SSB) identity were included as random intercepts to account for the hierarchical structure of the data in both my species richness and abundance models. Site identity (SSBS) was also included as a random intercept in the species richness models to correct for overdispersion present in this model (Rigby, Stasinopoulos, & Akantziliotou, 2008). All fixed effects used in this analysis had a Variance Inflation Factor (VIF) of under 2.9, and so showed sufficiently limited collinearity for a robust statistical analysis. To model mammal species richness, I ran a Poisson mixed-effects model using the “glmer” function from the “lme4” package Version 1.1-26 in R. To model the total abundance of mammal species, I fitted a linear mixed-effects model using the ‘lmer’ function of the same R package. I $\log_e$-transformed the abundance estimates, adding a value of 1 to account for zeros in the data. It was not possible to use generalized linear models for abundance, because abundance values are recorded in the PREDICTS database using very heterogeneous metrics and often given in non-integer values. For both the species richness and total abundance models, I conducted a backward stepwise selection of fixed effects using the “GLMERSelect” function from the “StatisticalModels” package Version 0.2-1 (Newbold, 2015b), testing interaction terms first, and then dropping them to test main effects. Main effects that are part of significant interaction terms were retained in the final model. The data used in this analysis are outlined in figure 4, together with the variables retained in the final model from the backward stepwise model selection process.

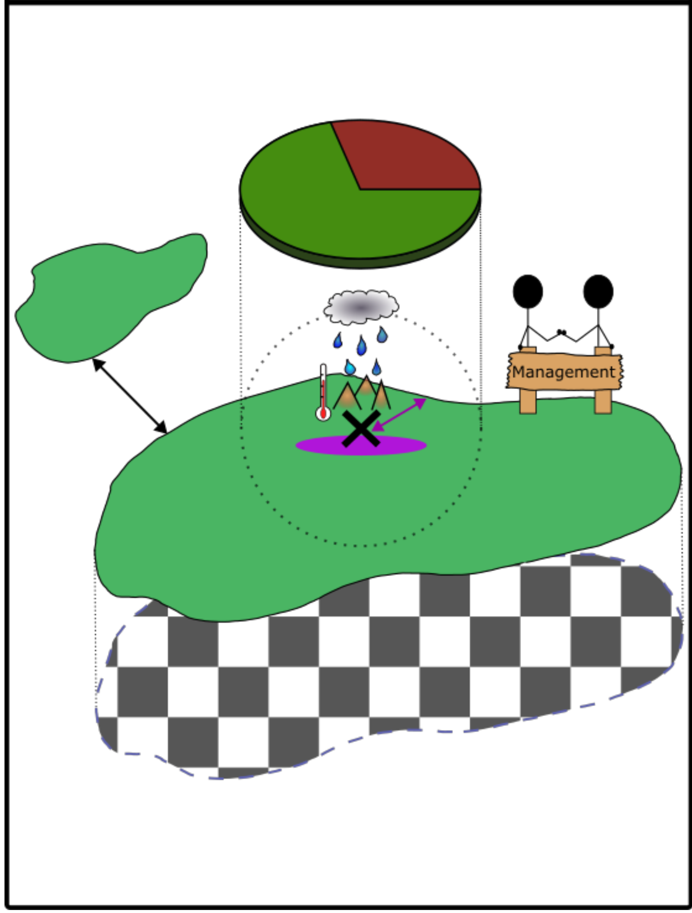


Key		Variable retained in backward stepwise model selection? Species abundance	Species richness
✕ Sampled site			
Protected area (inside/outside)	Fixed effects	✓	✓
Total annual precipitation	Fixed effects	✗	✗
Mean annual temperature	Fixed effects	✗	✗
Elevation	Fixed effects	✗	✗
Predominant land use of site	Fixed effects	✗	✓
Random intercepts			
Study (SS)		✓	✓
Spatial block (SSB)		✓	✓
Site identity (SSBS)		NA	✓

Figure 4. Overview of the data used to investigate the effect of protection status on mammal biodiversity outcomes. The fixed effects and random intercepts included in the total species abundance and species richness models are listed, together with the main effects retained as part of significant interaction terms in the final model from the backward stepwise model selection process.

Protected area characteristics analysis

For my second analysis, I examine the characteristics of protected areas that influence mammal biodiversity measures within protected areas. Features of protected areas considered were the size of the protected area, the management category, the governance type, the distance to the nearest other protected area, and the complexity of the protected area's border. I also used explanatory variables that are specific to the sampling site: predominant land use, the percentage of surrounding natural habitat, distance to the nearest protected-area border, elevation, mean annual temperature and total annual precipitation. Percentage of surrounding natural habitat, protected-area size, distance to protected-area edge, and elevation were $\log_e$-transformed, scaled and centred. Border complexity (fractal dimension) values were also scaled and centred, while distance to the nearest other protected area was $\log_e$-transformed, adding a value of one to account for zeros in the data, as well as being scaled and centred. I considered interactions between the effects of percent natural habitat and: IUCN category, predominant land use, the distance to the edge of the protected area, and elevation. These interactions were selected based on the following expectations: in protected areas classified as strict nature reserves, a higher percentage of natural habitat can have a stronger positive impact on biodiversity compared to protected areas that have a less strict IUCN category (Timmers et al., 2022); having a larger amount of natural habitat surrounding locations in artificial land uses, such as urban environments, can have stronger positive impacts on biodiversity than amount of natural habitat surrounding locations in natural habitat (Bradfield, Nagy, Weckel, Lahti, & Habig, 2022); natural habitat that is further inside a protected area is less exposed to pressures outside of a protected area (Volenec & Dobson, 2020), and so is more likely to have positive impacts on biodiversity; and lastly natural habitat that is at lower elevation is more likely to have positive impacts on biodiversity as it can potentially support more species (Kamenišťák et al., 2020). All fixed effects used in this analysis had a VIF of under 3.4, and so showed sufficiently low collinearity for a robust analysis. 19 sites with biodiversity data had to be excluded from this analysis because of unknown land use, precipitation and/or temperature, or not being able to determine the distance to the nearest protected area (because the shape of some protected areas meant that the nearest protected area was the same as that in which biodiversity was sampled). As before, species richness was modelled using a Poisson generalized linear mixed-effects model, and $\log_e$-transformed total abundance (+ 1) with a linear mixed-effects model. Random effects were as in the first set of models, with the addition of a random intercept of the unique protected area ID (WDPAID), to account for the nested structure of the data where there could be multiple study sites within the same protected area. Again, I conducted backward stepwise selection of fixed effects using the GLMERSelect function. The data used in this analysis are outlined in figure 5, together with the variables retained in the final model from the backward stepwise model selection process.



Key	Variable retained in backward stepwise model selection? Species abundance	Species richness
Sampled site		
Protected area		
Fixed effects		
Total annual precipitation	✗	✗
Mean annual temperature	✗	✗
Elevation	✓	✓
Predominant land use of site	✗	✗
Percentage of natural habitat in 100km surrounding site	✓	✓
Total protected area size	✗	✗
PA border complexity	✗	✗
Distance from sampled site to edge of PA	✓	✗
Distance from PA border to nearest other PA	✗	✗
IUCN management category of PA	✗	✗
Governance type of PA	✗	✗
Random intercepts		
Study (SS)	✓	✓
Spatial block (SSB)	✓	✓
Site identity (SSBS)	NA	✓
PA ID	✓	✓
Interaction terms		
Natural habitat : Elevation	✓	✓
Natural habitat : IUCN management category of PA	✗	✗
Natural habitat : Predominant land use of site	✓	✗
Natural habitat : Distance from sampled site to edge of PA	✗	✗

Figure 5. Overview of the data used in the protected area characteristics analysis. The fixed effects and random intercepts included in the species abundance and species richness models are listed, together with the main effects retained as part of significant interaction terms in the final model from the backward stepwise model selection process.

Results

Mammal species richness was 11% higher in protected areas compared to locations outside (χ^2=6.33, df=1, p=0.012) (figure 6), whereas total mammal abundance was not significantly different between areas with or without protection (χ^2=1.12, df=1, p=0.290) (supplementary material, table 1). The fixed effects included in the species richness model accounted for 6% of the variance in the response variable (marginal pseudo-R^2 = 0.063), and the proportion of the variance explained by both the fixed and random effects was 84% (conditional pseudoR^2 = 0.837). In the species abundance model, fixed effects accounted for 5% of the variance in the response variable (marginal pseudo-R^2 = 0.051), and both fixed and random effects accounted for 84% of the variance (conditional pseudo-^{2} = 0.842). The deviance of the species richness model was 1,585, and the species abundance model was 4,750.

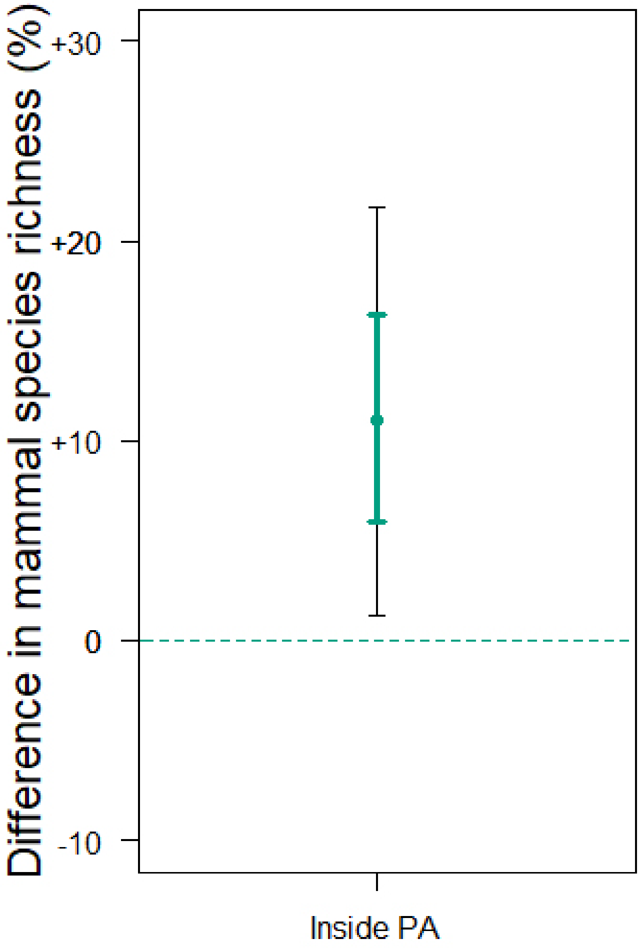


Figure 6. The percentage difference in mammal species richness inside protected areas ('Inside PA') compared to outside protected areas (dotted green line). Points represent model-estimated median mammal species richness, the black error bar represents 95% confidence, and the green error bar 67% confidence intervals around the modelled median estimate.

Sampled mammal total abundance within protected areas increased the further inside a protected area the sample was taken (χ^2=4.54, df=1, p=0.033), increasing approximately three-fold on average between sites immediately inside protected-area borders to those 75 km inside a protected area (figure 7). Natural habitat didn't have a significant effect on its own (χ^2=1.10, df =1, p=0.294), but did have a significant interactive effect with distance to border (χ^2=11.65, df=1, p=0.001) and elevation (χ^2=5.71, df=1, p=0.017). Natural habitat had a positive association with mammal abundance further from the edge of protected areas (figure 8), and at low elevations (figure 9), but had a much weaker and slightly negative association near the edge of protected areas or at high elevations. All other variables considered had non-significant effects on mammal total abundance (supplementary material, table 2). The fixed effects included in this model accounted for 12% of the variance in the response variable (delta marginal pseudo-R^2 = 0.124), and the proportion of the variance explained by both the fixed and random effects was 91% (delta conditional pseudo-R^2 = 0.913). The deviance of the model was 1,411.

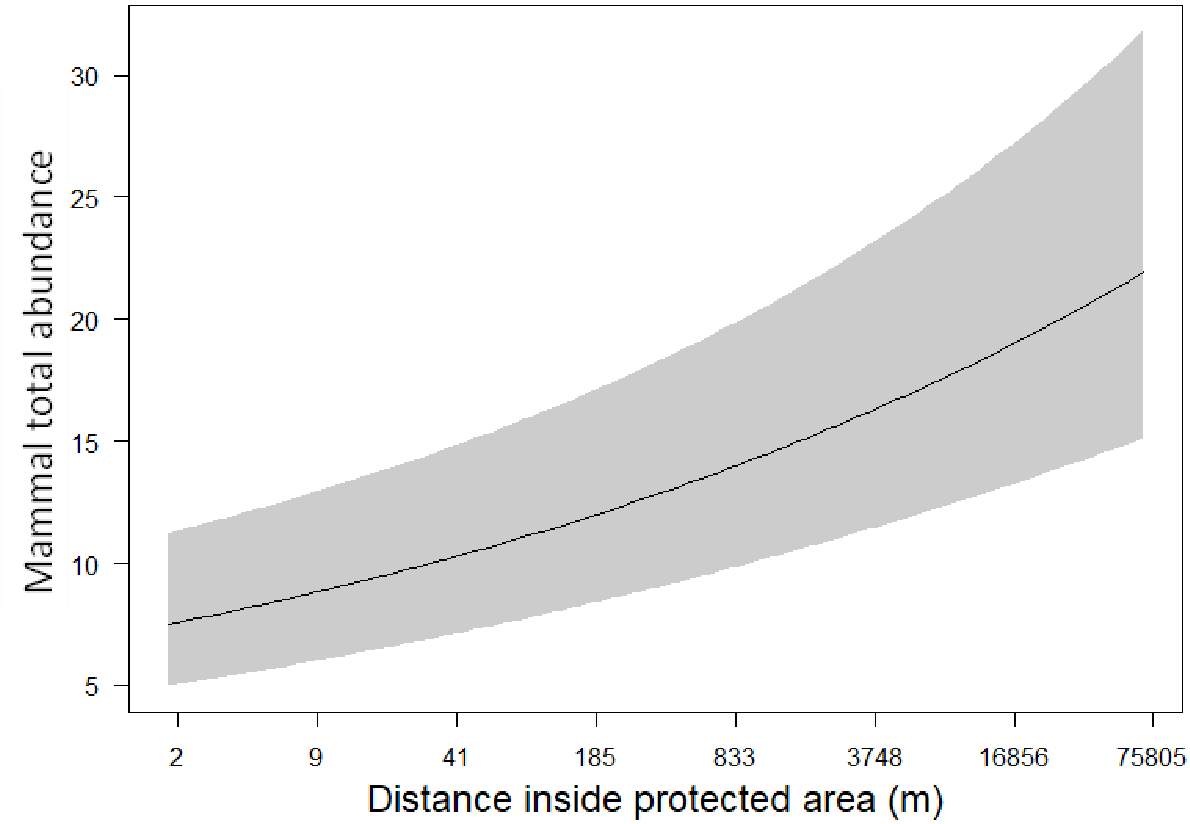


Figure 7. Model-fitted relationship between distance to the edge of a protected area and the sampled total abundance of mammals. The black line represents the model-estimated mean total abundance, and grey shading represents ± 1 standard error.

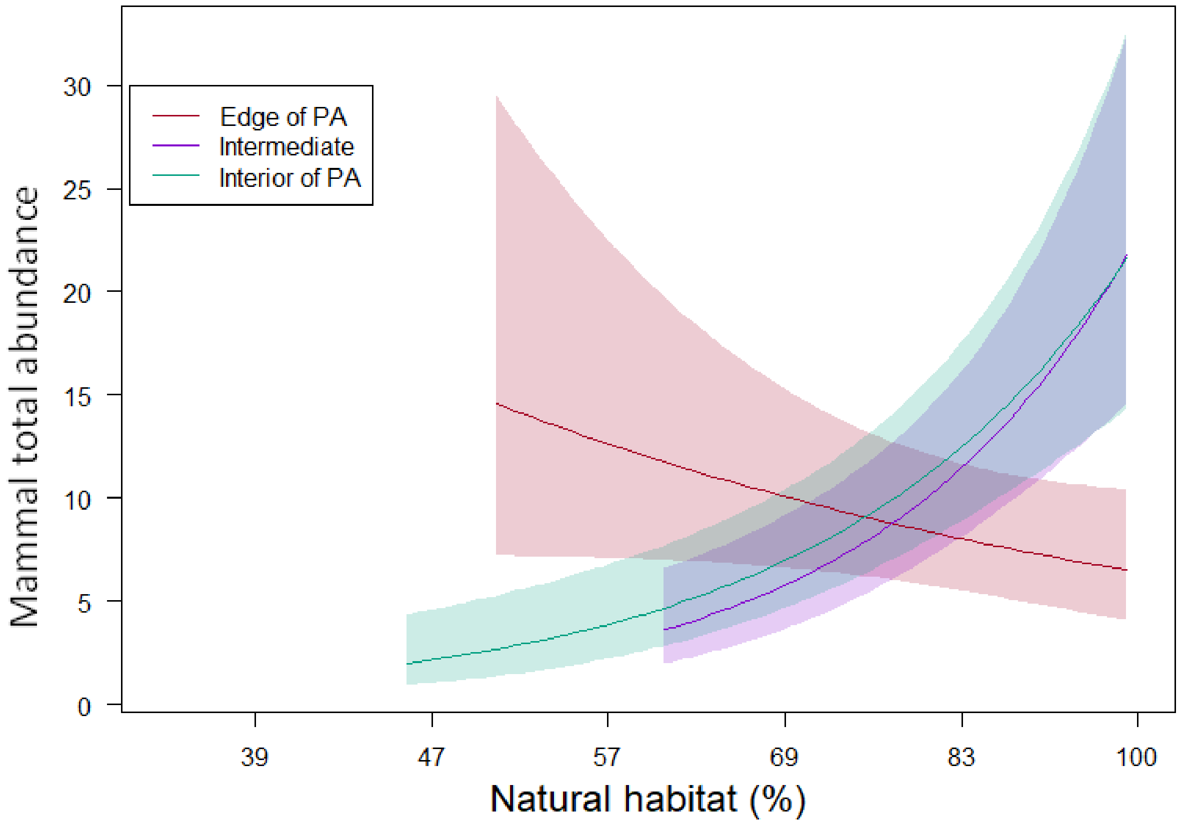


Figure 8. Model-fitted relationships between the percentage of natural habitat surrounding sampled sites, and the sampled total abundance of mammals, for sites at different distances from the border of the protected area. Shown are relationships for sites near the edge of a protected area (red line; at the 2.5th percentile among sampled sites – 34 m distance), at intermediate distances to the border (purple line; 50th percentile – 896 m), and in the interior of a protected area (green line; 97.5th percentile – 10.64 km). Sampled mammal total abundance is fitted to a $\log_e$+1 scale and natural habitat is fitted to a $\log_e$ scale. Lines represent model-estimated mean values, while shading shows ± 1 standard error.

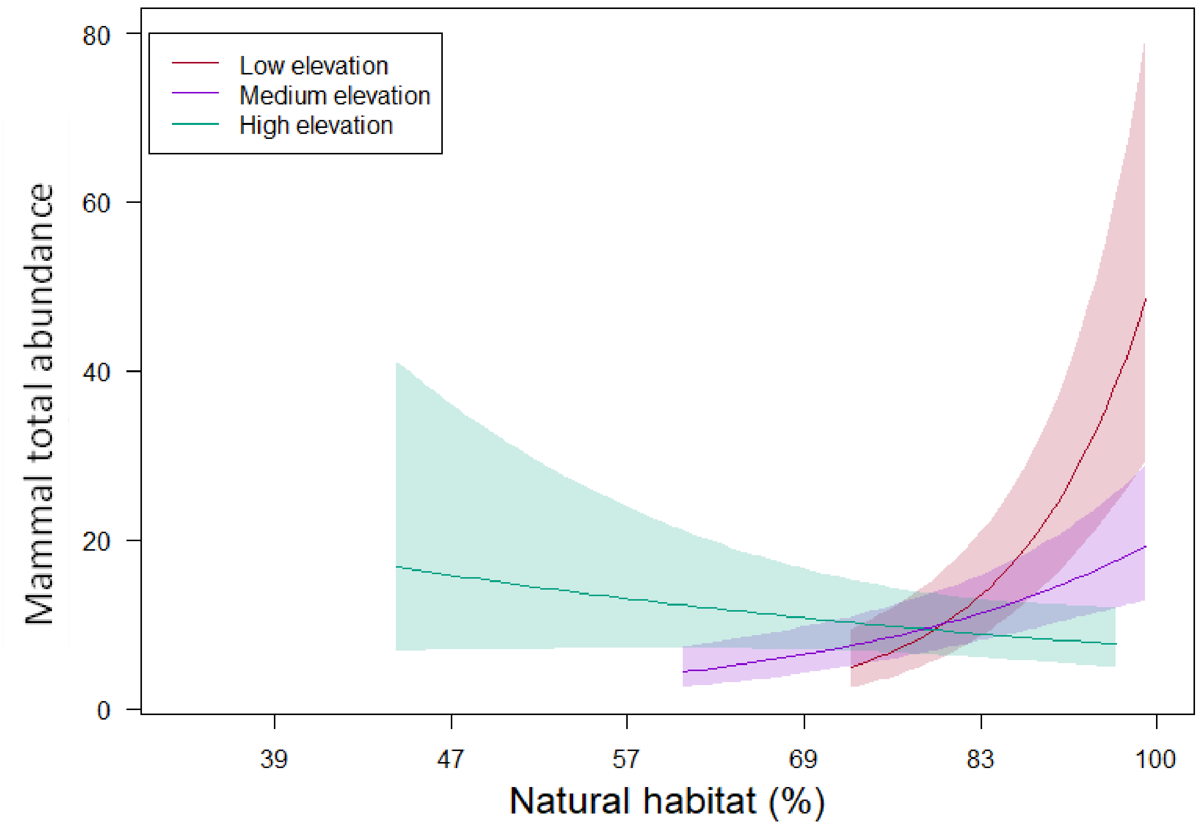


Figure 9. Model-fitted relationships between the percentage of natural habitat surrounding sampled sites, and the sampled total abundance of mammals, for sites at different elevations. Shown are the relationships for sites at low elevations (red line; at the 2.5th percentile among sampled sites – 13 m elevation), medium elevations (purple line; 50th percentile – 203 m) and high elevations (green line; 97.5th percentile – 1,633 m). Sampled mammal total abundance is fitted to a log_e+1 scale and natural habitat is fitted to a log_e scale. Lines represent model-estimated mean values, while shading shows ± 1 standard error.

Species richness decreased in areas of high percentage natural habitat at low and medium elevations, but increased slightly with natural habitat at high elevations (χ^2=8.74, df=1, p=0.003) (figure 10). None of the other variables considered in the species richness model had a significant effect on mammal species richness within protected areas (supplementary material, table 2). The fixed effects included in this model accounted for 19% of the variance in the response variable (delta marginal pseudo-R^2 = 0.193), and the proportion of the variance explained by both the fixed and random effects was 82% (delta conditional pseudo-R^2 = 0.820). The deviance of the model was 419.

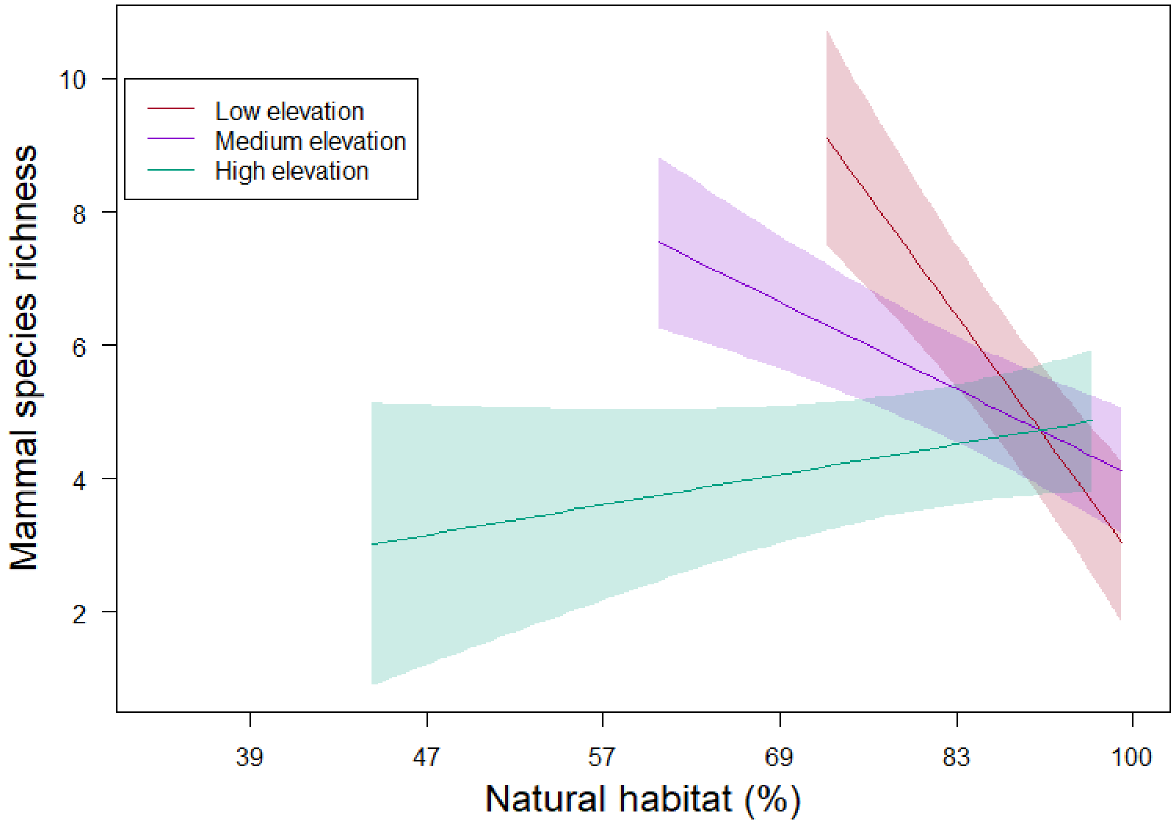


Figure 10. Model-fitted relationships between the percentage of natural habitat surrounding sampled sites, and the sampled total species richness of mammals, for sites at different elevations. Shown are the relationships for sites at low elevations (red line; 2.5th percentile among sampled sites, 13 m elevation), medium elevations (purple line; 50th percentile – 203 m) and high elevations (green line; 97.5th percentile – 1,633 m). Natural habitat is fitted on a $\log_e$ scale. Lines represent model-estimated mean values, while shading shows ± 1 standard error.

Discussion

In this chapter I explore whether protected areas have higher mammal biodiversity than no protection, as well as which characteristics of protected areas have greatest impact on mammal species richness and abundance. I show that the characteristics of protected areas have a significant and strong effect on mammal total abundance and species richness. Particularly important for conserving high levels of biodiversity is to have a protected area core (far from the edge of the protected area) that has a high percentage of natural habitat. Furthermore, my results support the use of protected areas as a way to conserve biodiversity, with mammal species richness 11% higher inside compared to outside protection. My findings can help ensure that protected areas effectively deliver internationally agreed biodiversity and sustainability targets (Dudley et al., 2022), such as those outlined in the Kunming-Montreal Global Biodiversity Framework (CBD, 2022).

The benefits of protected areas for biodiversity are well documented. Many studies point to biodiversity being higher inside protected areas than outside (Coetzee et al., 2014). For example, a global study of multiple groups of species (including mammals) found that species richness is 10.6% higher and species abundance 14.5% higher inside protected areas compared to outside (Gray et al., 2016). For mammals, there are also reported benefits of protection for species. A recent global study that examined mammal taxonomic and functional diversity using over 8,000 camera traps in 23 countries concluded that taxonomic diversity of terrestrial mammals increases with the percentage coverage of protected areas (Chen et al., 2022). In my analysis, mammal species richness was found to be 11% higher inside protected areas compared to areas without protection (figure 6). My work thus contributes to a growing body of research highlighting how terrestrial protected areas can sustain higher levels of biodiversity than comparable unprotected areas.

It is important to consider that 11% higher mammal species richness inside protected areas compared to outside protected areas could have a disproportionate conservation value if the additional species are those of most conservation concern. For example, in a camera trap study of a selection of protected areas in Brazil, of the 21 mammal species assessed, species richness was twice as high in areas with stricter protection. The difference was even more pronounced for nationally threatened species, with 2.7 times more species per site in strictly protected areas, compared to 2.4 times more species per site for non-threatened species (G. B. Ferreira et al., 2020). This suggests that even modest increases in species richness within protected areas can have significant implications for the preservation of vulnerable species, particularly when protection measures are most strict. Furthermore, species that are most vulnerable to extinction, as listed on the Alliance for Zero Extinction (AZE), are most likely to downlisted to either vulnerable, near threatened or least concern when they receive significantly more law and policy conservation actions or species management such as restoring species, than species that remained on the AZE list (Luther et al., 2021). This further emphasizes the importance of protected areas under effective management for safeguarding species most vulnerable to extinction. At a larger scale, the area of land under protection in Africa, Eurasia, and the Saharo-Arabian zone are more important for predicting threatened vertebrate species richness compared to other zoogeographic regions (Howard, Flather, & Stephens, 2020). This may suggest that conservation efforts in such regions might have disproportionate impact in conserving threatened species. Whilst I did not consider the threat status of species in my analysis comparing local samples of biodiversity inside protected areas compared to areas without protection, identifying the proportion of threatened species within the heightened species richness found inside protected areas could be important for future research, as it would help us to understand further the conservation impact of protected areas.

There is a wide range of literature that documents the importance of natural habitat for the conservation of biodiversity. Good quality natural habitat in surrounding landscapes leads to higher species abundance for a range of taxa (Anlauf-Dunn et al., 2014; Cosset et al., 2019; Nicolè et al., 2011; Outhwaite et al., 2022), as well as acting as a buffer against climate change (Suggitt et al., 2018; Xu et al., 2022). The influence of natural habitat on mammal biodiversity has been explored in several case studies. For example, dense vegetation is associated with positive trends in elephant populations in Africa (Duffy & Pettorelli, 2012), while in Canada mammal biodiversity outcomes in protected areas are higher in areas that have higher amounts of natural habitat (Stewart, Volpe, et al., 2019). Even within working landscapes (those used for agriculture, farming and forestry), there are benefits associated with natural habitat, specifically habitat that consists of plant species that are native to the area. These benefits can include supporting biodiversity from nearby protected areas, by offering ecological corridors and stepping stones through working landscapes (Garibaldi et al., 2021). There is a strong need for a well-connected network of protected areas, as this can increase species resilience to climate change, facilitate species migrations and increase gene flow between populations (Brennan et al., 2022).

I show a consistent additional benefit globally of natural habitat on mammal abundance, over the protection of habitat alone. Specifically, I show that in the interior of protected areas, an increased amount of natural habitat is associated with increased total abundance of mammal species. Conversely, I did not detect an effect of natural habitat on species abundance near the inside edges of protected areas (figure 8). This could be for a number of reasons, including anthropogenic impacts and edge effects that may spill over into protected area boundaries, offsetting any positive impact from the availability of natural habitat. Livestock incursions and illegal grazing within protected areas is a well-known edge effect (Butt, 2014) that can lead to mortality of large carnivores through human-wildlife conflict at protected area borders (Balme et al., 2010; Woodroffe & Ginsberg, 1998). Such conflict may impact mammal abundance more severely than any potential benefit provided by heightened natural habitat in the surrounding area. It is expected that the borders of protected areas are also the most visited by ecotourists as they are easiest to access and serve as entry points, although the spatial distribution of tourists within protected areas is something that requires more research (Torsney & Buckley, 2023). Human presence itself, such as through high footfall, is known to have complex interactions with biodiversity (T. Xu, Chen, Carver, & Wu, 2024). Protected area boundaries may also be more susceptible to poachers who find it easier to access these areas (Duporge, Hodgetts, Wang, & Macdonald, 2020), and this can also impact measures of biodiversity, although this can be countered by heightened ranger patrols (Moore et al., 2018). Pressures within the wider landscapes surrounding protected areas from agriculture, construction and habitat fragmentation also contribute to detrimental edge effects (Fuente et al., 2020; Hansen & DeFries, 2007). In particular agricultural incursions, such as cocoa planting encroaching on protected tropical forests (Brobbey et al., 2020) and slash and burn farming that can lead to uncontrolled wildfires spreading within protected areas (Mistry & Bizerril, 2011) can lead to: increased temperature variability, heightened desiccation and wind exposure, and leave species that depend on a certain habitat type vulnerable to predation or with insufficient resources to reproduce (Laurance, 2000). Other examples of edge effects reported in the literature include how disturbance found within the surrounding natural habitats of protected areas in Alberta has been linked to detrimental impacts on mammalian biodiversity within protected areas of that region (Stewart, Volpe, et al., 2019). Similarly, forest clearing at the edge of protected areas in the Amazon can lead to tree mortality within protected areas (Laurance, 2000). Furthermore, within the Amazonian forests, edge effects together with other forest disturbances can cause as much biodiversity loss as deforestation itself (Lapola et al., 2023). Other studies have shown how potential negative impacts of fragmentation on biodiversity can be overcome when the cumulative area of habitat is large (Fahrig, 2017; Fahrig et al., 2019). My results highlight the importance of having protected areas that are surrounded by high quality natural habitat, or that are large enough that the benefits of natural habitat can operate within the interior. There are many examples of the benefits of large protected areas on biodiversity in the literature. For example, larger protected areas have been shown to harbour greater mammal species richness within their borders (Ramesh et al., 2016), and also outside due to spill over (Brodie et al., 2023). While I didn’t find an effect of protected area size on samples of local mammal abundance in my study, the fact that mammal abundance increases further inside protected areas (figure 7), and that natural habitat has a positive effect on mammal abundance further inside protected areas (figure 8), indicates that large protected areas do benefit mammal biodiversity.

I show that for mammals at lower elevations (but not higher elevations), total abundance increases with the amount of surrounding natural habitat (figure 9). This difference may be because at low elevations, species are limited mainly by the availability of natural habitat, whereas at high elevations other climatic conditions may be more important, such as temperature range and oxygen availability (Grytnes & Mccain, 2007). My results also show that at lower elevations with increasing levels of natural habitat, surprisingly, there were lower levels of mammal species richness (figure 10). It is important to note that measures such as species richness and total abundance may overlook unique species found at high elevations that nevertheless require protection and natural habitat. As I did not consider the identity of the species involved, I cannot know if the species present in these areas are habitat specialists or generalists. It may be that there are mammal species more tolerant of human disturbance and low levels of natural habitat, such as rodents, in these areas (Rodewald & Gehrt, 2014; Spear et al., 2013). Furthermore, species with distinct traits may respond differently to the characteristics of protected areas. For example, it may be expected that larger protected areas are more beneficial for species with larger home ranges or body sizes, as these species require larger areas to obtain resources and reproduce (Biedermann, 2003; Pe'er et al., 2014). In a study on just under 500 protected areas globally, it was found that larger-bodied species inside protected areas had more positive population trends than smaller bodied species (Barnes et al., 2016), showing how species body size can influence the benefits derived from protected area size. However, in a study on 21 mammal species in Finland, although 90% of species has different habitat usage (either through range contraction, expansion, or range shifts through adapting to different conditions) depending on whether the species population was located inside or outside a protected area, these changes in habitat use could not be significantly attributed to the species traits measured in the study, which included habitat specialisation, body size, diet, and species threat status on the IUCN red list (Santangeli et al., 2022). This demonstrates that other studies have found little effect of traits on species interaction with protected areas. To further explore the influence that species traits may have on species responses to protected area characteristics, further study is needed that considers the identities and traits of species. Particularly important is the influence of protected areas on species that are at a greater threat of extinction, as these species often exist in areas that face more extreme anthropogenic threats (Gonçalves-Souza, Verburg, & Dobrovolski, 2020), and often have intrinsic characteristics that make them more at risk (Chichorro, Juslén, & Cardoso, 2019), and can therefore be more dependent on protected areas to avoid such threats for their continued existence.

At most elevations and distances within a protected area boundary, there were opposing effects of natural habitat on mammal species richness (largely negative effects at low and medium elevations), and total mammal abundance (largely positive effects at low and medium elevations). Further insights into these opposing patterns could be gained from considering the mammal species composition of sampled sites. For example, in grasslands with large herds of herbivores, increases in natural habitat in the form of grazing land might be associated with increases in species abundance, as the carrying capacity of the landscape increases (Hobbs, 2024). Carnivores can regulate the abundance of herbivores through top down control, however in the absence of carnivores, such as through management strategies that reduce or remove them from the ecosystem – increased abundance of a few species can be the outcome (Martinez, Dugelby, Foreman, Miller, & Noss, 2001). High abundance but low richness of herbivorous species, in areas of high natural habitat could in this way be indicative of degraded mammal fauna with few predators, and thus indicate where protected area management need be revised (Found, 2016). Future study that considers the identities of species, would help further understand the impacts of protected area management on biodiversity.

My study is limited by the relatively small sample size of 64 protected areas for which there were mammal biodiversity data. It is also important to note that the placement of protected areas is biased. Those established before 2004 were placed in areas of low agricultural suitability and high elevation (Joppa & Pfaff, 2009b), which tend not to be areas with high concentrations of threatened vertebrates (Venter et al., 2018). I attempted to control for potential confounding effects caused by non-random placement of protected areas by including climate and elevation as control variables in my analyses. Climate not only determines agricultural suitability (X. Zhang & Cai, 2011), and thus the placement of some protected areas, but also influences biodiversity itself (Coelho et al., 2023). Another limitation of the analysis of mammal species richness and abundance within protected areas is that it doesn't consider the baseline mammal biodiversity present in each region, which is known to vary depending on ecoregion or latitude, and which may also covary with some of the variables I considered in the analysis; for example there is heightened species richness of mammals in the tropics compared to the poles (Ceballos & Ehrlich, 2006; Willig, Kaufman, & Stevens, 2003). Although I include the identity of studies from which data originated and also the identity of the protected areas as random intercepts in the analysis to account for such regional differences, directly controlling for baseline biodiversity should be explored in future analyses, and may reduce the overdispersion observed in the results. Some interesting insights that could be gained from this approach include whether certain characteristics of protected areas are more effective in regions with lower/higher baseline species richness, and would be a valuable addition to the literature for future study. Lastly, although the age of protected areas has been shown to influence biodiversity outcomes in marine (Edgar et al., 2014b) and terrestrial protected areas (Gray et al., 2016), I decided not to include this in my analysis, as my focus was on factors that could be manipulated in designing future protected areas or adjusting the management of existing protected areas. Despite this, I recognise that certain characteristics of protected areas may take longer before their benefits on biodiversity can be recorded, such as the time it takes for effective protected area management to establish. This therefore may have caused the benefits of some protected area characteristics to be underestimated.

Finally, it is important to highlight that utilising a backward stepwise model selection approach means that some of the variables selected for analysis were not retained in the final model. This has the benefit of reducing the final model complexity, however, it can also mean that some of the contextual information for the response variable is lost. For example, in the analyses that explore the impact of protection status on biodiversity outcomes, the fixed effects: total annual precipitation, mean annual temperature and elevation are all excluded in the final recommended model. As previously mentioned, these variables are often key determinants of species abundance and richness, and their exclusion could oversimplify the model. Furthermore, in the species abundance model, the predominant land use of the sampled site was excluded as it did not independently predict mammal abundance after accounting for protection status, however this does not rule out its importance in other contexts. When all variables were included in a full model, these excluded variables were not statistically significant, and so we can be confident in their exclusion. The full model used to explain species richness and species abundance explains 84% of the variation in both response variables, however on their own the fixed effects explained relatively little.

In the analyses that look at the impact of the characteristics of protected areas on biodiversity outcomes, as well as the climatic variables of total annual precipitation and mean annual temperature being excluded, the size of the protected area, border complexity, the predominant land use of the sampled site, as well as the IUCN management category and governance type of the protected area were not included as fixed effect in either the species richness or species abundance models. The distance between the sampled site and the edge of the protected area was also not included in the final model for species richness. The skewed nature of the data in these variables, together with a small sample size of protected areas could be influencing their exclusion, however if this study were to be replicated on a larger subset of protected areas, I would recommend their continued consideration for the final model design. The full model used to explain species richness and species abundance explains 82% and 91% of the variation in the response variables respectively.

It is particularly important to consider the wording from target 3 of the Convention of Biological Diversity (CBD, 2022), which emphasises that protected areas should be integrated into the wider landscape. My findings underscore this principle by demonstrating the enhanced conservation value of protected areas that are surrounded by a high proportion of natural habitat. Given the importance of natural habitat, there are important implications to prioritise the land use management surrounding protected areas. This could involve implementing protected area buffer zones and reducing natural habitat fragmentation in areas surrounding protected areas. Furthermore, with a wider sample of protected areas, it may be possible to further explore the relationship of the IUCN management categories and governance on biodiversity outcomes. These two aspects would be a very useful contribution to knowledge as governments across the world are deciding which areas should count towards being part of the 30% that is considered protected by 2030, and how those sites should be managed (Bailey et al., 2022).

My study contributes to understanding which characteristics of terrestrial protected areas make them successful in the conservation of mammal biodiversity. I show that protected area design has important effects on total mammal abundance and richness, whereas protection itself has an important effect on mammal species richness - with sampled locations within protected areas on average 11% higher in mammal species richness than equivalent unprotected locations. Monitoring effectiveness and understanding which characteristics of protected areas have the most impact on biodiversity outcomes is important, as it allows protected-area managers to adapt their practices and allocate resources to areas that can have the greatest impact on biodiversity. My results show that it is important to have protected areas that are sufficiently large, to realise the potential benefits of natural habitat on local measures of mammal biodiversity within a protected area's interior. Studies like this are vital for guiding the actions that need to be taken in order to meet local, national, and global conservation objectives, especially as countries around the world strive to meet internationally agreed environmental targets, such as protecting 30% of land and seascapes by 2030.

Supplementary Material

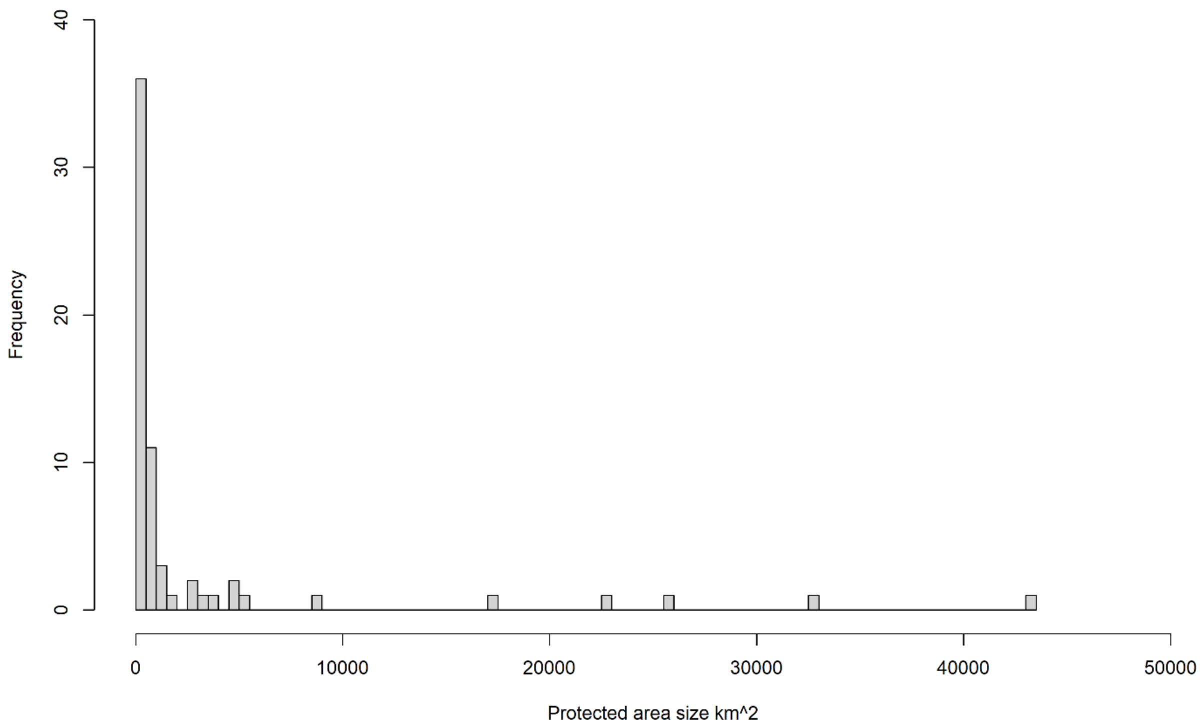


Figure 1. Histogram of the sizes of the 64 protected areas included in this study. These protected areas also contained at least one sample of mammal biodiversity recorded in the PREDICTS database.

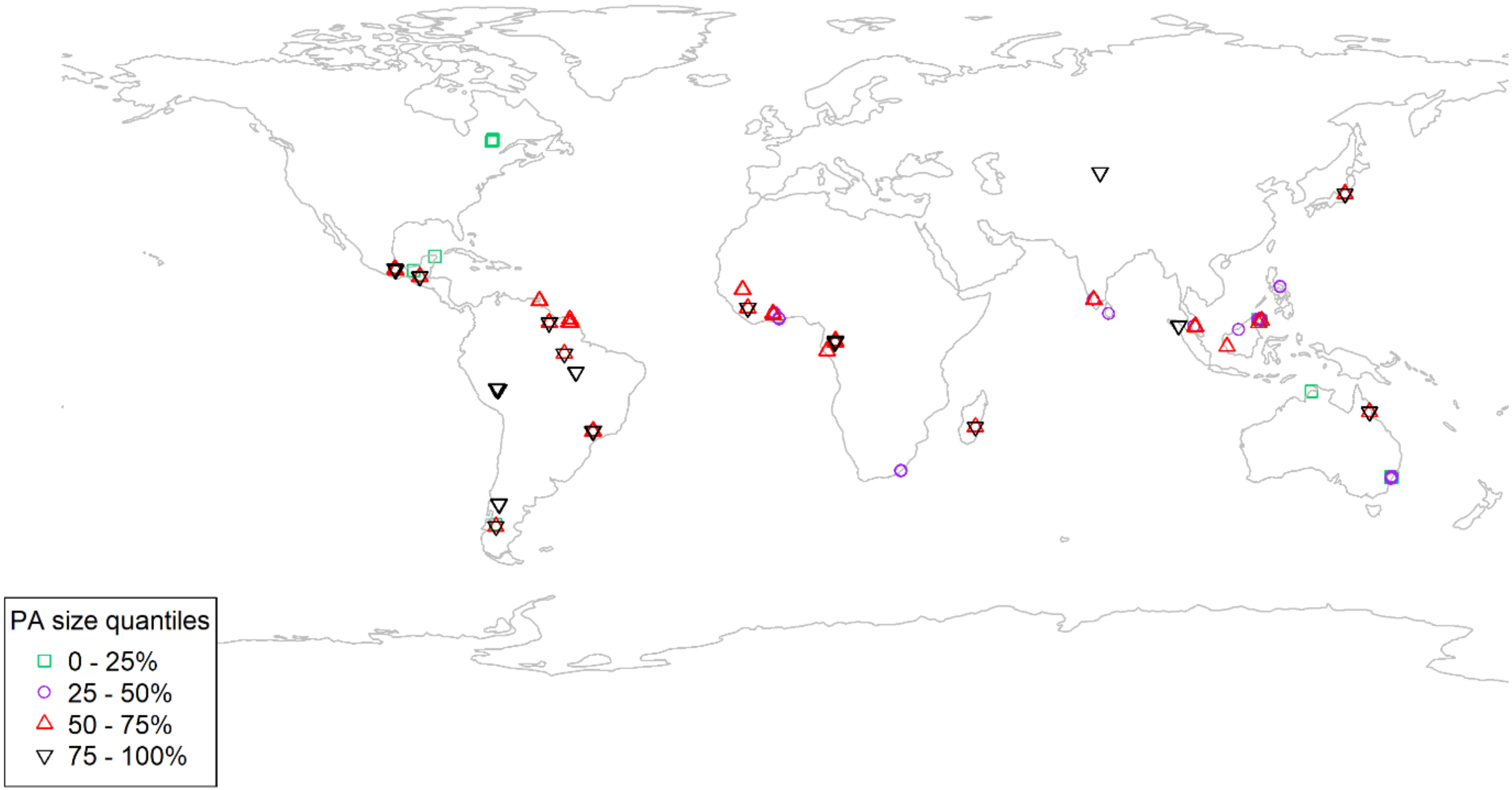


Figure 2. Location of sites of mammal biodiversity in the PREDICTS database that also fall within a protected area. Point colour and shape represents the size of the protected area in which biodiversity was sampled: quantile 0 – 25% (green square) includes protected area sizes up to 27.9km^2, quantile 25 – 50% (purple circle) includes protected area sizes up to 288.4km^2, quantile 50 – 75% (red upward triangle) includes protected area sizes up to 11,116.5km^2, quantile 75 – 100% (green downward triangle) includes protected area sizes up to the largest included in this study at 43,115.9km^2. Plotted in the WGS84 geographic coordinate system.

Table 1: Results of mixed effects models investigating effect of protection status on mammal biodiversity outcomes. To model mammal species richness, we ran a Poisson mixed-effects model using the “glmer” function from the “lme4” package Version 1.1-26. To model the total abundance of mammal species, we fitted a linear mixed-effects model using the lmer function of the same R package. I $\log_e$-transformed the abundance estimates, adding a value of 1 to account for zeros in the data. In bold are the significant values that have also been retained in the best-fitting model.

	Mammal species richness				**Mammal species abundance**			
Terms	χ^2	DF	P	dAIC	χ^2	DF	P	dAIC
Protection status	6.33	1	**0.012**	4.328	1.12	1	0.290	2.072
Predominant land use	43.34	9	**<0.001**	25.340	52.66	9	**<0.001**	-16.819
Elevation	2.26	1	0.133	0.256	3.63	1	0.057	-0.166
Temperature	1.55	1	0.213	-0.446	0.21	1	0.647	-1.018
Precipitation	1.67	1	0.196	-0.328	7.01	1	**0.008**	-1.707

The random effects in the species richness model that investigates the effect of protection status on mammal biodiversity outcomes included the study (SS) (SD = 0.946), and spatial block (SSB) (SD = 0.323) and the spatial sample (SSBS) (SD = 0.115). The random effects in the species abundance model included the study (SS) (SD =405.2), and spatial block (SSB) (SD = 0.00).

Table 3: Results of mixed effects models that examine the effects of characteristics of protected areas (PA) on mammal biodiversity outcomes. Features of protected areas considered were the size of the protected area, the management category, the governance type, the distance to the nearest other protected area, and the complexity of the protected area's border. I also used explanatory variables that are specific to the sampled site: predominant land use, the percentage of surrounding natural habitat, distance to the nearest protected-area border, elevation, mean annual temperature and total annual precipitation. I considered interactions between the effects of percent natural habitat and: IUCN category, predominant land use, the distance to the edge of the protected area and elevation (see main text for justification for considering these interactions specifically). Species richness was modelled using a Poisson generalized linear mixed-effects model, and $\log_e$-transformed total abundance (+ 1) with a linear mixed-effects model. In bold are the significant values that have also been retained by the best fitting model.

	Mammal species richness				**Mammal species abundance**			
Terms	χ^2	DF	P	dAIC	χ^2	DF	P	dAIC
PA size	0.97	1	0.326	-1.036	0.16	1	0.686	-1.837
Distance inside PA	3.84	1	0.050	1.839	4.54	1	**0.033**	2.541
PA connectivity	0.36	1	0.547	-1.638	0.07	1	0.783	-1.924
PA border complexity	0.20	1	0.653	-1.798	2.26	1	0.132	0.264
IUCN management category	0.11	2	0.946	-3.888	0.96	2	0.620	-3.043
IUCN governance type	4.48	4	0.345	-3.519	7.16	4	0.128	-0.842
Natural habitat	1.01	1	0.314	-0.985	1.10	1	0.294	-0.898
Predominant land use	0.06	1	0.806	-1.939	1.85	1	0.174	-0.151
Elevation	0.20	1	0.651	-1.795	3.85	1	**0.050**	1.846
Temperature	3.21	1	0.073	1.208	0.00	1	0.958	-1.997
Precipitation	0.23	1	0.631	-1.769	0.82	1	0.364	-1.177
Interaction: IUCN management and natural habitat	2.46	2	0.291	-1.536	5.34	2	0.069	1.338
Interaction: predominant land use and natural habitat	1.29	1	0.256	-0.712	0.07	1	0.787	-1.927
Interaction: distance inside PA and natural habitat	0.63	1	0.427	-1.368	11.65	1	**0.001**	9.647
Interaction: elevation and natural habitat	8.74	1	**0.003**	6.742	5.71	1	**0.017**	3.710

The random effects in the species richness model that investigates the effects of the characteristics of protected areas on mammal biodiversity outcomes included the protected area ID (SD = 0.000), study (SS) (SD = 4.913), and spatial block (SSB) (SD = 0.000). The random effects in the species abundance model included the protected area ID (SD = 0.176), study (SS) (SD = 2.066), and spatial block (SSB) (SD = 0.162).

Chapter 3

Consideration of Minimum Area Requirements enables Identification of Areas That Do Not Contain Enough Contiguous Habitat for Mammal Conservation under Future Climate Change

Abstract

Climate change and land-use change are causing species range shifts and biodiversity changes, with substantial losses for some species and regions. Areas currently set aside for species conservation may not be situated in suitable locations or of sufficient size to support biodiversity given future climate changes. To effectively conserve species both at present and in the future, we need to ensure that the space available for them to exist is climatically suitable, contains appropriate habitat, and is also large enough to support species' populations. In this study, I impute the minimum area requirements of all mammal species globally. I use these estimates to identify areas of suitable climate and habitat that are expected to be large enough to support the continued survival of mammal species, under 4 different climate scenarios for the year 2070. I test whether projected changes in species' distributions are larger when accounting for minimum area requirements than when not accounting for them. I predict that when accounting for minimum area requirements, species at a greater risk of extinction will have a larger discrepancy between their total amount of projected suitable habitat and the total size of all habitat patches that are large enough to support future populations of a species, than less threatened species. This area discrepancy is referred to as the area shortfall. Furthermore, I examine which areas key to meeting a large proportion of mammal species minimum area requirements under future climate conditions, are not currently under any form of protection. In this study, I find that by not taking into account minimum area requirements for species, we could be overestimating future suitable area projections for species in some locations, and that critically endangered species undergo a greater area shortfall when we consider their minimum area requirements. Large parts of Western Europe, Central and South America, the African savanna and Eastern Asia do not contain enough contiguous areas of suitable habitat and climate to meet the needs of a large proportion of

mammal species projected otherwise to be able to exist in those areas. I also find that large parts of ecologically important areas of the globe, such as in the Brazilian Amazon, the African savanna and Southeast Asia containing habitat that is crucial for a large number of species to meet their minimum area requirements, are not currently under any form of protection. This study highlights the importance of incorporating minimum area requirements in future species distribution projections, so that we can ensure that key areas important for mammal species' persistence are preserved, as well as highlighting areas that are consistently failing to provide enough contiguous habitat for species, so that we may heighten conservation efforts for mammals in these places.

Introduction

Climate change is already exerting detrimental impacts on biodiversity (Habibullah et al., 2022), and its effects are expected to accelerate in the future. Climate change can cause species range shifts (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012) which affect interspecies interactions (Brambilla et al., 2020) and can change future biome distributions (Boonman et al., 2022). Species may adapt to climate impacts by altering their spatial habitat use, shifting their temporal patterns via changing the time of day or season they are most active (S. J. Cunningham, Gardner, & Martin, 2021), shifting breeding season (Cole, Regan, & Sheldon, 2021), or through evolution, for example by adapting greater temperature tolerance over time (Bellard et al., 2012). However, the impacts of climate change are not felt equally across geographic regions, through a combination of varying magnitude of conditions such as extreme temperatures and droughts, and the velocity of such changes (Garcia et al., 2014). Likewise, some species are more sensitive to climate change than others, for example Tropical and Mediterranean biodiversity are predicted to show more negative responses to climate change than in other regions (Newbold, Oppenheimer, Etard, & Williams, 2020).

Governments across the globe have committed to limiting global warming increase to 2°C above pre-industrial levels (Delbeke, Runge-Metzger, Slingenberg, & Werksman, 2019), recognising the irreversible impact to our planet if this were to be surpassed. Under a strong mitigation scenario of 2°C warming, 2% of ecological assemblages will have at least 20% of their corresponding species suddenly exposed to extreme temperatures within one decade. However, under a high-emissions scenario of 8.5°C, an average of 71% of species within any ecological assemblage could be suddenly exposed extreme temperatures within one decade (Trisos, Merow, & Pigot, 2020). This can cause extinctions of species that are abruptly placed outside of their thermal limits (Román-Palacios & Wiens, 2020), interspecies interactions integral to their existence to change (Brambilla et al., 2020), or changes in species range sizes (Pacifici et al., 2020). Changes in projected species ranges are predicted to be observed between global warming scenarios that only differ by 0.5ºC (Warren, Price, Graham, Forstenhaeusler, & VanDerWal, 2018), highlighting the importance to limit warming scenarios through emission reduction as much as possible; as well as the importance of considering multiple climate circumstances when modelling future scenarios. Understanding the impact of climate change on species, especially on their geographical distributions is key to creating effective policies that are robust in the face of expected future climate changes.

In conjunction with limiting global warming, it is also important to halt the detrimental impacts of land-use change on biodiversity. Land-use change is being driven predominantly by anthropogenic demands made on the planet's resources, such as agricultural expansion to meet the demands of a growing population, which is propelling deforestation (Pendrill et al., 2022). The sequence of land use change and its effects on biodiversity is being seen again and again. One example land use change trajectory is where first natural habitat is converted to agriculture, removing biodiversity from highly productive lands whilst maintaining biodiversity in marginal lands, and later the change to focus on technical innovation sees population expansion into previously marginal areas, which further reduces biodiversity (Huston, 2005). Globally, land-use change is associated with average reductions of 11% of total assemblage species abundance and 14% of species richness between the year 1500 and the present day, with a further 3% decrease in species richness projected by the year 2100 under a business as usual land use scenario (Newbold et al., 2015). Furthermore, community species assemblages are being restructured because of differential effects of land use on different functional groups (Newbold, Bentley, et al., 2020). Alterations to land use may result in species facing extinctions years later, as loss of biodiversity accumulates over time. Indeed habitat change to any land use, but especially to agriculture, can result in an extinction debt that is paid between 10-15 years later (Semper-Pascual et al., 2018), so the damage to ecosystems may not be evident until it is too late to reverse, compromising ecosystem resilience.

It is important for studies to address land-use and climate change together if we are to have a more complete vision of the future. These two pressures are amongst the most consequential threats currently faced by biodiversity (Sharma, Sharma, Sharma, & Sharma, 2022; Titeux et al., 2017). A combination of both land-use and climate change is predicted to cause a further 5-16% habitat decline for mammals, on average across the globe, by the year 2050 (Baisero et al., 2020), although the pressures of both will be felt unevenly across regions. Land-use change is predicted to have the greatest influence on biodiversity loss in the tropics and temperate zones, as opposed to other regions, whereas climate change will initially most influence biodiversity loss at the poles (Dobson, Rowe, Berger, Wholey, & Caro, 2021). Furthermore, the absolute magnitude of climate change is expected to be greater at high latitudes, but research also points towards greater sensitivity of biodiversity to climate change in tropical systems. In future scenarios it is predicted that the effects of climate change on species loss will likely exceed the effects of land-use change by the year 2070 (Newbold, 2018), emphasising the importance of including both in studies on global biodiversity impacts.

Areas that are expected to have suitable climate and habitat are key for biodiversity conservation. However, these areas may not sustain species into the future if they don't meet the minimum area requirements for population persistence. Minimum area requirements represent the smallest area that a species needs to have access to for survival and will be different for each species, although in the past generalisations have been used for whole taxa (Flather, Hayward, Beissinger, & Stephens, 2011; Traill, Bradshaw, & Brook, 2007). In China it has been assessed that the minimum area requirements of mammals are not fully represented within protected areas, especially for large carnivores and threatened species (Wang, Zhang, Qiu, Yang, & Dai, 2023). Threatened species may be less able to meet their minimum area requirements as they often exist in areas that face more extreme anthropogenic threats (Gonçalves-Souza et al., 2020), meaning that suitable patches can be more fragmented and isolated than for less threatened species (Kuipers et al., 2021). Furthermore, the protected area network at a global scale has been shown as too small to support more than half of the worlds mammals' population persistence into the future (D. R. Williams, Rondinini, & Tilman, 2022).

Using imputed minimum area requirements for each mammal species, published projections of suitable climate for mammals (Newbold, 2018), and suitable habitat for species as defined by the IUCN Red List, I identify areas of continuously connected suitable habitat and climatic conditions under 4 different climate scenarios for 2070. With this information I assess the effect of accounting for the estimated minimum area requirements of species on habitat and climate change suitability projections for mammals globally. I test the hypothesis that incorporating minimum area requirements in the calculations of total suitable area for species in the future will lead to a greater projected decrease in suitable area between now and future scenarios, than not incorporating them. I also predict that when incorporating minimum area requirements, species at a greater risk of extinction will have a larger discrepancy between their total amount of projected suitable habitat and the total size of all habitat patches that are large enough to support future populations of species (area shortfall), than less threatened species. Lastly, I explore the extent to which protected areas preserve land that is expected to have suitable climate and habitat for species, and to be of sufficient size to meet species' minimum area requirements.

Methods

I identify areas of continuously connected suitable climate and habitat under 4 different Representative Concentration Pathways (RCP) scenarios for 2070 using: projections of suitable climatic area for species (Newbold 2018), the habitat requirements of species (as listed on the IUCN Red List, 2022), a global map of habitat types corresponding with the types listed for species on the IUCN Red List (Jung et al., 2020), and an imputed list of minimum area requirements for all mammals based on traits in the PanTHERIA dataset (Jones et al., 2009). I also undertake a comparative analysis with published empirical minimum area requirements for a subset of mammal species (Verboom et al., 2014) (supplementary material).

Climatic suitability

Based on current global commitments and actions to mitigate climate change, it is likely that we will exceed 1.5 degrees average warming by the year 2100, and even 2 degrees is currently likely to be exceeded (IPCC, 2023). Under a future scenario of RCP 2.6, global average temperatures are projected to reach about 2 degrees of warming by the year 2100, whereas under RCP 8.5, temperature would exceed 4 degrees of average global warming by the year 2100 (IPCC, 2023). Therefore, although I use projections based on low (RCP 2.6), intermediate (RCP 4.5), high (RCP 6.0) and very high (RCP 8.5) emissions scenarios for all analyses, I focus the results on the intermediate emissions scenario (RCP 4.5), which is the most likely outcome under current commitments (UNFCCC, 2022).

Predictions of where mammals will be in the year 2070, under the climate scenarios RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5, were obtained from a published study that utilises species distribution models to link expert-drawn species distribution maps of all vertebrates to 4 climatic variables thought to be important in determining vertebrate distributions (Newbold, 2018): minimum temperature of the coldest month, total annual precipitation, growing degree days and water balance. Whilst these climatic variables were expected to be generally important in determining the distribution of species, different species may respond to different climatic variables.

Newbold (2018) fitted distribution models using 5 different distribution modelling algorithms: Maxent, Generalised Linear Models (GLM), Random Forests, BIOCLIM and DOMAIN, and then projected mammal distributions into the year 2070. It is important to use different modelling algorithms when making projections of biodiversity into the future, to capture uncertainty caused by different methods for representing relationships between climatic variables and distributions (Thuiller, Guéguen, Renaud, Karger, & Zimmermann, 2019). For the purposes of my study, I use the outputs derived from the random forest method only, as they gave the most central projections among the algorithms used (Newbold, 2018). This is sufficient for the aims of my study, in which I needed only to compare projections between the present day and the future, with and without incorporating minimum area requirements.

Species distributions projected to the year 2070 considered dispersal ability of species from their current day distributions to the future. An intermediate dispersal estimate of 3 km per year was utilised for all mammal species (Newbold, 2018). This is an important caveat as, in reality, species vary widely in their dispersal ability. Dispersal is associated with intrinsic characteristics such as range size (Alzate & Onstein, 2022), home range area, body size (Whitmee & Orme, 2013), and diet type (Sutherland, Harestad, Price, & Lertzman, 2000), and also limited by extrinsic factors such as landscape habitat configuration (Årevall, Early, Estrada, Wennergren, & Eklöf, 2018) and geographic obstacles such as water bodies. However, the inability to consider species-specific dispersal ability is shared by most studies that project potential climate impacts on species (Newbold, 2018; Warren et al., 2013).

Habitat suitability

The IUCN classifies terrestrial habitats into 47 categories within the groupings of forests, savanna, shrubland, grassland, wetlands, rocky areas, caves, desert and artificial habitats across the globe (IUCN, 2024). I downloaded a land-use map containing the IUCN terrestrial habitat type/land uses at a spatial resolution of 100 m (Jung et al., 2020). I also obtained a list of all the habitats in which each mammal species can survive (IUCN, 2023). The suitability of habitat for mammals is classified either as: suitable – the species occurs in the habitat regularly or frequently; marginal – the species occurs in the habitat irregularly or infrequently, or only a small proportion of individuals are found in the habitat; or unknown – the habitat is of unknown importance to the species (IUCN, 2024). If a habitat is not listed, then it is assumed that it is most likely not used by that species. There is a further classification within suitable habitat, which considers if a habitat is of major importance to the species, such as being required by the species for breeding or as a critical food source (IUCN, 2024). In this study, I include all habitats listed as being suitable or marginally suitable for species, not taking into account whether a habitat is of major importance or not. This is appropriate for the scope of this study, as I aim to identify areas where species are likely to experience habitat constraints due to insufficient continuously connected suitable habitat, rather than assessing the relative importance of specific patches within those areas.

For each mammal species I overlay the individual maps of where species are predicted to have suitable climate in the present day or in 2070 with the map of current habitat types. I extract these areas, and group contiguous patches of suitable habitat and climate together using the clump function (Hijmans & van Etton, 2023a) from the raster package (version 3.6) in R (version 3.5). More detail on this can be found in the "Spatial Analysis" section below.

Minimum area requirements

The minimum area required by a species for its population to persist into the future can be determined using the following equation:

minimum area requirement = minimum viable population / species density

Whilst there are density estimates for many mammal species, accurate estimates of minimum viable population are often lacking (Verboom et al., 2014). The minimum viable of a species refers to the smallest population size that can persist into the future without facing extinction. Research on minimum viable population for mammals is extensive, but there is no consistently applied method for determining the minimum viable population of species (Flather et al., 2011; Traill et al., 2007). The most comprehensive estimates of minimum viable population were collated by Verboom et al. (2014). This dataset also used estimates of population density in turn to estimate minimum area requirements for the same mammal species, totalling 80 species distributed in different parts of the world.

In light of the limited information on empirical minimum area requirements for species, I imputed minimum area requirements for all mammal species using a trait-based approach. It is important to be aware that because there are only empirical minimum area requirements for a small subset of species, there will be considerable uncertainty in imputed estimates. However, minimum area requirements are strongly correlated with species traits. For example, there is a positive correlation between mammal body mass and the minimum area requirement for mammals (Verboom et al., 2014). I imputed minimum area requirements based on a combination of species traits expected to be associated with minimum area requirements: body mass, diet breadth, habitat breadth, home range size of a group and of an individual, maximum longevity, population density, basal metabolic rate, dispersal age at which young permanently leave their parent, population group size in which an individual spends the majority of their time and the social group size of their social cohesive unit (table 1). PanTHERIA is a species-level database describing the traits of extant mammals globally (Jones et al., 2009), which I used as the source of trait estimates for imputing minimum area requirements.

Table 1. Traits included in the imputation of species' minimum area requirements, and their expected influence on minimum area requirements. Traits from the PanTHERIA database.

Mammal species trait	Predicted influence on minimum area requirements
Body mass	Mammal species with higher body mass are expected to have larger minimum area requirements (Biedermann, 2003; Pe'er et al., 2014).
Home range size (group and individual)	Species with larger home range sizes are expected to have larger minimum area requirement. Home range area is already part of the equation used to calculate minimum area requirements in birds (Verboom et al., 2014).
Habitat breadth	A positive relationship exists between species' habitat breadth and range size (Slatyer, Hirst, & Sexton, 2013), which may be associated with larger minimum area requirements.
Diet breadth	There is expected to be a complex relationship between diet breadth and minimum area requirements (Pe'er et al., 2014; Price & Hopkins, 2015). However, in general, it is expected that species with a broad diet will be able to exploit a wide range of food resources, allowing them to use a wider range of habitats with diverse resource availability, and potentially reducing their minimum area requirements.
Basal metabolic rate	Species with a higher basal metabolic rate are expected to have larger minimum area requirements, as they require more resources, for which they need more space (D. A. Kelt & Van Vuren, 2001).
Population density / population group size / social group size	Species that live in denser populations or in larger groups are expected to have smaller minimum area requirements. Population density is already an accepted part of the equation to calculate minimum area requirements for species in mammals (Verboom et al., 2014).
Maximum longevity	Species that live for longer will be able to undergo more movement in their lifetime (Sutherland et al., 2000), and will require more resources to sustain them, and so are expected to have larger minimum area requirements (D. A. Kelt & Van Vuren, 2001).
Dispersal age	Species with a later dispersal age (when young permanently leave their parent) are expected to have lower minimum area requirements as they will have less time to undergo movement in their lifetime, although the relationship is expected to be complex (Alzate & Onstein, 2022).

I also included 10 phylogenetic eigenvectors in this imputation (which provide insight into how species are evolutionarily connected to each other), enough to minimise imputation error as determined by other published works (Penone et al., 2014; Wang et al., 2023). The phylogenetic eigenvectors were extracted from the class-specific phylogenies listed in the PHYLACINE database (Faurby et al., 2020), using the PVR package in R (Santos, Diniz-filho, Rangel, & Bini, 2012). I create the first modelled estimates of minimum area requirements for all mammal species at a global scale.

I undertook taxonomic matching between the Verboom et al. (2014) and PanTHERIA datasets (table 2). Of the 80 mammal species represented in Verboom et al. (2014), 13 needed manual taxonomic matching to the binomial list in PanTHERIA (Table 2). I used the Catalogue of Life (GBC, 2022) as the taxonomic authority to determine synonyms.

Table 2: taxonomic matching between the PanTHERIA and Verboom et al. (2014) datasets, using the Catalogue of Life as the taxonomic authority to determine synonyms (GBC, 2022).

Species Binomial in PanTHERIA	**Species Binomial in Verboom et al. (2014)**
Saimiri oerstedii	*Saimiri oerstedii citrinellus*
Zyzomys palatilis	*Zyzomys palatalis*
Antilocapra americana	*Antilocapra americana sonoriensis*
Equus caballus	*Equus caballus przewalskii*
Canis lupus	*Canis rufus*
Chlorocebus aethiops	*Cercopithecus aethiops*
Rucervus eldii	*Cervus eldii*
Ovis dalli	*Ovis dalli dalli*
Elephas maximus	*Elephas maximas*
Ursus thibetanus	*Ursus thibetanus japonicus*
Cercocebus galeritus	*Cercocebus galeritus galeritus*
Puma concolor	*Felis concolor*
Ursus arctos	*Ursus arctos horribilis*

The empirical estimates of minimum area requirements (Verboom et al., 2014) were compared to imputed values using a leave-one-out evaluation. There was a moderate positive correlation between the empirical and imputed estimates of ($\log_e$) minimum area requirements (Pearson $r = 0.59$, $p < 0.001$). Due to the relatively high uncertainty in individual estimates of minimum area requirements, I test the robustness of my results by repeating all spatial analyses detailed below with the empirical estimates from Verboom *et al*. (2014) (supplementary material).

Spatial analysis

The world habitat map (Jung et al., 2020) and each individual species projected climatic suitability map (Newbold, 2018) were projected into the Behrmann Cylindrical Equal Area projection in Geographic Coordinate System, World Geodetic System 1984 (GCS WGS 1984), using R version 4.0.2. The species climatic suitability maps (Newbold, 2018) were disaggregated using the disaggregate function in the raster package (Hijmans & van Etton, 2023b) from 10-km resolution to match the habitat map. Cells were identified as suitable if the habitat in the world habitat map matched either a suitable or marginally suitable habitat type for the species in question, as well as being inside a cell that was considered climatically suitable for that species in the year 2070. The final suitable area for a species is therefore made up of the cells that have projected suitable climate in the future and currently have habitat that is suitable. The resulting maps are at a 833 m x 1,111 m resolution.

To assess which areas had suitable climate and habitat, and also met the minimum area requirements of the species in question, these extracted cells were grouped together using the clump function from the raster package (Hijmans & van Etton, 2023a), setting the direction to 8, meaning that cells would be considered a group if they joined one another either diagonally, horizontally or vertically. The sum of each clump was then added, and clumps that do not meet the minimum area requirements for a given species were filtered out. The area shortfall between the two measures is calculated as a percentage for each species. To demonstrate how climate, habitat and minimum area requirements are combined to sum a total suitable area for each species, I provide figure 1.

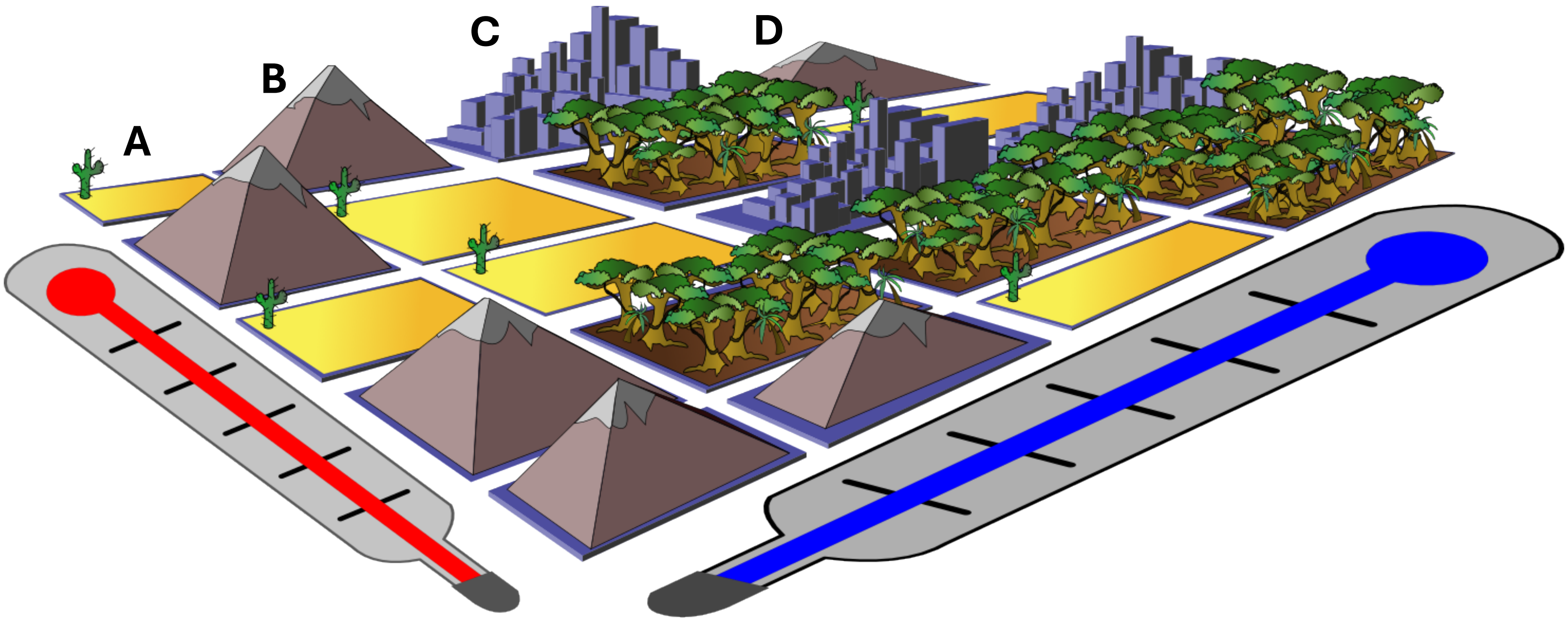


Figure 1. My own graphic illustration of how climate, habitat and minimum area requirements are combined to sum a total suitable area for each species. This example considers a hypothetical species that needs 4 squares of habitat to support its future existence and meet its minimum area requirement; this species can only live in mountainous regions, and it needs a climate that can only be provided by the two rows on the far left (row A and B). This means that this species has a total of 10 squares that are the right climate, within that, 5 squares that are the right climate *and* the right habitat (mountains), however, there are no patches that are large enough to support its future existence – as the biggest patch of suitable contiguous habitat and climate is only 3 squares large. This species had a minimum area requirement of 4.

I repeat this process for the climatic scenarios RCP 2.6, 4.5, 6.0 and 8.5 in the year 2070, as well as for present day mammal distributions as projected in published work (Newbold, 2018). To test if there is a significant difference in the area shortfall between present and future climatic scenarios, I use a Kruskal-Wallis rank sum test, as well as a Dunn's post hoc test. To estimate species richness, I combine all the individual species maps using the ArcPy module using Python version 2.7, to create species richness maps. I add maps together in batches of 20 using the sum argument in the CellStatistics function, and iteratively accumulate this into a single map that represents total mammal species richness (ArcGIS, 2021a).

Variation among Species with Different Extinction Risk

I downloaded the IUCN Red List status for all mammal species (IUCN, 2023), which attributes one of the following extinction-risk statuses to each species: least concern, near threatened, vulnerable, endangered, critically endangered, extinct or data deficient. I match the IUCN status to the percentage of area that is suitable climate and habitat for species, but does not meet a species minimum area requirements, also referred to as the area shortfall. Using an ANOVA I determine whether there is a statistically significant difference in the area shortfall in 2070 among IUCN Red List categories for the RCP 4.5 intermediate-emissions climate-change scenario. I also use a Tukey HSD test to analyse pairwise differences among groups.

Representation of Sufficiently Large Suitable Areas Within Protected Areas

I download the April 2023 version of the World Database on Protected Areas (WDPA), considering all protected-area types, including: strict nature reserves, wilderness areas, national parks, natural monuments, habitat or species management areas, protected landscapes or protected area with sustainable use of natural resources (Protected Planet, 2024). This dataset is split into spatial polygons delineating the boundaries of protected areas on the map, and point data that lack specific drawn boundaries, but that have accompanying metadata describing protected area size. For protected areas represented as points, I draw a circular buffer around each point data with a diameter corresponding to the listed protected area size. As point data represents 9% of all protected areas in the WDPA, it is generally recommended to utilise these protected areas in analyses where possible (Bingham et al., 2020). Using the "ExtractByMask" function from the "sa" package in ArcPy (ArcGIS, 2021b), I extract areas from the full species richness map detailed in "spatial analysis" above, that fall outside the boundaries of the spatial polygons, or buffered point data. The species richness map used is the projected species richness when taking into account suitable climate and habitat, as well as the minimum area requirements of mammals. This aims to determine which parts of the world, key to meeting the minimum area requirements of mammals, are not currently under protection.

Results

When estimating changes in projected suitable area between the present day and the future, taking into account minimum area requirements leads to a greater mean percentage decrease in total available area for species, with the strongest average differences observed under representative concentration pathway (RCP) 8.5 (figure 2). Results for species with empirical estimates of minimum area requirements only are in supplementary materials figure 5.

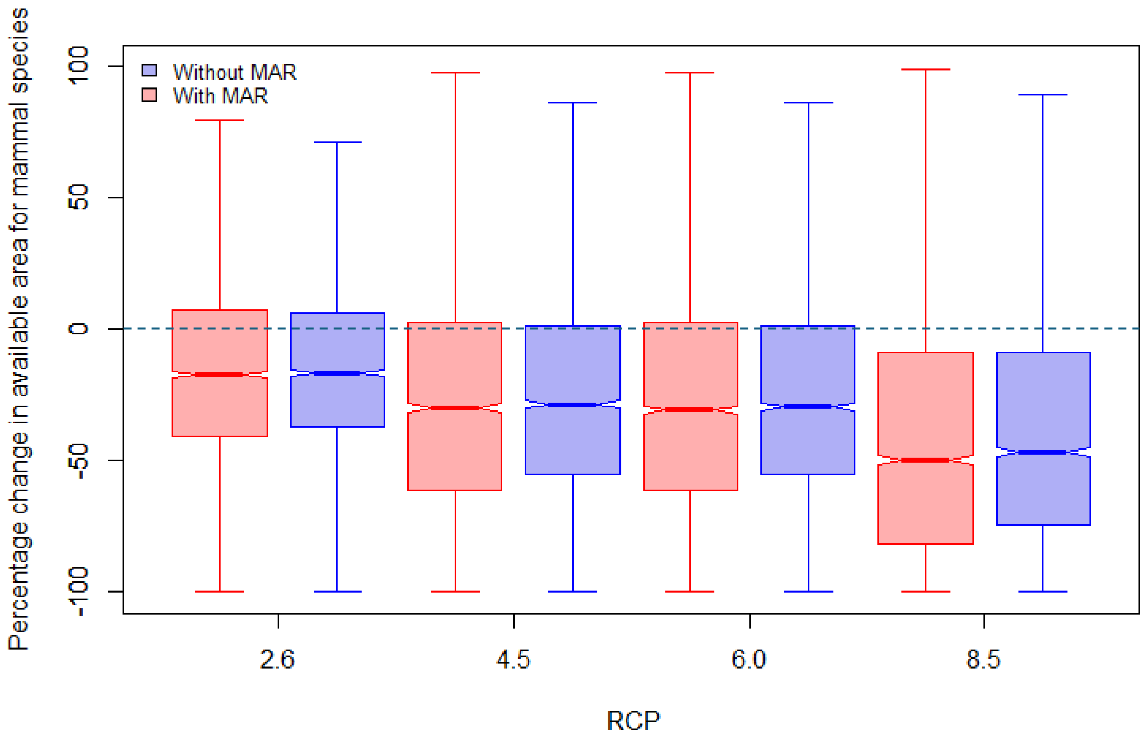


Figure 2. Comparison of the total suitable climate and habitat available for mammals with (red bars) and without (blue bars) taking into account a species minimum area requirements (MAR), under the RCP 2.6, 4.5, 6.0 and 8.5 future climatic scenarios for the year 2070. Values are compared to a present-day baseline scenario (dashed line at 0 percentage change).

I examine the percentage of a species range that has suitable habitat and is projected to have suitable climate in the future, but that doesn't meet the minimum area requirements of the species, referred to here as the area shortfall. The percentage area shortfall showed an overall significant difference among the present day and the future climate scenarios considered (Kruskal-Wallis rank sum test: $\chi^2 = 209.32$, d.f. = 4, $p < 0.001$). A Dunn's post-hoc test revealed that the area shortfall was significantly different between the present day and all future climate scenarios, and among all pairs of future climatic scenarios except RCP 4.5 and RCP 6.0 (table 3). The mean present day area shortfall is -28.6%. In 2070, I predict the area shortfall to be -31.4%, -34.1%,

-34.2% and -38.3% for scenarios RCP 2.6, 4.5, 6.0, and 8.5 respectively. By not taking into account minimum area requirements, we could be overestimating the area available to species in the future by between 2.8% – 9.7%, depending on the climatic scenario.

Table 3. Dunn's post hoc test comparing the area shortfalls of present and future climatic scenarios. Values reported are for the Z value (Z), and a post-hoc effect size derived from the Dunn’s test (R), numbers in bold represent a highly significant difference ($p < 0.001$) in the means between groups compared.

	Present day		RCP 2.6		RCP 4.5		RCP 6.0	
	Z	R	Z	R	Z	R	Z	R
RCP 2.6	**3.700**	**-0.041**						
RCP 4.5	**7.898**	**-0.087**	**4.198**	**-0.046**				
RCP 6.0	**7.948**	**-0.088**	**4.248**	**-0.047**	0.050	-0.001		
RCP 8.5	**13.614**	**-0.150**	**9.920**	**-0.110**	**5.727**	**-0.063**	**5.676**	**-0.063**

Under higher emissions scenarios, a greater proportion of species face large area shortfalls when taking into account their minimum area requirements (figure 2). In RCP 2.6, 7.6% of mammal species face a 90% or more area shortfall when incorporating minimum area requirements, and under RCP 8.5 this increases to 12.3% of mammal species (figure 3). When considering the percentage of species that undergo a 50% of more area shortfall, this accounts for 18.9% of mammal species under RCP 2.6, and 25.6% of species under RCP 8.5. Results for species with empirical estimates of minimum area requirements only can be found in the supplementary material figure 6.

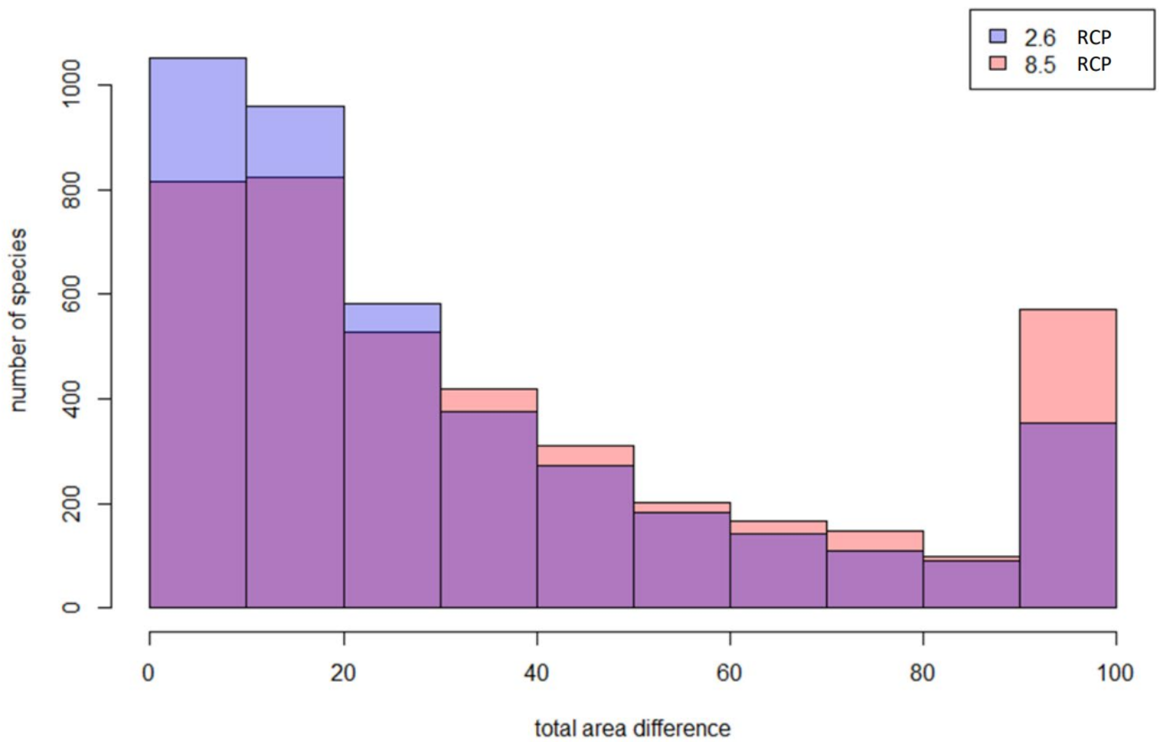


Figure 3. The distribution of percentage area shortfalls across species when incorporating minimum area requirements between one of the lowest-emissions climate scenarios – RCP 2.6 (blue) – to one of the highest – RCP 8.5 (red), for the year 2070. Areas of overlap are shown in purple.

Species considered more at risk of extinction, as classified by the IUCN red list of species, are expected to lose a greater proportion of their projected suitable area when factoring in species minimum area requirements. Overall, I find significant differences in the area shortfall, under RCP 4.5, among the IUCN red list categories (ANOVA: $F = 34.77$, d.f. = 6, $P < 0.001$), and a Tukey HSD test showed that there were significant pairwise differences between most of the groups (figure 4b).

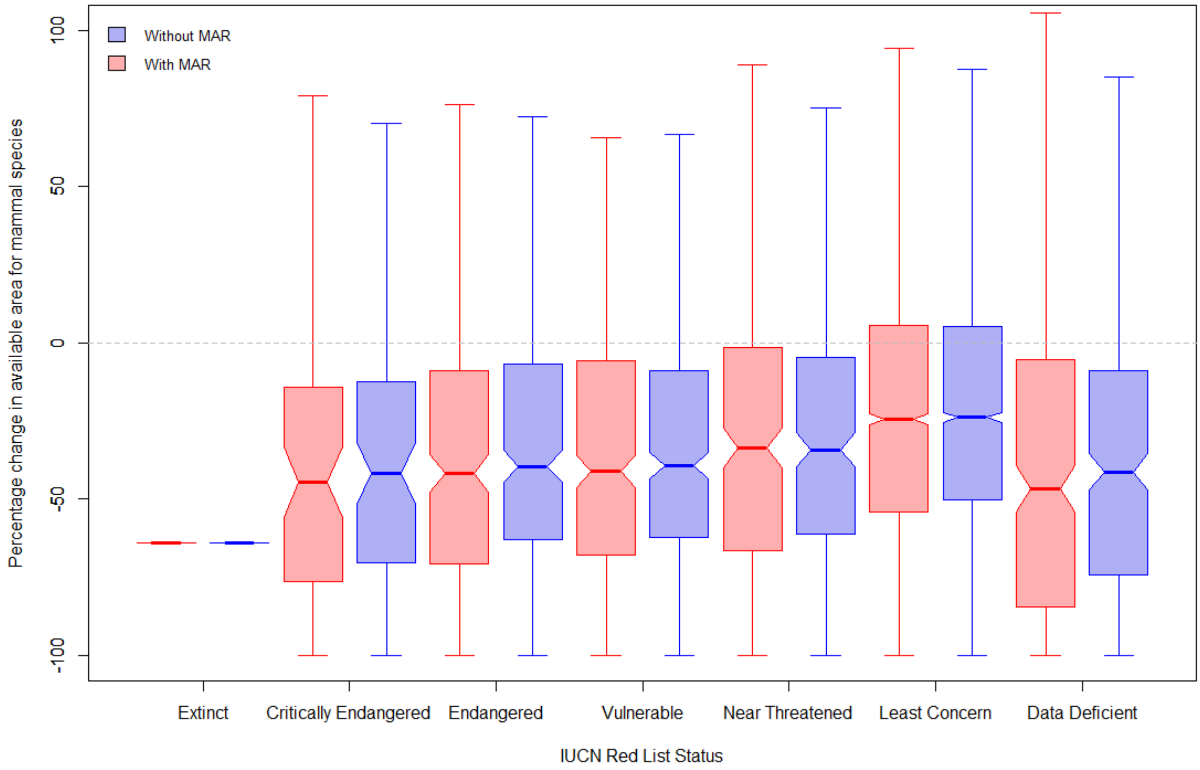


Figure 4a. Comparison of the total projected suitable climate and habitat available among mammal species with different extinction-risk statuses, with (red) and without (blue) taking into account a species minimum area requirements (MAR), under the RCP 4.5 climate scenario for 2070. Values are compared to a present-day baseline scenario (dashed line at 0 percentage change).

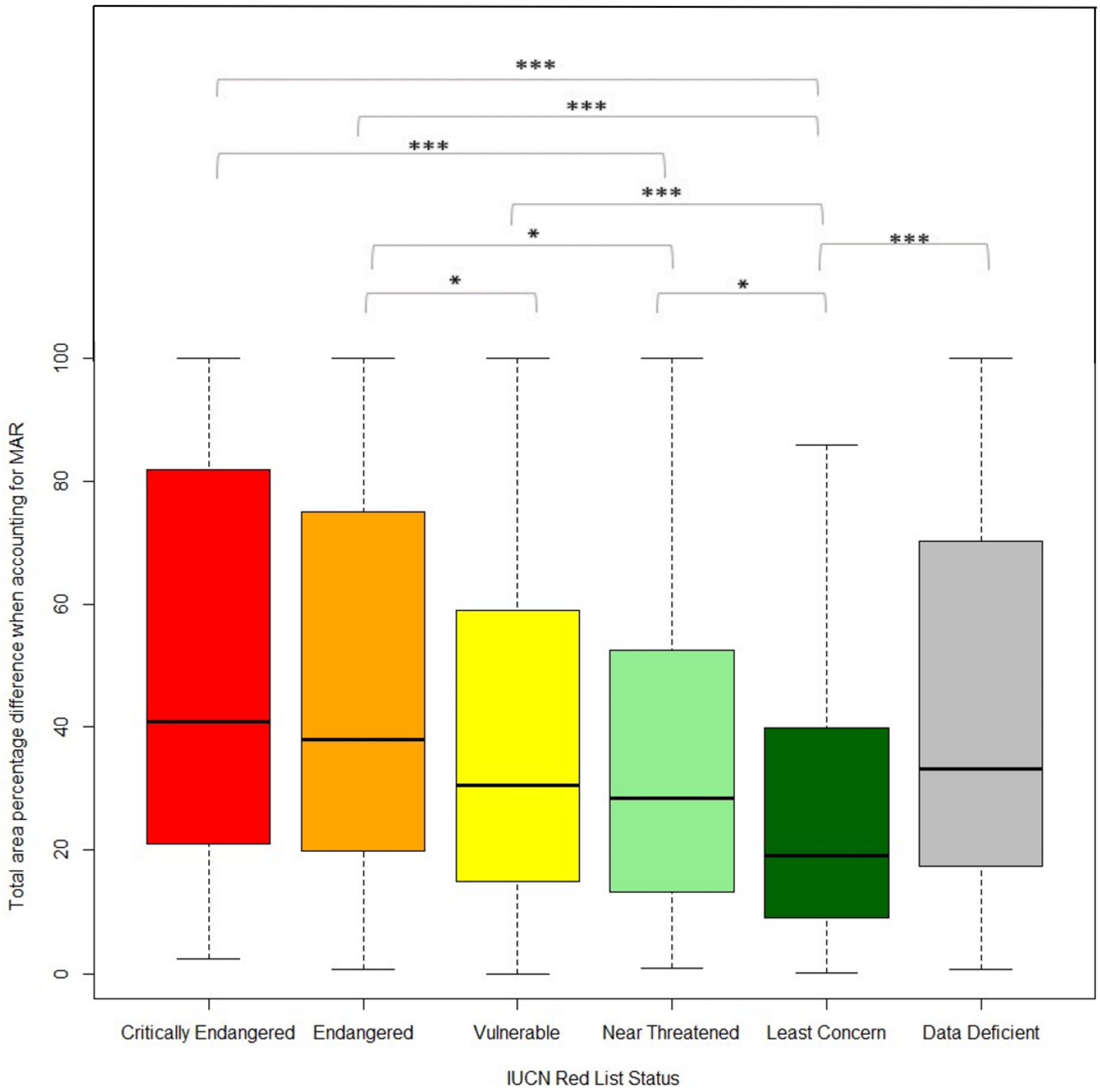


Figure 4b. Comparison of the percentage area shortfall when accounting for species minimum area requirements (MAR) among species with different extinction-risk status, under an intermediate-emissions climate-change scenario (RCP 4.5), for the year 2070. A higher positive value means that there is more of an area shortfall, as a larger area of habitat patches are too small to meet a species minimum area requirements.

When comparing future climatic scenarios to the present day, factoring in minimum area requirements does not lead to significant differences in the average percentage change in mammal species richness across grid cells (figure 5). However, some regions of the world saw very large discrepancies, with a species-richness shortfall of nearly 100% in some locations. Areas with particularly large species-richness shortfalls when accounting for minimum area requirements included the arc of deforestation around the Amazon, Central America, African savanna areas, as well as large areas of Western Europe and China (figure 6). Supplementary figure 1 displays the two input maps used to create this percentage difference map, and supplementary figure 3 is the same analysis, but only for those species for which we have empirical estimates of minimum area requirements.

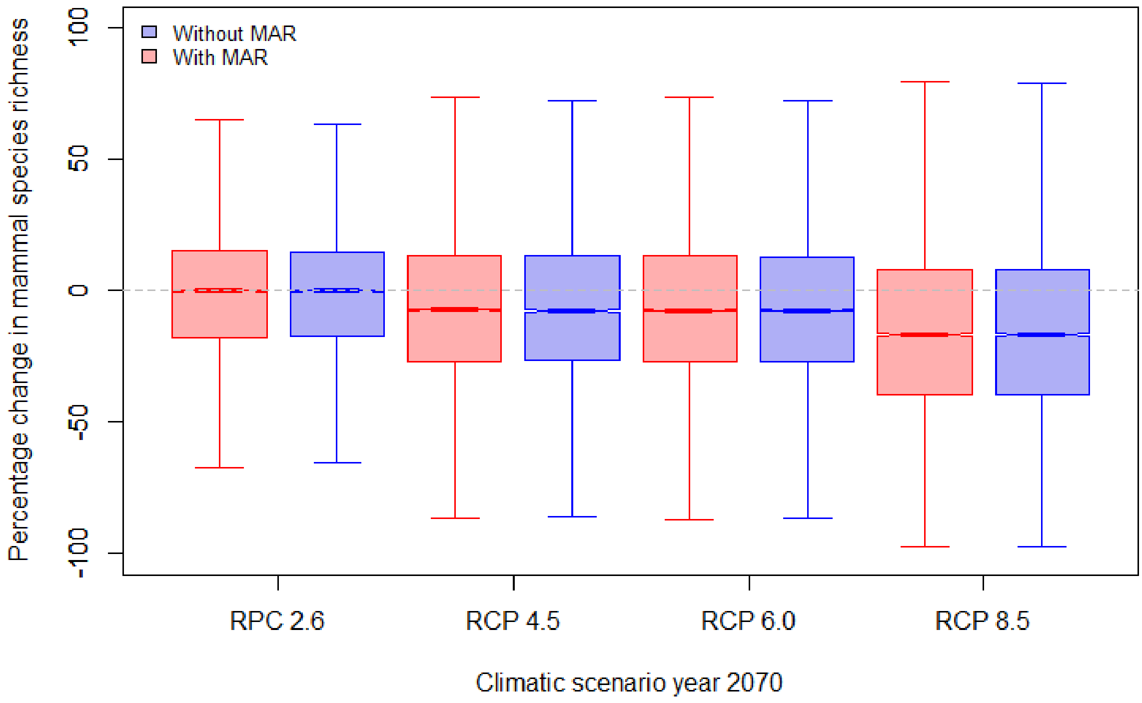


Figure 5. Comparison of the average percentage change in mammal species richness across grid cells globally between the present day and the year 2070, incorporating (red) or not (blue) species' minimum area requirements (MAR). The dashed grey line at no percentage change represents the present day.

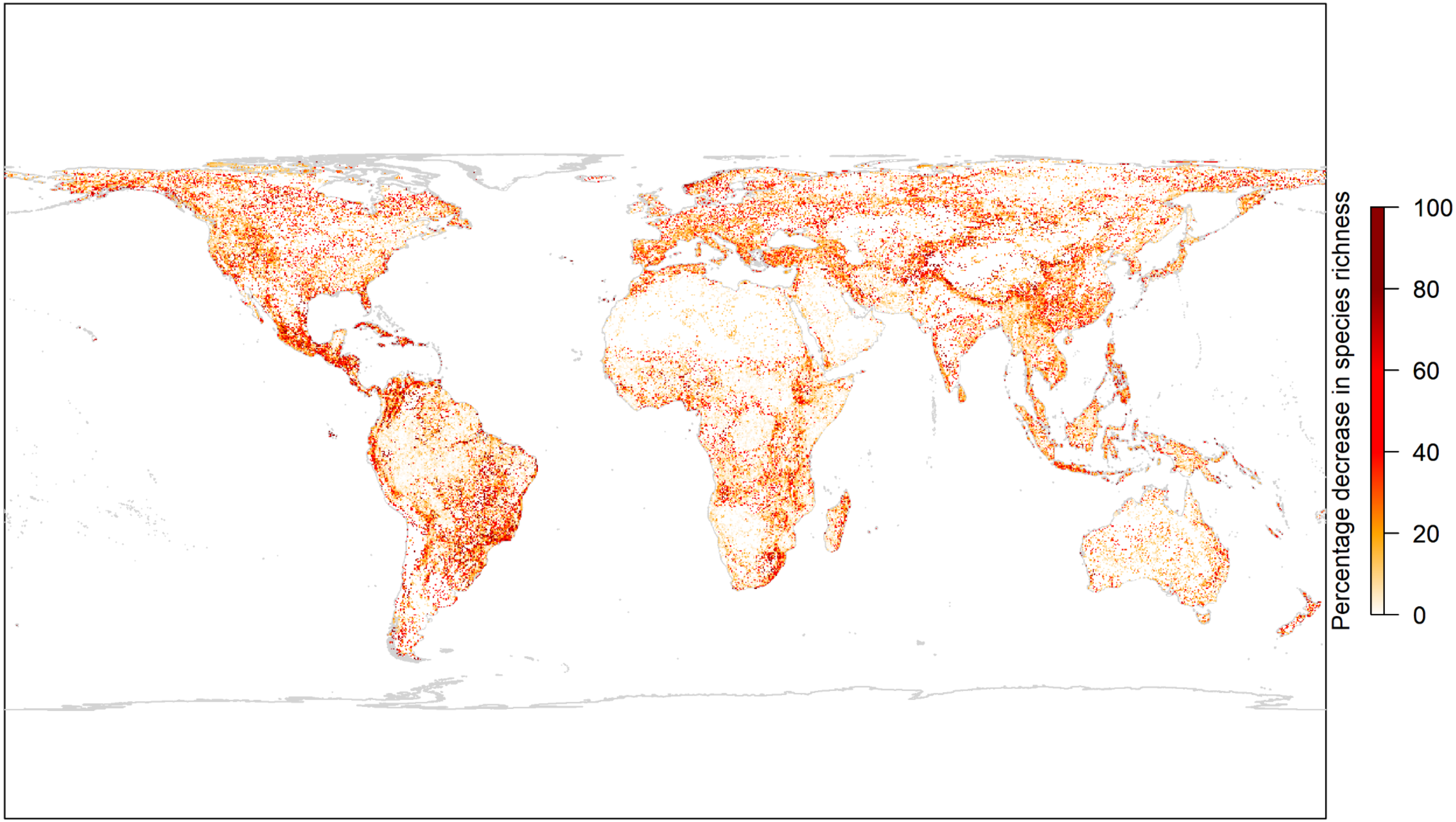


Figure 6. The percentage of species lost from a cell when accounting for species' minimum area requirements, under an intermediate-emissions climate change scenario (RCP 4.5) for the year 2070. Areas highlighted in darker red do not contain enough contiguous areas of suitable climate and habitat to meet the needs of a large proportion of the species projected to exist in those areas according to just climate and habitat suitability, and not incorporating minimum area requirements.

The Brazilian Amazon, Indonesia and parts of Western and Central Africa are projected to see some of the greatest absolute changes in mammal species richness between the present day and 2070, under the RCP 4.5 scenario, when considering suitable climate, habitat and areas that meet the minimum area requirements of species (figure 7). Supplementary figure 2 displays the two input maps used to create this absolute difference map, and supplementary figure 4 is the same analysis repeated only using species for which we have empirical estimates of their minimum area requirements.

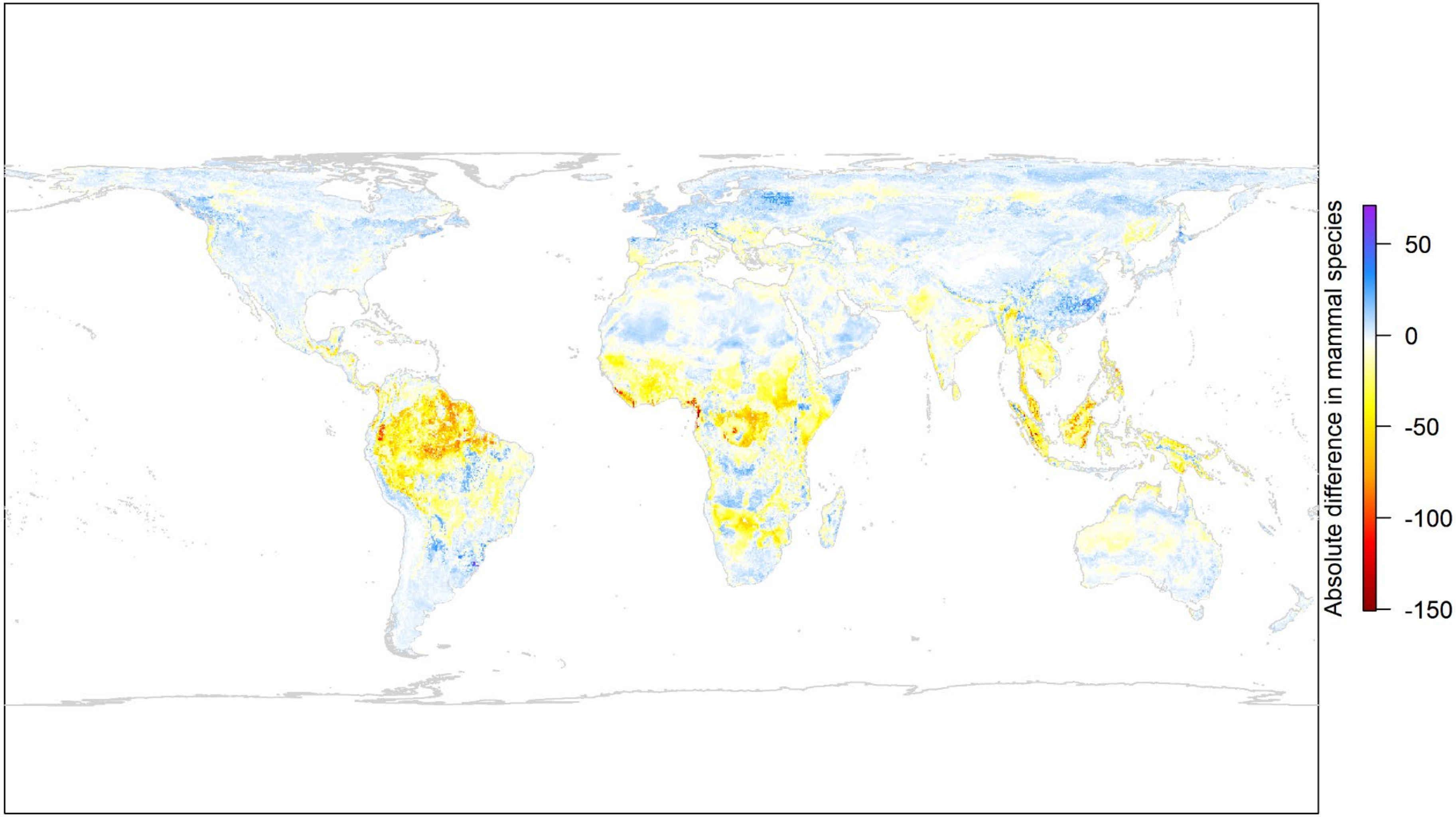


Figure 7. Absolute difference in mammal species richness between the present day and 2070, under an intermediate-emissions climate scenario (RCP 4.5), when taking into account future climatic suitability, the current existence of suitable habitat and species' minimum area requirements. Areas in blue and purple colours represent predicted absolute gains in species richness, white colours represent limited change in species richness, and yellows, oranges and reds show projected losses in species richness between the present day and 2070.

Areas of the Amazon, Sub-Saharan Africa and Southeast Asia are identified as being of the highest priority both for establishing new protected areas, and for maintaining extisting protection, as these areas are projected to support the most species in the year 2070 by having sufficiently large areas of suitable climate and habitat (figure 8).

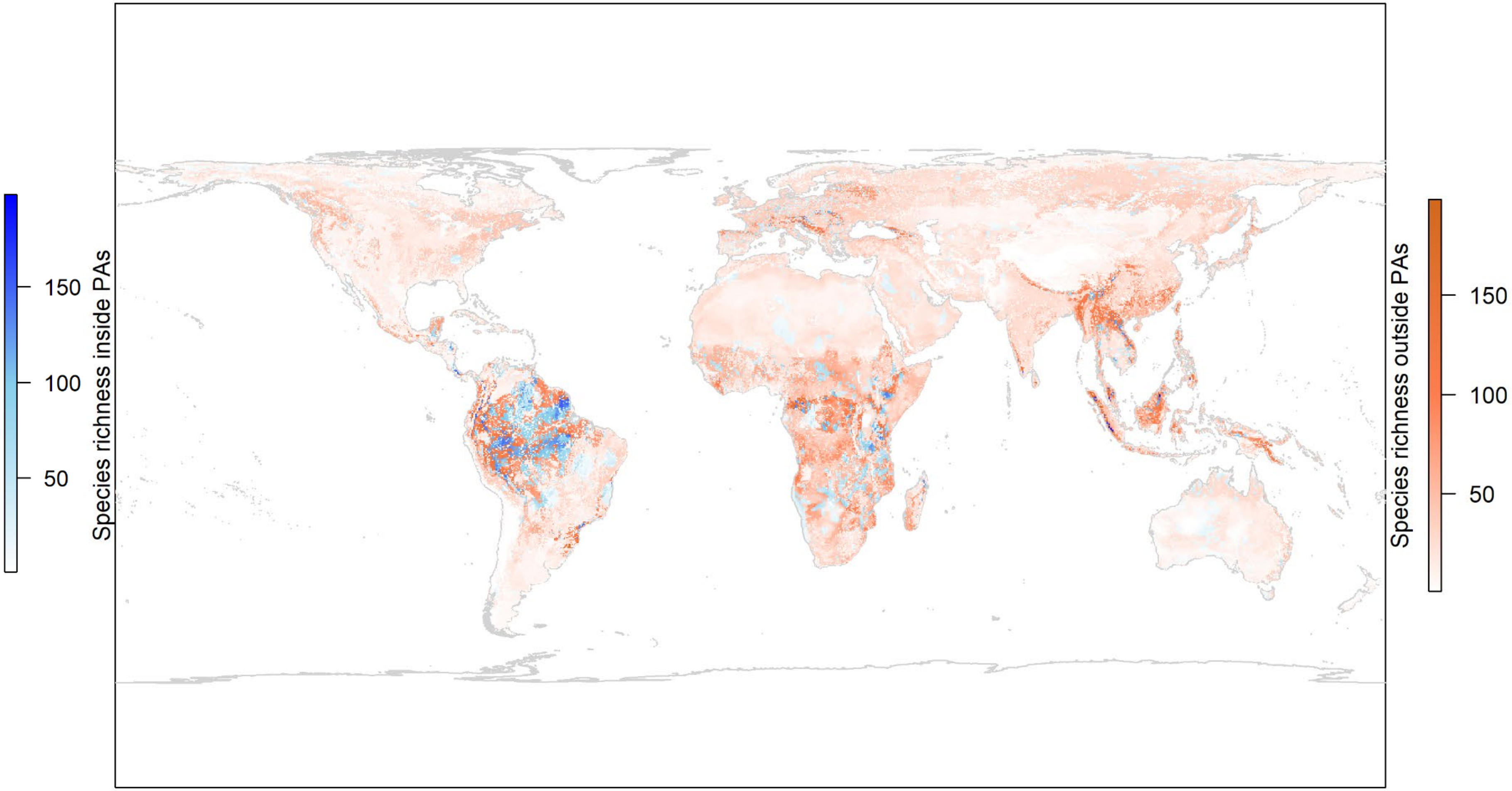


Figure 8. Total mammal species richness in areas of suitable climate and habitat, and that meet the minimum area requirements of species in the year 2070 under RCP 4.5. Grid cells with at least some area inside a protected area (PA) are plotted in blue, while grid cells that fall entirely outside of a protected area are plotted in red.

Discussion

In this chapter I explore whether incorporating minimum area requirements in the calculations of total suitable area for species in the year 2070, will lead to a greater projected decrease in suitable area between now and future scenarios, than not incorporating them. Current projections of future species distributions may be overly optimistic as they often don't take into account a combination of habitat suitability, climate suitability and the minimum area required by a species to enable the population to persist. By taking into account all of these factors, I find that we could be underestimating the projected losses of suitable area, compared to considering just climate and habitat suitability. Shortfalls of suitable area for the largest number of species are expected to occur in areas such as the arc of deforestation around the Amazon, in Central America, savanna areas of Africa, and in Southeast Asia. Furthermore, my analysis has shown that species considered to be critically endangered or endangered according to the IUCN Red List are predicted to have a significantly greater area shortfall when incorporating minimum area requirements, than species considered near threatened and least concern (figure 4b). I also find that whilst there are no significant differences in the global average percentage decrease in species richness when accounting for minimum area requirements, there are large areas of the world that are projected to not be able to fulfil their total potential species richness as they do not contain contiguous areas of sufficiently large size that consist of suitable climate and habitat (figure 6).

I have found that neglecting to consider minimum area requirements can lead to a substantial overestimation of the total area available to mammal species, which can present significant challenges for biodiversity conservation, and could lead to global and local conservation strategies that are not optimally targeted (Ford et al., 2021). The area shortfall (the area that contains suitable climate and habitat, but is not large enough to meet a species minimum area requirements) is greater under more extreme climatic scenarios (figure 2). For approximately 600 mammal species, greater than 90% of the range that is projected to have suitable habitat and climate in 2070 will not meet minimum area requirements under the most extreme climate scenario (figure 3). This effect can be explained by the higher degree of climate warming that will restrict species ranges, as well as leaving fewer sufficiently large patches of habitat available for mammals (Pacifici et al., 2020).

Factoring in species minimum area requirements has a stronger effect for species that are at higher risk of extinction according to the IUCN (figure 4b). This points to a greater level of habitat fragmentation within the climatically suitable range of critically endangered species, which prevents a species from fulfilling its minimum area requirements. A study on the predicted mammal species loss from ecoregions of the world showed that an average of 11% of species per ecoregion are predicted to become extinct due to habitat loss and fragmentation (Kuipers et al., 2021). Fragmentation of habitats in particular is a key predictor of extinction risk for terrestrial mammal species (Crooks et al., 2017; Ramírez-Delgado et al., 2022). The large area shortfalls for species that are at a greater threat of extinction may not only be due to habitat fragmentation, but also because these species are more sensitive to climate change. For example, some threatened species might exist in areas that are more vulnerable to climate change (Chowdhury, 2023). Research has also shown that endangered species threatened by climate change face an additional 33% increase non-climatic threats (compared to species at a lower threat of extinction), such as: transportation, residential development, human disturbance, invasive species, severe weather, mining and energy production, natural system modification, pollution, agriculture/aquaculture, and biological resource use (Fortini & Dye, 2017). The combination of potential heightened sensitivity to climate change and habitat fragmentation, makes it crucial to prioritise these species in conservation efforts, as these combined impacts reduce the probability of a species being able to meet its minimum area requirements. My finding is also in line with research on the protected area network in China, that shows that the minimum area requirements for threatened species are often not met (Wang et al., 2023). My own data from this study showed that in general species at a higher risk of extinction did not have larger minimum area requirements than species at a lower risk of extinction (supplementary materials, figure 9). This suggests that the greater area shortfalls in species at a greater threat of extinction are not due to larger habitat needs, but may be due to these species facing increased habitat fragmentation and being more sensitive to climate change.

Areas that do not meet the minimum area requirements for large numbers of species include the arc of deforestation around the Amazon, in Central America, savanna areas in Africa, large areas of Western Europe and China, and in the North of India - just south of the Himalayas (figure 6). Some of this will be natural fragmentation due to a matrix of natural habitat types (Chetcuti, Kunin, & Bullock, 2021), which will provide its own benefits to species and climate resilience. For example the south of the Himalayas, known for its high mammal diversity compared to the northern slope, undergoes steep elevational changes that will provide unique climatic conditions for different species (Hu et al., 2018). This will naturally fragmenting the landscape both climatically, and through habitat type as we have rapid habitat changes from artificial habitats, to forest, to grassland and rocky habitats - as shown in the global terrestrial map of habitat types (Jung et al., 2020). However, in other areas, such as the arc of deforestation in the Amazon, habitat fragmentation is caused mostly by anthropogenic land conversion, such as deforestation (Lapola et al., 2023; Palmeirim, Santos-Filho, & Peres, 2020). Similarly in Central America, the high number of endemic species and ongoing loss of natural habitat due to land use change (Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000), may be driving habitat fragmentation, so that species are not able to meet their minimum area requirements. Focusing conservation efforts on improving the connectivity of habitat patches in these areas will enable us to preserve large number of species that would otherwise be lost (Ramírez-Delgado et al., 2022), and there will be important habitat availability thresholds to maintain for some species if we are to prevent abrupt species decline (Estavillo, Pardini, & Da Rocha, 2013).

With shifts and changes in the area of species distributions, some areas of the globe will see a reduction in the number of mammal species that they support in the future, and some areas will be predicted to see an increase in mammal species richness (figure 7). In some parts of the Sahara there is predicted to be relative increases in species richness in the year 2070 compared to the present day. This perhaps seems unlikely given the known future impacts of climate change on this region that will increase desertification and reduce distributions of important carnivore species (Karssene, Chammem, Khorchani, Nouira, & Li, 2017). It is important to note that my study only considers current habitat type, and not future habitats that are likely to exist given the projected change in climates - this might be influencing some of this pattern. Across all areas of the globe, it is expected that there will be increased interspecies competition in the areas that are predicted to increase in mammal species richness (Douglas A. Kelt et al., 2019), due to the species range shifts between now and the future. Increased resource demands on areas that will see an absolute increase in mammal species could mean that that species will not establish itself in its modelled future area due to competition (Marion & Bergerot, 2018), although this relationship is very complex.

When utilising mammal species with empirical estimates of minimum area requirements (Verboom et al., 2014), areas that do not meet the necessary habitat size for many species include parts of North America, African savannas, and large parts of East Asia and Europe (supplementary materials, figure 3). A key difference between these results and those using imputed minimum area requirements for all mammal species is the absence of South America, including the arc of deforestation, as a critical region unable to meet minimum habitat requirements. When utilising imputed minimum area requirements, South America is an important region noted as unable to meet these minimum habitat requirements (figure 6). The geographic differences between these two analyses are most likely attributed to the species composition of the empirical dataset, which when comparing the Americas, is biased towards species native to North America. Furthermore, differences also exist when we compare the maps that examine the areas of the globe that will see a reduction/increase in the number of mammal species that they support in the future, when looking at species for which we have empirical estimates of their minimum area requirements (supplementary materials, figure 4) compared to those for which this has been imputed (figure 7). North America is picked up as an important region for species gains in the future, but this is most likely reflecting the same bias in the empirical dataset (Verboom et al., 2014).

Maps such as those presented in this study (figure 6) can provide insight into where conservation efforts will need to be concentrated if we are to meet the minimum area requirements of species. In understanding which areas could support species long-term conservation, we can then look towards facilitating species movements to reach these key areas (Littlefield et al., 2017). Increasing habitat connectivity is perhaps the most important conservation strategy that has a multitude of recognised benefits including facilitating species dispersal (especially in smaller mammal species that have limited dispersal abilities) (Iezzi et al., 2022), and assisting species to track climate change (Robillard, Coristine, Soares, & Kerr, 2015). This also provides a flexible way forward, given the likely high levels of uncertainty in model outputs from this study.

My predictions of which areas will be suitable for species in the year 2070 are based on the assumption that habitat will remain distributed as it is in the present day. There is a greater chance of limiting land-use change, particularly from natural to artificial habitat, within protected areas (Figueroa & Sánchez-Cordero, 2008; Lucas N. Joppa & Pfaff, 2011; Wolf, Levi, Ripple, Zárrate-Charry, & Betts, 2021). Land inside protected areas is also generally considered to be of a higher quality than the surrounding habitat matrix, with more natural habitat and less fragmentation (Santiago-Ramos & Feria-Toribio, 2021). Greater levels of natural habitat are beneficial for many species (Outhwaite et al., 2022), for example, the gaur and Asian elephant have both been shown to use areas of higher quality habitat when dispersing across a landscape (Gangadharan, Vaidyanathan, & St. Clair, 2017). In 2011 it was reported that an average of 54% of carnivorous mammals' range is considered as high quality habitat, with limited fragmentation, and only 5.2% of that range was protected (Crooks, Burdett, Theobald, Rondinini, & Boitani, 2011). Another study in China has been able to demonstrate where protected area expansion can occur in order to meet the minimum area requirements of mammals in the present day, as at present we are not meeting these requirements for threatened species or large carnivores (Wang et al., 2023).

Currently, over half of the land that is afforded some level of protection at a global scale is not climatically connected (Parks, Holsinger, Abatzoglou, Littlefield, & Zeller, 2023). Climate connectivity is important as it allows for species to track suitable climate niches across a landscape, resulting in species range shifts as a response to climate change. Achieving large scale climate connectivity is theoretically achievable, although there will always be constraints and costs to implementation. Research into climate connectivity at large scales such as in North America has taken place, using least cost pathways and circuit theory to model corridors between protected areas that improves current climate connectivity whilst considering the human modification of the landscape (Barnett & Belote, 2021). It is critical that we understand where will be suitable for species in the future, as this will help to meet global targets such as effectively protecting 30% of terrestrial habitats by 2030. This will mean that we can ensure any newly designated sites are not only located in climatically suitable continuously connected suitable habitat, but are also of a sufficient size to support species conservation, and will remain relevant into the future.

In the year 2070 there is projected to be high species richness outside of protected areas, especially in Southeast Asia (figure 8), presenting significant challenges and opportunities for biodiversity conservation. The need for broader, landscape-scale conservation strategies that extend beyond the boundaries of legally binding protected areas, such as other effective conservation measures (OECMs) (Dudley et al., 2018), community managed conservation areas (Esmail et al., 2023), and establishing actively managed buffer zones (Lanzas, Hermoso, de-Miguel, Bota, & Brotons, 2019) is evident; focusing solely on the expansion of existing protected areas is unlikely to safeguard biodiversity into the future (Kremen & Merenlender, 2018; Maxwell et al., 2020). Southeast Asia, as one of the most biodiverse regions in the world, could place high biodiversity areas under community managed conservation, integrating local communities into conservation work, as well as providing livelihoods. This approach of community-based management is established in Southeast Asia for mangrove management, and its success is heightened by granting local communities ownership of extracted resources (Datta, Chattopadhyay, & Guha, 2012). Where lands are working landscapes, the importance of leaving at least 20% natural habitat has been highlighted, which can improve both food security as well as increasing the connectedness of existing protected areas for species (Garibaldi et al., 2021). This will protect critical habitats and ensure the sustainable management of human-dominated landscapes. Areas projected to hold high species richness in the future that fall outside of protected areas are unlikely to retain their current habitat, as these areas aren't be protected from future land use change and other anthropogenic pressures (Geldmann et al., 2013). Without some form of conservation action, such as those mentioned above, species projected to occupy these sites will not have sufficient suitable habitat to persist into the future.

Policy applications of this research include using the minimum are requirements of species to inform where to expand existing protected areas, as well as where to establish a variety of new areas dedicated to sustainable land practices and biodiversity conservation (figure 8). It can also highlight the importance of ensuring that areas which are projected to have high mammal species richness have an established buffer zone where extraction of natural resources and land use change is restricted. Furthermore, through highlighting the impacts of climate change, I highlight the importance of limiting warming to as low as possible, as under increasing RCPs habitat becomes more fragmented for species as there are less patches contained within suitable climatic conditions (figure 2). Nature based solutions such as habitat restoration that can both increase carbon sequestration as well as reduce habitat fragmentation is perhaps one of the most important policy implications of this work.

This study is subject to some limitations. First, I assume that mammals can't traverse unsuitable habitat types at all. Some habitat types, whilst unsuitable for a mammal species to live in, might be tolerated by a species when moving (O'Neill, Durant, & Woodroffe, 2020). If species are in fact able to cover at least short distances across unsuitable habitat or climate space, we may to some extent over-estimate the area shortfall for species. For example, rivers may prevent species from accessing habitat on the other side however, shallow rivers might be possible to cross for some mammal species. Second, I did not incorporate individual species' dispersal distances into the projections of future distributions. Instead, the projections of future suitable climate space assumed a single dispersal distance of 3 km per year for all mammal species

(Newbold, 2018). Whilst it would have been possible to model dispersal distances for each species, this approach was beyond the scope of this study, and the uncertainty in the estimates of minimum area requirements could be compounded by uncertainty in estimates of dispersal distances, leading to a very large overall uncertainty in future projections of distributions. Third, I didn't consider interactions among species when making projections of future distributions and thus species richness. Finally, the temperature that a species is actually exposed to on the ground might differ from that represented by the coarse-scale climate maps that underpinned this analysis, for example through canopy shading (Bütikofer et al., 2020).

In conclusion, current estimations of future species distributions are over optimistic because they don't take into account habitat suitability, climate suitability and the minimum area required by an animal to enable the population to persist into the future. I present a more conservative estimation of where species will be in the future, which can serve as a more realistic basis for predictions, showing that incorporating species' minimum area requirements has the most profound effect for species that are currently considered already to be at a higher risk of extinction, and in areas of the world where habitats are particularly fragmented by human activities. In highlighting areas that do not contain enough contiguous habitat to support a species' minimum area requirements (figure 6), I also provide an indication of where conservation efforts, such as restoration, may be focussed, in order to try to limit natural habitat fragmentation and so enhance biodiversity. I emphasize the importance of taking into account the minimum area requirements of species when looking into the future of mammal conservation, and thus a priority for future conservation biology should be to obtain empirical measures of minimum area requirements for as many species as possible.

Supplementary material

All Mammals

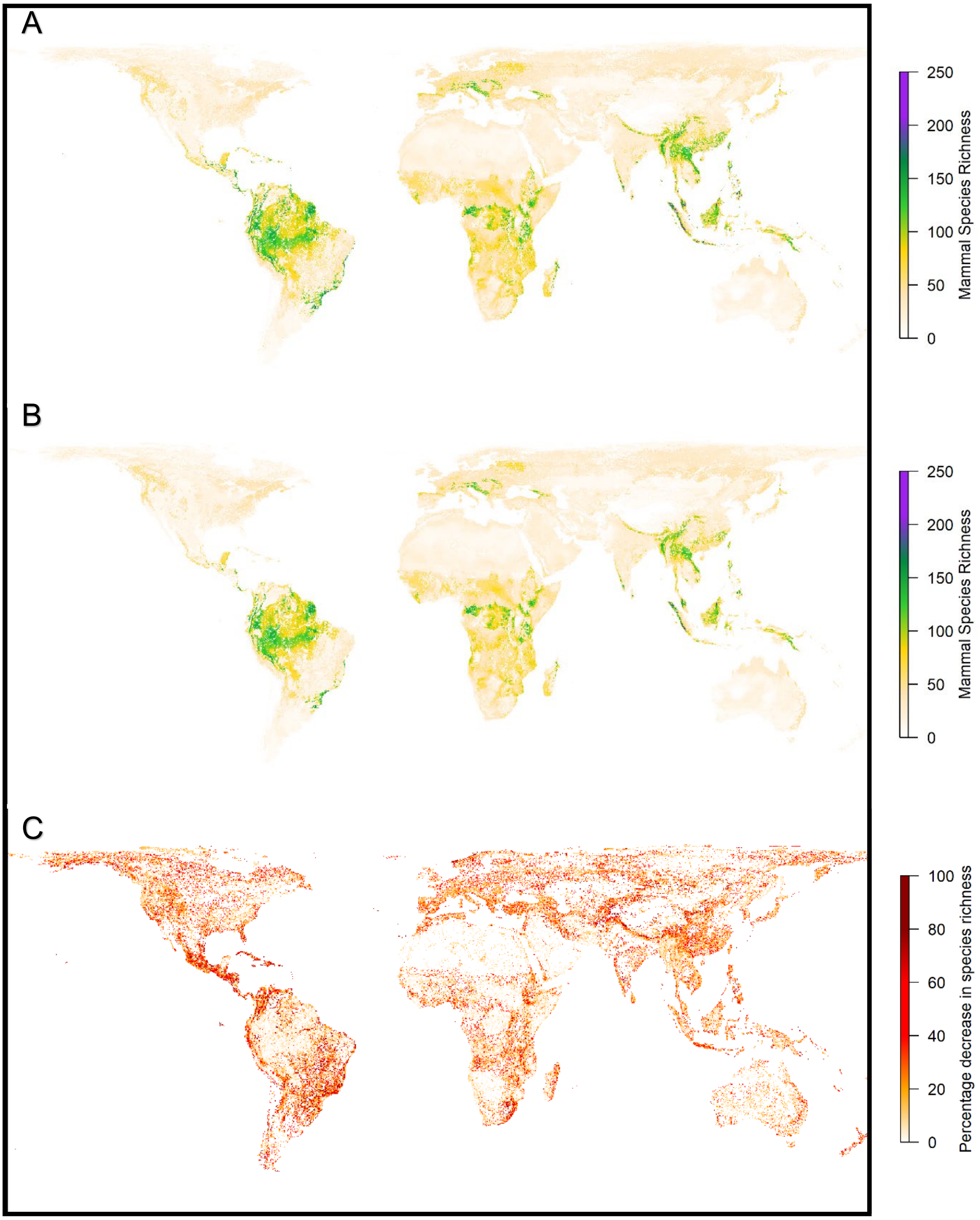


Figure 1. A: projected mammal species richness based on climate and habitat suitability for 2070 under RCP 4.5. B: projected mammal species richness for 2070 under RCP 4.5 when also incorporating minimum area requirements. C: Percentage difference in mammal species richness between A & B.

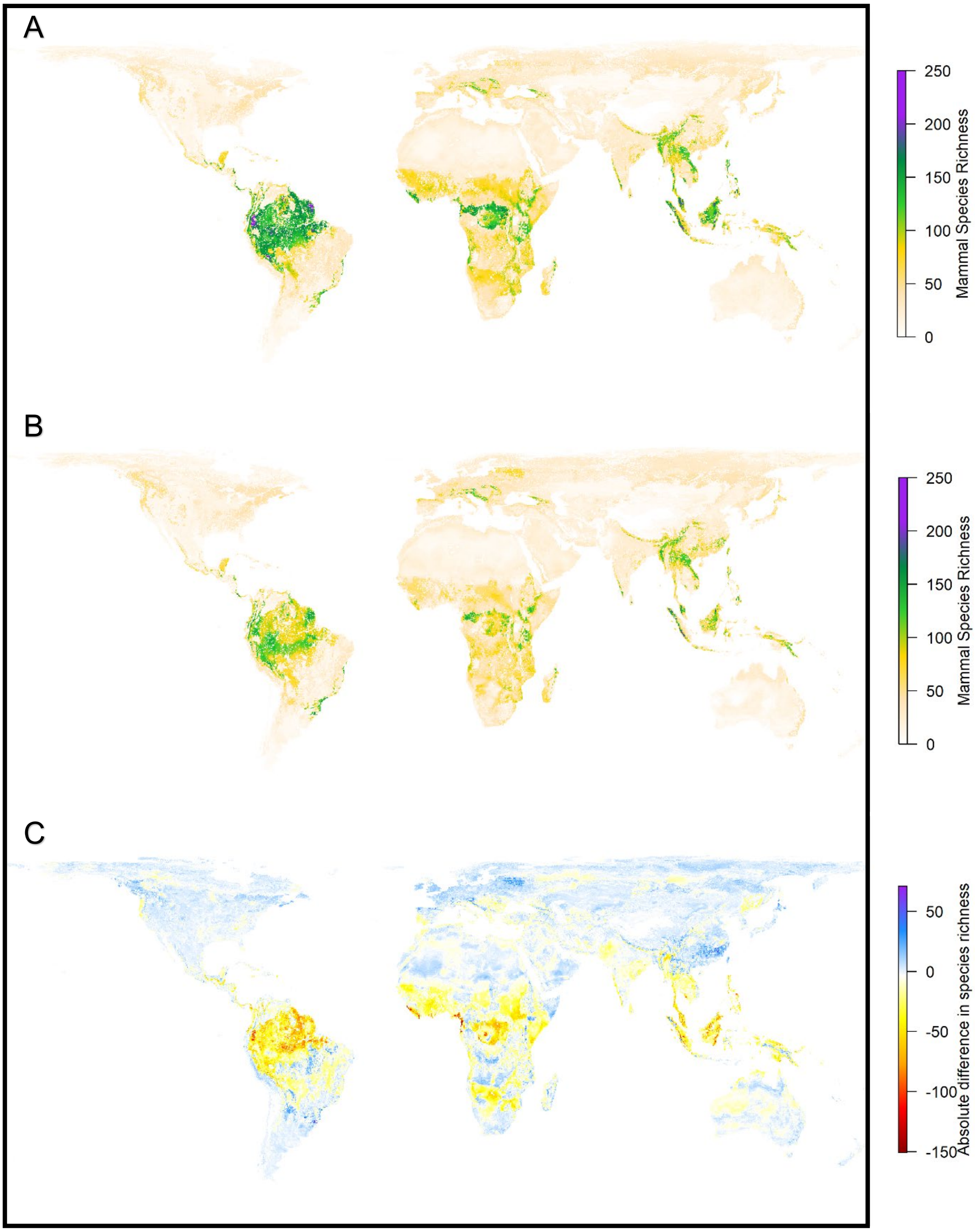


Figure 2. A: projected present-day mammal species richness when accounting for suitable climate, habitat, and minimum area requirements of species. B: mammal species richness when accounting for suitable climate, habitat, and minimum area requirements in the year 2070 under RCP 4.5. C: the absolute difference in mammal species richness between A & B.

Comparisons Projections based on only Empirical Minimum Area Requirement Estimates

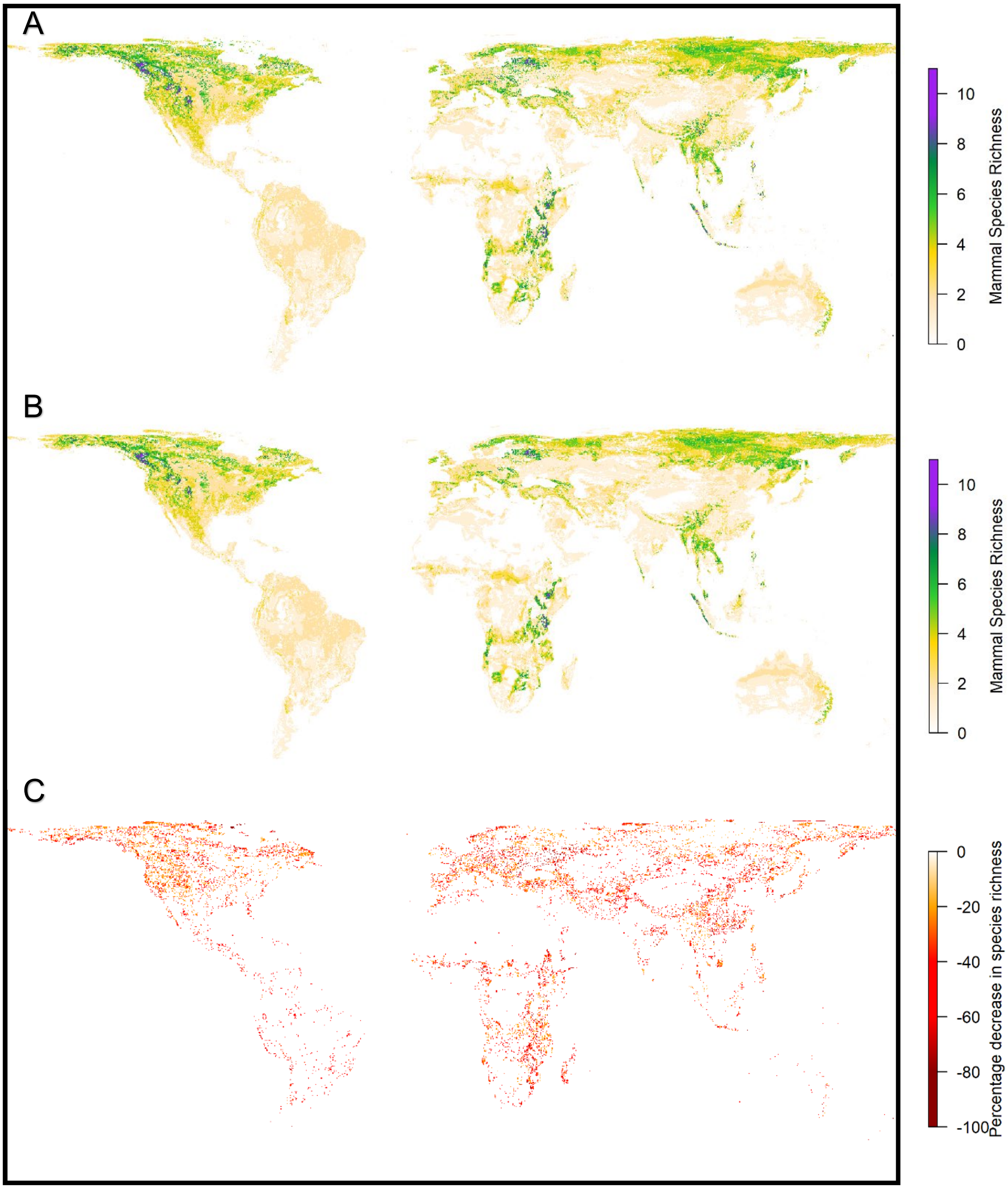


Figure 3. Focusing only on species with empirical estimates of minimum area requirements, A: projected mammal species richness based on climate and habitat suitability for 2070 under RCP 4.5; B: projected mammal species richness in 2070 under RCP 4.5 when also incorporating minimum area requirements of species; C: Percentage difference in mammal species richness between A & B.

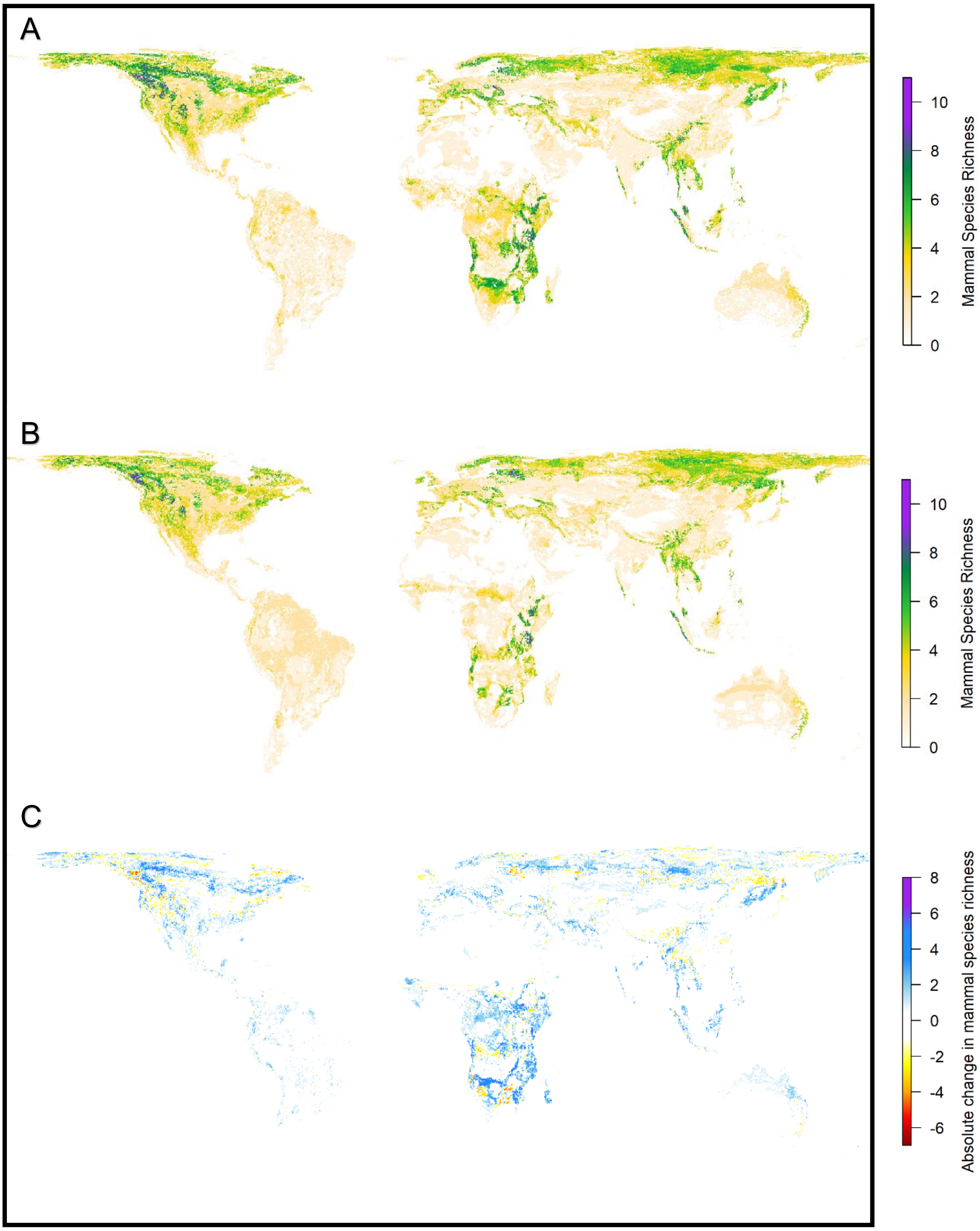


Figure 4. Focusing only on species with empirical estimates of minimum area requirements, A: projected present-day mammal species richness when accounting for suitable climate, habitat, and minimum area requirements of species; B: mammal species richness when accounting for suitable climate, habitat and minimum area requirements in the year 2070 under RCP 4.5; C: the absolute difference in mammal species richness between A & B.

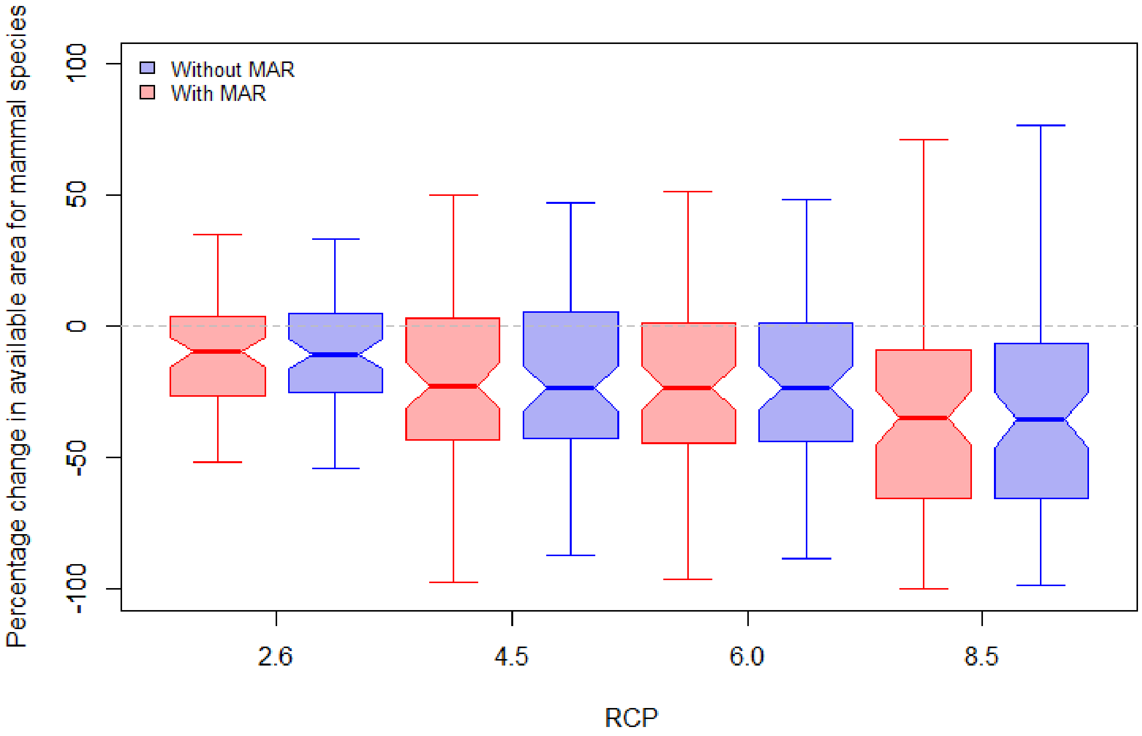


Figure 5. Comparison of the total suitable climate and habitat available for mammals with (red bars) and without (blue bars) taking into account a species minimum area requirement (MAR), under the RCP 2.6, 4.5, 6.0 and 8.5 future climatic scenarios for the year 2070. Values are compared to a present-day baseline scenario (dashed line at 0 percentage change). Data for species with empirical estimates of minimum area requirements only (Verboom et al., 2014).

For species with empirical estimates of minimum area requirements, I examine the percentage of a species range that has suitable habitat and is projected to have suitable climate in the future, but that doesn't meet the minimum area requirements of the species. There was no significant difference in the area shortfall between present and future climate scenarios for species that have empirical estimates of minimum area requirements (Kruskal-Wallis rank sum test: $\chi^2 = 2.991$, df = 4, p = 0.559). However, as we only have empirical minimum area requirements for a small subset of 80 mammal species, detecting a significant difference here is more unlikely.

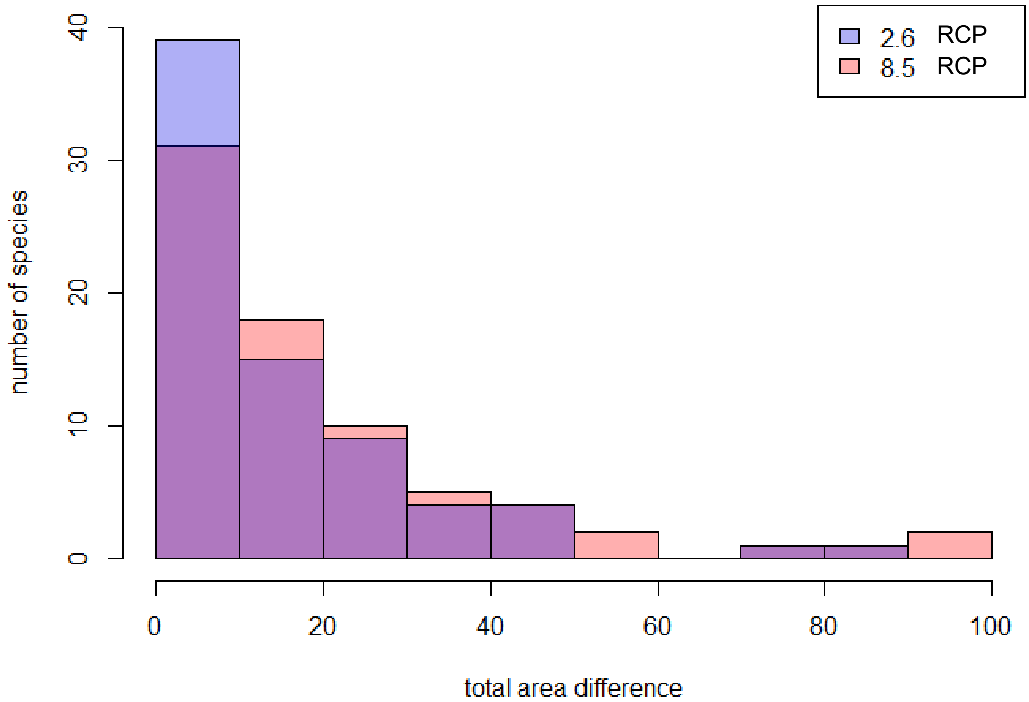
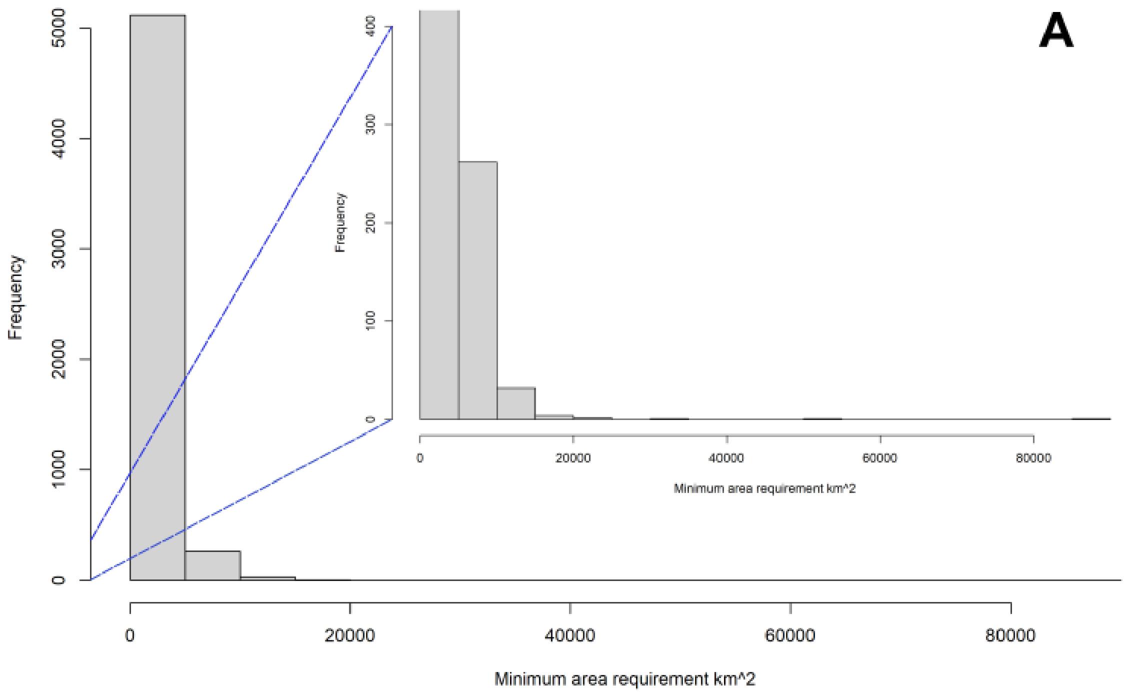


Figure 6. The distribution of percentage area shortfalls across species when incorporating minimum area requirements between one of the lowest-emissions climate scenarios – RCP 2.6 (blue) – to one of the highest – RCP 8.5 (red), for the year 2070. Areas of overlap are shown in purple. Data for species with empirical estimates of minimum area requirements only (Verboom et al., 2014).



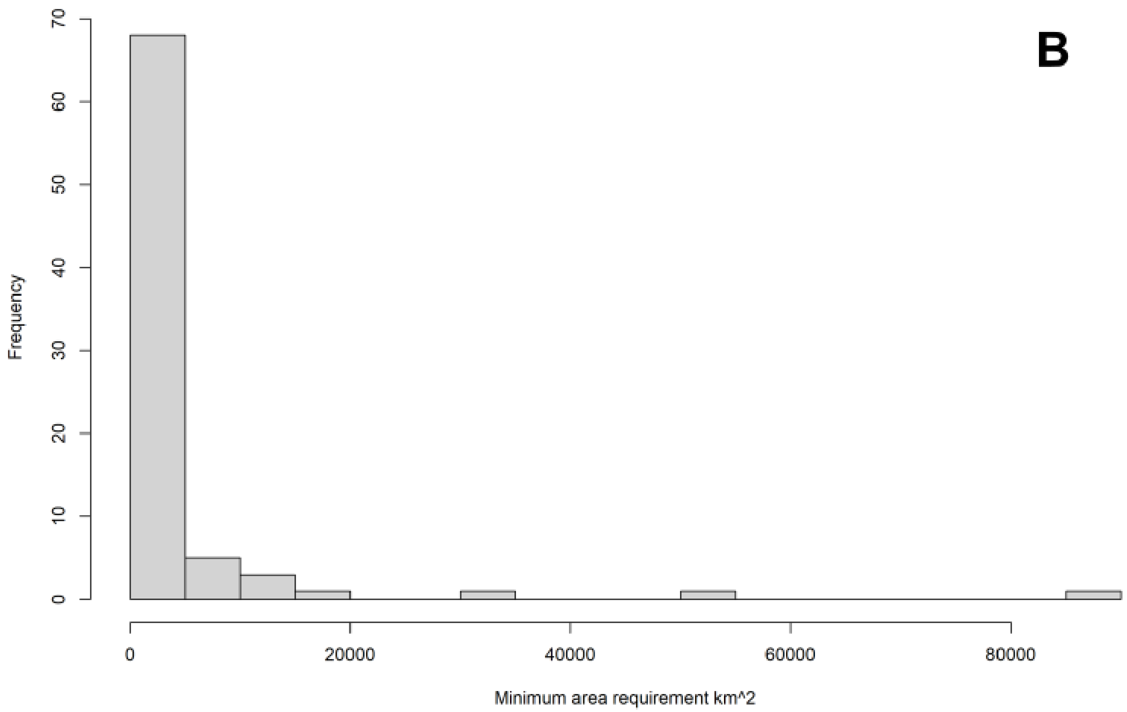


Figure 7. A: Histogram for all mammal species using imputed minimum area requirements. On the y axis, 0-400 is also enlarged to view some of the larger minimum area requirement species that would otherwise not be visible in the histogram due to the small frequency of these species. B: Histogram for species with empirical estimates of minimum area requirements only (Verboom et al., 2014).

Table 1. The 80 mammal species for which empirical minimum area requirement estimates as provided in Verboom et al. (2014), and their subsequent imputed minimum area requirements. The imputation took place for all mammal species across the globe, however only this subset of 80 mammal species is shown here. I imputed these values based on a combination of species traits expected to be associated with minimum area requirements: body mass, diet breadth, habitat breadth, home range size of a group and of an individual, maximum longevity, population density, basal metabolic rate, dispersal age at which young permanently leave their parent, population group size in which an individual spends the majority of their time, and the social group size of their social cohesive unit.

Species binomial	Minimum area requirement empirical estimate km^2	Minimum area requirement imputed value km^2
Acinonyx jubatus	18,675.23	9,024.76
Aepyceros melampus	248.01	1,395.86
Ailuropoda melanoleuca	396.33	7,372.52
Antilocapra americana	24.21	1,039.35
Babyrousa babyrussa	1,268.31	1,960.19
Bison bonasus	1,109.33	12,660.98
Bos taurus	9,334.14	1,536.74
Brachyteles arachnoides	75.21	2,648.19
Bubalus mindorensis	183.60	3,246.65
Burramys parvus	0.22	1,719.20
Canis lupus	7,215.16	12,695.20
Canis rufus	411.00	373.88
Canis simensis	1,265.82	1,640.41
Capra hircus	85.37	5,014.01
Castor fiber	128.56	2,087.66
Cercocebus galeritus	1,906.05	194.39
Cervus elaphus	1,447.96	3,934.78
Chlorocebus aethiops	925.52	191.22
Crocidura russula	25.01	390.99
Dama dama	13.23	860.24
Dicerorhinus sumatrensis	38.43	3,230.99
Diceros bicornis	5,048.15	5,944.53
Dipodomys stephensi	17.02	1,449.28
Elephas maximus	1,463.38	5,140.77
Equus caballus	303.33	5,644.74
Equus zebra	49.29	1,275.92
Gorilla gorilla	1,675.44	3,847.37
Gulo gulo	13,966.43	31,192.70
Gymnobelideus leadbeateri	4.42	868.92
Hippotragus equinus	1,305.86	7,241.11
Hylobates lar	5.35	896.11
Hylobates moloch	4.64	347.64
Lagorchestes conspicillatus	334.91	415.52

Leontopithecus rosalia	45.78	752.34
Loxodonta africana	4,432.12	6,785.66
Lycaon pictus	2,220.53	1,3861.23
Lynx lynx	7,205.84	9,564.78
Lynx rufus	1,1998.70	4,435.49
Macaca Silenus	7.41	1,034.69
Macropus robustus	364.91	3,955.73
Marmota flaviventris	171.79	715.22
Marmota marmota	12.97	236.15
Martes americana	1,173.04	1,745.93
Meles meles	372.04	1,610.74
Mustela nigripes	92.85	5,185.68
Neofelis nebulosa	365.25	2,969.26
Odocoileus virginianus	2,354.15	218.74
Ovibos moschatus	586.03	2,987.15
Ovis aries	380.97	423.49
Ovis canadensis	49.26	697.35
Ovis dalli	1,259.32	2,563.04
Ozotoceros bezoarticus	39.70	393.58
Pan troglodytes	16.42	11,663.12
Panthera leo	50,584.06	7,570.30
Panthera tigris	30,984.87	10,300.07
Papio cynocephalus	756.00	1,399.72
Peromyscus maniculatus	1.15	342.28
Petauroides volans	0.46	269.73
Petaurus gracilis	3.74	3,524.08
Petraurus australis	64.89	372.61
Phacochoerus aethiopicus	701.52	1,588.24
Phascolarctos cinereus	121.07	872.10
Puma concolor	7,575.01	11,822.09
Rangifer tarandus	466.44	3,978.62
Rhinoceros sondaicus	4,090.79	13,237.47
Rhinoceros unicornis	1,773.80	2,306.17
Rhinopithecus brelichi	32.37	986.46
Rucervus eldii	1,219.79	15,868.53
Saimiri oerstedii	2.69	158.00
Sciurus niger	4.40	228.51
Sus scrofa	1,463.38	934.13
Tapirus bairdii	381.90	2,336.17
Trichosurus caninus	9.95	1,030.14
Trinomys eliasi	61.74	672.69
Urocyon littoralis	37.56	2,162.86
Ursus americanus	1,129.01	5,462.34
Ursus arctos	10,441.77	19,518.73
Ursus maritimus	88,943.22	7,907.71
Ursus thibetanus	1,832.06	13,323.75
Zyzomys pedunculatus	21.99	455.02

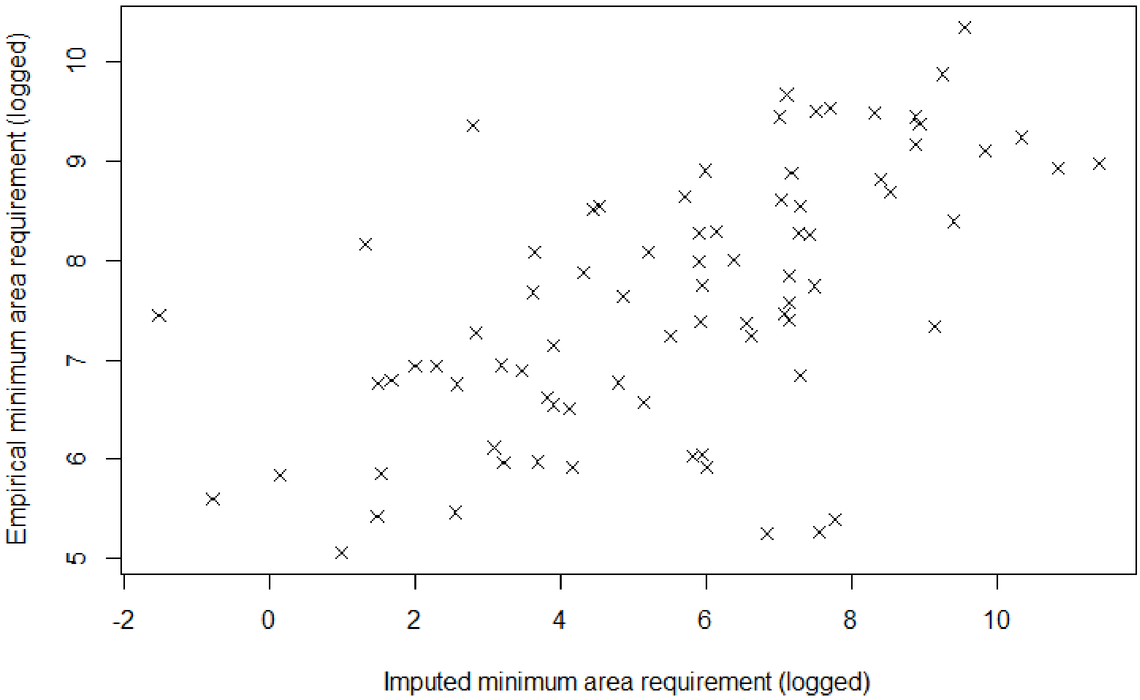


Figure 8. The 80 mammal species for which empirical minimum area requirement estimates as provided in Verboom et al. (2014), and their subsequent imputed minimum area requirements logged and plotted against each other. There was a moderate positive correlation between the empirical and imputed estimates of (log_e) minimum area requirements (Pearson r = 0.59, $p < 0.001$). The imputation took place for all mammal species across the globe, however only this subset of 80 mammal species is shown here. I imputed these values based on a combination of species traits expected to be associated with minimum area requirements: body mass, diet breadth, habitat breadth, home range size of a group and of an individual, maximum longevity, population density, basal metabolic rate, dispersal age at which young permanently leave their parent, population group size in which an individual spends the majority of their time, and the social group size of their social cohesive unit.

Species at a greater risk of extinction on the IUCN red list do not have greater minimum area requirements compared to species that are less threatened with extinction (Kruskal – Wallis $\chi^2 = 6.762$, df = 6, p = 0.344) (figure 9).

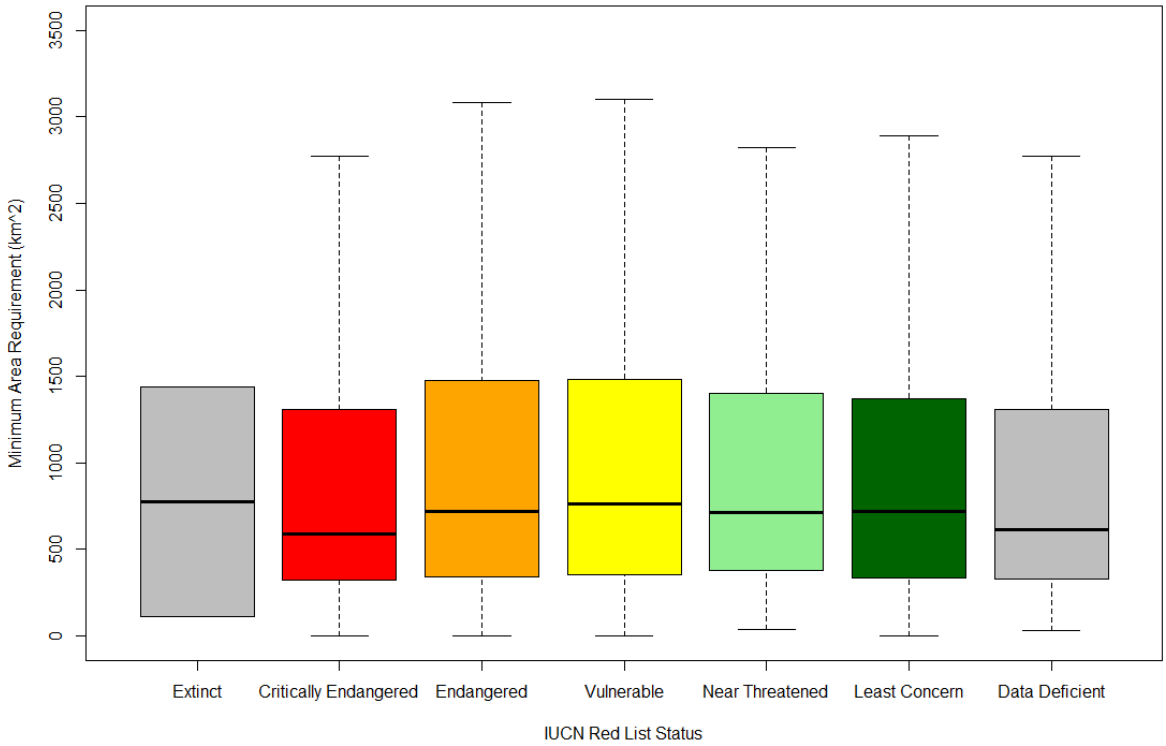


Figure 9, boxplot for all mammal species, comparing imputed minimum area requirements (km^2) to the IUCN red list status of those species (grey = extinct, red = critically endangered, orange = endangered, yellow = vulnerable, light green = near threatened, dark green = least concern, grey = data deficient).

Chapter 4

Habitat Restoration Priorities that Conserve Mammal Species Richness in the Year 2070 Under Climate Change

Abstract

Habitat restoration makes a very important contribution to the conservation of species, potentially reversing some of the detrimental effects to biodiversity caused by anthropogenic land use, which is one of the greatest present-day drivers of biodiversity loss. Identifying habitat restoration priorities can permit the most efficient use of scarce resources for conservation to conserve the greatest possible number of species. Restoring areas of anthropogenic land use to natural habitat can also enhance natural habitat connectivity, thus increasing the total area of contiguous habitat available to species. Previous studies into restoration do not generally consider the effects of climate change on future habitat suitability for species, nor do they incorporate the minimum area required by a species to persist into the future. Utilising projections of where mammals will be in the year 2070 under an intermediate climate change scenario, I identify patches of habitat that if restored would contribute to meeting species minimum area requirements. South and Central America, Western and Eastern Africa, Eastern and Southeast Asia, as well as large parts of Europe are highlighted as restoration priorities that conserve the greatest number of mammal species in the year 2070, whilst incorporating climate suitability projections of species, as well as ensuring that contiguous habitat is above mammal species' minimum area requirements. This result highlights how there is considerable potential for habitat restoration at a global scale, however, this study does not look at the feasibility of restoration within priority areas as I do not account for the direct and opportunity costs associated with such efforts. My results also show that the hypothetical habitat restoration in line with the priorities identified, would lead to a greater percentage increase in range area for mammal species with a greater extinction risk. This underscores the benefits of targeted conservation actions focussed on threatened species in mitigating biodiversity loss. The restoration priority maps produced in this research can act as guidance for conservation practitioners seeking to undertake more targeted and localised research, and they endeavour to understand the likely outcomes and practicalities of habitat restoration in specific local contexts.

Introduction

In the face of escalating climate and land-use change, which have important effects on biodiversity (Habibullah et al., 2022; Jantz et al., 2015; Newbold et al., 2015), prioritizing habitat restoration has emerged as a critical strategy for reversing species and habitat loss (Banks-Leite et al., 2020; Rey Benayas, Newton, Diaz, & Bullock, 2009). Some of the global targets currently in place for restoration include: at least 30% of all degraded ecosystems need to be under effective conservation by the year 2030 (CBD, 2024a); restoring degraded forests, land and soil (UNDP, 2024); and countries signing up to restore 1 billion hectares globally (United Nations, 2024). The benefits of habitat restoration, the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed (Mcdonald, Gann, Jonson, & Dixon, 2016), are numerous. Restoration can increase the size of a specific habitat area, providing resources for species, creating corridors and increasing connectivity, which facilitates species dispersal, and increases the number of species that naturally occur within a location (Török & Helm, 2017).

Land use change is causing the loss of multiple natural habitat types (Lehsten et al., 2015). Increases in human population is partly driving this change, as natural habitats are being converted to artificial land types such as urban areas (Güneralp, Reba, Hales, Wentz, & Seto, 2020) and agricultural landscapes (Genet, 2020), although land use change trajectories differ between the global South and the global North (Winkler, Fuchs, Rounsevell, & Herold, 2021). A study that looked at the projected impacts of meeting global targets for habitat restoration found projected increases in tree cover of 4 million km^2 by the year 2050, however, it also determined that these targets did not prevent the projected losses of other habitats such as grasslands (Wolff, Schrammeijer, Schulp, & Verburg, 2018). This emphasizes the importance of land management that avoids exclusively prioritising one habitat type, such as tree cover, and instead aims to conserve a range of natural habitat types.

The impact of land use change on species is also largely detrimental (Keil, Storch, & Jetz, 2015), and can lead to extinctions of species years later as isolated populations lose access to key resources for their survival (Halley, Monokrousos, Mazaris, Newmark, & Vokou, 2016). Before extinction occurs, there may be time to reverse the course of extinction through habitat restoration (Kuussaari et al., 2009). Under current habitat conditions, 8% of mammals, amphibians and birds are expected to become extinct due to the lagged effects of habitat loss; restoring just 15% of converted land globally is predicted to reduce that global extinction debt by 63%, through averting expected extinctions (Strassburg et al., 2020).

Rapid climate change means that areas restored to the naturally prevailing habitat may not remain climatically suitable for the target species in the future (Harris, Hobbs, Higgs, & Aronson, 2006). Climate change is a leading cause of biodiversity loss across the globe (Habibullah et al., 2022), causing substantial shifts in species ranges (Bellard et al., 2012; Kerr et al., 2015) and biomes (Boonman et al., 2022), and is disrupting interspecies interactions (Brambilla et al., 2020). It has been suggested that climate change be included in the design of habitat restoration by selecting sites based on projected climate changes, and accounting for the future distribution of the target species, while also acknowledging the uncertainty in future climate trajectories – although in practice restoration to date rarely combines all of these aspects (Simonson et al., 2021).

Ensuring that restored areas will remain effective into the future, is as much about ensuring that they are located in climatically appropriate areas, as it is about ensuring that they are large enough to support their target species. The minimum area requirement, the smallest area that a species can persist in to gain all its resources required for survival and reproduction to maintain a stable population, is a good way to set goals as to how large a habitat patch should be (van der Hoek, Zuckerberg, & Manne, 2015). Minimum area requirements are beginning to be used to inform conservation studies (Pe'er et al., 2014; Verboom et al., 2014; Wang et al., 2023), however, their usage is far from widespread. Indeed, there are potential failures of restoration efforts that don't encompass a sufficient size to accommodate the target species (Gittman et al., 2018; Morrison, Lindell, Holl, & Zahawi, 2010).

Some areas of the world are expected to be higher priority for restoration efforts due to their potential to conserve a higher number of species (Lewis et al., 2022). Regions currently experiencing rapid loss of habitat and land degradation, where there are larger quantities of agriculture and urban landscapes, may also be higher priorities for restoration efforts to help mitigate biodiversity loss (Ricketts & Imhoff, 2003). For example, tropical forests are an illustration of both aspects. They face accelerated loss of habitats driven by a demand for resources, such as agricultural expansion driving deforestation (Hoang & Kanemoto, 2021). They are also key to the health of our planet, not least because of the carbon capture and long term storage potential of trees and soils in these habitats (Koch & Kaplan, 2022), but also because of the heightened species richness of mammals in the tropics (Ceballos & Ehrlich, 2006; Schipper et al., 2008; Willig et al., 2003).

Some species are also expected to be higher priority for restoration efforts due to their vulnerability to habitat loss. Species that are at a greater risk of extinction often face more extreme anthropogenic threats (Gonçalves-Souza et al., 2020), meaning that suitable habitat patches can be more fragmented and isolated than for less threatened species (Kuipers et al., 2021). While restoration may increase the amount of habitat for species, the degree to which this occurs for species at a greater risk of extinction is uncertain.

In this study, I conduct a global analysis that identifies habitat restoration priorities that conserve mammal species richness in the year 2070 under future climate change. I take the minimum area requirements of species, as presented in Chapter 3 and use these to identify areas where habitat restoration could allow the creation of sufficiently large habitat patches that conserve the highest possible number of mammal species under climate change. I quantify gains in mammal species richness as a result of hypothetical restoration efforts, relative to expected mammal species richness levels without any restoration. Previous work identifying priorities for habitat restoration at a global level has not considered future projections of species distributions under climate change (Strassburg et al., 2020), although its importance has been highlighted (Simonson et al., 2021). Thus, I provide a new perspective on restoration priorities by accounting for climate change impacts on species distributions. I also aim to provide insight into the hypothetical restoration of some tropical forests, as I expect that these areas will be amongst a collection of sites that have the most to gain from restoration (Brancalion et al., 2019).

In this context I pose the following question - which areas of land, if restored to the prevailing natural habitat, have the potential to benefit the most mammal species when compared to a scenario without any restoration, and considering future climate-change impacts on species distributions. I predict that areas that are most exposed to anthropogenic pressures within naturally biodiverse regions will have the most potential to conserve mammal species. I also predict that species at greater risk of extinction will have a larger percentage increase in the total size of all habitat patches that are large enough to support future populations of a species after identified hypothetical restoration takes place, than less threatened species.

Methods

I identify areas where restoration of natural habitats could be feasible, and from these areas identify priorities where restoration is expected to conserve the greatest average local number of mammal species, given species' expected distributions in 2070 under an intermediate climate change scenario (RCP 4.5), and requiring that areas of habitat meet the minimum area requirements of species. For each species, I start from the maps produced in Chapter 3, which identify areas of intact habitat that are situated in climatically suitable areas in the year 2070 (see Chapter 3, "Spatial Analysis" for methods). These projections of suitable climate come from expert-drawn species distribution maps of mammal species under 4 climatic variables important to determining vertebrate distributions: minimum temperature of the coldest month, total annual precipitation, growing degree days, and water balance (Newbold, 2018). I also identify areas of artificial habitat from a global map of current habitat types, that corresponds to those listed on the IUCN Red List (Jung et al., 2020), compared against the naturally occurring habitat type within those areas, from a global map of naturally occurring habitat types before anthropogenic influence (Jung, 2020). I use the habitat suitability of species (as listed on the IUCN Red List, 2022; see Chapter 3, "Habitat Suitability" for detailed methods), to see if a conversion of artificial land to naturally occurring habitat would benefit each species. For an area of suitable climate and habitat to be considered able to support the persistence of species, it must provide enough contiguous land (restored and original suitable habitat) to meet a species' minimum area requirement. I use the imputed minimum area requirement estimates for all mammal species presented in Chapter 3 to determine this threshold (see Chapter 3, "Minimum Area Requirements" for full methods). Imputations were based on species' body mass, home range size, habitat breadth, diet breadth, basal metabolic rate, population density, maximum longevity and dispersal age, for which trait estimates were obtained from the PanTHERIA database (Jones et al., 2009). The final areas identified as priorities for habitat restoration were those expected to conserve the greatest average local number of mammal species by creating areas of contiguously intact suitable habitat within climatically suitable areas, large enough to meet species' minimum area requirements. More precise details about each of these steps are given in the following sections.

Habitat restoration feasibility

I only consider as candidates for restoration, areas currently under the terrestrial artificial habitat category (Jung et al., 2020), which is land that has been severely modified by humans away from its natural state. I do not consider rural gardens or urban areas as candidates for restoration (table 1), which is in line with other published research that only considered cropland or pastureland as suitable for restoration (Strassburg et al., 2020).

Table 1. List of terrestrial artificial habitat types and their definitions (Jung et al., 2020), and whether they are considered feasible candidates for restoration to a natural habitat type.

Terrestrial Artificial Habitat Types	Definition	Candidate for Restoration
Arable land	Cereal fields, rice paddies, perennial crops, orchards and groves.	Yes
Pastureland	Permanent grasslands, sometimes treated with herbicides, with degraded flora and fauna. Also includes secondary grasslands and wooded farmland.	
Plantations	Planting of trees and shrubs that are maintained on economic bases other than that of subsistence farming.	
Subtropical tropical heavily degraded former forest	Former subtropical or tropical forest that has been extensively cleared or impacted by human activities.	
Rural gardens	Small plots that are often in close proximity to houses, they usually employ fences and have a high intensity of land use. These gardens have a mix of annual, semi-permanent and perennial crops, and also provide space for the raising of small animals. Sometimes these areas are the only source of income for the rural poor.	No
Urban areas	Usually metropolitan and commercial areas that are dominated by asphalt, concrete and roof. Includes buildings, lawns and parks.	

If the habitat currently existing in an area is a candidate for restoration, then I use a map which predicts the distribution of 8 terrestrial habitats that would naturally occur (under 1970-2015 average climatic conditions) if there was no anthropogenic influence in the landscape (Jung, 2020). To assess whether each species can live in the naturally occurring habitat of an area, I downloaded a list of the habitats in which each mammal species can survive (IUCN, 2023). The suitability of habitat for mammals is classified either as: suitable – the species occurs in the habitat regularly or frequently; marginal – the species occurs in the habitat irregularly or infrequently, or only a small proportion of individuals are found in the habitat; or unknown – the habitat is of unknown importance to the species. Habitats listed as being suitable or marginally suitable for species are considered potentially beneficial for species in this study. The broad habitat categories I use are appropriate for a global-scale analysis, where I aim to identify the broad areas where species might be conserved in 2070, if the artificial land type were to be restored to its naturally occurring land type. The linkage between the fine scale present day habitat / land use map and coarser habitat classification of naturally occurring land types is the same as used in the published present day habitat / land use map (Jung et al., 2020) (table 2).

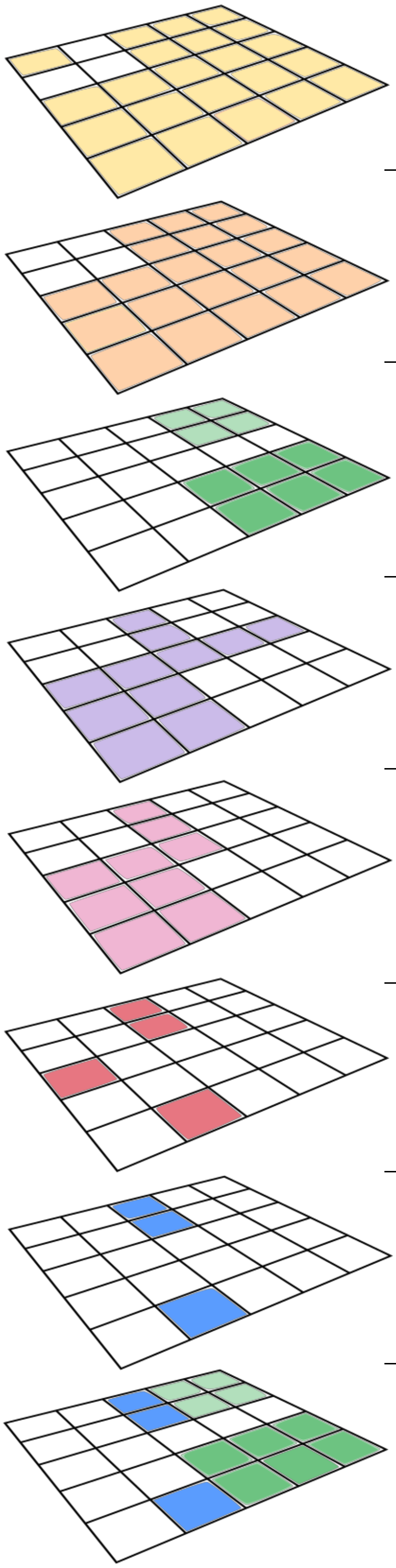
Table 2. Mapping between fine-scale and coarse-scale terrestrial habitat classifications, as proposed by Jung et al. (2020) in their habitat/land use map. I use the coarse-scale terrestrial habitat type to define whether habitat is suitable for species, and if it should be recommended for hypothetical restoration.

Fine-Scale Terrestrial Habitat	Coarse-Scale Terrestrial Habitat
Forest boreal	
Forest subarctic	
Forest subantarctic	
Forest temperate	
Forest subtropical tropical dry	Forest
Forest subtropical tropical moist lowland	
Forest subtropical tropical mangrove vegetation above high tide level	
Forest subtropical tropical swamp	
Forest subtropical tropical moist montane	
Savanna dry	Savana
Savanna moist	
Shrubland subarctic	
Shrubland subantarctic	
Shrubland boreal	
Shrubland temperate	Shrubland
Shrubland subtropical tropical dry	
Shrubland subtropical tropical moist	
Shrubland subtropical tropical high altitude	
Shrubland mediterranean type shrubby vegetation	
Grassland tundra	
Grassland subarctic	
Grassland subantarctic	
Grassland temperate	Grassland
Grassland subtropical tropical dry	
Grassland subtropical tropical seasonally wet flooded	
Grassland subtropical tropical high altitude	
Wetlands inland permanent rivers streams creeks includes waterfalls	
Wetlands inland seasonal intermittent irregular rivers streams creeks	
Wetlands inland shrub dominated wetlands	
Wetlands inland bogs marshes swamps fens peatlands	
Wetlands inland permanent freshwater lakes over 8 ha	
Wetlands inland seasonal intermittent freshwater lakes over 8 ha	
Wetlands inland permanent freshwater marshes pools under 8 ha	
Wetlands inland seasonal intermittent freshwater marshes pools under 8 ha	
Wetlands inland freshwater springs and oases	
Wetlands inland tundra wetlands inc. pools and temporary waters from snowmelt	Wetlands
Wetlands inland alpine wetlands inc. temporary waters from snowmelt	
Wetlands inland geothermal wetlands	
Wetlands inland permanent inland deltas	
Wetlands inland permanent saline brackish or alkaline lakes	
Wetlands inland seasonal intermittent saline brackish or alkaline lakes	
Wetlands inland permanent saline brackish or alkaline marshes pools	
Wetlands inland seasonal intermittent saline brackish or alkaline marshes	
Wetlands inland karst and other subterranean hydrological systems inland	
Rocky areas e.g. inland cliffs mountain peaks	Rocky
Caves and subterranean habitats non-aquatic caves	Caves
Caves and subterranean habitats non-aquatic other subterranean habitats	
Desert hot	
Desert temperate	Desert
Desert cold	

Spatial analysis

I start with projections of the climatically suitable distribution of species in 2070, under RCP 4.5 (Newbold, 2018) (figure 1: Climate). These maps are projected using the World Geodetic System 1984 (WGS84) at a resolution of 10 km × 10 km. I disaggregate these maps to 833 m × 1,111 m to match the final resolution of the species richness maps produced from Chapter 3, and to allow for a comparative spatial data analysis. For each species I identify contiguous areas of suitable climate using the clump function from the raster package (version 3.6) in R (version 4.0.2). Cells are considered a group if they are adjacent to one another either diagonally, horizontally or vertically (figure 1: Climate MAR). Groups of adjacent cells that have a combined area of less than the minimal area requirement of the species in question are removed from the map, as I only want to identify restoration in areas that are climatically suitable and could potentially meet species minimum area requirements. Methods to determine the minimal area requirements of mammals are described in Chapter 3, “Minimum Area Requirements”.

Maps for each species containing areas of suitable climate and habitat are derived from Chapter 3 (figure 1: Climate & Habitat). I use these individual species maps to identify from the areas within the suitable climate that do not currently have suitable habitat for species, and thus are potential candidates for restoration (figure 1: Suitable Climate & Currently Unsuitable Habitat). Of these areas, I consider as feasible candidates for restoration those where the potential naturally occurring habitat is suitable for the species in question (figure 1: Natural Habitat) and the current habitat is artificial and considered potentially feasible to restore to natural habitat (figure 1: Artificial Habitat). Finally, I consider as potentially beneficial for the species only those areas (including both restored habitat and currently suitable habitat) that are above the minimum area requirements of the species (figure 1: Beneficial Hypothetical Restoration). The resulting areas recommended for restoration for each species are plotted on top of each other to make species richness maps that highlight priorities for restoration across the globe.



Label	Description
Climate	Suitable climate for species. Projections from Newbold (2018).
Climate MAR	Suitable climate for species that also meets the species minimum area requirements.
Climate & Habitat MAR = dark green Climate & Habitat = light green	Areas that currently have suitable habitat for the species (woodland in this case), which are located in climatically suitable areas (Climate). Dark green patches (Climate & Habitat MAR) meet the minimum area requirements of the species, light green patches (Climate & Habitat) are smaller than the minimum area required by the species. Derived from maps presented in Chapter 3.
Suitable Climate & Currently Unsuitable Habitat	Areas within the suitable climate that do not currently have suitable habitat for the species, and thus are potential candidates for restoration.
Natural Habitat	Areas within those considered as potential candidates for restoration (Suitable Climate & Currently Unsuitable Habitat) that would have appropriate natural habitat after restoration. E.g. These areas would naturally be forest habitat, the preference for this example species, regardless of what habitat currently exists in these areas. Naturally occurring habitat maps from Jung (2020).
Artificial Habitat	Areas within those considered potential candidates for restoration (Natural Habitat) where the current habitat is artificial and considered feasible for restoration. E.g. These areas are currently croplands. Current day habitat/land use maps from Jung et al. (2020).
Beneficial Hypothetical Restoration	Cells that have a combination of: naturally occurring appropriate habitat for the species (Natural Habitat), considered feasible for restoration (Artificial Habitat), and also when added to the Climate & Habitat layer make patches that are above the minimum area requirement threshold for the species.
Climate & Habitat MAR = dark green Climate & Habitat = light green Restored = blue	Final map that shows the gains from restoration. Dark green patch is now one square larger owing to hypothetical habitat restoration, while the light green patch is now large enough to meet the minimum area requirements of this species (6 squares).

Figure 1. Graphic illustration of how I identified candidate areas where restoration is expected to allow a species to persist in areas that would be unsuitable without restoration. The hypothetical species depicted requires 6 squares of intact habitat to meet its minimum area requirements (MAR) and has a preference for forest habitats. The identification of beneficial hypothetical habitat restoration proceeds from top to bottom of this figure.

Potential for Area Gains for Species with Different Levels of Extinction Risk

I downloaded the IUCN Red List status for all mammal species (IUCN, 2023), which attributes one of the following extinction-risk statuses to each species: least concern, near threatened, vulnerable, endangered, critically endangered, extinct or data deficient. I then assess the percentage increase in predicted available area for species with compared to without hypothetical habitat restoration among species with different levels of extinction risk. As percentage gains in range area are not normally distributed, I perform a Kruskal Wallace test to explore if there are significant differences in the hypothetical gains in range area among groups of species with different levels of extinction risk.

Results

The areas where the greatest number of mammal species are expected to benefit from restoring artificial habitat to the naturally occurring habitat type, given predicted species distributions in 2070 under an intermediate-emissions climate scenario, include large parts of South America, especially Brazil, the Central America region, large parts of Eastern Africa, including Madagascar, Uganda, Rwanda, Burundi and South Sudan, large parts of Eastern Asia, in particular China, large parts of Southeast Asia, including Indonesia, as well as Southern Europe, including Croatia and Slovenia (figure 2). The hypothetical restoration identified contributes to meeting species' minimum area requirements, either through increases in the size of suitable patches that already satisfy a species' minimum area requirement, the extension or joining of patches of existing suitable habitats that were previously too small to meet a species' minimum area requirements, or through the creation of entirely new patches of habitat.

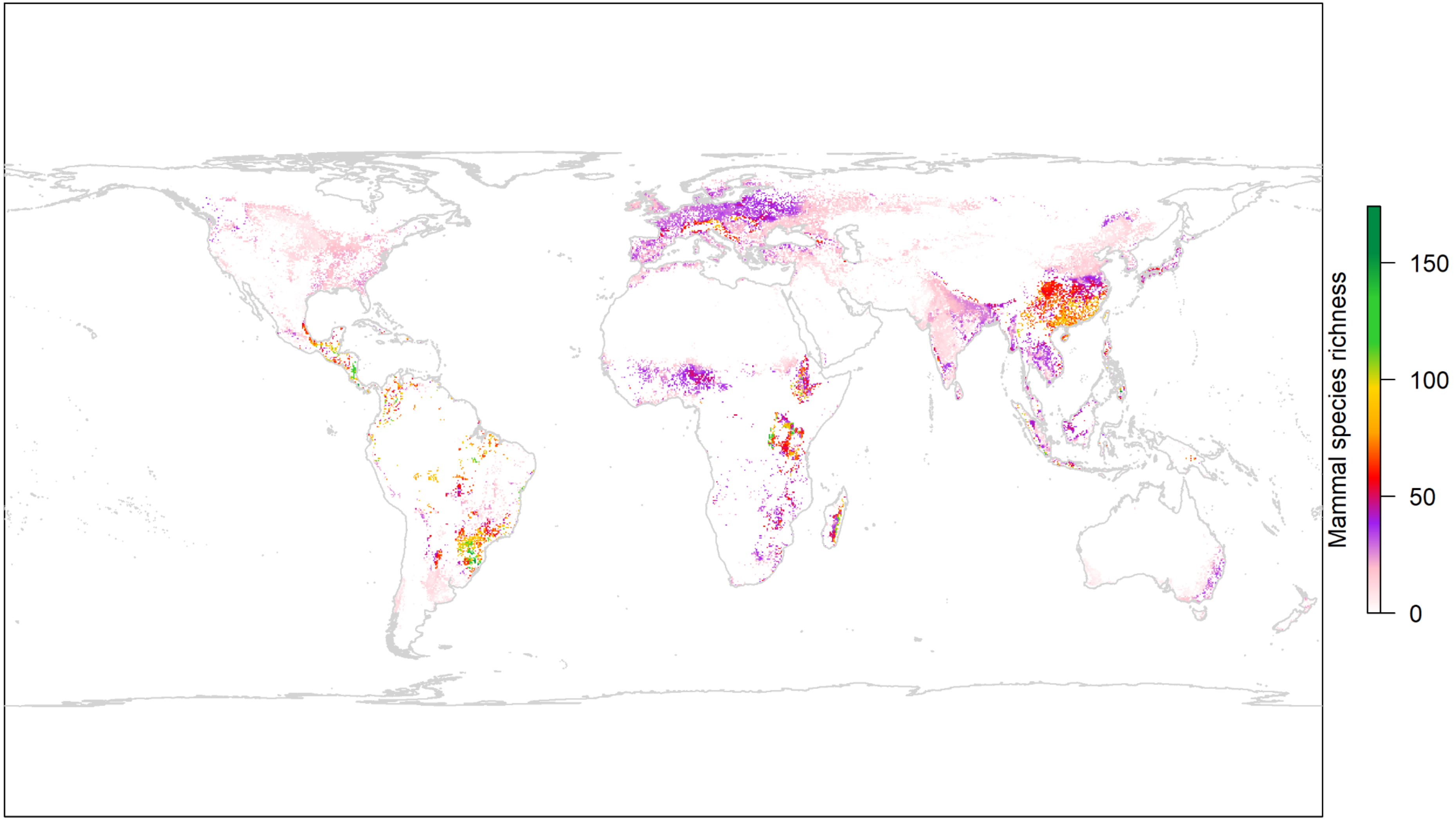


Figure 2. Assuming expected future species distributions, under an intermediate-emissions climate change scenario (RCP 4.5) in 2070, the number of mammal species that would meet their minimum area requirement by restoring an area to its natural habitat type. Expected gains are achieved by the creation of new habitat patches, or by the extension/joining of existing patches to meet species' minimum area requirements.

The correlation coefficient between the area of restored habitat that adds to the minimal area requirements of a species (figure 1, Beneficial Hypothetical Restoration), and the area of newly connected habitat that is now large enough to meet a species minimal area requirement (figure 1, Climate & Habitat) is $r = 0.92$, indicating a strong positive linear relationship between the two variables ($n = 4625$, $p < 0.001$). I used a linear regression model to examine the relationship between restoration and newly connected land; for every 10km of habitat restored, 1.64km of habitat that was previously too small to meet minimum area requirements but contained suitable habitat and climate (figure 1, Climate & Habitat), is connected up that meets a species' minimum area requirements (estimate = 0.164, se = 0.001, $p < 0.001$).

If the areas identified in figure 2 were restored to their naturally occurring habitat types, then the projection of mammal species richness under an intermediate climate change scenario in the year 2070 derived from my analysis in Chapter 3 taking into consideration species minimal area requirements (figure 3), will lead to more habitat that meets more species minimum area requirements. I present the prediction of mammal species richness in the year 2070 under an intermediate climate change scenario that includes hypothetically feasible restored habitat and newly connected habitat that now meets or surpasses a species minimum area requirement (figure 4).

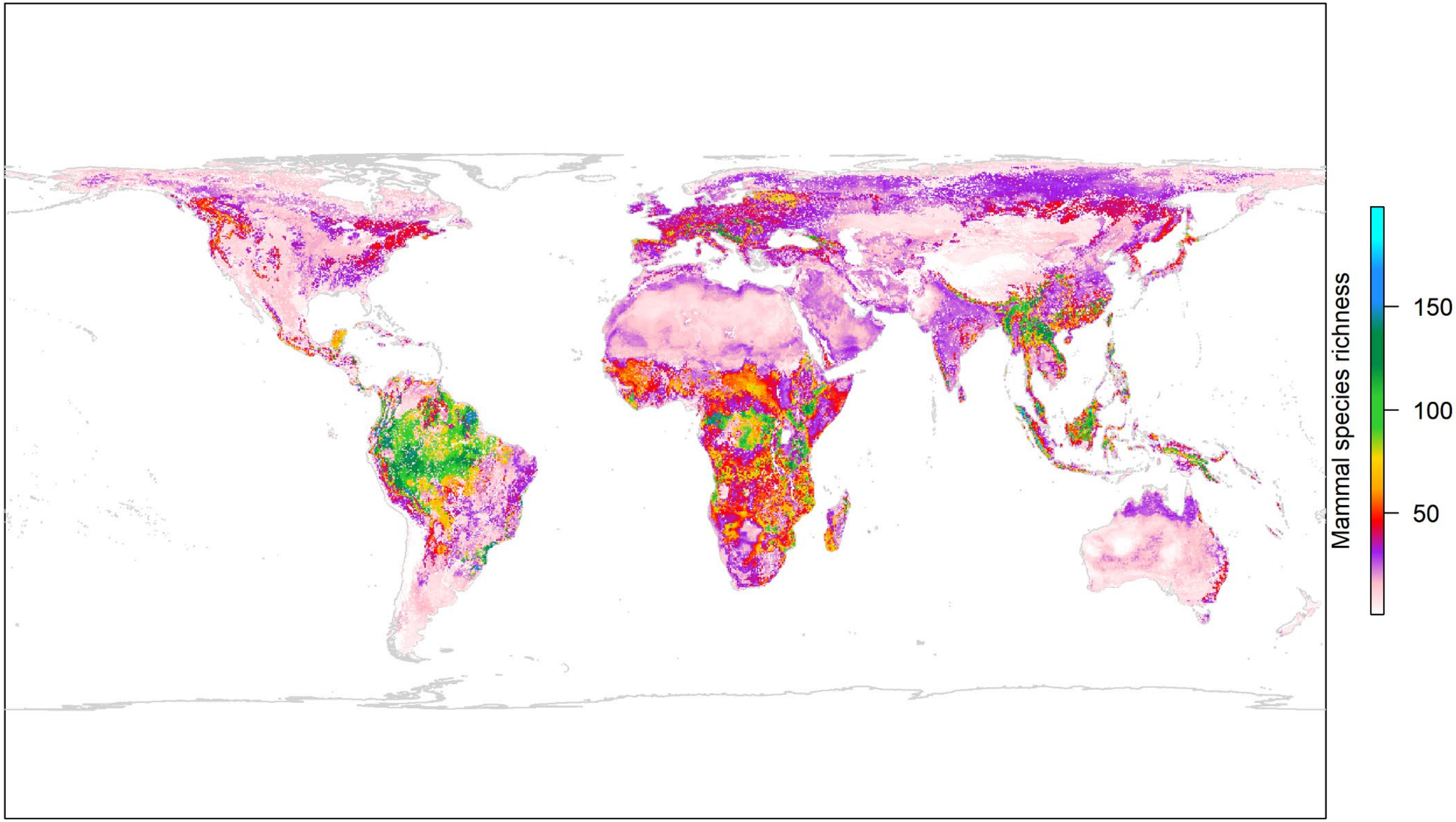


Figure 3. Projected mammal species richness in 2070 under the RCP 4.5 climate scenario, taking into account climate suitability, habitat suitability and the minimum area requirements of species, assuming that current land use/cover is maintainted to the year 2070. This map is based on the data presented in Suplimentary material Figure 1B in Chapter 3 of my thesis, presented again here for direct comparison with projections based on the restoration of habitat (Figure 4).

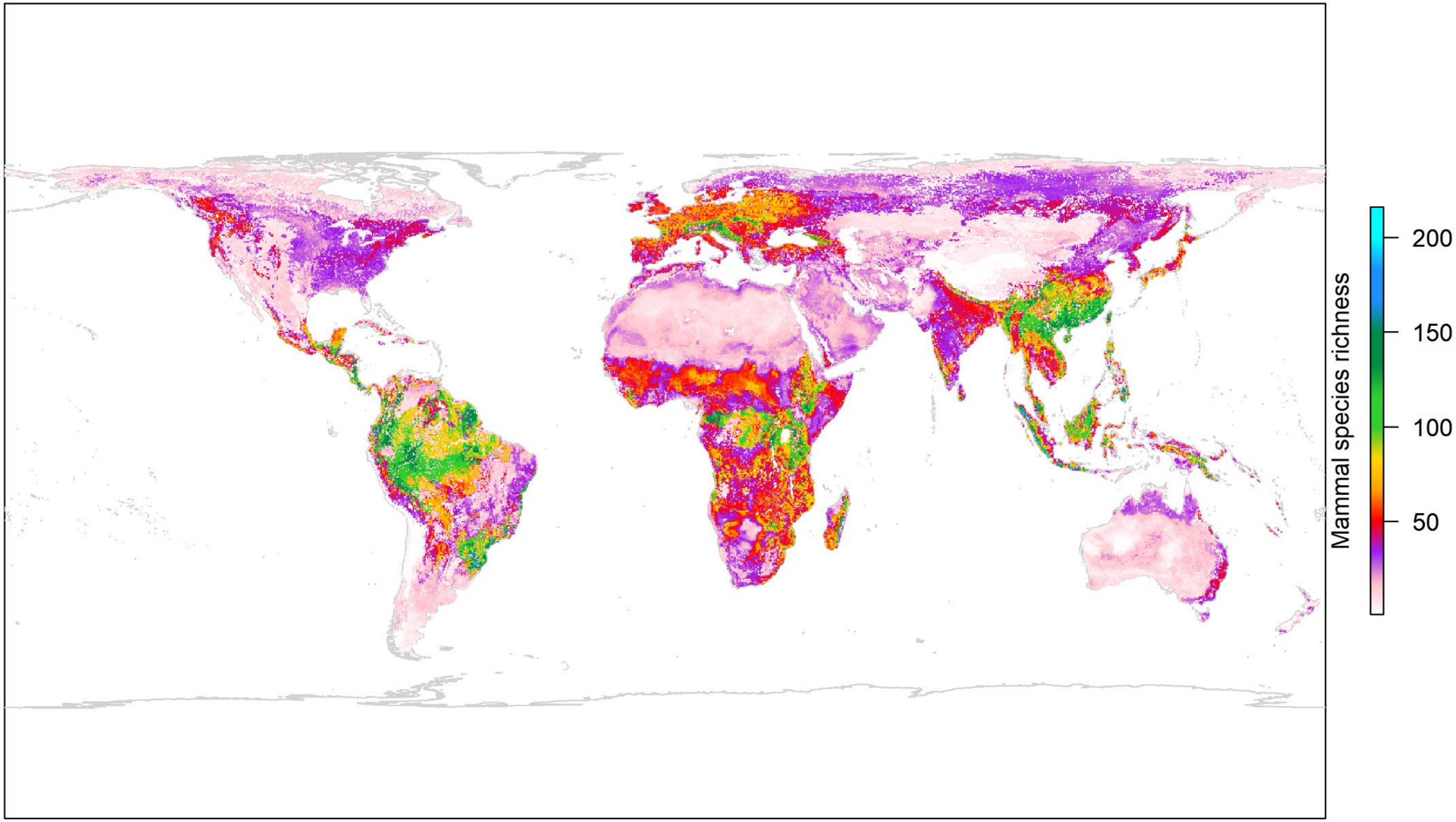


Figure 4. Projected mammal species richness in 2070 under the RCP 4.5 climate scenario, taking into account climate suitability, habitat suitability and the minimal area requirements of species, and assuming the hypothetical restoration of natural habitat in areas that will create new natural habitat that contributes to meeting the minimum area requirement of species in future climatically suitable areas.

It is important to highlight that some countries are more biodiverse than others, and so while restoration in these areas has the potential to support a higher absolute number of mammal species, restoration in other areas may lead to greater relative benefits. Relative benefits of habitat restoration were greatest in Central America, the Caribbean, South America – in particular in Brazil, Chile, Ecuador, Columbia and Venezuela, the east coast of North America, Southern Europe – in particular in Portugal and the South of Spain, parts of Western Africa – in particular in Nigeria, Eastern Africa – in particular in Madagascar, and the countries surrounding Lake Victoria (Kenya, Tanzania and Uganda), Eastern Asia – in particular in central China, and Southeast Australia (figure 5).

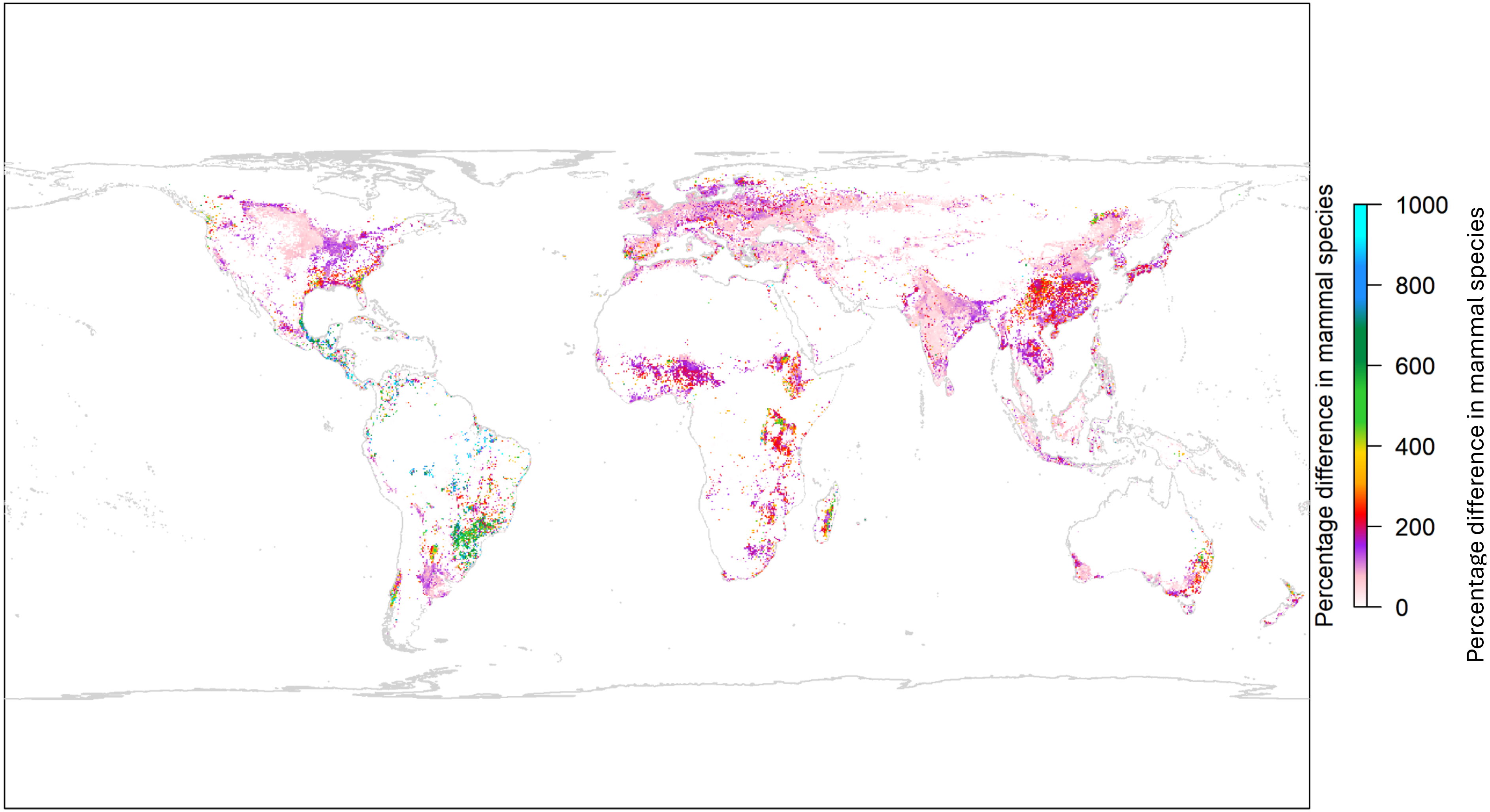


Figure 5. Percentage difference in expected mammal species richness in 2070 given projected species distributions under the RCP 4.5 climate scenario, between a situation with no restoration of habitats (figure 3), and where habitats have been restored in areas where the creation of natural habitats supports the meeting of species' minimum area requirements (figure 4).

Of the countries that stand to gain the most for mammal species richness from restoration, Brazil, China and Madagascar are currently some of the most biodiverse in the world, and face increased anthropogenic pressures from expanding agricultural practices and urbanisation. I take each of these countries in turn to explore some of the patterns in detail.

Brazil case study

Land use change, such as the anthropogenic impacts of agricultural expansion within the arc of deforestation (a region where agricultural land is currently replacing forested land), are identified as restoration priorities that would enable large amounts of mammal species to meet their minimum area requirements (figure 6.2.A). The artificial habitat in the North of the country (figure 6.2.F) is also largely considered to be suitable for restoration, as it meets the conditions outlined in the methods of this study. It is also in the North where the greatest benefits of habitat restoration for mammal species richness are expected (figure 6.2.B), as well as where species richness is projected to increase under climate (figure 6.2.C) and climate and habitat (figure 6.2.D), when comparing the present day to the year 2070. By looking at projected changes in species richness caused by climate alone, we can see that climate plays a large part in determining mammal species richness. There are two main naturally occurring habitat types in Brazil, forest in the North and South, and savanna habitat in the centre (figure 6.2.E). In Brazil it appears that forest compatible species have the most to gain from restoration, as forested areas conserve more mammal species than within naturally occurring savannah habitat.

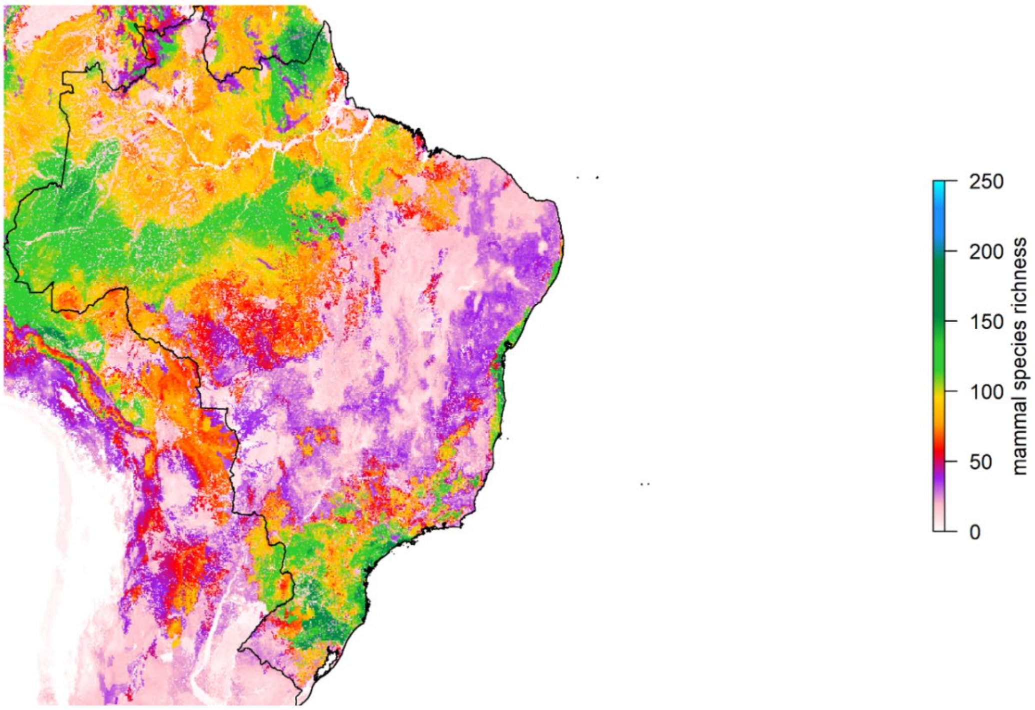


Figure 6.1. Mammal species richness in 2070 under RCP 4.5 in a post restoration scenario that takes into account the minimum area requirements of mammals. Map derived from figure 4 and cropped to extent of Brazil.

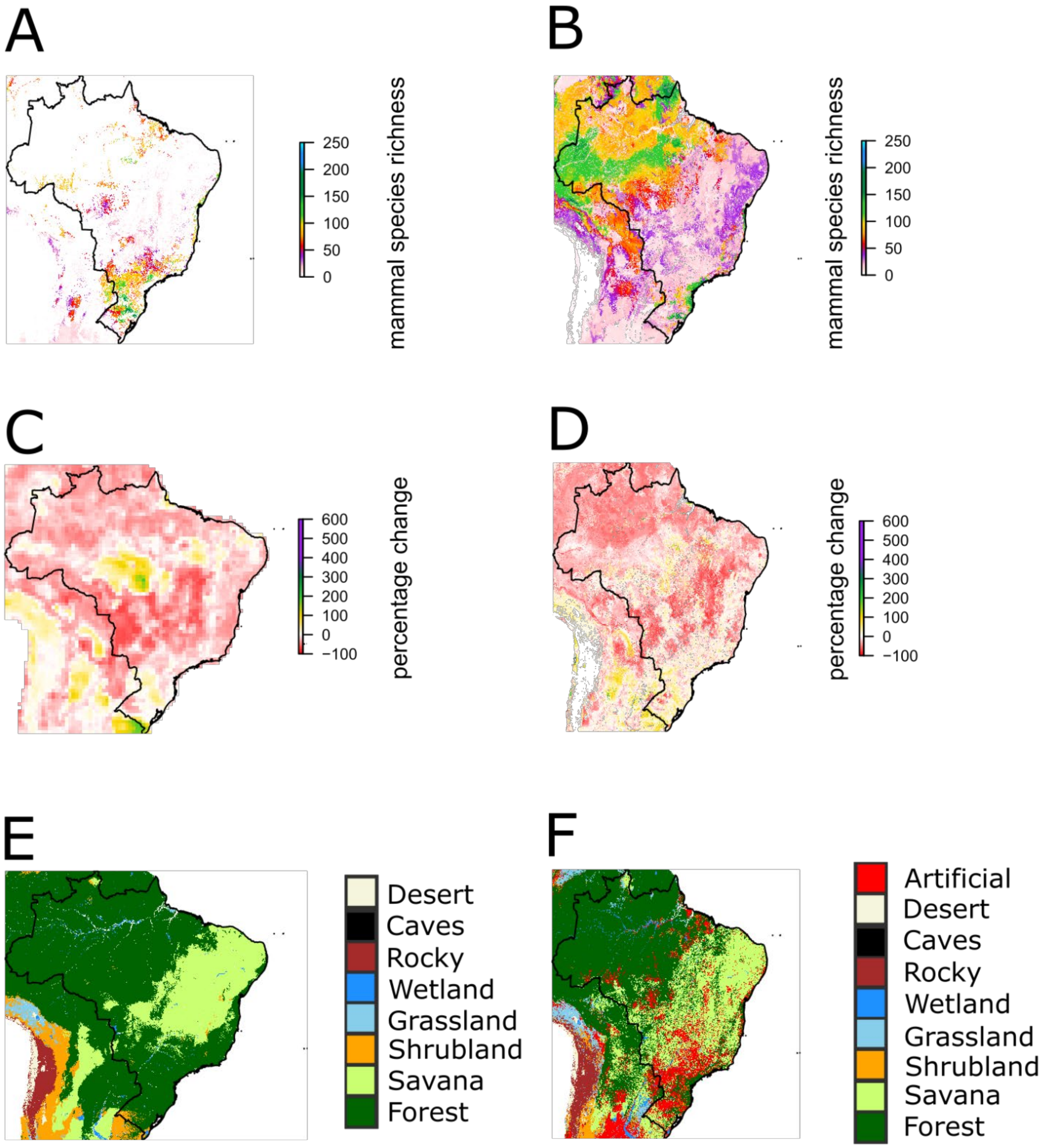


Figure 6.2. Each map cropped to extent of Brazil. A, areas hypothetically recommended for restoration as they add to the minimal area requirements of species in the year 2070 under RCP 4.5, derived from figure 2. Number of species to benefit from hypothetical restoration depicted in species richness; B, projected mammal species richness under suitable climate and suitable habitat in the year 2070 under RCP 4.5, without restoration, derived from figure 3; C, percentage difference in suitable climate for species between current day and year 2070 RCP 4.5, without taking into account species minimum area requirements; D, percentage difference in suitable climate and habitat for mammal species between current day and year 2070 RCP 4.5, without taking into account minim area requirements; E, naturally occurring habitat before anthropogenic influence (Jung, 2020); F, present day land use / habitat type (Jung et al., 2020)

China case study

Large parts of the east of China if restored will lead to more species being able to meet their minimum area requirements in the year 2070 (figure 7.2.A). In particular, restoration in the southeast will increase the total area for the most amount of mammal species. This area is historically forest habitat (figure 7.2.E), however currently largely contains artificial habitat (figure 7.2.F). Climatically this area is also projected to become suitable for a larger amount of species in the future than during the present day (figure 7.2.C), even when considering current habitat restraints (figure 7.2.D).

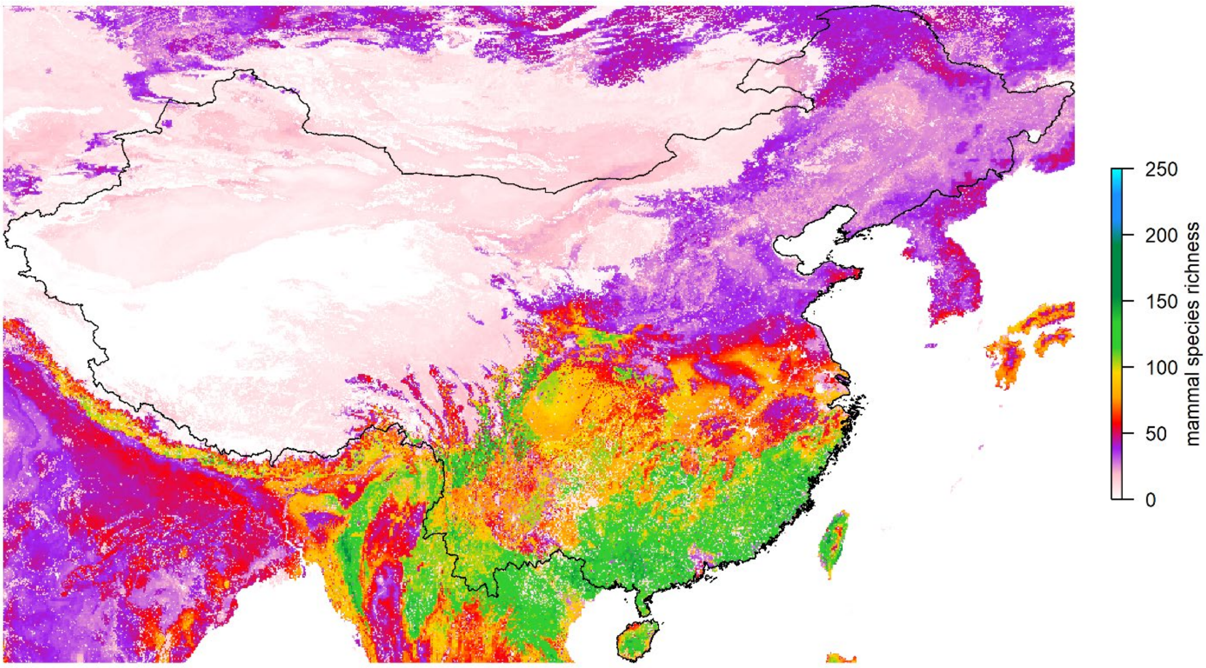


Figure 7.1. Mammal species richness in 2070 under RCP 4.5 with restoration completed and taking into account the minimum area requirements of mammals. Map derived from figure 4, and cropped to extent of China.

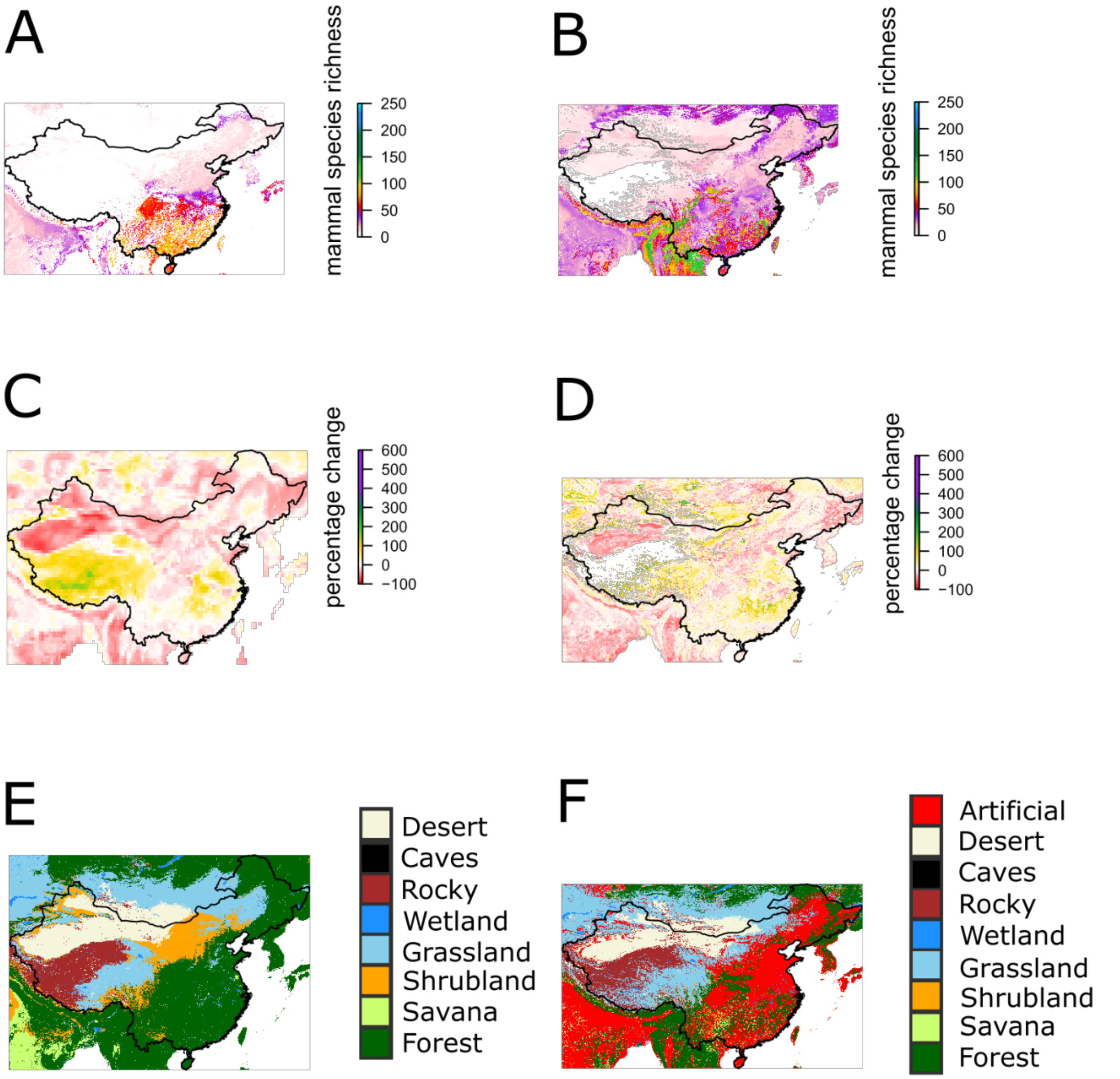


Figure 7.2. Each map cropped to the extent of China. A, areas hypothetically recommended for restoration as they add to the minimal area requirements of species in the year 2070 under RCP 4.5, derived from figure 2. Number of species to benefit from hypothetical restoration depicted in species richness; B, projected mammal species richness under suitable climate and suitable habitat in the year 2070 under RCP 4.5, without restoration, derived from figure 3; C, percentage difference in suitable climate for species between current day and year 2070 RCP 4.5, without taking into account species minimum area requirements; D, percentage difference in suitable climate and habitat for mammal species between current day and year 2070 RCP 4.5, without taking into account minim area requirements; E, naturally occurring habitat before anthropogenic influence (Jung, 2020); F, present day land use / habitat type (Jung et al., 2020).

Madagascar case study

Madagascar historically is made up of savanna habitat on the East and South coasts, shrubland in the centre, and forest habitat in the remaining majority of the island (figure 8.2.E). It is striking that today the majority of the island is now filled with savanna habitat, and what was shrubland is now largely artificial habitat (figure 8.2.F). It is the centre of the island that has been largely identified as increasing the number of mammals that will meet their minimum area requirements if restored to the naturally occurring habitat type (figure 8.2.A). This will greatly improve the outlook for mammal species richness in the year 2070 when comparing a before restoration (figure 8.2.B) and after restoration scenario (figure 8.1). Looking to the climate change projected to occur in this area, it is largely the East coast of the island that is projected to see increases in mammal species richness when comparing the present day to the year 2070 (figure 8.2.C), and this is also the case when current day habitat use is considered (figure 8.2.D).

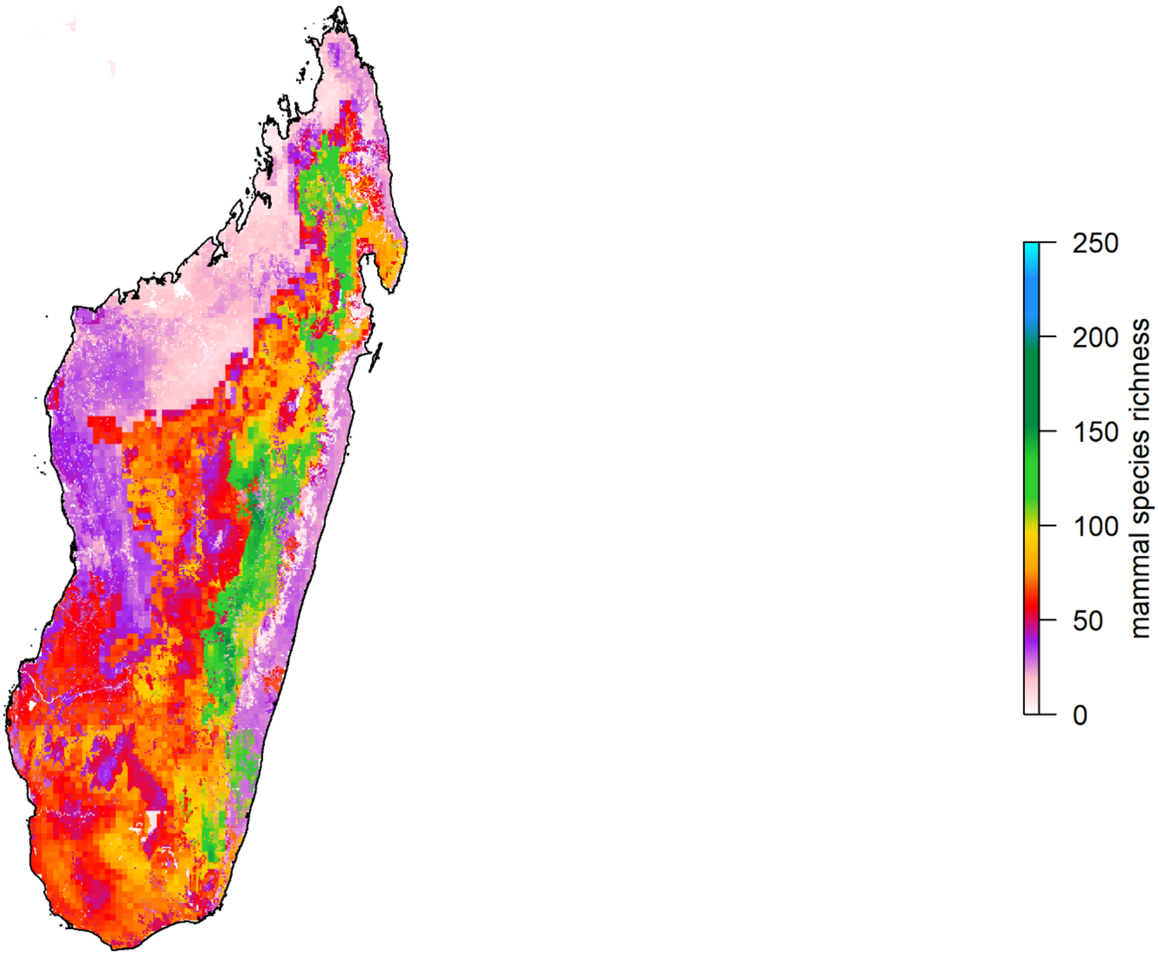


Figure 8.1. Mammal species richness in 2070 under RCP 4.5 with restoration completed and taking into account the minimum area requirements of mammals. Map derived from figure 4, and cropped to extent of Madagascar.

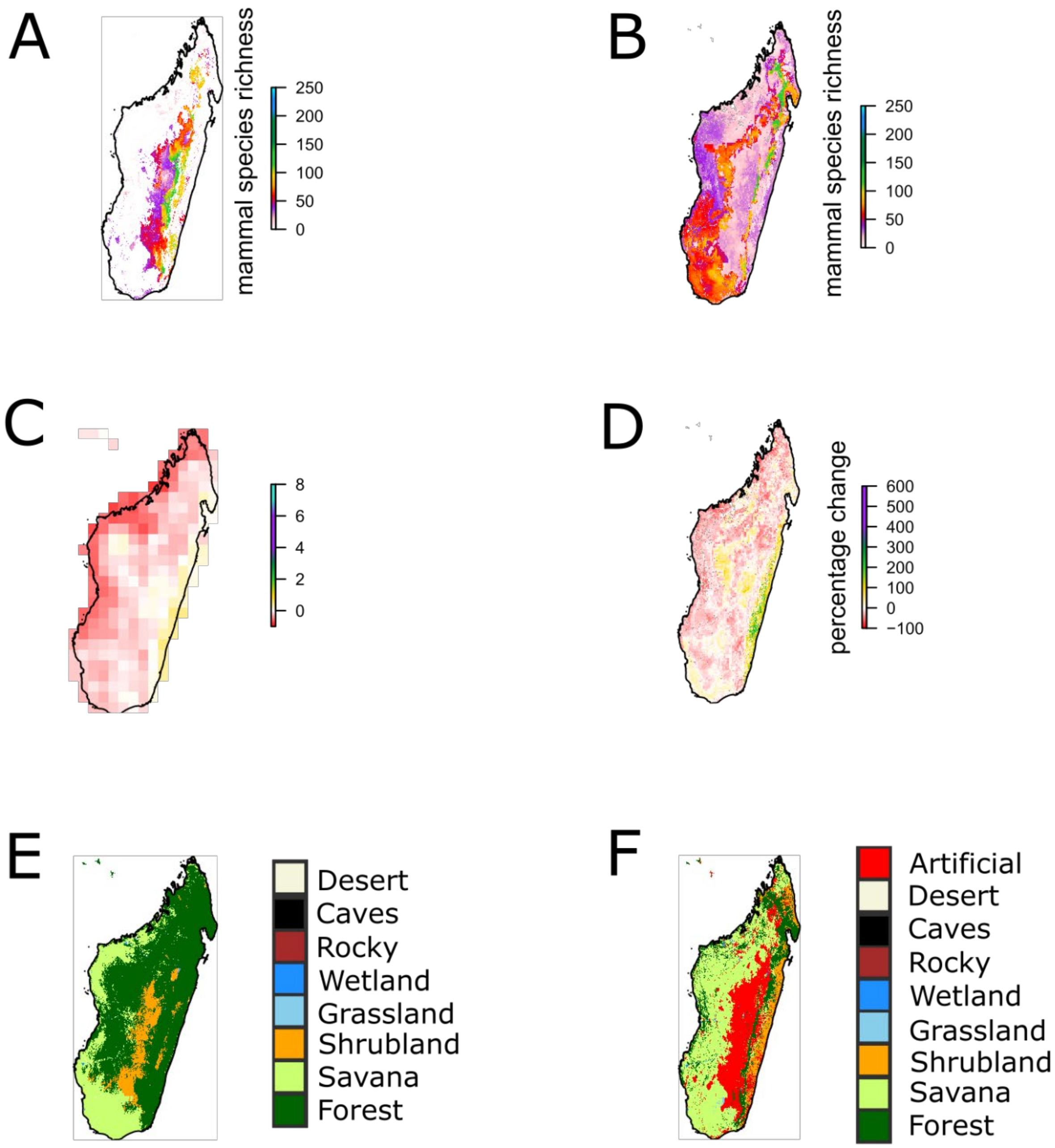


Figure 8.2. Each map cropped to the extent of Madagascar. A, areas hypothetically recommended for restoration as they add to the minimal area requirements of species in the year 2070 under RCP 4.5, derived from figure 2. Number of species to benefit from hypothetical restoration depicted in species richness; B, projected mammal species richness under suitable climate and suitable habitat in the year 2070 under RCP 4.5, without restoration, derived from figure 3; C, percentage difference in suitable climate for species between current day and year 2070 RCP 4.5, without taking into account species minimum area requirements; D, percentage difference in suitable climate and habitat for mammal species between current day and year 2070 RCP 4.5, without taking into account minim area requirements; E, naturally occurring habitat before anthropogenic influence (Jung, 2020); F, present day land use / habitat type (Jung et al., 2020).

IUCN red list

Species considered to be at a higher risk of extinction have higher potential increase in total available habitat that meet their minimum area requirements under hypothetical habitat restoration than species at a lower risk of extinction (figure 9). A Kruskal Wallace test showed significant difference in the expected percentage increase in suitable area for species (suitable climate and habitat of sufficient size to meet species' minimum area requirements) that could be achieved by habitat restoration depending on the extinction-risk category of species ($\chi^2 = 31.69$, df = 5, $p < 0.001$). In particular, using a Dunns test I could determine that there was a significant difference between the endangered and least concern groups ($Z = 3.31$, $p = 0.007$), as well as between the data deficient and: vulnerable ($Z = -3.70$, $p = 0.001$), endangered ($Z = -4.28$, $p < 0.001$) and critically endangered groups ($Z = 3.50$, $p = 0.004$).

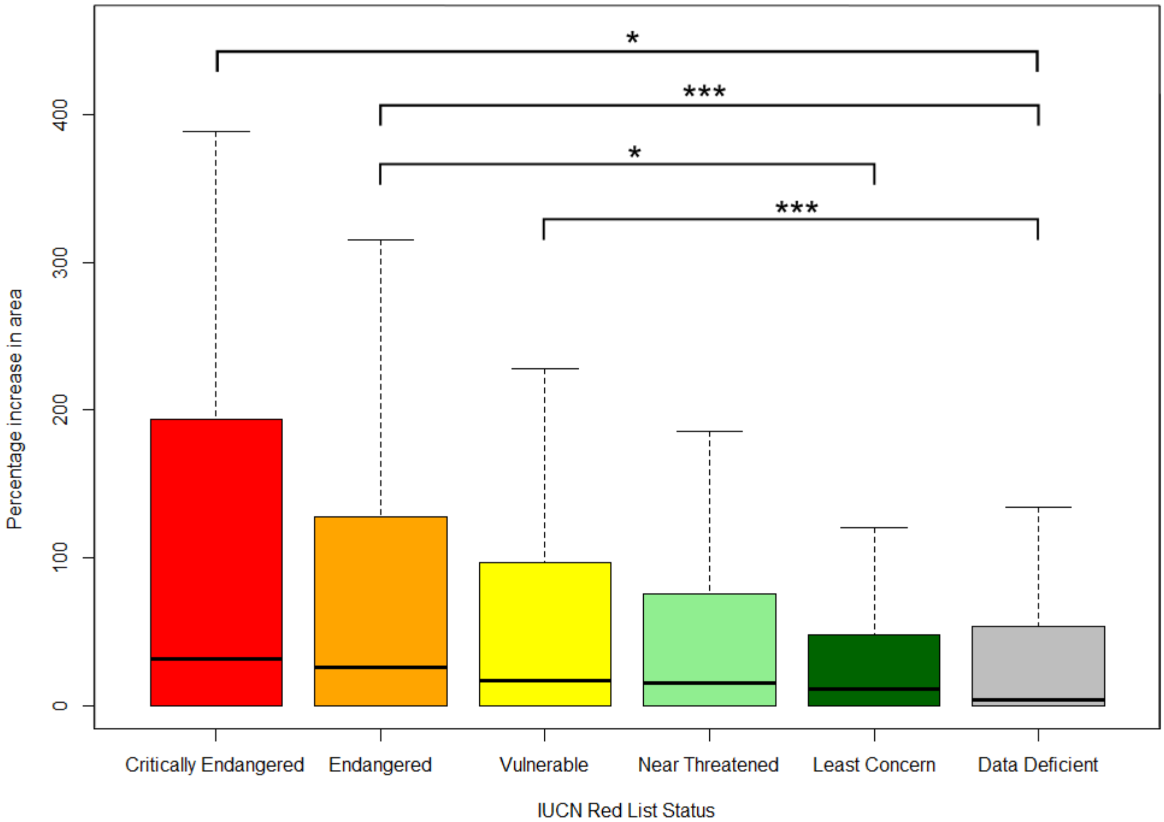


Figure 9. The increase in percentage area that has suitable climate and habitat in patches that meet a species' minimum area requirements between a situation in which no restoration takes place and when all hypothetically feasible areas are restored to natural habitat that could allow a species to meet its minimum area requirement, assuming expected future species distributions under the RCP 4.5 scenario. Species are classified by the IUCN in terms of their extinction risk, as critically endangered (red), endangered (orange), vulnerable (yellow), near threatened (light green), least concern (dark green) or data deficient (grey).

Discussion

This study identifies areas where restoration is expected to conserve the greatest number of mammal species, over those that would be projected to exist in the year 2070 without restoration having taken place. Crucially, my identified priorities for restoration are in areas expected to be suitable in 2070 under expected future climate change, and also ensure that the estimated minimum area requirements of species are met. My results suggest that tropical forest restoration could conserve some of the highest numbers of mammal species. Previous attempts to identify habitat restoration priorities have typically neglected the expected impacts of future climate change on species distributions (Strassburg et al., 2020), and when they have considered future climate, modelled just a few species (Rather, Ahmad, Dar, & Khuroo, 2022).

Large parts of Europe, Eastern and Southeastern Asia, Western and Eastern Africa, as well as Central and South America are identified as areas where habitat restoration is expected to lead to the conservation of the greatest number of mammal species into the future. Many of these regions are facing significant anthropogenic pressures at present. Europe, East and Southeast Asia, and parts of Central and South America are under high exposure to multiple drivers such as human use of the landscape (through crop, pasture, and urban cover, as well as forest loss), high human population and pollution, and in Western and Eastern Africa as well as parts of South America, high exposure to climate change (Bowler et al., 2020). The rapid loss of suitable area for species through land-use change and climate change (Baisero et al., 2020) reflects the urgent need to address ecosystem degradation on a global scale, if we are to conserve the maximum potential of mammal species richness into the future. The maps I present can act as a guide to where to focus restoration efforts that will connect future climatically suitable habitat into patches that are large enough to support mammal species.

The areas that I have identified for restoration are currently preventing habitat connectivity for many species in landscapes projected to have suitable climate in the future owing to their current land use, particularly for those species that are unable to tolerate anthropogenic habitats. These areas are currently either arable land, pastureland, plantations, or subtropical/tropical heavily degraded former forest. It is important to note that species that can tolerate such heavily human-modified habitats may not be considered as beneficiaries of the restoration considered in this study. Previous studies have highlighted the species-specific nature of restoration outcomes (Boron et al., 2019; Lawer, Mupepele, & Klein, 2019). Nevertheless, restoration of natural habitats is expected to benefit species that rely heavily on natural habitats for their existence (Deere et al., 2020; Hannibal, Cunha, Figueiredo, Teresa, & Ferreira, 2020), and improves habitat connectivity for these species (de Oliveira, Gonçalves, Machado, & Galetti, 2023).

The areas that I identify as priority areas for natural habitat restoration mostly match those identified in a previous study that did not take into account climate-change impacts on species, or species' minimum area requirements (Strassburg et al., 2020). In contrast to this previous study, I use species richness as a measure of restoration priority in my research, although there are known limitations of using this as a measure of biodiversity (Fleishman, Noss, & Noon, 2006). For example, some species are more important for ecosystem function than others (Brodie, Williams, & Garner, 2021). Functional diversity, a measure of the range of traits exhibited by species related to how they interact with their habitat to perform ecological functions (for example seed dispersal), is a way of measuring importance of species for ecosystem function. This measure is recommended for use in biodiversity monitoring, and it has been shown that species composition changes with age of the restoration patch to more closely resemble the reference ecosystem (Derhé, Murphy, Preece, Lawes, & Menéndez, 2018). However, for the purposes of my study, species richness is appropriate to identify habitat restoration priorities that benefit the greatest number of species, whilst maximising potential conservation impact.

Incorporating the minimum area requirements of species ensures that patches of habitat are large enough to support species survival into the future. Other tools, such as 'Optimal Restoration of Altered Habitats' (OPRAH) allow for restoration to be modelled for individual or small groups of species, incorporating a user-defined input of a species minimal area requirement, although this tool considers only whether the total area of all habitat patches meets a species' requirements rather than considering the size of individual habitat patches (Lethbridge et al., 2010). To my knowledge, no other global-scale study on restoration priorities has included individual species' minimum area requirements.

The overall potential benefit of restoration differs for species in different categories of extinction risk. In general, my study shows that as the extinction risk increases, a post-restoration scenario has a greater potential to increase the total area available to species, composed of contiguous habitat patches that meet species minimum area requirements. In a global study on the primate order of mammals, it has been shown that species that can tolerate artificial land covers are less threatened with extinction (Galán-Acedo et al., 2019). It would make sense that the opposite is also true, that species less able to tolerate artificial land are more threatened with extinction; therefore, restoring artificial land to natural habitats can increase total available area the most for these species. This result underscores the importance of targeted conservation actions in mitigating biodiversity loss.

The in-country variation of identified restoration areas can mostly be explained by patterns in climate and habitat. The areas identified as restoration priorities in large part reflect the areas that are predicted to have the greatest numbers of species after the impacts of future climate change. Restoration priorities are also often in places where the current natural habitat is fragmented by anthropogenic land use, and thus where habitat restoration could lead to gains in the numbers of species expected to persist by connecting habitat patches. I have identified three areas of the world within tropical forest regions to explore these patterns further, based on my results showing that these areas could conserve some of the highest number of mammal species richness. In Brazil the South of the country has the most to contribute to increasing species richness, due to the underlying natural forest habitat (figure 6.2.E), high current artificial land use (figure 6.2.F), and a mostly positive projected increase in species richness in the year 2070 compared to the present day when considering only suitable climatic conditions (figure 6.2.C). The arc of deforestation, a region where agricultural land is currently replacing forested land, is also unsurprisingly highlighted as a priority area to undertake restoration (figure 6.2.A). As highlighted in Chapter 3, the north coast of Brazil surrounding the Rio de Janeiro region as well as the arc of deforestation are areas that are projected to lose species in the year 2070 when accounting for species' minimum area requirements (Supplementary materials, figure 2A). These areas could conserve species through restoration of habitats (Supplementary materials, figure 2B), leading to a percentage increase in expected mammal species richness in 2070 when comparing a situation with no restoration of habitats and where habitats have been restored to meet species' minimum area requirements (Supplementary materials, figure 2C). Restoring habitats in these regions can help reduce the projected loss of species by 2070, though there are some areas where restoration alone may not be sufficient to prevent species declines, highlighting the need for additional conservation measures.

In China, the Hu line, an imaginary line dividing the Northwest from the Southeast of the country, which reflects differences in human land use (Zou, Wang, & Bai, 2022), is very evident in the identified priorities for restoration. More areas are identified as priorities for hypothetical restoration in the Southeast, where anthropogenic land use is more extensive (figure 7.2.F), combined with a largely suitable climate (figure 7.2.C). In the Northeast of the country, it is striking that although there is a large amount of artificial habitat, and naturally occurring forest habitat, this area is not identified as a priority for habitat restoration. This could largely be due to the unsuitability of the projected future climate in this area. East, south central and southwest China are areas projected to lose species in the year 2070 when accounting for species' minimum area requirements (Supplementary materials, figure 2A). Restoration is mostly recommended in East and south central China (Supplementary materials, figure 2B), however restoration alone does not appear to be sufficient to prevent species declines in southwest China as species do not increase in this region when comparing the situations with no restoration of habitats to that of where habitats have been restored to meet species' minimum area requirements (Supplementary materials, figure 2C).

Lastly, in Madagascar, it is striking the amount of savanna habitat that is identified as forest habitat through the process of classifying potential naturally occurring habitat types (Jung, 2020) (figure 8.2.E&F). This is partly a limitation of using the Jung map, as it does not provide insights into historical habitats lost to land use change. My study does not recommend converting the savanna habitat to forest, instead I identify where species richness can be conserved through the restoration of anthropogenic land uses to forest and shrubland. The east cost of Madagascar is projected to lose the most species in the year 2070 when accounting for species' minimum area requirements (Supplementary materials, figure 2A). In contrast, it is mostly the central highlands of this country that are recommended for restoration (Supplementary materials, figure 2B), which will also lead to significant species conservation in this area (Supplementary materials, figure 2C). However, the area that is currently shrubland on the east coast (figure 8.2.F) could be an area for conservation actions other than habitat restoration, as this area will be climatically suitable for a large proportion of mammal species in the year 2070 (figure 8.2.C&D). Only 45% of studies that focused on the responses of mammal biodiversity to restoration of habitat structure include habitat preference of species in their analysis (Hale, Blumstein, Mac Nally, & Swearer, 2020). Focusing on these three country case studies shows the importance of considering the habitat preference of mammals when recommending areas for restoration, in combination with suitable climate and minimum area requirements, which are all important factors for understanding which areas species can inhabit.

Some terrestrial areas, whilst not the most species rich in absolute terms, have a greater potential to increase their relative species richness through habitat restoration (figure 5). This is an important point to consider when global targets for restoration are made, as applying the same area restoration target to each country may not be the best use of that country's resources. Whilst this work has shown the significant potential for mammal conservation within tropical forests, it is important to highlight that focussing only on forest restoration can lead to the loss of other habitat types such as grasslands (Wolff et al., 2018), a habitat that has great potential for biodiversity conservation (Staude et al., 2023).

The benefits of habitat restoration if completed by indigenous and local communities are numerous, including benefits for communities such as sustainable extraction of natural resources, and benefits for habitats such as intimate knowledge of ecosystems which can help with the restoration itself as well as monitoring there after (N. S. Santini & Miquelajauregui, 2022). Community-led restoration initiatives could be a crucial component of conservation strategies, particularly in regions where formal protection (such as protected areas) may be limited. Whilst I do not consider the location of protected areas in this chapter of my thesis, future research could identify communities that are willing to uptake community lead restoration of habitats, in priority restoration areas that fall outside of protected areas. Furthermore, where there are projected to be species losses in the year 2070 when accounting for species' minimum area requirements, and hypothetical restoration of habitats does not lead to the recouperation of these potential losses, nature-based solutions could be explored. Where habitat restoration is the recovery of ecosystems that have been destroyed or degraded, for the benefit of nature, nature-based solutions simultaneously benefit both nature and people, whilst addressing societal challenges through providing ecosystem services (Waylen et al., 2022). For example, agroforestry (where forest or shrubland habitats are integrated with crop cultivation or livestock farming) can both increase native biodiversity, enhance soil health and improve livelihoods (Quintero-Angel, Cerón-Hernández, & Ospina-Salazar, 2023). Sites that have not been considered as suitable for hypothetical restoration in my research could also benefit from nature based solutions, such as green roofs in urban areas; improving air and water quality, as well as reducing heat island effects (Quintero-Angel et al., 2023). Integration of local communities in habitat restoration, as well as the use of nature-based solutions where traditional habitat restoration is unsuitable are effective complimentary conservation actions that should be considered in the priority areas identified in my research.

The maps presented in this chapter would be beneficial to organisations such as the World Conservation and Monitoring Centre (UNEP-WCMC), who are partnered with the Protected Planet – who host the most up to date and complete source of data on protected areas and other effective area-based conservation measures (OECMs) (Protected Planet, 2024). The United Nations Environmental Program would also be a suitable place to host maps that prioritise restoration for species. One of the most recent collaborations of UNEP is with the Convention on the Conservation of Migratory Species of Wild Animals (CMS), who have launched an atlas of global ungulate migration (Global Initiative on Ungulate Restoration) to inform conservation action and aid in spatial planning of infrastructure (CMS, 2024). The priority areas identified in my thesis could be used to prioritise more localised studies that assess the feasibility of the hypothetical restoration identified here. Both local and global studies have merit in conservation, with global studies benefiting from a wider perspective of systems, and more local studies benefiting from being species location specific, whilst also allowing for specific management responses (Linnell, 2005). There are some tensions between the two approaches, especially where human wildlife conflict exists. In some areas where a global study may have identified large carnivores as a priority for conservation action, local communities in those areas may not wish for these species to be conserved, for the safety of the community and their livestock. Such conflicts can be overcome through ensuring that the following enabling conditions are established: transparent and fair governance systems for natural resources, capacity for wildlife linked enterprises, local empowerment and involvement in decision making, monitoring and evaluating the quality of coexistence, and ensuring sufficient financial resources to support conservation actions (Durant et al., 2021). Furthermore, it is important be exhibit care when recommending top-down conservation action, as this often comes management power imbalances (Linnell, 2015). Local conservation studies based on global prioritisation studies can better address local nuances such as uneven biodiversity distribution, anthropogenic pressures and local needs (Brooks et al., 2006). Integrating global prioritisation with locally tailored conservation research can allow for more effective and context-specific management, ensuring both broader conservation goals and the needs of local communities are addressed.

There are multiple limitations to this research. First, I do not take into consideration when restoration at this scale could realistically be completed, or even if restoration is possible at all, as most of the land identified will be under private ownership (Cameron, Schloss, Theobald, & Morrison, 2022), or will be in areas where food production is of a higher priority than species conservation. Second, although biodiversity may recover after restoration, it may take several years to do so (Loch, Walters, & Cook, 2020). Third, whilst I assume that species will populate the restored habitat, I acknowledge that this is not always the case (Hale et al., 2020; Tattersall, Burgar, Fisher, & Burton, 2020), as even if habitat is restored, species may not be able to reach the newly suitable areas due to being limited by their dispersal distance. For the majority of mammals, dispersal distance is well known, or can be determined by home range size (Bowman, Jaeger, & Fahrig, 2002). Therefore, whilst it would have been possible to model a species dispersal ability to better understand which areas species would be able to reach, the complexity involved would have made this study better placed on other modelling software such as OPRAH. The potential dispersal distance that a species would be able to undertake by the year 2070 is indirectly included in this study by utilizing climate projections for mammals from published research. These projections are based on a standardised dispersal distance of 3km per year for all mammals (Newbold, 2018). A further limitation in my study is that I also assume that mammals can't traverse unsuitable habitat types, for example where rivers divide a landscape. In this scenario, while two habitat patches together may meet the minimum area requirements of a species, if those habitat patches are separated by a river, then they would not count as meeting minimum area requirements, even if a species could reach them by traversing the unsuitable area. Lastly, whilst I do consider connectivity of habitats in relation to having patches of contiguous habitat that is above the threshold for a species minimum area requirement, I do not consider connectivity of climate that allows species to track climate change.

In conclusion, this study has been able to identify terrestrial areas globally that if restored are expected to conserve the largest number of mammal species, whilst meeting species minimum area requirements in climatically suitable habitat in the year 2070. However, global restoration studies such as mine should only be used as a guide as to where to focus efforts on conducting finer-scale studies that consider the local context in order to design restoration schemes (Wyborn & Evans, 2021). While the restoration of many habitats does improve biodiversity compared to its degraded state, natural intact ecosystems still maintain significantly higher biodiversity (Rey Benayas et al., 2009). It is therefore important that the first step always be to conserve what we have, and then to compliment this with restored areas (Mcdonald et al., 2016). The reality and practicalities of restoration on the ground will inevitably be quite different to the generalities modelled in large-scale studies such as mine. Importantly though, I find that species with increased extinction risk could gain more range area from the hypothetical restoration of artificial habitats than species at a lower risk of extinction. My results highlight the importance of considering future climate change and the minimum area requirements of species alongside the suitability of habitat in restoration studies, if we are to unlock the full potential of conservation through restoration.

Supplementary material

I undertook a per “continent exploration of the kind of land that the models developed in this chapter recommend being hypothetically restored (figure 1). I utilised the continent boundaries as supplied by the “World Continents” basemap layer from Esri Data and Maps (Esri, 2024), and extracted the current habitat type (Jung et al., 2020) and potential natural habitat type (Jung, 2020) per continent, using the areas recommended for hypothetical restoration (main chapter, figure 2) as a mask. The majority of land that is recommended for restoration in every continent is artificial habitat. Of the land recommended for restoration, potential natural habitat in: Africa includes 46% savanna and 26% forest, Asia includes 63% forest and 13% savanna, Australia includes 48% forest and 39% shrubland, Europe includes 77% forest, North America includes 58% forest and 26% grassland, Oceania includes 89% forest, and South America includes 61% forest and 26% savanna.

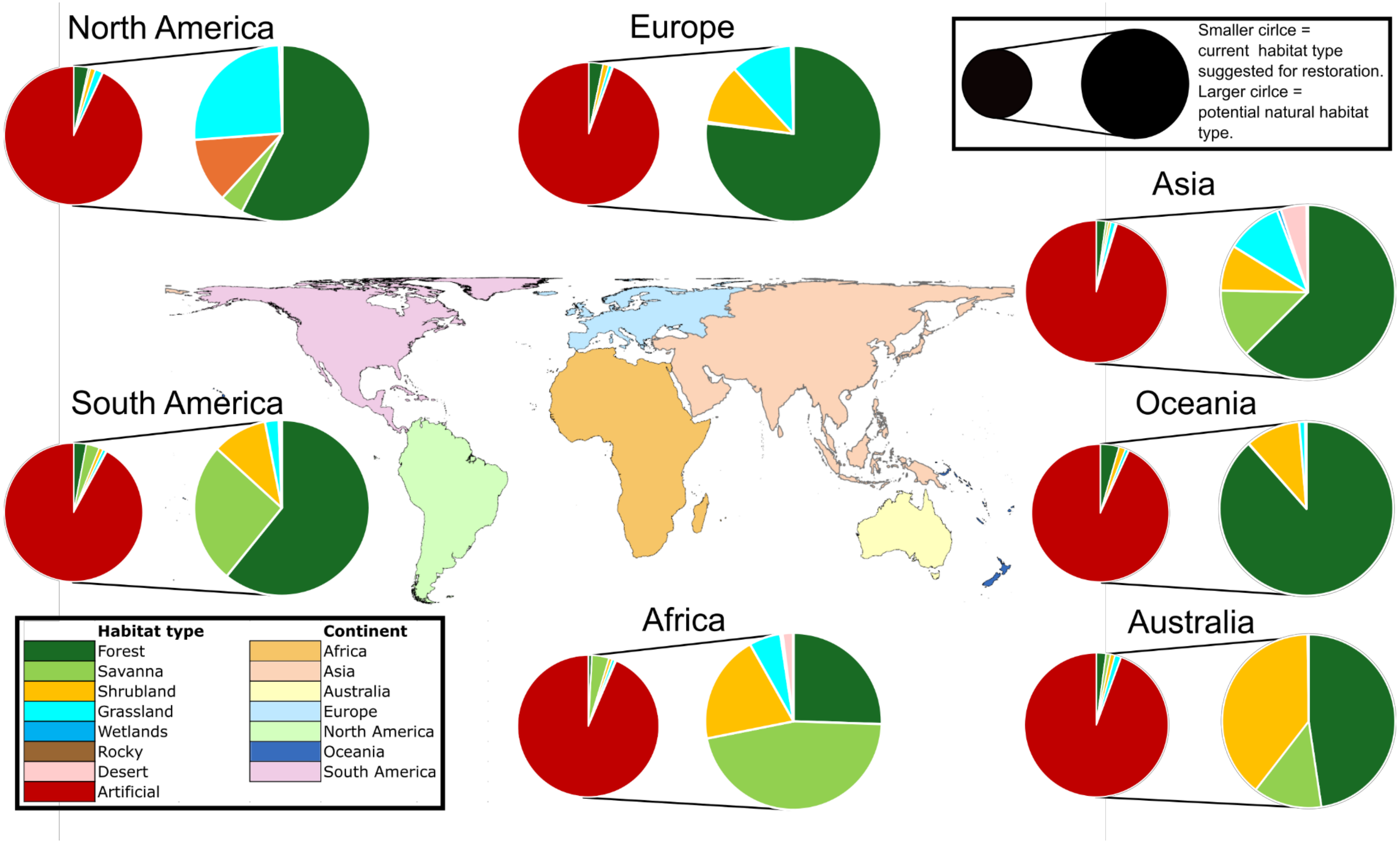


Figure 1. The habitat types that the models developed in this chapter suggest being restored. Current habitat type suggested for restoration is represented per continent in the small circles, and the potential natural habitat that the current habitat type could be restored to is represented in the larger circles. This figure is an exploration of figure 2 from the main chapter.

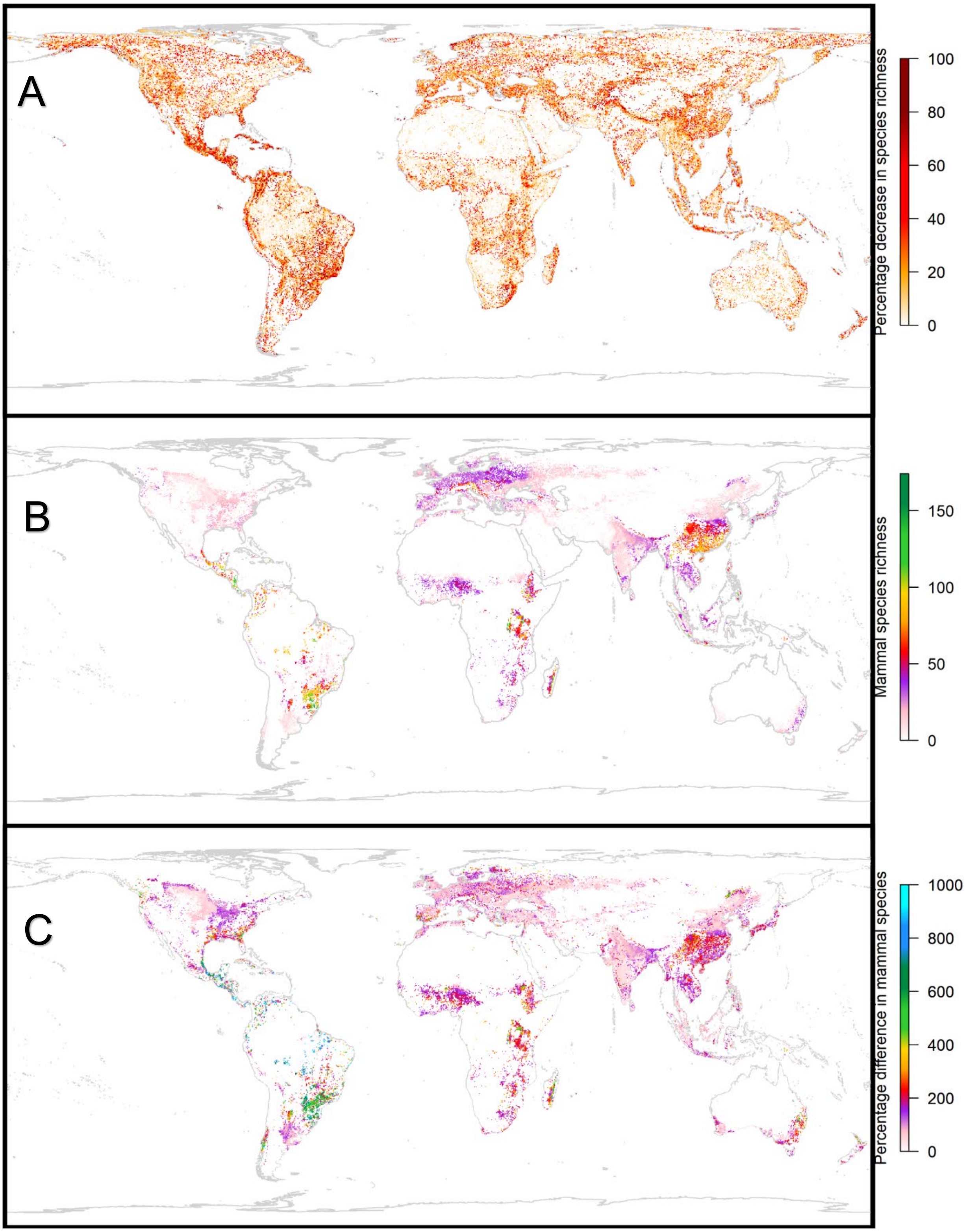


Figure 2. A: The percentage of species lost from a cell when accounting for species' minimum area requirements, under an intermediate-emissions climate change scenario (RCP 4.5) for the year 2070. Areas highlighted in darker red do not contain enough contiguous areas of suitable climate and habitat to meet the needs of a large proportion of the species projected to exist in those areas according to just climate and habitat suitability, and not considering minimum area requirements. This map is based on the data presented in figure 6 in Chapter 3 of my thesis, presented again

here for comparison. B: Assuming expected future species distributions, under an intermediate-emissions climate change scenario (RCP 4.5) in 2070, the number of mammal species that would meet their minimum area requirement by restoring an area to its natural habitat type. Expected gains are achieved by the creation of new habitat patches, or by the extension/joining of existing patches to meet species' minimum area requirements. This map is based on the data presented in figure 2 in Chapter 4 of my thesis, presented again here for comparison C: Percentage difference in expected mammal species richness in 2070 given projected species distributions under the RCP 4.5 climate scenario, between a situation with no restoration of habitats (Chapter 4, figure 3), and where habitats have been restored in areas where the creation of natural habitats supports the meeting of species' minimum area requirements (Chapter 4, figure 4).

Chapter 5

General Discussion

The emergence of ambitious global agreements for biodiversity conservation, such as the Global Biodiversity Framework (GBF) (Convention on Biological Diversity, 2022), signal a rising recognition in governments across the world of the importance of a healthy, biodiverse natural environment. There are a myriad of tools at the disposal of governments, non-governmental organisations and the private sector, available to help achieve these goals. These include protected area establishment and expansion (Chen et al., 2022), habitat restoration (Strassburg et al., 2020), species reintroductions (Ruble, Verschueren, Cristescu, & Marker, 2022), urban biodiversity planning (Kirk et al., 2021), and sustainable agriculture (Tahat, Alananbeh, Othman, & Leskovar, 2020), to name just a few. These tools can help us to address some of the main threats to biodiversity, including anthropogenic climate change and land-use change, human population growth, as well as invasive species (Bowler et al., 2020; Jaureguiberry et al., 2022). My thesis focuses on the role of protected areas and habitat restoration in biodiversity conservation, assessing their effectiveness now and in a future with accelerating climate change. I show that protected areas conserve more biodiversity than areas outside of protection, and that certain characteristics of protected areas are associated with differing levels of biodiversity. I also explore where species are projected to be in the year 2070 under climate change, whilst also taking into consideration suitable habitat type, as well as the size of projected suitable areas in relation to species' minimum area requirements. Lastly, I explore where we can conserve the most species through habitat restoration in areas currently heavily modified by anthropogenic activities. Throughout, I have focussed on mammals as they are among the best sampled groups of species, allowing us to obtain data on species distributions and traits.

Protected areas are a conservation method that protect both biodiversity and natural resources by often preventing natural habitat loss (Gonçalves-Souza, Vilela, Phalan, & Dobrovolski, 2021; Santiago-Ramos & Feria-Toribio, 2021) or leading to habitat management that is more compatible with biodiversity conservation (Campos-Silva et al., 2021), acting as a climate refuge for species (Lehikoinen, Santangeli, Jaatinen, Rajasärkkä, & Lehikoinen, 2019; Mi et al., 2023), and containing higher levels of biodiversity (Gray et al., 2016). Some of the characteristics that are important to consider when looking at protected areas include their IUCN management category. For example, it has been shown that areas under stricter levels of protection are better at preventing forest loss (Leberger, Rosa, Guerra, Wolf, & Pereira, 2020), as well as being better at conserving larger mammals and mammal species at a greater risk of extinction (G. B. Ferreira et al., 2020). Other characteristics of protected areas, such as their size and the level of connectivity between them, also increases the benefits to biodiversity (Brennan et al., 2022; Cho, Thiel, Armsworth, & Sharma, 2019; Lawton et al., 2010).

I show in Chapter 2 that there are, on average, 11% more mammal species in locations inside protected areas than in locations outside of protection, supporting the use of protected areas as an effective tool for conserving mammal biodiversity. One of the potential reasons for heightened biodiversity inside protected areas is their success, in general, at preventing land-use change (Figueroa & Sánchez-Cordero, 2008; Gonçalves-Souza et al., 2021), which in turn leads to a higher quantity of natural habitat, which is positively associated with different measures of biodiversity (Outhwaite et al., 2022). Whilst studies exist that show heightened biodiversity inside protected areas (Cooke et al., 2023; Gray et al., 2016), to my knowledge there are no global studies that specifically explore which characteristics of protected areas make them most effective at preserving mammal species richness. Preserving and expanding the protected-area network should therefore be a main focus of conservation biology, in particular through improving effective management (Adams, Iacona, & Possingham, 2019), if we are to continue to conserve mammal species.

I also find support for the use of protected areas that are of a large size, that contain high quantities of natural habitat to obtain desired biodiversity outcomes. My results from Chapter 2 show that total local mammal abundance increased with distance inside protected areas, especially in areas with a greater percentage of natural habitat within 100 km of the sample site. This is in line with other studies that show the importance of protected area size (Bond, Ozgul, & Lee, 2023; da Silva, Paviolo, Tambosi, & Pardini, 2018; Ramesh et al., 2016), as well as the importance of natural habitat for biodiversity (Outhwaite et al., 2022). This underscores the importance of the landscape context in shaping mammal biodiversity within protected areas, as well as lends support to the importance of the 30by30 target. This target focuses not only on the amount of the terrestrial area that is protected, but also stipulates that protected areas need to be managed effectively, be ecologically representative, as well as integrated into wider landscapes (CBD, 2024b). My research supports the integration of protected areas into the wider landscapes of which they are part, by showing the benefits for mammal biodiversity of having a high proportion of natural habitat both within and surrounding a protected area. This result is consistent with other published research that focuses on the importance of integration of high-value biodiversity habitat into protected areas (Mokany et al., 2020), as well as the importance of conserving natural habitat for biodiversity (Outhwaite et al., 2022). However, to ensure that conservation measures remain relevant into the future, it is important to predict species distributions under changing environmental conditions (Monzón, Moyer-Horner, & Palamar, 2011; Newbold, 2018), thus preventing static conservation and promoting dynamic models that capture future predictions (Zurell et al., 2022).

It is also important to note some of the limitations of protected areas, for example some protected areas that exist on maps are not effectively managed or enforced, these are also known as paper parks (Di Minin & Toivonen, 2015). Furthermore, some forms of governance are more effective than others depending on the region and resources available. A review of the effectiveness of different governance types within protected areas globally suggest that community-based and co-managed governance types are some of the most effective for conservation that favours both people and nature (Y. Zhang et al., 2023). However, governance that excludes local communities is also prevalent. For example, a local community within the Sahariya forest community witnessed the removal of 1,650 of their households from the Kuno Sancturary in India; a wildlife sanctuary established to protect a range of wildlife such as antelopes, primates and carnivores. This was a community dependent on natural resources for income, and each displaced household saw a 50% decrease in their income (Kabra, 2009). Another example is in Peru, where the establishment of the Allpahuayo-Mishana National Reserve placed restrictions on extraction of natural resources, and resulting in the economic displacement of many locals (Cardozo, 2011). My own experience of the Pacaya Samiria Nature Reserve in the Peruvian Amazon (Metcalfe, Yaicurima, & Papworth, 2022) has also exposed me to the mismatch between local needs, wildlife conservation and management decisions. For example, in 2018 the Marañón River (an important Peruvian Amazon River for wildlife and people) was being considered for intensive dredging to allow for larger boats to travel along it, responding to both increased levels of tourism and increased transport of natural resources along this river, furthermore, there were also a number of hydrodam proposals (IUCN, 2020). Both of these actions would pose significant threats to unique biodiversity in this region, however, they are still being considered by government (Campbell et al., 2023). Iquitos's economy, the largest town with entry to the Pacaya Samiria Reserve, is increasing its income through ecotourism, like many places in similar situations. It is important to both engage and empower local stakeholders, involve local knowledge (even more relevant as this region in Peru supports over 14 indigenous peoples), and protect wildlife so that the benefits of ecotourism can be enjoyed for years to come. I would expect that in general if the effectiveness of protected areas increased through effective management and equitable governance, there would be an even greater potential for biodiversity gains within protected areas above those highlighted in Chapter 2.

Anthropogenic climate change is one of the major threats to biodiversity, and is causing increases in the total number of species threatened by extinction (Habibullah et al., 2022; Urban, 2015), species range shifts (Hetem et al., 2014), and habitat degradation in some areas due to increased water limitations and climate variability (Forzieri, Dakos, McDowell, Ramdane, & Cescatti, 2022). Some of the world's most biodiverse regions for terrestrial mammals, including South America, Eastern Africa and Southeast Asia, are also the areas that are most vulnerable to projected climate change (Paniw et al., 2021). Whilst mammals can modify their behaviour to lessen the impacts of climate change, such as through seeking shade, basking and changing activity times (Cunningham et al., 2021), existing in habitats outside of their thermal limits can exert extreme stress on their existence, interfering with their metabolism and water retention ability (Fuller, Maloney, Blache, & Cooper, 2020). Depending on the ecosystem a species inhabits, the pressures from climate change differ. For example, mammals that live in drylands will face reduced water availability and increased daily temperatures (Fuller et al., 2021), while those that live in the Amazon face an intensification of floods and droughts (Bodmer et al., 2018). However, climate change will not impact all species that live within the same landscape in the same way (Yusefi, Safi, Tarroso, & Brito, 2021), and indeed some traits of mammals can impact their responses to climate change. For example, in mammal species that have more restrictive diets (so are less able to exploit a range of food resources), slow reproductive rates, and larger body mass, are generally less able to adapt to rapidly changing climates (Pacifici et al., 2017). In Chapter 3 I explore how current projections of future species distributions may be overly optimistic as they often don't take into account a combination of habitat suitability, climate suitability and the minimum area requirements required by a species to enable a population to persist. By utilising trait based data to obtain estimates of species minimum area requirements, I have been able to show that some of the largest shortfalls in suitable habitat area (area shortfall relates to the discrepancy between a species total amount of projected suitable habitat, and the total size of all habitat patches that are large enough to support future populations of species) are projected in highly biodiverse regions such as the Amazon, Central America, Southeast Asia and the African savanna. As mentioned above, these are also some of the areas most vulnerable to projected climate change impacts. Furthermore, in my study species that were at a greater threat of extinction are expected to face greater area shortfalls than those that are at a lesser threat of extinction. My results confirmed that the threat of extinction was not linked the size of a species minimum area requirements. Thus other factors, such as species at a greater threat of extinction may also be facing greater pressures from habitat fragmentation and climate pressures; contributing to greater area shortfalls. Future research that focuses on the spatial distribution of threatened species and unique anthropogenic and climate pressures in those regions could be a good way to understand how we can mitigate such impacts on threatened species.

Another major driver of biodiversity loss is land-use change, driven by increased anthropogenic demand on planetary resources (Davis et al., 2016; Huang, Yeh, & Chang, 2010). Land-use change can lead to habitat fragmentation (Semper-Pascual et al., 2021), edge effects which can increase species exposure to anthropogenic pressures (J. N. G. Willmer, Püttker, & Prevedello, 2022), and loss of natural habitat (Baisero et al., 2020), all of which can have detrimental effects on mammal biodiversity. In a global analysis of the effects of current habitat loss and fragmentation on mammals, there was found to be an average relative loss of 11% mammal species across the 804 terrestrial ecoregions of the world. In particular, some of the highest mammal species loss was shown to be in South America, Western and Eastern Africa, as well as in Southeastern Asia (Kuipers et al., 2021). Anthropogenic land uses can cause ecological communities to change, and some species are less able to adapt to these changes than others. For example, it has been shown that certain functional groups, such as carnivores, are disproportionately reduced in anthropogenic landscapes compared to other functional groups (Newbold, Bentley, et al., 2020). Furthermore, within disturbed neotropical forest habitats, ecological functions performed by mammals such as: browsing, large seed dispersal, small and large seed depredation and medium and large sized vertebrate predation become more vulnerable, and the mean body mass and species richness of mammals also decreases (Magioli et al., 2021). In Chapter 3, areas such as the arc of deforestation in the Amazon were highlighted to have significant area shortfalls for mammal species. This is an area that is undergoing significant anthropogenic land use change due to the expansion of agricultural habitats into forested regions (Lapola et al., 2023). This is also an area of the world that has important endangered carnivores such as jaguar (*Panthera onca*, near threatened on the IUCN red list (IUCN, 2023)), that are sensitive to habitat fragmentation (Espinosa, Celis, & Branch, 2018). Studies already exist that recommend agricultural expansion in the Amazon should be limited to existing pastures, as these areas have already undergone land use change and have limited conservation value for wild mammals in these areas (Boron et al., 2019). I would also concur that agricultural expansion should not expand into forested areas of the Amazon, as my results show we are already facing projected mammal species declines due to a combination of climate change and insufficient area to meet the minimum area requirements of species in these regions.

Good quality natural habitat contributes to a thriving ecosystem (Carvalheiro, Seymour, Veldtman, & Nicolson, 2010; Outhwaite et al., 2022). While larger habitat patches are usually better for biodiversity (Bradfield et al., 2022; Magioli et al., 2021), it is vital to understand how large a habitat patch needs to be in order for benefits to biodiversity to be exhibited. By looking at the minimum area requirements of species, the minimum area required by a species for its population to persist into the future, a landscape can be conserved or restored so that it meets such requirements. In China, it has been shown that minimum area requirements are not met for large carnivores or for threatened species inside their protected area network (Wang et al., 2023). However, a lack of empirical minimum area requirements for terrestrial mammals has prevented broader-scale studies on how well we meet the minimum area requirements of species. Indeed, the largest global dataset of terrestrial mammal empirical minimum area requirement estimates represents just 80 species (Verboom et al., 2014).

Using species traits that are correlated with minimum area requirements of mammals: body mass (Biedermann, 2003; Pe'er et al., 2014), home range size (Verboom et al., 2014), habitat breadth (Slatyer et al., 2013), diet breath (Pe'er et al., 2014; Price & Hopkins, 2015), basal metabolic rate (Kelt & Van Vuren, 2001), population density (Verboom et al., 2014), maximum longevity (Kelt & Van Vuren, 2001), and dispersal age (the age at which young permanently leave their parent) (Alzate & Onstein, 2022), I imputed the minimum area requirement for each mammal species as shown in Chapter 3. The most complete dataset of empirical estimates for minimum area requirements of mammals is only for 80 species presented in Verboom et al. (2014). Using imputed measures comes with substantial uncertainty, and so it should be a priority to increase the number of species for which their minimum area requirements are known. However, the alternative of ignoring minimum area requirements entirely will lead to very large overestimations of the area that can be occupied by most species, as the habitat will often not be large enough to support the species population into the future (Gurd, Nudds, & Rivard, 2001; Qing et al., 2016).

My results demonstrate the importance of including the minimum area requirements of species in conservation planning. I show in Chapter 3 that with the inclusion of minimum area requirements, projected species richness is reduced the most in areas such as the arc of deforestation in the Amazon, central America, the African Savana, as well as large parts of Western Europe and China, compared to what we would expect when ignoring minimal area requirements. The overestimation of potential species richness is to a relatively large extent because of the high levels of habitat fragmentation in these areas, that prevent a contiguous habitat patch from meeting the minimum area requirements of species. I also show that we are likely overestimating the total suitable area available for species the most in groups that are more at risk of extinction.

The importance of protected areas being sufficiently large to accommodate species needs is well represented in both the scientific literature and policy (Bailey et al., 2022; Chundawat, Sharma, Gogate, Malik, & Vanak, 2016; Lawton et al., 2010; Ramesh et al., 2016). A large protected area can better protect against habitat disturbance (Gonçalves-Souza et al., 2021), enhance biodiversity (Di Minin et al., 2013), and facilitate movement of individuals between habitat patches (Barnett & Belote, 2021). Too often protected areas are not large enough to provide such benefits for mammals (Bowyer et al., 2019). My research has highlighted key areas of the world that are projected to have high species richness under future climate change, where the patches of suitable climate and habitat are sufficiently large to meet the minimum area requirements of species, and yet are not contained within the current protected area network. This leaves habitat vulnerable to land-use change, and other anthropogenic pressures on wildlife, such as pollution. Large areas of the Amazon rainforest, African savanna, and tropical forests of Southeast Asia lack any type of formal protection. These areas are also projected to hold the most species under future climate conditions if current natural habitat is maintained.

Furthermore, this chapter highlights the importance of limiting global warming. The representative concentration pathways (RCP) are projections of possible climate warming scenarios at the end of the century, based on the concentration of CO^2 released into the atmosphere. Countries are working to avoid future scenarios of RCP4.5, RCP6.0 and RCP8.5, which would see a global increase of temperature by 2.4, 2.8 and 4.3 degrees Celsius respectively (UK Met Office, 2018). Carbon compensation can help countries to reach their goals within the Paris Agreement, of limiting global warming to under 2 degrees Celsius by the end of the century (Delbeke et al., 2019), and also meet a combination of the Sustainable Development Goals (ONU, 2022). I highlight that under increasing RCPs habitat becomes more fragmented for species, as there are fewer patches contained within suitable climatic conditions, and therefore it becomes more difficult for mammal species to meet their minimum area requirements.

Promoting carbon offsetting (where carbon dioxide or other greenhouse gas emissions made in one area are compensated for in another) is one such way that we can limit global warming. There are several options available, although some methods are more effective in limiting climate change than others. Carbon compensation allows for the trade of carbon credits through the voluntary carbon market (VCM); one credit is equal to one tonne of reduced or avoided carbon emissions. These credits are certified for their impact within carbon reduction projects. In 2021 Ecosystem Market reported that the VCM made just under $1 billion in transactions, and that just under 25 million metric tonnes of carbon dioxide equivalent were traded (Donofrio, Maguire, Myers, Daley, & Lin, 2021). As the demand for these services increases, there needs to be price transparency and project quality checks to ensure that carbon capture and reduction is effective at limiting climate change in the long term. The Dasgupta Review talks about how our financial economy is embedded within nature (R. Fletcher, 2021), and thus carbon credits should be priced according to the damage that the emissions would cause in the atmosphere (Kaskeala, Salo, & Pakkala, 2021). Emissions can stay in the atmosphere from anywhere between 300-1000 years (Alan Buis, 2019), so both reducing emissions and increasing the permanence of this carbon capture is of high importance. For example, in projects that use afforestation to capture carbon, it is important that the trees remain for an extended time frame, as if trees are logged soon after planting then any sequestered carbon will be released back into the atmosphere. It is recommended that such afforestation projects have a minimum life span of 100 years to be effective (Fairs, 2021).

Chapter 4 of my thesis focused on where we can benefit the most mammal species through restoration of natural habitats in places that are currently dominated by artificial habitat types. Restoring natural habitats can enhance ecosystem resilience (Török & Helm, 2017), improve species functional diversity (Derhé et al., 2018) and increase species richness and abundance (Tonietto & Larkin, 2018). However, it is also important to acknowledge the opportunity costs of restoration. This can include for example potential conflict in converting agricultural land back to natural habitat, as while restoration can lead to gains in ecosystem services and biodiversity (Schüler & Bustamante, 2022), it can also impact local people's livelihoods (Torres et al., 2023). The potential of restoration as a tool for supporting species conservation is also recognised in the global restoration target from the Convention on Biological Diversity, whereby at least 30 per cent of areas of degraded terrestrial ecosystems need be under effective restoration to enhance biodiversity by the year 2030 (CBD, 2024a)

The response within different world regions and of individual species to habitat degradation varies (Banks-Leite et al., 2020). Producing priority maps for restoration can therefore help decide the broad regions on which to focus efforts. To my knowledge, there has been no attempt at creating a global restoration priority map for all mammal species that takes into account their individual habitat and climate needs, whilst projecting individual species future distributions, despite reviews highlighting the importance of considering climate-change impacts in the way that restoration is carried out (Harris et al., 2006; Simonson et al., 2021), as well as species-specific responses to habitat degradation and restoration (Banks-Leite et al., 2020). By incorporating projections of the future climatic suitability of areas for species, with knowledge of suitable habitat types, and ensuring that contiguous habitat is above the minimum area requirement for each species, I identify South and Central America, Western and Eastern Africa, Eastern and Southeast Asia, as well as large parts of Europe as restoration priorities expected to conserve the greatest number of mammal species in 2070.

Individual species responses to climate and land use change vary widely. The IUCN red list risk classification acts as a way to determine which species may need to become a conservation priority if we are to prevent their extinction, however so far it has made little consideration of the potential impacts of future climate change. A study that focussed on the most threatened plant species in South Africa found that species ranges were more represented within the protected area network under future climate change scenarios than they are in the present day, however this was attributed to species range contractions outside of protected areas (Hoveka, van der Bank, & Davies, 2022). My work in Chapter 3 has shown that not only are mammal species with a greater extinction risk more likely to have their species distributions overestimated when their minimum area requirements are not taken into account, but I also reveal that mammal species with a greater extinction risk gain more percentage area from hypothetical restoration than those at a lower risk in Chapter 4. This underscores the importance of targeting conservation actions towards threatened species to have the greatest effect in mitigating biodiversity loss, although conservation priorities are likely to change through time as certain threats intensify or abate.

My thesis contributes to the field of conservation biology by focussing on how we can future proof mammal conservation, using conservation tools such as protected areas and restoration, whilst considering not only the suitability of different habitat types for different species, but also the impacts of future climate change on species' distributions. Global studies such as mine can provide a broad understanding of where, without further conservation action, mammal biodiversity is most at risk. Such studies can identify priorities for where local field studies that investigate locally specific conservation action should take place (Wyborn & Evans, 2021). Using a global study to select such regions can ensure the effective use of limited resources for local-scale work. Using a combination of approaches this way can result in realistic conservation plans that address some of the greatest threats to specific regions. A practical recommendation going forward includes greater emphasis being placed on involving local communities in decision-making, which will require closer collaboration between global targets, national governance and local stakeholders.

My research provides further evidence for the benefits of continuous investment in protected area establishment and expansion, as well as effective management of existing protected areas. I highlight the importance of natural habitat for sustaining mammal abundance within protected areas. I emphasize the importance of taking into account the minimum area requirements of species when projecting the future situation for mammal conservation under climate change, and thus a priority for future conservation biology should be to obtain empirical measures of minimum area requirements for as many species as possible. And lastly, I underscore the importance of incorporating restoration into broader conservation strategies, so that we can achieve a species rich future in the face of climate change. The implications of my work for setting conservation priorities include enhancing the protection of natural habitat, and the integration of climate change in future projections of species distributions, so that we can ensure conservation action remains relevant into the future. Overall, my work is supportive of the idea that we can positively impact the future of mammal conservation if we act in a targeted manner, through strengthening the implementation of existing conservation tools in a way that is considerate of species-specific characteristics.

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Appendix

I was a lead author on a policy briefing with the British Ecological Society entitled “Protected Areas and Nature Recovery. Achieving the goal to protect 30% of UK land and seas for nature by 2030.”

The following pages show an extract from this briefing, “What is the current state of protected areas and what are their biodiversity trends?” which I co-authored.

SECTION 3

WHAT IS THE CURRENT STATE OF PROTECTED AREAS AND WHAT ARE THEIR BIODIVERSITY TRENDS?

Chloë Alexia Metcalfe and Constance M. Schéré

SUMMARY

A 2021 analysis of terrestrial and coastal Common Standards Monitoring (CSM) data in the United Kingdom's (UK's) statutory protected sites found that 43% – 51% are in favourable condition. Most sites and features classed as unfavourable are reported as recovering, but differences in reporting approaches between country agencies make it difficult to generalise.

Not all of the UK's species are well represented within protected areas (PAs), however PAs remain important spaces for conserving species and can achieve effective nature conservation. Overall, PAs support higher species richness than unprotected sites, but more monitoring of biodiversity (and its trends) is required.

EVIDENCE GAPS

The condition of statutory site features has been quite widely monitored in the recent past, while trends in biodiversity (e.g., number of species or individuals of a species) have not. Both sets of information are needed to fully understand and manage biodiversity change.

Statutory agencies are struggling to meet the level of monitoring set out in the original CSM statement, so up-to-date information about condition is often missing or out of date, making it difficult to monitor site condition at scale. Meanwhile, there is no central inventory of the scale of habitat recreation and restoration, meaning the planned scale and pace of efforts is unknown.

Existing national schemes to monitor biodiversity are extremely valuable (e.g., Breeding Birds Survey, UK Butterfly Monitoring Scheme), but are not always suitable for understanding local site-specific trends because they were designed to report trends at large scales. There is currently no scheme to assess species abundances or overall biodiversity in PAs, or for comparable areas outside them. There is also a data shortfall for priority species, of which there are 2,890 in the UK, and changes in relative abundance and distribution have only been assessed for 7%, and 14% of these species respectively.

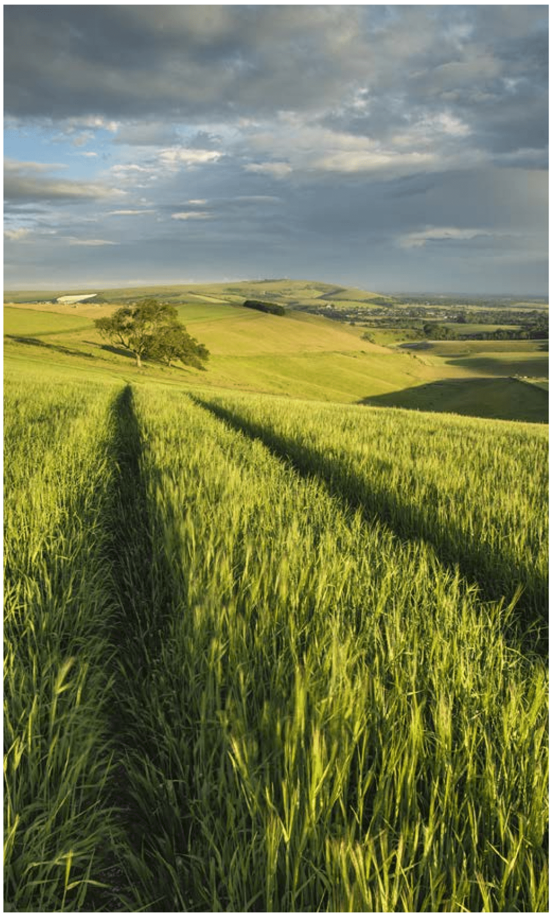
3.1 THE STATE OF PROTECTED AREAS

A 2021 analysis of terrestrial and coastal condition monitoring data at UK statutory protected sites revealed that only 43% – 51% of sites were in a favourable condition[1]. When considering the strictest International Union for the Conservation of Nature (IUCN) categories (Ia - IV), which make up less than 11.6% of UK land area, the study concluded that the proportion of effectively protected land might be as little as 4.9% of UK land. Terrestrial PAs have often been placed where there is relatively limited historical economic development potential[2,3], such as at high altitudes or on steep slopes. Indeed, land use change for economic growth (converting natural habitats to urban areas, arable and pastureland), is one of the main drivers of biodiversity loss[4]. Even when an area is designated, activities that are detrimental to the environment cannot always be prevented. For example, studies have shown that PAs have not prevented some forms of intensive land management that is damaging nature in the UK's uplands[5]. Meanwhile at sea, a recent report found that bottom trawling was taking place in 98% of UK offshore Marine Protected Areas (MPAs), and between 2015 and 2018, benthic habitats[i] were subjected to about 90,000 hours of bottom trawl fishing[6]. The UK's exit from the European Union (EU) may provide more opportunities to halt bottom trawling within PAs[7].

Common Standards Monitoring (CSM) is the existing, agreed UK approach to measuring the state of PAs. It involves setting targets that reflect the desired state of habitats and species, and collecting evidence to determine whether those targets have been met; a species or habitat that meets its target is said to be in favourable condition. The results of CSM assessments are combined to produce one of the UK Biodiversity Indicators, illustrating trends over time in the condition of Areas/Sites of Special Scientific Interest (ASSI/SSSIs). Since 2005, there has been little improvement, with about 50% of ASSI/ASSIs in favourable condition[8,9]. CSM results have also contributed to assessments of the broader concept of Favourable Conservation Status (FCS), a conservation goal that works at a much larger geographical scale than PAs alone[10]. FCS assessments[11] draw on a range of evidence sources, including CSM, wider species surveillance schemes, general biological recording and habitat maps, integrating results from site-specific and broader monitoring schemes.

National Parks and Areas of Outstanding Natural Beauty (AONB) cover large areas of land that offer prime opportunities for the recovery of nature in the UK and can provide ecosystem services. However, these areas were not specifically designated for biodiversity, and so species and habitats are exposed to many of the pressures driving declines elsewhere. A 2018 article reported that SSSIs outside England's National Parks and AONBs were more likely to be in favourable condition than those inside[12]. This may be because most National Parks are located in the uplands where there has been, and remains, widespread ecologically damaging land management, for example through overgrazing and burning[13]. Further to this, a review of the condition of SSSIs located within the seven National Parks in the English uplands[ii], reported that roughly the same percentage are in favourable condition inside National Parks compared to outside them (20% favourable condition inside upland National Parks and 18% favourable condition in the wider uplands)[14]. A major reform is necessary to ensure these designations are significantly improved for biodiversity.

National Parks and AONBs have not been set up in a way that allows them to secure effective protection and management for nature, because they were not designated primarily for nature conservation[15], meaning that nature may not be prioritised where there are perceived conflicts with their other primary purposes. The authorities responsible for these landscapes own little, if any, land and have no legal powers to secure the appropriate management of land across their areas[16]. Nature conservation outcomes within landscape designations might not be favourable due to insufficient management plans, inadequate implementation of management plans, or external pressures that cannot be controlled by the managing body's actions. Case Study 3.1 displays some of the complexities of achieving favourable condition.



South Downs National Park

[i] Benthic habitat is found at the lowest level of a body of water, for example the ocean floor.

[ii] Altitudes of more than 300m.

CASE STUDY 3.1

Llyn Tegid/Bala Lake

AFON DYFRDWY/RIVER DEE AND LLYN TEGID/BALA LAKE

The Afon Dyfrdwy/River Dee flows through north Wales and into north-west England. This freshwater ecosystem is covered by Sites of Special Scientific Interest (SSSIs) and Special Area of Conservation (SAC) designations that stretch from Llyn Tegid/Bala Lake (which is also a Ramsar site) to the Aber Afon Dyfrdwy/Dee Estuary; part of the river also falls within the Clwydian Range and Dee Valley AONB, and the estuary itself has additional Special Protection Area (SPA) and Ramsar status. Collectively, the SAC and SSSI designations recognise a variety of habitat, species and earth science features, with seven species features (five fish, one mammal, one plant) being common across the two designations. The SSSI recognises additional invertebrate, plant and habitat features. A recent exercise to assess the indicative condition of features considered most of them to be in unfavourable condition[1].

The Dyfrdwy/Dee faces various pressures both in-river and across the catchment. The river is highly regulated and there is a long history of modification for navigation, agricultural drainage, and development. Its flow has been controlled for around 200 years. The catchment provides drinking water for a large population in England and north-east Wales, it is popular for fishing and tourism, and is surrounded by farmland for most of its length[2]. Physical modifications such as channel straightening, removal of trees, embankments causing disconnection of the floodplain, and many weirs all contribute to habitat degradation[3]. Diffuse pollution from both rural and urban areas and point source pollution also threaten the species present[4].

Designation is just the start of the process to achieve positive biodiversity outcomes for a site, supporting the implementation of management that aims to maintain or bring about the favourable condition of recognised features. The complex mixture of pressures that act upon the river and its features make bringing them all into favourable condition a challenging and ongoing enterprise. There have been several management initiatives for the Dyfrdwy/Dee over the past 15 years, including the launch of a catchment partnership in 2013 to implement a catchment-based approach. More recently, the Dee LIFE project[5] represents a significant investment in actions aimed at restoring freshwater features in the River Dee and Bala Lake/Afon Dyfrdwy, a Llyn Tegid SAC.

[1] Cyfoeth Naturiol Cymru/Natural Resources Wales, 2020. *Protected sites baseline assessment 2020.* [online] Available at: https://naturalresources.wales/evidence-and-data/research-and-reports/protected-sites-baseline-assessment-2020/?lang=en [Accessed 04 February 2022].

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[4] Cyfoeth Naturiol Cymru/Natural Resources Wales and Environment Agency, 2014. *Dee Management Catchment Summary.* [online] Available at: https://naturalresources.wales/media/3225/dee-management-catchment.pdf [Accessed 04 March 2022].

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3.2 BIODIVERSITY WITHIN PROTECTED AREAS

PAs have historically been established in areas of high biodiversity or because of a feature of interest; this could be small (such as a patch of habitat) or large (such as a unique landscape). Over the last 40 years, sites with high levels of protection and/or high topographic variation have often been most effective at achieving long-term conservation outcomes[17].

Geographic distributions of species must be represented by the PA network. A recent analysis[18] of 5,254 habitat specialist species (covering reptiles, amphibians, bryophytes, lichens, insects, and non-insect invertebrates) in statutory protected sites found that representation (measured as the proportion of each species' predicted suitable habitat that overlaps with statutory protected sites) is less than 10% of species' potential habitat. Specialists' suitable habitats were better represented by PAs than generalists (except in Northern Ireland). Building on studies like this, it is important to account for specialist and generalist species when assessing how representative the PA network is.

To track biodiversity trends in PAs and other effective area-based conservation measures (OECMs), it is important to monitor PA condition as well as trends in ecological parameters (e.g., species richness and abundance). Within the UK, there are several long-term terrestrial monitoring schemes, such as the Breeding Bird Survey[19], the National Bat Monitoring Programme[20], and the UK Butterfly Monitoring Scheme[21]. Although none of these schemes were designed specifically to measure the effectiveness of PAs or OECMs, their spatially replicated design makes it possible for biodiversity trends to be investigated.

For the broader set of terrestrial PAs (i.e., National Parks as well as other designations), a recent national analysis has reported higher invertebrate species richness inside PAs than in areas with no recognised protection[22,23]. Meanwhile, a study of abundance data for birds and butterflies (as well as records for invertebrates, bryophytes, and lichens) has recently found that sites within PAs support higher species richness, but for nearly all groups of species there were negligible differences in species population abundance trends (i.e., change through time) inside compared with outside PAs[24]. Analysis of local extinctions of bird species in National Parks, AONBs and the wider countryside in England showed that AONBs afford only marginal additional protection, and that National Parks afforded no more protection to species than the wider countryside[25]. A key finding of this report is the lack of studies reporting trends in biodiversity within UK PAs[26] and OECMs, due to limited monitoring at the appropriate form and scale[27]. Indeed, there is also a data shortfall for priority species, of which there are 2,890 in the UK, and changes in relative abundance and distribution have only been assessed for 7%, and 14% of these species respectively[28]. Although studies such as the above do contain useful information for biodiversity trends, they do not offer an authoritative answer for biodiversity.

3.3 MONITORING AND INDICATOR SPECIES

There are many biodiversity metrics, such as species richness, abundance, genetic diversity and ecosystem diversity, that can be used to monitor how well an area designated for conservation is performing for biodiversity. Monitoring can be undertaken via citizen science recording schemes, such as Royal Society for the Protection of Birds (RSPB) Big Garden Birdwatch[29] and through apps such as iNaturalist[30], and long-term monitoring projects, such as the Environmental Change Network[31]. Technologies such as camera traps, computer vision, eDNA (environmental DNA) and passive acoustic monitoring are just some of the methods used to monitor biodiversity, and combining such monitoring with computer modelling can help to predict species range shifts in the face of anthropogenic pressures and climate change[32]. Software programmes can be used to assess risks for biodiversity to help businesses limit detrimental impacts. One such recent development is the Integrated Biodiversity Assessment Tool[33], which combines data from the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species, the World Database on Protected Areas, and the World Database of Key Biodiversity Areas. Other software programmes are able to undertake systematic conservation planning that designs efficient marine protected areas (MPAs)[34].

Indicator species (Box 3.2) are one way to monitor PAs, and they can provide insights into progress towards management goals and the health of an ecosystem if they react to certain characteristics of the habitat. They may signal the presence of other species, an ecosystem function or environmental condition. Indicator species are best used if they are selected to help achieve management objectives and inform actions[35], such as in CSM. However, they should not be used in isolation, nor as a substitute for wider research into a PA's ability to meet its conservation objectives[36].

BOX 3.2: INDICATOR SELECTION

The following steps should be followed when selecting an indicator: the management objective for the PA must be defined; alternative management actions and candidate indicator species should be named; the best indicator species that provides the best management outcomes has been chosen; selected actions are put in place; the process is evaluated; and learning is implemented[37]. Used correctly, indicator species can be of great use as they can be used to represent what is happening to wider biodiversity, without needing to monitor every part of a system. However, it is important to note that no single species can monitor the conservation goals of all UK PAs.

Indicator Group: Bees

Bees can indicate pollution impact[1], and they are also vital to the maintenance of semi-natural and agricultural systems[2].

Indicator Group: Seals

Seals are considered a top predator in certain marine systems and regulate food webs and cycle nutrients[3], thus, they are indicative of ecosystem function[4].

Indicator Group: Sea pens

Sea pens are the only octocorals capable of living in soft sediments and they are considered important indicators of good quality mud habitats and associated communities[5].

Indicator Group: Mussels

Mussels can form biogenic reefs that support numerous communities of species[6].

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